



Fast ice variability in East Antarctica: observed repercussions for emperor penguins

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ABSTRACT: As a species highly reliant on stable fast ice as a breeding platform, emperor penguins are increasingly challenged in their breeding attempts due to changes in fast ice conditions. We collated habitat information of 27 emperor penguin colonies in East Antarctica (43°–167° E) from 2018 to 2023 using European Space Agency Sentinel-2 satellite images. Our objective was to examine the variability in habitat and ice conditions and associated repercussions for colony location and breeding success. Variables, such as location, colony movement and inter-annual variability in these parameters, were used to assess the adaptability of emperor penguins when local conditions change markedly. The major challenge emperor penguins currently face throughout Antarctica is untimely loss of breeding habitat resulting in increased or complete breeding failure, as observed in 9 colonies at least once during the study. One small colony at the West Ice Shelf lost its breeding area and has not been seen since 2021. The inter-annual movement of some colonies demonstrates the species' adaptability and the need for ongoing monitoring of the global emperor penguin population using satellite imagery. We highlight caveats, such as availability of suitable satellite images and movement of colonies, that need to be accounted for to ensure sound interpretation of the monitoring findings. Ongoing Antarctic-wide monitoring is essential to quantify the impact of changing fast ice conditions on emperor penguins and also the cumulative impacts of other threats such as disease. The information presented is to provide background and empirical data for researchers, policy makers and managers.

KEY WORDS: Emperor penguins · East Antarctica · Colony diversity · Adaptability · Breeding failure

1. INTRODUCTION

Emperor penguins *Aptenodytes forsteri* live in a highly dynamic environment, and extreme events have likely been part of their history. Having existed for nearly 1 million yr (Vianna et al. 2020), these penguins have had to be resilient and been able to adapt to new circumstances, for example, by shifting colonies to new locations or breeding on non-traditional platforms (e.g. ice shelves rather than fast ice). To breed successfully, emperor penguins need a reliably stable breeding platform, a relatively flat surface and access to fresh snow (Le Maho 1977). Stable land-fast sea ice

(fast ice) is required for about 10 months a year and crucial to rear their chicks (March–December).

Conditions in Antarctica are changing at an unprecedented rate and processes like the now rapid warming of the Amundsen Sea may be irreversibly underway (Naughten et al. 2023). Recent reports about extensive breeding failure at various colonies due to untimely loss of their breeding area (e.g. Kooyman et al. 2007, Schmidt & Ballard 2020, Fretwell et al. 2023) and record low sea ice extent Antarctica-wide in 2022 and 2023 (NSIDC 2023a,b) may indicate rapidly worsening conditions for emperor penguins. Being a long-lived, late-maturing species with low

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annual reproductive output and low genetic diversity (Younger et al. 2017), the capacity of emperor penguins to adapt physiologically and otherwise to accelerating environmental change is limited.

Previous studies provide valuable information about how future environmental change is likely to affect the global emperor penguin population (e.g. Jenouvrier et al. 2014, 2020). Based on long-term projections of loss of habitat and habitat quality (Jenouvrier et al. 2009), the International Union for Conservation of Nature uplisted the species from Least Concern to Near Threatened in 2012 (BirdLife International 2024). Recent studies modelling the trajectory of the global emperor penguin population project that 65% of colonies may become quasi-extinct by 2050 even if the global temperature rise were limited to 1.5°C. Change processes already underway in the climate system do not reverse immediately when carbon neutrality is reached but continue on their trajectory well into the future because of lags inherent in the climate system (Jenouvrier et al. 2021). Given the rapid change of environmental conditions in Antarctica, there have been calls to uplist the species status to Vulnerable (Trathan et al. 2020).

Organisations and government departments are beginning to take notice of the threats to emperor penguins. For example, in 2022, the US Fish and Wildlife Service listed emperor penguins as a threatened species under the Endangered Species Act after a comprehensive analysis of the best available science was carried out; the time horizon for major changes was the year 2050 (US Fish and Wildlife Service 2022). The Endangered Species Act recognises a species as endangered when it is threatened with extinction in part or all of its range (US Fish and Wildlife Service 1973). Internationally, discussions are ongoing among member nations of the Antarctic Treaty Consultative Meeting (ATCM) about the listing of emperor penguins as Specially Protected Antarctic Species (ATCM 2023).

In addition to models examining long-term changes in habitat, optical medium- and high-resolution satellite imagery is a useful tool to assess some key habitat characteristics (e.g. type of breeding platform, distance to fast ice edge), as well as environmental parameters, such as the regional variability in duration, extent and area of fast ice (e.g. Fraser et al. 2023). Importantly, it enables annual determination of the locations of all emperor penguin colonies and assessment of conditions at individual colonies. Local impacts may be regionally insignificant, but they can have serious consequences for individual colonies

and need to be considered when determining the status of a colony.

It is imperative to understand the complexity of the highly colony-specific variability in changes in local conditions and populations, as well as the complex dynamics of fast ice rather than total sea-ice extent to assess habitat quality. In this study, we gathered detailed information on selected habitat characteristics of 27 colonies in East Antarctica (43°–167° E), including location, distance to fast ice edge, fast ice extent, colony movement and inter-annual variability in these parameters. We used European Space Agency (ESA) Sentinel-2 satellite images to examine changes in habitat and fast ice conditions from 2018 to 2023. Our objectives were to (1) examine the variability in habitat and ice conditions and associated repercussions for colony movements and breeding success, (2) assess the adaptability of emperor penguins when local conditions changed markedly and (3) understand how, particularly, changes in fast ice conditions affect shifts in colony locations and the occurrence of disastrous breeding failures. In addition to discussing the challenges emperor penguins currently face in the region, we consider the need for ongoing monitoring of the global emperor penguin population and highlight caveats that need to be considered when using satellite imagery to assess local population changes. The information presented here is to provide background and empirical data for researchers, policy makers and managers in their assessments of threats to the future of emperor penguins.

2. MATERIALS AND METHODS

2.1. Survey area and imagery

We examined 27 emperor penguin colonies along ~6000 km of coastline, covering 124° longitude (43°–167° E) and spanning 5.8° latitude (645 km), from 64.9° to 70.7° S (Fig. 1). Twenty-three of the study colonies occurred within the region extending from Breitunga (glacier tongue) (25° E) to the Mertz Glacier (144° E), which comprises about half the fast ice in Antarctica (Fraser et al. 2021).

Detailed descriptions of individual study colonies are provided in Tables S1 & S2 (in the Supplement at www.int-res.com/articles/suppl/n055p001_supp.pdf), which highlight the great diversity in habitat and local environmental conditions, and for some of the colonies, their mobility, as well as details about colony history, and where available, new estimates

of population sizes (Table A1 in the Appendix, Table S2).

We covered the period from early September to late December from 2018–2023, when optical light satellite images are available. Importantly, this time coincides largely with the chick rearing period of emperor penguins; thus, certain events can affect their breeding success. Clear images available in April were checked for the presence of penguins to determine their location at the onset of the breeding season.

We mainly used freely available, high resolution (10 m horizontal in RGB) Sentinel-2 images and downloaded them via the ESA Sentinel Playground from 2018 to 2023. Sentinel Playground has recently been replaced with ESA's Copernicus browser (<https://browser.dataspace.copernicus.eu/>). We applied the method of Fretwell & Trathan (2021), but inspected all images regardless of cloud cover to assess the number of useful images for each colony and season. When none were available at key dates, we used NASA's Landsat-8 and Landsat-9 imagery (30 m horizontal resolution in RGB). Information on regional sea-ice extent was obtained from the NASA Earth Observing System Data and Information System (EOSDIS) (www.worldview.earthdata.nasa.gov), an open-source code application from NASA's EOSDIS that provides lower-resolution (250 m horizontal), daily, global satellite images taken by MODIS satellites (for further detail see <https://space.oscar.wmo.int/satelliteprogrammes/view/eos> and <https://www.nesdis.noaa.gov/news/satellite-imagery-rgbs-adding-value-saving-time>).

2.2. Colony environments and ice conditions

To compare the state of the 27 emperor penguin colonies, we defined 4 habitats based on colony substratum and distance from the coast, where 'coast' is the edge of the continent, not the edge of an ice shelf or glacier:

(1) Coastal: fast ice <10 km from coast, often in small embayments. The surface of the fast ice here tends to be relatively smooth as it forms *in situ* due to loss of heat from the ocean to the atmosphere (thermodynamic formation, Fraser et al. 2023).

(2) Fast ice sheet: fast ice and ice tongues > 10 km from coast, often near or among grounded icebergs. The fast ice surface here is often rough as it forms where ice rubble (pack ice or reconfigured fast ice) becomes consolidated under the influence of winds and currents. This dynamic process produces pressure ridges and generates an uneven surface (dynamic formation, Fraser et al. 2023).

(3) Land-based: on land throughout the breeding season.

(4) Ice shelf/glacier: on or near an ice shelf or iceberg tongue off a glacier. At times, colonies may relocate from the fast ice onto the shelf or berg if it is accessible. These habitats are potentially affected by environmental variables, such as persistence of fast ice and exposure to katabatic winds.

We manually recorded colony locations indicated by brown pixels from each available cloud-free image taken in September to December. Small colonies (<1000 pairs) can be difficult to spot as the staining of the ice is less intense than in large colonies (several thousand pairs). Changes in position of faintly stained pixels indicate colony movement.

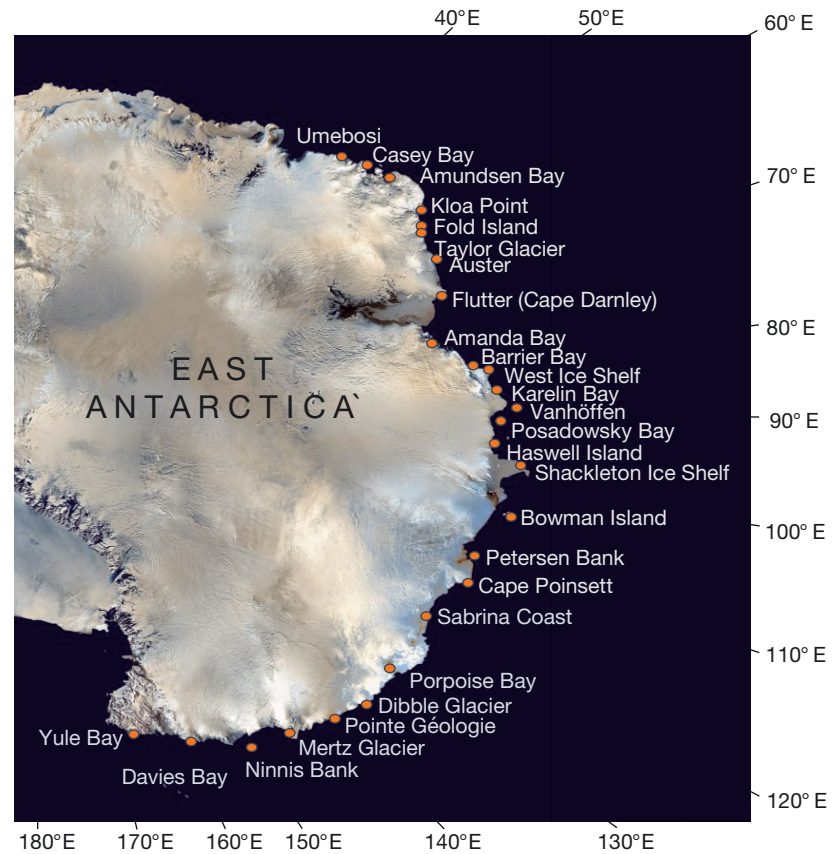


Fig. 1. Locations of study colonies of emperor penguins in East Antarctica. Background image created by Dave Pape using NASA's Blue Marble data set (https://en.wikipedia.org/wiki/File:Antarctica_6400px_from_Blue_Marble.jpg)

To assess the variability in fast ice extent within and between colony locations, we estimated the maximal distances between colonies and the fast ice edge in late September/mid-October when the extent reaches its maximum (Fraser et al. 2021). When Sentinel-2 images were not available, we examined images in the NASA's Worldview application (<https://worldview.earthdata.nasa.gov>), also used to estimate the annual regional fast ice extent. While Sentinel-2 delivers high-resolution images several times per month, Worldview provides daily data, albeit at lower resolution, allowing evaluations of major changes in fast ice conditions such as the timing of break-out events that may not have been captured by Sentinel-2. Worldview images are available for Antarctica from 24 February 2000 onwards and enable a comparison with conditions pre-2018.

When using optical light satellite images, cloud cover limits observations, making it difficult to determine when fast ice forms or breaks out. Since these processes are gradual, exact dates may not be necessary. However, catastrophic breakouts occur rapidly, and recording their accurate time and extent is needed to assess the impact on a colony. The date of fast ice loss is indicative of additional chick mortality. When the breeding platform disintegrates before early December, it is highly likely that all chicks perish (complete breeding failure). When the ice breaks out before the end of December, when peak fledging occurs in East Antarctica, chicks at an advanced stage of development may survive, but those whose plumage is not yet waterproof die. There is thus additional mortality due to the break-out event (reduced breeding success).

Overall sea-ice conditions were the lowest on record in 2022 and 2023. Since colony locations were generally similar in both years, changes in the distance to the fast ice edge were largely due to changes in fast ice conditions. For each colony, we compared the distance to the fast ice edge in mid-December 2022 and 2023, when chicks are not yet ready to go to sea, to examine whether any effect was apparent given the unprecedented sea-ice conditions in both years.

When comparing distances, we used the Mann-Whitney U -test at $p < 0.05$, calculated in Microsoft Excel, Microsoft 365. All means are reported ± 1 SD.

2.3. Colony movements

We used Sentinel-2 images to examine interannual changes in colony locations, consistency of use of certain areas and distance moved within seasons. For these exercises, we chose colony locations in October

of each year when good-quality satellite imagery is often available. When not available, we chose the closest date to mid-October in late September or early November. Emperor penguin colonies often divide into various suburbs during chick rearing. When separated by >1 km, we chose the coordinates of the largest suburb for these comparisons.

Where possible, we estimated how far colonies had moved historically by comparing previously reported positions with current ones, considering only colonies that had relocated more than 10 km. We calculated great circle distances using the latitude/longitude distance calculator provided by the National Hurricane Center (2023).

Names of features and locations were those of the Composite Gazetteer of the Antarctica of the Scientific Committee on Antarctic Research (SCAR) hosted by the Australian Antarctic Data Centre (<https://data.aad.gov.au/aadc/gaz/scar/>).

2.4. Number of useable Sentinel-2 images

Sentinel-2 satellite image quality varies. To examine variables of emperor penguin colonies most likely to be successfully monitored using Sentinel-2 imagery, we determined the number of useable images taken each year from 1 September to 31 December. Images were classified as 'cloud-covered' when a colony area could not be detected (this included cloud cover obscuring a colony) and 'cloud-free' when the colony was visible. The dates of the first cloud-free images for each of the 27 study colonies ranged from 1 March to late August/early September 2018.

2.5. Historical information

Detailed information is presented in Table S2. We searched the published literature for estimates of population size and also used our own counts. No precise population data are presently available for recently discovered colonies.

For well-known colonies, we searched field records and notebooks of the Australian Antarctic Division for visits to emperor penguin colonies and information on colony locations and population estimates. We also contacted expeditioners who took part in these endeavours to verify numbers and to obtain images. Population information from these records needs to be handled with care as it is rarely the result of a systematic count. Since the number of penguins attending a colony varies throughout a breeding season, dif-

ferences in the timing of colony visits, the methods employed to estimate numbers and the count units used (adults, chicks, penguins) affect the results. Hence, historical information is often anecdotal and unreliable for the study of populations. However, it serves to confirm the presence of emperor penguins in a given location.

2.6. Updates on population numbers

We have been conducting systematic counts of emperor penguins continuously at Taylor Glacier since 1988 (ground photography), at Amanda Bay since 2011 (ground and aerial photography) and intermittently at Fold Island (ground photography), Flutter (Cape Darnley), Barrier Bay and the West Ice Shelf (all aerial photography). The time of the photography was kept as constant as possible, but logistic and weather-related issues meant this was not always possible.

We also attempted to photograph distant colonies. Inclement weather and lack of aircraft access can be challenging when trying to visit these colonies. However, in November/December 2022, aerial images were taken of 10 colonies either from helicopters (750 m separation distance) or fixed wing aircraft (900 m separation distance). In September 2022, ground visits had been made to 2 western colonies (Kloa Point, Fold Island) (Table A1).

High quality photographs enable repeatable counts, more accurate than ground counts, and provide archival records. Our well-overlapping images were put together by colony in Adobe Photoshop and manually counted. The same person (B. Wienecke) counted to avoid observer variability (for further detail see Robertson et al. 2014).

Both the number of adults and chicks were counted. We used this information to determine changes in the adult to chick ratio during chick rearing at all colonies. For comparison, we added information from other colonies in the Ross Sea from Kooyman & Mullins (1990).

3. RESULTS

3.1. Colony habitats and fast ice conditions

Colony habitats were highly diverse and all habitat types, except land-based, occurred throughout the study region (Fig. 2). Coastal colonies (n = 13) were the most common type and varied greatly in their distances to the fast ice edge in September/October (Fig. 2).

Colonies located on fast ice sheets (n = 6) or near ice shelves or glacier (n = 6) were closest to the fast ice edge (Fig. 2). Among the fast ice sheet colonies, Auster was an exception, with a distance to the ice edge that consistently averaged around 50 km. Gen-

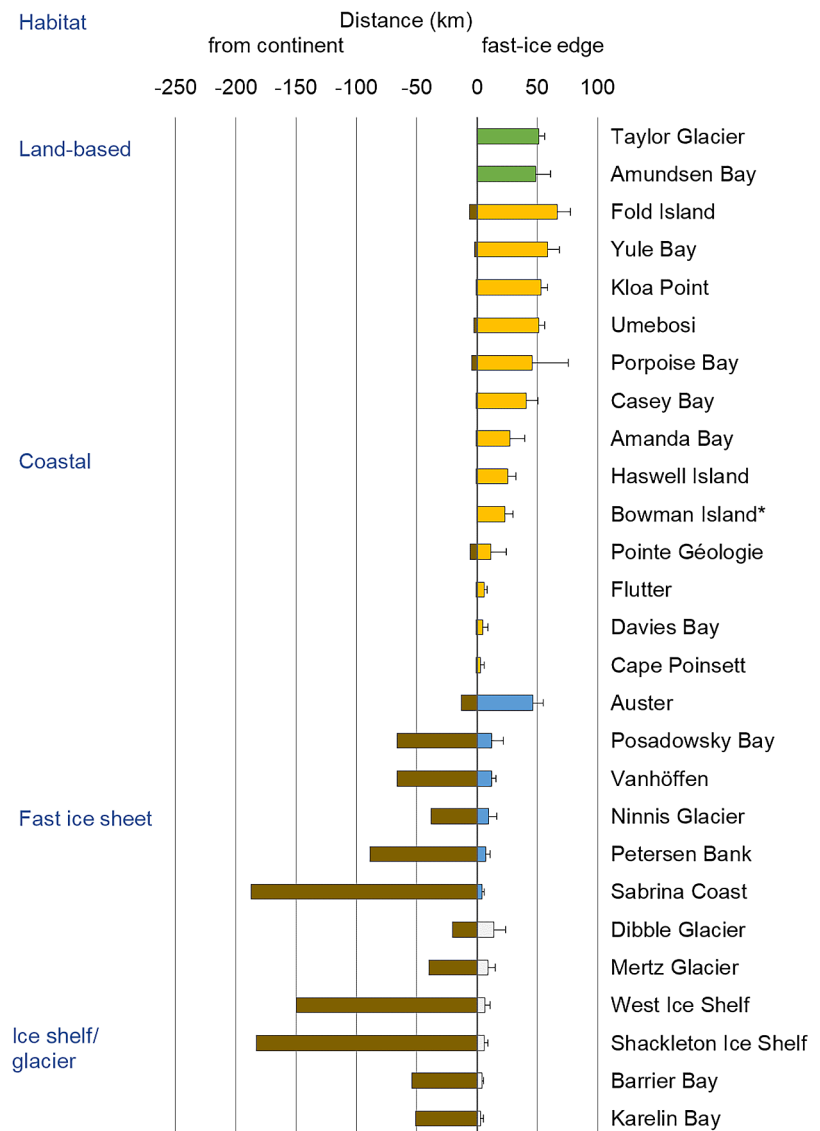


Fig. 2. Colonies sorted by habitat type according to decreasing mean (\pm SD) distance between the colony and the fast ice edge. Distances from the colony to the coast are included to demonstrate the overall variability in habitat

erally, fast ice sheet and ice shelf/glacier colonies were most distant from the continental coast. The West Ice Shelf, Shackleton Ice Shelf, and Ninnis Bank colonies are >100 km from the coastline, but <10 km from the edge of the fast ice. The colony north of iceberg C-31 at the Shackleton Ice Shelf (see Table S2, Colony 16) is the northernmost study colony (~64.9° S), while the Ninnis Bank colony (~66.7° S) is located farthest north on an extensive fast ice sheet. Like the Shackleton Ice Shelf colony, the West Ice Shelf colony is also at the northern edge of an iceberg, D-15A (see Table S2, Colony 10).

The 2 land-based colonies (Amundsen Bay, Taylor Glacier) exist in the western part of the study area where winter fast ice is extensive. Amundsen Bay is at the western side of Enderby Land, where the fast ice often reaches west as far as the Stanjukovicha Ice Shelf (west of the Riiser-Larsen Peninsula), covering >63 000 km², while Taylor Glacier is east of Enderby Land, where the fast ice area can cover >31 000 km². Penguins from both colonies regularly travelled >50 km to the fast ice edge (Fig. 2).

The geographic distribution of the colonies highlights inter-colony differences in the median distances between colonies and fast ice edge. The western study colonies (Umebosi to Auster) were generally >40 km from the ice edge, while most colonies east of Flutter at Cape Darnley (69.7° E) were about half that distance or less (Fig. 3, Table 1). Two exceptions were the Porpoise Bay, which experienced the largest interannual variability, and Yule Bay, where distances to the fast ice edge regularly exceeded 50 km.

Annually and seasonally, fast ice conditions change frequently and differ among colonies. Four examples show the change in the distance between individual colonies and the nearest fast ice edge from September to December each year (Fig. 4). The number of data points differs by location and season due to the varying numbers of useable images used to estimate the distances.

From 2018 to 2022, the distances between colony and the fast ice edge remained most constant at the Kloa Point and Auster colonies, where long distances were typical in spring/summer. The peaks at Auster occurred when pack ice concentrated at the

eastern side of the fast ice sheet, increasing the distance temporarily. Davies Bay consistently experienced the shortest distances, while the most marked inter-seasonal variability at Porpoise Bay was due to the formation of a polynya (areas of open water within the sea ice) (Fig. 4). Here, the penguins had to cope with widely varying travel distances to the fast ice edge. For example, in November 2019, the distance was 72 km, compared to <1 km in October/November 2022 (Fig. 4, see Table S2 for further details).

In 2023, at 3 of the 4 example colonies (Auster, Kloa Point, Porpoise Bay) fast ice was lost rapidly (Fig. 4). Most pronounced was the situation at Auster, where the fast ice area decreased in mid-December at a rate previously only seen in late January/February. At Kloa Point and Porpoise Bay, the ice edge retreated more in December than in other years, but 20–30 km of fast ice remained. At Porpoise Bay, the fast ice extent was greater in 2023 than in previous years. In Davies Bay, where the distance to the fast ice edge rarely exceeded 10 km, there were only about 11 km² of fast ice. Two suburbs had formed; both were <0.16 km from the fast ice edge in November (see Table S2).

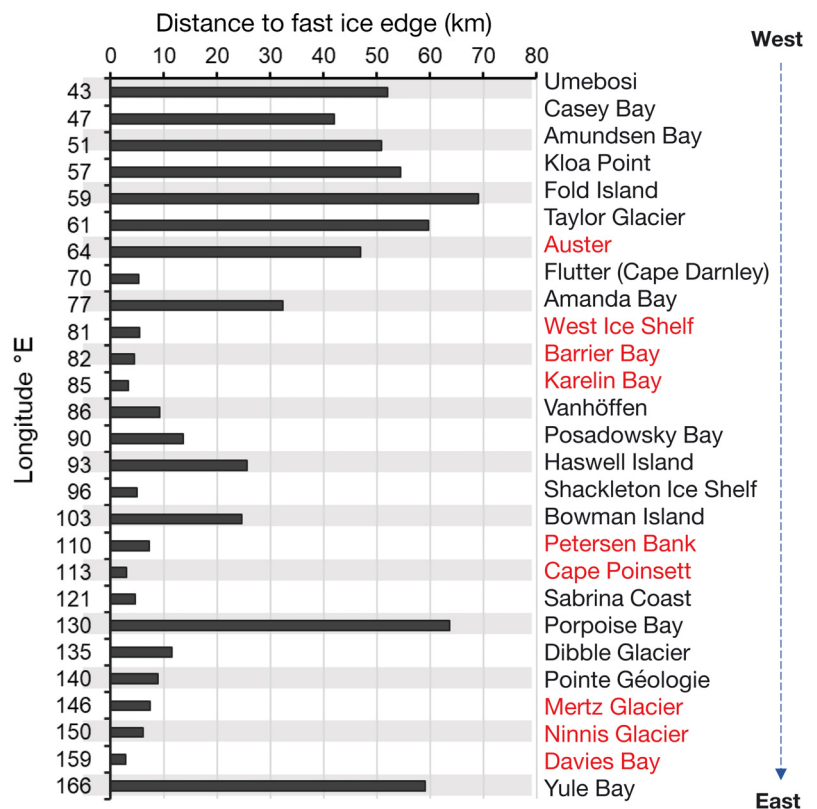


Fig. 3. Median distance from colonies to the fast ice edge by longitude (°E) from September to December from 2018 to 2023. Red names indicate colonies with reduced or complete breeding failure at least once in 6 years

Table 1. Comparison of selected parameters between western and eastern colonies in the study area for the study period 2018–2023

	Western colonies (43° E to 76° E)	Eastern colonies (81° E to 167° E)
Colony type (n)		
Land-based	2	0
Coastal	6	7
Fast ice sheet	1	5
Iceberg/glacier	0	6
Mean ± SD distance to fast ice edge (km)	54.1 ± 19.4	21.8 ± 18.0
Median ± SD distance to fast ice edge (km)	58.0	18.0
Mean ± SD interannual colony movement (km)	0.6 ± 0.8	2.9 ± 2.9
Median interannual colony movement (km)	0.3	2.0
Maximal interannual colony movement (km)	3.6	13.1

3.2. Fast ice conditions in 2022 and 2023

In 15 colonies, representing all 4 habitat types, fast ice conditions were similar (<5 km difference) in mid-December of both years, and 12 colonies were <5 km from the fast ice edge (Fig. 5). Of these, 7 (Karelin Bay, Petersen Bank, Cape Pointette, Sabrina Coast, Porpoise Bay, Ninnis Glacier and Davies Bay) had experienced reduced or complete breeding failure by mid-December 2022 and 3 (West Ice Shelf, Petersen Bank and Davies Bay) had lost their breeding platform by mid-December 2023. In 2023, fast ice conditions changed dramatically at Auster and Amanda Bay. At Auster, from early to mid-December, the distance to the fast ice edge decreased from 35 km to 6 km within about 2 wk, and by late December, the fast ice had completely disintegrated. At Amanda Bay, where the fast ice extent was already 22 km less than in September 2022, the fast ice started to recede in the last week of

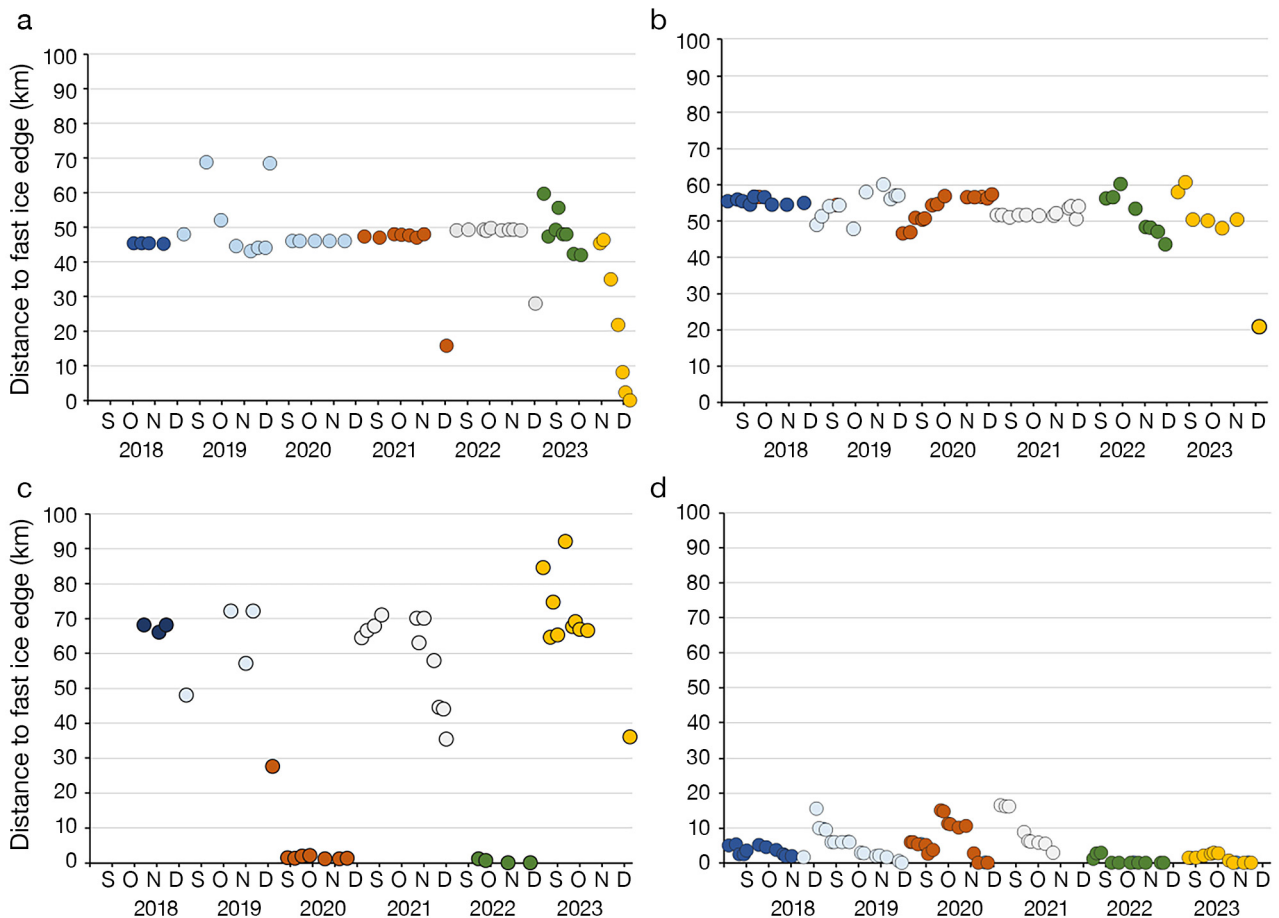


Fig. 4. Distance to fast ice edge of 4 colonies estimated for the months from September to December each year from 2018 to 2023. (a) Auster, (b) Klua, (c) Porpoise Bay, (d) Davies Bay. The number of points varies among years because of differences in the number of available images

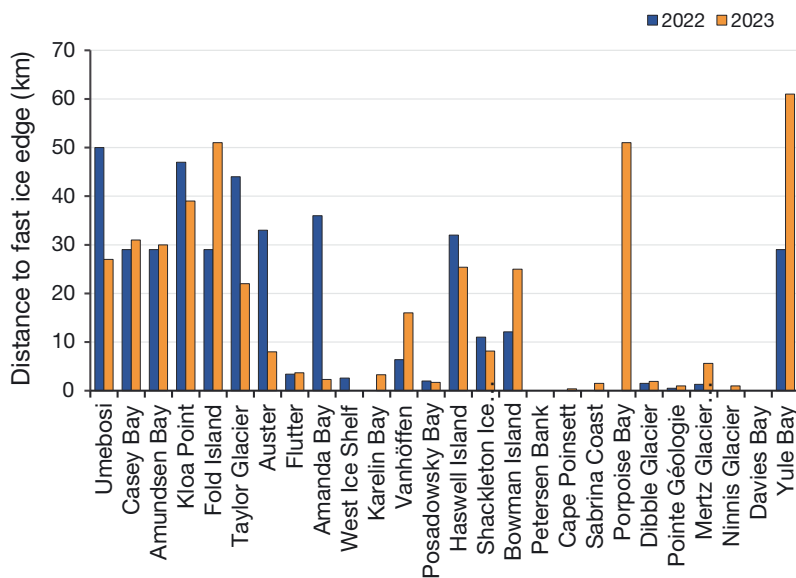


Fig. 5. Comparison of the distances between colonies and the fast ice edge in December 2022 and December 2023

October 2023 and was only about 2 km from the colony by mid-December 2023.

The 9 western colonies from Umebosi (~43° E) to Amanda Bay (76.8° E) generally encountered extensive fast ice. Except at the Casey Bay and Flutter colonies, where fast ice conditions were unchanged, the distances to the fast ice edge differed significantly (Mann-Whitney $U = 65.5$, $p = 0.030$), averaging 43 ± 18 km in 2022 compared to 23 ± 15 km in 2023 (medians 49 and 23, respectively). The largest change occurred at Amanda Bay with a 34 km shorter distance in 2022 than in 2023.

In comparison, at the 17 eastern colonies the distances were similar or greater in 2023 than in 2022 at the same time of year (2022: 5 ± 9 km; 2023: 17 ± 25 km), but statistically not significant (Mann-Whitney $U = 115$, $p = 0.159$). The Barrier Bay colony was not included as no penguins had been present at the previous colony location since mid-September 2021. In 2023, 12 of the 17 eastern colonies were <10 km from the fast ice edge in mid-December. The greatest interannual difference occurred at Porpoise Bay and Yule Bay, where, unlike at most other colonies, the ice edge was farther away in 2022 than in 2023 (51 and 32 km, respectively).

3.3. Interannual relocation distances

From 2018 to 2023, interannual movements of the 27 colonies varied, averaging a modest 2.1 ± 2.5 km.

Only the Shackleton Ice Shelf and the Porpoise Bay colonies relocated >10 km during this period (Fig. 6).

The western colonies (Umebosi to Amanda Bay) remained faithful to their colony location. Colonies nearest the fast ice edge generally moved several kilometres interannually and 4 coastal colonies all situated near rocky outcrops or islands (Haswell Island, Pointe Géologie, Davies Bay, Yule Bay) moved only 1 km or less.

Historical observations of 7 colonies were intermittent and discontinuous, and movement distances were determined over periods ranging from 3 to 58 yr (Fig. 7). Three colonies had moved >40 km since they were discovered. The Shackleton Ice Shelf moved farthest over 52 yr, shifting 73 km from 64.67° S, 97.50° E in 1960 to 64.86° S, 96.02° E in 2008. It has remained north of the ice shelf since, but relocated >10 km twice more since 2018 (Fig. 7).

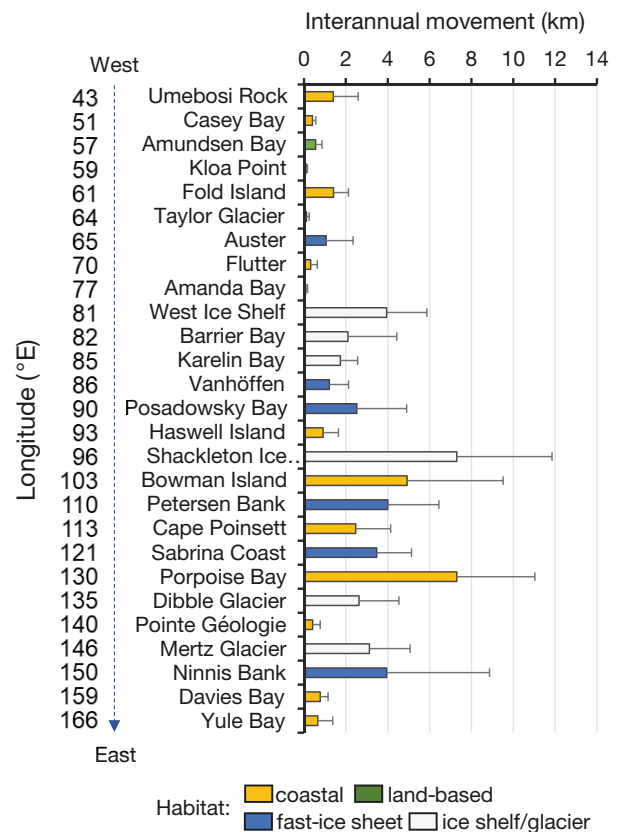


Fig. 6. Mean (\pm SD) distances that colonies moved interannually during the study period 2018–2023

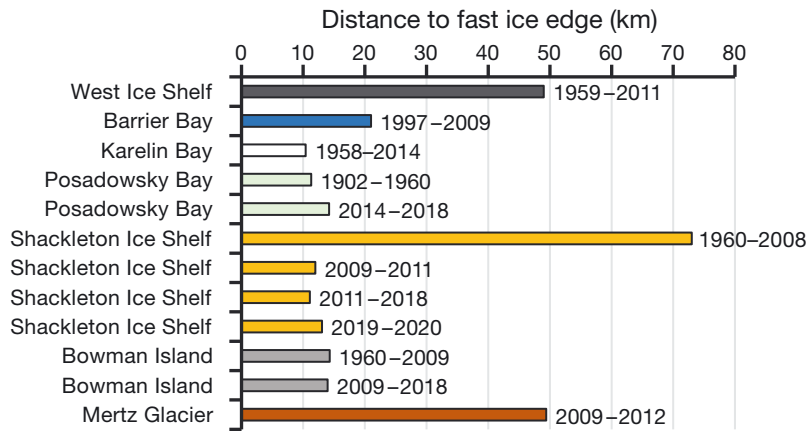


Fig. 7. Historical changes of locations of 7 colonies. Each bar indicates a major relocation and the distance (km) a colony had moved between two observations. Since the exact timings of relocations are unknown, the years at the end of each bar indicate the period during which a relocation must have occurred

The West Ice Shelf and Mertz Glacier colonies moved approximately 49 km from their historical position. The latter relocated quite recently and abruptly after a very large iceberg (B-9B) collided with the Mertz Glacier Tongue in mid-February 2010 (NASA 2010), causing it to split off and destroy the colony area in the process. The colony moved southwards (Ancel et al. 2014).

The Bowman Island and Karelin Bay colonies shifted moderate distances (28 and 11 km, respectively), probably due to changes in the environment. At Bowman Island, ice conditions were poor at the 1960 site in 15 of the 23 years from 2000 to 2023. When the colony moved to the eastern side of the island is unknown. The Karelin Bay colony was gradually forced northwards by the advancing West Ice Shelf.

3.4. Number of useable Sentinel-2 images

In the study area for the period 1 September to 31 December each year, the total number of images per year ranged from 321 in 2018 to 600 in 2021, and per colony from 67 (Posadowsky Bay) to 167 (Davies Bay).

Of the 3037 classified images, 1465 (48%) were cloud-covered and 1574 (52%) were cloud-free (Fig. A1). The percentages of cloud-covered versus cloud-free images varied among colonies. At 4 colonies, cloud-covered images comprised 60% or more of the images considered: Karelin Bay (61%), Ninnis Bank (62%), Vanhöffen (63%), and West Ice Shelf (70%). These colonies occur either at the northern edge of ice shelves/icebergs or on fast ice sheets. Colonies where >60% of

images were cloud-free were Yule Bay (60%), Dibble Glacier (64%), Pointe Géologie (64%), Davies Bay (65%), Kloa Point (66%), and Auster (66%) (Fig. A1). Except Auster (fast ice sheet), these colonies are coastal.

3.5. Updates on population numbers

In September 2022, Kloa Point and Fold Island were photographed from the ground. At Kloa, only adult penguins were counted ($n = 3740$). In the densely packed colony many chicks were still being brooded and hence invisible. The Fold Island colony was spread out, but the chick count is likely

incomplete because chicks were still being brooded here as well.

The largest penguin aggregations occurred at the Shackleton Ice Shelf (adults = 1339, chicks 10 738) and Amanda Bay (adults = 1424, chicks = 10 485). Four colonies comprised several thousand chicks, ranging from 2390 at Bowman Island to 8207 at Flutter. Posadowsky Bay, the smallest study colony, probably had a poor season with barely more chicks ($n = 155$) present than adults ($n = 123$). Petersen Bank was photographed, but due to rapid ice loss in November/early December, only a colony remnant was still present.

Adult to chick ratios decrease from mid-September to late December. After early October, chicks outnumber adults in the colonies (Fig. 8).

4. DISCUSSION

The data presented here document the local variability of emperor penguin colonies and recent changes.

Outside the scope of this paper, there is another serious threat to Antarctic seabirds, including emperor penguins: the introduction of infectious pathogens in Antarctic populations as another consequence of climate change (Grimaldi et al. 2015). The recent discovery of bird (and mammal) deaths due to a highly pathogenic strain of avian influenza at high latitudes has been reported widely (e.g. Anthes 2024, Bourke 2024). The introduction of pathogenic microorganisms into Antarctic seabird colonies, causing high morbidity and mortality, will increase the pressure on already vulnerable populations.

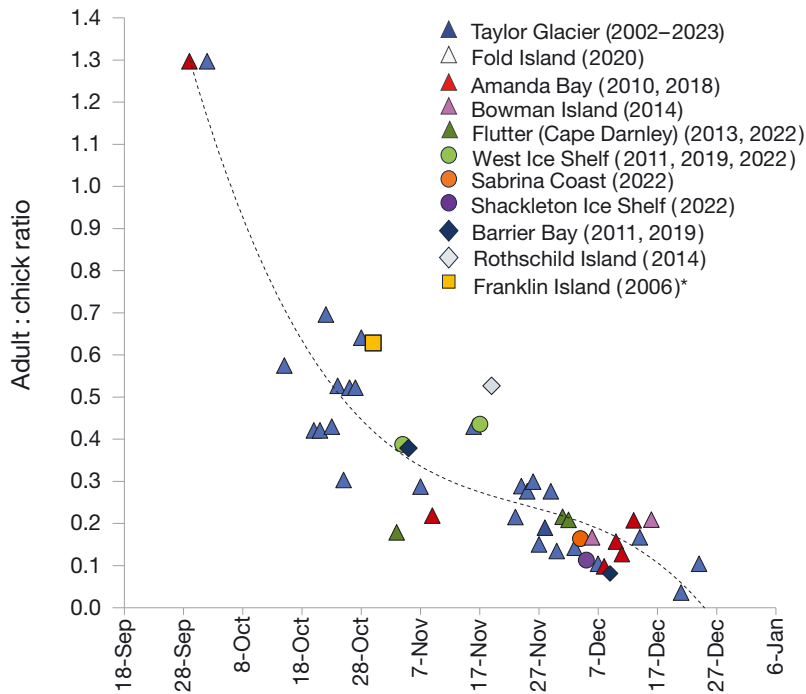


Fig. 8. Adult to chick ratio from September to December. Data were obtained from several colonies for comparative purposes, including 2 (Franklin Island, Rothschild Island) outside the study region. *Datum from Kooyman & Ponganis (2017)

4.1. Regional fast ice conditions

The stationary fast ice zone occurs in a circumpolar, discontinuous band of varying width comprising only 4–13% of the total sea ice (Fraser et al. 2023), and is different from the mobile pack-ice zone that drifts westwards with the Antarctic Coastal Current (Fraser et al. 2012). While the overall sea-ice extent peaks in September (Fraser et al. 2021), fast ice reaches its maximal extent in late September/early October. The timing varies by region. From 2000–2018, the date of fast ice maximum ranged from 16 or 17 September (day of year, DOY 260) in the sector 103–146° E, where 8 study colonies occur (Bowman Island to Mertz Glacier) to 11 or 12 October (DOY 285) at the 3 most easterly colonies (Ninnis Glacier, Davies Bay and Yule Bay) in sector 146–172° E. In the region from Amanda Bay to the Shackleton Ice Shelf (8 colonies), fast ice extent peaked around 1 or 2 October (DOY 275), and in the westernmost section comprising the remaining 8 colonies (Umebosi to Flutter), around 20 or 21 September (DOY 264) (Fraser et al. 2021). Maximum fast ice extent occurs when emperor penguins provide for thermally independent chicks. In the western part of the study area, especially in sector 43–64° E, the fast ice was most extensive, and adults from these mainly coastal colonies potentially travelled the longest distances to the fast ice edge.

The distance between colony and fast ice edge varies seasonally (Fraser et al. 2021). Important for emperor penguins is that the greater the distance, the longer adults travel to access open water (individuals may forage briefly in tide cracks) and therefore food. Long distance travel means that a parent can feed the chick only about every 2–3 weeks.

Fast ice quality also matters. Occasionally, colonies are located on reliable, several metre thick, multi-year fast ice that exists throughout the year. This provides a reliable breeding platform and enables a timely start to the breeding season. (Fig. A2). The icescape is unlikely to change much between seasons compared to areas with first-year fast ice. Where new ice forms, the quality (e.g. rugosity), characteristics (e.g. ice thickness, distance to fast ice edge) and the icescape (e.g. presence of icebergs) of the area may change, potentially rendering a site

unsuitable as a breeding ground. When required conditions are not met, emperor penguins may skip a season or move to a different location (LaRue et al. 2015).

The timing of fast ice formation and breakup can affect the breeding cycle (Fig. S3). Delays in fast ice formation in autumn may shift back the onset of the breeding season and early fast ice breakup further shortens the season. The earlier fast ice is lost, the more dire the consequences for breeding success. Complete breeding failure occurs when the fast ice disappears before the chick moult commences. For example, in 2021, the fast ice broke out at the Barrier Bay and Cape Poinsett colonies in mid-September and mid-October, respectively.

Around the second week of November, the oldest chicks show the first signs of moult. Within about 25 d after showing the first signs of moult, a chick progresses from a full down cover to a stage where most down is lost on the ventral surface, on the back and around the head (Pütz & Plötz 1991). At this stage a chick's plumage is waterproof although it still carries down. Within approximately another week, all down is lost. Over a period of about 33 d, most fledglings depart the colony. Some chicks may remain at the colony, but they are no longer cared for by their parents; unable to fend for themselves, they perish (Robertson 1992). At Taylor Glacier, the peak fledging lasted from 25 December 1988 to 3 January in 1989, when 52% of the

fledglings departed the colony. Thus, in 1988, the first chicks probably commenced their moult in mid-November and the last in mid-December.

Emperor penguins have a limited potential to adapt to a shorter fast ice season (e.g. Fig. S3). Their protracted courtship period of about 6 wk (Ancel et al. 2013) could potentially be shortened. However, the development and growth of their offspring probably cannot be shortened. Increasing the growth rate of chicks is associated with shortening the life-span (see Geiger et al. 2012).

4.2. Variability in colony environments

Generally, fast ice is stationary for many months, but its overall stability varies with location. Its extent and area can change rapidly under the influence of tides and ocean swells that can penetrate deeply into the pack-ice zone (Ushio 2006). The western colonies (43–64° E) should experience more stable conditions than many of the eastern ones as they occupy regions with extensive (~50 km wide) fast ice that forms along 100s of km of coast (Fraser et al. 2012, Table S1).

Most of the colonies east of Cape Darnley are farthest from the coast but relatively near the fast ice edge. Whether this affects breeding success is largely unknown. In our study area, long-term data on breeding success are available for only 1 of the 27 colonies, the Taylor Glacier colony. Over 30 yr (1988–2010), breeding success at this land-based colony fluctuated but was not affected by the consistent 60–70 km distance to the fast ice edge during chick rearing (Robertson et al. 2014). The penguins at Taylor Glacier adapted to the extended travels and poor breeding success was likely caused by factors other than distance to the fast ice edge. In comparison, at Pointe Géologie, the distance between colony and fast ice edge was more variable than off Taylor Glacier, and breeding success was highly correlated with fast ice extent. For example, in 1993, 1998 and 1999, when fast ice extent was well below the regional average, and distance to the fast ice edge was <10 km, breeding success exceeded 75%. In contrast, record low breeding success in 1992 and 1994 occurred when the distance to the fast ice edge exceeded 60 km (Massom et al. 2009). It is unknown how the emperor penguins from Taylor Glacier cope with the recurrently protracted travel across the fast ice, while those from Pointe Géologie are more challenged by long distance travel when rearing chicks. This comparison shows that events considered extreme at some colonies are standard conditions at others.

Fast ice extent is not static but can change throughout the chick-rearing period. In the western part of

the study area with extensive fast ice, the width of the fast ice usually decreased gradually and significant reductions generally occurred in mid- to late December without threatening colonies. For example, the distances between colony and fast ice edge averaged 51 ± 5 km and 53 ± 4 km, respectively, for the Umebosi and Kloa Point colonies from September to December 2018–2023.

In comparison, 15 of the 17 colonies east of 80° E were much closer to the fast ice edge than the western colonies. Seven colonies (West Ice Shelf, Barrier Bay, Karelin Bay, Petersen Bank, Cape Poinsett, Ninnis Bank and Davies Bay) experienced complete breeding failure or greatly reduced (Davies Bay) breeding success at least once during the study period, while others narrowly avoided additional or complete breeding failure. Early ice loss brought the fast ice edge to <2 km of the colonies during late chick rearing at least once during the study years. Only the Haswell Island and Yule Bay colonies remained safe at distances averaging 26 ± 7 km and 59 ± 10 km, respectively.

Pack ice at the edge of the fast ice can affect the travel distance of adults, especially at colonies at the eastern side of fast ice sheets (Posadowsky Bay, Ninnis Bank). When eastwards-drifting pack ice consolidates off the fast ice edge, it becomes near-impenetrable, thereby extending the ice-covered surface temporarily. Consolidated pack ice can also break out suddenly, greatly reducing the travel distance.

The Porpoise Bay colony experienced the most pronounced distance changes between years and within seasons. It occurs at the southwestern side of the Blodgett Iceberg Tongue (130° E) among a vast field of icebergs and at the eastern side of the 150 km-wide Porpoise Bay, where the iceberg tongue usually comprises multi-year fast ice (Fraser et al. 2012). Assuming the penguins chose the shortest route independent of direction, they travelled potentially in different directions to reach the fast ice edge. From September to December, the shortest travel distances averaged 62, 58 and 69 km in 2019, 2021 and 2023, respectively, compared to 6 km and 1 km in 2020 and 2022, respectively, and the penguins would have had to travel west, north-west or north-east.

Noticeable intra-seasonal changes in distances also occur. For example, in early August 2019, a polynya formed in the eastern part of Porpoise Bay, putting the fast ice edge about 31 km northwest from the colony. The ocean surface refroze in September/October and large leads formed at the fast ice edge either 125 km north or 72 km northeast of the colony. Either way, the penguins would have travelled a much longer distance than in early August. When the

polynya formed again in 2020, the colony was 28 km from the fast ice edge in early September 2020, but only about 1 km 3 weeks later.

The distance between the coast and an emperor penguin colony is also important, albeit less than the distance to the fast ice edge. It provides some measure of a colony's exposure to katabatic winds (downslope, gravity and pressure-driven surface winds formed by cooling air while moving over sloping surface; Vihma et al. 2011). In Antarctica, these often-fierce winds are a constant feature, particularly in winter, when they flow from the continent's interior towards the coast (Vignon et al. 2019), and are especially prominent in the coastal zone of East Antarctica (Turner et al. 2009). Coastal colonies, such as Umebosi, Fold Island and Amanda Bay, are exposed to persistently strong winds.

Katabatic winds contribute to the formation of some polynyas in winter (Nihashi & Ohshima 2015). During the study period, 6 of the 9 colonies near polynyas lost their breeding platform (Barrier Bay) or experienced complete breeding failure (Karelin Bay, Petersen Bank, Cape Poinsett, Mertz Glacier and Ninnis Bank). However, proximity to the fast ice edge does not necessarily lead to the premature loss of a breeding ground. Much seems to depend on the local conditions. For example, the median distance from the Flutter colony (69.7° E) to the fast ice edge was only 5 km (see Fig. 3), but fast ice remained *in situ* in spring/summer, despite the proximity to the Cape Darnley polynya. Katabatic winds flowing off MacRobertson Land in concert with the nearly continuous flow of cold continental air off the Lambert Glacier Basin maintain the large ice tongue on which the colony is located (Carpentier 2007).

4.3. Observations during 2023

Antarctic sea-ice extent has generally been decreasing since 2016, but in 2023, it reached its lowest extent since records began in 1979, and followed 2022 when sea-ice coverage was also extremely low. On 10 September 2023, the maximal sea-ice extent was estimated at only 16.96 million km², 1.03 million km² less than the previous record low of 1986 (National Snow and Ice Data Centre 2023a). Antarctica-wide, the maximal extent also occurred 13 d earlier than in 1981–2010 (range 18–30 September, median date 23 September) (National Snow and Ice Data Centre 2023a). Although possibly part of the long-term variability of the sea ice system, the reductions in sea ice extent in 2022 and 2023 may be indicative of a new regime (Purich & Doddridge 2023). Regardless,

recent changes in sea ice conditions have already affected multiple colonies Antarctica-wide (e.g. Fretwell & Trathan 2019, Fretwell et al. 2023).

As highlighted here, fast ice must be distinguished from the overall sea ice; the latter comprises mainly pack ice and usually forms slowly from mid-March to late September, then it recedes comparatively quickly from mid-October until early February. In comparison, fast ice tends to reach its minimal extent in early to mid-March and then grows rapidly. It persists from mid-May to late October before it starts to decrease (Fraser et al. 2012).

Our study colonies experienced highly variable conditions. In 2023, untimely breakout of fast ice caused reduced or complete breeding failure at 5 colonies (Auster, West Ice Shelf, Petersen Bank, Mertz Ice Shelf, Davies Bay) some of which had experienced premature fast ice loss in previous years, and others narrowly escaped (Karelin Bay, Cape Poinsett). Several polynyas formed, greatly reducing the distance between the fast ice edge and nearby colonies. The Barrier Bay colony was again not seen at the last known location nor elsewhere along the coast. It is unknown whether the penguins from the Barrier Bay colony had joined the West Ice Shelf colony, the nearest colony approximately 100 km farther north, or other colonies in the region (Amanda Bay, about 245 km west, and Karelin Bay, ~172 km east) or had skipped the season altogether.

Unexpectedly, in 2023, the year of record Antarctica-wide low sea ice extent (NSIDC 2023b), the Barrier Bay polynya did not form. Instead, Barrier Bay froze and extensive fast ice (>20 000 km² on 16 October 2023) stretched from the Vestfold Hills in the west to the north-eastern part of D-15A. The distance from the last known colony location in 2020 to the fast ice edge was 90 km in October, but open water occurred by 21 December 2023. Had the penguins returned to their previous location, conditions would have been highly unfavourable.

Since 2000, the only year when the regional fast ice was similarly extensive in Barrier Bay as in 2023 was in 2008, when winds drove much of the pack-ice in the area southwards where it compacted against the continent. Along the Leopold and Astrid Coast, the ice was 1.9 m thick in winter, the thickest in the decade 2001–2010 (Heil et al. 2011). In the 2008 spring and summer, >25 400 km² of fast ice extended west of the West Ice Shelf, and the distance from colony location in 2009 (Wienecke 2012) to the fast ice edge was about 128 km; most of the fast ice persisted well into January 2009 and extended ~80 km from the colony (details in Table S2).

Also unusual in 2023 was the low snow cover at colonies. Throughout spring and summer, satellite images showed consistently large, bare blue ice areas, indicating a lack of snow at the colonies, which has potentially 2 effects. During winter, penguins deposit substantial amounts of faecal material where they spend most of their time. In summer, these patches absorb heat, and the ice surface becomes brittle and pocketed. When snow is lacking, the albedo of the ice is low and heat is absorbed, leading to a decrease in fast ice quality and stability. Also, snow is the only source of water for incubating males during winter and chicks awaiting the next delivery of food in spring. At this stage, it is unclear whether the lack of access to snow influenced breeding success.

Throughout the annual cycle, changing environmental conditions that affect fast ice extent and duration may reduce the survival of colonies and individuals, particularly when the duration is shortened over which suitable breeding habitat is available to the penguins. The situations described are not unique to East Antarctica (Fretwell et al. 2023).

4.4. Interannual changes in colony locations

Since flat islands, or other terrestrial areas, are rare along the Antarctic coastline, emperor penguins most commonly establish colonies on the relatively flat fast ice because of their need for social thermoregulation (Jouventin 1971), particularly during incubation.

Several study colonies (e.g. Kloa Point, Fold Island, Amanda Bay) accessed multi-year fast ice and maintained their position within a small area for decades. Minor adjustments were made in years when the fast ice broke out in summer, but these colonies have consistently occupied the same areas since they were discovered in 1956 (Fold Island, Amanda Bay) and 1957 (Kloa Point) (Willing 1958).

Changes in local conditions can induce a colony to relocate; the distance from the previous site depends on the kind and extent of the local change. An extreme event occurred at the Mertz Glacier Tongue and caused a colony relocation (Ancel et al. 2014). In October 2002, the Mertz Glacier colony was at 66.93° S, 146.45° E (Fretwell & Trathan 2009) on a narrow band of fast ice (~7 km wide) at the northeastern side of the ice tongue that at the time reached 66.78° S. In early February 2010, a giant iceberg (~30 × 96 km), B-9B, which had been grounded for 18 yr ~70 km farther east, became unstuck and collided with the Mertz Glacier Tongue. Since it was summer, the fast ice had already disappeared and with it the

emperor penguins. Due to the impact, ~80% of the ice tongue broke off, producing another giant iceberg (~36 × 78 km) (Young et al. 2010). The 2002 colony location was now ~50 km north of the remaining ice tongue. Since then, the former breeding area has been covered in pack ice and has become unsuitable as breeding habitat. In November 2012, 2 breeding sites existed near the Mertz Glacier Tongue: one was on fast ice at the northeastern side of the ice tongue, and the other on fast ice about 18 km west in a small embayment off a rift at the northern side of the ice tongue (Ancel et al. 2014). Exposed to the open ocean, the western location had no fast ice in all but one year from 2013–2018. Probably soon after 2012, these 2 colonies reunited and still occupy the fast ice immediately adjacent to the eastern side of the Mertz Glacier Tongue. Events at this colony show that major changes in fast ice conditions can arise overnight. On 11 December 2020, approximately 1700 km² of fast ice extended from the Mertz Glacier Tongue eastwards to the Ninnis Glacier. On 12 December 2020, only ~620 km² remained. Simultaneously, several large floes (the largest ~15 × 50 km) broke off in the eastern fast ice area overnight and ~290 km² of fast ice including the colony area shattered into floes, most <100 m long. The colony narrowly avoided disaster only because it had occupied multi-year fast ice (<1.3 km²) that remained attached to the ice tongue. Similarly, in 2018, the colony was ~2 km farther south when the fast ice in the colony area broke out on 21 November, well before the chicks started to moult, leading to complete breeding failure. The rapid change in fast ice conditions, although minor on a geographic scale, was disastrous for the colony.

The Barrier Bay colony experienced a different extreme situation. Located on top of an iceberg in 2009, the colony lost its access to this breeding location (year unknown), and by 2018 had moved into a narrow area of fast ice between iceberg D-15 and the West Ice Shelf. In the coming years, 3 factors affected the colony: the proximity to the Barrier Bay Polynya, the movement of the ice shelf and the calving of a small iceberg, D-27, in May 2020. When D-27 calved, the embayment became shorter and its opening widened substantially. The ensuing premature loss of fast ice in the colony area resulted in total breeding failure in 2020 and 2021. In 2022, only a thin layer of ice covered the embayment, insufficient to provide a breeding platform; no colony has since formed here or elsewhere in the area.

Although records are limited, historically, some study colonies had to find new breeding areas, often for unknown reasons. Colonies near ice shelves or ice

tongues can be affected by calving events that alter the local conditions. For example, in November 1956, a large emperor penguin colony occurred north of the West Ice Shelf at 65.92° S, 81.92° E near a giant iceberg referred to as 'Penguin Island' (Korotkevich 1964). A large ice tongue, the Chelyuskintsy ice tongue, probably split off the West Ice Shelf sometime before March 1965, and moved 29 km west grounding at ~82° E (Ledenev & Yevdokimov 1967). This event likely changed local ice conditions and caused the colony to reposition. Today, the West Ice Shelf colony is about 41 km farther south than in 1956; the previous location is nowadays in the pack-ice. Similarly, a large colony north of the Shackleton Ice Shelf at 64.67° S, 97.5° E in October 1960 (Korotkevich 1964) was probably the same colony sighted at 64.86° S, 96.02° E in 2008 near the western extension of the Shackleton Ice Shelf (Table S2). What caused this colony to move >70 km is unknown, as is the time frame over which this shift occurred. Even today, the Shackleton Ice Shelf colony is among the most mobile in the study area.

Outside the breeding season, such events probably have a relatively minor impact on emperor penguins. If a traditional site no longer suffices, the penguins may miss a breeding season while searching for a new suitable area. As long-lived seabirds, they can cope with disruptive incidents, provided these do not occur frequently.

Not all change of breeding locality is due to catastrophic change. For example, the Karelin Bay colony in the central section of the West Ice Shelf region was about 13 km farther north in 2023 than in 1958. The gradual northward movement of the ice shelf has nudged the penguins away from the 1958 position. Similarly, at the Mertz Glacier Tongue, the ice tongue is pushing slowly north, and with it the colony location; in 2023, it was approximately 9 km farther north than in 2012.

Occasionally, a colony shifts location and moves to a different habitat type. For example, historically, the Shackleton Ice Shelf colony moved from an extensive fast ice area in 1960 onto the top of iceberg C-31, where it resided from 2012 to 2021. In 2022 and 2023, the colony relocated onto the fast ice, right at the edge of the iceberg. Why this move happened is unclear; ice breaking off the edge of the berg may have eliminated the penguins' access.

In Adélie Land, the colony had occupied the fast ice at the Pointe Géologie Archipelago for several decades, but in 2022 and 2023, it gathered on continental ice near a nunatak just south of its traditional breeding area, likely due to deteriorating fast ice conditions.

These behaviours document the adaptability of emperor penguins, but such shifts can only occur where abrasion at the edge of an iceberg or the pla-

teau generates relatively gentle slopes accessible to the penguins (e.g. Fretwell et al. 2014). Where steep ice (or rock) cliffs border a colony area rendered unsuitable, the penguins must find alternative breeding areas, potentially 10s of km distant (see e.g. Fretwell & Trathan 2019).

However, this adaptive behaviour comes with risks. On top of icebergs or iceshelves, emperor penguins lack shelter from wind, encounter crevasses, lose access when access routes collapse and may have less snow cover, potentially with consequences for their ability to breed successfully.

4.5. Monitoring emperor penguin colony locations

Given the recent chick deaths due to deteriorating fast ice conditions in numerous emperor penguin colonies (e.g. this study, Fretwell & Trathan 2019, Fretwell et al. 2023), we need a 2-tiered approach to assess the conservation status of the species: (1) improve our understanding of the effects of environmental change on emperor penguins at the local, regional and global scale; (2) improve the modelling of local and global population trajectories. Monitoring emperor penguin colonies with regard to changes in sea ice conditions requires a focus on fast ice rather than the entire sea-ice zone. Fast ice comprises only a small percentage of the total sea ice and its extent and dynamics vary significantly with region as does the timing of fast ice minima and maxima (Fraser et al. 2023). The large-scale distribution of fast ice can be determined remotely (e.g. Fraser et al. 2023), but methods are still being developed to examine other factors influencing the longevity of fast ice (e.g. quality, thickness, surface rugosity). Should fast ice conditions be poor, colonies can reposition themselves over distances of 10s of km relatively quickly. Hence, when determining locations of colonies, the wider region needs to be searched should a colony not be detected at its previous site.

Rediscovering a colony may take some years. For example, in October 2013, 6 small groups of emperor penguins occupied the top of iceberg D-21 that had calved from the north-eastern part of the West Ice Shelf (north of Zavadovski Island) in May 2013. This iceberg broke free in early May 2014, but the colony was not resighted until early December 2022 (P. Fretwell pers. comm.), when it occurred 21 km east of its 2013 position. Sentinel-2 images showed that the colony had been there since 2018 and had moved only 3 km by 2023. This so-called Vanhöffen colony is the most recently discovered one in the study area (Fretwell 2024).

Much remains unknown about newly discovered colonies, since high-resolution imagery has become available relatively recently. Many of these colonies appear to be quite small, raising the question of for how long they have existed and whether they have split off larger colonies. Given the potential for change in colony locations, we need to determine whether a colony has simply relocated or whether it is indeed new. To achieve some level of certainty, colonies should be monitored annually Antarctica-wide and dates of sightings must be recorded with colony locations.

Also, the varying number of occupied colonies (see LaRue et al. 2015) necessitates annual monitoring of active colonies. Satellite imagery is likely to be the most efficient way to accomplish this, but may not provide insights into the whereabouts of penguins when a colony does not form. Achievable and necessary tasks include the determination of colony positions, proximity to the fast ice edge, and the occurrence and possible impact of early ice breakouts. Habitat characteristics effectively assessable from satellite imagery include the distance from the Antarctic coast, the distance to the edge of the fast ice, the substratum where colonies form, and impacts of early ice break-outs. The frequency and area coverage of the Sentinel-2 satellites were not set up specifically for this work. While cloud-free images can capture colonies, the number of images available per month is not constant because of a slight shift in position of the satellites. For 21 of the 27 colonies, 6 images were usually available from September to December. Occasionally 7 or 8 images included a particular colony location. Since September 2022, 14 colonies are captured in only 3 images per month (every 10 d). In cloudy areas, colonies may be undetectable for several weeks, making it difficult to verify their fate. Search areas must be larger than colony areas of a previous season, especially where colonies are quite mobile. Some colonies experience pressures that may encourage sections of a colony to relocate. Since many of the most recently discovered colonies are relatively small, this process possibly indicates that emperor penguins are attempting to adapt to changing local conditions.

4.6. Monitoring emperor penguin colony populations

Monitoring changes in emperor penguin populations is crucial to determining the species' threat status both locally and globally, but is logistically more difficult to achieve than determining changes in colony locations. Estimating emperor penguin

numbers based on satellite images requires consideration of various caveats. For example, as colonies move throughout the season, ice areas with faecal stains are not representative of colony size. Also, only adult numbers were previously estimated (Fretwell et al. 2012). However, the number of adults in a colony decreases throughout the season (see below). Also, consistent timing of estimates, needed for effective relative interannual comparisons, is affected by cloud cover. Thus, accurate population counts are presently not possible with the available 30 cm resolution satellite imagery; hence the paucity in data for most colonies.

Estimates based on the number of adults are likely underestimates (see below). From October onwards, chicks tend to outnumber adults and provide a more accurate estimate of population size. However, due to the lack of contrast between chick plumage and ice background, they are very difficult to count from satellite images; ground and aerial surveys are imperative to monitor colony populations accurately. The number of adults in a colony varies throughout the breeding season. The population size of a colony is most accurately estimated in mid-winter when only males are present. Although not every male attending a colony during incubation carries an egg (e.g. Budd 1962, Robertson 1992), the number of males is the most accurate estimate of colony size. However, this is also a highly sensitive time, and disturbance can lead to significant egg losses. In addition, access to most colonies in winter is severely limited by operational (few daylight hours) and weather-related constraints. Females returning to the colonies from mid-July onwards add to the number of adults. Since the return of the females is quite asynchronous, and males do not depart immediately upon their partner's return, the number of adults is no longer equal to the number of breeding pairs.

From September onward, chicks start to crèche, grow quicker and require more energy than during the brood and guard stage. Thus, both parents have to provide for their offspring and the number of adults in the colony decreases as the season progresses. From late October onwards, chicks outnumber adults noticeably. In October, there are on average 2 chicks per adult; this increases to 4 chicks per adult in November and 7 chicks per adult in early to mid-December (see Fig. 8). The number of adults rapidly decreases, and from mid-to late December the chick to adult ratio increases to 28–40 chicks per adult (Barber-Meyer et al. 2008). At colonies separated into several suburbs, the ratio of adults to chicks is not always constant. In November 2022, the West Ice Shelf colony comprised 5 distinct

groups, where adult to chick ratios ranged from 0.2 to 0.4. In comparison, in December 2013, this ratio was 0.2 for 4 distinct groups at the Flutter colony.

Barring unforeseen events, absolute chick numbers remain quite stable from October to December as chick mortality is noticeably lower than in the early chick-rearing period (Kirkwood 1997, Barber-Meyer et al. 2008). From late November onwards, non-breeding birds (unsuccessful breeders, sub-adults, yearlings) may return to the colony to moult, adding to any population counts. Timing of population estimates is important and must be as consistent as possible to reduce errors. Census work should be undertaken before early December, as chicks advanced in their final moult can be difficult to distinguish from adults. Although previous losses of eggs and chicks cannot be accounted for, late in the season, the number of chicks is more representative of colony size than the number of adults and relative comparisons between years are possible, provided counts occur, if possible, consistently at the same time of year. Adults should also be counted, as adult to chick ratios may help determine whether shifts occur in the breeding phenology at particular colonies.

4.7. Conclusions

The 27 study colonies occur in different and variable environments, where changes in local conditions range from insignificant to disastrous. The most impactful change to colonies is an untimely, early loss of breeding habitat when chicks are not yet able to fend for themselves. These changes are multidirectional, non-linear, highly colony-specific and important at a local scale. Of concern are the number of colonies affected by reduced or complete breeding failure in just 6 yr (2018–2023). The 13 colonies < 10 km from the nearest fast ice edge appear to be particularly at risk. Eight of these 13 colonies experienced reduced or complete breeding failure at least once during the study period. Even a colony like Auster, situated on a vast fast ice sheet and a long way from the ice edge, experienced rapidly changing conditions just as the chicks were moulting. The situations described here are not limited to the study colonies. Habitat changes rendering breeding areas unsuitable for emperor penguins also are known to have occurred off the coast of Marie Byrd Land, West Antarctica (LaRue et al. 2015) and in the eastern Weddell Sea (Fretwell & Trathan 2019).

What also needs to be examined, but was out of scope of this paper, is the effect of changing fast ice

conditions on the moult habitat of emperor penguins. Pre-moult, adults disperse widely and are not reliant on areas as specific as breeding areas. However, penguins still require a platform that persists for 4 to 6 wk in late summer. Untimely loss of breeding habitat curtails breeding success, and if frequent, recruitment of new breeders. Loss of moult habitat can limit the survival of adults, with potentially significant downturns in the size of the breeding population. Should recruitment become limited and adult survival decreases, emperor penguins are heading for a crisis point from which they may not recover.

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Appendix.

Table A1. Results of the most recent counts of 9 emperor penguin colonies in 2022. For further details see Table S1. Colony visits to all colonies except the Bowman Island and Shackleton Ice Shelf colonies occurred at times when chicks are quite independent and colonies are usually spread out, making individuals recognisable. On the flight on 6 December 2022, it was noted that a small number of chicks had departed from the colony and were seen near the fast ice edge

Colony	Date	Method	Number of adults	Number of chicks
Kloa Point	22 Sep 2022	Ground photography	3470	—
Fold Island	20 Sep 2022	Ground photography	361	234
Flutter	3 Nov 2022	Aerial photography	1378	7707
Amanda Bay	23 Nov 2022	Aerial photography	1424	10 485
West Ice Shelf	3 Nov 2022	Aerial photography	2480	7786
Posadowsky Bay	3 Nov 2022	Aerial photography	123	155
Shackleton Ice Shelf	6 Dec 2022	Aerial photography	1339	10 738
Bowman Island	6 Dec 2022	Aerial photography	399	2372
Petersen Bank	2 Dec 2022	Aerial photography	ice broke out in November	
Sabrina Coast	2 Dec 2022	Aerial photography	672	4278

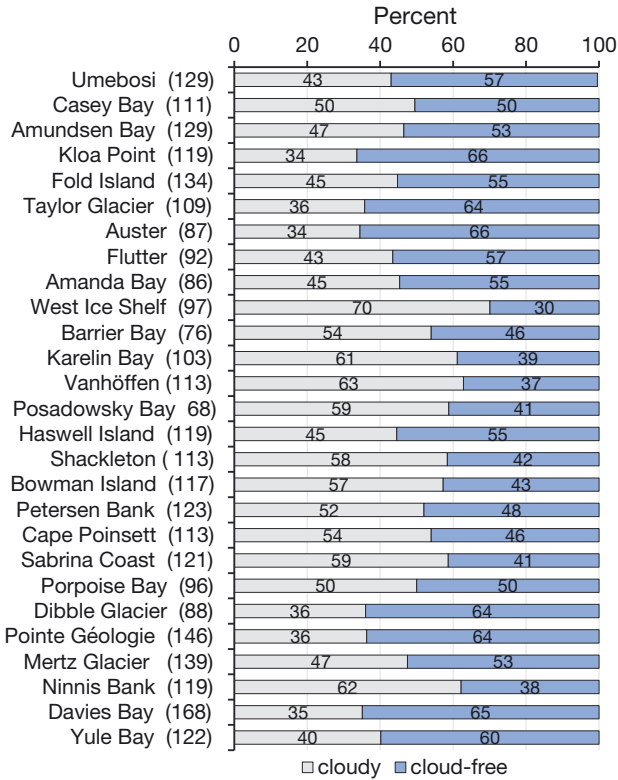


Fig. A1. Percentage of cloud-free and cloud-covered Sentinel-2 images by colony from September to December over the study period 2018–2023

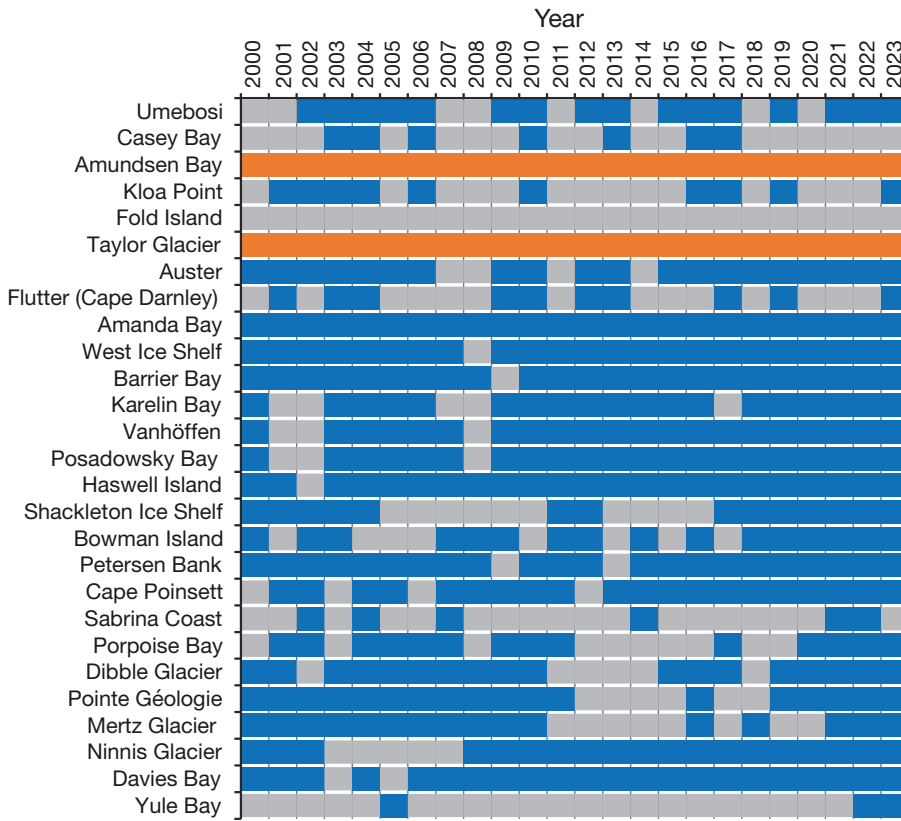


Fig. A2. Fast ice conditions at 27 emperor penguin colonies in East Antarctica, 2000–2023 showing 1-year fast ice (blue) and multi-year fast ice (grey). Amundsen Bay and Taylor Glacier are land-based colonies (orange) and as such independent of fast ice formation