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When sea-ice clock is ahead of Adélie penguins' clock

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Abstract

1. In Polar Regions, the extent and dynamics of sea-ice are changing. This affects the ocean productivity which consecutively impacts plankton communities and polar top predators like penguins. Yet, the underlying behavioural and physiological mechanisms remain poorly understood.

2. Here we monitored the ecophysiological responses of Adélie penguin (*Pygoscelis adeliae*) pairs during two seasons of contrasting timing of sea-ice retreat. Beside classical breeding parameters like foraging trip duration, body mass and reproductive success, we also investigated food-related stress (*via* plasma corticosterone concentration), nutritional state (*via* metabolite levels) and the use of penguins' habitat (*via* blood isotopic values).

3. Body mass and reproductive success remained unchanged but foraging trips were shorter when sea-ice retreated earlier. Constant plasma corticosterone concentrations indicated that none of the feeding conditions resulted in a food-related stress. However metabolite levels were lower when sea-ice retreated early, suggesting that the foraging performance and the quality/quantity of food differed. Indeed isotopic ratios indicated that coastal prey like fish contributed more to the penguins' diet when sea-ice retreated prematurely.

4. The early sea-ice retreat was related to higher chlorophyll concentrations, known to favour krill recruitment. Paradoxically, this was not associated to a higher krill contribution in the penguins' diet. We propose that a shift in the phytoplankton quality (rather than quantity), affecting krill recruitment, forced penguins to switch to more available prey like coastal fish.

5. In some Antarctic regions, sea-ice is retreating earlier and earlier. In the present study, even though the timing of sea-ice retreat and the consecutive ocean productivity differed drastically between the 2 years, Adélie penguins were not severely affected because they were able to adjust their at-sea behaviour and thus maintained their body condition and reproductive success unchanged.

6. This suggests that the timing of sea-ice retreat does not represent an important threat to populations of Adélie penguins at least as long as alternative resources are still available and other environmental parameters like winter sea-ice extent are not dramatically altered.

Key-words: food availability, krill, phytoplankton, seabird, sea-ice retreat

Introduction

From a predator's perspective, the quality of a particular habitat can be considered as the matching between its requirements and the food available in terms of timing, abundance and accessibility (Durant *et al.* 2007). When the breeding season is conditioned by resource availability, several alternatives are possible for potential breeders when a decrease in food resources happens: animals may (1) skip one breeding season (Drent & Daan 1980), (2) breed but shift their breeding timing according to food availability (Barbraud & Weimerskirch 2006), (3) breed without altering their breeding phenology but mismatch the peak of food availability. In this latter case, animals may change their foraging behaviour and shift to other preys to cope with the lower availability of their usual food resource (Croxall, Reid & Prince 1999; Miller & Trivelpiece 2008; Nicol *et al.* 2008).

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Fig. 1. Adélie penguins on sea-ice edge. Photo by Michaël Beaulieu©.

Because the quality of the habitat is likely to induce effects on the animal physiology and behaviour, the examination of the adequacy between food availability and the animal requirements can be carried out by the investigation of its manifestations on the animal itself. For instance, corticosterone levels have been proposed as a reliable measure of food-related stress and as a consequence a direct measure of food availability in free-living birds (Kitaysky, Piatt & Wingfield 2007). This stress hormone plays an important role in the regulation of feeding, locomotor activity and energy metabolism (see Landys, Ramenofsky & Wingfield 2006) and may affect foraging decisions (Angelier *et al.* 2008). Similarly, plasma metabolite levels highly depend on food intake and can be used as indicators of the nutritional state of free-living animals (Jenni-Eiermann & Jenni 1998). For instance, triglyceride levels reflect the amount of food absorbed and the time since when it was ingested, while uric acid levels characterize protein breakdown which occurs once a critical threshold has been reached in the depletion of body fuel reserves or may result of high muscular activity. Moreover, metabolite levels may also depend on the seasonal requirements of animals; for instance in female birds, before egg laying, triglyceride and uric acid levels reflect the increased liver activity involved in lipid and protein production for oogenesis (Vézina & Williams 2003; Kern *et al.* 2005). Finally a shift in the use of the habitat can be examined by the measurement in animal tissues of stable isotope ratios which indicate simultaneously the trophic position, through $^{15}N : {}^{14}N$ ratio (further expressed as $\delta^{15}N$), and the spatial distribution, through $^{13}C : {}^{12}C$ ratio (further expressed as $\delta^{13}C$), of the consumer. Indeed, in marine food-webs, low values of $\delta^{15}N$ reflect a diet based on preys found at the bottom of the food-web and high values of $\delta^{13}C$ are found in coastal foragers (for the principle of this measurement, see Inger & Bearhop 2008).

In the Southern Ocean, interactions between algae and krill (mainly *Euphausia superba*) represent the basis for energy flux to higher trophic levels like fish, seabirds and mammals. Krill is essentially herbivorous and grazes on phytoplankton. The intensity of its reproduction is therefore highly correlated with annual primary production in the water column, which in turn depends on sea-ice extent and the timing of its retreat (Quetin & Ross 2001). As a result, the summer krill density and quality (reproductive krill are more energetic) correlate positively with chlorophyll concentrations (Cripps *et al.* 1999; Atkinson *et al.* 2004). In the Arctic, it has been shown that the timing of sea-ice retreat affects the timing of the phytoplankton bloom (Hunt & Stabeno 2002). Indeed sea-ice acts as a physical barrier between the atmosphere and the ocean, preventing daylight from penetrating into the water column. The timing of sea-ice retreat may be variable since sea-ice is relatively thin and is therefore vulnerable to perturbations from the ocean and the atmosphere. In certain regions of Antarctica, on top of a decrease in its extent (Moline *et al.* 2008), sea-ice is also forming ~55 days later and retreating ~30 days earlier than 40 years ago (Stammerjohn *et al.* 2008). As a result, these premature retreats are likely to modify the timing and the intensity of the spring phytoplankton bloom (Moline *et al.* 2008) which by a cascade effect may affect the whole food-web structure.

In this study, we focused on two successive austral summers in Adélie Land which presented contrasting conditions in sea-ice retreat and therefore followed the general trend observed in some Antarctic regions. In 2006–2007, fast sea-ice retreated in late September consecutively to a strong windstorm while in 2007–2008, it retreated, more typically, 3 months later in late December (Fig. 2). This difference of timing was likely to induce consequences on the subsequent phytoplankton bloom, krill and krill-eating predators. Here we examined the link between habitat quality in terms of timing and abundance of phytoplankton and the reproductive and ecophysiological responses of Adélie penguins (*Pygoscelis adeliae*, Fig. 1). During the breeding season in Adélie Land, Adélie penguins principally feed upon krill *Euphausia superba*. However they are not krill-specialists since they can also feed upon Antarctic fish (*Pleuragramma antarcticum*, Ridoux & Offredo 1989; Clarke *et al.* 1998; Wienecke *et al.* 2000). Adélie penguins present a high degree of seasonality: in Adélie Land, they arrive on the breeding grounds in mid-October, lay 1–2 egg(s) in mid-November that hatch in mid-December, chicks are then guarded until mid-January and left in crèches until mid-February (Fig. 3). Food requirement peaks during the chick-rearing period (guard and crèche stages, Chappell *et al.* 1993) when parents have to feed their growing chick(s) and insure their own maintenance. In addition, Adélie pen-

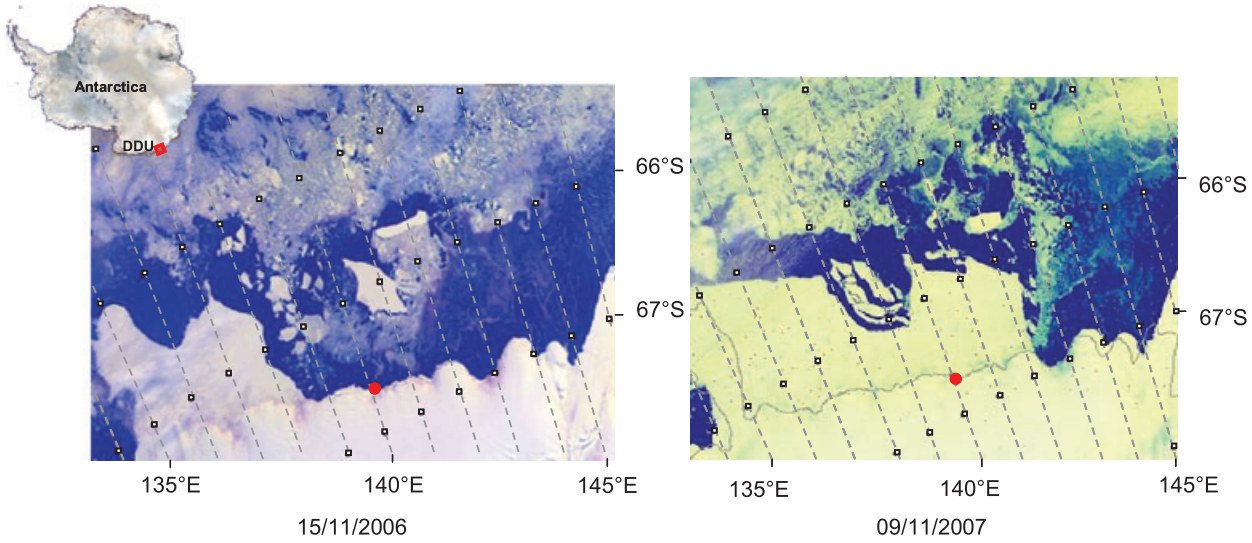

Fig. 2. Satellite images showing sea-ice conditions in Adélie Land in November 2006 and November 2007. Open water areas are represented in blue while ice is represented in white (2006) or yellow (2007). Dumont d'Urville Station (DDU), located on the coast, is symbolized by a red circle. These images were provided by Météo France.

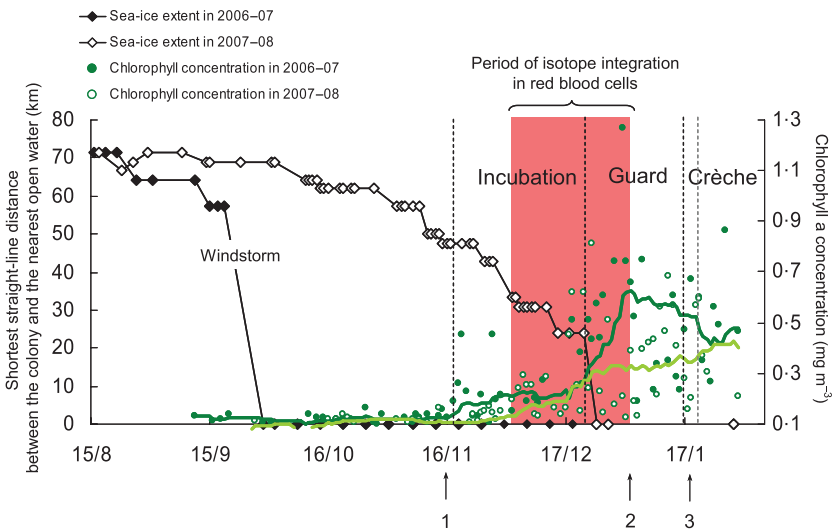

Fig. 3. Evolution of the shortest distance from the colony to the nearest open water due to fast-ice retreat (2006–2007: black symbols, 2007–2008: white symbols) and the consecutive chlorophyll concentration in open water (2006–2007: green-filled symbols, 2007–2008: green-unfilled symbols) from 15 August to 31 January. The moving averages of chlorophyll concentration are represented to facilitate the visualization of its evolution (2006–2007: dark-green line, 2007–2008: light-green line). The breeding phenology of Adélie penguins is superimposed: the limits between two stages were the same in 2006–2007 and 2007–2008 except the limit between the guard and the crèche stages which tended to differ – although non significantly –between the 2 years (2006–2007: black-dashed line, 2007–2008: grey-dashed line). Penguins were weighed and bled twice (arrows 1 and 2) and chicks were weighed at the end of the guard stage (arrow 3). The red area represents the period of isotope integration in red blood cells for the second blood sample.

guins are forced to forage in a limited area (30–110 km from the colony, Angelier *et al*. 2008) because of the constraint to feed chicks regularly. Since sea-ice retreat was premature in 2006–2007, a mismatch between phytoplankton bloom (and presumably krill recruitment) and the requirements of Adélie penguins was likely to happen. In our study, we examined whether differences in the timing of sea-ice retreat affected the timing and/or the abundance of phytoplankton and to what extent it may have affected Adélie penguins' body condition, metabolisms of lipids and proteins, foraging decisions, diet quality and ultimately breeding success.

Materials and methods

FIELD PROCEDURE

In 2006–2007, at the end of the courtship period, 32 birds from 16 different pairs from Dumont d'Urville, Pétrel Island (66°40′S, 140°01′E;

Fig. 2), were captured on their nest and weighed with an electronic balance (Ohaus, ±2 g). The birds were then identified with a Nyanzol-D mark painted on the breast feathers and with a subcutaneous passive transponder (Renner & Davis 2000). To minimize disturbance due to consecutive captures on the same nest, the partner underwent a similar treatment 2 days later.

Until the end of the guard stage, the 16 nests were observed from a blind overhanging the nests, about 20 m apart, every 2 h at worst and continuously at best to monitor copulation behaviours, laying, foraging trip duration and reproductive success. Laying date was defined as the laying date of the first egg. Provisioning rate was defined from the chick perspective and was calculated as the number of parent returns (male + female) from the sea during the guard stage. The number of chicks in crèche was used to estimate the final reproductive success of the focal pairs since at this stage, chick mortality is low in Adélie penguins (Davis & McCaffrey 1986; Clarke *et al.* 2002).

The birds were captured and weighed a second time during the guard stage (40–45 days after laying), after a nest relief and just before leaving the colony to forage at sea (Fig. 3). Body mass loss was defined as the difference between the first and the second weighing.

Blood was collected during the two captures (courtship and guard stage, Fig. 3) from the wing vein with a heparinized syringe. After centrifugation, plasma and red blood cells were quickly stored at −20 °C. Because the capture and the restraint constitute an acute stress that may influence baseline parameters in blood (Jenni-Eiermann & Jenni 1998; Cockrem *et al.* 2008), most attention was paid to minimize the stress for birds. The head of the penguin was covered by a hood (Cockrem *et al.* 2008) and handling duration was minimized and timed from the approach of the experimenter towards the nest until the end of blood sampling. A 5-min threshold was chosen since it has been shown that handling durations < 5 min had no effect on corticosterone levels in Adélie penguins (Vleck *et al.* 2000). Timing of blood sampling depended on the bird departure and therefore occurred at any time of the day. However corticosterone concentration is not affected by daytime in Adélie penguins (Vleck & Van Hook 2002, Angelier *et al.* 2008).

At the end of the guard stage, the chicks were weighed on their nest with a spring balance (Salter, ±20 g) when they were left unguarded for the first time.

In 2007–2008, at the end of the courtship period and twice during the incubation period, all the nests occupied by pairs in 2006–2007 were checked with a hand held antenna to search for penguins identified with transponders. For the rest of the breeding cycle, the procedure was strictly the same as that described in 2006–2007.

In both years, adults were sexed by a combination of parameters including cloacal inspection before egg laying, copulatory position and incubation routine (Taylor 1962; Kerry, Clarke & Else 1993). Sex determination carried out in 2007–2008 totally confirmed the sexing of all birds achieved 1 year before.

LABORATORY ANALYSES

Analyses of the plasma concentrations of corticosterone, triglycerides and uric acid were conducted at the IPHC-DEPE, France. Corticosterone levels were determined by immunoassay (AssayMax Corticosterone ELISA Kit; AssayPro, St. Charles, Missouri, US) and concentrations of triglycerides and uric acid were measured using enzymatic colorimetric tests (Sigma Diagnostic, St. Louis, Missouri, US). Intra- and inter- assay variations were 5% and 7%, respectively for corticosterone measurements and were comprised between 1% and 3% for metabolite measurements. In addition, the cross-reactivity of the corticosterone antibody with other steroids is low (comprised between 0 and 2%, Assay Pro). No relationship between handling time and corticosterone levels was found (courtship 2006: $r_s = 0{\cdot}04$, $P = 0{\cdot}86$; courtship 2007: $r_s = -0{\cdot}26$, $P = 0{\cdot}29$; guard stage 2006–2007: $r_s = -0{\cdot}03$ $P = 0{\cdot}91$; guard stage 2007–2008: $r_s = -0{\cdot}20$ $P = 0{\cdot}41$), so that we considered these corticosterone levels reflected baseline values.

Tissue isotopic values mirror the diet throughout the period of tissue synthesis (Bearhop *et al.* 2002). We chose to investigate isotopic values of red blood cells, which require 3–4 weeks to turn-over (Hobson & Clark 1993; Haramis *et al.* 2001; Bearhop *et al.* 2002) and thus integrated the diet of the bird from the end of the incubation period to the early guard stage (second blood sample, Fig. 3). Before isotopic analyses, red blood cells were lyophilized (48 h) and powdered (Hobson, Gibbs & Gloutney 1997). Lipids were not extracted as this is not necessary when using red blood cells (Cherel *et al.* 2005). Stable-carbon and nitrogen isotope assays were carried out at the Centre de Recherche sur les Ecosystèmes Littoraux Anthropisés (CRELA), L'Houmeau, France. Results are expressed in the standard δ notation (‰) relative to PDB belemnite for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. Intra-assay coefficients of variation for $\delta^{13}C$ and $\delta^{15}N$ values of standard acetanilide were 0·88% and 0·63%, respectively. Inter-assay coefficients of variation for $\delta^{13}C$ and $\delta^{15}N$ values of standard acetanilide were 0·42% and 0·24%, respectively.

ENVIRONMENTAL ANALYSIS

In both years, we measured the shortest straight-line distance between the colony and the nearest open water on cloud-free satellite images (resolution: 1 km) provided by Météo France. To measure chlorophyll concentration, we used SEAWIFS satellite data (NASA-OrbImage, resolution: 1 km) that provided mean chlorophyll *a* concentration in open-water areas in a region that extended latitudinally from 65°00′S to 66°40′S and longitudinally from 135°00′E to 145°00′E (Fig. 2). Since chlorophyll concentration varies as a function of daytime (McMinn *et al.* 2007), it was measured only between 13:00 and 15:00 local time. Environmental data were analysed from 15 August to 31 January.

DATA ANALYSIS

A population is characterized by diversity and variance as it is composed of animals of different age, experience, quality etc. In order to perform inter-annual comparisons and avoid confounding factors due to inter-individual variability, two alternate sampling protocols are conceivable: (1) sample each year a large number of individuals equally sampling all the categories found in the population (or even better in the species) or (2) repeatedly sample each year the same number of animals so that the experimenter is sure that the confounding factors due to sampling are the same year after year. As the first alternative is logistically too difficult, we chose the second option thus assuming that the potential inter-individual confounding factors were the same each year. Since newly-established pairs have a lower breeding success in Adélie penguins (Ainley, Leresche & Sladen 1983) and that a change of mate may increase corticosterone levels (Angelier *et al.* 2007), we removed the potential bias due to pair stability by considering only stable pairs from 2006–2007 to 2007–2008. This resulted in the exclusion of five pairs that divorced or in which one mate was absent in 2007–2008. Moreover, because metabolic levels do not lead to the same interpretation during incubation and chick-rearing periods (see introduction) and corticosterone levels may also

change within a breeding season (Lanctot *et al.* 2003), we conducted comparisons between the 2 years during the incubation period and during the guard stage independently.

The concentrations of chlorophyll were compared between the 2 years after the chlorophyll bloom (15 November) with a Mann–Whitney test. Using the date of laying as the reference date, we assessed with general linear models whether the dates of manipulation and sampling differed between the 2 years. Almost all other comparisons were carried out using general linear mixed models to avoid the problem of pseudoreplication since our statistical analyses involved repeated observations of the same subjects. Individuals were considered as a random factor while the year, the sex and their interaction were used as fixed factors. Normality of residuals was assessed by Shapiro-Wilk tests. When this condition was not fulfilled, we used generalized linear models with a normal distribution (duration of the first foraging trip during incubation) or a gamma distribution of dependent data (plasmatic parameters, foraging trip duration during the guard stage). Generalized linear models with a Poisson distribution were also used in the case of count data (reproductive success) considering the stage (egg laying, hatching, guard stage and crèche stage), the year and the interaction of these two factors as fixed factors. Multiple comparisons were undertaken using the post hoc Bonferroni test.

All analyses were conducted using SPSS 16.02 (SPSS Inc., Chicago, IL, USA). Results are expressed as means ± SE and significance level was set at $\alpha = 0{\cdot}05$.

Results

ENVIRONMENTAL PARAMETERS

The distance from the colony to the nearest open water was similar (70 km) in mid-August 2006 and 2007. In 2006–2007, open water reached the coast of the colony 3 months before it did in 2007–2008 (Fig. 3). Chlorophyll concentrations began to increase at the same time in both years (15 November). After this date, chlorophyll mean concentration was 30% lower in 2007–2008 ($0{\cdot}287 \pm 0{\cdot}024$ mg m^{-3}) than in 2006–2007 ($0{\cdot}404 \pm 0{\cdot}035$ mg m^{-3}, $U = 880$, $P = 0{\cdot}006$, Fig. 3).

PRE-LAYING PERIOD

There was no difference in the handling date between the 2 years ($F_{1,\ 39} = 1{\cdot}05$, $P = 0{\cdot}31$) and females and males were manipulated at the same time ($F_{1,\ 39} = 3{\cdot}29$, $P = 0{\cdot}08$). The interaction year × sex was not significant ($F_{1,\ 39} = 2{\cdot}28$, $P = 0{\cdot}14$, Table 1).

Before egg laying, males were heavier than females ($5{\cdot}12 \pm 0{\cdot}10$ and $4{\cdot}53 \pm 0{\cdot}10$ kg, respectively; $F_{1,\ 38} = 18{\cdot}12$, $P < 0{\cdot}001$) but neither the year ($4{\cdot}83 \pm 0{\cdot}10$ kg in 2006 and $4{\cdot}82 \pm 0{\cdot}10$ kg in 2007, $F_{1,\ 38} = 0{\cdot}01$, $P = 0{\cdot}94$) nor the interaction sex × year ($F_{1,\ 38} = 0{\cdot}74$, $P = 0{\cdot}40$) had an effect on body mass (Fig. 4).

Concentrations of corticosterone were similar between males and females ($2{\cdot}32 \pm 0{\cdot}51$ and $1{\cdot}86 \pm 0{\cdot}53$ ng mL^{-1}, respectively; Wald $\chi^2 = 0{\cdot}39$, d.f. = 1, $P = 0{\cdot}53$) and between years ($1{\cdot}92 \pm 0{\cdot}46$ in 2006 and $2{\cdot}26 \pm 0{\cdot}45$ ng mL^{-1} in 2007, Wald $\chi^2 = 0{\cdot}40$, d.f. = 1, $P = 0{\cdot}53$). The interaction sex × year was also not significant (Wald $\chi^2 = 1{\cdot}83$, d.f. = 1, $P = 0{\cdot}18$, Fig. 4).

Plasma concentrations of uric acid and triglycerides followed the same trends: metabolite concentrations were lower in males than in females (uric acid: $0{\cdot}21 \pm 0{\cdot}01$ and $1{\cdot}16 \pm 0{\cdot}08$ mmol L^{-1}, respectively; Wald $\chi^2 = 9{\cdot}88$, d.f. = 1, $P = 0{\cdot}002$, triglycerides: $1{\cdot}33 \pm 0{\cdot}12$ and $10{\cdot}96 \pm 1{\cdot}26$ mmol L^{-1}, respectively; Wald $\chi^2 = 58{\cdot}21$, d.f. = 1, $P < 0{\cdot}001$) and there were differences between years (uric acid: $0{\cdot}60 \pm 0{\cdot}04$ in 2006–2007 and $0{\cdot}77 \pm 0{\cdot}05$ mmol L^{-1} in 2007–2008, Wald $\chi^2 = 15{\cdot}46$, d.f. = 1, $P < 0{\cdot}001$, triglycerides: $3{\cdot}09 \pm 0{\cdot}73$ in 2006–2007 and $9{\cdot}20 \pm 0{\cdot}78$ mmol L^{-1} in 2007–2008, Wald $\chi^2 = 54{\cdot}51$, d.f. = 1, $P < 0{\cdot}001$). The interaction sex × year (uric acid: Wald $\chi^2 = 9{\cdot}88$, d.f. = 1, $P = 0{\cdot}002$, triglycerides: Wald $\chi^2 = 48{\cdot}74$, d.f. = 1, $P < 0{\cdot}001$) indicated that metabolite concentrations remained stable in males (uric acid: $P = 0{\cdot}79$, triglycerides: $P = 0{\cdot}13$) while they increased between 2006–2007 and 2007–2008 in females (uric acid: $P = 0{\cdot}001$, triglycerides: $P < 0{\cdot}001$, Fig. 4).

INCUBATION PERIOD

There was no difference in the laying date between both years ($F_{1,\ 9} = 0{\cdot}02$, $P = 0{\cdot}90$, Table 1). The first foraging trip was longer in 2007–2008 than in 2006–2007 ($13{\cdot}47 \pm 0{\cdot}32$ and $10{\cdot}83 \pm 0{\cdot}26$ days, respectively; Wald $\chi^2 = 45{\cdot}68$, d.f. = 1, $P < 0{\cdot}001$) but neither the sex (Wald $\chi^2 = 1{\cdot}64$, d.f. = 1, $P = 0{\cdot}20$) nor the interaction year × sex affected its duration (Wald $\chi^2 = 0{\cdot}15$, d.f. = 1, $P = 0{\cdot}70$, Fig. 4). Egg hatching

Table 1. Principal dates of the breeding cycle of the studied Adélie penguin pairs and dates of handling

	2006–2007		2007–2008	
	Females ($n = 11$)	Males ($n = 11$)	Females ($n = 11$)	Males ($n = 11$)
Duration between the first handling and egg laying (days)	−5·8 ± 0·9	−2·8 ± 0·9	−5·4 ± 0·9	−5·09 ± 0·9
Date of laying	17/11 ± 0·6 days	–	17/11 ± 1·1 days	–
Date of hatching	23/12 ± 0·8 days		23/12 ± 0·8 days	
Duration between egg laying and the second handling (days)	41·2 ± 0·6	41·3 ± 0·6	40·6 ± 0·6	40·2 ± 0·6
Duration of the guard stage (days)	25·2 ± 1·5		28·7 ± 1·6	

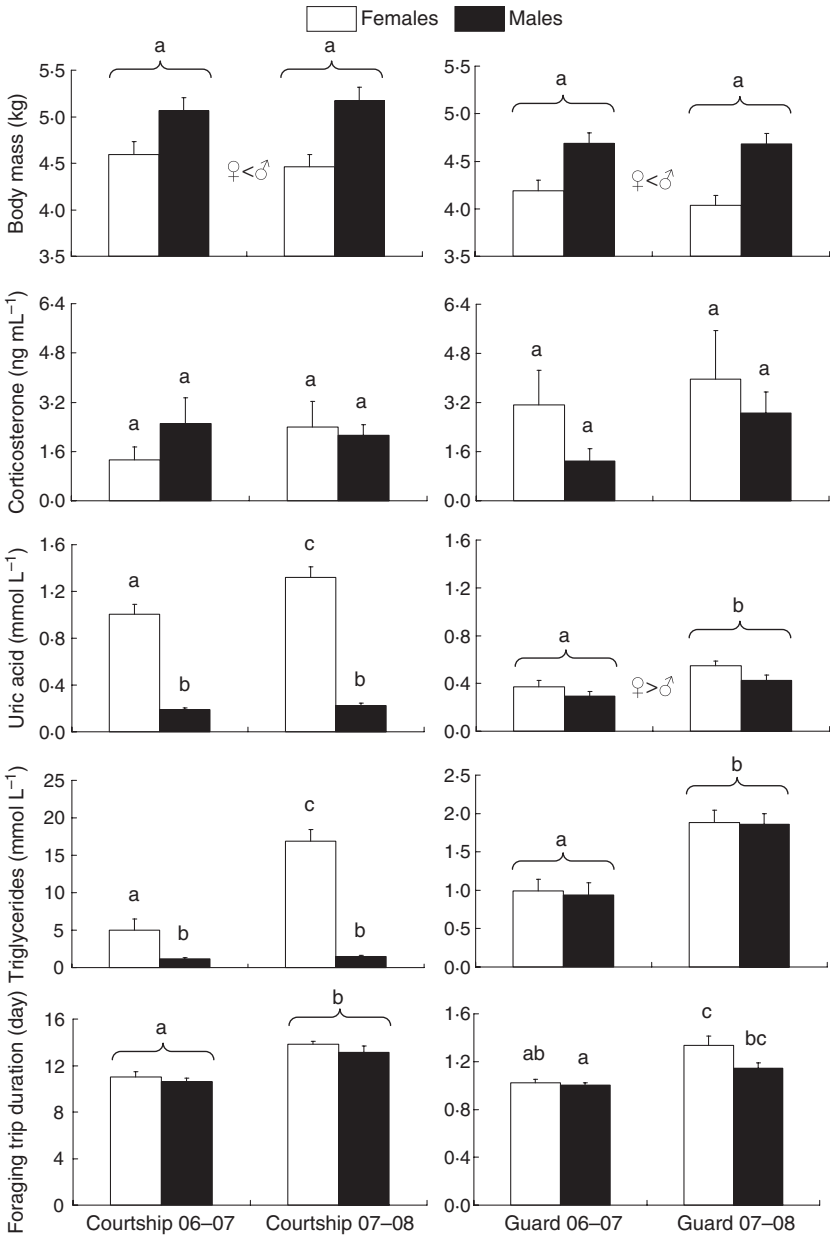

Fig. 4. Body mass, plasmatic parameters (corticosterone, uric acid and triglyceride) and foraging trip duration during the courtship and the incubation periods (left column) and during the guard stage (right column) in 2006–2007 and 2007–2008. White histograms refer to females and black histograms refer to males. Results are presented as means ± SE. Comparisons were carried out during the courtship and the incubation periods and during the guard stage independently. Different letters correspond to significant differences between two groups for a considered parameter and the brackets indicate the results of the comparison between the 2 years whatever the sex of the individuals.

happened at the same date ($F_{1,\ 9} = 0{\cdot}03$, $P = 0{\cdot}88$) in 2006–2007 and in 2007–2008 (Table 1).

GUARD STAGE

There was no difference in the handling date during the guard stage between the 2 years ($F_{1,\ 36} = 2{\cdot}13$, $P = 0{\cdot}15$), between sexes ($F_{1,\ 36} = 0{\cdot}04$, $P = 0{\cdot}84$) and the interaction year × sex was not significant ($F_{1,\ 36} = 0{\cdot}16$, $P = 0{\cdot}69$, Table 1).

Body mass was higher in males than in females (4·69 ± 0·10 and 4·11 ± 0·10 kg, respectively; $F_{1,\ 18} = 16{\cdot}08$, $P = 0{\cdot}001$) but neither the year (4·44 ± 0·08 kg in 2006–2007 and 4·36 ± 0·08 kg in 2007–2008, $F_{1,\ 17} = 1{\cdot}73$, $P = 0{\cdot}21$) nor the interaction sex × year ($F_{1,\ 17} = 1{\cdot}57$, $P = 0{\cdot}23$) influenced body mass (Fig. 4). Body mass changed similarly between the pre-laying period and the guard stage (mean body mass loss: 393 ± 59 g) in both years ($F_{1,\ 16} = 0{\cdot}41$, $P = 0{\cdot}53$) and in males and females ($F_{1,\ 17} = 1{\cdot}74$, $P = 0{\cdot}21$). The interaction sex × year was not significant ($F_{1,\ 17} = 0{\cdot}78$, $P = 0{\cdot}79$).

Corticosterone remained constant between males and females (2·07 ± 0·47 and 3·54 ± 0·82 ng mL^{-1}, respectively; Wald $\chi^2 = 2{\cdot}41$, d.f. = 1, $P = 0{\cdot}12$) and between years (2·21 ± 0·59 in 2006–2007 and 3·40 ± 0·87 ng mL^{-1} in 2007–2008, Wald $\chi^2 = 1{\cdot}07$, d.f. = 1, $P = 0{\cdot}30$). The interaction sex × year was also not significant (Wald $\chi^2 = 0{\cdot}10$, d.f. = 1, $P = 0{\cdot}75$). Metabolite concentrations were higher in 2007–2008 than in 2006–2007 (uric acid: 0·49 ± 0·03 and 0·33 ± 0·03 mmol L^{-1}, respectively, Wald $\chi^2 = 16{\cdot}74$, d.f. = 1, $P < 0{\cdot}001$, triglycerides: 1·87 ± 0·10 and 0·96 ± 0·11 mmol L^{-1}, respectively; Wald $\chi^2 = 54{\cdot}42$, d.f. = 1, $P < 0{\cdot}001$) and sex had only an effect on uric acid concentrations (uric acid: 0·36 ± 0·03 mmol L^{-1} in males and 0·46 ± 0·04 mmol L^{-1} in females, Wald $\chi^2 = 1{\cdot}11$, d.f. = 1, $P = 0{\cdot}04$, triglycerides: 1·40 ± 0·13 mmol L^{-1} in

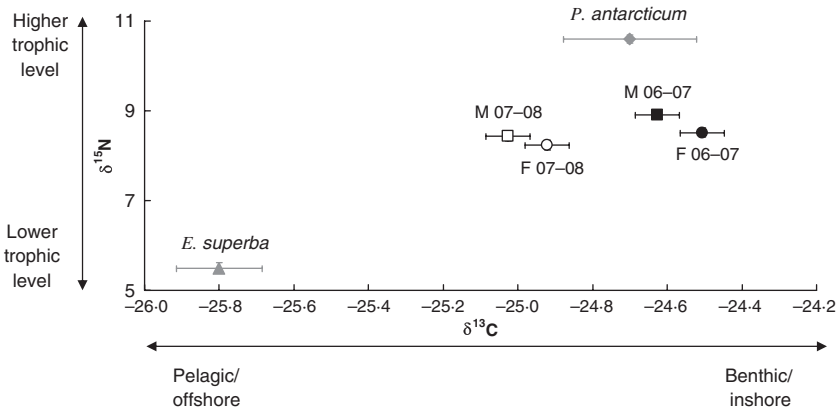

Fig. 5. Mean $\delta^{15}N$ and $\delta^{13}C$ (± SE) values of adult Adélie penguins, males (squares) and females (circles) in 2006–2007 (filled symbols) and 2007–2008 (empty symbols). Values for *Euphausia superba* and *Pleuragramma antarcticum* are also represented (from Cherel 2008).

males and 1·44 ± 0·12 mmol L^{-1} in females, Wald χ^2 = 0·04, d.f. = 1, P = 0·84). The interaction sex × year was not significant neither for uric acid (Wald χ^2 = 0·29, d.f. = 1, P = 0·59) nor for triglycerides (Wald χ^2 = 0·01, d.f. = 1, P = 0·91, Fig. 4).

During the guard stage, foraging trip duration was affected by the sex (1·07 ± 0·03 days in males and 1·17 ± 0·04 days in females, Wald χ^2 = 4·12, d.f. = 1, P = 0·04), the year (1·01 ± 0·02 days in 2006–2007 and 1·24 ± 0·04 days in 2007–2008, Wald χ^2 = 28·03, d.f. = 1, P < 0·001) and the interaction sex × year (Wald χ^2 = 3·98, d.f. = 1, P = 0·05) with males performing 15% longer foraging trips in 2007–2008 than in 2006–2007 (P = 0·001) and females performing 30% longer foraging trips in 2007–2008 than in 2006–2007 (P < 0·001, Fig. 4). Over the guard stage, the provisioning rate was similar in 2006–2007 and in 2007–2008 (2006–2007: 22·70 ± 1·54 parent returns, 2007–2008: 20·44 ± 1·63 parent returns, $F_{1, 17}$ = 1·01, P = 0·33). This was due to the nearly significantly longer guard stage (~3·5 days) in 2007–2008 than in 2006–2007 ($F_{1, 9}$ = 4·14, P = 0·07, Table 1), since provisioning rate was significantly different between the 2 years after controlling for the duration of the guard stage (2006–2007: 24·06 ± 0·98 visits, 2007–2008: 18·93 ± 1·04 visits; $F_{1, 16}$ = 12·14, P = 0·003).

Isotopic values differed according to the sex and the year: males had higher levels of $\delta^{15}N$ than females (8·7 ± 0·1 ‰ and 8·4 ± 0·1 ‰, respectively, $F_{1, 18}$ = 6·29, P = 0·02) but $\delta^{13}C$ values were similar in both sexes (males: −24·8 ± 0·1 ‰, females: −24·7 ± 0·1 ‰, $F_{1, 18}$ = 2·67, P = 0·12). Both $\delta^{15}N$ and $\delta^{13}C$ values were different between the 2 years with higher $\delta^{15}N$ values in 2006–2007 than in 2007–2008 (8·7 ± 0·1 ‰ and 8·3 ± 0·1 ‰, respectively, $F_{1, 18}$ = 23·20, P < 0·001), associated with higher $\delta^{13}C$ values (2006–2007: −24·6 ± 0·1 ‰, 2007–2008: −25·0 ± 0·1 ‰, $F_{1, 18}$ = 74·35, P < 0·001). The interaction sex × year was not significant neither for $\delta^{15}N$ values ($F_{1, 18}$ = 1·67, P = 0·21) nor for $\delta^{13}C$ values ($F_{1, 18}$ = 0·03, P = 0·87, Fig. 5).

REPRODUCTIVE SUCCESS AND BROOD MASS

Even though the breeding stage had an effect on reproductive success (Wald χ^2 = 35·56, d.f. = 3, P < 0·001, Fig. 6), there was no difference between the 2 years (Wald χ^2 = 0·30, d.f. = 1, P = 0·59) and the interaction stage × year was not significant (Wald χ^2 = 1·64, d.f. = 3, P = 0·65). At the end of the guard stage, brood mass was similar in 2006–2007 and in 2007–2008 (3·01 ± 0·34 kg and 3·02 ± 0·35 kg, respectively, $F_{1, 9}$ = 0·00, P = 0·98).

Discussion

Few studies have tried to establish a link between ecological, behavioural, dietary and physiological parameters in wild animals. Here, we showed that a 3-months earlier fast-ice retreat was associated to a 30% higher chlorophyll production in open water and it affected Adélie penguins who performed shorter foraging trips, and fed on a diet with higher $\delta^{15}N$ and $\delta^{13}C$ values. They presented lower plasma metabo-

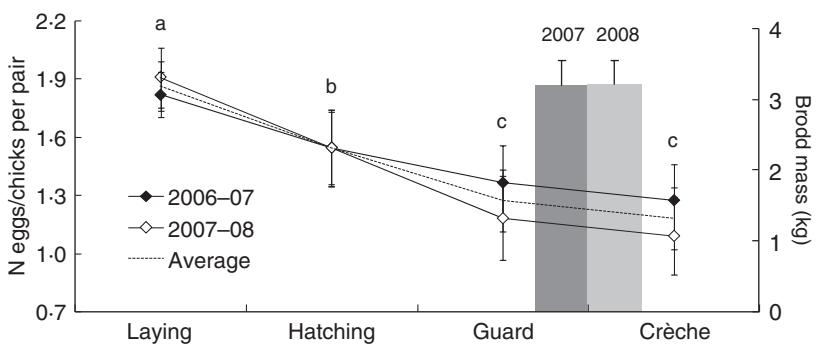

Fig. 6. Reproductive success of Adélie penguin pairs as a function of the number of eggs laid, hatched, the number of chicks during the guard and the crèche stages in 2006–2007 and 2007–2008. Histograms represent brood mass at the end of the guard stage. Results are presented as mean ± SE. Different letters correspond to significant differences between two consecutive stages for the mean reproductive success.

lite levels but corticosterone levels, body mass and reproductive success were not altered.

Interestingly, the early fast sea-ice retreat did not result in a premature phytoplankton bloom as previously described in the Arctic (Hunt & Stabeno 2002). As a result, Adélie penguins, who did not modify their breeding phenology, did not mismatch the peak of primary productivity. This match in timing between phytoplankton bloom and Adélie penguin breeding season occurred probably because both rely on the same environmental cues (i.e. daylight duration and intensity). However the early fast-ice retreat was followed by a 30% higher peak of primary production. In 2006–2007, krill stocks were thus expected to be more abundant and presumably more energetic since the recruitment must have been higher (Cripps *et al*. 1999; Quetin & Ross 2001; Atkinson *et al*. 2004). However, looking at isotopic values, higher values of $\delta^{15}N$ indicated that penguins did not feed more at lower trophic levels (krill) than at higher trophic levels (fish) in 2006–2007. This discrepancy between expected krill availability (estimated through chlorophyll concentration) and krill exploitation by Adélie penguins may come from a mismatch between phytoplankton bloom and krill recruitment in 2006–2007. Adult krill is known to feed on the phytoplankton bloom at the ice edge (Nicol 2006). In 2006–2007, as the ice edge had totally disappeared, krill recruitment may have been altered. Indeed it has been shown that an early sea-ice retreat was associated with the dominance of 'small' pico-nanophytoplankton (< 20 μm, cryptophytes) on 'large' microphytoplankton (> 420 μm, diatoms; Montes-Hugo *et al*. 2008). As a result, even if the overall chlorophyll concentration was higher in 2006–2007 than in 2007–2008, a shift in the size distribution of the phytoplankton community is likely to have occurred, with small phytoplankton prevailing in 2006–2007. As the grazing efficiency of *Euphausia superba* decreases significantly with particles < 20 μm (Moline *et al*. 2004), these specific conditions could have led to a lower krill recruitment in 2006–2007 than in 2007–2008. As a result, a high chlorophyll production is not necessarily associated with high krill recruitment. This may explain why, in 2006–2007, Adélie penguins were forced to partially shift to a diet with a higher contribution of fish resulting in higher $\delta^{15}N$ plasma values. Ainley *et al*. (2003) also found that Adélie penguins eat more fish in years with less sea-ice in the Ross Sea, suggesting that a low sea-ice cover may increase the relative abundance and/or the accessibility of fish.

As suggested by isotopic values, *Pleuragramma antarcticum* inhabits more coastal areas (higher $\delta^{13}C$ values) than *Euphausia superba* (lower $\delta^{13}C$ values, Cherel 2008). In agreement with this, isotopic measures showed that penguins fed more on higher trophic levels in coastal areas (higher $\delta^{15}N$ and $\delta^{13}C$ values) while they fed more on lower trophic levels in pelagic areas (lower $\delta^{15}N$ and $\delta^{13}C$ values, Fig. 5). Two non-exclusive reasons can explain why penguins fed more predominantly on krill in more pelagic areas in 2007–2008: (1) the presence of the fast-ice forced the penguins to reach the limit ice-edge/open water, 20–30 km away from the colony (Fig. 3), where krill is present (Nicol 2006), (2) Adélie penguins are known to feed preferentially on gravid energetic female krill (Clarke *et al*. 2002; Nicol *et al*. 2008) that live and spawn offshore (Nicol 2006). This may also explain why penguins performed longer foraging trips in 2007–2008, even when fast-ice disappeared during the guard stage.

The absence of changes in body mass and corticosterone levels between the 2 years suggested that none of the environmental conditions in the 2 years induced a food-related stress for birds. The fact that the diet differed between both years does not necessarily mean that 1 year was inferior to the other in terms of food availability. Overall food availability (krill and/or fish) may not have been drastically different and because Adélie penguins are generalist feeders, they were able to adjust their diet to the contrasting environmental conditions. Nevertheless, our results may have been biased by our selective sampling method since only birds remaining in a stable pair and present each year in the colony were included in the analysis; we may have thus selected only the most competitive birds able to respond to different levels of food availability without experiencing any food-related stress.

Metabolite levels were higher in 2007–2008 than in 2006–2007. The diet richer in krill (2007–2008) could be therefore considered as more profitable for birds than the diet richer in fish (2006–2007): as triglyceride and uric acid levels were higher in 2007–2008, one can hypothesize that birds consumed larger amount of food, stored more fat and had a higher-protein diet in 2007–2008 than in 2006–2007. However, body mass was not higher in 2007–2008 than in 2006–2007. Moreover protein content is similar in krill and fish (*Euphausia superba*: 10% of wet weight, *Pleuragramma antarcticum*: 11% of wet weight, Reinhardt & Van Vleet 1986) and lipid content is lower in krill than in fish (*Euphausia superba*: 5% of wet weight, *Pleuragramma antarcticum*: 10% of wet weight; Clarke 1980; Friedrich & Hagen 1994). One alternative explanation could be that krill lipids and proteins may be better assimilated than those of fish. Another way to interpret higher observed uric acid levels in 2007–2008, is that penguins increased protein breakdown by providing a higher muscular effort (Jenni-Eiermann & Jenni 1998) when they foraged on krill in more pelagic areas and during longer foraging trips. In the same line of thought, since foraging trip duration was longer in females than in males, females may have to provide a greater effort than males to obtain the same diet, which may explain why their uric acid levels were higher than those of males.

Comparing our results to other studies dealing with Adélie penguins facing different environmental conditions, it is interesting to notice that all parameters are not similarly modified in all studies (Table 2). The laying date, the laying success or the hatching date did not vary in any study. In contrast, some parameters changed in all studies (foraging trip duration, decreased meal size, duration of the guard stage) and can therefore be considered as sensitive indicators of a modification in the environment of Adélie penguins. Arrival body mass, diet quality, breeding success and fledgling mass varied in some studies but not in others. This is likely to be due to variable differences in food availability between the two

Table 2. Comparison of four studies dealing with consequences of inter-annual environmental conditions and breeding in Adélie penguins

	This study	Clarke *et al.* 2002*	Nicol *et al.* 2008;	Olmastroni *et al.* 2004;	Clarke *et al.* 2002†
Location	Dumont d'Urville	Béchervaise Island	Béchervaise Island	Edmonson Point	Béchervaise Island
Difference in primary production	30%	NI	NI	NI	NI
Difference in krill availability	NI	NI	70%	NI	NI
Decreased arrival body mass	No	No	No	Yes	No
Decreased laying success	No	NI	No	No	NI
Delayed laying	No	No‡	No	No‡	No‡
Delayed hatching	No	NI	No	No	NI
Increased foraging trip duration	F (30%) M (15%)	F (30%) M (20%)	F (50%) M (40%)	NI	F (150%) M (30%)
Change in diet quality	Yes	No	Yes	NI	No
Increased corticosterone levels	No	NI	NI	NI	NI
Different metabolic state	Yes	NI	NI	NI	NI
Decreased meal size	NI	Yes	Yes	NI	Yes
Delayed crèching date	(Yes)	NI	Yes	Yes	NI
Decreased breeding success	No	Yes	Yes	Yes	Yes
Decreased fledgling mass	No	Yes	No	NI	All chicks died

Studies are presented from the left to the right according to the percentage of increased foraging trip duration. Data from Clarke *et al.* (2002) are presented for years 1993–1994 (†) and 1997–1998 (*) and are completed with data provided by Emmerson *et al.* (2003). For some studies, the laying date was approximated by the female departure after egg laying (‡). The increase in foraging trip duration is presented in percentage for females (F) and males (M) during the guard stage. 'Yes' indicates a difference and 'No' indicates no differences between the two considered years (the reference year being that when foraging trips were the shortest). NI indicates that the parameter was not investigated.

considered years. It is also important to note that most studies, like ours, usually consider a limited number of years with different level of food availability and thus do not cover the full spectrum of feeding conditions. Some parameters vary with a small difference between two environmental situations while others vary only if this difference is important. For instance, we did not detect any effect of environmental variability on breeding success while other studies did. It is likely because the birds of our study experienced the smallest modification of their environment compared to other studies. This is in agreement with foraging trip duration which increase was one of the smallest of all studies.

In Béchervaise Island, between 1997 and 1998, foraging trip duration increased similarly as in our study (Clarke *et al.* 2002). However, in contrast to our data, their breeding success decreased the year when penguins foraged for a longer time. This discrepancy may come from the possibility that our penguins had to change the quality of their diet so that they could feed their chicks properly. This shift in diet was not observed in Béchervaise Island between 1997 and 1998, and may explain why breeding success was affected. This hypothesis is reinforced by Nicol *et al.* (2008): in their study, even though foraging trip duration increased more importantly than in our study, breeding success remained unchanged. Birds may have been able to maintain their breeding success because, like in our study, they were able to modify their diet.

Our study is a first attempt to relate environmental conditions to behavioural, dietary, breeding and physiological parameters in Adélie penguins. This approach is promising but proved to be an uneasy task because it integrates many levels (sea-ice, phytoplankton, krill, fish, penguins' behaviour and physiology). Consequently results are sometimes difficult to interpret. Unfortunately we were not able to compare our physiological data to other data since no other studies, examining the effects of contrasting environmental conditions on Antarctic top predators, investigated the animals' physiology (Table 2). In the other studies dealing with Adélie penguins, birds appeared to have experienced more severe modifications of their environment so that their physiological response is likely to have been different to that in our study. In addition, we have considered the isotopic values of prey as constant over time while they may also have fluctuated between years. To better understand the underlying mechanisms between environmental constraints and ecophysiological responses of Antarctic top predators, further studies should integrate data on animals' behaviour, prey, endocrinology and physiological state over a large spectrum of environmental conditions.

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