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Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean

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Summary

1. Climatic variation outside the breeding season affects fluctuations in population numbers of seabirds and marine mammals. A challenge in identifying the underlying biological mechanisms is the lack of information on their foraging strategies during winter, when individuals migrate far from their breeding grounds.

2. We investigated the temporal variability in resource partitioning within the guild of five sympatric Subantarctic penguins and fur seals from Crozet Islands. The stable isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) for whole blood were measured for penguins and fur seals, as were the isotopic ratios for penguin nails and food. Animals were sampled at two periods, during breeding in summer and at their arrival in the colonies in spring (hereafter winter, since the temporal integration of blood amounting to several months).

3. In summer, $\delta^{13}C$ and $\delta^{15}N$ for blood samples defined three foraging areas and two trophic levels, respectively, characterizing four nonoverlapping trophic niches. King penguins and female Antarctic and Subantarctic fur seals are myctophid eaters foraging in distinct water masses, while both macaroni and rockhopper penguins had identical isotopic signatures indicating feeding on crustaceans near the archipelago.

4. Isotopic ratios were almost identical in summer and winter suggesting no major changes in the species niches, and hence, in the trophic structure of the guild during the nonbreeding period. A seasonal difference, however, was the larger variances in $\delta^{13}C$ (and also to a lesser extent in $\delta^{15}N$) values in winter, thus verifying our hypothesis that trophic niches widen when individuals are no longer central place foragers.

5. Winter isotopic ratios of macaroni penguins and male Antarctic fur seals had large variances, indicating individual foraging specializations. The range of $\delta^{13}C$ and $\delta^{15}N$ values of male fur seals showed, respectively, that they dispersed over a wide latitudinal gradient (from Antarctica to north of the archipelago) and fed on different prey (crustaceans and fish).

6. By comparing summer and winter isotopic ratios and examining the summer diet, we highlight the feeding habits of marine predators that were not previously addressed. The findings have a number of implications for understanding the functioning of the pelagic ecosystem and on the demography of these species.

Key-words: fur seal, nonbreeding period, penguin, resource partitioning, trophic level.

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Introduction

Environmental variability is known to influence avian and mammalian population dynamics. In seabirds and pinnipeds, there is increasing evidence that climatic variations outside the breeding season affects fluctuations in population numbers, in many cases operating on variation in adult survival (Boyd *et al*. 1995; Grosbois & Thompson 2005; Sandvik *et al*. 2005; Jenouvrier, Barbraud & Weimerskirch 2006). Understanding how climate affects trophic interactions and interspecific relationships are almost nonexistent, although studies of long-lived seabirds suggest that such interactions are important (Saether, Sutherland & Engen 2004; Sandvik *et al*. 2005). However, for seabirds and pinnipeds, a major challenge in identifying the underlying biological mechanisms is the lack of information on their foraging strategies during the nonbreeding season, when they migrate far from their breeding grounds.

The lack of winter dietary and habitat-use information is particularly relevant for penguins and fur seals, because, unlike flying seabirds, the swimming and diving habits of these flightless predators make them cryptic organisms when foraging, thus precluding accurate visual identification and quantification at sea. Consequently, almost nothing is known about their winter biology, although increasing use of electronic devices has already provided new insights into their annual diving patterns (Green *et al*. 2005) and foraging areas (Boyd, Staniland & Martin 2002). This lack of information is of special concern, because penguins number about 113 millions of individuals (Van Franeker, Bathmann & Mathot 1997) and form 90% of seabird biomass in the Southern Ocean (Woehler 1993), where they constitute a key group of marine consumers within the pelagic ecosystem (Woehler 1995; de Brooke 2004). Stomach contents have been the primary means for determining the diet and resource partitioning of sympatrically breeding penguins (Adams & Brown 1989; Ridoux 1994; Hindell, Robertson & Williams 1995). However, the method is temporally limited to the chick-rearing period, when parent birds are accessible and feed their chicks in the colonies, and so gives no indication on dietary variations over the annual cycle of migrating species.

Measurements of stable isotopes in animal tissues can be a powerful alternative to the conventional ways of analysing diets by collecting stomach contents or faeces (Hobson, Piatt & Pitocchelli 1994; Kelly 2000; Bearhop *et al*. 2004). Depending on tissue-specific isotopic turnover, stable isotope measurements reflect average dietary records over days to years and have thus the potential to resolve nutritional variation at different time-scales (Dalerum & Angerbjörn 2005). Traditionally, stable nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) and carbon ($^{13}C/^{12}C$, $\delta^{13}C$) isotope measurements have been used primarily in dietary analyses. Consumers are enriched in ^{15}N relative to their food and consequently $\delta^{15}N$ measurements serve as indicators of a consumer trophic position (McCutchan *et al*. 2003; Vanderklift & Ponsard 2003). By contrast, $\delta^{13}C$ values vary little along the food chain and are mainly used to determine primary sources in a trophic network (Kelly 2000; McCutchan *et al*. 2003). In the marine environment, $\delta^{13}C$ values can also indicate inshore vs. offshore, or pelagic vs. benthic, contribution to food intake (Hobson *et al*. 1994). As lower-latitude plankton food bases are enriched in ^{13}C relative to higher-latitude waters, geographical $\delta^{13}C$ gradients have been also used as an effective way for investigating the winter foraging areas of seabirds in the Southern Ocean (Cherel, Hobson & Weimerskirch 2000; Quillfeldt, McGill & Furness 2005; Cherel *et al*. 2006), including penguins (Cherel & Hobson 2007).

The primary objective of this study was to assess the temporal variability in resource partitioning within a guild of large air-breathing diving predators, focusing on the poorly known winter period. Species where individuals forage in a range of geographical areas are likely to show more variation in the stable isotope signatures of their tissues than those from more sedentary populations (Bearhop *et al*. 2004). We thus hypothetized that, because penguins and fur seals are no longer central place foragers and disperse after breeding, their trophic niches widen in winter thus leading to larger variances in $\delta^{15}N$ and $\delta^{13}C$ values than in summer.

As the stable isotope method is at its most powerful when combined with conventional approaches (Bearhop *et al*. 2004; Karnovsky *et al*. 2007), stable isotope analyses were also performed for penguin food to create a basis for the interpretation of the isotopic signatures of predators. Food analysis also helped to investigate summer segregation occurring through the consumption of different prey classes, prey species and prey size within the guild. Summer was considered as the control period to help interpretation of winter values, because much information is available on summer feeding ecology of penguins and fur seals, including their food, foraging areas and diving patterns (Cherel & Ridoux 1992; Ridoux 1994; Bost *et al*. 1997; Tremblay & Cherel 2003; Bailleul *et al*. 2005). Fieldwork was performed at Crozet Islands (southern Indian Ocean) where no Antarctic krill *Euphausia superba* occurs and where, instead, the seabird community feeds on a larger diversity of prey, including other euphausiids, hyperiid amphipods and mesopelagic myctophid fishes (Ridoux 1994). This makes the archipelago an ideal location to investigate interspecies resource partitioning in the absence of the masking effect of the superabundance of a single prey on segregating mechanisms (Croxall, Prince & Reid 1997).

Methods

FIELD STUDY

Fieldwork was carried out at Possession Island, Crozet Archipelago. According to physical oceanography, the islands (46–47°S) lie in the middle of the Polar Frontal

Table 1. Stable isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) and C/N ratio for whole blood, nails and food samples of penguins and fur seals from Crozet Islands

Species and status	Period of integration	Tissue	*n*	$\delta^{15}N$ (per mil)	$\delta^{13}C$ (per mil)	C/N mass ratio
Antarctic fur seals						
Lactating females	Summer	Blood	10	10·99 ± 0·19	–20·61 ± 0·77	3·60 ± 0·12
Breeding males	Winter	Blood	11	11·41 ± 1·50	–21·76 ± 2·66	3·59 ± 0·08
Arriving females	Winter	Blood	11	10·99 ± 0·25	–19·82 ± 0·53	3·56 ± 0·03
Subantarctic fur seals						
Lactating females	Summer	Blood	10	10·79 ± 0·29	–19·40 ± 0·19	3·52 ± 0·05
Breeding males	Winter	Blood	5	11·87 ± 0·33	–19·31 ± 0·37	3·47 ± 0·02
Arriving females	Winter	Blood	5	11·15 ± 0·50	–19·08 ± 0·31	3·54 ± 0·01
King penguins						
Chicks	Summer	Food	10	7·77 ± 0·62	–22·84 ± 0·48	3·76 ± 0·18
	Summer	Blood	10	10·28 ± 0·23	–22·60 ± 0·12	3·61 ± 0·07
Breeding adults	Summer	Blood	10	10·07 ± 0·18	–22·42 ± 0·13	3·48 ± 0·02
	Unknown	Nails	10	10·89 ± 0·61	–21·56 ± 0·28	3·35 ± 0·04
Moulting adults	Winter	Blood	10	9·83 ± 0·35	–21·78 ± 0·75	3·46 ± 0·07
Macaroni penguins						
Chicks	Summer	Food	10	3·07 ± 0·30	–21·61 ± 0·39	3·95 ± 0·11
	Summer	Blood	10	7·49 ± 0·31	–21·18 ± 0·32	3·55 ± 0·06
Breeding adults	Summer	Blood	10	6·97 ± 0·22	–20·40 ± 0·14	3·45 ± 0·03
	Unknown	Nails	10	6·86 ± 0·42	–19·53 ± 0·81	3·32 ± 0·07
Arriving females	Winter	Blood	10	6·60 ± 0·66	–20·99 ± 1·38	3·72 ± 0·13
Arriving males	Winter	Blood	10	6·85 ± 0·58	–20·70 ± 1·30	3·46 ± 0·04
Rockhopper penguins						
Chicks	Summer	Food	7	4·41 ± 0·67	–21·47 ± 0·35	3·72 ± 0·09
	Summer	Blood	10	6·82 ± 0·28	–21·15 ± 0·14	3·54 ± 0·06
Breeding adults	Summer	Blood	11	7·51 ± 0·53	–20·87 ± 0·46	3·48 ± 0·05
	Unknown	Nails	10	7·11 ± 0·80	–19·43 ± 0·54	3·37 ± 0·14
Arriving adults	Winter	Blood	10	7·62 ± 0·29	–19·73 ± 0·53	3·46 ± 0·02

Zone, between the Subantarctic Front in the north and the Polar Front in the south (50°S). The western Indian Ocean is marked by the strong confluence of three fronts, the Subantarctic, Subtropical and Agulhas Return Current Fronts into a single frontal structure, the Crozet Basin Frontal Zone, which is located in the north of the islands (41–43°S) (Park & Gambéroni 1997).

The guild of large air-breathing diving vertebrates feeding on pelagic prey includes four species of penguins and three species of pinnipeds at Crozet Islands. All species are summer breeders, except the gentoo penguin *Pygoscelis papua* (Forster, 1781) and elephant seal *Mirounga leonina* Linnaeus, 1758, which reproduce in winter and were thus not considered in the present work. The five investigated species were two crested penguins, the rockhopper *Eudyptes chrysocome filholi* Hutton, 1879, and macaroni *E. chrysolophus* Brandt, 1837, penguins, the king penguin *Aptenodytes patagonicus* Miller, 1778, and two congeneric fur seals, the Antarctic *Arctocephalus gazella* (Peters, 1875) and Subantarctic *A. tropicalis* (Gray, 1872) fur seals. All species were studied within the same year (2002), first in summer during the chick-rearing period of penguins (adults and chicks) and lactating period of fur seals (females), and second in spring when animals went back to the colonies for breeding after their winter migration (adult penguins, and male and female fur seals). As the king penguin breeding cycle involves more than one year, adult birds present in the colony in spring include both breeding birds at the end of one cycle and non-breeding birds. We consequently selected birds arriving to moult ashore, because they were at the beginning of a new moult/reproductive cycle and consequently they were not in charge of chicks during the previous winter period.

Five to 11 randomly chosen individuals were blood-sampled for each group of penguins and fur seals in summer and spring (Table 1). Using allometric equations between body mass and carbon half-life in avian red blood cells (Carleton & del Rio 2005), half-lives in penguin blood was estimated to amount to 27–45 days. The isotopic signature in spring was thus considered as representative of the trophic niche of the animals during the last winter months at sea. Although the sampling periods were separated by a southern winter, they are protracted during spring and summer months. Depending on penguin species, a 3–5-month interval separated the two spring (October–November) and summer (February) sampling periods within a given breeding cycle. The interval was 1 month only (December/spring, January/summer) for female fur seals. We are therefore confident that penguin samples were representative of winter and summer months, respectively, but the sampling interval in female fur seals was the

minimal duration to detect potential dietary shifts between the end of winter and summer. Samples from the same tissue (here blood) were compared because it is the most straightforward approach to resolve temporal diet variation (Dalerum & Angerbjörn 2005) and to minimize the tissue effect on $\delta^{15}N$ and $\delta^{13}C$ values (Kelly 2000; Vanderklift & Ponsard 2003). Blood has also the advantage that its isotopic signature is only marginally affected by the nutritional status of the animals (Cherel *et al*. 2005a).

Blood was collected into a heparinized syringe by venepuncture of a penguin flipper vein and of an interdigital vein in fur seal hind-flipper. Seventy per cent ethanol was then added to whole blood, because, in many cases, freezing was not possible in the field and storage in 70% ethanol does not alter the isotopic composition of tissues (Hobson, Gibbs & Gloutney 1997). Using the stomach lavage method, food samples were collected from adult penguin rearing-chicks and the tip of nail from the median toe was cut on the same individuals. Fresh faecal samples (scats) of fur seals were collected from areas used by lactating females. All samples were subsequently kept at –20 °C until analysis.

DIETARY ANALYSES

In the laboratory, each fur seal scat was thawed in warm waters and rinsed through 1·0 and 0·5 mm sieves to collect hard prey remains. Penguin food samples were thawed overnight over a sieve to remove the liquid fraction. The solid fraction was then placed in a large flat-bottomed tray and fresh remains were divided into broad prey classes (crustaceans, fish and cephalopods), which were weighed to estimate their proportions by fresh/wet mass in the diet.

Total numbers of each prey item were counted in each individual fur seal scat and penguin stomach content. Prey was identified using published keys and descriptions and by comparison with material held in our own reference collection. For crustaceans, total length, carpus length and eye diameter were determined using an ocular scale in a binocular microscope. Total length (TL) of amphipods and euphausiids was measured from the front of eye to the tip of the longest uropods, and from the tip of rostrum to the tip of uropods, respectively. For digested specimens, TL was estimated from carpus length or eye diameter measurements by the use of allometric equations (Ridoux 1994; authors' unpublished data), as was estimated the standard length (SL) of fish by the use of sagittal otoliths (Williams & McEldowney 1990; Cherel, Guinet & Tremblay 1997).

STABLE ISOTOPE ANALYSIS

Before isotopic analysis, whole blood and penguin food samples were dried in an oven at +60 °C. Food samples and nails were then powdered and treated with a 2 : 1 chloroform : methanol solution to remove lipids and cleaned of surface contaminants, respectively. The low lipid content of blood does not necessitate lipid extraction (Cherel, Hobson & Hassani 2005b), as verified here by its consistently low values of C/N mass ratio (Table 1). As food samples from both species of crested penguins contained crustacean prey, they were soaked in 0·1 N HCl to remove carbonates. Relative abundance of ^{13}C and ^{15}N were determined by continuous-flow isotope-ratio mass spectrometry. Results are presented in the usual δ notation relative to PDB belemnite and atmospheric N_2 (Air) for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (albumin, keratin) indicate measurement errors of $\pm 0{\cdot}1$‰ and $\pm 0{\cdot}3$‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

STATISTICS

Data were analysed statistically using SYSTAT 9 for WINDOWS. Values are mean ± SD, significance at 0·05 level.

Results

SUMMER DIET

Analysis of food samples showed that king penguins fed more on fish than macaroni and rockhopper penguins (91·9, 6·5 and 23·8% by fresh mass, respectively), and that crested penguins were mainly crustacean eaters (90·7 and 64·8% for macaroni and rockhopper penguins, respectively). Cephalopods constituted a minor but significant proportion of the penguin diet (8·1, 2·8 and 11·5% for king, macaroni and rockhopper penguins, respectively).

Prey identification and quantification from scats and food samples showed two groups of predators with fur seals and king penguins being fish eaters (> 91% of the total number of prey items) and crested penguins preying upon crustaceans (84–98% by number). Four macrozooplanktonic species, including two euphausiids and two amphipods, formed the bulk of the food of crested penguins (Table 2). The two main differences between macaroni and rockhopper penguins were the relative importance of *Themisto gaudichaudii* and *Thysanoessa macrura/vicina* in their diet (45 vs. < 1%, and 8 vs. 30% by number, respectively). Fishes of the family Myctophidae were by far the dominant fish prey of all the five predators (94–99% of the total number of fish). *Krefftichthys anderssoni* was the main myctophid prey of penguins, forming, together with *Electrona carlsbergi* the staple food of king penguins (68 and 19% of the total number of prey, respectively). Fur seals were also myctophid eaters, but they primarily targeted species of the genus *Gymnoscopelus* (70–71% by number), *G. piabilis* being the main prey of Antarctic fur seals, and *G. fraseri* and *G. piabilis* the main prey of Subantarctic fur seals. Scats from Antarctic fur seals contained on average less otoliths (n = 23 vs. 39 per scat, respectively), which were more eroded (39 vs. 23% of the total number of sagitta), than those of Subantarctic fur seals.

Table 2. Main prey species (> 1% by number for at least one predator) of fur seals and penguins from Crozet Islands in summer

Prey species	Antarctic fur seal $N = 36$ *n* (%)	Subantarctic fur seal $N = 39$ *n* (%)	King penguin $N = 10$ *n* (%)	Macaroni penguin $N = 10$ *n* (%)	Rockhopper penguin $N = 10$ *n* (%)
Crustaceans	0·0	1·4	0·0	97·9	84·1
Euphausiacea					
Euphausia vallentini				27·9	25·7
Thysanoessa macrura/vicina				8·5	29·7
Decapoda					
Nauticaris marionis		1·4		< 1	1·2
Amphipoda					
Themisto gaudichaudii				45·4	< 1
Primno macropa				16·1	26·5
Fish	91·8	94·4	97·6	1·9	11·8
Myctophidae					
Electrona carlsbergi	1·8	< 1	19·1		
Electrona subaspera	3·8	5·4			
Gymnoscopelus fraseri	10·3	28·6			
Gymnoscopelus nicholsi	9·4	4·4	< 1	< 1	
Gymnoscopelus piabilis	26·9	26·4			
Gymnoscopelus sp. (eroded otoliths)	24·2	10·4			
Krefftichthys anderssoni	< 1	< 1	68·2	1·8	11·2
Metelectrona ventralis	1·8	3·3	1·0		
Protomyctophum choriodon	< 1	1·2		< 1	
Protomyctophum tenisoni	< 1	1·0	6·9	< 1	
Myctophidae sp. (eroded otoliths)	11·2	10·0			
Osteichthyes sp. (eroded otoliths)	< 1	1·2			< 1
Cephalopods	8·2	4·2	2·4	0·2	3·9
Gonatidae					
Gonatus antarcticus	< 1		< 1	< 1	1·5
Brachioteuthidae					
Slosarczykovia circumantarctica	7·0	3·7	< 1		
Oegopsida sp. (unidentified).	< 1	< 1	< 1	< 1	1·7
Others	0·0	0·0	0·0	0·0	0·2
Total (*n*)	913	1606	576	27061	5752

N, number of scats and stomach contents of fur seals and penguins, respectively.

When feeding on the same prey species, the myctophids *G. piabilis* and *G. fraseri*, Antarctic and Subantarctic fur seals caught individuals of the same size classes (SL: 132 ± 10 and 130 ± 8 mm, and 83 ± 6 and 82 ± 6 mm, respectively). On the other hand, king penguins targeted larger individuals of *K. anderssoni* (no clear mode, range: 31–57 mm SL) than crested penguins (mode at 10 mm SL) (Fig. 1). Macaroni and rockhopper penguins preyed upon the same size of *Primno macropa* (mode at 15 mm TL, Kolmogorov–Smirnov test, $P = 0{\cdot}812$), different sizes of *T. macrura/vicina* ($P < 0{\cdot}0001$) and two size classes of the Subantarctic krill *Euphausia vallentini* (modes at 15 and 23 mm TL). Macaroni penguins, however, fed more on the larger size class of *E. vallentini* and rockhopper penguins on the smaller one ($P < 0{\cdot}0001$).

STABLE ISOTOPES

Penguins in summer. Within each penguin species, summer food samples and tissues differed in univariate analysis by both $\delta^{13}C$ and $\delta^{15}N$ values (ANOVA, king penguin: $F_{3,36} = 36{\cdot}83$ and 89·07, macaroni penguin: $F_{3,36} = 36{\cdot}06$ and 406·73, rockhopper penguin: $F_{3,34} = 45{\cdot}59$ and 42·95 for $\delta^{13}C$ and $\delta^{15}N$ values, respectively, all $P < 0{\cdot}0001$). Stable-carbon isotope values were almost identical among food samples and blood of adults and chicks, but adult nails were consistently more enriched in ^{13}C than food and blood (*post hoc* Tukey Honest Significant Difference multiple comparison tests, all $P \leq 0{\cdot}001$). Stable-nitrogen isotope values were almost identical among bird tissues, but, as expected, food was always depleted in ^{15}N when compared with blood and nails (all $P < 0{\cdot}0001$) (Fig. 2).

Penguin species were segregated by both $\delta^{13}C$ (ANOVA, $F_{5,51} = 50{\cdot}61$, $P < 0{\cdot}0001$) and $\delta^{15}N$ values of chick food and blood ($F_{5,51} = 356{\cdot}80$, $P < 0{\cdot}0001$). King penguins differed from crested penguins in $\delta^{13}C$ values (all $P < 0{\cdot}0001$), while those of macaroni and rockhopper penguin food and blood were similar. $\delta^{15}N$ values of chick blood showed differences between the three penguin species, and, interestingly, king penguin food and macaroni penguin blood had identical $\delta^{15}N$ values

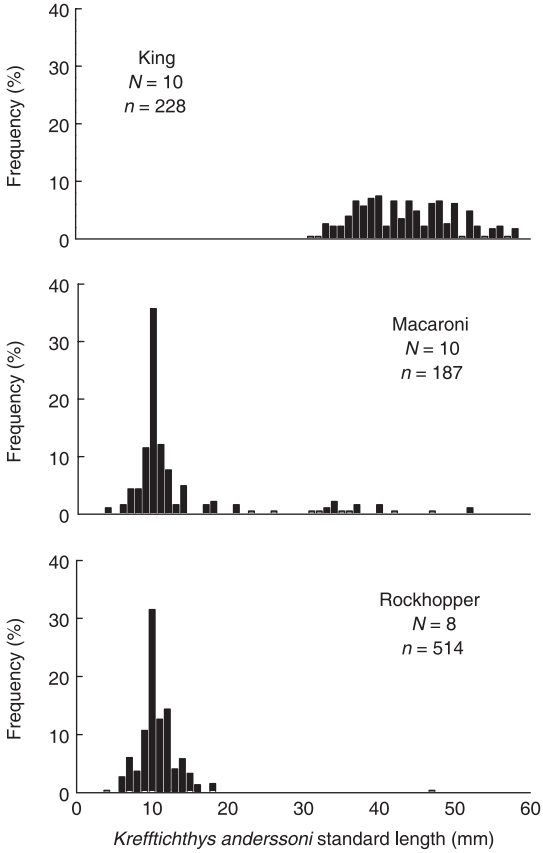

Fig. 1. Length-frequency distribution of the myctophid fish *Krefftichthys anderssoni* in the diet of penguins from Crozet Islands in summer. *N*, number of food samples; *n*, number of measured otoliths. Kolmogorov–Smirnov test, $P < 0{\cdot}0001$ between king and crested penguins, and $P = 0{\cdot}011$ between macaroni and rockhopper penguins.

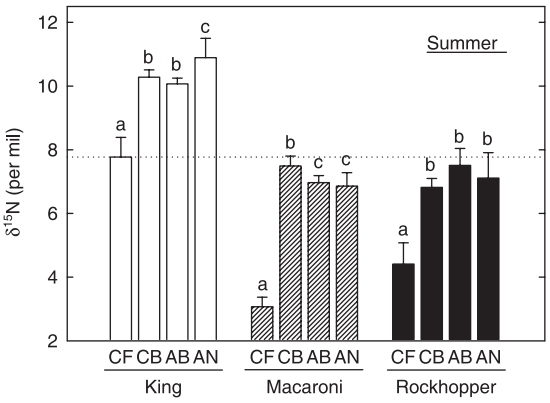

Fig. 2. Stable isotopic ratios of nitrogen ($\delta^{15}N$) of penguins from Crozet Islands in summer. CF, chick food; CB; chick blood; AB, adult blood; AN, adult nails. Within each penguin species, values not sharing the same superscript letter are significantly different. Dotted line illustrates the identical trophic level of king penguin food and crested penguins (see text).

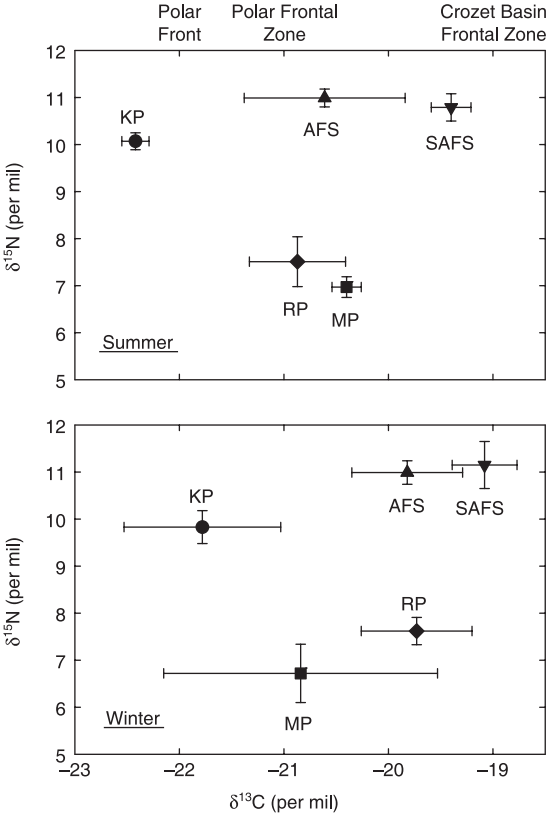

Fig. 3. Stable isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) for blood of adult penguins and female fur seals from Crozet Islands in summer (upper panel) and winter (lower panel). Estimated foraging zones are indicated above the upper panel. AFS, Antarctic fur seal; KP, king penguin; MP, macaroni penguin; RP, Rockhopper penguin; SAFS, Subantarctic fur seal.

(Fig. 2). Penguins were also segregated by their $\delta^{13}C$ (ANOVA, $F_{2,25} = 40{\cdot}56$, $P < 0{\cdot}0001$) and $\delta^{15}N$ values of adult nails ($F_{2,25} = 121{\cdot}79$, $P < 0{\cdot}0001$). King penguins had lower and higher $\delta^{13}C$ and $\delta^{15}N$ values, respectively, than crested penguins (all $P < 0{\cdot}0001$), while macaroni and rockhopper penguins had identical nail isotopic signature.

Community in summer and winter. In summer, sympatric adult penguins and female fur seals differed by their overall isotopic signatures (MANOVA, Wilks' lambda, $F_{8,90} = 158{\cdot}85$, $P < 0{\cdot}0001$) and, in univariate analysis, both $\delta^{13}C$ (ANOVA, $F_{4,46} = 67{\cdot}32$, $P < 0{\cdot}0001$) and $\delta^{15}N$ blood values ($F_{4,46} = 368{\cdot}06$, $P < 0{\cdot}0001$). King penguins had significantly lower and Subantarctic fur seals had significantly higher $\delta^{13}C$ values than crested penguins and Antarctic fur seals, respectively, with no differences between the latter three species. All $\delta^{15}N$ values were significantly different among species, except between the Antarctic and Subantarctic fur seals (Fig. 3).

The structure of the community in winter was overall the same as in summer, with the five species segregating by both their $\delta^{13}C$ (ANOVA, $F_{4,51} = 11{\cdot}63$, $P < 0{\cdot}0001$) and $\delta^{15}N$ values ($F_{4,51} = 227{\cdot}45$, $P < 0{\cdot}0001$). Again, all $\delta^{15}N$ values were significantly different among species, except between the Antarctic and Subantarctic fur seals. Winter $\delta^{13}C$ values of the community also showed the same trend as in summer with king penguins and Subantarctic fur seals having the lowest and highest values, respectively. However, due to overall larger variances in winter than in summer, winter $\delta^{13}C$ values overlapped between species during the nonbreeding season with, for example, no significant differences

between the $\delta^{13}C$ values of rockhopper penguin and the two fur seal species (Fig. 3).

Seasonal variations in $\delta^{13}C$ and $\delta^{15}N$ values within each species showed either moderate or low changes, ranging between 0·3 and 1·1‰, and between 0·0 and 0·4‰, respectively (Table 1). Stable-carbon isotope values in summer and winter were similar for macaroni penguins, marginally different for Subantarctic and Antarctic fur seals and for king penguins (U = 8·5, 19·5 and 14·5, P = 0·043, 0·012 and 0·007, respectively), and they were highly significantly different for rockhopper penguins (U = 4·0, $P < 0·0001$). Seasonal $\delta^{15}N$ values were similar within each species, except for the king penguin (Mann–Whitney, U = 81·5, P = 0·017).

As the stable isotopic signatures of macaroni penguins suggested gender-related feeding strategies in the southern Atlantic (Bearhop *et al.* 2006), we looked at such potential differences in birds from Crozet Islands during the nonbreeding season. At the latter locality, male and female macaroni penguins were not segregated by their overall isotopic signatures in winter (MANOVA, Wilks' lambda, $F_{2,17}$ = 2·19, P = 0·142). The large variance in their $\delta^{13}C$ values, however, suggested individual specialization within the population (Fig. 3). Indeed, individual $\delta^{13}C$ values can be grouped in a continuum from –21·4 to –18·9‰ together with a cluster of five birds that showed lower values (–22·7 ± 0·1 vs. –20·2 ± 0·8‰, U = 75·0, P = 0·001). Interestingly, these individuals (including two males and three females) also had higher $\delta^{15}N$ values than the others (7·5 ± 0·4 vs. 6·5 ± 0·4‰, U = 3·0, P = 0·003) (Fig. 4).

Fur seals in winter. Female and male Subantarctic fur seals did not segregate by their isotopic signatures in winter. On the other hand, female and male Antarctic fur seals had different signatures with males showing very large variances in both $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 4). Male Antarctic fur seals can be split into three distinct groups according to their $\delta^{13}C$ values (n = 3, 5 and 3, –25·5 ± 0·2, –21·2 ± 1·0 and –19·0 ± 0·2, respectively, Kruskal–Wallis, H = 8·73, P = 0·013), the three groups also having different $\delta^{15}N$ values (9·3 ± 0·6, 11·9 ± 0·6 and 12·7 ± 0·2, respectively, H = 8·73, P = 0·013). Interestingly, the group of males with the lowest $\delta^{13}C$ values had an identical signature than Adélie penguins, but fur seals and penguins segregated by their $\delta^{15}N$ values (Mann–Whitney, U = 30·0, P = 0·011).

Females of the two fur seal species segregated by both their $\delta^{13}C$ and $\delta^{15}N$ values in winter (U = 0·00 and 50·0, both P = 0·002). When presumably foraging in the same wintering area (i.e. when they had the same $\delta^{13}C$ values), male Antarctic fur seals had higher $\delta^{15}N$ values than male Subantarctic fur seals (U = 15·0, P = 0·024) (Fig. 4).

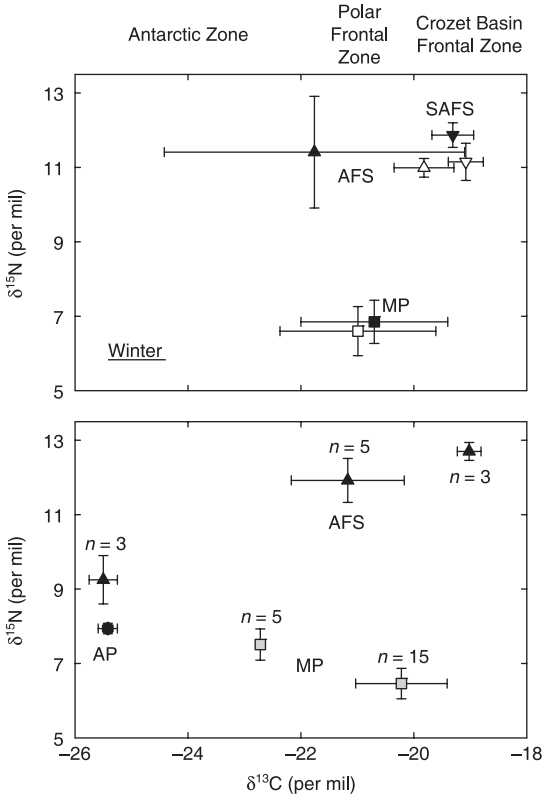

Fig. 4. Stable isotopic ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) for blood of females (open symbols) and males (filled symbols) of macaroni penguins and fur seals from Crozet Islands in winter (upper panel), and of groups (see text) of macaroni penguins and male Antarctic fur seals in winter (lower panel). Estimated foraging zones are indicated above the upper panel. The winter signature of Adélie penguins (AP) from Adélie Land illustrates the $\delta^{13}C$ values of a species known to live in Antarctica all year long. AFS, Antarctic fur seal; MP, macaroni penguin; SAFS, Subantarctic fur seal.

Discussion

To our knowledge, this study is the first to use the stable isotope method to investigate the feeding ecology of a guild of large air-breathing marine predators in winter (but see Ainley, Ribic & Fraser 1992). The isotopic signature of whole blood provided dietary information during the pre-breeding period corresponding to the late winter months. Blood has also the advantage to allow a comparison between sympatric diving seabirds and marine mammals, an issue that was rarely investigated in the past (Croxall, Reid & Prince 1999).

SEGREGATION IN SUMMER

The summer isotopic signature of adult penguins and female fur seals indicated a strong trophic segregation between the five species breeding sympatrically at the Crozet Islands. Blood $\delta^{13}C$ and $\delta^{15}N$ values defined three foraging areas and two trophic levels, respectively, thus allowing characterization of four distinct and nonoverlapping trophic niches. Importantly, due to the temporal integration of whole blood, the isotopic signatures indicated that this trophic structure occurred over the long term (spring and summer). Prey determination from penguin stomach contents and fur seal scats were in agreement with two distinct trophic levels,

with king penguin and the two species of fur seals preying upon myctophid fishes, and macaroni and rockhopper penguins feeding mainly on crustaceans. Myctophids are also crustacean eaters (Pakhomov, Perissinotto & McQuaid 1996; Gaskett *et al*. 2001) and they consequently occupy the same trophic level as crested penguins, thus explaining why king penguin food samples and macaroni and rockhopper penguin tissues had identical $\delta^{15}N$ values.

The main segregating mechanism between the three species of myctophid consumers operate at the spatial scale with each predator foraging in a distinct zone. Using latitudinal variations in $\delta^{13}C$ values of marine organisms in the Southern Ocean (Quillfeldt *et al*. 2005; Cherel & Hobson 2007), our data indicate a spatial gradient from the southern and colder foraging zone of king penguins to the northern and warmer feeding areas of female Subantarctic fur seals. These results are in general agreement with animals satellite-tracked over different summers. Breeding king penguins forage in the south of Crozet Islands where they reach the Polar Front (Bost *et al*. 1997), female Antarctic fur seals in oceanic waters in the vicinity of the archipelago, and Subantarctic fur seals further north (Bailleul *et al*. 2005). Separation of trophic niches also includes other temporal and dietary mechanisms. King penguins are diurnal deep divers feeding on small- and medium-sized myctophids (Cherel & Ridoux 1992; Kooyman *et al*. 1992; this study), while both species of fur seals are night-time shallow divers preying upon larger fish (Robinson *et al*. 2002; this study). Female Antarctic fur seals furthermore dive at shallower depths and have longer foraging trips than Subantarctic fur seals (Bailleul *et al*. 2005; Luque *et al*. unpublished data), which is in agreement with fewer and more eroded otoliths found in Antarctic than in Subantarctic fur seal scats.

Unlike fur seal species, the congeneric macaroni and rockhopper penguins had identical mean $\delta^{13}C$ and $\delta^{15}N$ values, thus suggesting a substantial overlap in their trophic niches in summer. Indeed, at other Subantarctic localities including Macquarie Island (where macaroni penguin is replaced with royal penguin), the two sympatric species overall forage in the same regions of the Polar Frontal Zone (Hull 1999), dive at the same depths (Hull 2000) and feed on the same prey (Cooper *et al*. 1990). More subtle segregating mechanisms however, take place, with a tendency for macaroni/royal penguins to forage further offshore (Hull 1999) and to feed more on fish (Cooper *et al*. 1990). Our data are in agreement with such mechanisms, with the two species feeding on the same prey, but in different proportions, and on different size classes of the Subantarctic krill *Euphausia vallentini*.

Previous investigations on dietary differentiation in Subantarctic penguin communities indicated clear separation between king and crested penguins and considerable similarity between the congeneric species pair (Ridoux *et al*. 1988; Adams & Brown 1989; Hindell *et al*. 1995). Our snapshot data on chick food were in agreement with this dietary segregation, and the $\delta^{15}N$ values of chick blood confirmed this and extended it to the whole chick-rearing period. However, food analyses were restricted to the chick diet only, with no information available on the feeding ecology of the adults during and outside the chick-rearing period. The stable isotope analysis of adult tissues filled that gap, indicating that the same differentiation also operated for adult birds. Within each penguin species, the $\delta^{13}C$ and $\delta^{15}N$ values of chick blood and those of adult blood and nails were essentially similar, suggesting that adults fed for themselves in the same area/water mass and on the same prey as those given to their chicks.

SEGREGATION IN WINTER AND INDIVIDUAL SPECIALIZATION

The guild of adult penguins and female fur seals essentially shows the same trophic structure in winter and summer. Again, two distinct trophic levels with no intermediary values segregate king penguins and fur seals from crested penguins. When compared with the dietary habits and the stable isotopic signature of the animals in summer, the most parsimonious explanation is that each predator species consumes the same prey all year round, with no important seasonal dietary shifts. However, a major seasonal difference was the larger variances in $\delta^{13}C$ (and also to a lesser extent in $\delta^{15}N$) values in winter than in summer, thus verifying our hypothesis that trophic niches widen in winter. At that time, adult penguins and female fur seals are no longer central place foragers constrained by their terrestrial breeding sites, and they have thus the potential to disperse over wide oceanic areas. Dispersion did not occur randomly, however, and, even if winter foraging zones overlapped between species, each predator had its own strategy. Interestingly, no very negative and positive $\delta^{13}C$ values indicative of foraging in Antarctic and subtropical waters, respectively, were found. The data therefore suggest that most penguins and female fur seals remain in waters of the Polar Frontal Zone and the Crozet Basin Frontal Zone all year long (but see below). This strategy contrasts with the wintering habits of Subantarctic petrels and albatrosses showing a wide latitudinal gradient of species moulting from Antarctic to subtropical waters (Cherel *et al*. 2000, 2006).

At the species level, our data add substantial information on the feeding ecology of penguins and fur seals and raise new questions about their winter biology. First, while satellite-tracking shows that breeding king penguins reach the distant Antarctic ice zone in winter (Bost *et al*. 2004), $\delta^{13}C$ values of moulting birds suggest that nonbreeding penguins remain in the vicinity of the Polar Front and in the Polar Frontal Zone at that time. Different wintering strategies for breeding and nonbreeding individuals thus merit further investigation using, for example, geolocation tags (Croxall *et al*. 2005).

Second, only one species, the rockhopper penguin, showed different $\delta^{13}C$ values in winter and summer, suggesting that birds shifted from Crozet waters to slightly lower latitudes during the interbreeding period. Almost no rockhopper penguins were seen in the south-western Indian Ocean in winter, but the few observations of birds of unknown status are in agreement with our findings and suggested that rockhoppers winter in the vicinity of the Subantarctic Front (Stahl *et al*. unpublished data). Third, macaroni penguins showed a large variance in their $\delta^{13}C$ values, indicating interindividual differences in their wintering foraging zone (Fig. 3). According to these values, most birds disperse north of the archipelago, which is in agreement with the few penguins observed at sea from Crozet waters towards the Subantarctic Front in winter (Stahl *et al*. unpublished data). Some of the macaroni penguins follow another distinct strategy, their negative $\delta^{13}C$ values (identical to that of the king penguin in summer) and higher $\delta^{15}N$ values suggesting wintering in colder waters where they fed more on fish.

In agreement with penguin data, the isotopic signature of female fur seals was essentially similar in winter and summer, both species showing identical trophic levels (based on $\delta^{15}N$ values) and a slight overlap in their wintering foraging zones ($\delta^{13}C$). Unlike females, almost nothing is known on the food and feeding ecology of adult male fur seals (Green 1997; Boyd *et al*. 1998). Breeding males are present and fast in the colony at the beginning of the reproductive cycle. They therefore retain the isotopic signature of their winter diet and foraging grounds, where they build up energy reserves. Within that context, it is noticeable that females and males of the Subantarctic fur seal had identical $\delta^{15}N$ and $\delta^{13}C$ values suggesting that both sexes fed on myctophids and foraged in warm waters in winter.

Stable-carbon and nitrogen isotopic signatures of fur seals showed relatively small variances, reflecting limited interindividual variation within each group. A major exception was breeding male Antarctic fur seals where individuals showed a remarkable range in their $\delta^{13}C$ values reflecting a wide latitudinal gradient, from Antarctica to the Crozet Basin Frontal Zone north of the archipelago. Using stable isotopes, such striking within-population variation in water mass utilization during the nonbreeding period was previously described in only one seabird species, the small planktivorous common diving petrel at Kerguelen (Cherel *et al*. 2006). When foraging in Antarctica, male Antarctic fur seals moreover showed lower $\delta^{15}N$ values, indicating feeding at a lower trophic level. The most likely explanation is that they fed not only on myctophids, but also on Antarctic krill, which is known to form the staple food of the species in Antarctic waters (Casaux *et al*. 2003). Interestingly also, when foraging in warm waters, male Antarctic fur seals had a significantly higher $\delta^{15}N$ values than male Subantarctic fur seals, indicating dietary differences in the male trophic niches during the winter months.

Conclusions

We have demonstrated how the food and feeding ecology of marine predators during the nonbreeding period can be determined using stable isotope ratios coupled with the traditional method of food analysis. Within the guild of Subantarctic penguins and fur seals, segregation in summer occurs primarily through different foraging areas and trophic levels, and secondarily through the consumption of different prey species and prey size.

A first major finding was that the trophic structure of the guild was almost identical in summer and winter, the main difference being a widening of the species trophic niches in winter. This finding has a number of implications on the functioning of the pelagic ecosystem, and on the demography of the species. A general assumption (almost never tested) when quantifying the impact of seabirds and pinnipeds on marine resources is to consider that summer chick food and female diet, respectively, correspond to adult prey over the whole annual cycle. Our data verify that assumption on penguins and fur seals and will help to quantify seasonal fluxes of matter and energy within the pelagic ecosystem of the Southern Ocean. Delineating winter foraging ecology is also a first and crucial step to disentangle causal mechanisms between extrinsic and intrinsic factors in the regulation of population parameters, including survival rate and body condition, all being primarily affected by winter changes in the marine environment.

A second major finding was the wide trophic niche of wintering macaroni penguins and male Antarctic fur seals. Several questions arise from these findings. First, do individual specializations occur over one winter or is it consistent over years? There is direct and indirect evidence that individual seabirds and marine mammals exploit the same staging areas in succeeding winters (Bradshaw *et al*. 2004; Croxall *et al*. 2005) but this requires further investigation. Second, is specialization related to individual quality or not? During the breeding period, specialization can influence individual reproductive output (Annett & Pierotti 1999; Golet *et al*. 2000). During the nonbreeding period, however, nothing is known on the consequences of individual foraging specialization on life-history traits and individual fitness of seabirds and fur seals. Finally, population models generally assumed that all individuals within a population are affected in the same way and to the same extent by environmental changes. Further modelling is therefore needed in order to investigate the effect of specialization on population dynamics and this has important implications in biological conservation (Durell 2000).

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References

Adams, N.J. & Brown, C.R. (1989) Dietary differentiation and trophic relationships in the sub-antarctic penguin community at Marion Island. *Marine Ecology Progress Series*, **57**, 249–258.

Ainley, D.G., Ribic, C.A. & Fraser, W.R. (1992) Does prey preference affect habitat choice in Antarctic seabirds? *Marine Ecology Progress Series*, **90**, 207–221.

Annett, C. & Pierotti, R. (1999) Long-term reproductive output in western gulls: consequences of alternative tactics in diet choice. *Ecology*, **80**, 288–297.

Bailleul, F., Luque, S., Dubroca, L., Arnould, J.P.Y. & Guinet, C. (2005) Differences in foraging strategy and maternal behaviour between two sympatric fur seal species at the Crozet Islands. *Marine Ecology Progress Series*, **293**, 273–282.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A. & MacLeod, H. (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology*, **73**, 1007–1012.

Bearhop, S., Phillips, R.A., McGill, R., Cherel, Y., Dawson, D.A. & Croxall, J.P. (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Marine Ecology Progress Series*, **311**, 157–164.

Bost, C.A., Georges, J.Y., Guinet, C., Cherel, Y., Pütz, K., Charrassin, J.B., Handrich, Y., Zorn, T., Lage, J. & Le Maho, Y. (1997) Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Marine Ecology Progress Series*, **150**, 21–33.

Bost, C.A., Charrassin, J.B., Clerquin, Y., Ropert-Coudert, Y. & Le Maho, Y. (2004) Exploitation of distant marginal ice zones by king penguins during winter. *Marine Ecology Progress Series*, **283**, 293–297.

Boyd, I.L., Croxall, J.P., Lunn, N.J. & Reid, K. (1995) Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. *Journal of Animal Ecology*, **64**, 505–518.

Boyd, I.L., McCafferty, D.J., Reid, K., Taylor, R. & Walker, T.R. (1998) Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Canadian Journal of Aquatic Sciences*, **55**, 845–852.

Boyd, I.L., Staniland, I.J. & Martin, A.R. (2002) Distribution of foraging by female Antarctic fur seals. *Marine Ecology Progress Series*, **242**, 285–294.

Bradshaw, C.J.A., Hindell, M.A., Sumner, M.D. & Michael, K.J. (2004) Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour*, **68**, 1349–1360.

de Brooke, M.L. (2004) The food consumption of the world's seabirds. *Proceedings of the Royal Society B Suppl.*, **271**, S246–S248.

Carleton, S.A. & Martinez del Rio, C. (2005) The effect of cold-induced increased metabolic rate on the rate of ^{13}C and ^{15}N incorporation in house sparrows (*Passer domesticus*). *Oecologia*, **144**, 226–232.

Casaux, R., Baroni, A., Arrighetti, F. & Ramon, A. (2003) Geographical variation in the diet of the Antarctic fur seal *Arctocephalus gazella*. *Polar Biology*, **26**, 753–758.

Cherel, Y., Guinet, C. & Tremblay, Y. (1997) Fish prey of Antarctic fur seals *Arctocephalus gazella* at Ile de Croy, Kerguelen. *Polar Biology*, **17**, 87–90.

Cherel, Y. & Hobson, K.A. (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series*, **329**, 281–287.

Cherel, Y. & Ridoux, V. (1992) Prey species and nutritive value of food fed during summer to king penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *Ibis*, **134**, 118–127.

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

Cherel, Y., Hobson, K.A., Bailleul, F. & Groscolas, R. (2005a) Nutrition, physiology, and stable isotopes: new information from fasting and molting penguins. *Ecology*, **86**, 2881–2888.

Cherel, Y., Hobson, K.A. & Hassani, S. (2005b) Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. *Physiological and Biochemical Zoology*, **78**, 106–115.

Cherel, Y., Phillips, R.A., Hobson, K.A. & McGill, R. (2006) Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters*, **2**, 301–303.

Cooper, J., Brown, C.R., Gales, R.P., Hindell, M.A., Klages, N.T.W., Moors, P.J., Pemberton, D., Ridoux, V., Thompson, K.R. & Van Heezik, Y.M. (1990) Diets and dietary segregation of crested penguins (*Eudyptes*). *Penguin Biology* (eds L.S. Davis & J.T. Darby), pp. 131–156. Academic Press Inc., San Diego, CA.

Croxall, J.P., Prince, P.A. & Reid, K. (1997) Dietary segregation of krill-eating South Georgia seabirds. *Journal of Zoology*, **242**, 531–556.

Croxall, J.P., Reid, K. & Prince, P.A. (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series*, **177**, 115–131.

Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V. & Briggs, D.R. (2005) Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science*, **307**, 249–250.

Dalerum, F. & Angerbjörn, A. (2005) Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia*, **144**, 647–658.

Durell, S.E.A. Le V. dit (2000) Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biological Reviews*, **75**, 503–518.

Gaskett, A.C., Bulman, C., He, X. & Goldsworthy, S.D. (2001) Diet composition and guild structure of mesopelagic and bathypelagic fishes near Macquarie Island, Australia. *New Zealand Journal of Marine and Freshwater Research*, **35**, 469–476.

Golet, G.H., Kuletz, K.J., Roby, D.D. & Irons, D.B. (2000) Adult prey choice affects chick growth and reproductive success in pigeon guillemots. *Auk*, **117**, 82–91.

Green, K. (1997) Diving behaviour of Antarctic fur seals *Arctocephalus gazella* Peters around Heard Island. *Marine Mammal Research in the Southern Hemisphere*, **1**, 97–104.

Green, J.A., Boyd, I.L., Woakes, A.J., Warren, N.L. & Butler, P.J. (2005) Behavioural flexibility during year-round foraging in macaroni penguins. *Marine Ecology Progress Series*, **296**, 183–196.

Grosbois, V. & Thompson, P.M. (2005) North Atlantic climate variation influences survival in adult fulmars. *Oikos*, **109**, 273–290.

Hindell, M.A., Robertson, G.G. & Williams, R. (1995) Resource partitioning in four species of sympatrically breeding penguins. *The Penguins* (eds P. Dann, I. Norman & P. Reilly), pp. 196–215. Surrey Beatty & Sons, Chipping Norton, NSW.

Hobson, K.A., Gibbs, H.L. & Gloutney, M.L. (1997) Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotope analysis. *Canadian Journal of Zoology*, **75**, 1720–1723.

Hobson, K.A., Piatt, J.F. & Pitocchelli, J. (1994) Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology*, **63**, 786–798.

Hull, C.L. (1999) The foraging zones of breeding royal (*Eudyptes schlegeli*) and rockhopper (*E. chrysocome*) penguins: an assessment of techniques and species comparison. *Wildlife Research*, **26**, 789–803.

Hull, C.L. (2000) Comparative diving behaviour and segregation of the marine habitat by breeding royal penguins, *Eudyptes schlegeli*, and eastern rockhopper penguins, *E. chrysocome filholi*, at Macquarie Island. *Canadian Journal of Zoology*, **78**, 333–345.

Jenouvrier, S., Barbraud, C. & Weimerskirch, H. (2006) Sea ice affects the population dynamics of Adélie penguins in Terre Adélie. *Polar Biology*, **29**, 413–423.

Karnovsky, N.J., Hobson, K.A., Iverson, S., Hunt, G.L. Jr & Spear, L.B. (2007) Seasonal changes in food habits of seabirds in the North Water Polynya: a multiple-indicator approach using stomach content, stable isotope and fatty acid analyses. *Marine Ecology Progress Series*, in press.

Kelly, J.F. (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, **78**, 1–27.

Kooyman, G.L., Cherel, Y., Le Maho, Y., Croxall, J.P., Thorson, P.H., Ridoux, V. & Kooyman, C.A. (1992) Diving behavior and energetics during foraging cycles in king penguins. *Ecological Monographs*, **62**, 143–163.

McCutchan, J.H., Lewis, W.M., Kendall, C. & McGrath, C.C. (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos*, **102**, 378–390.

Pakhomov, E.A., Perissinotto, R. & McQuaid, C.D. (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Marine Ecology Progress Series*, **134**, 1–14.

Park, Y.H. & Gambéroni, L. (1997) Cross-frontal exchange of Antarctic Intermediate Water and Antarctic Bottom Water in the Crozet Basin. *Deep-Sea Research*, **II** (**44**), 963–986.

Quillfeldt, P., McGill, R.A.R. & Furness, R.W. (2005) Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Marine Ecology Progress Series*, **295**, 295–304.

Ridoux, V. (1994) The diets and dietary segregation of seabirds at the Subantarctic Crozet Islands. *Marine Ornithology*, **22**, 1–192.

Ridoux, V., Jouventin, P., Stahl, J.C. & Weimerskirch, H. (1988) Ecologie alimentaire comparée des manchots nicheurs aux Iles Crozet. *Revue d'Ecologie (Terre Vie)*, **43**, 345–355.

Robinson, S.A., Goldsworthy, S.G., van den Hoff, J. & Hindell, M.A. (2002) The foraging ecology of two sympatric fur seal species, *Arctocephalus gazella* and *Arctocephalus tropicalis*, at Macquarie Island during the austral summer. *Marine and Freshwater Research*, **53**, 1071–1082.

Saether, B.E., Sutherland, W.J. & Engen, S. (2004) Climate influences on avian population dynamics. *Advances in Ecological Research*, **35**, 185–209.

Sandvik, H., Erikstad, K.E., Barrett, R. & Yoccoz, N.G. (2005) The effect of climate on adult survival in five species of North Atlantic seabirds. *Journal of Animal Ecology*, **74**, 817–831.

Tremblay, Y. & Cherel, Y. (2003) Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. *Marine Ecology Progress Series*, **251**, 279–297.

Van Franeker, J.A., Bathmann, U.V. & Mathot, S. (1997) Carbon fluxes to Antarctic top predators. *Deep-Sea Research*, **II** (**44**), 435–455.

Vanderklift, A. & Ponsard, S. (2003) Sources of variation in consumer-diet $\delta^{15}N$ enrichments: a meta-analysis. *Oecologia*, **136**, 169–182.

Williams, R. & McEldowney, A. (1990) A guide to the fish otoliths from waters off the Australian Antarctic Territory, Heard and Macquarie Islands. *ANARE Research Notes*, **75**, 1–173.

Woehler, E.J. (1993) *The Distribution and Abundance of Antarctic and Subantarctic Penguins*. Scientific Committee on Antarctic Research, Scott Polar Research Institute, Cambridge.

Woehler, E.J. (1995) Consumption of Southern Ocean marine resources by penguins. *The Penguins* (eds P. Dann, I. Norman & P. Reilly), pp. 266–294. Surrey Beatty & Sons, Chipping Norton, NSW.

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