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Maëlle Connan, Patrick Mayzaud, Colette Trouvé, Christophe Barbraud, Yves Cherel. Interannual dietary changes and demographic consequences in breeding blue petrels from Kerguelen Islands. *Marine Ecology Progress Series*, 2004, 373, pp.123-135. 10.3354/meps07723 . hal-00359279

HAL Id: hal-00359279

<https://hal.science/hal-00359279>

Submitted on 14 Apr 2021

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Interannual dietary changes and demographic consequences in breeding blue petrels from Kerguelen Islands

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ABSTRACT: Interannual variation in summer diet and demographic parameters of blue petrel *Halobaena caerulea* were investigated to understand how changes in the marine environment affect the reproduction of an oceanic seabird from the Southern Ocean. Lipids from stomach oil were used as trophic markers of prey consumed by adult birds when they self-fed during long trips, and conventional food analyses allowed determination of the food delivered to chicks after long and short adult foraging trips. Biochemical analysis of stomach oil showed little differences in lipid classes and in fatty acid and fatty alcohol compositions, with most oils deriving from triacylglycerol- and wax ester-rich myctophid fishes over the 4 yr study period (1996, 2000, 2001 and 2002). Accordingly, stomach content analysis showed that chick food was dominated by mass by crustaceans and fish, with myctophids as the main fish items. Important interannual variations in chick diet occurred, most prominently featuring an almost lack of fish in 2002. Summer 2002 was also marked by the lowest fledging success, lowest mass of chicks at fledging and lowest summer survival of adults during the period 1986–2002. In contrast to 1996, 2000 and 2001, summer months in 2002 were also characterized by an intense warm event in Kerguelen waters. Overall, results strongly suggest causal links between climatic anomalies, availability of myctophids and dietary shifts with poor reproductive performance and lower survival in blue petrel. Furthermore, they emphasize the importance of lipid-rich prey in seabird nutrition.

KEY WORDS: Crustacean · Euphausid · Lipids as trophic markers · Myctophid · Seabird · Southern Ocean

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INTRODUCTION

The Southern Ocean (south of the Subtropical Front) is marked by high spatial and temporal variability in its primary and secondary productivities which affects the whole pelagic ecosystem. Other characteristics of the Southern Ocean include the diversity, numerical importance and biomass of its populations of air-breathing consumers, with about 363 and 15 million breeding seabirds and seals, respectively (van Franeker et al. 1997). Seabirds and fur seals reproduce on land

and feed at sea and this spatial segregation leads to limited prospecting ranges during the breeding period. Consequently, any oceanographic variation within the feeding area of these central-place foragers could potentially affect their foraging success and, hence, their reproductive output at that time. Indeed, it has long been recognized that the availability of a key-stone foodweb species such as Antarctic krill *Euphausia superba* determines the breeding success of many species of seabirds and marine mammals (Croxall et al. 1988). Antarctic krill dominates the pelagic ecosystem

in high-Antarctic waters and around South Georgia, located in the southwestern Atlantic. Further north, however, where no Antarctic krill occurs, air-breathing predators target a larger diversity of pelagic organisms, including other euphausiids, hyperiid amphipods and mesopelagic fish (Ridoux 1994). The greater complexity of these predator–prey relationships is likely to be the reason why trophic mechanisms linked to variations in breeding parameters of subantarctic consumers have rarely been investigated (Olsson & van der Jeugd 2002), despite more and more evidence that environmental variability shapes population dynamics in subantarctic consumers (Inchausti et al. 2003, Nevoux & Barbraud 2006, Nevoux et al. 2007).

The goal of the present study was to investigate the summer dietary habits and potential demographic consequences of their variation in a subantarctic seabird, the blue petrel *Halobaena caerulea*, breeding at Kerguelen Islands, southern Indian Ocean. Long-term studies have documented that demographic parameters of *H. caerulea* are affected by environmental conditions during both summer and winter, probably reflecting spatio-temporal changes in food availability, a key selective agent (Guinet et al. 1998, Barbraud & Weimerskirch 2003, 2005). During the chick-rearing period, adults use a dual foraging strategy, regularly alternating long trips (LT) to Antarctic waters with short trips (ST) in closer oceanic waters (Chaurand & Weimerskirch 1994, Cherel et al. 2002). They lose mass during ST during which they maximize food delivery to the chick, and gain mass during LT. Consequently, self-feeding during LT is crucial for the success of ST, because most of the energy used during ST is probably derived from that stored during LT (Weimerskirch et al. 2003). In summer, blue petrels feed their chicks on a large diversity of prey species, mainly pelagic swarming crustaceans and schooling mesopelagic fish (Cherel et al. 2002). However, the diet of adult birds when they self-feed during LT remains unknown, but the presence of digested remains of Antarctic krill in LT food samples suggests that krill comprises a large proportion of blue petrel diet. Blue petrels store oil from dietary origin in their stomach during LT only (Cherel et al. 2002). This, together with a much slower passage rate of lipid than aqueous digesta in the stomach (Clarke 1989) indicates that oil reflects the diet of adult birds before they collect food for their chicks. Consequently, the biochemical composition of oil was recently tested and used as an efficient tool to investigate the food of adult procellariiform seabirds when they feed for themselves (Connan et al. 2005, 2007a,b).

In the present work, we studied over 4 yr the diet of blue petrels by using both the conventional method of stomach content analysis and lipids of stomach oil as trophic markers to determine the summer food of

chicks and adult birds, respectively. Demographic consequences of interannual dietary variation were assessed by measuring chick fledging mass, and breeding success and adult survival rate in our long-term study colony during the same 4 yr.

MATERIALS AND METHODS

Collection of stomach contents. The diet of blue petrels breeding at Mayes Island (49° 28' S, 69° 57' E; Kerguelen Archipelago) (Fig. 1) was examined during 4 austral summers (1996, 2000, 2001 and 2002). Stomach contents were collected from 118 adults using either the water-offloading method (Wilson 1984) or spontaneous regurgitation during handling. 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 oily fraction. The solid and oily fractions were then frozen (−20°C) until subsequent analyses in France. Oily fractions were kept at −80°C in the laboratory before lipid analyses.

Stomach oil analyses. Total lipids were quantitatively extracted from each of 51 oily fractions recovered from 69 LT food samples according to the Bligh & 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 MKV TH10 thin-layer chromatography-

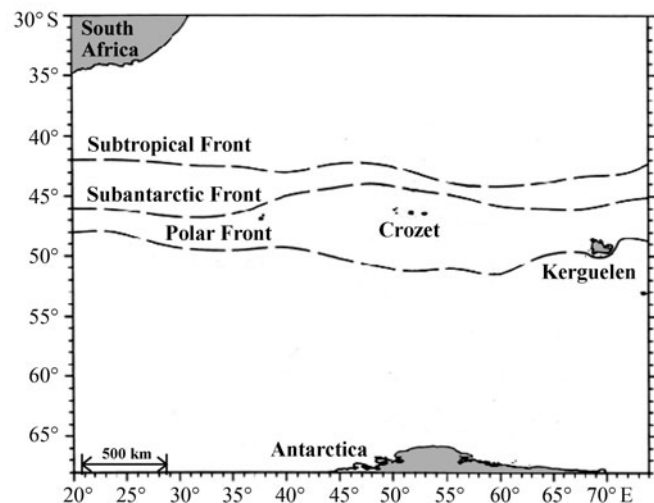


Fig. 1. Location of Kerguelen Islands and oceanographic fronts in the southwestern Indian Ocean. Front positions follow indications of Park et al. (1993)

flame-ionization detector (TLC-FID), and after methylation (fatty acids [FA] from both wax esters [WE] and triacylglycerols [TAG]) or acetylation (fatty alcohols [FAlc] from WE), FA and FAlc profiles were determined using an Autosystem XL gas chromatograph (Perkin-Elmer) equipped with a polar column Fameswax (Restek; 30 m length \times 0.32 mm internal diameter) and an FID.

Conventional dietary approach. Each solid fraction was thawed and drained by gravity overnight to separate the solid items from the residual liquid fraction. In the solid fraction, accumulated items were discarded (squid beaks, 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 counted 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 (FO) and numerical importance. FO of a given taxon was calculated as the total number of food samples containing this taxon as a percentage of the total number of food samples. 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. Interannual variability of oil lipid composition was evaluated using a combination of univariate and multivariate analyses. First, normality (Shapiro-Wilks test) and homogeneity of variance (Fisher test) were verified to run ANOVA followed by multiple range tests. When normality or homoscedasticity were not verified, the non-parametric Kruskal-Wallis test was used to evaluate differences between the 4 yr. Second, forward stepwise discriminant analyses (FSDA) were conducted to identify the main FAs and FAlcs discriminating the oils of the 4 yr. Wilk's λ and the number of observations correctly classified were used to test the significance of the FSDA (F-to enter = 4, F-to remove = 4) to separate among years and to evaluate the performance of the FSDA, respectively.

The predator-prey relationship (dietary origin of oils) was approached by linear discriminant analyses (LDA). To achieve meaningful comparisons between FAlc and FA patterns from potential prey species and stomach oils, 3 databases were built using the majority of published studies on subtropical, subantarctic and Antarctic potential prey (databases available on request from M. Connan). They included the main species of meso- and macrozooplankton, micronekton and nekton of the Southern Ocean (details in Connan

et al. 2005), plus the nototheniid *Dissostichus eleginoides* (Wilson 2004), and the myctophids *Electrona antarctica*, *E. carlsbergi*, *Gymnoscopelus nicholsi*, *Krefflichthys anderssoni* and *Protomyctophum bolini*, (authors' unpubl. data). To investigate the origin of WE recovered in stomach oils, 2 prey databases were constructed: a WE fatty alcohol database (WEAL database) regrouped 80 FAlc profiles of 9 crustacean and fish species, and a WE fatty acid 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) where 17 crustacean, fish and squid species were grouped. The prey species were then classified by LDA based on either FAlc or FA patterns. The outliers were removed from each group *a priori* defined after verification of the homogeneity of FA or FAlc profiles with the use of Mahalanobis distance and chi-squared tests. The number of descriptors considered in the LDA was limited to the data available in the literature: 8, 17 and 16 descriptors for WEAL, WEAC and TAG databases, respectively. Stomach oils, used as supplementary observations and thus not integrated in the definition of 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 normalised using the arcsine transformation (Zar 1996).

Demographic parameters. Data on breeding performances and demographic parameters of blue petrels were obtained from a long-term study (from 1985–86 to 2001–02, hereafter 1986–2002) conducted in the so-called 'demographic' colony on Mayes Island (details in Guinet et al. 1998, Barbraud & Weimerskirch 2003, 2005). A number of measures of the overall breeding performance were made during each breeding season: (1) breeding success was calculated as the number of chicks fledged from the number of eggs laid, (2) hatching success as the number of eggs hatched from eggs laid, and (3) fledging success as the number of chicks fledged from eggs hatched. Chick body mass was measured year after year at the end of the chick-rearing period, before fledging. Demographic parameters came from capture-mark-recapture of adult birds from the study colony. Annual and seasonal adult survival probabilities were estimated using the Cormack-Jolly-Seber model implemented in the MARK computer program (White & Burnham 1999). Adult survival estimates were modeled as in Barbraud & Weimerskirch (2003), starting with a model in which season and time dependence in both survival and recapture probabilities adjusted for trap dependence. Annual survival was defined as the probability of survival from November of Year t to November of Year $t + 1$, summer survival as the probability of sur-

vival from November of Year t to April of Year $t + 1$, and subsequent winter survival as the probability of survival from April of Year $t + 1$ to November of Year $t + 1$.

RESULTS

A total of 118 birds were caught during the 4 yr. Since the presence of stomach oil and/or Antarctic krill indicates LT (Cherel et al. 2002), adult food samples were divided into 2 groups according to the presence (presumably LT) or absence (presumably ST) of oil and/or Antarctic krill. Forty-nine samples were recovered after ST (22, 7, 15 and 5 in 1996, 2000, 2001 and 2002, respectively) and 69 after LT (17, 14, 24 and 14 in 1996, 2000, 2001 and 2002, respectively). Yellow to deep orange oil was collected from 51 LT samples (13, 13, 12 and 13 in 1996, 2000, 2001 and 2002, respectively). The volume of stomach oil tended to be lower in 1996 and 2002 than in 2000 and 2001 (2.1 ± 2.6 , 5.2 ± 4.9 , 4.0 ± 3.0 and 2.7 ± 1.9 ml, mean \pm SD, in 1996, 2000, 2001 and 2002, respectively; Kruskal-Wallis, $H = 7.37$, $p = 0.061$).

Interannual variation in oil lipid composition

Lipid class composition

Three neutral lipid classes (TAG, WE and diacylglycerol-ethers [DAGE]) dominated in oils (>90% of total lipids) (Fig. 2). TAG and WE proportions did not differ between years (WE: ANOVA, $F_{3,51} = 1.07$, $p = 0.370$;

TAG: $F_{3,51} = 1.12$, $p = 0.350$), while oils were significantly richer in DAGE in 1996 and 2002 (12.8 ± 7.9 , 8.9 ± 8.4 , 5.6 ± 3.4 and $18.7 \pm 20.6\%$ in 1996, 2000, 2001 and 2002, respectively; $H = 8.44$, $p = 0.037$). Other lipid classes (hydrocarbons, free FAs, cholesterol, diacylglycerols and polar lipids) were absent or present in small amounts only (<3% of total lipids).

Fatty alcohol and fatty acid profiles

Interannual differences were found in the FALc and FA profiles of WE- and TAG-oils over the 4 yr. Seventeen FALcs were identified in the WE fractions (>0.5% of total FALcs) (Table 1). More than half were monounsaturated (MUFALc; 53 to 60%), while saturated FALcs represented 38 to 44% of the total FALcs. Very few polyunsaturated FALcs were identified in the oils. The 4 dominant FALcs were 16:0, 18:1n-9, 18:1n-7 and 20:1n-9. Using 3 FALc discriminators (Table 2) (68% of correctly assigned profiles), FSDA showed that oils from 1996 and 2002 were clearly separated from those from 2001 and 2000 ($\lambda_{\text{Wilks}} = 0.273$, $F = 8.41$, $p < 0.001$) (Fig. 3A). Oils from 1996 were positively related to DF 1 (79.4% of variability), which was associated with higher 18:2n-6 percentages. DF 2 (17.9% of variability) slightly separated 1996 and 2002 oils (richer in 18:0) from 2000 and 2001 oils. Overall, MUFALc percentages were significantly higher in 2001 and 2002 than in 1996 and 2000 ($H = 8.61$, $p < 0.05$).

In WE fractions, 23 different FAs were identified (Table 3). Profiles were dominated by large amounts of monounsaturated FAs (MUFAs), followed by polyunsaturated (PUFAs) and saturated (SFAs) FAs. MUFAs

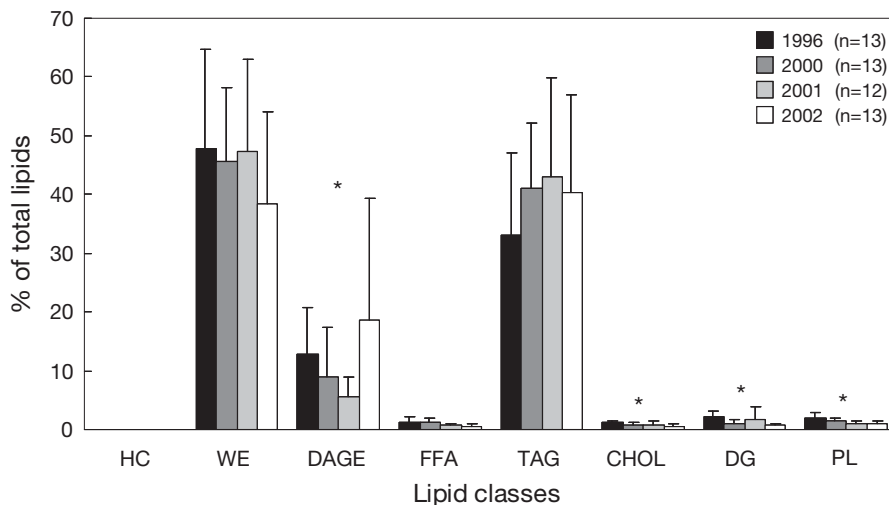


Fig. 2. *Halobaena caerulea*. Lipid composition (% of total lipids; mean \pm SD) of stomach oils. HC: hydrocarbons; WE: wax esters; DAGE: diacylglycerol-ethers; FFA: free fatty acids; TAG: triacylglycerols; CHOL: cholesterol, could include other sterols; DG: diacylglycerols; PL: polar lipids; *: significant difference between years

were dominated by 18:1n-9, 16:1n-7, 20:1n-9 and 18:1n-7. WE fractions from 1996 and 2002 were richer in MUFAs ($F_{3,51} = 5.33$, $p < 0.01$) and poorer in PUFAs ($H = 29.35$, $p < 0.001$) than those from 2000 and 2001.

FSDA showed that 4 FAs were largely responsible for interannual variation ($\lambda_{\text{Wilks}} = 0.094$, $F = 14.03$, $p < 0.001$) (Fig. 3B), and these 4 FA discriminators correctly assigned 80.4% of individuals (Table 2). The first DF (75.1% of variability) separated oils from 1996 from those from the 3 other years, while the second DF (23.1% of variability) isolated most of the 2002 oils. Oils from 2002 were significantly poorer in 22:6n-3 ($H = 27.97$, $p < 0.001$) and 20:5n-3 ($F_{3,51} = 8.14$, $p < 0.001$) than 2000 and 2001 oils.

Table 1. *Halobaena caerulea*. Wax ester fatty alcohol compositions of stomach oils (%; mean \pm SD). Others: all fatty alcohols present at $< 0.5\%$; SFAlc: saturated fatty alcohols; MUFAlc: monounsaturated fatty alcohols; PUFAlc: polyunsaturated fatty alcohols

	1996 (n = 12)	2000 (n = 13)	2001 (n = 12)	2002 (n = 13)
14:0	7.35 \pm 1.47	8.80 \pm 3.43	7.87 \pm 1.84	6.80 \pm 2.29
16:0	31.71 \pm 4.21	27.85 \pm 5.84	26.65 \pm 5.24	26.00 \pm 5.43
iso17:0	0.62 \pm 0.09	0.53 \pm 0.13	0.49 \pm 0.10	0.51 \pm 0.10
iso18:0	0.55 \pm 0.11	0.49 \pm 0.17	0.44 \pm 0.09	0.48 \pm 0.15
18:0	2.23 \pm 0.26	2.14 \pm 0.51	2.01 \pm 0.44	2.56 \pm 0.55
16:1n-7	3.55 \pm 0.54	4.22 \pm 0.87	3.63 \pm 0.72	3.11 \pm 0.65
18:1n-9	15.48 \pm 3.83	11.26 \pm 5.48	9.38 \pm 3.42	10.54 \pm 5.27
18:1n-7	10.44 \pm 1.56	8.71 \pm 3.19	9.28 \pm 2.85	11.83 \pm 2.02
18:1n-5	0.95 \pm 0.13	0.81 \pm 0.20	0.80 \pm 0.20	0.78 \pm 0.18
20:1n-9	12.63 \pm 5.57	19.07 \pm 8.68	23.61 \pm 9.62	22.15 \pm 10.00
20:1n-7	1.99 \pm 0.55	1.39 \pm 0.66	1.59 \pm 0.41	1.53 \pm 0.67
22:1n-13+11	2.57 \pm 0.97	5.20 \pm 4.25	4.80 \pm 1.54	3.89 \pm 0.83
22:1n-9	2.43 \pm 0.78	3.08 \pm 1.03	3.35 \pm 1.04	3.23 \pm 0.82
22:1n-7	0.59 \pm 0.24	0.30 \pm 0.17	0.35 \pm 0.21	0.31 \pm 0.12
24:1n-9	1.11 \pm 0.39	1.34 \pm 0.38	1.45 \pm 0.49	1.55 \pm 0.48
18:2n-6	0.64 \pm 0.13	0.55 \pm 0.15	0.42 \pm 0.09	0.39 \pm 0.13
Others	5.15 \pm 0.56	4.25 \pm 0.76	3.88 \pm 0.66	4.34 \pm 0.87
SFAlc	44.12 \pm 5.28	41.67 \pm 6.01	38.94 \pm 7.04	38.24 \pm 7.95
MUFAlc	53.11 \pm 4.88	56.65 \pm 6.22	59.54 \pm 7.26	60.38 \pm 8.21
PUFAlc	2.77 \pm 0.72	1.68 \pm 0.35	1.52 \pm 0.30	1.39 \pm 0.33

Eighteen different FAs were found at levels exceeding traces ($> 0.5\%$ by mass) in TAG fractions (Table 4). MUFAs dominated over both SFAs and PUFAs. Two FAs dominated by mass: the oleic (18:1n-9) and palmitic (16:0) acids, followed by 18:1n-7, 20:1n-9, 16:1n-7, 14:0 and 20:5n-3. All together, these 7 FAs accounted for 76 to 79% of total FAs. FSDA indicated little interannual variation ($\lambda_{\text{Wilks}} = 0.532$, $F = 5.69$, $p < 0.001$), with only 51% cases correctly assigned using 2 FA variables (85 and 75% cases correctly assigned for 1996 and 2001 oils, respectively) (Table 2). The first DF accounted for 71.3% of variability, and separated 1996 oils (poorer in 20:1n-7, $H = 13.38$, $p < 0.01$) from those from the 3 other

Table 2. *Halobaena caerulea*. Discriminant analyses of stomach oil fatty acid and fatty alcohol data, comparing the years 1996, 2000, 2001 and 2002 (51.0, 80.4 and 68.0% of allocated cases were correctly classified for wax ester fatty alcohol, wax ester fatty acid and triglyceride fatty acid fractions, respectively)

Allocated group	Predicted group membership				n	Fatty alcohols (or acids) used in separation	Standardised discriminant function coefficients	
	1996	2000	2001	2002			Function 1	Function 2
Wax ester fraction								
Fatty alcohols								
1996	10	1	0	1	12	18:0	-0.396	1.077
2000	2	6	4	1	13	20:1n-7	1.262	-0.054
2001	0	2	7	3	12	18:2n-6	0.755	0.887
2002	1	0	1	11	13			
Fatty acids								
1996	12	1	0	0	13	14:0	-1.130	-0.003
2000	1	8	4	0	13	16:1n-5	1.814	0.067
2001	0	2	9	1	12	18:1n-5	-0.751	-0.230
2002	0	0	1	12	13	22:6n-3	0.173	0.954
Triglyceride fraction								
Fatty acids								
1996	11	1	1	0	13	20:1n-7	0.696	0.723
2000	2	3	3	5	13	22:6n-3	0.775	-0.637
2001	0	3	9	0	12			
2002	3	4	3	3	13			

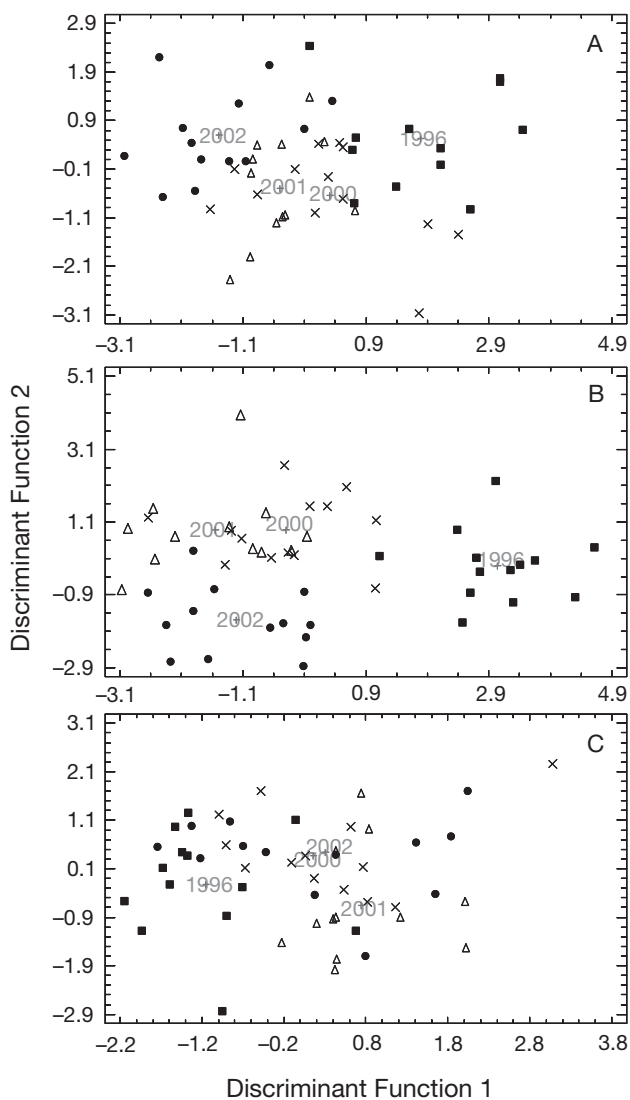


Fig. 3. *Halobaena caerulea*. Discriminant scores of (A) fatty alcohol and (B) fatty acid fractions of wax esters, and (C) fatty acid fractions of triglycerides from stomach oils (year-group labels are located over respective group centroids [+])

years (Fig. 3C). The second DF discriminated most of the 2001 oils that were significantly richer in 22:6n-3 ($F_{3,51} = 6.14$, $p < 0.01$) and 20:5n-3 ($H = 11.1$, $p < 0.05$), and poorer in 18:1n-9 ($H = 13.4$, $p < 0.01$).

Dietary origin of stomach oil

Dietary origins of WE- and TAG-oils were investigated using LDA. A first LDA was performed using the WEAL database. Nine classes corresponding to the 9 potential prey species were defined *a priori*: copepods (*Calanoides acutus*, *Paraeuchaeta antarctica*, *Rhincalanus gigas*), euphausiids (*Euphausia crystalloro-*

phias, *Thysanoessa macrura*) and myctophids (*Electrona antarctica*, *Electrona carlsbergi*, *Gymnoscopelus braueri*, *Krefflichthys anderssoni*). The first DF, representing 69% of total variance, contrasted between *Electrona carlsbergi* and *T. macrura*, which have high percentages of 18:1n-9, and *Euphausia crystallorophias*, *R. gigas* and *P. antarctica*, which are marked by high levels of 14:0 and 16:0. The second DF segregated *C. acutus* (with high levels in 16:1, 20:1 and 22:1 FAlc) from *Electrona carlsbergi* and *Euphausia crystallorophias*. Using the classification model calculated from DF, 100% of prey profiles were correctly assigned. The 50 profiles of oil FAlc 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 2 myctophid species *Electrona antarctica* and *G. braueri* for >80% of FAlc profiles (Table 5).

The same kind of analysis was performed for the WEAC. Eight similar classes have been defined consisting of all of the above species except *Electrona carlsbergi*. The first DF (54% of total variance) clearly separated *Thysanoessa macrura* (rich in 16:0) from the 7 other classes. The second DF separated *E. antarctica* (rich in 18:1) from *Calanoides acutus*. One hundred percent of cases were correctly assigned with this second model, and the prediction of stomach oil WEAC allocation indicated highest probability of association of >88% FA profiles with the myctophid *Krefflichthys anderssoni* (Table 5).

Comparison of TAG FA patterns of stomach oils with the literature data was performed using 82 FA profiles from 6 crustacean, 9 fish and 2 squid species described by 16 FAs. Four classes of prey were defined in a first LDA: 2 crustacean classes (euphausiids: *Euphausia crystallorophias*, *Euphausia superba*, *Euphausia valentini*; other species: *Calanus propinquus*, *Euchirella rostromagna* and *Themisto gaudichaudii*), 1 fish class (*Dissostichus eleginoides*, *E. carlsbergi*, *Gymnoscopelus nicholsi*, *Pagothenia borchgrevinki*, *Protomyctophum bolini*, *Trematomus bernacchii*, *Trematomus hansonii*, *Trematomus newnesi* and *Trematomus pennellii*), and 1 squid class (*Moroteuthis ingens* and *M. robsoni*). The first DF, accounting for 70% of total variance, clearly separated the fish and squid classes from the crustacean class. The second DF separated the squid class from the fish class, and the euphausiid class from the other crustacean class. With this last model of DF, 100% of the cases were correctly assigned, and comparison of TAG oil samples with the prey data showed that stomach oils presented the highest probability of grouping with the fish class. A second LDA was then conducted with only fish profiles (56 profiles described by 32 FAs). Nine classes were defined corresponding to the 9 fish species. The first

Table 3. *Halobaena caerulea*. Wax ester fatty acid compositions of stomach oils (%; mean ± SD). Others: all fatty acids present at <0.5%; SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids

	1996 (n = 13)	2000 (n = 13)	2001 (n = 12)	2002 (n = 13)
14:0	3.82 ± 1.90	3.79 ± 2.11	5.15 ± 3.78	6.30 ± 3.11
16:0	3.57 ± 1.51	3.61 ± 2.22	4.51 ± 2.99	5.42 ± 2.77
18:0	0.48 ± 0.18	0.62 ± 0.44	0.77 ± 0.47	0.88 ± 0.46
14:1n-7	0.49 ± 0.10	0.34 ± 0.13	0.43 ± 0.15	0.54 ± 0.17
16:1n-7	17.17 ± 1.92	15.21 ± 1.23	14.54 ± 1.14	14.57 ± 2.13
16:1n-5	0.57 ± 0.08	0.38 ± 0.10	0.38 ± 0.08	0.46 ± 0.08
17:1	0.58 ± 0.06	0.59 ± 0.06	0.70 ± 0.31	0.59 ± 0.09
18:1n-9	39.79 ± 2.98	32.47 ± 8.36	32.46 ± 5.30	38.04 ± 6.74
18:1n-7	6.58 ± 0.48	6.09 ± 2.17	6.11 ± 1.07	7.49 ± 1.29
18:1n-5	0.59 ± 0.08	0.56 ± 0.16	0.67 ± 0.10	0.74 ± 0.11
20:1n-9	6.15 ± 0.88	6.67 ± 1.47	7.44 ± 1.35	7.47 ± 2.11
20:1n-7	0.48 ± 0.06	0.59 ± 0.16	0.66 ± 0.20	0.65 ± 0.20
22:1n-13+11	2.60 ± 0.67	3.08 ± 1.42	2.72 ± 0.73	2.48 ± 0.68
22:1n-9	1.79 ± 0.43	1.55 ± 0.24	1.54 ± 0.46	1.44 ± 0.41
18:2n-6	1.96 ± 0.66	2.08 ± 0.49	1.70 ± 0.18	1.88 ± 0.53
16:4n-1	0.17 ± 0.10	1.09 ± 1.28	0.64 ± 0.43	0.10 ± 0.14
18:4n-3	0.71 ± 0.29	1.86 ± 1.32	1.34 ± 0.64	0.35 ± 0.23
20:4n-6	0.34 ± 0.14	0.52 ± 0.29	0.42 ± 0.16	0.33 ± 0.07
20:4n-3	0.34 ± 0.10	0.60 ± 0.32	0.52 ± 0.15	0.31 ± 0.11
20:5n-3	4.24 ± 2.78	8.86 ± 5.08	8.04 ± 3.63	3.08 ± 1.90
22:5n-3	0.22 ± 0.06	0.54 ± 0.51	0.42 ± 0.17	0.18 ± 0.08
22:6n-3	2.21 ± 0.88	3.18 ± 0.75	3.47 ± 1.40	1.34 ± 0.67
Others	5.15 ± 0.43	5.70 ± 0.49	5.36 ± 0.42	5.33 ± 0.66
SFA	9.29 ± 3.76	9.27 ± 4.88	11.49 ± 7.44	14.27 ± 6.59
MUFA	77.97 ± 5.28	68.69 ± 8.57	68.72 ± 6.80	75.60 ± 8.32
PUFA	12.58 ± 4.97	21.78 ± 9.68	19.49 ± 6.32	9.94 ± 3.24

sample mass in 2000 ($H = 16.67$, $p < 0.001$). Chick diet was dominated by fresh mass by crustaceans every year, but more fish (about 30%) was consumed in 1996 and 2001 than in 2000 and 2002 (Fig. 4). Cephalopods and other organisms were minor items.

A total of 17 878 prey belonging to 63 taxa were recovered from the 69 LT food samples. By number, blue petrel diet was dominated by crustaceans that accounted for >99% of the total number of prey. Chick food was almost identical in 1996, 2000 and 2001, with the euphausiid *Thysanoessa macrura/vicina* being by far the main crustacean prey (>86%), and Antarctic krill occurring in a significant number of food samples (FO > 62%). In 2002, however, *Thysanoessa macrura/vicina* was partly replaced by the hyperiid amphipod *Themisto gaudichaudii* (67 and 31%, respectively), and Antarctic krill was rarely identified (FO = 29%) and occurred in smaller numbers (<1% versus 2–4%). Fish were found in 71% of LT food samples. The fish diet was dominated

DF (74% of data variability) separated nototheniids (except *D. eleginoides* which is poorer in PUFAs) from the 4 other species. This second model correctly classified 100% of fish profiles. Comparisons of TAG oil samples with prey data showed that stomach oils presented the highest probability of grouping with myctophids (*G. nicholsi* and *Electrona carlsbergi* with >72 and 11% of FA profiles, respectively) and nototheniids (*D. eleginoides* >13% of FA profiles) (Table 5).

No clear interannual variation was observed in the dietary origin of oil WE and TAG over the 4 yr.

Food samples

Long trips

Depending on year, mean (±SD) mass of LT food samples ranged from 15.3 ± 6.5 to 24.3 ± 5.1 g, with lower

Table 4. *Halobaena caerulea*. Triacylglycerol fatty acid composition of stomach oils (%; mean ± SD). Others: all fatty acids present at <0.5%; SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids

	1996 (n = 13)	2000 (n = 13)	2001 (n = 12)	2002 (n = 13)
14:0	6.60 ± 2.04	5.04 ± 1.38	6.15 ± 1.65	5.16 ± 1.42
16:0	13.63 ± 1.92	12.70 ± 1.64	14.51 ± 1.98	13.35 ± 2.06
18:0	2.04 ± 0.33	2.12 ± 0.55	2.04 ± 0.28	2.25 ± 0.60
16:1n-7	8.45 ± 1.77	7.62 ± 1.69	8.38 ± 1.28	8.07 ± 1.57
18:1n-9	27.35 ± 1.75	26.90 ± 5.89	22.55 ± 2.23	26.67 ± 5.01
18:1n-7	9.92 ± 1.61	9.02 ± 2.10	8.75 ± 2.03	8.73 ± 2.23
18:1n-5	0.61 ± 0.11	0.72 ± 0.14	0.69 ± 0.10	0.68 ± 0.13
20:1n-9	7.70 ± 3.21	9.13 ± 1.73	7.81 ± 2.16	8.80 ± 2.03
20:1n-7	0.56 ± 0.16	0.84 ± 0.25	0.72 ± 0.20	0.81 ± 0.22
22:1n-13+11	1.71 ± 0.75	2.53 ± 1.09	2.45 ± 1.24	2.76 ± 1.15
22:1n-9	1.69 ± 0.50	2.10 ± 0.56	1.90 ± 0.78	2.06 ± 0.75
24:1n-11	0.43 ± 0.27	0.39 ± 0.19	0.46 ± 0.24	0.55 ± 0.34
24:1n-9	0.76 ± 0.28	0.77 ± 0.20	0.87 ± 0.30	0.84 ± 0.30
18:2n-6	1.39 ± 0.29	1.38 ± 0.62	1.28 ± 0.25	1.19 ± 0.33
18:4n-3	0.53 ± 0.15	0.63 ± 0.31	0.67 ± 0.09	0.45 ± 0.10
20:5n-3	5.21 ± 1.63	5.68 ± 1.48	7.17 ± 1.32	5.30 ± 1.32
22:5n-3	0.36 ± 0.14	0.57 ± 0.24	0.66 ± 0.48	0.51 ± 0.15
22:6n-3	3.50 ± 1.11	4.11 ± 1.00	5.39 ± 1.12	4.09 ± 1.28
Others	7.57 ± 0.83	7.74 ± 0.96	7.54 ± 0.38	7.74 ± 1.10
SFA	24.46 ± 3.77	22.12 ± 3.17	24.72 ± 3.30	23.04 ± 3.70
MUFA	60.82 ± 4.65	61.61 ± 3.65	56.21 ± 3.67	61.63 ± 4.34
PUFA	14.38 ± 3.25	15.68 ± 2.82	18.61 ± 2.52	14.78 ± 2.77

Table 5. *Halobaena caerulea*. Predicted species classification from linear discriminant analyses

Predicted species membership		Predicted classification				Total
		1996	2000	2001	2002	
Wax esters						
Fatty alcohols	<i>Calanoides acutus</i> (copepod)	0	2	1	3	6
	<i>Electrona antarctica</i> (myctophid)	11	4	1	6	22
	<i>Krefflichthys anderssoni</i> (myctophid)	0	1	2	0	3
	<i>Gymnoscopelus braueri</i> (myctophid)	1	6	8	4	19
	Total	12	13	12	13	50
Fatty acids	<i>Electrona antarctica</i> (myctophid)	1	1	0	0	2
	<i>Krefflichthys anderssoni</i> (myctophid)	11	11	11	12	45
	<i>Gymnoscopelus braueri</i> (myctophid)	1	1	1	1	4
	Total	13	13	12	13	51
Triglycerides						
Fatty acids	<i>Electrona carlsbergi</i> (myctophid)	1	0	4	1	6
	<i>Gymnoscopelus nicholsi</i> (myctophid)	10	11	7	9	37
	<i>Protomyctophum bolini</i> (myctophid)	0	0	1	0	1
	<i>Dissostichus eleginoides</i> (nototheniid)	2	2	0	3	7
	Total	13	13	12	13	51

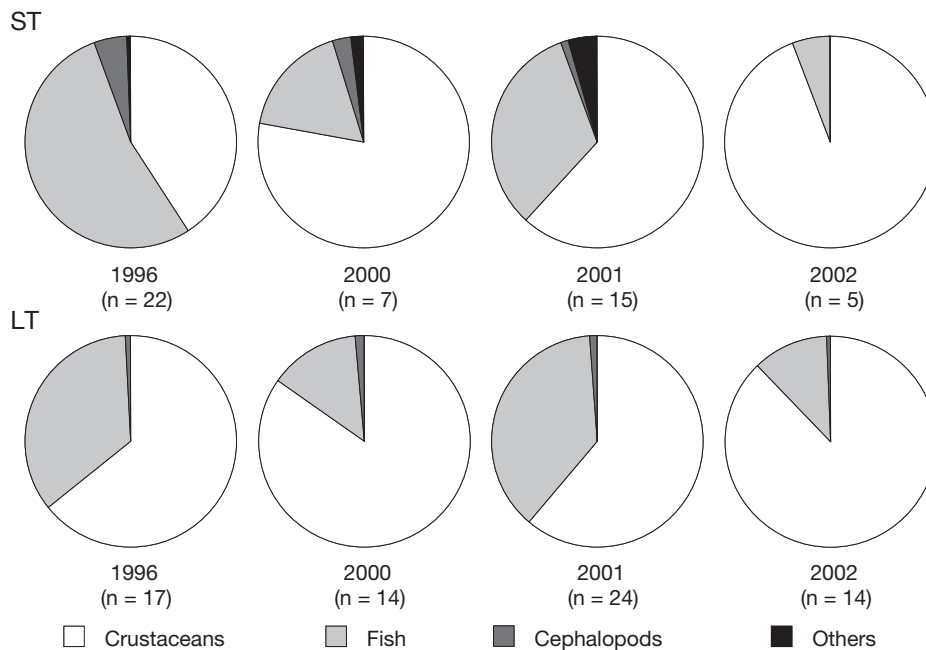


Fig. 4. *Halobaena caerulea*. Interannual dietary variation in broad prey classes (percentages by fresh mass) at Kerguelen Islands. LT: long trips; ST: short trips

by myctophids, including *Electrona antarctica*, *Krefflichthys anderssoni* and *Protomyctophum bolini*, and by the gempylid *Paradiplospinus gracilis* (Table 6).

Short trips

The wet mass of the 49 ST samples averaged 14 g (from 8.8 ± 2.3 to 21.1 ± 5.2 g, mean \pm SD), with significant differences between years ($F_{3,49} = 7.71$, $p < 0.001$, $2002 = 2001 < 1996 < 2000$). Crustaceans dominated

the diet by mass every year, except 1996 during which fish ranked first and crustaceans second (54 and 41% by mass, respectively). Fish was a minor item (6%) in 2002 (Fig. 4).

A total of 8750 prey belonging to 43 taxa were recovered from the ST food samples. Again crustaceans dominated the diet (>96% by number). *Thyanoessa macrura/vicina* and *T. gaudichaudii* were the 2 main crustacean prey, with the former dominating in 2001 and 2002, and the latter in 1996 and 2000. The dietary importance of subantarctic krill *Euphausia vallentini*

Table 6. *Halobaena caerulea*. Prey species identified from stomach contents of 118 blue petrels at Kerguelen Islands. FO: frequency of occurrence; Nb: % by number

	Long trips								Short trips							
	1996 (n = 17)		2000 (n = 14)		2001 (n = 24)		2002 (n = 14)		1996 (n = 22)		2000 (n = 7)		2001 (n = 15)		2002 (n = 5)	
	FO	Nb	FO	Nb	FO	Nb	FO	Nb	FO	Nb	FO	Nb	FO	Nb	FO	Nb
Crustaceans	100.0	98.3	100.0	99.4	95.8	99.1	100.0	99.6	100.0	96.9	100.0	99.3	100.0	98.1	100.0	99.9
Euphausiacea																
<i>Euphausia superba</i>	70.6	4.5	64.3	1.9	62.5	2.1	28.6	0.5								
<i>Euphausia vallentini</i>	-	-	14.3	1.1	12.5	0.2	14.3	0.1	4.5	4.1	57.1	19.2	26.7	3.7	20.0	0.1
<i>Euphausia</i> sp.	29.4	0.5	21.4	0.3	20.8	0.9	7.1	< 0.1	9.1	0.1	-	-	20.0	1.6	-	-
<i>Thysanoessa macrura/vicina</i>	94.1	87.0	92.9	91.0	87.5	86.2	100.0	67.0	50.0	18.6	28.6	1.1	60.0	54.5	100.0	65.4
Amphipoda																
<i>Polycheria kergueleni</i>	-	-	-	-	-	-	-	-	13.6	1.6	-	-	6.7	3.4	-	-
<i>Uristes gigas</i>	-	-	-	-	-	-	-	-	-	-	-	-	6.7	1.0	20.0	1.5
<i>Cylopus magellanicus</i>	47.1	0.8	14.3	0.1	70.8	1.4	42.9	0.2	86.4	2.5	100.0	4.9	86.7	6.0	60.0	0.8
<i>Vibilia antarctica</i>	52.9	1.4	14.3	0.1	20.8	0.2	21.4	0.1	68.2	1.6	100.0	5.1	66.7	3.7	60.0	0.6
<i>Hyperiella antarctica</i>	29.4	0.4	21.4	0.1	16.7	0.3	14.3	< 0.1	18.2	0.1	28.6	0.2	6.7	0.7	40.0	0.2
<i>Themisto gaudichaudii</i>	100.0	2.6	85.7	4.4	75.0	7.1	100.0	31.3	100.0	67.9	100.0	68.9	100.0	23.1	100.0	31.1
Fish	82.4	1.4	71.4	0.5	75.0	0.8	50.0	0.1	95.5	1.0	85.7	0.4	73.3	1.4	20.0	0.1
Myctophidae																
<i>Electrona antarctica</i>	17.6	0.1	21.4	0.1	16.7	0.1	14.3	< 0.1	9.1	0.1	28.6	0.1	-	-	-	-
<i>Electrona carlsbergi</i>	11.8	0.1	7.1	< 0.1	4.2	< 0.1	-	-	9.1	0.1	14.3	< 0.1	6.7	0.1	-	-
<i>Gymnoscopelus microlampas</i>	-	-	-	-	-	-	-	-	-	-	-	-	6.7	0.1	-	-
<i>Gymnoscopelus nicholsi</i>	-	-	-	-	4.2	< 0.1	7.1	< 0.1	-	-	-	-	6.7	0.1	-	-
<i>Krefflichthys anderssoni</i>	29.4	0.3	14.3	< 0.1	16.7	0.1	-	-	27.3	0.2	-	-	13.3	0.1	-	-
<i>Protomyctophum bolini</i>	29.4	0.4	7.1	< 0.1	16.7	0.1	-	-	9.1	0.1	14.3	< 0.1	13.3	0.1	-	-
<i>Protomyctophum choriodon</i>	-	-	-	-	20.8	0.1	-	-	-	-	-	-	20.0	0.3	-	-
Unidentified Myctophidae	23.5	0.2	7.1	< 0.1	20.8	0.1	-	-	18.2	0.1	-	-	20.0	0.2	-	-
Muraenolepididae																
<i>Muraenolepis marmoratus</i>	-	-	-	-	-	-	-	-	9.1	0.1	-	-	-	-	-	-
Nototheniidae																
<i>Lepidonotothen mizops</i>	-	-	-	-	-	-	-	-	-	-	-	-	6.7	0.1	-	-
Gempylidae																
<i>Paradiplospinus gracilis</i>	23.5	0.1	-	-	20.8	0.1	14.3	< 0.1	31.8	0.2	14.3	< 0.1	26.7	0.3	20.0	0.1
Unidentified fish	17.6	0.1	21.4	0.1	8.3	0.1	14.3	< 0.1	18.2	0.1	14.3	< 0.1	6.7	0.1	-	-
Cephalopods	23.5	0.1	28.6	0.1	12.5	0.1	21.4	0.1	18.2	0.1	57.1	0.2	20.0	0.2	-	-
Others	23.5	0.3	-	-	4.2	0.1	21.4	0.2	63.6	1.9	28.6	0.1	13.3	0.3	-	-

greatly varied between years, being a main item in 2000 and almost absent in 2002. The latter year was also marked by very low numbers (<1%) of the amphipods *Cylopus magellanicus* and *Vibilia antarctica*. Fish prey during ST again included mostly mesopelagic fish with the gempylid *Paradiplospinus gracilis* and various myctophids (*Krefflichthys anderssoni*, *Protomyctophum* spp. and *Electrona* spp.). The only identified fish item from the 2002 food samples was *Paradiplospinus gracilis* (Table 6).

Demographic parameters

Hatching, fledging and breeding success of blue petrels averaged 49, 77 and 38%, respectively, and they all showed interannual variations over the 17 yr study period (1986–2002; $\chi^2_{16} = 83.5, 134.7$ and 100.9 , all $p < 0.01$). Within the 4 yr of the dietary investigation

and when compared to other years, 2002 was noticeably marked by the lowest breeding success (24%), which was due to the lowest fledging success (56%) ever recorded during the 17 yr study period. Summer 2002 was also characterized by the lowest mass of chicks at fledging (ANOVA over 1989–2002, $F_{13,555} = 17.292$, $p < 0.0001$, with post hoc Tukey HSD multiple comparison tests showing that 2002 was different from 1996, 2000 and 2001, all $p < 0.0001$) and the lowest summer survival of adults (0.870, average survival = 0.963) recorded during the study period (Table 7).

DISCUSSION

Stomach oil and fresh portions of food samples are indicators of prey items mainly caught at different time scales, and thus on different foraging zones. Stomach oil reflects the adult diet when they self-feed

Table 7. *Halobaena caerulea*. Demographic parameters for the study period. Sea surface temperature (SST) anomalies were averaged over the oceanic sector 48–65° S and 55–85° E for the summer months of December, January and February

Year	Monitored burrows (n)	Hatching success (%)	Fledging success (%)	Breeding success (%)	Summer survival	Winter survival	Annual survival	Mean fledgling mass (g)	Mean (max) SST anomaly (°C)
1996	238	58.8	83.3	49.0	0.923	0.846	0.833	217	-0.38 (0.74)
2000	182	54.3	88.0	47.8	0.988	0.922	0.813	187	-0.25 (0.53)
2001	200	37.5	83.3	31.3	0.980	0.888	0.969	194	-0.15 (0.97)
2002	200	43.4	55.8	24.2	0.870	0.851	0.828	141	0.23 (2.23)
Mean 1986/2002	175 ± 50	49.1 ± 8.7	76.7 ± 1.01	38.0 ± 9.7	0.963 ± 0.015	0.914 ± 0.015	0.871 ± 0.008	196 ± 24	-

far away their breeding grounds during LT, while the fresh portion of food samples includes prey taken for the chicks either on the way back to the colony at the end of LT or during ST. Both biochemical and conventional methods are thus complementary and result in new insights on the summer feeding ecology of breeding blue petrels at Kerguelen Islands. Biochemical analysis highlighted the consistent importance of myctophid fish over years in the nutrition of adult birds, while analysis of chick food depicted significant interannual dietary variation leading to demographic consequences on the short-term (fledging mass and fledging success), but also on the medium-term (summer adult survival).

Biochemical analysis of adult stomach oils: importance of myctophid fish

Overall, biochemical analysis showed little interannual variation in lipid classes and FALC and FA compositions of WE and TAG, suggesting relatively low interannual changes in the diet of adult blue petrels at Kerguelen Islands during LT. In agreement with a previous study conducted in South Georgia (Clarke & Prince 1976), lipid class analysis indicated that birds fed mainly on WE- and TAG-rich prey species during all 4 yr, and that they caught some DAGE-rich prey in 1996 and 2002. WE and TAG are the 2 main forms of lipid storage in marine organisms (Lee et al. 2006), but DAGE is a rare lipid class that, so far, has only been found in some squids and pteropods in the Southern Ocean (Phleger et al. 2001, Phillips et al. 2002). Seabirds are known to feed on cephalopods but rarely on pteropods (Karnovsky et al. 2008). Accordingly, DAGE from stomach oil was recently found in association with squid remains (Connan et al. 2007a). However, this does not preclude birds feeding on pteropods nor on other DAGE-rich prey species that have yet to be analysed. More detailed biochemical analyses are needed to investigate the trophic origin of DAGE of stomach oils.

Interannual variation in FA composition of WE and TAG and in FALC composition of WE were underlined by FSDA assigning 51–80% of individual oils to the correct year. Both FALC and FA compositions of WE grouped oils from 2001 and 2000, with differences between 1996 and 2002 oils, and FA composition of TAG isolated 1996 oils from those from the 3 other years (Fig. 3). For example, 1996 and 2002 oils contained less PUFAs (20:5n-3, 22:6n-3) than 2000 and 2001 oils in their WE fraction. Despite these differences, no clear interannual changes were detected in the dietary origin of stomach oils, with most oils deriving from myctophid lipids in all the 4 yr. This mismatch points out the need for much more information on lipid composition of marine organisms (including the different species of myctophids) and on their spatio-temporal variation to build up a more accurate database to better interpret the FA and FALC profiles of predators.

A myctophid origin of stomach oils of blue petrels is consistent with recent investigations on oils of various procellariiform seabirds, underlining the importance of mesopelagic fish in the nutrition of adult birds when they self-feed (Connan et al. 2005, 2007a,b). Surprisingly, no stomach oil fit the lipid patterns of euphausiids, including those of the TAG-rich Antarctic krill and of the WE-rich *Thysanoessa macrura*. The latter species (and/or the closely-related *T. vicina*) is the main prey by number of blue petrels at Kerguelen, and digested remains of Antarctic krill commonly occur in LT food samples, suggesting that it is one of the main prey targeted by birds reaching Antarctic waters (Cherel et al. 2002, present study). While our study does not preclude blue petrels feeding on Antarctic krill in the southern Indian Ocean (Ryan & Cooper 1989), it emphasizes a more important role for myctophids than previously thought. The only crustacean species whose lipid pattern fits well with those of stomach oils was *Calanus acutus*. Copepods rarely occur in the chick diet at Kerguelen (Cherel et al. 2002, present study), but they are minor dietary items of blue petrels in South Georgia (Prince 1980). Finally, a few stomach oils probably originate from lipids of the Patagonian

toothfish *Dissostichus eleginoides*. Toothfish is a large species targeted by longliners in Kerguelen waters, but the blue petrel is not a ship-attracted species and it was not observed feeding on fishery waste (Cherel et al. 1996). The FA profile of toothfish TAG is dominated by MUFAs (Wilson 2004), which also compose the majority of FA of TAG-rich myctophids (Saito & Murata 1998, Lea et al. 2002). Consequently, the similarity of some stomach oils with toothfish lipids may be a methodological artifact that again underlines the need for more data on the lipid profiles of myctophids and other marine organisms from the Southern Ocean to better disentangle trophic links.

Conventional analysis of chick food: interannual dietary changes

Stomach content analysis showed that blue petrels fed on a large diversity of prey and that chick food was dominated by mass by crustaceans and fish, with cephalopods and other organisms being minor items (Cherel et al. 2002, present study). Euphausiids and *Themisto gaudichaudii* are consistently the major crustacean prey, and mesopelagic fish, including various myctophids, the main fish items at Kerguelen and elsewhere (Prince 1980, Steele & Klages 1986, Ridoux 1994, Cherel et al. 2002). Noticeably, the importance of WE-rich (e.g. *Electrona antarctica*, *Krefflichthys anderssoni*) and TAG-rich (e.g. *E. carlsbergi*, Lea et al. 2002, authors' unpubl. data) fish species fit well with the FA and FAlc compositions of stomach oils indicating feeding on myctophids during LT for Kerguelen birds. On the other hand, the main crustacean prey in LT and ST samples, the WE-rich *Thysanoessa* spp. and the TAG-rich *Themisto gaudichaudii*, respectively (Nelson et al. 2001, Mayzaud et al. 2003), were not identified from biochemical analyses, suggesting they were less important items than myctophids for the nutrition of adult birds when self-feeding during LT.

Important interannual variation in the chick diet occurred in both LT and ST samples. For example, sub-antarctic krill was much more abundant in ST food samples collected in 2000 than in the 4 other years. The most prominent feature, however, was that the chick diet in 2002 was clearly different from 1996, 1998, 2000 and 2001. Overall, adult blue petrels brought back less fish and accordingly more crustaceans to their chicks in 2002. ST samples that year contained more *Thysanoessa macrura/vicina* and less *Euphausia vallentini*, *Cylopus magellanicus* and *Vibilia antarctica*, while LT samples included almost no Antarctic krill, less *Thysanoessa macrura/vicina*, but more *Themisto gaudichaudii* (Cherel et al. 2002, present study). All together the data indicate that 2002 was an unusual foraging

summer for blue petrels rearing chicks, which was probably related to changes in prey availability in the pelagic ecosystem in Kerguelen and Antarctic waters. To our knowledge, such year-to-year dietary variations were not previously found in blue petrels. However, similar changes have been observed in a related species, the Antarctic prion at South Georgia, where, surprisingly and contrary to other seabirds, the poor-krill year had no effect on chick growth rate and survival, or accordingly on breeding success (Liddle 1994). The causes and consequences of the 2002 dietary changes were consequently further investigated in terms of demographic parameters of blue petrels breeding at Kerguelen Islands and of potential relationships with environmental variability in the southern Indian Ocean at that time.

Environment, demography and summer diet of blue petrels

Interannual variability in reproductive performance is a common feature in seabirds, including the blue petrel (Chastel et al. 1995a, Guinet et al. 1998). In blue petrels, breeding success is driven more by hatching success than fledging success, with body condition at the beginning of the breeding cycle determining both reproductive decision and reproductive success (Chastel et al. 1995a,b). Within that context, the breeding season of 2002 was unusual, being marked by a low breeding success that mainly resulted from the lowest fledging success on record. Summer 2002 was also characterized by a very low fledgling mass when compared with data from the 17 yr study period. All together, poor reproductive output and poor chick body condition strongly suggested poor foraging performance of adult blue petrels, and thus a causal link between demographic parameters and dietary changes observed in summer 2002. The main dietary feature was the near lack of mesopelagic fish in both ST and LT food samples, suggesting a substantial decrease in the availability of myctophids during the chick-rearing period in 2002 when compared to other years.

Food availability comprises a complex interaction of factors that integrates abundance, accessibility, taxonomic composition and quality of the prey items. No information on mesopelagic fish in Kerguelen waters is available for the study period, but it is likely that a decrease in myctophid abundance and accessibility to foraging flying seabirds occurred in summer 2002. Shifting from a mixed fish/crustacean to an almost exclusively crustacean diet decreased the overall quality of the food. Due to a size effect, single amphipods and euphausiids contain less energy than a single fish. Moreover, myctophids are protein- and lipid-rich

organisms; they thus possess a high energy density and are considered as food with a high nutritional quality (Donnelly et al. 1990, Cherel & Ridoux 1992). Indeed, it is well documented worldwide that dietary shifts from lipid-rich fishes to lipid-poor items result in low breeding success and reproductive failure in seabirds (Monaghan 1992, Regehr & Rodway 1999, Takahashi et al. 2001). Moreover, experimental investigations showed that nestlings fed rations of fatty fish experienced higher growth rates than nestlings fed lean items, which could be expected to have effect on pre- and post-fledging survival of nestlings in the wild (Romano et al. 2006).

Interestingly, summer 2002 was also marked by a decrease in survival probability of adult blue petrels. In this species, summer survival is relatively high and varies little between years; consequently, annual survival is driven by changes in winter survival (Barbraud & Weimerskirch 2003). At Kerguelen, winter survival is linked to climatic factors, being lower during anomalous warm events (Barbraud & Weimerskirch 2003). Accordingly, in contrast to 1996, 2000 and 2001, summer months in 2002 were characterized by intense positive sea-surface temperature anomalies in Kerguelen waters (Table 7), suggesting that adult survival may also be sensitive to extreme warm events occurring in summer. Data collected in the abnormal summer of 2002 therefore suggest the following sequence of causal events linking environment and seabirds: warm climatic event → lower mesopelagic fish availability → less myctophids in diet and decreased nutritional value of food → higher adult mortality and altered chick growth rate, and thus lower fledging mass and higher chick mortality. A recent investigation linked a major population decrease of blue petrels to an increase in adult winter mortality in response to a long warming event (Barbraud & Weimerskirch 2003). Our data therefore suggests that further modeling must also include summer demographic parameters in order to better depict the effect of climate change on seabird population dynamics (Jenouvrier et al. 2005, Lee et al. 2007).

Acknowledgements. The authors thank the numerous field workers (including P. Bocher, S. Chamailé, V. Chartendraul, N. Delelis, C. Vanpé and O. Villa) who collected food samples at Kerguelen Islands, M. Boutoute and R. Cattaneo for helping with lipid analyses, C. F. Phleger, P. D. Nichols, M. M. Nelson, K. L. Phillips and G. Wilson for supplying detailed chromatographic data, and P. Bocher for the 1996 dietary data. Fieldwork was supported financially and logistically by both the Institut Paul-Emile Victor (IPEV, Programme No. 109, H. Weimerskirch) and the Terres Australes et Antarctiques Françaises. This research was supported by CNRS through UMR 7093 and UPR 1934, and a doctoral scholarship to M.C. from Paris VI University. Protocols and procedures were approved by the Ethical Committee of the IPEV.

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Editorial responsibility: Hans Heinrich Janssen, Oldendorf/Luhe, Germany

Submitted: May 6, 2008; Accepted: September 2, 2008
Proofs received from author(s): December 12, 2008