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Evidence of emperor penguins' sensitivity to sea ice fluctuations

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Using satellite-derived abundance indices over 20 years, we investigated population change among the seven Ross Sea emperor penguin (*Aptenodytes forsteri*) colonies. We found a 90% probability that the Ross Sea metapopulation had lower springtime attendance between 2005 and 2024 (mean change = −23%; 95% CI: −46 to +20%). We identified two distinct phases of change: slightly increasing 2005 to 2019/2020, followed by a steep decline 2020–2024, resulting in a decrease of approximately 23 000 birds in 5 years or approximately 32% of the regional population. Over the 20 years, the two southernmost colonies, Cape Crozier and Cape Colbeck, increased in size, yet Beaufort, Coulman, Roget and Washington declined, resulting in a negative population trend especially evident from 2021. Asynchronous population change suggests metapopulation dynamics, with immigration from western colonies possibly driving increases at Colbeck and Crozier. Winter and spring sea ice concentration anomalies (5 year lag) and El Niño phases (1 year lag) statistically explained the most variance in our time series. Our results indicate that emperor penguins may be sensitive to sea ice fluctuations, offering insight into how this species may have adapted throughout their history and emphasizing the need for timely re-evaluation of targeted conservation strategies in an era of sea ice change.

1. Introduction

Antarctic penguins (Spheniscidae) are a prime example of species that employ the demographic buffering strategy, trading limited offspring production for adult survival in harsh conditions [1], exemplifying taxa that have evolved to persist in highly variable polar environments [2]. These adaptations for Adélie (*Pygoscelis adeliae*) and emperor (*Aptenodytes forsteri*) penguins are closely tied to the seasonal dynamics of sea ice, which regulate both reproductive success and trophic interactions [3]. However, recently the extent and persistence of summer and winter sea ice in the Southern Ocean have changed [4–6]. Because emperor penguins are sea ice obligates (breeding and chick rearing on fast ice and moulting on pack ice), it stands to reason that populations may be impacted by these changes [7–10]. Here, we evaluate the relative

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contribution of large-scale climate and sea ice variables to the variation in abundance of Ross Sea emperor penguins.

One of two penguin species endemic to Antarctica, emperor penguins have evolved in extreme conditions for millions of years [11]. Reaching sexual maturity between 3 and 8 years, emperor penguins produce just one egg per year and can 'skip breed' [7,12]. Lasting nine months, their breeding cycle takes place entirely on fast ice and is constrained by its formation and retreat [13]. The Southern Ocean marine environment is therefore of paramount importance to the persistence of the species. Notably, the *Aptenodytes* genus diverged from other extant penguin species more than 20 Ma, while emperor penguins diverged from their closest relative, the king penguin (*A. patagonicus*), approximately 3 Ma [11]. The species has therefore persisted through several glacial–interglacial periods, with varying sea levels, sea ice covers and extents [14–16]. Under the demographic buffering hypothesis, variability in breeding success and juvenile survival can fluctuate in response to short-term environmental perturbations, such as early break-up of fast ice [17,18], yet combined with predictably high adult survival [8,19], the expectation would be relatively invariable population growth rates [1,20,21]. However, sustained environmental change that increases variability in adult survival or results in extended periods of poor reproductive output can eventually erode this buffering capacity, leading to accelerated population decline and heightened risk of localized extinctions [21,22].

Prior to 2014, the Ross Sea region experienced increasing seasonal sea ice extent (SIE) and duration, advancing one month sooner and retreating one month later, contributing to an increasing circumpolar SIE trend between 1979 and 2008 [23,24]. However, large-scale sea ice trends have since changed; following an annual average SIE peak in 2014, there were 3 years of decline, reaching what was at the time a record low (since observations began in 1978) in 2017 [24]. In the years since, large-scale Southern Ocean SIE has continued to decline. Winter SIE in 2023 and 2024 was lower than the 2017 minimum [5,25,26] and summer SIE was the lowest on record in 2022, 2023 and 2024 [6,27]. Recently, satellite observations have indicated an unexpected increase in surface salinity and decrease in upper ocean stratification in the Southern Ocean, which coincided with observed sea ice declines since 2016 [28]. As the warmer, saltier, less stratified surface waters are less likely to freeze, the Southern Ocean may have transitioned to a period of sustained, reduced sea ice coverage [4,28]. These observations highlight the time-sensitive nature of improving our understanding of the physical Southern Ocean environment and possible relationships to ice-obligate species.

Studying emperor penguins is difficult owing to the formation of their breeding colonies in winter and their preferred fast ice habitat, yet some Ross Sea populations have been observed consistently for decades in spring, by ground count, aerial survey or high-resolution satellite imagery [29–33]. To date, possible links between abundance and drivers of change across spatial scales have remained elusive. Springtime counts represent indices of abundance derived from colony attendance. At this stage of the breeding cycle, chicks are thermally independent and adults often visit only briefly to feed chicks before departing on another foraging trip [13,33,34]. Thus, the number of birds present can fluctuate independent of breeding numbers. Abundance indices therefore require careful inference [32,35,36]. Despite the limitations, springtime censuses provide some of the only long-term, Antarctic-wide datasets for emperor penguins, may still capture relative variation in colony size linked with demographic processes, and yield insights into population trends that cannot be obtained otherwise [29,30,32].

To advance our understanding of environmental connections with emperor penguin abundance indices (representing springtime colony attendance), we investigated environmental influences on their springtime attendance in the Ross Sea, at colony and regional scales. Drawing on previous state-space models [32] and extending the time series to 2000–2024, we modelled attendance at each Ross Sea colony and the Ross Sea region overall across 20+ years and related annual change in abundance indices (growth rates) to environmental variables. Specifically, we aimed to assess relationships between emperor penguin abundance indices and seasonal sea ice concentration anomalies (SICa), fast ice persistence and broad-scale climate variables (e.g. El Niño). We focused on SIC owing to its relationship to both foraging conditions and moulting habitat for emperor penguins [37–40] and the greater precision of SIC data over SIE (i.e. SIE cells are binary indicating if more than 15% of the cell is covered in ice, whereas SIC indicates percentage cover for each cell). We hypothesized that metapopulation growth would be correlated to large-scale climate variables, such as El Niño Southern Oscillation (ENSO) Index [41] and regional-scale SICa. We hypothesized that colony-level dynamics would be related to local pack ice and fast ice conditions. By including broad-scale climate drivers alongside SIC, we aimed to test whether penguin demography responds only to sea ice or if there are additional pathways of influence (e.g. ENSO-driven prey redistribution or altered ocean productivity [41]).

2. Methods

(a) Study area

The Ross Sea (165° E–150° W, 65°–79° S, figure 1) represents the most productive stretch of the Southern Ocean [42]. The region's food web is described as 'wasp-waist' when considering species diversity, with an intact predator guild (e.g. Weddell seals (*Leptonychotes weddellii*), Adélie penguins, killer whales (*Orcinus orca*), Antarctic toothfish (*Dissostichus mawsoni*)), and relatively few prey species (e.g. Antarctic silverfish (*Pleuragramma antarcticum*), Antarctic krill (*Euphausia superba*) and crystal krill (*E. crystallorophias*)) [43]. The Ross Sea region also contains one of the world's largest marine protected areas. The region is home to large numbers of emperor penguins, an estimated 30% of the global population [31,32], with colonies varying in size from approximately 1000 birds at Beaufort Island and Cape Crozier to greater than 20 000 birds at Coulman Island and Cape Colbeck [30,32].

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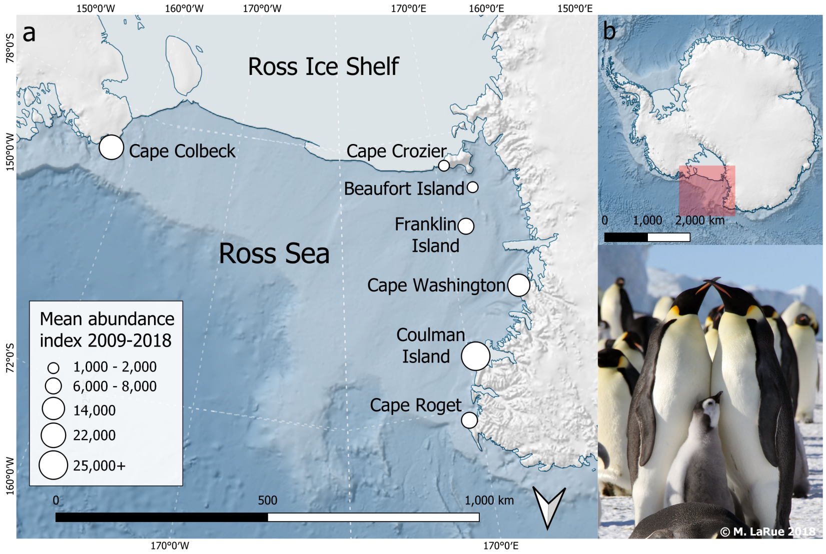

Figure 1. (a) Map of the Ross Sea, Antarctica (165° E–150° W, 65°–79° S) and the seven emperor penguin breeding colonies analysed in this study. Mean abundance index based on LaRue *et al.* [32]. (b) Antarctica with the extent of panel A in red. Emperor penguin image taken at Cape Crozier by LaRue (Permit: ACA no. 2019-006).

(b) Data coverage

Our study period spanned 2000–2024 and used very high resolution (VHR) optical satellite imagery and published ground/aerial survey counts to estimate abundance indices at every Ross Sea colony. To identify satellite imagery available for analysis, we reviewed imagery through Discover Maxar (https://xpress.maxar.com/), searching for images from the austral spring (September–November) between 2000 and 2024. Imagery availability varied by location: the earliest images were obtained for Cape Crozier and Franklin Island in 2002 and Cape Roget in 2004. We incorporated aerial survey data from Barber-Meyer *et al.* [29], Kooyman & Ponganis [30] and MAPPPD (https://www.penguinmap.com/). From these sources, we obtained aerial counts for Beaufort Island from 2000 onwards, Franklin Island and Cape Crozier from 2001 onwards and Cape Washington from 2004 onwards (see electronic supplementary material). Our analysis spanned all Ross Sea colonies from 2005 to 2024, representing the longest continual study of regional population trends for the species conducted to date.

(c) Satellite imagery analysis

We analysed VHR optical satellite imagery (0.31–0.6 m resolution) captured during the springtime (September–November). Imagery was acquired through Maxar (previously DigitalGlobe) satellite constellations (QuickBird-2, WorldView-2 and WorldView-3). We analysed near-infrared, blue and green bands, depending on the satellite platform of the image. We analysed imagery using a supervised classification algorithm within ArcGIS Pro (v. 3.4.0 [44]), calculating the total area covered by penguins in each image using the approach described by Fretwell *et al.* [31] (electronic supplementary material, figure S1). We analysed a total of 142 images for all Ross Sea colonies spanning 2002–2024 and converted the estimated penguin areas to an index of abundance, representing springtime colony attendance, using the modelling framework described below.

(d) Population modelling

We used an openly available Bayesian state-space (BSS) model to transform penguin area to an index of abundance [32]. Through the inclusion of 'day of year' and 'image quality' covariates, the BSS model considered observation error (resulting from variation in the ability of observers to accurately estimate population size) and process error (the actual variation in population size driven by abiotic and biotic processes) [32]. We excluded data that fell outside the optimum springtime population estimation window (i.e. estimates from before 1 September and after 31 November), as colony attendance fluctuates considerably across the spring as failed breeders depart, successful breeders forage and non-breeders arrive [13,34]. If we observed no evidence the colony was occupied in any available imagery for that year, we recorded it as an absence (0). However, we excluded colony absences identified after 1 November, as the colony status was too uncertain that late in the season and it was unclear if the colony was occupied earlier. If the ice was no longer formed when the image was captured, we recorded an NA at that location as we could not confirm if birds had been present prior to the ice breakout. For further detail on the BSS model development, see LaRue *et al.* [32].

We calculated the mean abundance index for each colony and the Ross Sea population overall each year, representing adult emperor penguins present at the colonies in spring. It is important to note that this index represents only a portion of the total population present during surveys and is therefore an underestimate of the true number of adult penguins in the Ross Sea. We calculated the standard error and credible intervals for the colony-specific and regional estimates, trends and change across the study period. To assess annual population change, we converted abundance indices from the current year $(\mathcal{X}_T)$ and year prior $(\mathcal{X}_{T-1})$ to annual growth rate using the following formula:

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$$\mathrm{Lognormal}\left(\frac{\mathcal{X}_{\mathcal{T}}}{\mathcal{X}_{\mathcal{T}-1}}\right).$$

(e) Environmental variables

We assessed seasonal SICa (localized, regional and moult sector; defined below), fast ice persistence (i.e. days per year that fast ice was present at the colony), fast ice breakout date, average yearly ENSO and southern annular mode (SAM) and seasonal averages for location (lat/lon) and strength (relative central pressure; RCP) of the Amundsen Sea low (ASL). We also assessed the importance of 1 and 5 year lags for each variable: 1 year lag to represent the conditions experienced by the adults during the previous year and 5 year lag to represent the estimated age of recruitment for emperor penguins [19,29], and thus the conditions experienced when the newly recruited breeders were chicks. We outline all variables tested in electronic supplementary material, table S1.

We calculated SICa based on monthly SIC data from the National Snow and Ice Data Centre [45] (https://masie_web.apps.nsidc.org/pub/DATASETS/NOAA/G02135/south/monthly/), comparing SIC for each month with the monthly average spanning 1995–2024 (encompassing our study period and a 5 year lag from the first year of observation). In R (v. 4.3.1 [46]), we calculated seasonally averaged SICa within a 200 km radius of each colony (based on maximum foraging range during the breeding season [47]), for the entire Ross Sea region (165° E–150° W, 65° S–79° S) and for the eastern Ross Sea-Amundsen Sea moult area in summer (155° W–135° W, 70° S–78° S [37]; electronic supplementary material, figure S2). We considered three monthly seasonal averages (Jan.–Mar., Apr.–June, July–Sep. and Oct.–Dec.), as each period relates to a different aspect of an emperor penguin annual cycle (electronic supplementary material, table S2 [12,29]).

We estimated fast ice persistence using the NASA Worldview MODIS tool (https://worldview.earthdata.nasa.gov/), estimating the date of fast ice formation and breakout at each colony each year (electronic supplementary material, figure S3). We observed imagery each day between August and April (when sunlight was available) each year between 2000 and 2024 to identify the earliest date that fast ice had broken out at each colony (i.e. when open water or loose pack ice was visible under the colony's estimated location) and the last date that the ice had formed at the colony location prior to the photoperiod ending, indicating the total number of days each year the colony had fast ice. We also created a binary variable that identified whether fast ice broke out early (prior to 15 December) as chicks may not be ready to fledge by that date [29,33].

To assess the role that broad-scale climate drivers may have on emperor penguins in the Ross Sea, we analysed ENSO, SAM and the relative strength and position of the ASL. We analysed yearly averaged Southern Oscillation Index (SOI) values (https://www.ncei.noaa.gov/access/monitoring/enso/soi) to identify ENSO phases, with El Niño phases (i.e. negative SOI values) associated with reduced winds, warmer sea surface and air temperatures and decreased SIE and SIC in the Ross Sea sector [41]. We hypothesized that fewer emperor penguins would breed during El Niño years or in the years following (1 and 5 year lags) owing to temperature changes, shifting sea ice conditions and the potential link to breeding and foraging conditions. We calculated yearly averages for SAM and hypothesized that positive SAM would positively affect Ross Sea emperor penguin populations owing to increasing westerly winds and upwelling, and thus greater large-scale SIE and, at smaller scale, larger, earlier polynya formation. We also analysed seasonal averages for the location and strength of the ASL owing to its link to wind speeds, SIC and ice drift in the Ross Sea [48]. We hypothesized that emperor penguin growth rates would be positively correlated with deeper RCP owing to the increased large-scale SIC, cooler winds and ice movement that may impact colony selection. We also hypothesized that this impact would be greater when the ASL was positioned closest to the Ross Sea sector (i.e. at its most westerly longitudes and higher latitudes). Because ASL and SAM are closely related climate patterns, they were analysed separately to avoid confounding their effects.

While colony spacing and size are shaped locally by intraspecific competition for prey and habitat availability [49], these dynamics may be synchronized by broad-scale environmental drivers that affect the entire region (i.e. the Moran effect [50–53]). We therefore hypothesized that Ross Sea colony dynamics may exhibit synchronous change. Alternatively, we hypothesized that negatively correlated change (i.e. one increasing while others decrease resulting in overall regional stability; hereafter referred to as asynchronous change [54]) may be driven by penguins responding to more localized pressures through inter-colony movement [55], thus facilitating a metapopulation [56,57].

(f) Statistical analysis

Statistical analyses were performed in R Statistical Software (v. 4.3.1 [46]). Following the BSS population analysis, we performed additional analyses on each full posterior trajectory to determine: (i) total change in abundance across the study period; (ii) per cent change across the study period; and (iii) average annual change. We ran these analyses on each of the 30 000 posterior draws to identify the mean, median and 95% confidence interval around each parameter. We identified an apparent phase shift in our time series and ran a break point analysis (*segmented* v. 2.4-1 [58]) on each posterior trajectory to determine if a significant change in slope occurred (electronic supplementary material, figure S4). We estimated the trend, total change (per cent and abundance) and annual per cent change for each phase prior to and following the estimated break point.

We plotted colony-specific abundance indices and ran a series of linear regressions to identify whether trends observed at each colony were significant over the study period. We calculated the coefficient of variation for each colony and the metapopulation to understand how much each colony fluctuated around its mean (electronic supplementary material, table S3). We aimed to determine if there were similar trends in population change among the Ross Sea colonies and visually identified potential synchronous fluctuations. To assess observed patterns of covariation, we assessed correlations between colony pairs using *cor*

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(*stats* package [46]) and *corrplot* (*corrplot* package, v. 0.92 [59]). We conducted synchrony analyses using the *community.sync* function in the *synchrony* package (v. 0.3.8 [60]), in which we treated each colony as a separate species within a community matrix to identify community synchrony values. We selected 'Pearson's' method and ran 999 randomizations to determine the significance of the observations. For community synchrony analyses, a value of 1 represents perfectly synchronous population change (positive or negative) and 0 indicates populations change independently of each other [60].

To understand the drivers of the observed fluctuations in abundance indices (analysed as annual growth rate), we used a generalized additive model (GAM) to model metapopulation change and a generalized additive mixed model (GAMM) with random effects to assess colony-specific change in R's *mgcv* package [61]. We opted to use GAMs owing to their ability to identify and estimate nonlinear effects. We used a thin plate basis regression spline (bs = 'tp'), default K and reduced maximum likelihood (REML) method. We checked for correlation between our covariates using R's *cor* function and *corrplot*. Variables with correlation coefficients greater than 0.5 were not included in the same model (electronic supplementary material, figure S5). We performed two sets of analyses, GAMs that analysed regional-scale drivers of metapopulation change ($n = 19$) and GAMMs that investigated local-scale drivers for colony-specific growth rates ($n = 147$). We identified temporal autocorrelation in our model residuals and remedied this by including an AR1 correlation component in each model.

For the metapopulation model, we assessed regional SICa from each season, summer SICa from the eastern Ross Sea (ERS) moult sector and climate drivers (ENSO, SAM and ASL). We also assessed 1 and 5 year lags. Owing to the small sample size ($n = 19$), we included a maximum of two variables in each candidate model to prevent overparametrization [62] and assessed various combinations of uncorrelated sea ice and climate covariates. We selected the best-supported metapopulation model by identifying the highest log-likelihood, adjusted R^2, deviance explained, Akaike weights and the lowest Akaike information criterion, corrected (AICc) (table 1; *MuMIn* package [64]). For the colony-specific model, we included 'site_number' and 'year' as random effects to account for any site-specific and annual variability not captured by the predictors. We analysed localized covariates, including fast ice persistence ('ice days'), local-scale SICa from autumn, winter and spring, early fast ice breakouts and lagged variables. Local summer SICa was not analysed as emperor penguins are not at breeding colonies in summer. We ran a global model with all available covariates and performed variable selection using 'select = TRUE' to penalize the smooths and reduce the effect size (F) of the non-important variables to zero [63]. We made inference about the effect of each variable based on the partial dependence plots produced through the model summary output. For both the metapopulation and colony-specific models, we ran two sets of analyses, one that analysed the entire time series up to 2024 and one that excluded data following the step change identified after 2020. We used gam.check to check residuals, test model convergence and the suitability of K for both models.

3. Results

We found a 90% probability that the Ross Sea metapopulation had lower springtime attendance between 2005 and 2024 (mean change = −22.6%; 95% CI: −49.3 to +19.6%). This corresponded to an estimated 17 216 fewer emperor penguins in 2024 than 2005. We estimated a mean annual change of −1.46% per year over 20 years. Abundance indices of the Ross Sea metapopulation reached a 20 year peak of 81 465 in 2019 and a low of 56 301 in 2024. We observed an apparent increase between 2005 and 2019/2020, followed by a decline between 2020 and 2024 (figure 2). Our break point analysis suggested a structural shift probably occurred in the final 6 years of observation (median = 2020, 78% probability a break point occurred after 2018; electronic supplementary material, figure S4). This corresponded to a change from a period of seemingly steady increase to a period of apparent rapid decline (figure 2). Between 2005 and 2020, we estimated an increase of 9.5%, corresponding to 6184 more birds present in the springtime across the region and an annual increase of +0.5% per year. From the estimated break point in 2020, the population was estimated to have declined by approximately 23 400 birds, corresponding to an estimated 32% decline and a mean annual change of −8.5% per year between 2020 and 2024.

At the colony level, the two southernmost colonies, Cape Crozier and Cape Colbeck, increased, Franklin Island was stable and Beaufort, Coulman, Roget and Washington decreased in size (figure 3, electronic supplementary material, table S4). We observed synchrony between Colbeck and Crozier (comm.sync = 0.995, p-value = 0.001), synchrony between the remaining five colonies (comm.sync = 0.85, p-value = 0.001) and asynchronous change between colonies across those two groups (electronic supplementary material, figures S6 and S7). The two largest western Ross Sea (WRS) colonies, Cape Washington and Coulman Island, approximately halved in size by the end of the study period, decreasing from 14 160 to 8278 and from 28 386 to 11 981, respectively. Cape Colbeck reached a maximum of 42 105 in 2020, making it the largest emperor penguin colony recorded to date. However, Colbeck also declined steeply in the last 3 years of observation. Beaufort Island steadily declined across 25 years, while its close neighbour, Cape Crozier, increased from 521 birds in 2002 to 1248 in 2024.

Environmental drivers of metapopulation growth differed depending on the years we included in models. Including the full time series (2005–2024), the best-performing model included 5 year lag springtime SICa and 5 year lag winter SICa (tables 1 and 2). We identified a negative correlation with 5 year lag spring SICa (i.e. growth rates were lowest 5 years following low spring SICa) and a quadratic effect of 5 year lag winter SICa (figure 4a). Excluding data after the break point in 2020, adjusted R^2 and deviance explained increased (table 1). The best-supported model (2005–2020) included 1 year lag ENSO (ENSO.1) and 5 year lag winter SICa (table 1, figure 4b). Growth rates were lowest the year after a strong El Niño event and we observed the same quadratic effect of 5 year lagged winter SICa (figure 4b). Competing models are presented in table 1. Colony-specific modelling identified relationships with winter, springtime and autumn SICa at various lags and fast ice persistence (figure 5, table 2). Highest and lowest regional SICa values for each season are presented in electronic supplementary material, table S5. Model diagnostics and additional results are presented in electronic supplementary material, figures S8–S19.

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Table 1. Results of GAMs assessing drivers of emperor penguin population change in the Ross Sea. We present the top five metapopulation models for the period up to 2020 and for the full time series (2005–2024). Models in bold were identified as 'best-supported' by assessing AICc, log-likelihood (LogLik), adj. R^2 and Akaike weights (wts). Metapopulation models were also assessed using deviance explained. Colony-specific models included 'year' and 'site_id' as random effects. Non-important variables (identified using 'select = T' [63]) were excluded. Additional GAM partial effect plots and model diagnostics are provided in electronic supplementary material.

	predictors	*n*	AICc	logLik	R^2 (adj.)	Dev. expl. (%)	ΔAICc	Akaike wts
metapopulation	**ENSO.1 + SICa_JAS.5**	**15**	**−220.4**	**42.22**	**0.760**	**84.5**	**0.0**	**0.887**
2005–2020	ENSO.1 + SICa_JAS.1	15	−214.9	37.04	0.608	69.1	5.5	0.057
	ENSO.1 + SICa_JFM	15	−213.7	37.32	0.605	70.2	6.7	0.031
	ENSO.1 + SICa_OND.5	15	−212.4	36.12	0.556	65.0	8.0	0.016
	ENSO.1 + ERS_SICa_JFM	15	−211.2	34.80	0.494	58.3	9.2	0.009
2005–2024	**SICa_JAS.5 + SICa_OND.5**	**19**	**−826.5**	**40.38**	**0.602**	**69.6**	**0.0**	**0.755**
	SICa_JAS.5 + SICa_JAS	19	−822.9	37.38	0.491	58.3	3.6	0.125
	SICa_JAS.5 + RCP_JFM	19	−822.6	36.59	0.465	54.6	3.9	0.107
	SICa_JAS.5 + SICa_JFM.5	19	−817.5	33.31	0.283	35.9	9.0	0.008
	SICa_JAS.5 + SAM	19	−816.3	32.56	0.236	30.6	10.2	0.005
colony-specific								
2000–2020	SICa_JAS + SICa_JAS.1 + SICa_JAS.5 + SICa_OND + SICa_OND.1 + SICa_OND.5 + SICa_AMJ.1 + ice_days + year + site_id	119	−170.62	104.31	0.194			
2000–2024	SICa_JAS + SICa_JAS.1 + SICa_JAS.5 + SICa_OND + SICa_OND.1 + SICa_OND.5 + SICa_AMJ.1 + ice_days + year + site_id	147	−224.00	133.00	0.142			

.1, 1 year lag; .5, 5 year lag; AMJ, Autumn (Apr, May, Jun); ENSO, El Niño Southern Oscillation; ERS, Eastern Ross Sea; ice_days, Fast ice persistence; JAS, Winter (Jul, Aug, Sep); JFM, Summer (Jan, Feb, Mar); OND, Spring (Oct, Nov, Dec); RCP, Relative Central Pressure (strength of the Amundsen Sea Low); SAM, Southern Annular Mode; SICa, Sea ice concentration anomaly .

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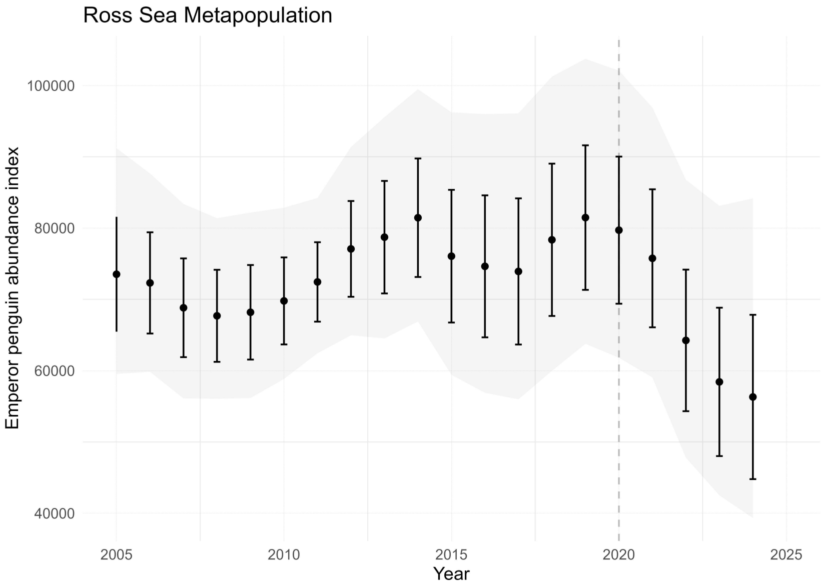

Figure 2. Annual abundance index estimates for the Ross Sea emperor penguin metapopulation between 2005 and 2024. Black points indicate the estimated abundance index, error bars indicate the standard error for each estimate and the grey ribbon represents the 95% confidence intervals. Vertical dashed line represents the estimated 'break point' when the metapopulation trend shifted from a period of increase to a period of decline (electronic supplementary material, figure S4).

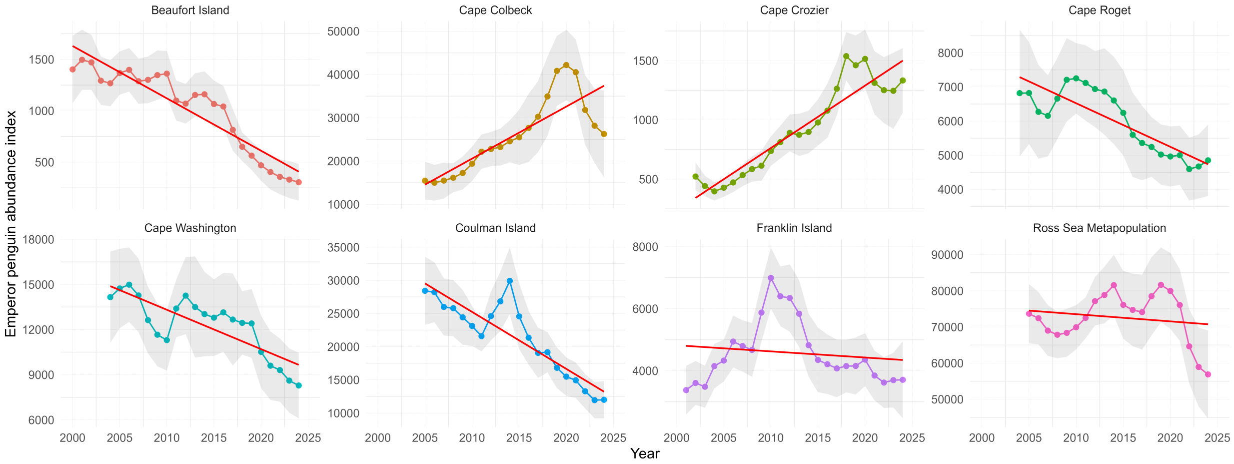

Figure 3. Colony-specific abundance indices (representing springtime colony attendance) for the seven Ross Sea emperor penguin colonies and the metapopulation. Grey ribbons indicate standard error and solid red lines indicate the linear regression trends for each location (electronic supplementary material, table S4).

4. Discussion

(a) Evidence of metapopulation dynamics

Over 20 years, we observed synchronous increases in emperor penguin populations at Cape Colbeck and Cape Crozier and asynchronous change between those two colonies and the remaining five, offering evidence to support metapopulation dynamics in the Ross Sea [56,57]. We suggest increases at the two southernmost colonies may be driven in part by immigration, both from the remaining Ross Sea colonies and possibly from outside the region [15]. Given the inherent instability of fast ice and the variable Southern Ocean environment, plasticity in colony selection may be an adaptation that allows this species to persist during times of environmental variability [17,55]. We further hypothesize that the region-wide decline after 2020 may also be owing to penguins emigrating out of the Ross Sea region completely [15,17].

Synchronous population change at the WRS colonies may be indicative of a broad-scale response to environmental pressures, specifically the Moran effect [50,51,53]. The Moran effect describes the phenomenon in which spatially separated populations exhibit synchronous abundance fluctuations owing to wide-ranging environmental variability [50,53]. This has been documented across taxa and ecosystems, particularly in cases where large-scale climatic drivers (e.g. ENSO) influence multiple populations simultaneously [51]. While the ability to disperse between colonies could buffer metapopulations from overall decline [57], if all subpopulations fluctuated synchronously, such as the declines at every colony in 2022 (and all except Roget in 2023), this could negate any advantage of migration between colonies and increase the vulnerability of metapopulations to disturbance [52,53]. The metapopulation decline may also be the result of each colony responding to a sustained large-scale environmental shift, which we explore further below.

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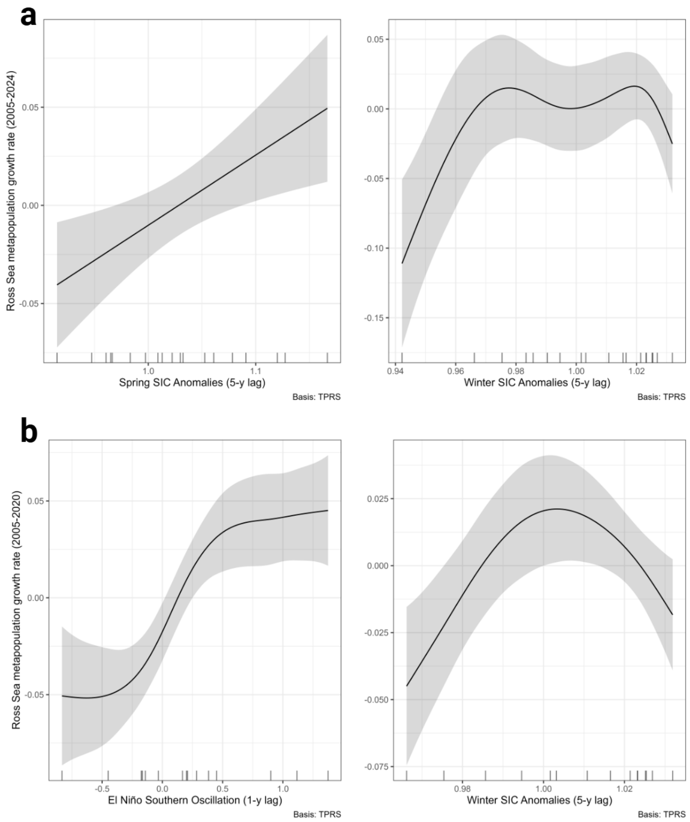

Figure 4. Partial dependence plots indicating results from GAMs built to determine drivers of emperor penguin population change in the Ross Sea; (a) the best-supported model explaining variation in the metapopulation growth rates between 2005 and 2024, highlighting the relationship with 5 year lag spring SICa and 5 year lag winter SICa; (b) the best-supported model to explain variation in the metapopulation growth rates between 2005 and 2020, highlighting the role of 1 year lag El Niño and 5 year lag winter SICa. See tables 1 and 2 for model details and electronic supplementary material, figure S8, for model diagnostics.

Table 2. Effect size and statistical significance of covariates included in the best supported GAMs to assess drivers of emperor penguin population change in the Ross Sea (table 1). We present effective degrees of freedom (edf), *F*-statistic (*F*) and *p*-values. See table 1 for abbreviations.

	predictors	edf	*F*	*p*-value
metapopulation	ENSO.1	2.944	4.284	0.0007
2005–2020	SICa_JAS.5	2.025	1.411	0.0301
2005–2024	SICa_JAS.5	3.336	1.772	0.0109
	SICa_OND.5	0.889	0.894	0.0090
colony-specific	SICa_JAS	1.000	5.592	0.0195
2000–2024	ice_days	1.815	5.424	0.0290
	SICa_JAS.1	1.000	3.204	0.0757
	SICa_JAS.5	1.000	3.119	0.0797
	SICa_OND.1	2.083	2.985	0.0588
	SICa_OND	1.000	1.896	0.1708
	SICa_AMJ.1	1.000	0.348	0.5564
	SICa_OND.5	1.742	0.142	0.8184
	year (re)	0.000	0.000	0.7562
	site_id (re)	0.000	0.000	0.4100

(b) Population status

Our results suggest Ross Sea emperor penguin colonies, representing greater than 30% of the global population [32], fluctuated substantially over a 20 year period and decreased overall owing to an apparent change in dynamics after 2020. From 2005 to 2020, indices of abundance for the metapopulation were stable and (slightly) increasing, with well-documented interannual colony fluctuations [29,30]. However, following the population peak that occurred in approximately 2019, the region decreased each year to 2024, displaying a negative trend that was especially evident from 2021. This steep decline resulted in an estimated approximately 23% decline in adult springtime attendance over the whole period, or 32% in the last 5 years. We therefore

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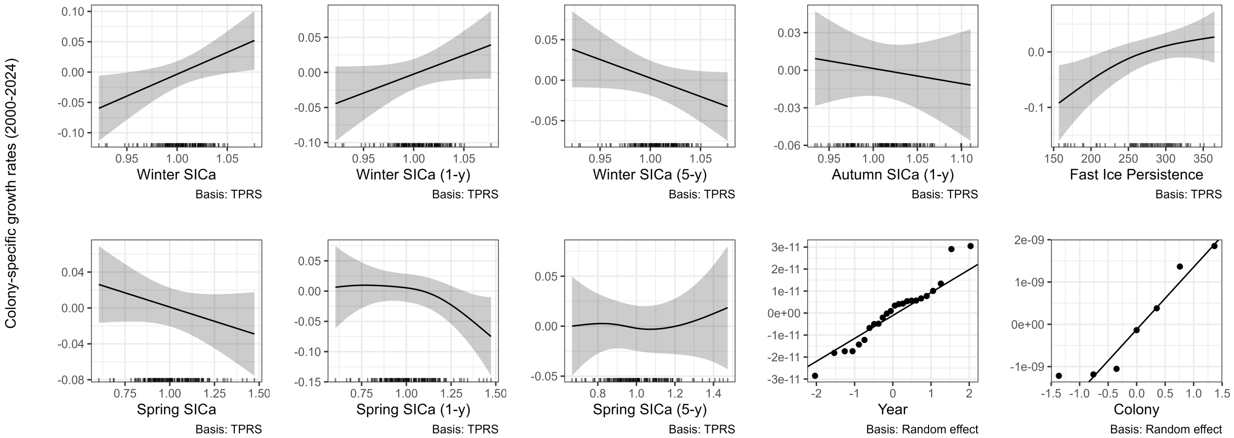

Figure 5. Partial dependence plots from the global GAMM to explain the variation in colony-specific emperor penguin growth rates in the Ross Sea between 2000 and 2024. Model includes winter SICa (no lag, 1 year lag and 5 year lag), spring SICa (no lag, 1 year lag and 5 year lag), autumn SICa (1 year lag) and fast ice persistence. Year and colony were random effects. Non-important covariates have been excluded from the figure. See tables 1 and 2 for model details. Model diagnostics presented in electronic supplementary material, figure S9, and the reduced time series model (2000–2020) is presented in electronic supplementary material, figure S10.

suggest that while emperor penguins may typically cope with environmental variability, they may be sensitive to substantial changes in regional sea ice characteristics, which is explored further below.

In light of recent evidence that springtime abundance indices are a proxy for fledgling abundance [65] and the suggested link between sea ice and food web dynamics [38–40], we posit that our results point to three (possibly additive) explanations: (i) fewer subadults (i.e. between fledging and their first breeding attempt at approximately 5 years old [19]) may be recruiting to the metapopulation in response to both too much and too little sea ice (the effect of a 5 year lag of winter SICa [12]); (ii) fewer emperor penguins may choose to breed following a strong El Niño event owing to its impact on sea ice and temperatures [41] and possible effects on the food web [38–40]; and (iii) emperor penguins from the WRS colonies may be emigrating east or possibly out of the region completely (indicated by the increases at Colbeck and Crozier and the declines observed after 2020). With increasing evidence that ocean changes are largely responsible for the persistently low SIE since approximately 2016 [4,27,28], the future recovery of Southern Ocean sea ice is uncertain, making it difficult to predict how ice-obligate species, like the emperor penguin, may respond.

We must note that while our model accounts for variability in the date of image acquisition [32], springtime indices of abundance are not a direct measure of breeding population (or chick production) and probably underestimate the total adults in the region. We therefore interpret our results with caution. Although adult and chick counts are not always comparable, our results corroborate with increasing trends and interannual fluctuations reported elsewhere [29,30,33].

(c) The role of sea ice

In different ways, we found that winter and spring SICa and fast ice persistence were related to springtime abundance indices (modelled as growth rate). For the overall metapopulation, we found low and high winter SICa from 5 years prior led to reduced springtime emperor penguin abundance indices. The three lowest Ross Sea regional winter SICa (when compared with 1995–2024) occurred in 2023, 2017 and 2016, while the highest winter SICa occurred in 2010 (electronic supplementary material, table S5). At a 5 year lag, these data correspond to declines that occurred between 2014 and 2015, and between 2020 and 2022. We therefore hypothesize that this correlation may be driven through effects on recruitment [9,12], and specifically, may indicate decreased chick and juvenile survival or condition during periods when winter SIC is both too low and too high.

In contrast, our colony-specific models indicated a positive relationship with winter SIC (current and 1 year lag). Therefore, we postulate that extensive sea ice in winter may exert dual influences, possibly enhancing prey availability and improving foraging conditions [38,40] leading to a positive response for adults, while negatively impacting chick/juvenile survival and condition by increasing wait times between feeds [8,9,66], impacting recruitment 5 years later. The apparent negative relationship between colony-specific growth rates and localized springtime SICa may be a result of increased travel times during foraging excursions, which could alter colony presence and chick survival during the provisioning period [67]. It is noteworthy, however, that this 5 year recruitment lag hypothesis may not fully explain the decrease that occurred after 2021, as the rate of decline exceeds that which may be attributed to poor recruitment. We therefore suggest that while some of the metapopulation change may have been linked with lagged SIC, a different factor may have contributed to the steep decline after 2021.

As long-lived seabirds, emperor penguins exhibit life history strategies consistent with the demographic buffering hypothesis [1,20]. Although early break-up of fast ice can lead to breeding failures, as recently suggested in the Bellingshausen and Weddell seas [17,18], such buffering means that anomalous breeding failures may not necessarily translate into sustained population declines. The *k*-selected natural history strategy of emperor penguins ‘prepares’ them to cope with such challenges. The issue arises, however, when breeding failure occurs repeatedly or when adult survival is reduced [21]. One lifecycle phase when this risk is particularly acute is during the annual summer moult. After their breeding cycle is complete, Ross Sea emperor penguins travel to the waters north of Marie Byrd Land, east of the Ross Sea, to moult on stable coastal fast ice or pack ice [37]. During the moult emperor penguins cannot enter the water as they are no longer waterproof [37,67], making them dependent on the persistence of stable sea ice platforms. Since 1995, sea ice in the ERS sector has changed considerably; when comparing

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ERS SIC between 1995 and 2024, we found the five lowest February SIC have occurred since 2017 (electronic supplementary material, figures S20–S23). Schmidt *et al.* [68] highlighted the threat this may pose for Adélie penguins, which also moult in the ERS, with the authors linking decreasing ERS SIC with banded bird return rates at Cape Crozier.

During years of minimal ERS SIC, we suspect that emperor penguins may travel farther east to find safe moulting substrate, increasing the return time to the WRS colonies. Increasing travel times may impact Ross Sea colony attendance through four possible mechanisms: (i) increased incidence of skip-breeding; (ii) birds may arrive late to their breeding colonies and be unable to find a mate; (iii) birds may breed at Cape Colbeck owing to its proximity to the moult area; or (iv) birds may breed somewhere other than the Ross Sea [37,55]. Such behaviour may explain the increasing trend at Colbeck, the relationship we observed between summer ERS SICa and the metapopulation growth rate prior to 2020 (electronic supplementary material, figure S14), and the decreasing trends in the final years of observation. Increased mortality is another possible driver of our observed population declines. At this stage, our results are unable to determine whether recent declines reflect an increased prevalence of skip-breeding, decreased recruitment, emigration out of the region or increased mortality. We suggest the lack of clear relationship identified between metapopulation growth and ERS SICa may be in part owing to the metapopulation dynamics presented earlier, in which low summer ERS SICa may have driven both the increases observed at Cape Colbeck via inter-colony movement and contributed to the decline after 2020.

(d) Evaluating our findings

We present evidence of the influence of sea ice conditions on the abundance of Ross Sea emperor penguin colonies and offer evidence in support of large-scale changes negatively affecting all colonies in the last 4 years of our study. Future research could explore individual-based evidence of metapopulation behaviour and responses. Currently, there exists no available technology to track the location of penguins for several years across their range [69]. Future technologies may offer alternatives to better elucidate the degree of emperor penguin philopatry and whether the observed changes are solely the result of changes in breeding propensity and recruitment [15,55]. Additionally, the study of breeding propensities, productivity and adult survival simultaneously at correlated colonies may also help to understand the nature of the observed population changes [56,70].

Further research could explore inter- and intra-specific competition as factors that may have influenced the population trends we report here [49,71]. It is notable that between 2019 and 2021 Cape Colbeck was estimated to have reached a size far beyond that of any emperor penguin colony recorded to date (approx. 40 000 birds), before declining to a size comparable to the previous maximum of WRS colonies (approx. 25 000). While speculative, this may possibly indicate the colony reached carrying capacity following eastward migration of birds, leading to greater resource competition and more birds departing the region. To further explore this hypothesis, increasing the spatial and temporal coverage of Ross Sea food web data should be prioritized considering recent ecosystem change.

5. Conclusion

Our results indicate the metapopulation of emperor penguins in the Ross Sea (as springtime indices of abundance) may have increased up to 2020 then declined steeply in the final years of observation, resulting in an overall decline of approximately 23% over 20 years. The mean change at the metapopulation scale from 2020, concurrent with record lows in winter and summer SIE, leads us to suggest that emperor penguins, although well-adapted to survive in an extreme and variable Antarctic environment, may respond negatively to sustained sea ice change. In support of metapopulation dynamics, our results indicate likely inter-colony movement through asynchronous change and increasing trends at the region's southernmost colonies. Winter and springtime SICa may influence emperor penguin colony presence across spatial and temporal scales, and SIC during the summer moult may also affect colony selection. Our observations offer insight into how emperor penguins may have adapted to environmental fluctuations throughout their existence and how the species may respond to future environmental change.

Ethics. Ethics approval was unnecessary for this study because we did not handle or interact with animals.

Data accessibility. Data and code required to recreate our analysis and results have been included in electronic supplementary material and are provided open-source via Dryad [72]. Supplementary material is available online [73].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. R.T.N.F.-D.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, validation, visualization, writing—original draft, writing—review and editing; D.I.: data curation, formal analysis, methodology, validation, writing—review and editing; L.S.: data curation, formal analysis, investigation, methodology, writing—review and editing; D.G.A.: investigation, validation, writing—review and editing; B.McD.: investigation, validation, writing—review and editing; S.S.: investigation, validation, writing—review and editing; L.V.: data curation, formal analysis, writing—review and editing; D.O.: data curation, formal analysis, writing—review and editing; A.E.S.: data curation, investigation, writing—review and editing; G.B.: data curation, investigation, writing—review and editing; C.H.: data curation, formal analysis, investigation, methodology, supervision, validation, writing—review and editing; J.D.T.: investigation, methodology, supervision, validation, writing—review and editing; M.LaR.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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