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ORIGINAL PAPER

Trophic ecology of Grey-headed albatrosses from Marion Island, Southern Ocean: insights from stomach contents and diet tracers

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Abstract During chick-rearing, albatrosses can alternate between long foraging trips that provide the main source of food for the adults and short foraging trips that they use to feed their young. This flexibility in foraging behaviour can lead to differences in diet composition between adults and chicks and implies that they may be vulnerable in different ways to food shortages. The trophic ecology of the Grey-headed albatross *Thalassarche chrysostoma* was investigated at the sub-Antarctic Prince Edward Islands during the chick-rearing period in April 2006 using a combination of approaches. Diets of adults and chicks were assessed using stable isotope ratios and fatty acid (FA) profiles of blood and/or stomach oils, in addition to stomach contents analysis. Fish from the family Macrouridae and cephalopods (particularly the onychoteuthid *Kondakovia longimana*) were the primary prey, whereas crustaceans (krill *Euphausia superba*) represented a smaller proportion of the stomach contents. Stomach oil FA profiles contained more monounsaturated FA than the profiles of plasma, which were richer in saturated FA and arachidonic acid (20:4n-6). There was also a distinct separation of adults from chicks, with higher levels of monounsaturates in chick plasma, and higher saturated FA levels (particularly 16:0) in the adult plasma. Stable carbon isotope ratios of whole blood were similar in adults and chicks, whereas stable nitrogen isotope ratios showed significant enrichment by >1‰ in chicks. The combined FA, stable isotopes and stomach contents analyses suggest clear differences in diet quality between adults and chicks, with chicks feeding at a higher trophic position through feeding more on highly nutritious fish and adults keeping much of the less nutritious zooplankton for themselves.

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Introduction

Seabirds represent an important trophic link in the transfer of nutrients between land and sea, deriving their nutrition from the ocean and returning to land during the breeding season. Procellariiform seabirds in the Southern Ocean are highly mobile and can perform foraging trips over thousands of kilometres (Waugh et al. 1999; Catard et al. 2000); therefore, determination of their diet has proven challenging. During the breeding season, the food intake of seabirds is limited by the availability of prey in geographically accessible foraging areas. Many species undertake foraging trips of variable length and distance (Weimerskirch et al. 1994), the duration depending on the body condition of the adults (Weimerskirch 1998), with food derived on short-term trips serving as the main source of nutrition for chicks and food derived on long-term trips largely providing nutrition for the adults (Weimerskirch et al. 2003; Cherel et al. 2005a). On foraging trips, seabirds must take

advantage of patchy and unpredictable distributions of their prey by successfully detecting and evaluating the relative value of prey patches (Nel et al. 2001). Flexible and complex behaviour and feeding patterns further complicate studies of procellariiform diet, and they also present the possibility that chicks can have diets markedly different from their parents because of both selective provisioning and the need to forage in areas close to the nest during chick provisioning. Furthermore, should adult and chick diets prove to be identical, chicks may metabolize and store their food in a manner that is different from adults.

Despite inherent difficulties in seabird ecological research, valuable data have been collected on the foraging habits and diet choices of several procellariiform species (e.g. Cherel et al. 2000; Xavier et al. 2003; Cherel et al. 2005a; Connan et al. 2007). The dependence of seabirds on land for chick-rearing provides ideal opportunities for field research. Traditionally, such studies involve analysis of stomach contents from adults and/or chicks (Barrett et al. 2007; Connan et al. 2007). This approach is limited because of the long distances involved, as assimilation of prey, particularly during long-term trips, renders many prey items unidentifiable (Cherel et al. 2002a). Moreover, for most species the method is restricted to the chick-rearing period, and it depicts the food of chicks and less of adults when they self-feed. Following the assumption that the elemental or molecular composition of consumers reflects that of their diet, tracer techniques such as stable isotope and fatty acid (FA) signatures have been utilized more recently to improve our general knowledge of seabird dietary sources. These methods are used to provide data on prey assimilated by a variety of organisms over ecologically meaningful periods (Barrett et al. 2007; Wang et al. 2009), and can be used in a complementary manner to derive seabird dietary information through non-lethal samples of blood, adipose tissue, feathers and stomach oil (Hodum and Hobson 2000; Cherel et al. 2002a; Connan et al. 2005; Wang et al. 2009). Non-lethal sampling is becoming increasingly important in view of the substantial decreases in population size experienced by numerous seabird species. Stomach oils contain dietary markers of pre-digested food, whereas blood, feather and tissue samples represent assimilated versions of the original diet. Thus, the most useful assessments of diet quality in seabirds use multiple methods to incorporate analysis at all levels at which nutrient modification can take place.

Grey-headed albatrosses (*Thalassarche chrysostoma*) typically breed once every two years, with their breeding season spanning several months (between September and May). These seabirds forage over an extensive area (up to 2,000 km from their breeding grounds), with short and longer trips lasting 5–26 days, respectively (Nel et al. 2001; Xavier et al. 2003). Prey items include fish (e.g. *Magnisudis prionosa*, myctophids), squid and Antarctic krill from cold Antarctic and sub-Antarctic oceanic waters in addition to shelf and slope regions of the sub-Antarctic islands of the Southern Ocean (Nel et al. 2001; Cherel et al. 2002b; Xavier et al. 2003). Satellite-tracking data (Nel et al. 2001) and the presence of high-latitude Antarctic prey species, including the krill *Euphausia superba* and the squid *Galiteuthis glacialis*, in stomach contents (Cherel et al. 2002b) have shown that *T. chrysostoma* forages over southern water masses and cold-core eddies. Approximately 7,000 pairs of Grey-headed albatrosses breed on Marion Island (Nel et al. 2002), the location of our study, which is situated within the Polar Frontal Zone between the sub-Antarctic Front to the north and the Antarctic Polar Front to the south.

In this study, we contribute to the growing research effort towards understanding energy acquisition and transfer through seabirds in the Southern Ocean. We assessed potential dietary differences between adult *T. chrysostoma* and their chicks using stomach content analysis, stable isotope signatures of whole blood, and FA profiles of plasma and stomach oil. We hypothesized that one or more of the techniques utilized would indicate differences in the diets of chicks and adults owing to selective provisioning of food to the chicks by the adults. FA profiles and stable isotope signatures of *T. chrysostoma* were compared with available published information on potential prey species and diving predators in the Southern Ocean.

Methods

Field collection

The study was carried out at the Grey-headed albatross colony at Rook's Peninsula on Marion Island (46°54′S, 37°51′E) during the end of the chick-rearing period in April 2006. Blood and stomach contents were collected from adults returning to the colony and chicks that had been recently fed. All seabirds were caught on the nest by hand or using a crook. Sixteen stomach contents were collected from 8 adults and 8 large chicks, which spontaneously regurgitated, and the samples were stored in plastic bags at −20°C. Syringes lined with heparin were used to draw blood from tarsal veins of the seabirds. Aliquots (1 ml) of whole blood from 11 adults and 12 chicks (of which only 3 formed adult/chick pairs) were preserved in 70% ethanol for subsequent stable isotope analysis. Aliquots (0.5–3.5 ml) of blood (from 5 adults and 5 chicks out of the original 23 individuals sampled for isotopes) intended for FA analysis were centrifuged following collection. The plasma layer of each blood sample was added to test tubes

containing 2 ml chloroform, covered with nitrogen gas and stored at −20°C (Budge et al. 2006). In the majority of cases, the stomach contents and blood samples were not collected from the same birds.

Laboratory analysis

In the laboratory, stomach contents were thawed, drained by gravity and sorted. Stomach oil droplets were pipetted from freshly thawed stomach contents of 4 adults and 8 chicks (oil was not present in all samples), added to 2 ml chloroform, topped with nitrogen and stored at −20°C for subsequent FA analyses. Food analysis followed Cherel et al. (2000). Fresh prey were divided into broad categories of fish, cephalopods, crustaceans and others and then weighed to provide proportional estimates of each category in the diet. Cephalopod beaks without flesh attached were considered accumulated items and not included in calculations of fresh prey. Prey were counted and identified to species whenever possible using published keys (Baker et al. 1990; Smale et al. 1995; Xavier and Cherel 2009) and an internal reference collection. Otoliths and bones were used to identify the fish, beaks for the cephalopod identifications and exoskeletons for crustaceans. Stomach contents results are reported as frequency of occurrence (the number and percentage of birds that contained a particular prey type in their stomachs) and total number of prey types (number and percentage) found within all stomach contents.

Total lipids of plasma and stomach oil samples were extracted/purified using a modified Folch procedure (Folch et al. 1957) within 7 months of collection. Samples were extracted in 2:1 (v/v) chloroform/methanol, with solvent volumes adjusted for each sample in an effort to obtain an 8:4:3 ratio (v/v/v) of chloroform/methanol/water. The lipid layers were removed using a double-pipetting method and combined following each of three chloroform washes (Parrish 1999). Fatty acid methyl esters (FAMEs) were prepared by heating the extracts suspended in hexane at 80°C for 1.5 h in the presence of 14% boron trifloride-methanol (method adapted from Parrish 1999). Gas chromatographic (GC) analyses of FAMEs were performed with a Hewlett Packard 5890A GC equipped with a bonded and crosslinked 78% cyanopropyl methylpolysiloxane fused silica capillary column (30 m length, 0.25 mm ID, 0.25 μm film thickness; Quadrex Corporation) with helium as the carrier gas. One-microlitre aliquots of sample were manually injected at 250°C with the oven set at 100°C. After 3 min, the oven temperature was raised to 150°C at 5°C min^{-1}, held for 1 min, and raised to 220°C at 3.5°C min^{-1}. The temperature of the flame ionization detector was set at 260°C. Peaks were integrated using 32 Karat 5.0 software (Beckman Coulter Inc.) and identified using mass spectral data derived from a subset of the samples (Thermo-Finnigan GC/MS fitted with same column as above) and by comparing retention times with those of known external standards (37 component FAMEs standard and marine PUFA no. 1, Supelco). Each FA was reported as a proportion of the total identified fatty acids (%TFA) in the shorthand form x:an-b, where x is the number of carbon atoms in the acyl chain, a is the total number of double bonds and b is the position of the first double bond from the methyl end of the molecule. Saturated fatty acids (SFAs) have no double bonds (e.g. 14:0), monounsaturated fatty acids (MUFAs) contain one double bond (e.g. 16:1n-7) and polyunsaturated fatty acids (PUFAs) have more than one double bond (e.g. 16:3n-4). Essential fatty acids (EFAs) include 20:4n-6, 20:5n-3 and 22:6n-3.

Whole blood samples were dried at 60°C and homogenized. Low lipid levels in whole blood, as indicated by low C:N mass ratios, precluded the necessity for lipid extraction (Cherel et al. 2005a). Stable isotope analyses were performed on 1 mg subsamples in a continuous-flow isotope ratio mass spectrometer (Micromass Isoprime) coupled to an elemental analyser (Euro Vector EA 3024) at the Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés, UMR 6217 du CNRS-IFREMER-ULR, L'Houmeau (France). Raw data were corrected using acetanilide internal standards, and analytical precision of the instrument was <0.15 and <0.30% for carbon and nitrogen measurements, respectively. Carbon and nitrogen isotope ratios are reported relative to Vienna-Pee Dee Belemnite and atmospheric nitrogen, respectively, in the traditional δ notation (‰; parts per thousand) derived from the equation: $\delta(‰) = (R_{sample}/R_{standard} - 1) \times 1{,}000$ (where δ is $\delta^{13}C$ or $\delta^{15}N$ and R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively).

Statistical analysis

To examine associations among the plasma and stomach oil samples from adults and chicks based on FA profiles, principal component analysis (PCA) was applied to arcsine square root transformed proportional data of all FAs. To test for statistical differences of FA profiles among groups, principal component 1 (PC1) and PC2 scores were used as dependent variables in two separate one-way ANOVAs (alpha level of $P < 0.05$ for all tests). Groups were considered distinct from one another if either or both of the PC1 or PC2 scores differed significantly in subsequent Tukey multiple comparisons tests. One-way ANOVAs were used to test for differences of total PUFA, MUFA and SFA among groups. To test for relatedness of the stomach oil and plasma profiles to prey, we ran a second PCA which included the published FA profiles (arcsine square root transformed %TFA data) of potential prey. Sixteen fatty

acids that occurred both in the different prey species and in *T. chrysostoma* (14:0, 15:0, 16:0, 17:0, 18:0, 22:0, 16:1n-7, 18:1n-9, 18:1n-7, 20:1n-9, 18:2n-6, 18:4n-3, 20:4n-6, 20:5n-3, 22:5n-3, 22:6n-3) were included in the prey/seabird PCA. Potential prey (all from the Southern Ocean except the macrourids, which were from the North Atlantic) were represented by notothenioids (Patagonian toothfish *Dissostichus eleginoides*), macrourids (*Coryphaenoides armatus*, *C. yaquinae*, *C. guentheri* and *C. ruspestris*), various teleosts (*Phosichthys argenteus*, *Salilota australis*, *Paradiplospinus gracilis*, *Arctozenus risso* and *Icichthys australis*), myctophids (*Electrona antarctica*, *E. carlsbergi*, *E. subaspera*, *Gymnoscopelus bolini*, *G. braueri*, *G. fraseri*, *G. nicholsi*, *G. piabilis*, *Lampichthys procerus*, *Metelectrona ventralis*, *Protomyctophum bolini*, *P. choriodon* and *P. tenisoni*), cephalopod digestive glands (*Brachioteuthis* spp., *Galiteuthis glacialis*, *Gonatus antarcticus*, *Histioteuthis eltaninae*, *Kondakovia longimana*, *Mastigoteuthis* sp., *Mesonychoteuthis hamiltoni*, *Moroteuthis ingens*, *Moroteuthis knipovitchi*, *Moroteuthis robsoni*, *Psychroteuthis glacialis* and *Todarodes* spp.) and zooplankton, including euphausiids (*Thysanoessa macrura*, *Euphausia lucens* and *E. superba*) and amphipods (*Themisto gaudichaudii*). Prey data, mainly mean values, were extracted from Nichols et al. (1994), Kattner et al. (1996), Phleger et al. (1998), Raclot et al. (1998), Hagen et al. (2001), Nelson et al. (2001), Phillips et al. (2001, 2002, 2003a, b), Lea et al. (2002), Wilson (2004), Drazen et al. (2009), Newland et al. (2009) and Stowasser et al. (2009a, 2009b). In this larger dataset, transformations were not successful in normalizing all of the FA variables, so an additional non-parametric multidimensional scaling (*n*-MDS) analysis was performed on the same data to substantiate the PCA findings. Two one-way ANOVAs were used to determine statistical differences between chick and adult whole blood carbon and nitrogen stable isotope signatures. In these isotope models, the samples were not entirely independent because three adult/chick pairs were contained within these data. Statistics were completed using PAST 1.42 (Hammer et al. 2001) or Systat 12.0. Variability is reported as one SD.

Results

Stomach contents

Stomach contents of *T. chrysostoma* (adults and chicks combined) were comprised of fish [59.6% of fresh mass (FM)], cephalopods (20.7% FM), crustaceans (0.3% FM) and carrion (19.4% FM). Fish also dominated the stomach contents by frequency of occurrence (81%), followed by cephalopods (63%) and crustaceans (38%). Crustaceans dominated the albatross diet only when considering total number of items found, all adults and chick stomachs inclusive. Specimens of the family Macrouridae (rattails) dominated the fish component, with 11 specimens identified from the 16 stomach contents. Fresh squids were mainly juveniles of the onychoteuthid *Kondakovia longimana*, while the main crustacean prey was the Antarctic krill *Euphausia superba* (Table 1). Adult albatrosses contained higher numbers of crustacean prey in their stomachs, but fewer fish and cephalopods, than chicks (Table 1).

Cephalopod beaks were enumerated separately from the fresh food, as they resist digestion and accumulate in seabird stomachs over time. Thirteen species of squid were identified, and the total number of beaks found in each stomach content sample ranged from 1 to 112, with a mean of 29 beaks per sample. The most dominant cephalopods

Table 1 *Thalassarche chrysostoma*

Prey	Frequency (%)		Number (%)	
	Adults	Chicks	Adults	Chicks
Fish	6 (75)	7 (88)	7 (19)	9 (47)
Phosichthys argenteus	–	1	–	1
Alepisaurus brevirostris	–	1	–	1
Coryphaenoides lecointei	2	1	3	2
Coryphaenoides sp. A	1	2	1	2
Macrouridae sp.	3	–	3	–
Dissostichus eleginoides	–	1	–	1
Unidentified fish	–	2	–	2
Cephalopods	5 (63)	5 (63)	7 (19)	5 (26)
Kondakovia longimana	2	1	4	1
?*Mastigoteuthis* A (Clarke)	1	–	1	–
Galiteuthis glacialis	–	1	–	1
Unidentified cephalopods	2	3	2	3
Crustaceans	3 (38)	3 (38)	22 (59)	3 (16)
Euphausia superba	1	1	15	1
Euphausia sp.	–	1	–	1
Neognathophausia gigas	1	1	1	1
Pasiphaea scotiae	1	–	1	–
Lepas australis	1	–	5	–
Others	1 (13)	2 (25)	1 (3)	2 (11)
Carrion	1	2	1	2
Total			37 (100)	19 (100)

Fresh food items in stomachs of Grey-headed albatrosses from Marion Island, April 2006

Frequency the number and % of birds that contained each item out of the eight stomach contents examined from adults and eight stomach contents from chicks; *Number* total number of food items counted, all stomach contents from adults or chicks inclusive; values in parentheses are percentages; ?, refers to an unconfirmed identification of cephalopod beaks

Table 2 *Thalassarche chrysostoma*

Cephalopods	Number	
	n	%
Ommastrephidae		
Ommastrephidae sp.	5	1.6
Onychoteuthidae		
Moroteuthis ingens	2	0.6
Moroteuthis knipovitchi	4	1.3
Kondakovia longimana	121	38.4
Psychroteuthidae		
Psychroteuthis glacialis	2	0.6
Psychroteuthis glacialis (small)	1	0.3
Brachioteuthidae		
Slosarczykovia circumantarctica	3	1.0
Gonatidae		
Gonatus antarcticus	4	1.3
Histioteuthidae		
Histioteuthis eltaninae	26	8.3
Neoteuthidae		
Alluroteuthis antarcticus	16	5.1
Mastigoteuthidae		
?*Mastigoteuthis* A (Clarke)	2	0.6
Batoteuthidae		
Batoteuthis skolops	11	3.5
Cranchiidae		
Galiteuthis glacialis	115	36.5
Mesonychoteuthis hamiltoni	1	0.3
Unidentifiable beaks (eroded)	2	0.6
Total	315	100.0

Cephalopod beaks found in stomachs of Grey-headed albatrosses from Marion Island, April 2006. Adults and chicks were not differentiated here, as only two adult stomachs contained squid beaks (representing 4 beaks in total), with the remainder occurring in nine chick stomachs (one chick contained accumulated items only)

Number total number and percentage of beaks counted (both upper and lower beaks in all stomach contents, $N = 16$); ?, refers to an unconfirmed identification of cephalopod beaks

(by percentage by number) recorded from these accumulated remains were *Kondakovia longimana* (38%) and *Galiteuthis glacialis* (37%), with *Histioteuthis eltaninae* (8%) and *Alluroteuthis antarcticus* (5%) being common prey items (Table 2).

Fatty acids

Twenty-eight FAs were detected in *T. chrysostoma* stomach oils, and twenty in plasma samples (Table 3). The most abundant FAs in all oil samples were 18:1n-9 (range 13–32% TFA), 16:0 (range 13–25%) and 16:1n-7 (range 10–19%). In contrast, the dominant FAs in plasma were 16:0 (range 30–45%), followed by 18:1n-9 (range 14–21%), 18:0 (range 5–14%) and 20:5n-3 (range 6–10%; Table 3). Plasma and stomach oil FA profiles were significantly different from one another (one-way ANOVA of PC1 scores: $F_{3,18} = 170.63$, $P < 0.001$, followed by Tukey pairwise comparisons of the 4 sample types—adult plasma, adult oil, chick plasma, chick

Table 3 *Thalassarche chrysostoma*

Fatty acid	Plasma		Stomach oil	
	Adults ($n = 5$)	Chicks ($n = 5$)	Adults ($n = 4$)	Chicks ($n = 8$)
14:0	5.2 ± 0.8	5.2 ± 2.3	8.3 ± 4.1	12.6 ± 3.5
15:0	0.7 ± 0.1	0.5 ± 0.2	0.6 ± 0.2	0.5 ± 0.2
i-15:0	–	–	0.2 ± 0.1	0.2 ± 0.2
16:0	41.3 ± 2.6	29.0 ± 3.2	16.9 ± 4.3	22.8 ± 3.6
17:0	0.6 ± 0.3	0.7 ± 0.2	0.3 ± 0.1	0.3 ± 0.2
ai-17:0	–	–	tr	0.4 ± 0.3
18:0	9.4 ± 1.0	10.2 ± 3.5	0.8 ± 0.2	1.0 ± 0.5
20:0	–	–	0.1 ± 0.1	0.1 ± 0.1
22:0	0.2 ± 0.1	0.3 ± 0.1	0.6 ± 0.1	0.4 ± 0.1
23:0	–	–	0.1 ± 0.0	0.1 ± 0.0
ΣSFA	57.4 ± 2.3[a]	45.8 ± 1.9[a]	27.9 ± 8.7[b]	38.2 ± 6.5[b]
14:1	–	–	0.6 ± 0.9	0.2 ± 0.2
15:1	–	–	0.1 ± 0.1	0.1 ± 0.0
16:1n-5	–	–	tr	0.3 ± 0.2
16:1n-7	3.2 ± 0.9	4.9 ± 0.8	15.3 ± 2.9	14.2 ± 2.4
17:1	0.2 ± 0.1	0.2 ± 0.1	–	–
18:1n-9	15.1 ± 0.7	19.9 ± 1.2	23.2 ± 7.5	18.1 ± 5.4
18:1n-7	3.7 ± 0.3	5.6 ± 1.0	9.4 ± 2.4	9.1 ± 2.2
20:1n-9	1.0 ± 0.1	1.9 ± 0.8	5.0 ± 1.3	5.0 ± 1.1
ΣMUFA	23.1 ± 1.5[a]	32.5 ± 1.4[a]	53.7 ± 9.7[b]	46.9 ± 7.6[b]
16:3n-4	–	–	0.6 ± 0.2	0.5 ± 0.2
16:4n-3	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.0	0.3 ± 0.1
18:2n-6	0.8 ± 0.1	1.7 ± 0.5	1.3 ± 0.2	1.1 ± 0.3
18:3n-3	0.1 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.3 ± 0.1
18:4n-3	–	–	0.7 ± 0.3	0.6 ± 0.3
20:2n-6	0.1 ± 0.1	0.1 ± 0.0	0.2 ± 0.1	0.2 ± 0.1
20:3n-6	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.0	0.1 ± 0.0
20:4n-6	5.7 ± 1.6	5.6 ± 2.0	0.6 ± 0.1	0.4 ± 0.1
20:5n-3	7.7 ± 1.4	8.4 ± 0.8	7.7 ± 0.6	6.5 ± 1.6
22:5n-3	0.5 ± 0.1	0.5 ± 0.2	0.7 ± 0.2	0.5 ± 0.2
22:6n-3	4.3 ± 0.4	4.6 ± 0.3	5.8 ± 0.9	4.6 ± 0.7
ΣPUFA	19.5 ± 0.3[a]	21.7 ± 1.7[a]	18.5 ± 1.1[ab]	14.9 ± 2.4[b]
ΣEFA	17.8 ± 2.1	18.6 ± 1.8	14.1 ± 1.1	11.5 ± 1.8
n-3/n-6	2.0 ± 0.7	1.9 ± 0.5	7.0 ± 0.5	7.5 ± 1.7

Fatty acid composition (%TFA, mean ± SD) of plasma and stomach oil. Superscript letters indicate significant differences among sample types (one-way ANOVA followed by Tukey pairwise comparisons, $P < 0.05$)

SFA saturated fatty acids; *MUFA* monounsaturated fatty acids; *PUFA* polyunsaturated fatty acids; *EFA* essential fatty acids; *i* iso; *ai* anti-iso; –, not detected; *tr* traces

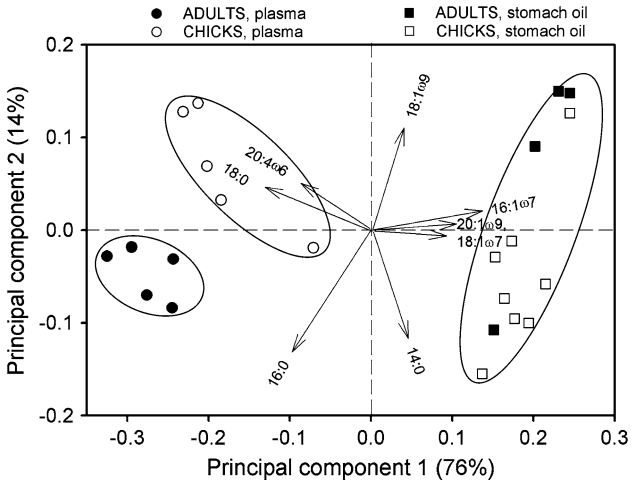

Fig. 1 *Thalassarche chrysostoma*. PCA ordination of stomach oil and plasma fatty acid profiles in adults and chicks. Percentage values represent the proportion of the variance explained by each principal component. Arrows running from centre denote the influence of fatty acids having loading values >|0.2| (although all fatty acids were included in the analysis). Sample groups within the same ellipses were not significantly different from one another (Tukey multiple comparisons, $P < 0.05$, following one-way ANOVAs of PC1 and PC2 scores). *Dashed lines* denote the origin

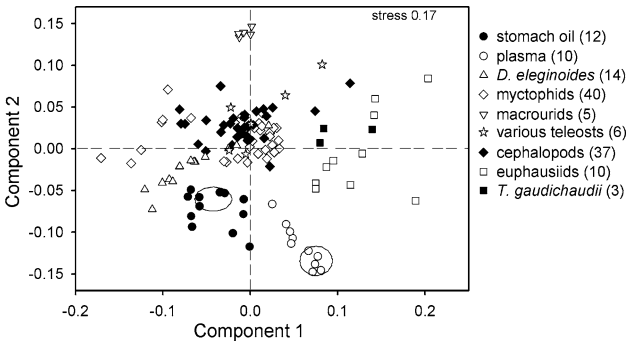

Fig. 2 *Thalassarche chrysostoma*. *n*-MDS ordination of stomach oil and plasma fatty acid profiles in relation to potential prey species in the Southern Ocean (%TFA; see "Methods" for species list, sources of prey data, and the 16 FAs used in the analysis). *Dashed lines* denote the origin, and ellipses distinguish the adult Grey-headed albatross samples (the remainder represents chicks). Numbers in brackets represent sample sizes. Stress is a measure of goodness-of-fit, with small values <0.15 indicating the best fit, and 0.17 indicating a reasonable fit

oil) based on higher levels of 20:1n-9, 18:1n-7, 16:1n-7 and 14:0 in the oils compared with higher levels of 20:4n-6, 16:0 and 18:0 in the plasma (Fig. 1). Plasma FA profiles in chicks and adults separated from one another along both PC1 and PC2, particularly owing to the influence of higher levels of MUFAs in the chicks relative to the adults, and higher SFA levels (particularly 16:0) in the adults ($P < 0.05$; Fig. 1, Table 3). Stomach oils from chicks and adults were more variable, overlapping within the PCA plot and thus were not distinct from one another in Tukey pairwise comparisons ($P = 0.788$; Fig. 1). PC1 explained 76% and PC2 explained 14% of the variation, in combination explaining 90% of the variance in the data.

Many of the species in our compiled prey database were not found in the stomach contents of Marion Island *T. chrysostoma* during this study, but the analysis provided a reasonable indication of the potential prey sources available to the albatrosses in the Southern Ocean. The output of PCA and *n*-MDS analyses of potential prey items and *T. chrysostoma* data revealed nearly identical patterns, and only the non-parametric *n*-MDS results are presented here (Fig. 2). Plasma profiles of adult and chick *T. chrysostoma*, which represent dietary fatty acids modified by metabolic processes, were markedly different from all of the prey. Most of the stomach oil samples, which represent unassimilated dietary fatty acids and the average signature of all recently ingested prey, were located nearest to the fish FA profiles (in particular the Patagonian toothfish *D. eleginoides*), but were distant from the zooplankton (Fig. 2), thus partially supporting the stomach contents findings. Cephalopods and myctophids represented the next-nearest neighbours to stomach oil in the *n*-MDS plot, and the macrourids (from the North Atlantic) were distant (Fig. 2).

Stable isotopes

Whole blood $\delta^{13}C$ signatures of chicks (-22.6 ± 0.3‰, $n = 12$) were not significantly different from those of adults (−22.4 ± 0.6‰, $n = 11$; $F_{1,21} = 2.79$, $P = 0.11$). In contrast, whole blood $\delta^{15}N$ signatures of chicks (12.1 ± 0.6‰) were significantly more enriched than those of the adults (10.7 ± 0.5‰; $F_{1,21} = 36.89$, $P < 0.001$). C:N mass ratios of chick blood (3.53 ± 0.09) did not differ significantly from those of adult blood (3.51 ± 0.11; $F_{1,21} = 0.28$, $P = 0.60$), indicating that lipid levels did not change with development stage of the albatrosses. Marion Island *T. chrysostoma* whole blood $\delta^{13}C$ signatures were intermediate between those of Southern Ocean diving predators from the Polar Frontal and Antarctic Zones, and they most resembled signatures of Crozet Island King Penguins (Fig. 3) whose primary foraging area in the summer is at the Polar Front (Cherel et al. 2007). Nitrogen signatures of *T. chrysostoma* were higher than those of crustacean feeders (Adélie penguins, Antarctic petrels, and Rockhopper and Macaroni penguins), approximately at the same level as fish predators (Emperor penguins, Antarctic fur seals and sub-Antarctic fur seals), but lower than those of a squid predator (Wandering albatrosses; Fig. 3).

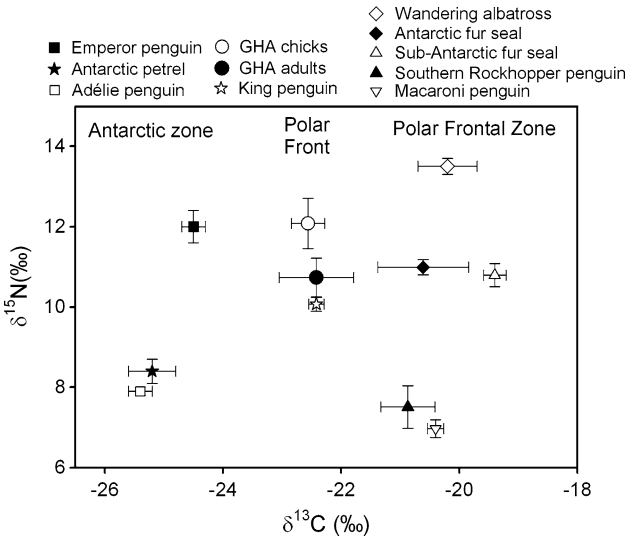

Fig. 3 *Thalassarche chrysostoma*. Stable carbon and nitrogen isotope signatures (‰ ±SD) in whole blood of Grey-headed albatrosses (GHA) from Marion Island and other air-breathing diving predators in the Southern Ocean. Data sources: Emperor penguin (Adélie Land, Antarctica; Cherel 2008), Antarctic petrel (East Antarctica; Hodum and Hobson 2000), Adélie penguin (Adélie Land, Antarctica; Cherel 2008), King penguin—indicative of foraging at the Polar Front (Crozet Island; Cherel et al. 2007), Wandering albatross (Crozet Island; unpubl data), Antarctic fur seal (Crozet Island; Cherel et al. 2007), sub-Antarctic fur seal (Crozet Island, Cherel et al. 2007), Southern Rockhopper penguin (Crozet Island; Cherel et al. 2007), Macaroni penguin (Crozet Island; Cherel et al. 2007)

Discussion

In our study of *T. chrysostoma* at Marion Island, stable isotope signatures revealed a trophic level change between adults and chicks; stomach content analysis revealed that chicks were fed predominantly fish, whereas adults had an increased consumption of crustaceans compared with the chicks, and FA groupings suggested differences in adults and chicks that originated either from differences in diet or in lipid metabolism/storage. Stomach contents analysis provided an indication of the recent prey of the Grey-headed albatross, which assisted in the determination of potential sources of the time-integrated dietary markers derived from stable isotope and FA signatures. Our results exemplify the benefits of utilizing three independent methods to explore the variability in seabird diets.

Stomach contents

Overall, stomach contents of *T. chrysostoma* at Marion Island, as measured using both frequency of occurrence and fresh mass, indicated a predominance of fish in their diets, followed by cephalopods and then crustaceans. These results are consistent with that of previous studies on *T. chrysostoma* inhabiting the Prince Edward Islands (Hunter and Klages 1989; Nel et al. 2001), although *Magnisudis prionosa* (Paralepididae) was previously found to dominate the fish portion of the diet, followed by myctophids (Nel et al. 2001), whereas these fish prey were not detected in our study. Surprisingly, rattails (mainly of the Genus *Coryphaenoides*) were the main fish prey in April 2006 at Marion Island. *Coryphaenoides* spp. are deep-sea fish (>2,000 m; Gon and Heemstra 1990) that are not usually available to seabirds at the sea surface. Some rattail species are regular bycatches of the Patagonian toothfish longline fishery in the Southern Indian Ocean (Duhamel et al. 1997), but they belong to the Genus *Macrourus* and live at shallower depths than *Coryphaenoides* spp. (Gon and Heemstra 1990). Thus, how albatrosses captured the latter species remains unclear, the most likely explanation being that they are eaten as carrion at the surface (Cherel and Klages 1998). For example, Sakamoto et al. (2009) showed that some albatrosses in the Southern Ocean actively followed a killer whale (*Orcinus orca*), potentially to feed on the food scraps left behind. The differences observed in our results relative to other studies conducted earlier in the chick-rearing period (Hunter and Klages 1989, Nel et al. 2001, Cherel et al. 2002b) may reflect seasonal and/or interannual changes in the prey community structure, and/or changes in the diet of chicks before they fledge, as our samples were collected during a few days in April at the end of the 2005–2006 breeding period. A diet rich in lipids may be particularly important in chicks just prior to fledging, as it may increase their probability of survival after they leave the colony.

The diet of *T. chrysostoma* varies with geographical location (Rodhouse et al. 1990), foraging distance of adults (Xavier et al. 2003) and with the occurrence and location of mesoscale oceanic phenomena such as eddies and fronts that can provide seabirds with access to concentrated patches of prey (Waugh et al. 1999; Nel et al. 2001). Geographic variability in *T. chrysostoma* diet may also arise in part from the establishment of non-overlapping foraging zones with any sympatric species to reduce interspecific competition (Waugh et al. 1999; Cherel et al. 2002b). As an example of geographical variation in prey availability in the southern Indian Ocean, Grey-headed albatrosses at Kerguelen Island (some 2,600 km east of Marion Island) feed primarily on squids, penguin flesh, fish and crustaceans, in decreasing order of importance (Cherel et al. 2002b). In the current study, *T. chrysostoma* did not appear to focus on penguin prey (identified either by feathers or skin pieces), but on fish, and squid was a significant component of its diet. *T. chrysostoma* at Marion Island were clearly ingesting large numbers of onychoteuthid squids (particularly juvenile *Kondakovia longimana*) and, if accumulated beaks are taken into account, cranchiids (adult *Galiteuthis glacialis*), all of which are sub-Antarctic

or Antarctic species. The latter squid species inhabits both oceanic and slope regions of the Antarctic and sub-Antarctic (Cherel and Weimerskirch 1999) and has been recorded in albatross diets (Rodhouse et al. 1990; Nel et al. 2001). Previous analysis of squid prey in *T. chrysostoma* from Marion Island indicated dominance of biomass by *Moroteuthis knipovitchi* in addition to *K. longimana* (Hunter and Klages 1989), with the lack of ommastrephids in the diet being unique compared with records of Grey-headed albatrosses from all other regions of the Southern Ocean (Cherel and Klages 1998; Cherel et al. 2002b).

The low frequency of crustacean occurrence in Marion Island Grey-headed albatross stomach contents is consistent with previous research, although the species composition tends to vary. Two crustacean prey species common in both our samples and an earlier study by Nel et al. (2001) were the krill *Euphausia superba* and the decapod shrimp *Pasiphaea scotiae*. In the Indian Ocean, *E. superba* occurs far south of the Antarctic Polar Front (Pakhomov et al. 1994); therefore, these prey were acquired on long-term foraging trips in Antarctic waters either at latitudes >59°S (see discussion in Cherel et al. 2002a) or from a cold-core eddy found closer to Marion Island, but originating in the south (Nel et al. 2001). The mysid *Neognathophausia gigas* and caridean shrimp *Pasiphaea scotiae* have been found in small proportions in the diets of related procellariiform seabirds and are considered a primary prey source (as opposed to secondary prey sources consumed by intermediate predators; Cherel et al. 2000). Depending on the prevalent oceanographic conditions, and hence the availability of prey in a particular location, crustaceans (particularly *E. superba*) can represent a major portion of *T. chrysostoma* diet (77% by mass and 90% by frequency of occurrence in South Georgia; Xavier et al. 2003).

Fatty acids

FA signatures in consumer body tissues reflect their diets despite the metabolic changes that occur during the assimilation of FAs from food. Adipose tissue biopsies provide a close reflection of diet over ecologically relevant time scales, although obtaining such samples without causing damage to birds can be challenging. Furthermore, to utilize FA profiles of adipose tissue and plasma most efficiently, feeding experiments are needed to deduce calibration factors for the transfer of FAs from diet to predator tissue (Käkelä et al. 2005; Käkelä et al. 2010). Since the FA profiles of seabird stomach oils represent relatively unmodified signatures of recently consumed food, they are the ideal samples for undertaking dietary studies as they eliminate the necessity for conducting calibration studies (Käkelä et al. 2005). Until recently, few studies have combined more than one method to examine the trophodynamics of seabirds (Connan et al. 2007; Käkelä et al. 2007; Williams et al. 2008).

Stomach oil of procellariiformes is derived directly from mechanical breakdown of lipid-rich prey, rather than secretions by the adults (Clarke 1989). As a result, stomach oil FAs represent the average signature of the dominant lipid-rich and undigested prey from previous meals, mainly derived from long-term foraging trips (Connan et al. 2005), and they show large intra- and inter-species variability (Warham et al. 1976; Connan et al. 2007). Nevertheless, the FA profiles of Marion Island *T. chrysostoma* stomach oil were remarkably similar to documented accounts (Clarke and Prince 1976; Warham et al. 1976), with 16-, 18- and 20-carbon MUFAs dominating the TFAs by >46% and the remainder composed of SFAs (mainly 14- and 16-carbon) and PUFAs (the essential fatty acids 20:5n-3 and 22:6n-3).

An ideal study using dietary biomarkers to determine food sources of consumers requires the collection of consumers and their potential prey species concurrently. In the case of long-distance foragers such as *T. chrysostoma*, this is not logistically possible. As a result, our comparisons of consumer stomach oil and plasma FA profiles were made with published accounts of potential Southern Ocean prey profiles. FA information on the species found in the stomach contents of *T. chrysostoma* (Table 1) is limited, and the existing data have been collected over a long time frame, introducing the problem of temporal variability in prey signatures. Our examination of the dietary origin of albatross stomach oil FAs was somewhat coarse and limited to broad prey categories (myctophids, notothenioids, macrourids, other teleosts, cephalopods and crustaceans), but will increase in resolution once the lipid content and composition of potential prey species become better understood. Lipid content (on a weight basis) of the main prey groups may have some influence on the dominant FA in seabird stomach oils, although these data are frequently reported using different units (% dry mass or % wet mass). The fish and krill tend to have substantial lipid contents [e.g. up to 53% dry mass (DM) in macrourids, 18% wet weight in myctophids, and 48% DM in krill; Hagen et al. 2001; Lea et al. 2002; Drazen et al. 2009], and even squid have high lipid contents when considering the digestive gland (up to 54% wet mass) rather than the mantle (2% wet mass; Phillips et al. 2002).

In general, notothenioid fish species such as the Patagonian toothfish *D. eleginoides* tend to contain high levels of PUFAs, the EFAs 20:5n-3 and 22:6n-3 in particular, but low levels of n-6 FAs such as the EFA 20:4n-6 (Nichols et al. 1994). This tendency may help explain the high n-3/n-6 ratios in *T. chrysostoma* stomach oils (Table 3). Our *n*-MDS analysis, which incorporated a variety of FA profiles primarily from Southern Ocean organisms, indicated

an association between Grey-headed albatross stomach oils and the Patagonian toothfish (*D. eleginoides*) and some similarities of the stomach oils with myctophids and cephalopods (Fig. 2). Of particular interest was the distant location of macrourid FA profiles relative to the stomach oils, as the albatross stomach contents were dominated by macrourid fish. This discrepancy probably arises from the lack of information on macrourid fish from the Southern Ocean (macrourid FA profiles depicted in Fig. 2 arise from North Atlantic samples, Drazen et al. 2009). Stomach oils showed the weakest association with the zooplankton profiles, although signatures from crustacean food sources commonly occur in higher predators as secondary prey signals, i.e. they arise from prey items within the guts of prey (Phillips et al. 2002). Previous research has shown that the food web encompassing copepods–myctophids–squids-higher predators may be a very prevalent and widespread energy pathway in the Southern Ocean (Phillips et al. 2001). Digestive glands in many squid species contain by far the greatest proportion of total lipids, and their FA profiles reflect the long-term diet of squid very closely because they are deposited with minimal metabolic modification (Phillips et al. 2002). These unique qualities of squid digestive glands also hinder studies on consumers of squid, as the squid FA profiles tend to reflect their own prey rather than unique squid signatures. Squid species such as *Moroteuthis ingens* feed mainly on myctophids; therefore, their digestive glands are likely to contain lipids originating from myctophids (Fig. 2; Phillips et al. 2001). Myctophids were not found in our stomach samples, but stomach oil FA profiles indicate that myctophid prey probably made up a proportion of the albatross diet. Myctophids are highly abundant and widely distributed throughout the Southern Ocean (Gon and Heemstra 1990), and they typically represent important prey during the long chick-rearing period, as seen in several petrel species (Connan et al. 2007). Further clarification of *T. chrysostoma* diet through FA analysis requires additional data on the potential prey species that encompasses their geographic, temporal and biological availability.

FA analysis of plasma in *T. chrysostoma* from Marion Island suggested the possibility of differences in diets of adults and chicks (Fig. 1), although we cannot exclude physiological and/or biochemical differences between adults and chicks, and some overlap in FA composition of stomach oils did not allow a definitive age-class separation (Table 3; Fig. 1). Similarly, Connan et al. (2007) found no significant differences between adult and chick stomach oils in White-chinned petrels *Procellaria aequinoctialis* from Crozet Island, and they concluded that the dietary origins of chick and adult oil were identical. Our findings of chick/adult diet segregation in Grey-headed albatrosses are compelling and warrant additional study to clarify the temporal variation and level of differentiation between adults and chicks.

Despite large variability among individuals, seabird plasma FA profiles were able to identify individual diets and differences in diet composition between colonies of Great skuas *Stercorarius skua*, gannets *Morus bassanus*, shags *Phalacrocorax aristotelis* and common guillemots *Uria aalge* in the Northeast Atlantic (Käkelä et al. 2006, 2007). Species such as the Great skua that do not contain stomach oil require added calibration steps to assess the modification of FAs from diet to plasma (Käkelä et al. 2005). Such calibration studies have shown that new FAs from food are incorporated rapidly into seabird plasma, although a complete turnover requires approximately 2 weeks (Käkelä et al. 2005), thus providing us with a potential integration period for *T. chrysostoma* plasma FAs. Variability among *T. chrysostoma* plasma FAs was not great (Table 3) despite large potential variability in diet among individuals and relatively larger variability among stomach oil FAs (Fig. 1), suggesting that intrinsic factors that modify the dietary signatures may shape the FA profiles of plasma in seabirds. For example, the main plasma FAs are remarkably similar in Marion Island *T. chrysostoma* and in seabirds from the North Atlantic (Käkelä et al. 2007). Higher PUFA levels in plasma relative to stomach oils indicated their preferred incorporation into plasma lipids of the Grey-headed albatrosses, and the EFA proportion of PUFAs were particularly high (Table 3). Levels of the marker 20:1n-9 in the stomach oils at $\sim$5.5% suggested some indirect consumption of calanoid copepods (Saito and Kotani 2000) via fish, euphausiids and other consumers. Despite the greater incidence of crustacean prey in adult stomach contents, higher levels of 20:1n-9 were not seen in the adult plasma or stomach oils relative to chicks. These FAs, if assimilated by albatrosses, may have been metabolically altered, as little trace of them was found in the plasma profiles (<2%). The FA 20:1n-9 and similar long-chain MUFAs were probably not dominant in the crustacean prey, although some of these markers may have existed as fatty alcohols, which were not analysed in this study.

Stable isotopes

Stable carbon isotopes generally show little change from one trophic level to the next; thus, seabird signatures tend to resemble those of their prey (Barrett et al. 2007). Carbon isotope signatures of whole blood from *T. chrysostoma* at Marion Island were relatively depleted (−22.6‰), in keeping with signatures derived from various tissues of procellariiform seabirds (range −25 to −15; Hodum and Hobson 2000; Cherel 2008). As plankton isotopic signatures vary in a predictable manner with latitude (Goericke

and Fry 1994), variation in $\delta^{13}C$ of seabirds also depends on the proportions of different prey species captured from different latitudes (Cherel et al. 2005a). The $\delta^{13}C$ signatures of Grey-headed albatrosses from Marion Island were consistent with those of the King penguins that forage at the Polar Front between the sub-Antarctic and Polar Fronts (Cherel and Hobson 2007), and fell between those of diving predators that forage either north or south of the Polar Front (Fig. 3). However, the larger variance in Grey-headed albatross whole blood $\delta^{13}C$ signatures relative to King penguins suggests that the albatrosses fed on prey derived from a broader area (i.e. in the vicinity of Marion Island, and also in oceanic waters both north and south of the Polar Front). Isotopic variance was greater in adult *T. chrysostoma* than chicks, as chicks integrate many meals collected by two parents over a medium time frame, thus buffering potential inter-individual variations in adult foraging ecology. Furthermore, chicks are fed with prey captured from a smaller geographic area, in the vicinity of the colony, than adult prey.

Stable nitrogen isotopes generally show a relatively large change from one trophic level to the next ($\sim$3‰), so that their signatures can indicate both diet sources and trophic level of a consumer (Cherel et al. 2005b). Nitrogen isotope signatures of whole blood from *T. chrysostoma* at Marion Island were enriched (range 10.2–13.3‰) relative to signatures derived from blood of crustacean-eating seabirds (range 7.0–9.0‰; Hodum and Hobson 2000; Cherel et al. 2007; Cherel 2008). *T. chrysostoma* $\delta^{15}N$ signatures, particularly in the chicks, were similar to those of Emperor penguins from Antarctica, but were slightly enriched relative to a variety of other Antarctic and sub-Antarctic fish-eating seabirds and fur seals (Fig. 3), thus indicating their top trophic level ranking relative to many other Southern Ocean predators. Anderson et al. (2009) also found relatively enriched $\delta^{15}N$ signatures in the whole blood of adult *T. chrysostoma* at South Georgia (mean 11.0‰), although chick blood samples were not provided for comparison. Enriched $\delta^{15}N$ in Marion Island Grey-headed albatross blood reflects the large masses of fish in their diets (particularly the chicks), as indicated by stomach contents analysis. Whereas stable carbon isotopes showed no variation between *T. chrysostoma* adult and chick whole blood samples in our Marion Island study, $\delta^{15}N$ signatures were significantly more enriched in chick blood relative to the adults (by $\sim$1.3‰; Fig. 3). This phenomenon has been documented in other seabird species. For example, Cherel (2008) reported that juvenile Adélie penguins were enriched in $\delta^{15}N$ by $\sim$1.2‰ relative to adults in Adélie Land, Antarctica. Antarctic procellariiformes have also shown this trend, which arises from adults provisioning their chicks with more $\delta^{15}N$-enriched food than themselves (i.e. fish rather than crustaceans, Hodum and Hobson 2000). Thus, enriched $\delta^{15}N$ in Marion Island chicks suggests that these chicks were provisioned with prey occupying a higher trophic level. Although it is possible that isotopic fractionation in predators changes with life stage and growth, this effect is minimal at fledging, i.e. when growth rates are slow (Sears et al. 2009). Several possibilities have been postulated to explain selective provisioning by adults: for example, chicks have greater nutritional requirements to accommodate growth; decreased salt loads to chicks would decrease metabolic stress levels; and delivery of more easily digested food would assist in promoting healthy development in chicks (Hodum and Hobson 2000). However, the salient point here is that adults provide their chicks with lipid-rich fish food and reserve the crustaceans (e.g. Antarctic zooplankton) for themselves. Given the relatively small sample sizes and the fact that individual diets can vary considerably, we recognize that paired samples, while statistically non-independent, might have provided a more conservative comparison of adults with chicks.

A thorough understanding of the trophic ecology of Southern Ocean seabirds is becoming increasingly important, particularly considering the decreasing sizes of many populations (Nel et al. 2002) and the continued exploitation of marine species via commercial fishing. The recovery of long-lived species such as the Patagonian toothfish from commercial exploitation is likely to be very poor relative to fast growing taxa such as cephalopods, and the loss of these resources is undoubtedly strongly affecting the trophic ecology of top predators like seabirds. Furthermore, global climate change is likely to affect Southern Ocean seabirds negatively by altering the distribution and properties of water masses and their associated prey communities. Consequently, understanding how and where different seabirds acquire their resources is of major significance from a conservation perspective. Generalizations of seabird diet are difficult given the limitations on sample size, the techniques available, and the regional variations in prey distribution, but the application of multiple methods to examine trophodynamics strengthens both the quality and quantity of the dietary information acquired. Independent methods have shown that Grey-headed albatrosses selectively provision their chicks with highly nutritious fish, and that cephalopods and crustaceans are less important in their diet. As FA profiles and isotopic signatures of potential prey species for these long-distance foraging seabirds become increasingly available, our ability to trace the variability in their diets will continue to improve.

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