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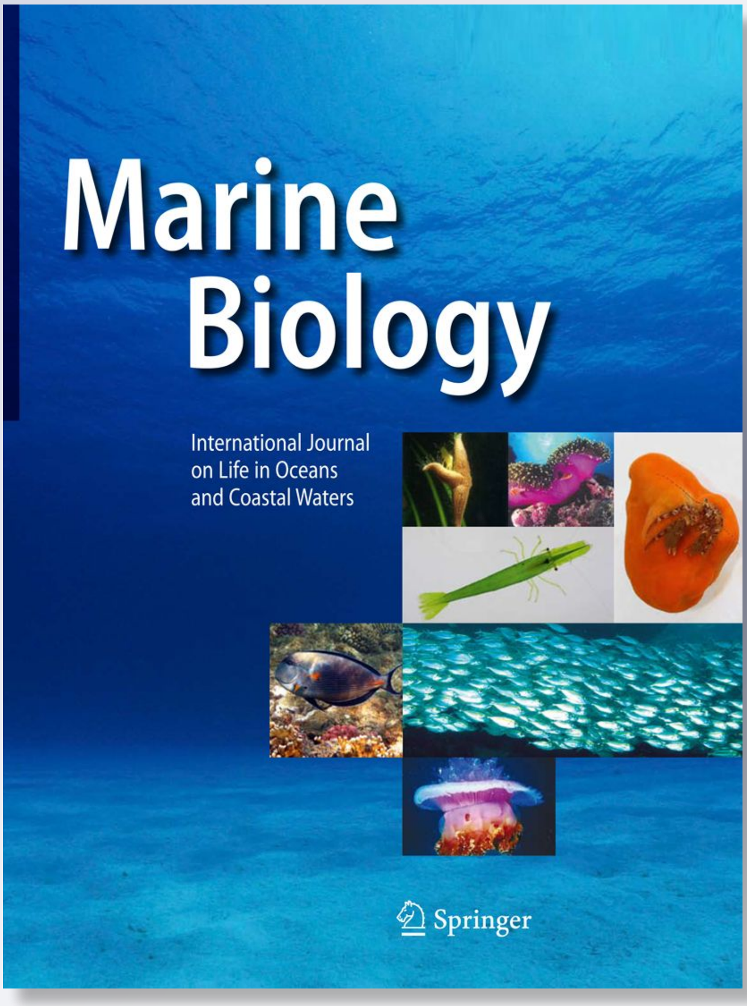

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ORIGINAL PAPER

Foraging strategies of male Adélie penguins during their first incubation trip in relation to environmental conditions

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Abstract Knowledge of habitat use by top marine predators in response to environmental conditions is crucial in the current context of global changes occurring in the Southern Ocean. We examined the at-sea locations of male Adélie penguins (*Pygoscelis adeliae*) breeding at Dumont d'Urville during their first, long incubation trip. Compared with the chick-rearing period, penguins performed longer trips, going to oceanic waters as far as 320 km from the colony. We observed 3 strategies: (1) five individuals covered large distances to the north, targeting open-ocean areas and following the currents of two persistent eddies; (2) five individuals foraged to the north-west, close to the Antarctic shelf slope at the limit of the pack ice; and (3) three individuals covered much shorter distances (northwards or eastwards). The foraging range also seemed to be limited by the body condition of the penguins before their departure to sea.

Introduction

In the current context of global environmental change, it is increasingly important to understand how Antarctic top predators use their habitat and cope with their constantly changing environment. The Adélie penguin (*Pygoscelis adeliae*) is one of the best-studied seabird species in the world. Because of its abundance (2.5 million breeding pairs) and its circumpolar distribution, it is considered as a relevant eco-indicator for the Southern Ocean (Ainley 2002). This species is well known to be sensitive to physical changes in its environment (Smith et al. 1999; Wilson et al. 2001; Ainley 2002; Croxall et al. 2002; Forcada and Trathan 2009). As an illustration of this, the sharp decrease in Adélie penguin populations in the north-west Antarctic Peninsula since 1974 has been related to the decrease in sea-ice extent in this area (Smith et al. 1999). The assessment of habitat use and distribution of penguins all around Antarctica therefore appears to be essential for long-term, large-scale monitoring of these populations. Accordingly, the foraging behaviour of Adélie penguins has been investigated with respect to sex, breeding stage and, especially, environmental conditions (e.g. Kerry et al. 1995; Watanuki et al. 1997; Clarke et al. 1998; Rodary et al. 2000; Wienecke et al. 2000; Kato et al. 2003, 2009; Lyver et al. 2011). Most studies on their at-sea distribution have taken place during the chick-rearing period (e.g.

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Kerry et al. 1995; Wienecke et al. 2000; Kato et al. 2003; Lyver et al. 2011). Few studies have investigated the first incubation trip (but see Davis and Miller 1992; Kerry et al. 1995; Clarke et al. 2006). During incubation, the obligatory presence of one adult to incubate the egg and the generally extensive sea ice (over which the penguins must walk to reach open water; Yoda and Ropert-Coudert 2007) force penguins to conduct long foraging trips, during which their partners must endure a prolonged fast. Prolonged incubation fast is a cause for abandonment of the egg in several seabirds (e.g. Chaurand and Weimerskirch 1994; Ancel et al. 1998; Groscolas et al. 2008; Spée et al. 2010). The body reserves of Adélie penguins can reach extremely low levels in this situation (Chappell et al. 1993; Spée et al. 2010). In particular, the males are present at the colony during the entire courtship period and also undertake the first incubation shift of the freshly laid eggs, while the females leave to sea to replenish their body reserves. The males have thus been fasting for up to 50 days by the time they begin their first foraging trip (Vleck and Van Hook 2002). This foraging trip is paramount to the successful continuation of their reproduction, because the adult males need to recover sufficient body condition to sustain their future energy demands, especially during the chick-rearing stage. Chick rearing is an energetically costly period since the adult has to feed its chick while ensuring its own survival.

In this context, the aim of our study was to identify the at-sea locations during the first incubation trips of male Adélie penguins breeding at Dumont d'Urville and to examine the relationships between these locations and the prevailing synoptic environmental conditions, including the position and evolution of the sea ice and the regional surface current field. Sea ice is well known to influence Adélie foraging behaviour (e.g. Watanuki et al. 1997; Ainley et al. 1998; Clarke et al. 2006). Oceanographic features, particularly wind-forced currents over the shelf and mesoscale eddies in the deeper ocean, may have an influence on prey availability as well as on swimming energetics. Oceanographic features such as fronts and eddies have been shown to influence foraging patterns in other penguin species (e.g. Jouventin et al. 1994; Sokolov et al. 2006; Wienecke et al. 2010). We also investigated the extent to which pretrip body condition and mass gained at sea were related to the at-sea foraging strategies of the birds. To the best of our knowledge, the latter issues have previously only been studied during the chick-rearing period in Adélie penguins (Watanuki et al. 2002; Angelier et al. 2008).

Materials and methods

This study was conducted at Pointe Géologie colony near the French polar station Dumont d'Urville (66°40′S, 140°01′E), Adélie Land, Antarctica, during the 2010–2011 reproductive season of Adélie penguins (during the austral summer).

Device deployment

Between 3 and 6 December 2010, 14 male Adélie penguins were equipped with GPS loggers to track their first foraging trips. Birds were captured on their nest before their departure to sea: the dirtier of the two partners was identified as the male as, in most cases, males take on the first incubation period (Ainley et al. 1983), and so females returning from sea usually have a cleaner plumage than the males. Molecular sexing was also performed to confirm the sex of each individual a posteriori. As expected, all captured penguins were males. An identification number was painted (using a temporary, biological dye, Nyanzol®) on the birds' chest for rapid identification at recapture.

The CatTraQ™ GPS logger (16 Mb memory, 230 mA lithium-ion battery, manufacturer Mr. Lee) were customized in our laboratory (IPHC–DEPE, Strasbourg, France). The initial packaging was removed, the main switch button replaced by a reed switch, and the units were then moulded into a resin. Finally, each unit was put in a heat-shrink tube for waterproofing. Final size was ca. 14 × 35 × 70 mm (representing around 1.7 % of the cross-sectional area of the penguin), and weight is 30 g. The GPS units were attached to the feathers of the birds with mastic and glue (Loctite® 401), strips of waterproof black Tesa® tape and two cable ties. Two different sampling protocols were used: (1) 1 point per hour ($n = 7$ individuals) and (2) 1 point every 5 min during 2 h per day (between midnight and 1 a.m. and noon and 1 p.m.; $n = 7$ individuals). Thus, for both sampling protocols, a maximum of 24 points was recorded per 24-h period.

Throughout the experiment, the nests of monitored birds were frequently checked (several times per day) in order not to miss the return of birds. At the end of each trip (between the 17 and 23 December 2010), equipped birds were recaptured on their nest, the logger removed and the data downloaded to a computer.

At each capture and recapture, birds were weighed with an electronic balance (Ohaus ± 2 g). At the recapture, flipper length was measured with a ruler (±1 mm), and 1–2 ml of blood was collected from the tarsus vein for sexing and stable isotope analyses (cf. Laboratory analyses, below). Capture and equipping lasted on average for 19 ± 2 min (range from 13 to 22 min), whereas the removal of the logger was faster (9 ± 2 min, range 6–16 min). An index of body condition (BCI) was calculated according to the following equation:

$$\mathrm{BCI} = \text{body mass in kg}/(\text{flipper length in mm})^3 \times 10^7 (\text{Cockrem et al. 2006}).$$

Laboratory analyses

All blood samples were kept at −20 °C until analyses. Sex determination was adapted from the protocol described by Kahn et al. (1998) and Ellegren (1996). DNA was extracted from blood samples according to the method used by Sambrook et al. (1989). Polymerase chain reaction–based sexing was performed using the 1237L/1272H primer pair (Kahn et al. 1998). The stable isotopic ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) were measured using red blood cells. This stable isotope analysis of Adélie penguins' diet is known to be relatively consistent with identification of prey found in their stomach content (Tierney et al. 2008). This method is used to get information on the trophic level of the prey (high values of δ^{15}N are related to prey with higher trophic levels) and the birds' foraging location (high levels of δ^{13}C are related to benthic/inshore prey). The complete turnover of whole blood is about 1 month (Cherel et al. 2007), which makes it the most appropriate and easily extractable tissue to investigate long foraging trips (about 15 days). Lipids were not extracted because the low lipid content of blood makes this step unnecessary (Cherel et al. 2005). The C/N mass ratios were verified for all samples (ratio ranged from 3.17 to 3.29, mean = 3.21 ± 0.04). Of each sample, 200 µl was lyophilized (48 h), powdered, weighed with a microbalance (0.51–1.17 mg) and then put into capsules for analysis. Stable carbon and nitrogen assays were performed at the 'Littoral Environnement et Sociétés' laboratory of La Rochelle (France). Results are presented in the usual δ notation (‰) relative to international standards (Pee-Dee Belemnite (PDB) for δ^{13}C and atmospheric nitrogen (N_2) for δ^{15}N). The measurement precision was ±0.03 ‰ and ±0.07 ‰ for δ^{13}C and δ^{15}N, respectively.

GPS data analysis

All GPS tracks were analysed using IGOR Pro (Wavemetrics, version 6.12A, Portland, USA) with the 'Spatial analysis' function of the Ethographer (version 2.0, Sakamoto et al. 2009) and Matlab (version 7.12, Mathworks, Natick MA, USA). Erroneous locations (travel speed > 12 km h^{-1}, Culik et al. 1994) were removed. Maximum foraging distance was calculated as the great-circle distance from the colony to the furthest point in the trip. Tracks were linearly interpolated at a rate of one point per 12 h for each bird to compare total distance travelled and travel speed. However, it should be noted that these travel distances are underestimated because of the large sampling interval. The deployed tags did not record dive activity or other relatively direct measures of foraging behaviour. However, we interpreted high track sinuosity and low swim speed as indicators of potential prey encounter (Pinaud 2008).

The Antarctic coastline data were obtained from The National Geophysical Data Center (NOAA, http://www.ngdc.noaa.gov/mgg/coast/) and the bathymetry of the study area from the Smith and Sandwell version 14.1 data set (Smith and Sandwell 1997). Daily sea-ice concentration data for December 2010 were obtained from AMSR-E passive microwave satellite estimates at 6.25 km resolution (Spreen et al. 2008), daily near-surface wind data were obtained from the NCEP/DOE Reanalysis 2 data set (http://www.esrl.noaa.gov/psd/), and daily geostrophic current data from satellite altimetry were obtained from AVISO (http://www.aviso.oceanobs.com). These daily data were processed into 5-day composites for comparison with track data.

Oceanographic model data

Physical oceanographic parameters and variability near the sea surface (temperature, salinity, currents) were estimated using a high-resolution ocean circulation model forced over the period from 1992 to 2007, similar to the one used in Hemery et al. (2011). The model has been successfully evaluated against oceanographic measurements taken in the vicinity of the George V and Adélie Basins and is able to resolve small-scale frontal features and eddies. The model is based on the Rutgers/UCLA Regional Ocean Model System (ROMS, Shchepetkin and McWilliams 2005). Note that the model does not cover the 2010 deployment season and so gives general information on the December oceanographic conditions of the region, rather than the specific conditions at the times of deployment.

Statistics

Statistical analyses were conducted in R 2.11.1 (R Development Core Team 2008). Values are presented as mean ± SD, and statistical significance was assumed at $p < 0.05$. In all cases, normality of residuals was assessed by Shapiro–Wilk tests. The relationships between pretrip body condition, foraging trip durations, distances travelled and mass gain at sea were tested using simple linear regression models followed by an analysis of variance. Because of the small number of individuals in each group, comparisons between main directions (north vs. north-west) were performed using a nonparametric test (Mann–Whitney–Wilcoxon). To compare the evolution of speed (repeated measures) during the trip and according to these main directions (north vs. north-west), a generalized estimating equation (GEE) with a gamma distribution was performed using the 'geepack' package in R.

Results

All equipped penguins were successfully recaptured after their trip. Of the 14 units, one did not record data (sampling protocol of 1 point per 5 min during 2 h per day), yielding a total of 13 reliable foraging trips. These trips lasted on average 15 ± 1 days, ranging from 13 to 17 days.

At-sea geographical range

We first compared the outputs of the two different sampling protocols, by examining the mean number of points recorded per day. Both sampling regimes were similar ($t = 1.4$, $p = 0.2$), with an average of 14 ± 2 points recorded per day. However, the sinuosity of tracks was clearer with the sampling of one point per hour (Fig. 1a, b). Events of high track sinuosity and low swim speed (which we assumed to be generally associated with periods of prey encounter) were localized over deep water (seabed depths down to 3,500 m), beyond the limit of the continental slope (Fig. 1a, b).

Mean maximum distances from the colony averaged 267 ± 45 km (range 196–323 km, see Table 1). Five out of the 13 penguins headed north-west (NW trips), while five others headed north (N trips) (Fig. 1a, b). Two other penguins covered shorter distances (208, 239 km) to the north and one to the east (200 km). Penguins going to the north went further away from the colony (mean maximum distance 310 ± 11 km) and covered greater net distances (mean total distance: 660 ± 87 km) compared to those going to the north-west (mean maximum distance: 254 ± 36 km, W = 0, $p = 0.02$; mean total distance: 550 ± 46 km, W = 0, $p = 0.001$) (Fig. 1a, b). Penguins in the north-west area foraged in or very close to the edge of the pack ice, whereas the foraging grounds to the north were almost ice free by December (Fig. 2). Penguins in the northern area appeared to forage at the edges of two fairly persistent eddies: a cyclonic eddy located at 141°E, 63.5°S and north of an anticyclonic eddy located at 140.5°E, 64.5°S. North of the shelf break, the birds travelling to the northern foraging grounds tended to follow the surface currents on the outward leg of their trip. The return leg was typically a more direct return to the colony (Fig. 2).

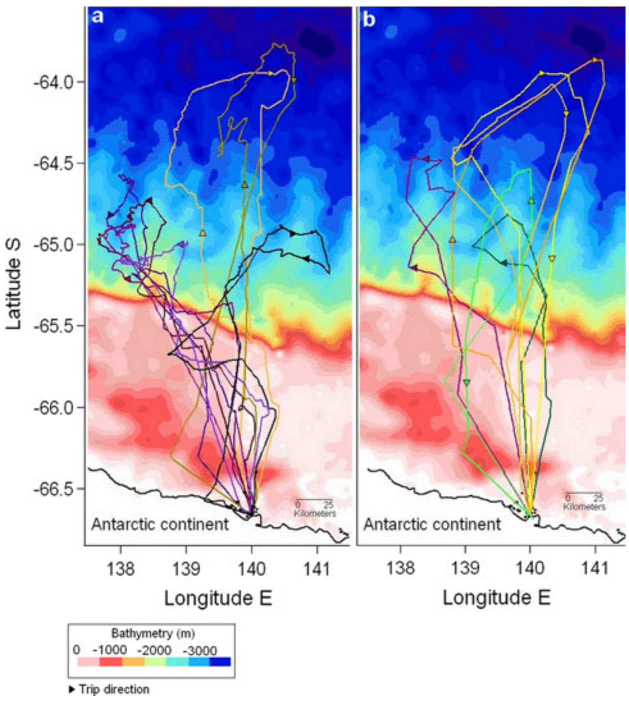

Fig. 1 Locations of 13 male Adélie penguins during their first incubation trip according to the bathymetry around Dumont D'Urville with a sampling of **a** 1 point per hour and **b** 1 point every 5 min during 2 h per day. *Colour gradients* of the *tracks* represent their predominant foraging direction: *orange* = north ($n = 5$), *purple* = north-west ($n = 5$), *green* = north but closer to the colony ($n = 2$) and *black* = east ($n = 1$). Colour version is available online

For both groups, travelling speed was higher at the beginning and at the end of the trip. However, in the middle of the trip (from 50 to 80 % of trip duration), penguins going towards the north-west had a significantly lower speed than those going towards the north (Fig. 3).

We then tested whether the distance travelled by penguins could be limited by their time spent at sea. However, the trip duration was not significantly correlated with the maximum distance ($F = 0.6$, $t = -0.7$, $r^2 = 0.05$, $p = 0.5$), nor with the total distance travelled ($F = 0.1$, $t = 0.3$, $r^2 = 0.01$, $p = 0.8$). This absence of relationship may be due to the small range (SD = 1 day) of trip durations.

Environmental conditions

Examination of the sea ice and wind data indicated that, in general, the timing of the first incubation trip coincided with the summertime decay of sea ice as it melted towards the coast. The relatively rapid retreat of sea ice during the latter part of the study period coincided with a corresponding change in wind direction from southerly to north-easterly, causing the sea ice to be compressed to a narrow banded area to the north-west of the colony (Fig. 2). The oceanographic model simulations showed that there is a series of transient anticyclonic eddies that propagate westwards roughly parallel with the 2,000-m bathymetric contour at about 64.5°S (Fig. 4). When the eddy locations coincide with the retreating sea-ice melt zone, sea-ice melt water can be transported offshore and concentrated by the eddies. This results in high concentrations of fresher water around each eddy core, as in Fig. 4. This transport of melt water off the shelf may also increase the nutrient

Table 1 Foraging trip parameters of 13 male Adélie penguins during their first incubation trip

Foraging trip direction	ID	Departure date	Trip duration (days)	Maximum distance from the colony (km)	Total distance travelled[a] (km)
North-west	64	03/12	17.0	295	578
	70	05/12	16.8	255	535
	72	05/12	16.2	260	526
	74	06/12	14.6	196	496
	75	06/12	16.0	262	613
North	66	06/12	14.4	305	712
	67	05/12	14.5	305	648
	68	04/12	13.9	323	763
	73	06/12	14.5	298	647
	77	07/12	13.3	318	724
North but closer to the colony	65	03/12	15.0	208	468
	71	08/12	12.8	239	489
East	76	7/12	15.8	200	618

[a] Data obtained using a 12-h interpolation to make both sampling protocols comparable

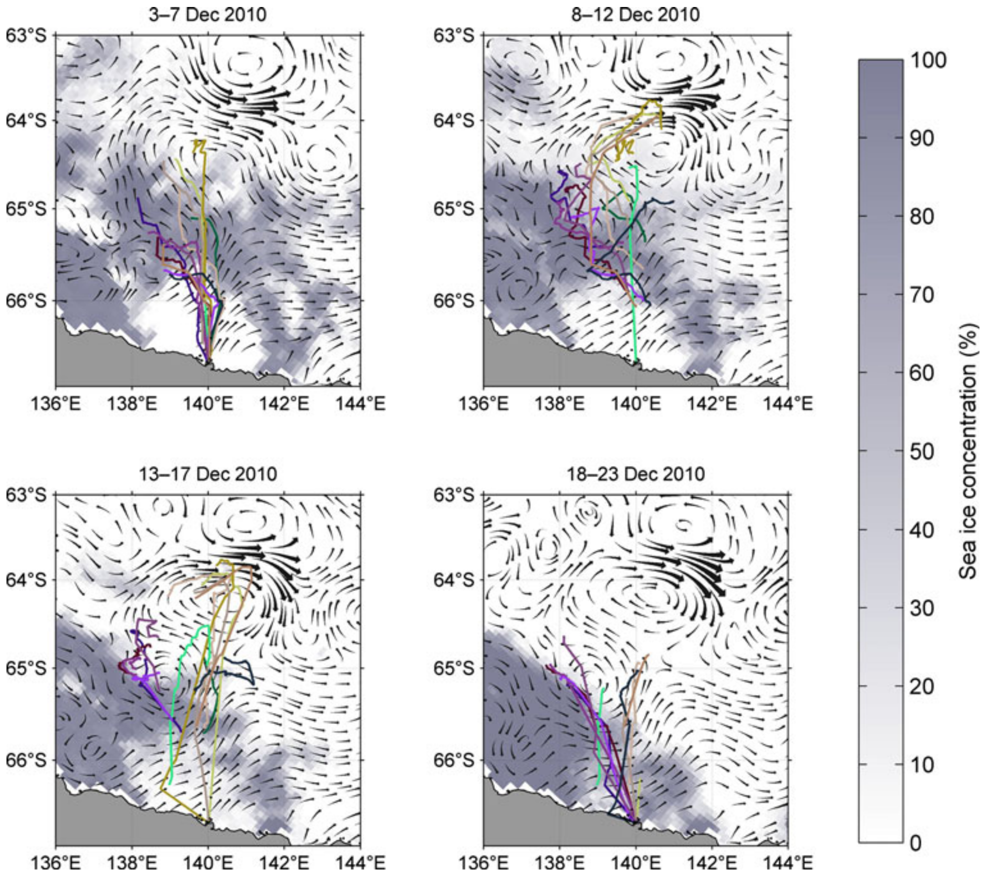

Fig. 2 Locations of 13 male Adélie penguins during their first incubation trip around Dumont D'Urville, in relation to surface geostrophic currents (*black arrows*) and sea-ice concentration (*background shading*). The *colours* of the tracks are as for Fig. 1. Colour version is available online

(particularly iron) content of the eddies above typical oceanic values (Lannuzel et al. 2007). The eddies are a persistent feature of the region, providing regularly alternating north/south transport of water. The eddies move from east to west at a rate of about 0.07° of longitude per day and so take about 3 weeks to move through the 1.5° of longitude where penguins forage.

Diet and body condition

All birds gained body mass during a trip: on average, 1.2 ± 0.3 kg per bird (range 1.0–1.7 kg). We tested whether the birds' condition before their departure (pretrip BCI) and the body mass gained during the trip were related to their at-sea behaviour. The foraging trip duration was

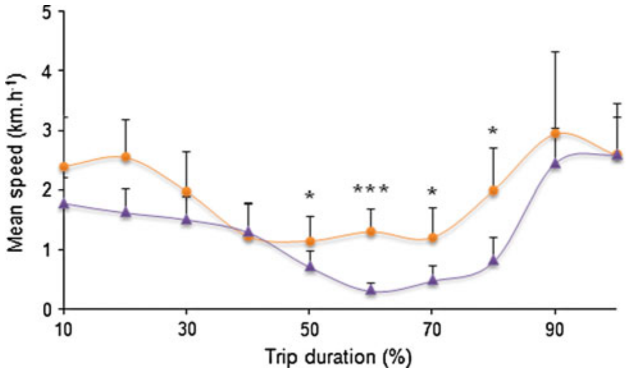

Fig. 3 Evolution of travelling speed (km h^{-1}) of 13 male Adélie penguins during their first incubation trip according to their predominantly foraging direction: north (*orange circles*, $n = 5$) versus north-west (*purple triangles*, $n = 5$). *Vertical bars* show SD (across the five individuals in both groups). * and *** indicate a significant difference ($p < 0.05$ and $p < 0.001$, respectively) between the two groups for a given percentage of the trip duration

not significantly related to the pretrip BCI ($F = 0.1$, $t = 0.3$, $r^2 < 0.01$, $p = 0.8$), nor to the body mass gained during the trip ($F = 0.4$, $t = 0.7$, $r^2 = 0.04$, $p = 0.5$). Moreover, no relationship between the body mass gained at sea and pretrip BCI was found ($F = 1.7$, $t = 1.3$, $r^2 = 0.1$, $p = 0.2$). However, there was a positive and significant relationship between their pretrip BCI and the maximum distance reached by penguins during their trip ($F = 10.6$, $t = 3.3$, $r^2 = 0.5$, $p = 0.008$) (Fig. 5). In addition, there was a positive relationship between the body mass gained and the maximum distance ($F = 7.8$, $t = 2.8$, $r^2 = 0.4$, $p = 0.02$) (Fig. 6). However, the body mass gain was not significantly correlated with the total distance travelled ($F = 4$, $t = 2$, $r^2 = 0.26$, $p = 0.07$) and was not significantly different between penguins going towards the north and those going towards the north-west (W = 19.5, $p = 0.2$).

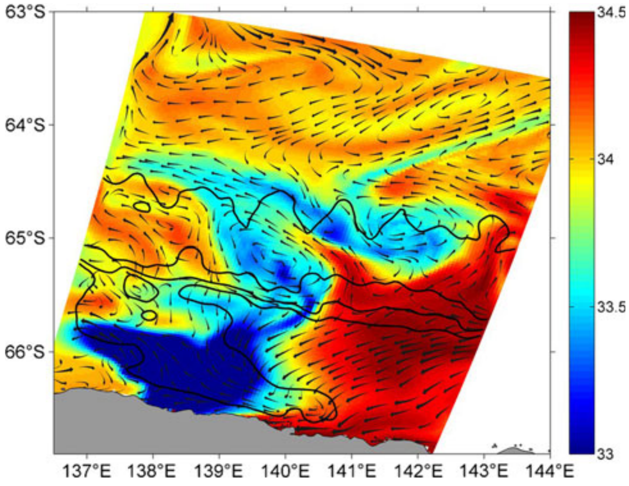

Fig. 4 December mean surface salinity (*background colours*) and near-surface currents (*arrows*) from the oceanographic model. The fresh water from sea-ice melt can develop into long tendrils drawn offshore by eddies and currents. Heavy *black lines* show bathymetric contours at 500-m interval. Colour version is available online

Neither $\delta^{13}C$ (index of foraging location) nor $\delta^{15}N$ (trophic level) values were significantly affected by the maximum distance reached by penguins ($\delta^{13}C$: $F < 0.01$, $t = 0.6$, $r^2 < 0.01$, $p = 0.96$; $\delta^{15}N$: $F = 0.6$, $t = 0.7$, $r^2 = 0.02$, $p = 0.47$). In addition, the penguins' main at-sea locations (N vs. NW) did not significantly relate to a difference in trophic levels used ($\delta^{15}N$, W = 14, $p = 0.8$). Because of one low value (penguin exploiting the NW area, $\delta^{13}C = -25.5$ ‰), the difference of $\delta^{13}C$ values was also not significant between these two groups (N vs. NW) (W = 3.5, $p = 0.07$). However, if this point was excluded, the difference became significant (W = 0, $p = 0.02$). The two penguins foraging in neritic waters closer to the colony had high $\delta^{13}C$ values (mean $\delta^{13}C = -24.9 \pm 0.1$ ‰) compared with those of other penguins. In contrast, the single bird foraging to the east had a relatively low $\delta^{13}C$ value (Fig. 7).

Discussion

The foraging extent of Adélie penguins in the region of Dumont d'Urville is known to range about from 5 to 120 km from the coast during chick rearing (Kerry et al. 1995; Wienecke et al. 2000; Angelier et al. 2008). In contrast, our recordings indicate that during the incubation period, Adélie penguins in this region forage much further from the colony (267 ± 45 km). Despite contrasting environmental conditions, these results are similar to those reported by Clarke et al. (2006) at Béchervaise Island (median maximal distance was 272 km for 5 years of observations). In the Béchervaise area, the constant presence of fast ice around the colony during the incubation

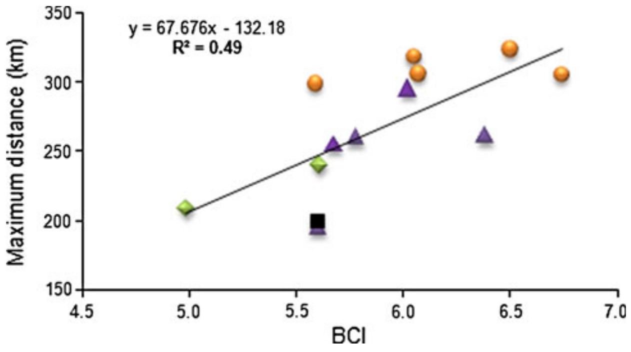

Fig. 5 Maximum distance reached by 13 male Adélie penguins during the first incubation trip according to their body condition index (BCI) before the trip and to their predominantly foraging direction: north (*orange circles*), north-west (*purple triangles*), north but closer to the colony (*green lozenges*) and east (*black square*)

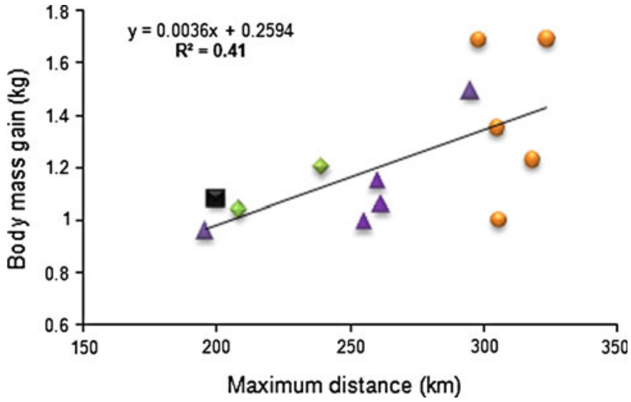

Fig. 6 Relationship between body mass gain at sea and maximum distance reached by 13 male Adélie penguins during their first incubation trip according to their predominantly foraging direction: north (*orange circles*), north-west (*purple triangles*), north but closer to the colony (*green lozenges*) and east (*black square*)

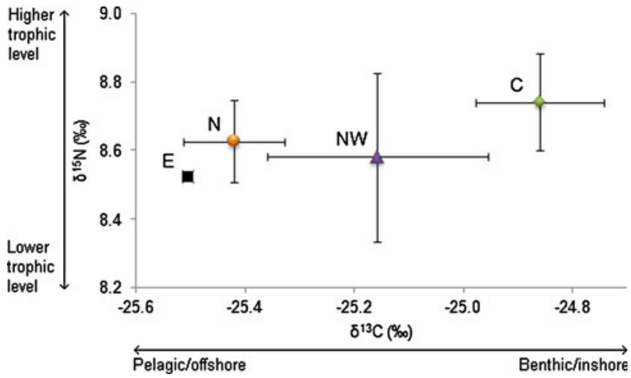

Fig. 7 Stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) for red blood cells of 13 male Adélie penguins during their first incubation trip according to their predominantly foraging direction: north (*N*, *orange circles*, $n = 5$), north-west (*NW*, *purple triangles*, $n = 5$), north but closer to the colony (*C*, *green lozenges*, $n = 2$) and east (*E*, *black square*, $n = 1$)

period forces penguins to walk several kilometres to reach the closest polynya. At Dumont d'Urville, the fast ice usually disappears during the months of November or December (indeed, no fast ice surrounded Dumont d'Urville at the beginning of December 2010). We suggest that increased foraging extents during the first incubation trip are due to (1) the poor body condition of the birds and their lower motivation to return ashore (cf. below) and/or (2) potentially low food availability near the colony during this period.

Energetics and temporal constraints

During chick rearing, foraging trip duration has been reported to be positively correlated with maximum distance travelled during this period (Clarke et al. 1998, 2006; Angelier et al. 2008). In our study, birds travelled further offshore than during chick rearing, and trip duration was not correlated with the maximum distance from the colony. During incubation, adults do not need to come back to the colony as regularly as during chick rearing when they have to provision their offspring. Although they still have to relieve their partner fasting on the nest, the major constraint for penguins during the incubation trip seems to be energetic rather than temporal. We showed here that there is a positive relationship between the maximum distance reached by penguins and the body mass gained during their trip. In many seabirds, including Adélie penguins (Ropert-Coudert et al. 2004), long and/or distant trips have been associated with journeys devoted to the replenishment of bird's own body reserves, in contrast to trips shorter and/or closer to the colony that aim to provision chicks on a regular basis (see Chaurand and Weimerskirch 1994).

Although we would expect that individuals with poorer body conditions would have gone farther, we found the opposite relationship: better-conditioned birds went farther. This suggests that penguins in good condition are physically able to go farther than penguins in poorer condition. This emphasizes the importance of body condition at the end of the fasting period, as birds with low body reserves could be limited in their foraging range. It has already been shown, for instance, that black-legged kittiwakes (*Rissa tridactyla*) in good condition spent less time foraging than those in poor condition (Angelier et al. 2007). However, our results show no significant relationship between pretrip BCI and body mass gain. This inability to forage at range may still have an impact on the capacity of birds to replenish their reserves in bad years, for instance when prey availability is poor or when prey patches are located farther from the colony.

Food availability

In addition to the high energetic constraint of the incubation fast, Adélie penguins might also need to deal with the low food availability during this period because the peak of primary productivity (i.e. the phytoplankton bloom) arrives later in the season, that is, during the chick-rearing period (see the evolution of chlorophyll concentration over two summer seasons (2006–2007 and 2007–2008) in Dumont d'Urville reported by Beaulieu et al. 2010, Fig. 3). In the ocean, phytoplankton is at the base of many food chains and can be used as an index of food availability as its concentration correlates positively with summer krill density (Atkinson et al. 2004). In Dumont d'Urville, penguins feed predominantly on euphausiid crustaceans (Antarctic and ice krill, *Euphausia superba* and *E. crystallorophias*, respectively) and also Antarctic silverfish (*Pleuragramma antarcticum*) during chick-rearing period (Wienecke et al. 2000). Although surveys of krill have been conducted near

Dumont d'Urville during the chick-rearing period (e.g. Nicol et al. 2000; Amakasu et al. 2011), data showing abundance and distribution of prey before the phytoplankton bloom are still scarce. According to Cherel (2008), nitrogen isotopic signatures of Adélie penguins' prey are distinguishable, ranging from ca. 5.5 and 7 ‰ for Antarctic and ice krill, respectively, to 11 ‰ for Antarctic silverfish in the Adélie Land region during spring. Our stable isotope data show a δ15 N of about 8.6 ‰, indicating that penguins likely feed on both krill and fish during this period. Amakasu et al. (2011) indicated that ice krill and Antarctic silverfish are dominant in neritic waters, whereas Antarctic krill is dominant in waters to the north of 66°S, with high densities located around 65.5°S and 64°S. In addition, Adélie penguins foraging in the deep ocean during the winter feed on a mixture of krill, myctophid fish and squid (Ainley et al. 1992). Although these results must be used cautiously (different year and different season), we hypothesize that Adélie penguins in Dumont d'Urville feed mainly on Antarctic krill and probably a mixture of Antarctic silverfish, myctophids and squid during their first incubation trip.

Both the north-west and northern foraging strategies are likely to be targeting processes that lead to predictable and consistently elevated prey densities. The spatial pattern and timing of sea-ice melt and accompanying change in winds are fairly consistent from year to year, leading to consistent sea-ice formation to the north-west of the colony. Pack ice and the continental slope are both often indicated as areas rich in food (Ainley and Jacobs 1981; Ainley et al. 1998; Ainley 2002). In particular, krill densities under the edge of the sea ice are typically much higher than those in the adjacent open water (Brierley et al. 2002). Together, these factors suggest that the north-west foraging grounds represent a reliable prey source from year to year. The northern, offshore foraging area is more dynamic, with transient eddies propagating through the area. The presence of eddies in this region has already been reported in the literature, although in that case they were mainly cyclonic eddies (Aoki et al. 2007). In such dynamic conditions, targeting a specific geographical location might therefore not be a particularly reliable strategy for finding food. However, the melted ice water, with high nutrient content (Lannuzel et al. 2007), is advected offshore and entrained by these eddies. This potentially presents a simple foraging strategy for the birds: follow the offshore current provided by a passing eddy, and this will lead to a concentration of food. This strategy is also potentially energy efficient, since the birds are following the currents, at least during the first half of the trip, that is, when they are in their lowest body condition. The return trip is conducted with less favourable currents, but it occurs after birds have replenished their body reserves. In early summer, the nearshore surface currents are fairly weak, allowing the penguins to easily move to the sea-ice melt edge which roughly corresponds with the continental shelf break and the lower edge of the offshore zone of eddies. Further studies may show whether this foraging strategy is consistent from year to year and provide stronger evidence for the role of synoptic oceanographic conditions on foraging strategies.

At-sea habitat preferences

Despite a relatively small sample size, we found that the penguins apparently present a geographical segregation in foraging effort at this stage of the breeding season. Of particular interest of our study is the unexpected presence of penguins foraging to the north in open-ocean areas. In the literature, the Adélie penguin has been identified as a pack-ice obligate species and also referred to as 'a creature of the Antarctic pack ice' (Ainley 2002). These birds typically forage in zones covered by ice floes, but our results show that their association with pack ice may not be as exclusive as these titles imply, at least concerning the summer breeding period.

Since we observed a geographical segregation in foraging location, we expected to see a corresponding difference in diet composition. However, the stable isotope measurements indicated that all penguins, regardless of their direction, fed on the same proportions of different trophic-level prey species (no δ^{15}N differences). It is possible that the absence of differences here might reflect the duration of the turnover of the blood cells (ca. 1 month) compared to the duration of the trip recorded (ca. 15 days). We observed two main foraging zones: the north and north-west areas. Both areas seem to be similarly productive, since we did not find any differences in the mass gained and distance travelled between the two groups of birds. We suggest that by using different areas, penguins might avoid intraspecific foraging competition. Competition with emperor penguins (*Aptenodytes forsteri*) is unlikely since their foraging areas do not overlap during this period: emperor penguins forage in shelf waters north-east of the Pointe Géologie colony, with maximum distances reaching 160 km (Zimmer et al. 2008). Adélie penguins may still compete with other krill consumers such as whales, seals and fish (Ainley et al. 2006), but such competition might be mitigated to some extent by the relatively large foraging ranges of the penguins at this time of the season.

Conclusions

Male Adélie penguins foraged up to 320 km from the colony during their first incubation trip. The high speeds observed at the beginning and at the end of each trip indicates that the penguins were not randomly searching for food. These results are consistent with the study of Weimerskirch (2007) showing that, at least at a mesoscale (i.e. 100–1,000 km), seabirds are foraging for predictable resources. We suggest that Adélie penguins used recurrent oceanographic features around Adélie Land, particularly eddies and pack-ice edges, for foraging.

The sample size of this study was relatively small, and so our interpretation of the observed patterns is somewhat tentative. In this study, individuals appeared to utilize one of two different foraging strategies: (1) using the prevailing currents to cover large distances to the north and targeting the persistent eddies in this region or (2) foraging to the north-west, close to the Antarctic slope and at the limit of the pack ice. We also hypothesize that the foraging range seems to be limited by the birds' body condition at the end of the fasting period. However, compared with the study of Clarke et al. (2006), the presence or absence of fast ice around the colony does not seem to influence the large distances travelled during this period. Rather, we wonder whether the crucial need for birds to replenish their body reserves as well as the possible low food availability at this stage might be more important determinants of foraging distances reached. The establishment of a long-term GPS monitoring programme at this colony should provide information essential to our understanding of the effects of climate change on Antarctic marine ecosystems. Contrary to the Antarctic Peninsula, there are no current indications of climate change–related decreases in Adélie Land penguin populations (Croxall et al. 2002). The data we collected in this area could thus be used as the baseline for long-term monitoring studies on Adélie penguins and help highlight modifications in penguins' foraging behaviour in relation to predictable changes in their at-sea habitat.

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