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Looking for new emperor penguin colonies? Filling the gaps

André Ancel[a,*], Robin Cristofari[a,b,c], Phil N. Trathan[d], Caroline Gilbert[e], Peter T. Fretwell[d], Michaël Beaulieu[f]

[a] Université de Strasbourg, CNRS, IPHC UMR 7178, F-67000 Strasbourg, France
[b] Centre Scientifique de Monaco, LIA-647 BioSensib, 8 quai Antoine I^{er}, MC 98000, Monaco
[c] University of Oslo, Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, Postboks 1066, Blindern, NO-0316, Oslo, Norway
[d] British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 OET, United Kingdom
[e] Université Paris-Est, Ecole Nationale Vétérinaire d'Alfort, UMR 7179 CNRS MNHN, 7 avenue du Général de Gaulle, 94704 Maisons-Alfort, France
[f] Zoological Institute and Museum, University of Greifswald, Johann-Sebastian Bach Straße 11/12, 17489 Greifswald, Germany

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ABSTRACT

Detecting and predicting how populations respond to environmental variability are crucial challenges for their conservation. Knowledge about the abundance and distribution of the emperor penguin is far from complete despite recent information from satellites. When exploring the locations where emperor penguins breed, it is apparent that their distribution is circumpolar, but with a few gaps between known colonies. The purpose of this paper is therefore to identify those remaining areas where emperor penguins might possibly breed. Using the locations of emperor penguin breeding colonies, we calculated the separation distance between each pair of geographically adjacent colonies. Based on mean separation distances between colonies following a circumpolar distribution, and known foraging ranges, we suggest that there may yet be six undiscovered breeding locations with half of these in Eastern and the remainder in Western Antarctica. Productivity in these regions suggests that food resources are likely to sustain emperor penguin populations.

Our analysis highlights a fundamental requirement, that in order to predict how species might respond to regional climate change, we must better understand their biogeography and the factors that lead to their occupation of particular sites. Regarding emperor penguins, remote sensing should target the identified gaps apparently devoid of penguins in order to update the total number of colonies, to re-evaluate both the regional and global population of emperor penguins, and to gain a better understanding of their biogeography.

1. Introduction

The climate of our planet is undergoing regional and global changes, which are driving shifts in the distribution and phenology of many plants and animals (Hansen et al., 2013). There are a number of ecosystems and communities where the physical drivers of ecological change might become apparent before anywhere else. For example, the impact of climate changes is more visible in coralline ecosystems, where small variation in temperature can lead to the massive bleaching of coral reefs (Hoegh-Guldberg et al., 2007). These climate changes are also visible in polar ecosystems where, for instance,

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* Correspondence to: CNRS/IPHC, UMR 7178, 23 rue Becquerel, 67087 Strasbourg Cedex 02, France.
E-mail addresses: andre.ancel@iphc.cnrs.fr (A. Ancel), robin.cristofari@iphc.cnrs.fr (R. Cristofari), pnt@bas.ac.uk (P.N. Trathan), caroline.gilbert@vet-alfort.fr (C. Gilbert), ptf@bas.ac.uk (P.T. Fretwell), miklvet@hotmail.fr (M. Beaulieu).

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small variation in temperature and sea ice cover can alter seabird populations (Croxall et al., 2002; Jenouvrier et al., 2012; Lynch and LaRue, 2014; Lyver et al., 2014). These regions provide examples that may foreshadow future events elsewhere on the planet.

Here, we focus on the southern polar region, which includes one of the most rapidly warming areas of the planet. For example, over the last 50 winters, the sea-level mean annual air temperature of the Antarctic Peninsula has become up to 6 °C higher than on the eastern side of the Antarctic continent (Reynolds, 1981; Turner et al., 2005; Malvaney et al., 2012). Among birds adapted to live in this extreme and variable environment, penguin species are the best known. As with other penguin species inhabiting more northerly locations, Antarctic penguins are restricted to a limited breeding latitudinal range at the shoreline of the continent (Ancel et al., 2013a), thereby limiting their ability to track latitudinally climate changes (Forcada and Trathan, 2009). Detecting and predicting how penguin populations respond to environmental variability represents a crucial challenge for their population management and their conservation (Jenouvrier et al., 2014; Trathan et al., 2014). This is particularly true for populations that exist at high latitudes, many of which are already exhibiting changes in population dynamics associated with global warming (Boersma, 2008; Baylis et al., 2012; Boersma and Rebstock, 2014; Lescröel et al., 2014). Notably this is the case for the emperor penguin (*Aptenodytes forsteri*), the only bird species that breeds in the midst of the Austral winter on the Antarctic continent (Stonehouse, 1952; Prévost, 1961).

Emperor penguin breeding sites are found at the edge of the Antarctic continent between latitudes 64°S and 77°S (Woehler, 1993; Lea and Soper, 2005; Ancel et al., 2013a). Within this circumpolar high-latitude distribution, the emperor penguin almost always breeds on stable fast ice near the coast (Mellick and Bremers, 1995; Coria and Montalti, 2000; Todd et al., 2004; Trathan et al., 2011), but a number of colonies have been reported on ice shelf (Wienecke, 2012; Fretwell et al., 2014) or land (see references in Fretwell et al., 2012, 2014) rather than on sea ice. Breeding colonies are usually located in areas where icebergs and ice cliffs shelter them from the prevailing winds (Prévost, 1961; Kooyman, 1993), but not far from open sea or polynyas, biologically productive areas of open water or reduced sea ice cover within the pack ice, where they feed (Ancel et al., 1992; Kooyman, 1993).

Available data on the abundance, distribution and phenology of the emperor penguin are far from complete. For instance, its phenology is only well known at the Pointe Géologie archipelago (67°S, 140°E) in Terre Adélie, where the colony has been surveyed for more than 60 years (Prévost, 1961). Generally, it is assumed that the phenology of all other colonies reflects that in Terre Adélie. The lack of information regarding other colonies is generally due to the logistic difficulties of reaching them. Indeed, due to the persistence of sea ice, few ships are able to reach most colonies before post-breeding adults disperse in early summer. During the breeding season in winter, access to colonies is even more difficult or impossible due to prevailing bad weather conditions and extensive pack ice.

Until recently, the location and size of emperor penguin colonies usually involved population counts and mapping on the ground (Prévost, 1961; Lea and Soper, 2005; Wienecke, 2010) or aerial photographs (Wienecke, 2012; Ancel et al., 2014; LaRue et al., 2015). Yet, these methods are laborious, time consuming and costly. As access to colonies is generally very difficult, it appears that a process of discovery is now best undertaken using remote sensing data from satellites (Barber-Meyer et al., 2007; Fretwell et al., 2012; LaRue et al., 2015). Indeed, several studies have recently demonstrated the utility of such remote-sensing imagery to identify and estimate the abundance of emperor penguin colonies (Barber-Meyer et al., 2007; Fretwell and Trathan, 2009; Fretwell et al., 2012, 2014). However, the total number of colonies remains uncertain. Currently, 54 colonies are thought to exist around the Antarctic continent (Fretwell et al., 2012, 2014; Wienecke, 2012; Ancel et al., 2014; LaRue et al., 2015). Of these, 48 are situated on fast-ice, four are permanently or occasionally located on ice-shelves (Barrier Bay, Shackleton Ice Shelf, Larsen Ice Shelf, Rupert Coast; (Fretwell et al., 2014)), one on rock (Taylor Glacier) and one on or near a frozen lake (Amundsen Bay). Four colonies have been recently identified by remote sensing and subsequently visited; two close to the Mertz Glacier and one close to Ragnhild during the austral summer of 2012–13 (Ancel et al., 2014), and one at Rothschild Island during 2015–2016 (Trathan et al., unpublished). The most recent satellite surveys include use of multiple images for each colony, with fine spectral and spatial resolution and high temporal resolution. Nevertheless, heavy cloud cover over the course of the breeding season may mean that colonies might be missed by satellite surveys. Detection during the winter is not feasible as optical satellite data is restricted by the lack of light. Further, especially towards the end of the breeding season, the break-out of sea ice may reduce the probability of detecting colonies. Complementary methods such as high-resolution imagery must therefore be found to locate these potentially missing colonies in winter.

When exploring the locations where emperor penguins breed, it is apparent that their distribution is circumpolar, but with a few gaps between known colonies (Fretwell et al., 2012). However, it is not yet known whether such gaps are actually devoid of emperor penguins, or if insufficient effort has been focussed on these regions to find if colonies actually exist. Interpreting the existence of a gap is complex as such a gap might truly result from low resource availability and/or inadequate sea ice structures and/or inadequate climatic conditions leading to a true absence of colonies, or alternatively the observed gap might result from a lack of observation effort. The purpose of this paper is therefore to identify regions, which might plausibly shelter emperor penguin breeding sites that we might be missing. Ultimately, remote sensing should target these gaps in order to update the total number of emperor penguin colonies, to re-evaluate both the regional and global population of emperor penguins, and to gain a better understanding of their biogeography.

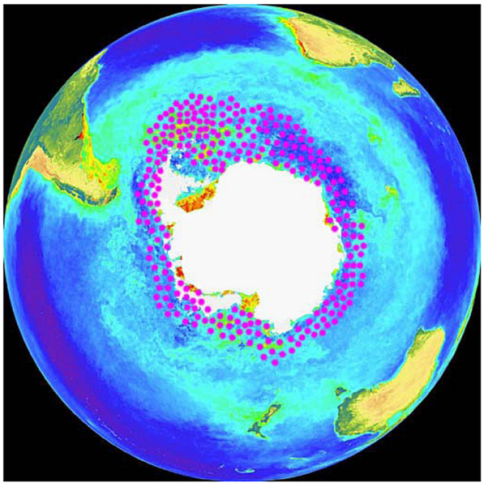

Fig. 1. Each pink dot represents the krill distribution around the Antarctic Continent. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Source: Courtesy of NASA/SeaWiFS Project.

2. Materials and methods

Using the remotely sensed locations of 46 emperor penguin breeding colonies determined by their guano stains on sea ice (Fretwell et al., 2012), combined with two colony locations close to the Mertz Glacier (Ancel et al., 2014) and four colony positions on ice-shelves (Fretwell et al., 2014) together with others (Wienecke, 2012; LaRue et al., 2015), we calculated the loxodromic separation distance, that is the shortest distance between two points on the surface of a sphere, between each pair of geographically adjacent colonies. We then apportioned each separation distance into classes of one hundred kilometres, which is the mean maximum distance a breeding adult can travel from the colony during the breeding period (Wienecke and Robertson, 1997; Zimmer et al., 2008). Finally, based on mean separation distances between colonies, and assuming a circumpolar distribution, we show the potential areas where emperor penguins might exist or could potentially settle. Such a separation distance is based on the assumptions that (1) there is competitive exclusion for food resources between individuals belonging to two adjacent colonies as shown for gentoo (*Pygoscelis papua*) and Adélie penguins (*P. adeliae*) (Cimino et al., 2016), and that (2) food resources (krill, squid and Antarctic silverfish) are distributed around the continent (Atkinson et al., 2009; Fig. 1), based on evidence from the location of polynyas and productivity of sea ice (Tamura et al., 2008; Nihashi and Ohshima, 2015). We therefore assembled several maps, consisting of colony plots, chlorophyll *a* concentration distribution and ice density around the Antarctic continent (see the legend of Fig. 4). As the distance between colonies may be the result of competitive exclusion between colonies, we also investigated whether the distance between two existing adjacent colonies could be linked to the number of penguins present in these colonies. Using linear regressions, we firstly correlated the size (number of pairs of penguins) of a given colony with its mean loxodromic distance between its two adjacent colonies, and secondly we correlated the loxodromic distance between two colonies with the sum of the size (number of pairs of penguins) of these two colonies ($N = 44$ and $N = 38$, respectively). We also undertook these analyses within each of the four quadrants of the Antarctic continent (North-East, South-East, South-West and North-West), to test whether competition would occur only in certain zones or in all zones.

3. Results

The loxodromic distance between one colony and the next nearest neighbour ranged between 19 and 899 km (Table 1) and averaged 311 km (±176 km SD, median = 324 km). The distance between colonies is less than 500 km in 88.9% of the cases, and less than 600 km in 94.5% of all cases (Fig. 2).

Based on these results (see Table 1 and Fig. 2), we suggest that there may be between three (distance between existing colonies >600 km) and six (distance between existing colonies >500 km) regions sheltering unknown colonies of emperor penguins. These potential new breeding sites are between the Sabrina Coast and Dibble Glacier, between Cape Crozier and Cape Colbeck, and between Rothschild and Snow Hill Island. Using the less conservative separation interval, we suggest that there may also be colonies between the Mertz Glacier East and Davis Bay, between Davis Bay and Cape Roget, and between the Larsen Ice Shelf and Dolleman (Fig. 3). Importantly, low sea ice density and high zoo-phytoplankton concentrations are present in these regions (Fig. 4), revealing polynyas and suggesting that food resources are present to sustain emperor penguins populations.

The known distribution of colonies surrounding the Antarctic shows a clockwise mean loxodromic separation distance of 268 ± 122 km SD, 275 ± 180, 337 ± 202 in three (0° to 90°, 90° to 180° and 270° to 360°, respectively) of the four quadrants

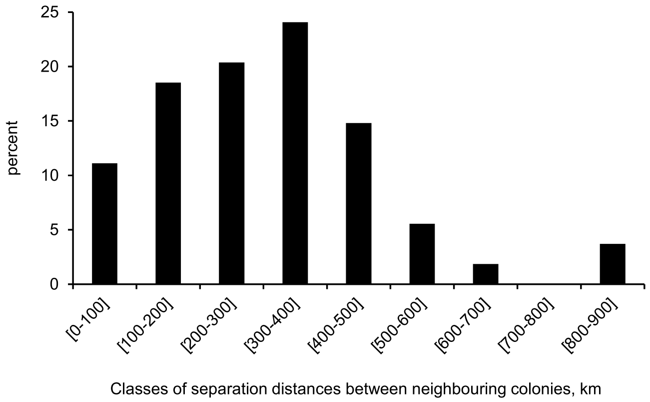

Fig. 2. Distribution of the 54 known emperor penguin colonies grouped according to the loxodromic separation distances between each pair of geographically adjacent colonies by class of 100 km.

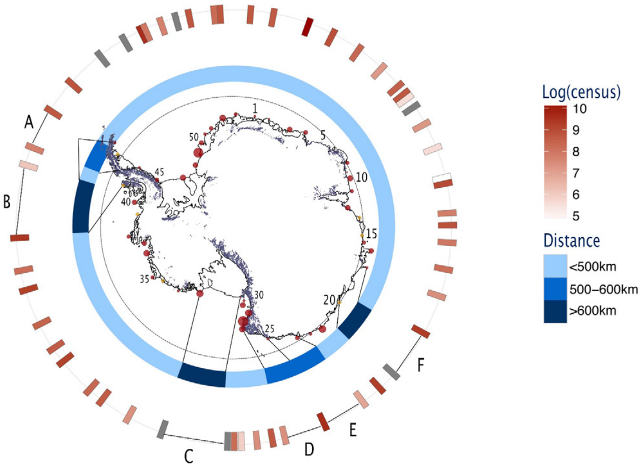

Fig. 3. Location of the 54 emperor penguin breeding colonies around the Antarctic continent. The outer circle represents population census estimates (log scale; grey: no data available). The inner circle represents the distance between neighbouring colonies. The area of the red circles symbolizing colonies is proportional to population size (yellow squares correspond to uncounted colonies). The numbers at the border of the continent refer to colonies in Table 1. The letters A–F represent the six hypothetical locations of undiscovered colonies (see Table 2).

(with 15–16 colonies in each quadrant). Only in the southwestern quadrant (from Cape Colbeck to Noville Peninsula; 180°–270°) is the mean separation between colonies slightly but not significantly more important than in the other quadrants (408 ± 211 km SD; GLM: $F_{3,49} = 1.316$, $P = 0.280$), and the number of colonies is much reduced (with seven colonies). In this quadrant, the number of wintertime polynya days (number of days during which a polynya is identified between June and September) is high (more than 70) and comparable to the other quadrants (more than 70), especially in its southern part (Kern, 2009), suggesting that resource availability is as high as in the other quadrants.

Considering all colonies, the size of a given colony was not correlated with the mean loxodromic distance between its two adjacent colonies ($r^2 = 0.0174$, $P = 0.393$, distance $= 322.9 - (0.00318 *$ colony size$)$). This result was similar within each of the four quadrants (North-East quadrant: $r^2 = 0.152$, $P = 0.169$, $N = 14$, distance $= 360.6 - (0.00918 *$ colony size$)$; South-East quadrant: $r^2 = 0.0701$, $P = 0.382$, $N = 13$, distance $= 325.3 - (0.00524 *$ colony size$)$; South-West quadrant $r^2 = 0.241$, $P = 0.322$, $N = 6$, distance $= 304.1 + (0.0160 *$ colony size$)$; North-West quadrant: $r^2 = 0.0493$, $P = 0.512$, $N = 11$, distance $= 247.1 + (0.00788 *$ colony size$)$). Similarly, the loxodromic distance between two colonies was not correlated with the sum of the size of these two colonies ($r^2 = 0.0228$, $P = 0.365$, distance $= 322.6 - (0.00282 *$ sum of colony size$)$). However, considering both equations, the two constants were significant ($P < 0.001$), and respectively of 322.6 and 322.9 km. This result was equivalent to the analyses within each quadrants (North-East quadrant: $r^2 = 0.193$, $P = 0.176$, $N = 11$, distance $= 367.1 - (0.00713 *$ sum of colony size$)$; South-East quadrant: $r^2 = 0.0574$, $P = 0.478$, $N = 11$, distance $= 301.3 - (0.00320 *$ sum of colony size$)$; South-West quadrant: $r^2 = 0.0933$, $P = 0.617$ $N = 5$, distance $= 862.1 - (0.0330 *$ sum of colony size$)$; North-West quadrant: $r^2 = 0.0438$, $P = 0.537$, $N = 11$, distance $= 233.6 + (0.00585 *$ sum of colony size$)$).

Table 1
Location of the 54 emperor penguin breeding colonies and loxodromic separation distance (km) between each pair of geographically adjacent colonies.

#	Name	Longitude	Latitude	Separation	Remarks	References
1	Astrid Coast	8.32°E	69.95°S			Fretwell et al. (2012)
2	Lazarev Ice Shelf	15.55°E	69.75°S	279		Fretwell et al. (2012)
3	Ragnhild	27.15°E	69.91°S	443		Fretwell et al. (2012)
4	Gunnerus Bank	34.38°E	68.76°S	318		Fretwell et al. (2012)
5	Umbeashi Rock	43.02°E	68.05°S	367		Fretwell et al. (2012)
6	Amundsen Bay	50.54°E	66.78°S	358	on a frozen lake	Fretwell et al. (2012)
7	Kloa Peninsula	57.28°E	66.64°S	297		Fretwell et al. (2012)
8	Fold Island	59.32°E	67.32°S	116		Fretwell et al. (2012)
9	Taylor Glacier	60.88°E	67.45°S	68	on land	Fretwell et al. (2012)
10	Auster	63.97°E	67.40°S	132		Fretwell et al. (2012)
11	Cape Darnley	69.70°E	67.89°S	246		Fretwell et al. (2012)
12	Amanda Bay	76.83°E	69.27°S	320		Fretwell et al. (2012)
13	Barrier Bay	81.82°E	66.55°S	374	on ice shelf	Fretwell et al. (2014)
14	West Ice Shelf	81.93°E	67.23°S	76		Wienecke (2012)
15	Burton Ice Shelf	89.70°E	66.27°S	363		LaRue et al. (2015)
16	Haswell Island	93.01°E	66.53°S	149		Fretwell et al. (2012)
17	Shackleton Ice Shelf	96.02°E	65.09°S	213	on ice shelf	Fretwell et al. (2014)
18	Bowman Island	103.07°E	65.16°S	329		Fretwell et al. (2012)
19	Peterson Bank	110.24°E	65.92°S	336		Fretwell et al. (2012)
20	Sabrina Coast	121.14°E	66.16°S	490		LaRue et al. (2015)
21	Dibble Glacier	134.80°E	66.00°S	618		Fretwell et al. (2012)
22	Point Geologie	140.01°E	66.67°S	241		Fretwell et al. (2012)
23	Mertz Glacier West	145.54°E	67.24°S	246		Ancel et al. (2014)
24	Mertz Glacier East	145.83°E	67.37°S	19		Ancel et al. (2014)
25	Davis Bay	158.49°E	69.35°S	543		Fretwell et al. (2012)
26	Cape Roget	170.60°E	71.99°S	509		Fretwell et al. (2012)
27	Coulman Island	169.62°E	73.35°S	154		Fretwell et al. (2012)
28	Cape Washington	165.38°E	74.64°S	190		Fretwell et al. (2012)
29	Franklin Island	168.44°E	76.19°S	190		Fretwell et al. (2012)
30	Beaufort Island	167.04°E	76.92°S	88		Fretwell et al. (2012)
31	Cape Crozier	169.33°E	77.47°S	82		Fretwell et al. (2012)
32	Cape Colbeck	157.71°W	77.09°S	819		Fretwell et al. (2012)
33	Rupert Coast	143.31°W	75.38°S	446	on ice shelf	Fretwell et al. (2014)
34	Ledda Bay	131.24°W	74.27°S	384		Fretwell et al. (2012)
35	Thurston Glacier	125.62°W	73.50°S	197		Fretwell et al. (2012)
36	Bear Peninsula	110.24°W	74.35°S	471		Fretwell et al. (2012)
37	Brownson Islands	103.63°W	74.35°S	198		Fretwell et al. (2012)
38	Noville Peninsula	98.45°W	71.77°S	339		Fretwell et al. (2012)
39	Bryan Coast	85.35°W	73.25°S	450		LaRue et al. (2015)
40	Smyley Island	78.82°W	72.30°S	245		LaRue et al. (2015)
41	Rothschild	72.23°W	69.52°S	401		Fretwell et al. (2012)
42	Snow Hill Island	57.44°W	64.52°S	899		Fretwell et al. (2012)
43	Larsen Ice Shelf	60.67°W	66.10°S	228	on ice shelf	Fretwell et al. (2014)
44	Dolleman Island	60.42°W	70.61°S	501		Fretwell et al. (2012)
45	Smith Peninsula	60.83°W	74.37°S	418		Fretwell et al. (2012)
46	Gould Bay	47.66°W	77.71°S	485		Fretwell et al. (2012)
47	Luitpold Coast	33.55°W	77.27°S	349		Fretwell et al. (2012)
48	Dawson-Lambdon Glacier	26.65°W	76.01°S	232		Fretwell et al. (2012)
49	Halley Bay	27.42°W	75.55°S	55		Fretwell et al. (2012)
50	Stancomb Wills	23.09°W	74.12°S	206		Fretwell et al. (2012)
51	Drescher Inlet	19.33°W	72.83°S	189		Fretwell et al. (2012)
52	Riiser Larsen	15.11°W	72.12°S	164		Fretwell et al. (2012)
53	Atka Bay	8.13°W	70.61°S	307		Fretwell et al. (2012)
54	Sanae	1.41°W	70.00°S	264		Fretwell et al. (2012)
	Astrid Coast	8.32°E	69.95°S	370		Fretwell et al. (2012)
				311	mean	
				176	SD	
				324	median	

4. Discussion

Based on distances between existing colonies, we found six regions potentially sheltering colonies of emperor penguins. Importantly, these regions do not fundamentally differ in terms of polynyas or primary production from regions where colonies of emperor penguins have already been identified. It is therefore possible that there are more than 54 colonies, as described until now (LaRue et al., 2015).

A mean separation of 311 km between adjacent colonies is likely to reduce overlapping foraging ranges. However, no correlations were found between colony size and distance between colonies, but with a constant distance between

Table 2
The six regions where emperor penguins might potentially breed, their expected mean coordinates and the presence of polynyas in the vicinity.

Name of regions	Coordinates	Polynyas
Wilkes Land	128.0°E–66.1°S	Yes
George V Land	152.2°E–68.4°S	Yes
Oates Land	164.6°E–70.7°S	Yes
Marie Byrd Land	174.2°W–77.3°S	Yes
Bellingshausen Sea	64.8°W–67.0°S	Presumably but not persistent
Western Antarctic Peninsula	60.6°W–68.4°S	Not established

colonies using two regression equations of 322 km. This result was also found when considering the four different quadrants separately (North-East, South-East, South-West, North-West). This suggests that local food resources are not a major determinant for colony location, this being similar for each Antarctic quadrant. Indeed during the breeding season in winter, the maximum distance emperor penguins can travel from their colony to their foraging grounds is approximately 100 km (Wienecke and Robertson, 1997; Zimmer et al., 2008), while total travelling distance is less than 300 km (Ancel et al., 1992), a value similar to the mean separation distance between colonies that we report here. During the inter-breeding period, travelling distances are much more important, as penguins are not restricted by the need to provision chicks, and can travel up to 3500 km (Ancel et al., 1992; Zimmer et al., 2008). The potential dispersal rate between colonies during the inter-breeding period is therefore likely to be very high, either with adults relocating from one breeding colony to another (Cristofari et al., 2016; Kooyman and Ponganis, 2016), or with juveniles joining a colony other than the natal colony after fledging (Kooyman et al., 1996; Thiebot et al., 2013; Ancel et al., 2014; LaRue et al., 2015). Consequently, future studies should endeavour to determine dispersal rate between colonies, which should then be taken into account in demographic models to predict the fate of the overall emperor penguin population (Cristofari et al., 2016).

In the Antarctic Peninsula region, one of the most rapidly warming parts of the planet during the latter part of the 20th century, one emperor colony has disappeared (Trathan et al., 2011), though it is plausible that small numbers of birds might still attempt to breed there, especially in years with extensive sea ice (such as 2015/2016 and 2016/2017). This colony would have sat within the gap between Rothschild and Snow Hill. Moreover, given that the Antarctic Peninsula is one of the most frequently visited and observed regions of the Antarctic, it is plausible that this gap might be real.

Interestingly, the three locations where colonies are close to each other (Table 1) –the two Mertz locations (19 km), Halley Bay/Dawson (55 km) and Barrier Bay/West Ice-Shelf (76 km) –are in very similar environments at the edge of large calving ice-shelves or ice tongues (P. Fretwell personal observation). The two existing Mertz locations show the emperor response to a recent calving event that led to the disintegration of the original Mertz colony. Possibly, both the Halley Bay/Dawson and Barrier Bay/West Ice-Shelf might also be the result of other ice shelf calving events. If so, this suggests that it is not uncommon for colonies to search multiple temporary locations in the short term until the best location is established. When sea ice forms too late for breeding, emperor penguins are also known to rear their chicks on ice-shelves as high as 30 m above sea level, which were previously thought to be inaccessible to emperor penguins (Fretwell et al., 2014). This highlights that emperors are able to leave their previous breeding grounds and relocate when conditions are not suitable for breeding (for instance because of unstable sea ice, lack of shelter from wind, or inadequate access to food resources). The stability and duration of the fast ice are as important as the ability to adapt to a possibly greatly changed prey landscape. Future impacts of climate change are still a threat and have the potential to be beyond the capacity of the penguins to adapt. That will in part depend upon the rate of change as well as the amplitude of change. Most importantly, such behavioural flexibility suggests that emperor penguins might mediate the future impact of climate changes in ways not hitherto foreseen. We suggest that this should be the focus of future research as already noted by Wilson et al. (2009) for Adélie penguins and LaRue et al. (2015) for emperor penguins.

It could be argued that emperor penguins might also adapt to new conditions through other behavioural changes, for instance by varying the timing of reproduction in response to changes in local conditions. However, emperor penguins do not appear to show much flexibility in this regard (Ancel et al., 2013a, b). Paleoecological records suggest that Antarctic penguins (Adélie, chinstrap (*Pygoscelis antarctica*), gentoo and emperor penguins) are indeed less likely to respond by local adaptation than by dispersal (Forcada and Trathan, 2009). Thus, shifts in species distribution are likely to be one of the major possible adaptations to changing environmental conditions in emperor penguins (Trathan et al., 2007; Peron et al., 2012). Identifying existing colonies, their variations in terms of location and population density, hence appears particularly important to help us to understand their adaptations to changing environments.

In winter, the distance of polynyas from the coastline varies from 10 to 100 km, and some of them are even located directly at the coast (Arrigo and van Dijken, 2003). Importantly, this indicates that penguins can easily reach these biologically productive areas during the breeding season in order to restore their body fuels (and especially for females after egg laying). The presence of sea ice (Kusahara et al., 2015), in which polynyas are present (Tamura et al., 2008; Kern, 2009; Haid and Timmermann, 2013) and regions of high productivity (Arrigo and van Dijken, 2003; McLeod et al., 2010) close to the gaps we identified, strengthens our hypothesis that these areas are likely to shelter unknown emperor penguin colonies, especially in zones B and C where primary production was high (Fig. 4). When data about sea-ice characteristics, polynyas characteristics,

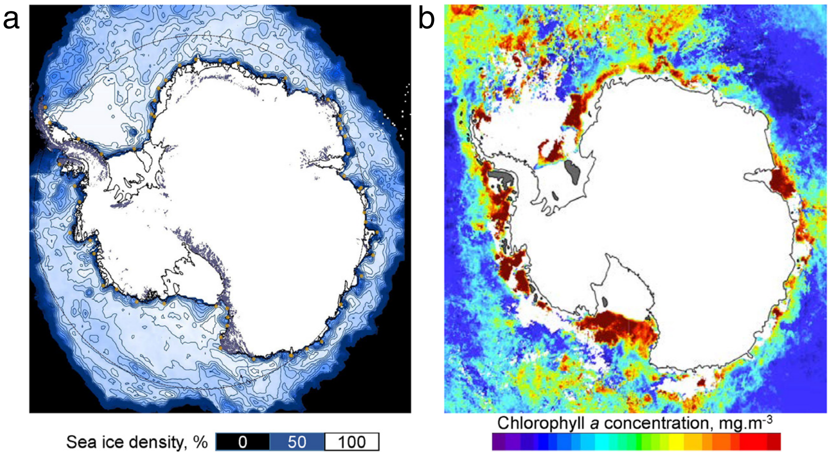

Fig. 4. Coastal concentrations of sea ice and chlorophyll *a* around the Antarctic Continent revealing polynyas. (a) Sea ice density (average July 2008–2014) from 0% (black) to 100% (white). Density isolines of 10% are shown. Orange squares symbolize known emperor penguin colonies. (b) Concentration of chlorophyll *a* (average summers 2002–2012) are represented from high (4 mg.m^{-3}, red) to low concentrations (0.1 mg.m^{-3}, blue). No data were available in white areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Source: Figure modified from R. Johnson, University of Tasmania, Australia (http://www.antarctica.gov.au/about-us/publications/australian-antarctic-magazine/2011-2015/issue-25-december-2013/science/measuring-phytoplankton-from-space). See also Nihashi and Ohshima (2015).

primary productivity, distance to open water are known for each breeding site, future studies should try to identify the factors determining the presence of a colony at a given location.

Of the gaps identified, we consider that some of the sites may have a lesser probability of holding an undiscovered colony. For example, in the Ross Sea (gap C), much of the potential habitat has previously been surveyed by aerial survey, so it is plausible that only small difficult to detect colonies exist within the gaps identified. Similarly, along the west Antarctic Peninsula, colonies might be unlikely to exist, as the west Antarctic Peninsula is one of the most-visited parts of Antarctica, so any other undiscovered colony would probably be small. However, along the West Antarctic Peninsula it is plausible that few birds still attempt to breed at the Dion Islands, a previously used breeding area, in some years, especially if sea ice is extensive. This was for instance the case in 2015/2016 and 2016/2017 within the gap between Rothschild and Snow Hill. This highlights the need to search repeatedly for emperor penguin colonies in the small number of gaps we identified. High resolution and cloud-free satellite imagery in these areas will be required to confirm the existence of emperor penguins colonies and to estimate their abundance. This global census will require a combination of ground counts, aerial counts (using helicopters or drones) and satellite imagery, coupled with a better appreciation of variable phenology related to latitude. Only such an approach will enable us to assess the overall population of emperor penguins. A further field of investigation will be to compare for each breeding site weather and sea ice conditions, zooplankton concentration, the closest distance to the open sea and/or polynya. Such information represents a necessary pre-requisite if we wish to understand and anticipate population changes in this emblematic Antarctic species. More generally, our analysis highlights a fundamental requirement, that in order to predict how species might respond to regional climate change (see for example Jenouvrier et al., 2014; Trathan et al., 2014), we must better understand their biogeography and the factors that lead to a species occupation of particular sites. Our study hence opens new avenues to determine the local and global characteristics of habitat choice and niche selection by emperor penguins, a species particularly adapted to polar climate.

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