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RESEARCH ARTICLE

Trophic relationships of white-chinned petrels from Crozet Islands: combined stomach oil and conventional dietary analyses

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Abstract The diet of white-chinned petrels *Procellaria aequinoctialis* breeding at the Crozet Archipelago (southern Indian Ocean) was studied using two complementary methods: lipid analysis of stomach oils as trophic markers together with the conventional dietary approach (i.e., stomach content analysis). Objectives were (1) to investigate the adult diet when they feed for themselves by analyzing stomach oil lipids, and (2) to compare the lipid signature of chick and adult oils. Stomach oils mainly consisted of triacylglycerols (TAG), diacylglycerol-ethers (DAGE) and wax esters (WE) (66, 14 and 11%, respectively). The dietary origin of TAG and WE was evaluated by linear discriminant analyses with fatty acid and fatty alcohol fractions. Analyses evidenced that stomach oils did not originate from Antarctic krill, but instead from myctophid fish, thus demonstrating the importance of mesopelagic fish in the nutrition of adult petrels. This result was consistent with the identification of digested remains of myctophids recovered from adult stomach contents after long foraging trips. Large amounts of a rare lipid class, DAGE (up to 76% of total lipids), were identified in two stomach oils, together with fresh remains of the squid *Gonatus antarcticus* (99% by mass), suggesting that DAGE could have the potential to be trophic markers of cephalopods. Moreover, six oils probably originated from Patagonian toothfish, thus confirming strong interactions between white-chinned petrels and fisheries. Comparison between chick and adult stomach oils indicated no major differences in their biochemical composition suggesting an identical dietary origin of oils, mainly myctophids. Both adult and chick oils can therefore be used to determine the feeding ecology of adult birds when they feed far away from their breeding grounds. Finally, food analysis of chick samples and adult samples collected after short and long trips indicated different foraging grounds during the two kinds of trips, and also between long trips performed in subtropical and Antarctic waters.

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Introduction

Understanding ecosystem functioning requires establishing and quantifying trophic relationships between key species of that ecosystem. Seabirds entirely rely on marine resources for food, coming back to the colony only for reproduction. They are thus an integral part of the marine food web. In the Southern Ocean, procellariiform seabirds (albatrosses and petrels) dominate the seabird community in terms of the number of species (about 105 species; Marchant and Higgins 1990). During the breeding season, several procellariiform species use a dual foraging strategy to feed their chicks: adults alternate short trips (ST) in the vicinity of the colony with long trips (LT) to more distant feeding areas (Chaurand and Weimerskrich 1994; Weimerskirch et al. 1994). During LT, adults feed for themselves and store energy in the form of endogenous reserves and stomach oil (Weimerskirch and Cherel 1998; Cherel et al. 2002), but their feeding habits during these trips remain essentially unknown (Cherel et al. 2005; Connan et al. 2005).

The diet of seabirds is classically studied during the chick-rearing period by the identification of prey items recovered from adult and chick stomach contents. This conventional dietary approach is limited to freshly ingested prey, thus precluding the determination of marine resources consumed by adult birds when they feed for themselves (Weimerskirch et al. 2003; Cherel et al. 2005). These limitations have led to the development of indirect techniques that do not depend on the recovery of stomach contents: e.g., the stable isotope ratios of carbon and nitrogen in consumer tissues (Hobson et al. 1994; Cherel et al. 2005) and lipids as trophic markers (adipose tissue: Horgan and Barrett 1985; Raclot et al. 1998; Dahl et al. 2003; plasma: García-Fuentes et al. 2002; Käkelä et al. 2005; stomach oil: Connan et al. 2005). The studies of stomach oil fatty acid (FA) and alcohol compositions have advantages over the studies of tissue FA fingerprints that have to be studied in the species which do not produce stomach oil. Different from the stomach oils, after breakdown in the digestion and subsequent rebuilding, the FA compositions of tissues are largely modified by the birds' metabolism. Thus the laborious feeding tests, necessary for calibrations between FA signatures of prey and bird plasma or adipose tissue (Käkelä et al. 2005, 2006), can be ignored in the species offering stomach oil to be analyzed.

The white-chinned petrel *Procellaria aequinoctialis* is the largest burrowing petrel, with a mass of 1.2 kg and a wing span of 1.5 m. During the austral summer it can be observed from tropical waters in the north to the edge of the Antarctic continent in the south, while breeding grounds are located on sub-Antarctic islands like the Crozet Archipelago, where the population was estimated to amount to 30,000 pairs (Jouventin et al. 1988). During the chick-rearing period, adults use the dual strategy to feed their chick, alternating ST (0–2 days) on the Crozet shelf edge and LT (3–11 days) to oceanic waters, mostly in the Antarctic zone (Catard et al. 2000).

Several studies investigated the white-chinned petrel diet using stomach content analysis (Cooper et al. 1992; Ridoux 1994; Catard et al. 2000). Moreover, two previous investigations have studied lipid composition of white-chinned petrel stomach oils sampled from chicks (Horgan and Barrett 1985; Warham et al. 1976). Our aim was thus to characterize the diet of white-chinned petrels breeding at the Crozet Archipelago using two complementary methods: lipid analysis of stomach oils as trophic markers together with the conventional dietary approach. We first investigated the adult diet by analyzing oil lipids. Since Antarctic krill *Euphausia superba*, a species restricted to Antarctic waters (Siegel 2005), was the most abundant species identified in chick stomach contents (Catard et al. 2000), we hypothesized that it was the main prey species targeted by adults during LT, and hence that adult stomach oils would be analyzed for a krill lipid signature. The second objective was to compare the lipid signature of chick and adult oils. Chick oil would result not only from the accumulation of oils from LT performed by the two parents, but also from lipids from prey (fresh remains) brought back to the colony by the adults after both LT and ST. We therefore hypothesized that the lipid signature of chick oil would be more complex than the adult ones, thus precluding its use to determine the adult diet during LT. Finally, since previous studies highlighted strong interactions between white-chinned petrels and Patagonian toothfish *Dissostichus eleginoides* fisheries at sub-Antarctic islands (Cherel et al. 1996; Weimerskirch et al. 2000), we compared lipids from seabird stomach oils with those of toothfish to quantify the importance of fishery waste in the birds' nutrition.

Materials and methods

Collection of stomach contents

Field work was carried out during the chick-rearing period of two consecutive austral summers (8 February–24 March 2000, and 12 February–2 March 2001) on Possession Island (46°26′S, 51°45′E; Crozet Archipelago) located in the south-western Indian Ocean (Fig. 1). Stomach contents were collected from both chicks and adults using either the water-off-loading method (Wilson 1984) or spontaneous regurgitation during handling. In most cases, birds were sampled at the nest. Immediately after sampling, the solid fraction of stomach contents was separated from the liquid fraction (oil and water) by gravity. Volumes of oil and water and mass of the solid fraction were then measured. To prevent lipid auto-oxidation, an antioxidant (butylated hydroxytoluene) was added to the oil fraction. The solid

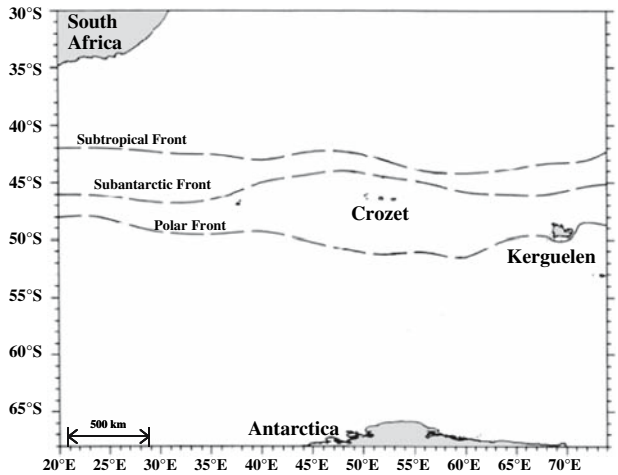

Fig. 1 Location of Crozet Archipelago in the south-western Indian Ocean. Front positions follow indications of Park et al. (1993)

and oil fractions were then frozen and stored at −20 and −80°C, respectively, until subsequent analyses in France.

A total of 51 birds were caught in 2000 and 2001: 21 stomach contents were recovered in 2000 (8 from adults and 13 from chicks), and 30 adult samples were collected the following year. Since the presence of stomach oil and/or Antarctic krill indicates LT (Weimerskirch and Cherel 1998; Cherel et al. 2002), adult food samples were divided into two groups according to the presence (presumably LT) or absence (presumably ST) of oil and/or Antarctic krill. Twenty adult samples were recovered after ST (2 in 2000 and 18 in 2001) and 18 after LT (6 in 2000 and 12 in 2001).

Stomach oil analyses

Total lipids were quantitatively extracted from each of 23 oil fractions recovered from the 51 food samples according to the Bligh and Dyer (1959) method. Crude extracts were placed in chloroform, concentrated under vacuum and stored at −80°C. All samples were then analyzed using the methods described by Connan et al. (2005). Briefly, the proportions of lipid classes were determined with an Iatroscan MK V TH10 thin-layer chromatography–flame-ionization detector (TLC–FID). Lipid classes were further isolated by preparative TLC, and the bands of wax esters (WE) and triacylglycerols (TAG) were then scraped off and eluted. Fatty acids (FA) from both WE and TAG, and fatty alcohols (FAlc) from WE were subsequently converted into methyl esters and acetates, respectively. Gas–liquid chromatography (GLC) analyses were performed with an Autosystem XL gas chromatograph (Perkin Elmer Corp.) equipped with a polar column Famewax (Restek, Bollende; 30 m length × 0.32 mm internal diameter) and a FID detector. Individual components were identified by reference to authentic standards and well-characterized fish oils (Capelin: Menhaden 1:1). In addition to the examination of esters and acetates recovered, one part of FA methyl ester or FAlc acetate samples was completely hydrogenated and the products examined qualitatively and quantitatively using GLC (details in Connan et al. 2005).

Conventional dietary method

Each solid fraction was thawed and drained by gravity overnight to separate the solid items from the residual liquid fraction. In the solid fraction, the accumulated items were discarded (squid beaks, and squid and fish lenses), while fresh remains were divided into broad prey classes (cephalopods, crustaceans, fish and others), which were weighed to estimate their proportion by fresh mass in the diet. Then, each prey item was numbered and identified to the lowest possible taxon, using published keys (Clarke 1986; Baker et al. 1990; Smale et al. 1995) and our own reference collection.

The abundance of each prey taxon was described by its frequency of occurrence and numerical importance. Frequency of occurrence was expressed as a percentage of the number of food samples containing a given taxon. Numerical importance was calculated as the total number of individuals of a given taxon found in all the samples as a percentage of the total number of all prey items ingested in all the food samples.

Statistical analyses

To compare chick and adult data, normality test (Shapiro–Wilk) and *F*-test for homogeneity of variances were run to verify that requirements were fulfilled to perform a Student's two-sample *t*-test. If not, a non-parametric test was used (Mann and Whitney *U*-test) (Zar 1996).

Concerning lipid analyses, chick and adult variabilities were tested by cluster analyses using Bray–Curtis similarity and complete linkage on lipid class composition, FAlc and FA profiles (Legendre and Legendre 1998). Then, the predator–prey relationship (dietary origin of oils) was investigated by linear discriminant analyses (LDA). To achieve meaningful comparisons between FAlc and FA patterns from potential prey species and stomach oils, three databases were built using the majority of published studies and some unpublished data on lipids of potential sub-Antarctic and Antarctic prey (databases are available on request to the authors). They included the main species of meso- and macrozooplankton, micronekton and nekton of the Southern Ocean (see details of references on crustaceans and squids in Connan et al. (2005), plus the pattern of the Patagonian toothfish [Wilson 2004], and those of the myctophids *Electrona antarctica*, *E. carlsbergi*, *Gymnoscopelus nicholsi*, *Krefftichthys anderssoni*, and *Protomyctophum bolini* [Connan et al. unpublished]). To investigate the origin of WE recovered from stomach oils, two prey databases were constructed: a WE FAlc database (WEAL database) regrouped 80 FAlc profiles of 9 crustacean and fish species, and a WE FA database (WEAC database) compiled 62 FA profiles belonging to 8 potential prey species. The origin of TAG oils was approached through a third database (TAG database), in which 17 crustacean, fish and squid species were grouped. Prey species were then classified by LDA based on either FAlc or FA patterns. Outliers were removed from each group a priori defined after verification of the homogeneity of FAlc or FA profiles with the use of Mahalanobis distance and Chi-square test. Stomach oils, used as supplementary observations and thus not integrated in the definition of the discriminant functions (DF), were then attributed to a pre-existing prey group with a classification model built from prey patterns. As normality was presupposed for most of these analyses, percentages were normalized using the arcsine transformation (Zar 1996).

Results

Stomach oils

Only one chick sample did not contain oil; the others contained from traces to 118 ml of oil (mean value 35.1 ± 42.2 ml). Concerning the adults, 88.9% of LT food samples contained variable amounts of yellow colored oil (mean value 12.7 ± 19.7 ml, from traces to 83 ml). The volume of oil was larger in chick than in adult samples, but the difference was not significant ($U = 85.5$, $P = 0.302$). Twenty-three oils were analyzed in terms of lipid classes, FA and FAlc compositions, with 10 oils sampled from chicks and 13 from adult birds.

Lipid class composition

Three neutral lipid classes (TAG, WE and diacylglycerol-ethers [DAGE]) dominated in chick and adult oils (Fig. 2). TAG were prevalent (66.2 ± 20.3 and 64.0 ± 21.2% of total lipids for chick and adult oils, respectively), followed by DAGE (14.0 ± 8.5 and 18.5 ± 20.3%) and WE (10.6 ± 14.9 and 12.0 ± 13.2%). Nineteen oils were mainly composed of TAG (9 chick and 10 adult oils), 2 adult oils of DAGE, and 1 chick and 1 adult oil of WE. However, even in the DAGE and WE rich samples, the TAG fraction represented between 17.1 and 36.4% of total lipids. Moreover, two chick oil samples contained high levels of hydrocarbons (13.6 and 6.6% of total lipids), while the other samples contained only traces or none of these compounds. Other lipid classes (free fatty acids, cholesterol, diacylglycerols, and polar lipids) were present in small amounts only (<3% of total lipids). Differences between chick and adult oils were significant for diacylglycerol amounts only ($U = 11$, $P = 0.001$).

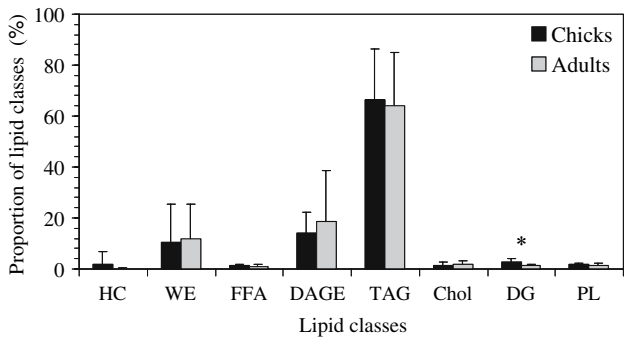

Fig. 2 *Procellaria aequinoctialis*. Lipid composition (% of total lipids; mean ± SD) of chick and adult stomach oils (*HC* hydrocarbons; *WE* wax esters; *FFA* free fatty acids; *DAGE* diacylglycerol-ethers; *TAG* triacylglycerols; *Chol* cholesterol, could include other sterols; *DG* diacylglycerols; *PL* polar lipids; *Significant difference between chick and adult oils)

Fatty acid and fatty alcohol patterns

In the TAG fraction, 19 different FA were found at levels exceeding traces (>0.5% by mass) (Table 1). The FA fractions of TAG from chick oil were very similar to the adult ones. Monounsaturated FA (MUFA; 53.1 ± 5.1 and 52.0 ± 5.6% for chick and adult oils, respectively) were more prevalent than both saturated FA (SFA; 29.1 ± 4.3 and 29.7 ± 5.6%) and polyunsaturated FA (PUFA; 17.3 ± 2.3 and 18.3 ± 5.0%) (Fig. 3). Two FA dominated by mass (>10%): oleic (18:1n-9; 25.1 ± 3.4 and 23.2 ± 3.8% for chick and adult oils, respectively) and palmitic acids (16:0; 17.1 ± 3.0 and 16.3 ± 1.7%). Together, these two main FA plus six other abundant FA (>5%; 14:0, 16:1n-7, 18:1n-7, 20:1n-9, 20:5n-3 and 22:6n-3) accounted for 81.2% (± 3.0% for chick oils) and 79.3% (± 3.9% for adult oils) of total FA. No difference in the FA composition of TAG was found between oil samples recovered from chicks and adults except for palmitoleic acid ($U = 18$, $P = 0.006$).

Thirteen oil samples contained significant amounts (>5% of total lipids) of WE (4 chick and 9 adult oils). Twenty-three different fatty acids were present in WE at levels >0.5% in oils (Table 2). MUFA dominated the profiles

Table 1 *Procellaria aequinoctialis*. Triacylglycerol fatty acid composition of 23 stomach oils (%; mean ± SD; Others include all fatty acids present at <0.5%;*Significant difference between chick and adult oils)

Fatty acids	Chicks ($n = 10$)	Adults ($n = 13$)
14:0	6.82 ± 2.00	7.45 ± 3.29
16:0	17.10 ± 2.98	16.26 ± 1.67
18:0	2.89 ± 0.69	2.70 ± 0.67
16:1n-7	7.20 ± 0.60	6.87 ± 1.99*
18 1n-9	25.10 ± 3.37	23.15 ± 3.80
18 1n-7	6.17 ± 1.44	5.74 ± 1.82
20:1n-9	7.33 ± 1.62	7.80 ± 2.40
20:1n-7	0.42 ± 0.12	0.51 ± 0.16
22:1n-13 + 11	2.16 ± 1.17	2.21 ± 0.85
22:1n-9	1.74 ± 0.46	1.62 ± 0.55
24:1n-11	0.49 ± 0.31	0.51 ± 0.31
24:1n-9	0.73 ± 0.32	0.74 ± 0.32
18:2n-6	1.27 ± 0.29	1.22 ± 0.38
18:4n-3	0.57 ± 0.12	0.51 ± 0.16
20:4n-3	0.55 ± 0.10	0.52 ± 0.15
20:4n-6	0.42 ± 0.13	0.51 ± 0.27
20:5n-3	6.04 ± 1.47	5.95 ± 1.83
22:5n-3	0.74 ± 0.08	0.67 ± 0.38
22:6n-3	5.40 ± 0.92	5.59 ± 3.28
Others	6.51 ± 0.85	8.72 ± 4.86

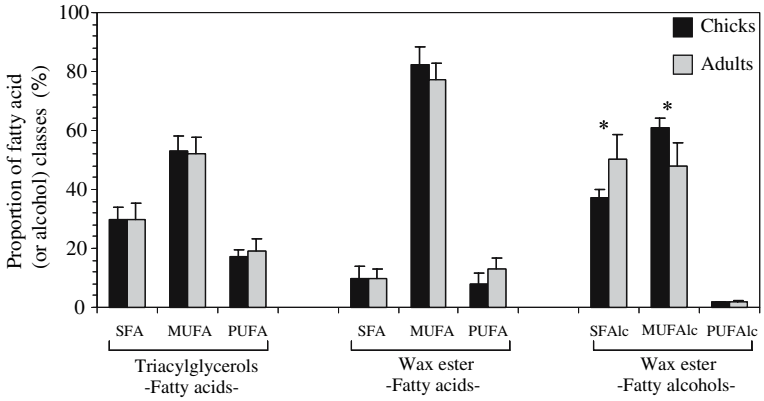

Fig. 3 *Procellaria aequinoctialis*. Fatty acid composition (% of total fatty acids; mean ± SD) of triacylglycerol and wax ester fractions, and fatty alcohol composition (% of total fatty alcohols) of wax ester fraction of chick and adult stomach oils (*SFA* saturated fatty acids, *MUFA* monounsaturated fatty acids, *PUFA* polyunsaturated fatty acids, *SFAlc* saturated fatty alcohols, *MUFAlc* monounsaturated fatty alcohols, *PUFAlc* polyunsaturated fatty alcohols; *Significant difference between chick and adult oils)

Table 2 *Procellaria aequinoctialis*. Wax ester fatty acid and fatty alcohol compositions of stomach oils (%; mean ± SD; Others include all fatty acids or fatty alcohols present at <0.5%; *Significant difference between chick and adult oils)

Fatty acids	Chicks (n = 4)	Adults (n = 9)	Fatty alcohols	Chicks (n=4)	Adults (n=9)
14:0	3.05 ± 2.30	2.97 ± 1.71	14:0	3.76 ± 0.47	7.58 ± 2.20*
16:0	3.80 ± 1.37	3.42 ± 1.39	15:0	0.66 ± 0.12	0.94 ± 0.38
18:0	1.49 ± 0.63	1.00 ± 0.37	16:0	23.17 ± 2.87	34.52 ± 6.18*
Phytanate	0.47 ± 0.10	0.61 ± 0.32	i17:0	0.60 ± 0.11	0.98 ± 0.22*
14:1n-7	0.88 ± 0.49	0.83 ± 0.44	i18:0	0.74 ± 0.10	0.73 ± 0.10
14:1n-5	0.71 ± 0.47	1.13 ± 0.52	18:0	5.66 ± 0.87	3.19 ± 1.54*
16:1n-7[a]	9.24 ± 3.29	14.11 ± 5.16	16:1n-7	2.25 ± 2.00	4.09 ± 0.60
16:1n-5	0.27 ± 0.15	0.69 ± 0.38*	17:1	0.39 ± 0.19	0.57 ± 0.29
17:1	0.66 ± 0.31	0.68 ± 0.30	18:1n-9	18.61 ± 13.16	22.08 ± 6.03
18:1n-9	39.53 ± 9.04	38.75 ± 7.31	18:1n-7	7.98 ± 3.04	8.92 ± 2.74
18:1n-7	4.98 ± 0.66	5.39 ± 1.69	18:1n-5	0.71 ± 0.26	0.78 ± 0.14
18:1n-5	0.51 ± 0.27	0.62 ± 0.22	20:1n-9	13.31 ± 5.12	5.19 ± 1.88*
20:1n-9[b]	15.34 ± 1.71	8.69 ± 6.30*	20:1n-7	2.35 ± 0.93	1.31 ± 0.78
20:1n-7	0.80 ± 0.24	0.74 ± 0.21	22:1n-13 + 11	5.50 ± 4.00	1.28 ± 0.76
22:1n-13 + 11	4.61 ± 1.36	2.26 ± 0.67*	22:1n-9	3.98 ± 2.61	1.07 ± 0.60
22:1n-9	2.16 ± 0.73	1.57 ± 0.45	22:1n-7	1.33 ± 0.91	0.20 ± 0.13
24:1n-11	0.95 ± 0.79	0.29 ± 0.13	24:1n-9	3.31 ± 2.11	1.28 ± 0.68
24:1n-9	0.74 ± 0.43	0.45 ± 0.29	18:2n-6	0.32 ± 0.22	0.55 ± 0.20
16:2n-4	0.47 ± 0.30	0.56 ± 0.22	Others	4.34 ± 0.96	3.52 ± 0.61
18:2n-6	1.21 ± 0.28	1.56 ± 0.41			
20:4n-6	0.36 ± 0.15	0.60 ± 0.37			
20:5n-3	1.38 ± 1.24	3.00 ± 1.35			
22:6n-3	1.58 ± 1.19	3.65 ± 2.11			
Others	4.83 ± 1.26	6.43 ± 0.92			

[a] Include some traces of 16:1n-9

[b] Include some traces of 20:1n-11

(82.2 ± 6.1 and 77.2 ± 5.4% for chick and adult oils, respectively; Fig. 3). The chick FA fraction contained less PUFA than the adult fraction (7.8 ± 3.8 and 13.1 ± 3.8% of total FA, respectively), but these differences were not significant. The major FA was 18:1n-9 (39.5 ± 9.0 and 38.8 ± 7.3% for chick and adult oils, respectively), and there were substantial amounts of 20:1n-9 and 16:1n-7 (15.3 ± 1.7 and 9.2 ± 3.3% for chick oils, 8.7 ± 6.3 and 14.1 ± 5.2% for adult oils, respectively). Chick oils were significantly richer in 20:1n-9 and in 22:1n-13 + 11 than adult oils (U = 4, P = 0.037 and U = 0, P = 0.007, respectively; Table 2).

In WE fractions, 18 different FAlc were identified (>0.5%; Table 2). Monounsaturated FAlc (MUFAlc) were dominant in chick oils (61.1 ± 3.1% of total FAlc) followed by saturated ones (SFAlc; 37.1 ± 3.1%), whereas

adult oils were dominated by SFAlc and then MUFAlc (50.3 ± 8.1 and 47.7 ± 8.0%, respectively; Fig. 3). MUFAlc amounts were significantly higher in chick oils than in adult oils ($U = 2$, $P = 0.017$), whereas the reverse was true for SFAlc ($U = 34$, $P = 0.017$). Very few polyunsaturated components were identified in WE oil. Palmitol (16:0) and oleol (18:1n-9) were the dominant fatty alcohols (23.2 ± 2.9 and 18.6 ± 13.2% in chick oils, and 34.5 ± 6.2 and 22.1 ± 6.0% in adult oils, respectively). The amounts of 14:0 and 16:0 were prevalent in adult oils ($U = 32$, $P = 0.037$ and $U = 35$, $P = 0.011$, respectively), while 18:0 and 20:1n-9 were more abundant in chick oils ($U = 4$, $P = 0.037$ and $U = 4$, $P = 0.037$, respectively).

Cluster analyses based on lipid classes, FA or FAlc compositions of chick and adult oils showed no clear discrimination between chick and adult oil samples (data not shown). Inter-individual variability in oil composition was thus more important than between chick and adult oils.

Dietary origin of oils

To investigate the origin of oil FAlc, a first LDA was performed using the WEAL database (9 prey species described by 8 FAlc). Nine groups were defined a priori corresponding to each potential prey species (Table 3, Database WEAL): the crustacean (*Calanoides acutus* [Caa], *Euphausia*

Table 3 Discriminant analyses of prey databases comparing wax ester fatty alcohol (WEAL), wax ester fatty acid (WEAC) or triacylglycerol fatty acid (TAG) signatures of prey species (see references in Connan et al. 2005) and stomach oils (*F* Fish; *C* Other crustaceans; *E* Euphausiids; *S* Squid; explanation of the fractions: Ea (2/4) means that two chick oils out of four showed similarities with *Electrona antarctica*, for example)

Species	First LDA			Second LDA
	Database WEAL	Database WEAC	Database TAG	Database TAG
Fish				
Dissostichus eleginoides	–	–	F	De
Electrona antarctica	Ea	Ea	–	–
Electrona carlsbergi	Ec	Ec	F	Ec
Gymnoscopelus braueri	Gb	Gb	–	–
Gymnoscopelus nicholsi	–	–	F	Gn
Krefftichthys anderssoni	Ka	Ka	–	–
Pagothenia borchgrevinki	–	–	F	Pb
Protomyctophum bolini	–	–	F	Pbol
Trematomus bernacchii	–	–	F	Tb
Trematomus hansoni	–	–	F	Th
Trematomus newnesi	–	–	F	Tn
Trematomus penellii	–	–	F	Tp
Crustaceans				
Calanoides acutus	Caa	Caa	–	–
Calanus propinquus	–	–	C	–
Euchirella rostromagna	–	–	C	–
Euphausia crystallorophias	Euc	Euc	E	–
Euphausia superba	–	–	E	–
Euphausia vallentini	–	–	E	–
Paraeuchaeta antarctica	Paa	Paa	–	–
Rhincalanus gigas	Rhg	Rhg	–	–
Themisto gaudichaudii	–	–	C	–
Thysanoessa macrura	Thm	Thm	–	–
Squids				
Moroteuthis ingens	–	–	S	–
Moroteuthis robsoni	–	–	S	–
				De (6/9)
Stomach oils (Chicks)	Ea (2/4)	Ea (1/4)	F (9/10)	Ec (2/9)
	Ka (2/4)	Ka (3/4)	S (1/10)	Gn (1/9)
			F (9/13)	
Stomach oils (Adults)	Ea (9/9)	Ea (1/9)	S (3/13)	Gn (6/9)
		Ka (8/9)	E (1/13)	Ec (3/9)

crystallorophias [Euc], *Paraeuchaeta antarctica* [Paa], *Rhincalanus gigas* [Rhg], *Thysanoessa macrura* [Thm]), and fish (*Electrona antarctica* [Ea], *E. carlsbergi* [Ec], *Gymnoscopelus braueri* [Gb], *Krefftichthys anderssoni* [Ka]) groups. The first DF, representing 69% of total variance, contrasted between *T. macrura* and *E. carlsbergi* that have high percentages of 18:1n-9, and *E. crystallorophias*, *P. antarctica* and *R. gigas* that have very high levels of SFAlc 14:0 and 16:0 (Fig. 4a). The second DF segregated

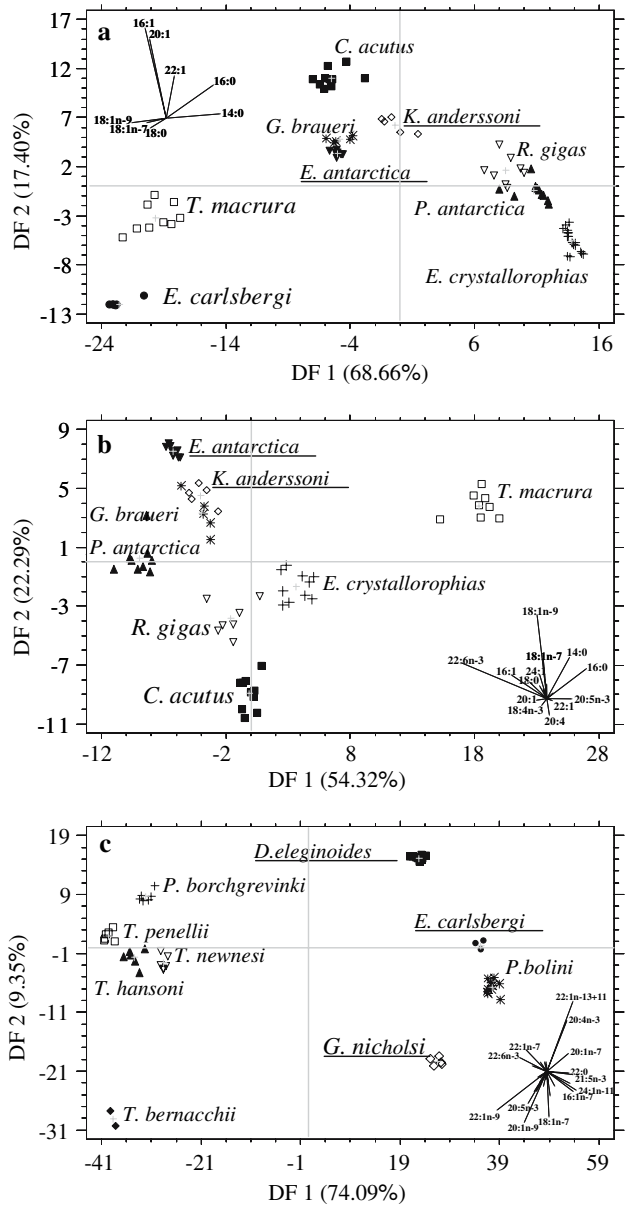

Fig. 4 *Procellaria aequinoctialis*. Linear discriminant analyses of fatty alcohol **a** and fatty acid **b** of wax ester patterns, and of fatty acid of triacylglycerol patterns **c** of prey species (*DF* discriminant function; prey species with similar patterns of oils are *underlined*). Variables are projected according to their relative contributions on the two discriminant functions. For clarity, only the major contributions of fatty acids (or alcohols) are included

C. acutus from *E. crystallorophias* and *E. carlsbergi* that almost lack 20:1 and 16:1 alcohols. Using the classification model calculated from DF, 100% of prey profiles were correctly assigned. The 13 patterns of stomach oil alcohols (from 4 chicks and 9 adults) were then used as test samples, and prediction of class allocation was achieved with the same model. The results indicated highest probability of grouping with two fish species *E. antarctica* (Ea) and *K. anderssoni* (Ka; Table 3, Database WEAL).

The same kind of analysis was operated for WEAC. Eight similar groups have been defined described by 17 FA, including all of the above species except for *E. carlsbergi* (Table 3, Database WEAC). The first DF (54% of variance) clearly separated the euphausiid *T. macrura*, rich in 16:0, from the seven others (Fig. 4b). The second DF (22% of variance) separated the fish *E. antarctica* rich in 18:1 fatty acids from *C. acutus*. 100% of the cases were correctly assigned with this second model, and the prediction of stomach oil WEAC allocation indicated highest probability of association with fish patterns (*K. anderssoni* [Ka] and *E. antarctica* [Ea]) in agreement with the earlier findings (Table 3, Database WEAC).

Comparison of stomach oils with the literature data for the TAG FA patterns was performed using 82 FA profiles from 6 crustacean, 9 fish, and 2 squid species described by 16 FA. Four groups of prey were first defined in Table 3 (First LDA, Database TAG): two crustacean groups (euphausiids: *Euphausia crystallorophias*, *E. superba*, *E. vallentini*, and others: *Calanus propinquus*, *Euchirella rostromagna*, *Themisto gaudichaudii*), one fish group (*Dissostichus eleginoides*, *Electrona carlsbergi*, *Gymnoscopelus nicholsi*, *Protomyctophum bolini*, *Trematomus bernacchii*, *T. hansoni*, *T. newnesi*, *T. pennellii*, *Pagothenia borchgrevinki*) and one squid group (*Moroteuthis ingens*, *M. robsoni*). The first DF, accounting for 69% of total variance, clearly separated the fish and squid groups rich in 24:1 from the crustacean class lacking or presenting very small amounts of 24:1. The second DF separated the squids from the fish. With this last model of DF, 100% of cases were correctly assigned, and comparison of TAG oil samples with the prey data showed that more than 77% of stomach oils presented the highest probability of grouping with the fish group (Table 3, First LDA, Database TAG). A second LDA was then conducted with only fish profiles (56 profiles described by 32 FA). Nine groups were defined corresponding to the nine fish species (Table 3, Second LDA, Database TAG). The first DF (74% of total variance) separated nototheniids (except toothfish *D. eleginoides*) from the four other species (Fig. 4c). This second model correctly classified 100% of fish profiles. Twelve oils had similarities with the myctophids *E. carlsbergi* and *G. nicholsi* (3 chick and 9 adult oils), and the six other chick oils were close to *D. eleginoides* (Table 3, Second LDA, Database TAG).

Finally, the dietary implications of stomach oil analyses showed no clear difference between chick and adult samples with a fish origin for the two types of oils (Table 3).

Food samples

Mean mass of 13 chick food samples was 54 ± 48 g (range 16–128 g; Table 4). Chick stomach contents were not significantly heavier than adult samples ($U = 229$, $P = 0.808$), with ST samples weighing 44 ± 27 g, and LT samples 52 ± 31 g. Similarly, contents collected after LT were not significantly heavier than those recovered after ST ($t = -0.810$, $P = 0.423$). Accumulated items, mainly vegetable matter and squid beaks, formed between 0.3 and 5% of the solid fraction; the remaining being fresh items. Samples were mainly dominated by fish, which accounted for 40–69% of the diet by fresh mass, followed by cephalopods, crustaceans and other various organisms (Table 4).

A total of 475 prey items belonging to 36 different taxa was recovered from chick and adult samples, including 98, 234 and 143 items from chick, adult ST and LT samples, respectively (Table 5). Species richness was twice as high in adult LT and chick samples compared to adult ST samples (27 and 22 vs 13 prey taxa). Fish occurred in 37 samples (72% of food samples), and the myctophid family was the most diverse and abundant fish family, particularly in chick and adult LT samples. The gempylid *Paradiplospinus gracilis* was the most common species in chick and adult ST samples, while the paralepidid *Notolepis coatsi* was the most abundant species in adult LT samples (17% of fish items). Cephalopods were recovered from 26 samples (51% of stomach contents), with the brachioteuthid *Slosarczykovia circumantarctica* accounting for most of the identified items (16 out of 38 individuals). The lack of buccal masses including beaks precluded the identification of most of the fresh squid remains after adult ST (8 out of 13 individuals).

Crustaceans dominated the diet by number, accounting for 72, 76 and 57% of the total number of prey in chick, and adult ST and LT samples, respectively, but, owing to their small size, crustaceans represented only 21, 2 and 1% by fresh mass of the samples, respectively (Tables 4 and 5). Chick and adult LT samples were mainly composed of the amphipod *Themisto gaudichaudii* and of the Antarctic krill *Euphausia superba* (29 and 24%, and 27 and 32% by number, respectively), whereas the euphausiid *Euphausia vallentini*, absent in LT samples, was the dominant prey species in adult ST samples (71% of total items). Finally, carrion and/or some unknown structures (possibly fish gut) were recovered in seven stomachs (from 3 chicks and 4 adults).

Discussion

This work is the first, to our knowledge, to describe the lipid classes, and FA and FAlc patterns of oils collected from adults of white-chinned petrels. Lipid analyses showed that the dietary origin of stomach oils was not from Antarctic krill, but instead from myctophid fish, thus demonstrating the importance of mesopelagic fish in the nutrition of adult petrels. This result was consistent with the identification of digested remains of myctophids recovered from adult stomach contents after LT.

Comparison with previous studies

Only two previous works have investigated lipid composition of stomach oils of white-chinned petrels. Horgan and Barrett (1985) described lipid classes from four chick oils, and Warham et al. (1976) described the FA and FAlc patterns from one chick oil. Our results are in general agreement with those earlier investigations showing a high inter-individual variability in the main lipid classes (oils dominated by either TAG or WE, and the presence of

Table 4 *Procellaria aequinoctialis*. Body mass and composition of chick and adult stomach contents at Possession Island, Crozet Archipelago (*ST* short trips; *LT* long trips; *n* sample size; mean ± SD; minimum–maximum)

	Chicks ($n = 13$)	Adults		
		ST ($n = 20$)	LT ($n = 18$)	Total ($n = 38$)
Bird body mass (kg)	1.3 ± 0.4 0.6–1.9	1.3 ± 0.1 1.1–1.5	1.3 ± 0.1 1.1–1.5	1.3 ± 0.1 1.1–1.5
Solid fraction (g)	54.2 ± 47.5 16–128	44.2 ± 26.6 10–104	51.9 ± 31.2 8–98	47.7 ± 28.7 8–104
Fresh items (g)	52.8 ± 47.9	44.1 ± 26.5	49.1 ± 33.1	46.4 ± 29.4
Accumulated items (g)	1.4 ± 1.3	0.1 ± 0.2	2.8 ± 7.6	1.3 ± 5.3
Overall composition (%)				
Fish	49.7	39.6	69.4	54.1
Cephalopods	22.9	53.6	22.0	38.2
Crustaceans	20.6	2.2	0.9	1.6
Others	6.9	4.7	7.6	6.1

Table 5 *Procellaria aequinoctialis*. Prey species in stomach contents of chicks (n = 13), and adults after short (ST; n = 20) and long (LT; n = 18) foraging trips at Possession Island, Crozet Archipelago

	Chicks				Adults											
					ST				LT				Total			
	Occurrence		Number		Occurrence		Number		Occurrence		Number		Occurrence		Number	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Fish	**8**	**61.5**	**14**	**14.3**	**14**	**70.0**	**37**	**15.8**	**15**	**83.3**	**32**	**22.4**	**29**	**76.3**	**69**	**18.3**
Phosichthyidae																
Phosichthys argenteus	1	7.7	1	1.0					1	5.6	1	0.7	1	2.6	1	0.3
Paralepididae																
Magnisudis prionosa	1	7.7	1	1.0					2	11.1	2	1.4	2	5.3	2	0.5
Notolepis coatsi	1	7.7	1	1.0					3	16.7	5	3.5	3	7.9	5	1.3
Anotopteridae																
Anotopterus vorax									1	5.6	1	0.7	1	2.6	1	0.3
Myctophidae																
Electrona antarctica									2	11.1	3	2.1	2	5.3	3	0.8
Electrona carlsbergi	1	7.7	1	1.0	1	5.0	1	0.4	1	5.6	1	0.7	2	5.3	2	0.5
Gymnoscopelus nicholsi									1	5.6	2	1.4	1	2.6	2	0.5
Gymnoscopelus sp.	1	7.7	1	1.0					1	5.6	3	2.1	1	2.6	3	0.8
Lampadena speculigera									1	5.6	1	0.7	1	2.6	1	0.3
Lampanyctus intricarius	1	7.7	1	1.0					2	11.1	2	1.4	2	5.3	2	0.5
Metelectrona ventralis					1	5.0	1	0.4					1	2.6	1	0.3
Unidentified myctophids	2	15.4	2	2.0					2	11.1	2	1.4	2	5.3	2	0.5
Gadidae																
Unidentified gadids	1	7.7	1	1.0					1	5.6	2	1.4	1	2.6	2	0.5
Scomberesocidae																
Scomberesox saurus									1	5.6	2	1.4	1	2.6	2	0.5
Melamphaidae																
Sio nordenskjöldii	1	7.7	1	1.0					2	11.1	2	1.4	2	5.3	2	0.5
Gempylidae																
Paradiplospinus gracilis	3	23.1	3	3.1	4	20.0	25	10.7					4	10.5	25	6.6
Unidentified fish	1	7.7	1	1.0	10	50.0	10	4.3	3	16.7	3	2.1	13	34.2	13	3.4
Cephalopods	**3**	**23.1**	**4**	**4.1**	**12**	**60.0**	**13**	**5.6**	**11**	**61.1**	**21**	**14.7**	**23**	**60.5**	**34**	**9.0**
Batoteuthidae																
Batoteuthis skolops					2	10.0	2	0.9					2	5.3	2	0.5
Brachioteuthidae																
Slosarczykovia circumantarctica	2	15.4	3	3.1					5	27.8	13	9.1	5	13.2	13	3.4
Cranchiidae																
Taonius sp.									1	5.6	1	0.7	1	2.6	1	0.3
Galiteuthis glacialis					1	5.0	1	0.4					1	2.6	1	0.3
Gonatidae																
Gonatus antarcticus									2	11.1	2	1.4	2	5.3	2	0.5
Histioteuthidae																
Histioteuthis atlantica					1	5.0	1	0.4					1	2.6	1	0.3
Histioteuthis eltaninae					1	5.0	1	0.4					1	2.6	1	0.3
Mastigoteuthidae																
Mastigoteuthis psychrophila									1	5.6	1	0.7	1	2.6	1	0.3
Unidentified cephalopods	1	7.7	1	1.0	8	40.0	8	3.4	4	22.2	4	2.8	12	31.6	12	3.2

Table 5 continued

	Chicks				Adults											
					ST				LT				Total			
	Occurrence		Number		Occurrence		Number		Occurrence		Number		Occurrence		Number	
	n	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
Crustaceans	**9**	**69.2**	**71**	**72.4**	**7**	**35.0**	**179**	**76.5**	**9**	**50.0**	**82**	**57.3**	**16**	**42.1**	**261**	**69.2**
Mysidacea																
Neognathophausia gigas	2	15.4	2	2.0												
Amphipoda																
Themisto gaudichaudii	6	46.2	28	28.6	6	30.0	14	6.0	3	16.7	34	23.8	9	23.7	48	12.7
Euphausiacea																
Euphausia sp.	1	7.7	8	8.2					1	5.6	1	0.7	1	2.6	1	0.3
Euphausia superba	7	53.8	26	26.5					7	38.9	45	31.5	7	18.4	45	11.9
Euphausia vallentini	1	7.7	1	1.0	5	25.0	165	70.5					5	13.2	165	43.8
Decapoda																
Pasiphaea scotiae	4	30.8	5	5.1					1	5.6	1	0.7	1	2.6	1	0.3
Unidentified decapod									1	5.6	1	0.7	1	2.6	1	0.3
Unidentified crustaceans	1	7.7	1	1.0												
Others	**4**	**30.8**	**9**	**9.2**	**3**	**15.0**	**5**	**2.1**	**5**	**27.8**	**8**	**5.6**	**8**	**21.1**	**13**	**3.4**
Unidentified nematods	2	15.4	3	3.1	2	10.0	2	0.9	3	16.7	5	3.5	5	13.2	7	1.9
Carrions	3	23.1	6	6.1	1	5.0	3	1.3	3	16.7	3	2.1	4	10.5	6	1.6

DAGE). However, the high amounts of free FA and free FAlc found by Warham et al. (1976) suggest a high level of lipid hydrolysis that precludes an accurate comparison with data from the present study.

A diet dominated by mass of fish (including mesopelagic fish and nototheniids), and by number of crustaceans (including *Euphausia superba, E. vallentini* and *Themisto gaudichaudii*) is consistent with two previous studies conducted at Crozet Islands in 1983 and 1997 (Ridoux 1994; Catard et al. 2000). Elsewhere, the diet was also dominated by mass of fish (Marion Island; Cooper et al. 1992), or of Antarctic krill *E. superba*, followed by fish (myctophids and nototheniids) and cephalopods (South Georgia; Berrow and Croxall 1999). Inter-site variability emphasized the opportunistic feeding habits of the species, because Antarctic krill does not occur in the vicinity of Crozet and Marion Islands, while it is the main marine resource in waters surrounding South Georgia.

Diet of adult white-chinned petrels inferred from stomach oil analysis

During the chick-rearing period, only LT are energetically profitable for breeders (Weimerskirch et al. 2003; Cherel et al. 2005). At that time, they build up energy reserves far away from their breeding grounds, and collect food for their chicks on the way back to the colony. Thus, adult diet cannot be studied by the conventional dietary approach, and, instead, indirect methods such as using lipid and fatty acid and alcohol patterns of stomach oils as trophic markers must be employed. Lipid class composition of stomach oils suggested that most birds sampled in the present study had fed on TAG-rich prey species. Some oils were, however, characterized by the dominance of DAGE (two samples) or WE (one sample). Oil lipid patterns hence indicated that white-chinned petrels preyed on a variety of prey during LT, in most cases TAG-rich, but also DAGE-rich or WE-rich organisms.

The analyses of FA (WE and TAG) and FAlc (WE) patterns highlighted for the first time the importance of mesopelagic fish in the diet of adults of white-chinned petrels. Indeed, WE recovered in oils would originate from myctophids (*Electrona antarctica* and *Krefftichthys anderssoni*), and most TAG oil signatures showed similarities with those of other myctophid species (*Electrona carlsbergi* and *Gymnoscopelus nicholsi*). Myctophids are the most diverse, widely distributed and abundant mesopelagic fish of the Southern Ocean, with four species contributing over 80% of the biomass (*Electrona antarctica, E. carlsbergi, K. anderssoni* and *Gymnoscopelus nicholsi*) (Sabourenkov 1991, 1992). Interestingly, otoliths from three of these species were found in small numbers in LT food samples, thus supporting the signature lipid indication that they were important prey of adult white-chinned petrels during LT. Noticeably, myctophids are fatty fish that store lipids either as WE (e.g. *E. antarctica*, *K. anderssoni*) or as TAG

(e.g. *E. carlsbergi*, *G. nicholsi*) (Phleger et al. 1999; Lea et al. 2002), thus explaining why both FA (WE and TAG) and FAlc (WE) patterns of oils showed similarity with myctophid-lipid patterns. Importantly also, and contrary to our initial expectation, the results indicated that Antarctic krill *Euphausia superba* and the amphipod *Themisto gaudichaudii*, the two most numerous species recovered in stomach contents (Table 5), did not contribute (or in very little amounts) to the oil composition.

The comparison between stomach oil and potential prey lipid signatures used in this study depends on prey databases composition. The three databases (TAG, WEAC and WEAL) gathered FAlc and/or FA signatures of 24 sub-Antarctic and Antarctic species. It must be noted that, on one hand, all the main macrozooplanktonic and nektonic species from the Southern Ocean were included in the databases, but, on the other hand, the lipid profiles of some common dietary items of white-chinned petrels, including the fish *Notolepis coatsi*, *Paradiplospinus gracilis* and *Lampanyctus intricarius*, and the squid *Slosarczykovia circumantarctica*, were not available or only one specimen was analyzed (Phillips et al. 2003). Our study thus highlights the need for more research on the lipid composition of pelagic organisms of the Southern Ocean and on its spatio-temporal variations.

Interestingly, one adult food sample contained oil characterized by large amounts of a rare lipid class (DAGE, 76% of total lipids) together with fresh remains of the squid *Gonatus antarcticus* (99% by mass). This squid species contains a high percentage of DAGE (45% of total lipids) in its digestive gland (Phillips et al. 2002), and this strongly suggests that stomach oil DAGE directly originated from the squid. DAGE has thus the potential to be trophic markers of specific cephalopods. However, the issue merits further investigation since DAGE has not only been found in squid (Phillips et al. 2002), but also in another group of pelagic organisms of the Southern Ocean, the pteropod *Clione limacina* (Phleger et al. 2001).

Comparison between chick and adult stomach contents

Overall, no major differences were found in the biochemical composition of chick and adult oils, and inter-individual variations within the two groups were higher than differences between groups. Consequently, the dietary origin of chick and adult oil was identical, with the lipid indication that fish, mainly myctophids, were the main items involved. Both adult and chick oil can therefore be used to determine the feeding ecology of adult birds when they feed far from their breeding grounds.

Food analysis also showed little differences between chick and adult stomach contents, which is consistent with chicks being fed exclusively by their parents during the chick-rearing period. More digested prey were found, however, in chick than in adult samples resulting in 76% of items being identified to the species level in chick samples, versus 90 and 83% in adult ST and LT samples, respectively. Chick samples and ST adult samples contained some prey (e.g. *Euphausia vallentini*, *Paradiplospinus gracilis* or *Slosarczykovia circumantarctica* more numerous in adult contents) rarely identified in LT adult samples, and reflecting different foraging grounds between ST and LT trips. Noticeable also was the presence of a few subtropical prey species (e.g. *Phosichthys argenteus* and *Lampadena speculigera*) indicating that some LT were performed in subtropical, not Antarctic waters, which is in agreement with satellite tracking of parent birds during the chick-rearing period (Catard et al. 2000).

Interactions with fisheries

Analysis of stomach oils have shown that the TAG fraction of six oils probably originated from lipids of the Patagonian toothfish and that eight oils contained hydrocarbons. We have no convincing explanation for the occurrence of hydrocarbons in white-chinned petrel oils, but the occurrence of toothfish lipids may be linked to trophic relationships between birds and fisheries. Patagonian toothfish is targeted by longliners in slope waters surrounding many sub-Antarctic islands, including Crozet and Kerguelen archipelagoes. In the Southern Indian Ocean, the white-chinned petrel is the most abundant ship—following seabird and the commonest species killed on longlines (Cherel et al. 1996; Weimerskirch et al. 2000). The species is known to feed on fishery waste, and diet analysis strongly suggests that a substantial part of its food is scavenged from behind fishing vessels (Jackson 1988).

A recent investigation at Crozet Islands (Catard et al. 2000) identified baits used by longliners together with remains of Patagonian toothfish in the food of white-chinned petrels after ST. We identified neither baits nor toothfish in samples of the present study, but some unidentified carrion could be offal collected behind fishing vessels. The fact that toothfish lipids were identified in chick oils only is again an indication that adult birds foraged in association with longliners in waters surrounding the archipelago and fed their chicks with fishery waste after ST. Indeed, during ST, satellite tracking showed that parent birds commute to the Crozet shelf-break, which is the area where both Patagonian toothfish and the fishery occur (Catard et al. 2000).

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