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ORIGINAL PAPER

# Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica

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**Abstract** The emperor and Adélie penguins are the only two species of penguins that co-occur at high-Antarctic latitudes. We first measured and compared their isotopic niches on the same year in Adélie Land in spring, when the two species co-exist. Emperor and Adélie penguins segregated by their blood isotopic signatures, with adult $\delta^{13}$C values ($-24.5 \pm 0.2$ and $-25.4 \pm 0.2$‰, respectively) suggesting that emperor penguins foraged in more neritic waters than Adélie penguins in spring. At that time, difference in their $\delta^{15}$N values (4.1‰, $12.0 \pm 0.4$ vs. $7.9 \pm 0.1$‰) encompassed more than one trophic level, indicating that emperor penguins preyed mainly upon fish (and squids), while Adélie penguins fed exclusively on euphausiids. Second, we compared the food of breeding adults and chicks. The isotopic signatures of adults and chicks of emperor penguins were not statistically different, but $\delta^{15}$N value of Adélie penguin chicks was higher than that of adults ($10.2 \pm 0.8$ vs. $9.0 \pm 0.2$‰). The difference showed that adult Adélie penguins captured higher trophic level prey, i.e. higher-quality food, for their chicks. Third, the isotopic signatures of Adélie penguins breeding in Adélie Land showed that adults fed on Antarctic krill in oceanic waters in spring and shifted to neritic waters in summer where they preyed upon ice krill for themselves and upon fish and euphausiids for their chicks. A comparison of isotopic niches revealed large overlaps in both blood $\delta^{13}$C and $\delta^{15}$N values within the community of Antarctic seabirds and pinnipeds. The continuum in $\delta^{15}$N values nevertheless encompassed more than one trophic level (5.2‰) from Adélie penguin and crabeater seal to the Weddell seal. Such a broad continuum emphasizes the fact that all Antarctic seabirds and marine mammals feed on varying proportions of a few crustacean (euphausiids) and fish (Antarctic silverfish) species that dominate the intermediate trophic levels of the pelagic neritic and oceanic ecosystems.

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## Introduction

The emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliae*) penguins are the only two species of penguins that live in Adélie Land, Antarctica (Micol and Jouventin 2001). They are arguably the two such species best adapted to polar existence, and are the only pair of penguins that co-occur at high polar latitudes. The food and feeding ecology of breeding emperor and Adélie penguins was heavily investigated over the past 15 years (Ainley 2002; Burns and Kooyman 2001), but, despite this long history of study, surprisingly little is known about the foraging ecology and habitat use where the two species co-exist in time and space. Emperor and Adélie penguins are winter and summer breeders, respectively, with temporal overlap in spring (October–November), when emperor penguins rear their chicks and Adélie penguins resume migration and begin their breeding cycle. The feeding habits of emperor penguins in spring are relatively well known (Kooyman and Kooyman 1995; Kirkwood and Robertson 1997; Zimmer et al. 2008), thus contrasting with the paucity of data available on the feeding ecology of Adélie penguins at that time. Most studies took place during summer when adult Adélie penguins are accessible and feed their chicks in the

colonies, and so give no indication on their feeding habits over the annual cycle.

Measuring the isotopic niche of animals can be a powerful alternative to the conventional means investigating various dimensions of their ecological niche (Newsome et al. 2007). The basic isotopic concept is that an animal's chemical composition is directly influenced by what it consumes. For example, consumers are enriched in $^{15}N$ relative to their food and consequently stable-nitrogen-isotope measurements ($^{15}N/^{14}N$, $\delta^{15}N$) serve as indicators of a consumer trophic position (Vanderklift and Ponsard 2003). By contrast, stable carbon signatures ($^{13}C/^{12}C$, $\delta^{13}C$) vary little along the food chain and, in the marine environment, $\delta^{13}C$ values are mainly used to indicate the foraging habitats of predators, including penguins (Cherel and Hobson 2007; Cherel et al. 2007). Surprisingly, no isotopic signature of emperor penguins is available in the scientific literature and only two studies detailed $\delta^{13}C$ values of nails and eggshells, not blood, of Adélie penguins (Ainley et al. 2003; Emslie and Patterson 2007).

The primary objective of this study was to define and compare the isotopic niches of emperor and Adélie penguins on the same year in Adélie Land, where the two species breed in significant numbers (Micol and Jouventin 2001). We focused in spring, during which the two species co-exist in time and space. Stable isotope analyses were also performed for chick food and prey to create a basis for the interpretation of the isotopic signatures of penguins within the pelagic ecosystem. The blood isotopic signatures of chicks were used first to check if breeding adults fed on the same prey as those given to their chicks, and second to help interpretation of blood $\delta^{15}N$ and $\delta^{13}C$ values of adult Adélie penguins in spring, because, as previously underlined, no dietary information is available at that time. Importantly, the stable isotope method is based on time-integrated assimilated food. Hence, the isotopic signature of blood was considered as representative of the isotopic niche of the penguins during the last months preceding sampling, thus contrasting with the snapshot method of collecting and analyzing food samples from stomach contents.

## Materials and methods

The study was carried out at Pointe Géologie Archipelago in Adélie Land, Antarctica. Emperor and Adélie penguins were studied within the same year (2002) during the chick-rearing period that took place in winter/spring and summer, respectively. Adélie penguins were also investigated in spring when they went back to the colonies for breeding after their winter migration. Eight to eleven randomly chosen individuals were blood-sampled for each group of penguins (Table 1). Due to temporal integration of whole blood in large birds, blood isotopic signature was considered as representative of penguin trophic niche during the last months at sea prior to sampling (Cherel et al. 2007), i.e. late winter for Adélie and emperor penguins that were sampled in spring, and summer for Adélie penguins sampled during the chick-rearing period. Samples from the same tissue were compared because it is the most straightforward approach to resolve temporal diet variation (Dalerum and Angerbjörn 2005) and to minimize the tissue effect on $\delta^{15}N$ and $\delta^{13}C$ values (Vanderklift and 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 venipuncture of a penguin flipper vein. Seventy-percent ethanol was then added to whole blood because storage in 70% ethanol does not alter the isotopic composition of tissues. Spontaneous vomits of emperor penguins ($n = 37$) were opportunistically collected on sea-ice in winter/spring, while food samples ($n = 10$) were collected from adult Adélie penguin rearing chicks in summer using the stomach lavage method. All samples were subsequently kept at −20°C until analysis.

In the laboratory, Adélie 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. Identification of prey relied almost totally on the examination of otoliths and bones for fish, chitinized beaks for cephalopods, and exoskeletons for crustaceans. Items were identified by comparison with material held in our own reference collection. Prey items were numbered in each stomach content. Food items were identified, but not numbered, in the numerous vomits of emperor penguins. Undigested and digested euphausiids, pieces of squid muscle and of digested fish items were collected from both Adélie and emperor penguin food samples for isotopic analysis.

Before analysis, whole blood, Adélie penguin food samples and penguin prey were dried in an oven at +60°C. Food samples and prey were ground to a fine powder and lipids were extracted using cyclohexane. The low lipid content of whole blood does not typically necessitate lipid extraction (Cherel et al. 2005b), as verified here by its consistently low C/N mass ratios (Table 1). Carbonates were removed from Adélie penguin food samples and euphausiids using 1 N HCl. Relative abundance of $^{13}C$ and $^{15}N$ were determined by continuous-flow isotope-ratio mass spectrometry. Results are presented in the usual $\delta$ notation relative to PDB and atmospheric $N_2$ (Air) for $\delta^{13}C$ and $\delta^{15}N$, respectively. Blood samples and prey samples were analyzed at the Department of Soil Science, University of

**Table 1** Stable isotopic signature and C/N ratio of whole blood and prey of penguins from Adélie Land

| Species and status | Sampling season | Tissue | *n* | $\delta^{13}$C (‰) | $\delta^{15}$N (‰) | C/N mass ratio |
|---|---|---|---|---|---|---|
| Emperor penguins (EP) | | | | | | |
| Breeding adults | Winter/Spring | Whole blood | 11 | −24.5 ± 0.2 | 12.0 ± 0.4 | 3.5 ± 0.1 |
| Chicks | Winter/Spring | Whole blood | 8 | −24.2 ± 0.3 | 12.4 ± 0.7 | 3.6 ± 0.1 |
| Prey | | | | | | |
| *Euphausia superba* | Winter/Spring | Whole body | 12 | −25.8 ± 0.4 | 5.5 ± 0.4 | 3.7 ± 0.1 |
| *Psychroteuthis glacialis* | Winter/Spring | Buccal mass | 10 | −25.0 ± 0.3 | 10.0 ± 0.7 | 3.6 ± 0.1 |
| *Pleuragramma antarcticum* | Winter/Spring | Pooled specimens | 5 | −24.7 ± 0.4 | 10.6 ± 0.3 | 3.8 ± 0.2 |
| Adélie penguins (AP) | | | | | | |
| Arriving males | Spring | Whole blood | 10 | −25.4 ± 0.2 | 7.9 ± 0.1 | 3.4 ± 0.1 |
| Breeding adults | Summer | Whole blood | 10 | −24.7 ± 0.3 | 9.0 ± 0.2 | 3.4 ± 0.1 |
| Chicks | Summer | Whole blood | 8 | −24.7 ± 0.3 | 10.2 ± 0.8 | 3.6 ± 0.1 |
| Prey | | | | | | |
| Adult stomach contents | Summer | Chick food | 10 | −24.4 ± 0.6 | 7.0 ± 1.2 | No data |
| *Euphausia crystallorophias* | Summer | Whole body | 10 | −25.4 ± 0.4 | 6.8 ± 0.7 | 4.0 ± 0.2 |
| *Euphausia superba* | Summer | Whole body | 10 | −25.4 ± 0.6 | 5.3 ± 0.5 | 3.8 ± 0.2 |

Values are means ± SD

Saskatchewan, Saskatoon (Canada), and at Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés, UMR 6217 du CNRS-IFREMER-ULR, L'Houmeau (France), respectively. Replicate measurements of internal laboratory standards (albumin and keratin, and acetanilide in Saskatoon and L'Houmeau, respectively) indicate measurement errors of <0.15 and <0.30‰ for $\delta^{13}$C and $\delta^{15}$N, respectively.

Various physiological and ecological processes may affect diet-tissue discrimination factors. In the present work, I used the $\delta^{15}$N discriminant factor ($\Delta^{15}$N) between diet and blood that was measured on captive penguins fed on a constant diet (Cherel et al. 2005b). $\Delta^{15}$N values do not differ between birds consuming fish, birds consuming invertebrates and mammals consuming fish (Robbins et al. 2005), and between penguins and phocid seals (Hobson et al. 1996; Lesage et al. 2002; Cherel et al. 2005b), thus allowing direct comparisons of the nitrogen signatures within and between these groups to investigate their respective trophic positions in the pelagic Antarctic ecosystem. Finally, I assumed that $\Delta^{15}$N values were identical between chicks and adult penguins, because firstly no experimental work tested the effect of growth per se on $\Delta^{15}$N in birds and mammals (but see Williams et al. 2007), and secondly modeling suggests that growing endotherms should show the same $\delta^{15}$N values as those of adults fed the same diet (Ponsard and Averbuch 1999).

Data were statistically analysed using SYSTAT 9 for WINDOWS (Wilkinson 1999). Values are means ± SD, significance at 0.05 level. The $\delta^{13}$C and $\delta^{15}$N values for penguin blood and prey were compared simultaneously using a multivariate analysis of variance (MANOVA) with the Wilk's lambda statistic. For each isotopic ratio ($\delta^{13}$C and $\delta^{15}$N), the effects of species (penguins and their prey) and period of collection were tested using analyses of variance (ANOVA). When significant differences were indicated, post hoc Tukey HSD multiple comparison tests were used to test for differences between pairs of values.

## Results

### Isotopic signature of penguins

Adélie and emperor penguins were segregated by their overall isotopic signatures (MANOVA, Wilk's lambda, $F_{8,82} = 41.38$, $P < 0.0001$) and, in univariate analysis, both $\delta^{13}$C (ANOVA, $F_{4,42} = 30.31$, $P < 0.0001$) and $\delta^{15}$N blood values ($F_{4,42} = 143.65$, $P < 0.0001$). Post hoc Tukey HSD multiple comparison tests indicated that adult Adélie penguins in spring had significantly lower $\delta^{13}$C values than emperor penguins and than Adélie penguins in summer (all $P < 0.0001$). Comparison tests showed that $\delta^{15}$N values of Adélie penguins were lower than those of emperor penguins, and that the three groups of Adélie penguins had different nitrogen signatures (all $P < 0.0001$) (Fig. 1). On the other hand, $\delta^{13}$C and $\delta^{15}$N values of adults and chicks of emperor penguins were not statistically different ($P = 0.118$ and 0.545, respectively).

### Penguin food

The food of Adélie penguin chicks was dominated by crustaceans that were found in all the samples and amounted to

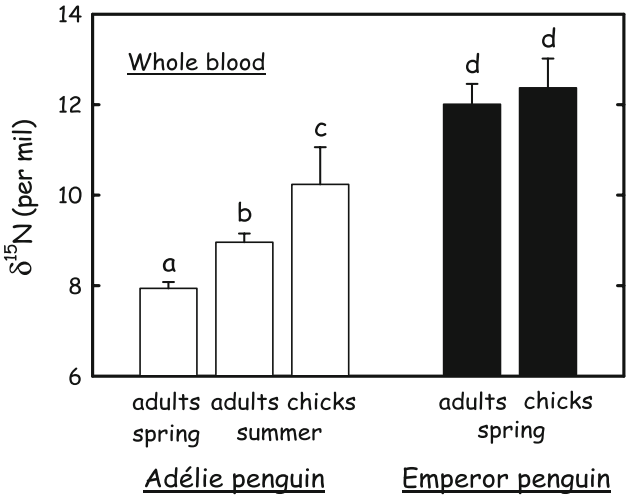


**Fig. 1** Stable nitrogen isotope values of Adélie and emperor penguins in Adélie Land, Antarctica, in spring and summer. Values are means ± SD. Values not sharing the same superscript letter are significantly different (ANOVA, $F_{4,42} = 143.65$, $P < 0.0001$, Post hoc Tukey HSD multiple comparison tests, all $P < 0.0001$)

93.6% of the diet by mass and 98.4% of the total number of prey. Fish ranked second (6.2 and 1.6% by mass and number, respectively) and squid was a minor dietary component (0.1 and <0.1%). By far the main prey species was the ice krill *Euphausia crystallorophias* (93.9% by number), followed by Antarctic krill *E. superba* (4.4%) and unidentified juvenile channichthyid fish (1.2%). The only fish and squid items that were identified to species level were Antarctic silverfish *Pleuragramma antarcticum* and *Psychroteuthis glacialis*, respectively.

Fresh preys of emperor penguins were not quantified in spontaneous regurgitations since they were opportunistically collected in the colony. The three main items identified were *E. superba* for crustaceans, *P. glacialis* for squid and *P. antarcticum* for fish. No specimen of *E. crystallorophias* was found. Accumulated items (i.e. items that resist to digestion and accumulate over time in penguin stomach) occurred regularly and they included stones and cephalopod beaks. The main cephalopod species identified from accumulated beaks ($n = 255$) was again *P. glacialis* (94.1% by number), followed by *Kondakovia longimana* (3.0%), *Alluroteuthis antarcticus* (1.8%), *Gonatus antarcticus* (0.7%) and *Slosarczykovia circumantarctica* (0.4%).

## Isotopic signature of prey

The three groups of *E. superba* (pooled digested specimens from emperor penguin food samples and undigested whole individuals from emperor and Adélie penguin samples) had statistically different $\delta^{13}C$, $\delta^{15}N$ and C/N values (ANOVA, $F_{2,33} = 46.25$, 19.21 and 31.26, respectively, all $P < 0.0001$). Post hoc tests indicated that digested krill specimens had significantly lower $\delta^{13}C$ ($-27.4 \pm 0.6$‰, $n = 14$) and $\delta^{15}N$ ($2.8 \pm 1.9$‰) values and higher C/N mass ratios ($5.2 \pm 0.8$) than the two other groups (all $P < 0.0001$). In contrast, isotopic signatures and C/N mass ratios of whole krill from emperor and Adélie penguin food samples were not statistically different (Table 1). Their $\delta^{13}C$ and $\delta^{15}N$ values were consequently pooled and the resulting means ($-25.6 \pm 0.6$ and $5.4 \pm 0.4$‰, respectively, $n = 22$) used for subsequent statistical analysis.

Penguin preys were segregated by their overall isotopic signatures (MANOVA, Wilk's lambda, $F_{6,84} = 43.77$, $P < 0.0001$) and, in univariate analysis, both $\delta^{13}C$ (ANOVA, $F_{3,43} = 6.74$, $P = 0.001$) and $\delta^{15}N$ values ($F_{3,43} = 225.10$, $P < 0.0001$). Overall, individual prey carbon signatures ranged from −26.8‰ (*E. superba*) to −24.2‰ (*P. antarcticum*), but average values encompassed a smaller range (< 1‰) with large overlaps between species (Fig. 2). $\delta^{13}C$ values of *P. antarcticum* and *P. glacialis*, and those of the two krill species were not different ($P = 0.626$ and 0.784, respectively), but the extreme values (*E. superba* and *P. antarcticum*) differed statistically ($P = 0.003$). More importantly, all nitrogen isotopic signatures of prey were different (all $P < 0.0001$), except those of *P. antarcticum* and *P. glacialis* ($P = 0.141$).

## $\delta^{15}N$ values of penguins and prey

Adélie penguins and prey segregated by their nitrogen isotopic signatures (ANOVA, $F_{7,77} = 101.87$, $P < 0.0001$). Post hoc Tukey HSD multiple comparison tests indicated that, as expected, $\delta^{15}N$ value of chick food was lower than

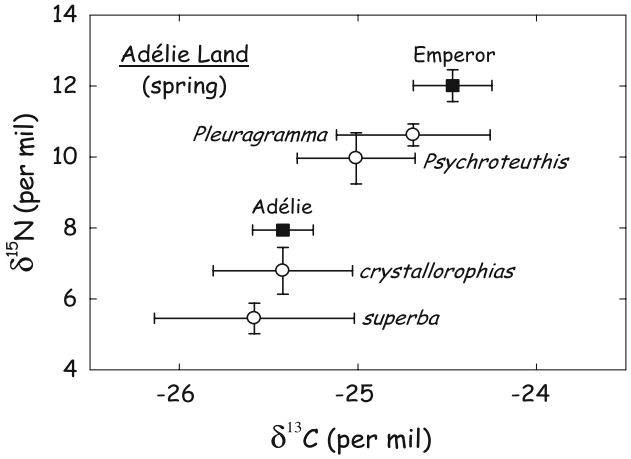


**Fig. 2** Stable carbon and nitrogen isotope values of emperor (chick-rearing) and Adélie (arrival to the colony) penguins and of their main prey in Adélie Land, Antarctica, in spring (see data in Table 1). Values are means ± SD. Abbreviations, *crystallorophias*: *Euphausia crystallorophias* (ice krill), *Pleuragramma*: *Pleuragramma antarcticum* (Antarctic silverfish), *Psychroteuthis*: *Psychroteuthis glacialis* (squid), *superba*: *Euphausia superba* (Antarctic krill)

those of the three groups of Adélie penguins and it was close to that of *E. crystallorophias* (Table 1). Adult Adélie penguins in spring and summer (chick-rearing period) had different $\delta^{15}$N values than prey, but it is noticeable that chick nitrogen signature was not statistically different from those of both *P. antarcticum* and *P. glacialis* (statistics not shown). Emperor penguins and prey also segregated by their nitrogen isotopic signatures ($F_{5,60} = 355.83$, $P < 0.0001$), with adults and chicks having significantly higher $\delta^{15}$N values than prey (all $P < 0.0001$) (Fig. 2).

## Discussion

This study is the first, to my knowledge, to investigate the dietary habits of emperor and Adélie penguins by comparing their isotopic signatures with the $\delta^{13}$C and $\delta^{15}$N values of their main prey.

### Methodological comments

Digested specimens of *Euphausia superba* had lower $\delta^{13}$C and $\delta^{15}$N values than undigested individuals. The most likely explanation is that digestion induced changes in krill biochemical composition, as reflected by the higher C/N mass ratio in digested specimens. Since lipids were extracted, such high C/N values cannot be related to a relative increase in fat content, but, instead, to an increase in the relative importance of exoskeleton. Indeed, exoskeleton resists better to digestion than other tissues, and the theoretical C/N mass ratio of pure chitin, a main biochemical component of exoskeleton, is higher than those of proteins and lipid-free whole crustaceans (Webb et al. 1998; Smyntek et al. 2007). Exoskeleton (chitin) has also lower $\delta^{15}$N values than muscle (protein) (Webb et al. 1998). Partial digestion thus probably accounts for some too low $\delta^{15}$N values of crustaceans in the literature (Cherel et al. 2005c). This finding has to be carefully taken into account when selecting prey items in food samples for subsequent isotopic analyses, because the use of erroneous crustacean isotopic signature can potentially lead to trophic misinterpretation within marine food webs.

The isotopic signature of the squid *Psychroteuthis glacialis* reported here is almost identical to the $\delta^{13}$C and $\delta^{15}$N values of specimens collected in 2001 (Cherel and Hobson 2005), suggesting little interannual variation in the isotopic niche of the species in Adélie Land. Like other cephalopod species (Hobson and Cherel 2006), *P. glacialis* has much higher $\delta^{15}$N values in muscle than in chitinized beaks (Cherel and Hobson 2005; Zimmer et al. 2007), the most likely explanation being again the $^{15}$N impoverishment of chitin when compared to protein (see above). Consequently, beak $\delta^{15}$N values must be corrected when comparing the isotopic signature of cephalopods with those from other organisms to trace pathways of organic matter (Cherel and Hobson 2005). No correction factor was applied to the beak $\delta^{15}$N values, including those from *P. glacialis*, in a recent investigation on Antarctic trophic relationships, thus precluding using its estimated $\delta^{15}$N values of emperor penguins (Zimmer et al. 2007).

### Trophic ecology of prey

Euphausiids, *P. glacialis* and *Pleuragramma antarcticum* were segregated by their nitrogen isotopic signatures, the difference being greater than one trophic level (i.e. about 3‰) between crustaceans, and fish and squid (Fig. 2). Accordingly, stomach content analysis showed that both *P. glacialis* and *P. antarcticum* were crustacean eaters. *P. glacialis* preys mainly upon *E. superba*, followed by fish (Kear 1992; Lu and Williams 1994), and *P. antarcticum* feeds on various crustacean taxa, including *Euphausia crystallorophias* and *E. superba*, with fish being a minor item (Hubold 1985; Dewitt et al. 1990). The average $\delta^{15}$N value of *P. antarcticum* from Adélie Land was similar to the nitrogen signature of specimens collected elsewhere (Burns et al. 1998; Hodum and Hobson 2000), suggesting no major differences in the foraging ecology of the species all over the Antarctic shelf.

The different isotopic signatures of *E. superba* and *E. crystallorophias* showed that they occupied different ecological niches. Overall, *E. crystallorophias* is a neritic species, while *E. superba* is mainly oceanic, but the latter species was also collected over the shelf in Adélie Land (Wienecke et al. 2000). Both species eat primarily phytoplankton, with a substantial contribution of heterotrophic food that varies according to season and location (Nicol et al. 2004; Schmidt et al. 2006). $\delta^{15}$N values of specimens sorted from Adélie penguin dietary samples suggest a more carnivorous diet for *E. crystallorophias* than *E. superba*, which is in agreement with gut content analysis of *E. crystallorophias* (Pakhomov et al. 1998). The identical isotopic signatures of *E. superba* from Adélie and emperor penguin food samples also indicate no significant dietary shift of *E. superba* between summer and late winter on the coast of Adélie Land in 2002 (Table 1).

### Trophic ecology of Adélie penguin

The food of Adélie penguin chicks is primarily composed of varying amounts of crustaceans (mainly *E. crystallorophias* and *E. superba*) and fish (mainly *P. antarcticum*) over its geographical range (Ainley 2002), including Adélie Land (Ridoux and Offredo 1989; Wienecke et al. 2000, this study). Taking into account the nitrogen signature of Adélie penguin chicks and the discriminant factor between

penguin food and blood (2.4‰, Cherel et al. 2005b), the theoretical $\delta^{15}$N value of chick diet was about 7.8‰. This value is higher than the nitrogen signature of euphausiids, confirming that fish constituted a significant part of the chick diet. Interestingly, adult penguins rearing chicks had lower $\delta^{15}$N value than chicks, suggesting that they preyed almost exclusively upon *E. crystallorophias*. Their nitrogen signatures therefore showed that adults fed for themselves on lower trophic level prey (euphausiids) and captured higher trophic level prey (fish, together with euphausiids) for their chicks. Such partial trophic segregation between adults and chicks were previously found in Antarctic procellariiforms, the higher trophic level of chicks being explained by adults provisioning offspring with higher-quality food to facilitate their growth (Hodum and Hobson 2000). Indeed, fish is more energetically valuable than euphausiids (Watanuki et al. 2002; Ainley et al. 2003), and fatty fish are known to be the best nutritional quality food promoting growth in penguin chicks (Heath and Randall 1985).

Little information is available on the feeding habits of Adélie penguins during the non-breeding season. In spring, breeding male Adélie penguins arrive at the colony after a critical period of hyperphagia at sea during which they build up large energy reserves (Ainley 2002). At that time, they had significantly lower $\delta^{13}$C values than chick-rearing adults in summer (Table 1). Taking into account the inshore/offshore $\delta^{13}$C gradient in Antarctic waters (Trull and Armand 2001) and the neritic habitat of breeding Adélie penguins (Wienecke et al. 2000), their carbon signature suggests that Adélie penguins foraged in oceanic waters during late winter, which is in agreement with visual observations of birds wintering well offshore in the pack-ice (Ainley et al. 1994). Their low $\delta^{15}$N values however precluded feeding on squid (Ainley et al. 1991), but, instead, fit well with a winter diet based mainly on *E. superba*. Accordingly, satellite tracks of a few individuals showed that penguins moved into known areas of high *E. superba* concentration at that time (Clarke et al. 2003). In brief, our isotopic data suggest that adult Adélie penguins breeding in Adélie Land feed on *E. superba* in oceanic waters in late winter and shift to neritic waters in summer where they prey upon *E. crystallorophias* for themselves and upon fish and euphausiids for their chicks.

## Trophic ecology of emperor penguin

The food of emperor penguins overall includes fish (mainly *P. antarcticum*), crustaceans (mainly *E. superba* and amphipods), and squid (mainly *P. glacialis*) (Kirkwood and Robertson 1997; Cherel and Kooyman 1998). In Adélie Land, the diet of emperor penguin chicks is by far dominated by fish (probably *P. antarcticum*, Cherel and Kooyman 1998), with *E. superba* and *P. glacialis* being minor items (Offredo and Ridoux 1986). The high nitrogen signature of emperor penguin chicks is in agreement with *P. antarcticum*, not euphausiids, being their main food item, thus suggesting no major changes in chick diet between the two years 1982 (Offredo and Ridoux 1986) and 2002 (this study). Chicks and breeding adults of emperor penguins had identical isotopic signatures, indicating that, unlike Adélie penguins, adults fed for themselves on the same prey as those given to their chicks. The isotopic data thus do not support the hypothesis based on diving behaviour that adult emperor penguins feed on different prey for their chicks on the last days of a foraging trip (Kooyman and Kooyman 1995). Instead, these shallower pelagic dives (Kooyman and Kooyman 1995) can be interpreted as travelling dives to the colony, thus contrasting with benthic feeding dives in the deep (Rodary et al. 2000a).

## Trophic segregation and Antarctic pelagic ecosystem

Emperor and Adélie penguins were segregated by their isotopic signatures in spring, indicating different feeding ecology during the late winter months. $\delta^{13}$C values suggest that migrating Adélie penguins and breeding emperor penguins foraged at that time in oceanic and neritic waters, respectively. Indeed, satellite tracking showed that Adélie penguins winter in oceanic waters (see above), while emperor penguins rearing chicks forage over the Antarctic shelf (Rodary et al. 2000a; Zimmer et al. 2008). The nitrogen signature of emperor penguins was also much higher (more than one trophic level) than that of Adélie penguins, thus underlining their fish (and squid) and euphausiid diet, respectively, during late winter. Spatially changing $\delta^{15}$N baseline level may theoretically also contribute to this difference, but, to my knowledge, no information is available on a $\delta^{15}$N gradient between oceanic and neritic Antarctic phytoplankton. The nitrogen signature of emperor penguins was also higher than that of chick-rearing Adélie penguins that are known to forage in neritic waters in summer. I am therefore confident that differences in the $\delta^{15}$N values of emperor and Adélie penguins reflect more dietary segregation than spatial/seasonal differences in $\delta^{15}$N of phytoplankton. Overall, emperor and Adélie penguins also segregate by their winter and summer breeding seasons, respectively, breeding sites (sea-ice vs. terrestrial) and diving behaviour. Adélie penguin is a shallow pelagic diver (Rodary et al. 2000b; Wienecke et al. 2000), while emperor penguin forages much deeper and performs both pelagic and benthic dives (Rodary et al. 2000a; Zimmer et al. 2008).

A comparison of trophic niches within the community of Antarctic seabirds and pinnipeds was rarely investigated in the past (Burns and Kooyman 2001). To minimize the tissue effect on $\delta^{15}$N and $\delta^{13}$C values (Vanderklift and

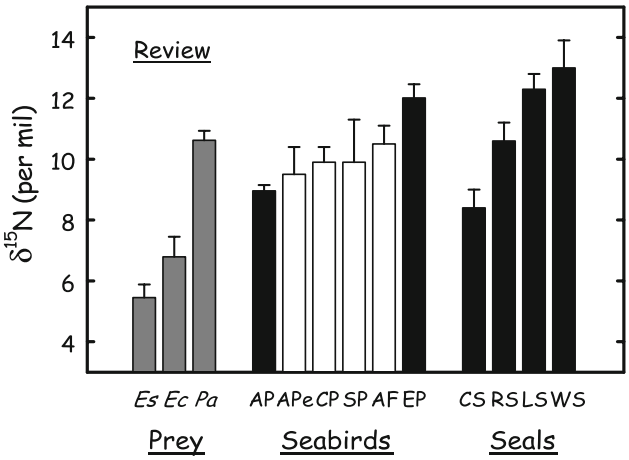


**Fig. 3** Stable nitrogen isotope values of prey (*grey*) and blood (whole blood, blood cells or serum) of adult air-breathing diving (*black*) and surface-feeding (*white*) vertebrates from Antarctica (data from Hodum and Hobson 2000; Zhao et al. 2004, this study). Values are means ± SD. *Es Euphausia superba*, *Ec Euphausia crystallorophias*, *Pa Pleuragramma antarcticum*, *AP* Adélie penguin, *Ape* Antarctic petrel, *CP* cape petrel, *SP* snow petrel, *AF* Antarctic fulmar, *EP* emperor penguin, *CS* crabeater seal, *RS* Ross seal, *LS* leopard seal, *WS* Weddell seal

Ponsard 2003), we therefore compared blood isotopic signatures of penguins (this study) with those of four petrels (Hodum and Hobson 2000) and four seals (Burns et al. 1998; Zhao et al. 2004; Hall-Aspland et al. 2005) living in high-Antarctic waters (Fig. 3). Overall, $\delta^{13}$C values encompass a small range and they are very negative (− 26.5 to −24.2‰), a distinctive feature of marine organisms living at high latitudes in the Southern Hemisphere. More variations, however, occur in $\delta^{15}$N values, the difference (5.2‰) being more than one trophic level between Adélie penguin (7.9‰, this study) and Weddell seal (13.1‰, Burns et al. 1998). The lower nitrogen signatures of Adélie penguin and crabeater seal are in agreement with an euphausiid-based diet (Zhao et al. 2004, this study), and the higher nitrogen signature of Weddell seal with a fish-based diet including some benthic prey (Burns et al. 1998; Zhao et al. 2004). Interestingly, the skin $\delta^{15}$N value (13.3‰) of C ecotype killer whale was only slightly higher than that of blood of Weddell seal and emperor penguin, which is consistent with their fish diet observed in the field (Krahn et al. 2006). Up to now, the highest $\delta^{15}$N value for a marine Antarctic consumer is that of the Antarctic toothfish (13.5‰, Burns et al. 1998). This does not preclude Weddell seal and C ecotype killer whale feeding occasionally and/or locally on toothfish (Krahn et al. 2006; Ponganis and Stockard 2007), but suggests that a fish, not a marine mammal or a seabird, occupies the highest trophic position in Antarctic waters. More information is however needed on the feeding habits and isotopic signature of other consumers to delineate the trophic structure of the upper levels of the high-Antarctic pelagic ecosystem, because poorly known groups of organisms potentially include top-level predators, e.g. cetaceans with B ecotype killer whale (Krahn et al. 2006) and cephalopods with colossal squid (Cherel and Hobson 2005).

Interestingly, isotopic signatures of Antarctic seabirds and seals showed a continuum of $\delta^{15}$N values, thus contrasting with the two well-defined trophic levels (crustacean and fish eaters) structuring the community of subantarctic air-breathing diving vertebrates (Cherel et al. 2007). Such a continuum emphasizes the fact that the diets of most Antarctic predators overlap extensively. Indeed, they feed on varying proportions of a few crustacean and fish species that dominate the intermediate trophic levels of the pelagic neritic and oceanic ecosystems. The study is thus in agreement with the importance of both Antarctic and ice krill together with Antarctic silverfish, and to a lesser extent *Psychroteuthis glacialis*, as key links between lower trophic levels and major consumers of the Southern Ocean like penguins and seals (Ainley and DeMaster 1990; Smith et al. 2007).

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