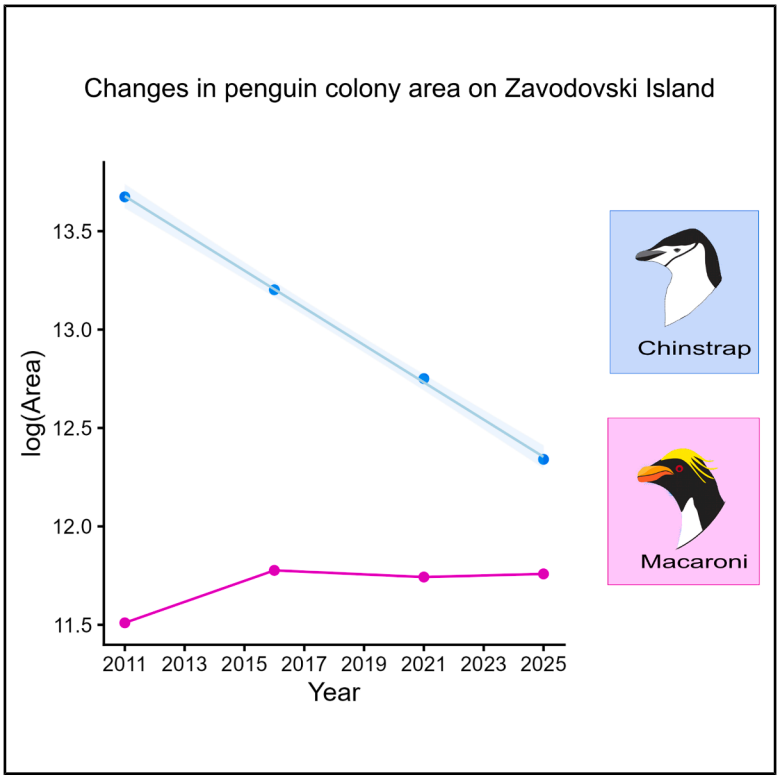
Article

Current Biology

Population declines and changes in community composition at the world's largest penguin colony

Graphical abstract



Highlights

- Chinstrap penguin numbers on Zavodovski have collapsed, while macaronis have increased
- Zavodovski has lost the title of largest penguin colony in the world
- The chinstrap penguin's global IUCN status meets the criteria for Endangered
- The changes show Zavodovski is moving from an Antarctic to a subantarctic state

Authors

Norman Ratcliffe, John Dickens, Gemma Clucas, ..., Heather Lynch, Peter Convey, Peter Fretwell

Correspondence

notc@bas.ac.uk

In brief

Ratcliffe et al. use drone and satellite surveys to show that chinstrap penguins on Zavodovski Island have declined rapidly while macaroni penguins have increased. Zavodovski is no longer the largest penguin colony in the world, and reconsideration of the chinstrap IUCN classification from Least Concern to Endangered may be warranted.

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Population declines and changes in community composition at the world's largest penguin colony

Norman Ratcliffe,[1,12,*] John Dickens,[1] Gemma Clucas,[2] Klemens Pütz,[3] Nathan Fenney,[1] Elizabeth Mackley,[1] Tom Hart,[4] Laure Cugniere,[4] Claudia Colesie,[5] Nicole Richter,[6] Mark Belchier,[7] Aliaksandra Skachkova,[1] Heather Lynch,[8] Peter Convey,[1,9,10,11] and Peter Fretwell[1]

[1]British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK
[2]Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA
[3]Antarctic Research Trust, Am Oste-Hamme-Kanal 10, 27432 Bremervörde, Germany
[4]School of Biological and Medical Sciences, Oxford Brookes University, Headington, Oxford OX3 0BP, UK
[5]School of GeoSciences, Climate Change Research Institute, University of Edinburgh, Edinburgh EH9 3FE, UK
[6]RWTH Aachen University, Lochnerstr. 4-20, 52056 Aachen, Germany
[7]Government of South Georgia and South Sandwich Islands, High Cross, Madingley Road, Cambridge CB3 0ET, UK
[8]Department of Ecology & Evolution, Stony Brook University, 650 Life Sciences Building, Stony Brook, NY 11794-5245, USA
[9]Department of Zoology, University of Johannesburg, Auckland Park, 2092, Johannesburg, South Africa
[10]Millennium Institute, Biodiversity of Antarctic and Sub-Antarctic Ecosystems, 8320150 Santiago, Chile
[11]School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK
[12]Lead contact
*Correspondence: notc@bas.ac.uk
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SUMMARY

The Antarctic Peninsula and Scotia Sea are experiencing the greatest pressures from climate change and fisheries in the Southern Ocean, with associated penguin population declines. However, surveys of the South Sandwich Islands in 2011 concluded that numbers there were stable. Zavodovski, the northernmost island in the archipelago, was then hailed as the largest penguin colony in the world. We show that, by 2025, rapid declines of maritime Antarctic chinstrap penguins mean this title has now been ceded to the Adélie penguin colony at Cape Adare, Ross Sea. Over the same period, the subantarctic macaroni penguins increased to become the most abundant species on Zavodovski, representing the largest community shift in Antarctic penguins that has been recorded at a single site. We infer that the most likely primary cause of the chinstrap decline was a reduction in krill availability associated with regional warming, as found across the rest of the Scotia Sea, rather than the volcanic eruption of Zavodovski in 2016 or competition from krill fisheries, macaroni penguins, or humpback whales. The declines of chinstrap penguins mean that reclassification of their global IUCN threat status, from Least Concern to Endangered, requires consideration.

INTRODUCTION

Climate change is causing rapid and widespread changes to the physical characteristics of the Antarctic Ocean, which cascade through the food web to affect the abundance of higher vertebrate predators.[1] Competition for food from fisheries or species expanding their ranges from lower latitudes has the potential to exacerbate such impacts.[2] Penguins are widespread, abundant consumers of krill and fish that are relatively easy to monitor, such that they have become one of the most prominent ecological indicators for the impacts of environmental and anthropogenic changes upon higher trophic level species in the Southern Ocean.[3–5] Studies on the Antarctic Peninsula, South Shetlands, South Orkneys, and South Georgia have detected declines in chinstrap *Pygoscelis antarcticus*, Adélie *P. adeliae*, and macaroni penguins *Eudyptes chrysolophus* over the past four decades.[3,4,6,7] However, their abundance in the South Sandwich Islands (SSIs), at the eastern boundary of the Scotia Sea, was found to be stable up to 2011.[8] This has allayed conservation concerns for chinstrap penguins, in particular, given the global importance of the archipelago for the species (~38% of the world population[9]).

The SSIs are a volcanic arc of eleven islands at the eastern edge of the Scotia Sea, situated within the seasonal sea ice zone and south of the Antarctic Circumpolar Current (ACC).[10,11] The islands are a UK Overseas Territory, with the surrounding seas managed according to regulations that apply within the South Georgia South Sandwich Islands Marine Protected Area (SGSSI MPA) and the Commission for the Conservation of Marine Living Resources (CCAMLR) Subarea 48.4.[12] Zavodovski Island (56.29°S, 27.57°W; hereafter Zavodovski), an active volcano that last erupted in March 2016,[13] is the northernmost island in the archipelago (Figure 1).

Zavodovski was hailed as the largest penguin colony in the world in 2011, comprising 600,000 chinstrap penguins and 90,000 macaroni penguins *Eudyptes chrysolophus*[8] (hereafter chinstraps and macaronis). These species are ranked as the top two avian consumers of marine prey by biomass in the world

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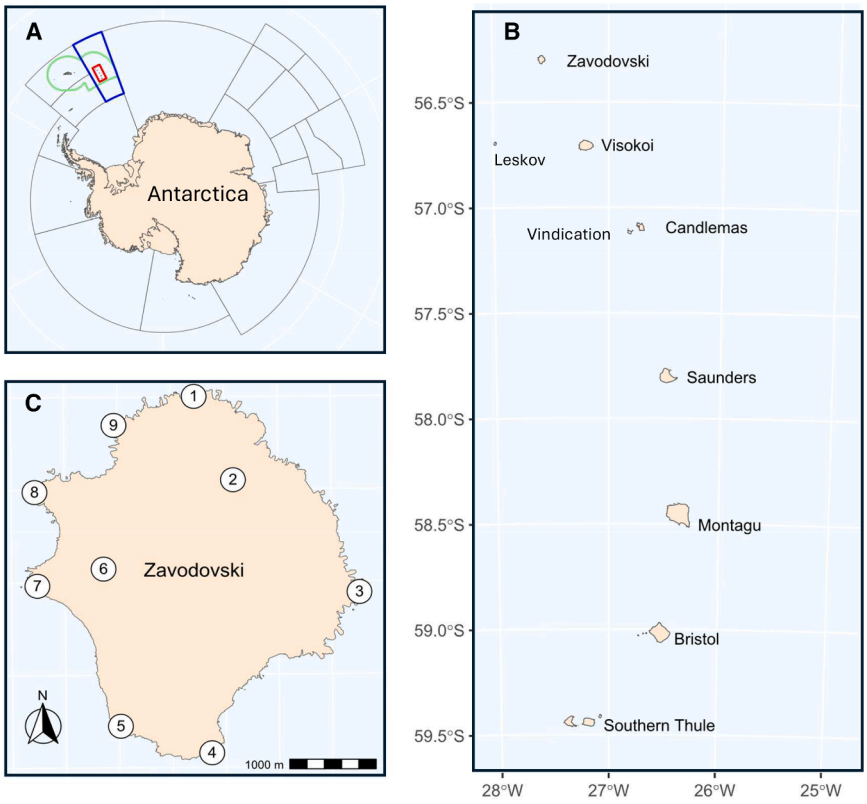


Figure 1. Maps showing the location of the study site

(A) The location of CCAMLR subarea 48.4 (blue rectangle), the South Georgia SSIs MPA (green polygon), and the extent of Figure 1B (red rectangle) in relation to the Antarctic continent.

(B) The SSIs archipelago with Zavodovski Island, our study site, in the north. Southern Thule comprises three islands: Thule, Cook, and Bellinghausen.

(C) Zavodovski Island with key place names numbered: (1) Reek Point, (2) Asphyxia Plain, (3) Pungent Point, (4) Fume Point, (5) Noxious Bluff, (6) Mount Curry, (7) Stench Point, (8) Acrid Point, and (9) Pacific Point.

and so play important roles in regional food webs.[14] Chinstraps are largely confined to the maritime Antarctic regions of the Scotia Sea and Antarctic Peninsula,[15] where they specialize in consuming Antarctic krill *Euphausia superba*[16] (hereafter krill). Macaronis are most abundant in the subantarctic region,[15] exhibiting a circumpolar range and a generalist diet that includes mesopelagic fish and a range of crustacean taxa.[16]

This paper presents the results of a drone survey of chinstraps and macaronis on Zavodovski Island, collected during an expedition in December 2023, and satellite surveys at approximately quintennial intervals between 2011 and 2025, which update information on penguin status and trends for the island. Potential drivers of change include effects of climate change upon food webs, the 2016 volcanic eruption of Zavodovski Island, interspecific competition and krill fisheries, evidence for which is evaluated from the patterns of population change, novel satellite tracking data from penguins, and reference to the scientific literature.

RESULTS

Colony area

The area of Zavodovski that was occupied by the chinstrap colony during the December 2023 drone survey was 20.83 ha. This survey omitted a portion of the western plateau that occupied 0.66 ha based on 2025 satellite images, bringing the total to 21.49 ha. The drone survey achieved complete coverage of macaroni colonies, which occupied 12.14 ha. The total area of penguin colonies of both species from drone imagery in December 2023 was 5.70% smaller than that from satellite imagery in January 2025. The area of the chinstrap colony based on the time series of satellite images showed a remarkably constant log-linear decline of −9.46% per annum (SE = 1.5; linear regression, t = −60.34, $p < 0.0005$, $R^2 = 0.99$, Figures 2 and 3). That of macaroni penguins showed an increase of 28.22% between 2011 and 2016, after which it remained stable (range of variation 3.33%, Figures 2 and 3).

Density estimates

The calibration between manual and classifier counts of apparently occupied nests (AON) within sample quadrats ($n = 114$) produced a slope estimate for chinstraps of 1.00 (lower 95% confidence interval [LCI] = 0.97, upper 95% confidence interval [UCI] = 1.03), which did not differ significantly from unity (linear regression; t = 0.032, $p > 0.9$), whereas that for macaronis was 0.981 (LCI = 0.97, UCI = 0.99), which is significantly lower (linear regression; t = −2.81, $p < 0.01$). The calibration-adjusted nesting density of chinstraps estimated from December 2023 drone imagery was 0.932 AON m^{-2} (LCI = 0.902, UCI = 0.968), and that for macaronis was 1.796 (LCI = 1.675, UCI = 1.783). The estimate of chinstrap density in January 2011 was 0.663 AON m^{-2} (LCI = 0.569, UCI = 0.774), which is lower than that estimated for December 2023.

Population estimates and trends

The adjusted classifier count of chinstraps in those parts of the island surveyed by the drone was 194,225 AON, while estimates for the omitted areas were 6,697 AON on the southwestern plateau and 130 AON at Stench Point, producing a total island-wide chinstrap count of 201,067 AON (LCI = 194,662, UCI = 207,088). Macaroni breeding distribution fell entirely within the area surveyed by the drone, and the adjusted population estimate was 218,109 AON (LCI = 213,625, UCI = 222,013).

The chinstrap population in January 2025, from satellite image analysis, was 201,182 AON (LCI = 193,999, UCI = 208,085) compared with 542,675 (LCI = 469,061, UCI = 635,845) in January 2011. This represents a 62.93% (LCI = −68.43, UCI = −56.91) decline at a constant annual population multiplication rate (λ) of 0.932 (LCI = 0.921, UCI = 0.942) throughout the period. This rate of decline is steeper than estimated for the Antarctic Peninsula and South Shetland Islands (λ = 0.980, LCI = 0.971,

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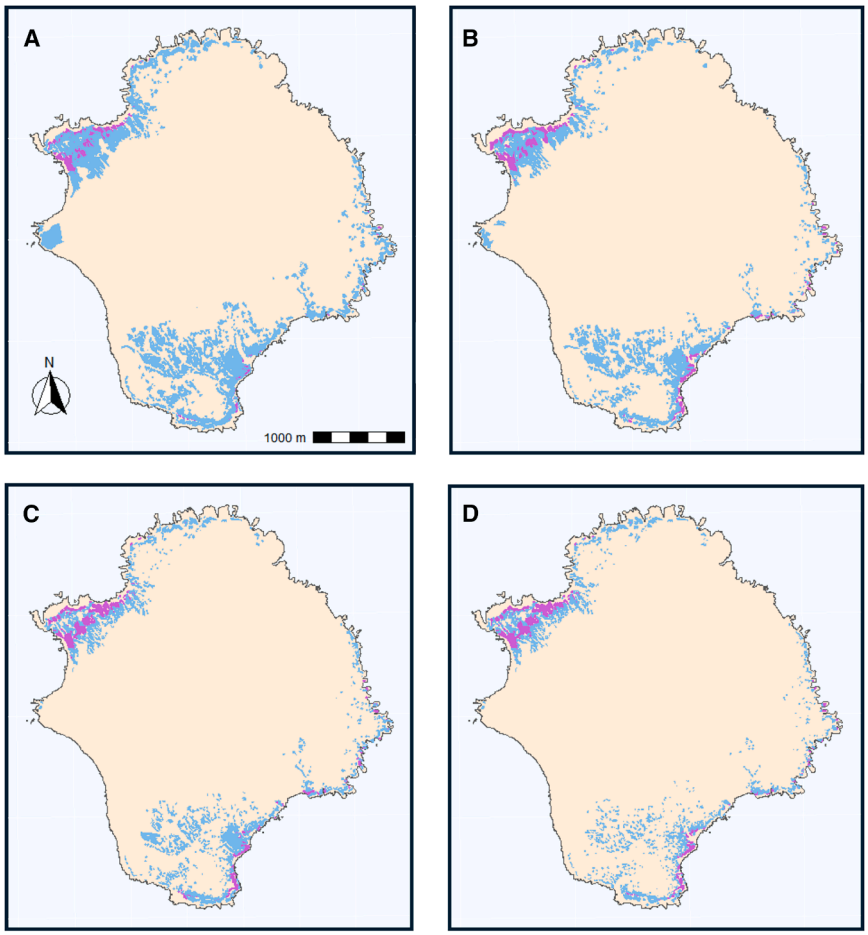


Figure 2. Distribution and extent of penguin colonies on Zavodovski Island

(A–D) Chinstraps are shown in blue and macaronis in magenta during (A) 2011, (B) 2016, (C) 2020–2022, and (D) 2025. Note the marked contraction and fragmentation of chinstrap colonies and the consistent absence of penguins along the northeast coast.

UCI = 0.989). Combining these regional rates of decline into global population trends over three generations reveals that 95.8% of the frequency distribution falls within the International Union for the Conservation of Nature (IUCN) category Endangered and the remainder in Vulnerable (Figure 4) based on Criterion A2. Macaronis numbered 216,606 AON (LCI = 209,334, UCI = 223,059) in 2025 and 168,936 (LCI = 163,265, UCI = 173,970) in 2011; an increase of 28.22% (LCI = 22.55, UCI = 34.04) that occurred between 2011 and 2016 at a λ of 1.051 (LCI = 1.041, UCI = 1.060).

Other taxa counted in the drone imagery were 1,265 Antarctic fur seal (*Arctocephalus gazella*) pups, 178 southern giant petrel (*Macronectes giganteus*) AON, and four active breeding attempts by king penguins (*Aptenodytes patagonicus*) (comprising two incubating adults and two crèche-stage chicks from the previous breeding season).

Penguin movements

One satellite tag on a chinstrap failed after 8 days and was excluded from further analysis, but the remainder produced tracks through to the end of the breeding season in late February. The data show that the two species exhibit different marine spatial distributions (Bhattacharyya's Affinity 0.303) and habitat use (sea surface temperature [SST] overlap 0.276). Macaroni penguins tended to utilize warmer waters to the northeast of Zavodovski and extended their range into the ACC, while chinstraps utilized cooler waters to the northwest and remained below the ACC's Southern Boundary (Figure 5). Chinstraps remained almost entirely within the SGSSI MPA, but the long trips of macaroni penguins extended beyond its northeastern boundaries (Table 1; Figure 5) into seas under the sole jurisdiction of CCAMLR Subarea 48.4. The closed areas of the MPA, in which krill fishing is prohibited, have afforded increasing protection to penguin foraging areas since 2013, and these now encompass almost three-quarters of chinstrap and half of macaroni time at sea during the breeding season (Table 1; Figure 5).

DISCUSSION

To date, conservationists have found comfort in the knowledge that the globally significant SSI population of chinstraps had avoided the declines seen in the wider Scotia Sea, but our study shows numbers here are now experiencing declines at a much faster rate than elsewhere in the region. Assuming that the alarming declines on Zavodovski are representative of those for the rest of the SSIs, and the region-specific losses continue exponentially through time, consideration should be given to reclassifying the IUCN status of chinstraps from Least Concern to Endangered, which goes beyond previous calls for the species' reclassification as Vulnerable.[17] Zavodovski now hosts a combined penguin population of 419,161 pairs, meaning it has ceded its title of the largest penguin colony in the world to the Adélie penguin colony at Cape Adare, Ross Sea (71.31°S, 170.20°E), which hosted a growing colony of 504,332 pairs in 2018.[18] The total loss of over a quarter of a million pairs of penguins from Zavodovski is likely to have repercussions for the structure of food webs in the SSI region, given their high per-capita rate of prey consumption.[14]

Penguin community shifts have been observed elsewhere in the Scotia Sea, where declines of chinstrap and Adélie penguins have been accompanied by growth in the numbers of gentoo penguins, *P. papua*, which are extending their range from lower latitudes.[3,4,6] However, gentoo penguin colonies are always relatively small compared with those of other species,[15] so the observed numerical shift from chinstraps to macaronis on Zavodovski represents the most striking change in penguin

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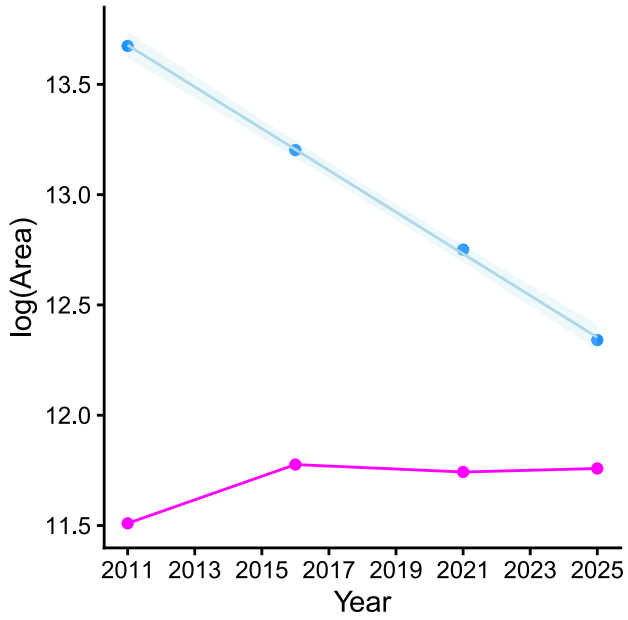


Figure 3. Changes in the total area of penguin colonies on Zavodovski Island

Chinstraps are shown in blue and macaronis in magenta. Note the use of a natural log scale on the *y* axis that allows changes to be seen clearly for both species on the same axis and emphasizes the exponential rate of decline of chinstraps (i.e., a constant percentage change per annum, which is characterized by a linear trend on a log scale). The blue line is the fit of the linear regression, and the ribbon its 95% confidence intervals.

community composition that has been observed at a single location in Antarctica to date. Similar shifts from high-latitude to low-latitude seabird communities have been observed on Svalbard in response to the borealization of the Barent's Sea in the Arctic.[19] The growth of the macaroni colony on Zavodovski means it is now the second largest in the Scotia Sea, after the Willis Islands on South Georgia.[7]

The most plausible explanation for the observed patterns of population change is that a climate-induced regime shift has occurred that has been detrimental to the maritime Antarctic chinstraps but has favored the subantarctic macaronis. Rapid warming has caused southward contraction of krill distribution in the northern Scotia Sea,[20] reducing food availability to chinstraps and creating a region-wide decline in their population,[3,4,6] which our study now shows to encompass the SSI. Chinstrap penguin distribution in environmental space occupies a narrow range of SSTs while avoiding sea ice.[21] Rising temperatures therefore place stress on populations in the north of the range, while sea ice, alongside a limited availability of land within the maritime Antarctic region, limits the scope for southward shifts in range. The dietary specialization of chinstraps means they are more vulnerable to declining krill stocks than the generalist macaronis,[16] whose foraging trips on Zavodovski extend into the ACC, where a more diverse macrozooplankton community provides alternative trophic pathways to krill.[22] Macaroni populations have declined at their Scotia Sea stronghold in South Georgia,[7] but warming at the southern limit of their range appears to have favored a growth in their numbers at Zavodovski. Macaronis are also increasing in abundance in the Antarctic Peninsula and South Shetland Islands, which lie at the southernmost limit of their range.[23] The growth of Antarctic fur seal numbers documented on Zavodovski compared with previous studies[8,24] and evidence for king penguin chicks surviving the winter may represent further signs of the island's shift toward a subantarctic state, given both species' regional population centers are on South Georgia.

Mount Curry on Zavodovski erupted in March 2016,[13] producing an ash cloud that traveled northeast across the island on the prevailing winds. Given ashfall and toxic gases from volcanoes are known to be detrimental to avian health,[25] fears were raised that the eruption might have caused a mass mortality of penguins.[26] However, the decline in chinstrap colony area was in progress prior to the eruption and continued at a constant rate thereafter, rather than being a step change as would be

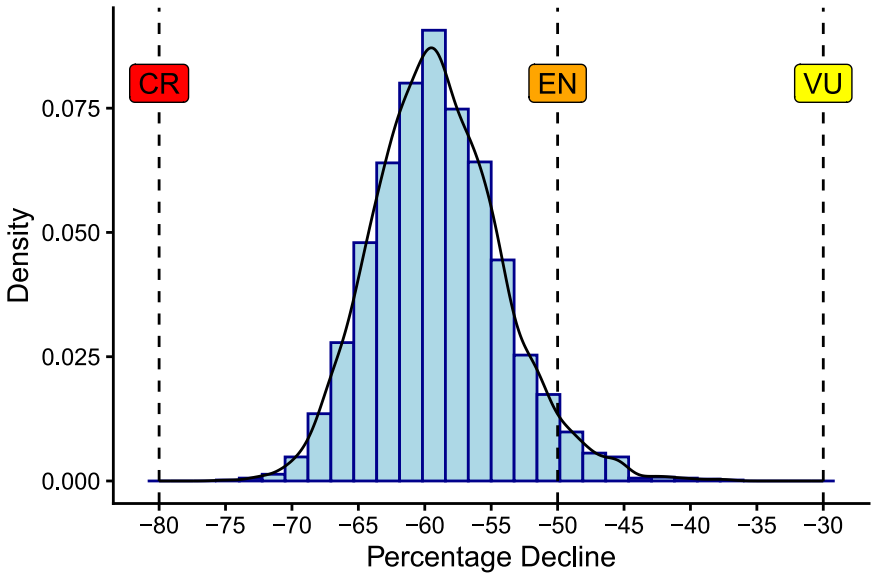


Figure 4. Frequency distribution of potential rates of change for global chinstrap penguin populations

This is expressed over three generations (28 years) in relation to IUCN thresholds. Values lower than the threshold fall into the given category: CR, Critical; EN, Endangered; VU, Vulnerable.

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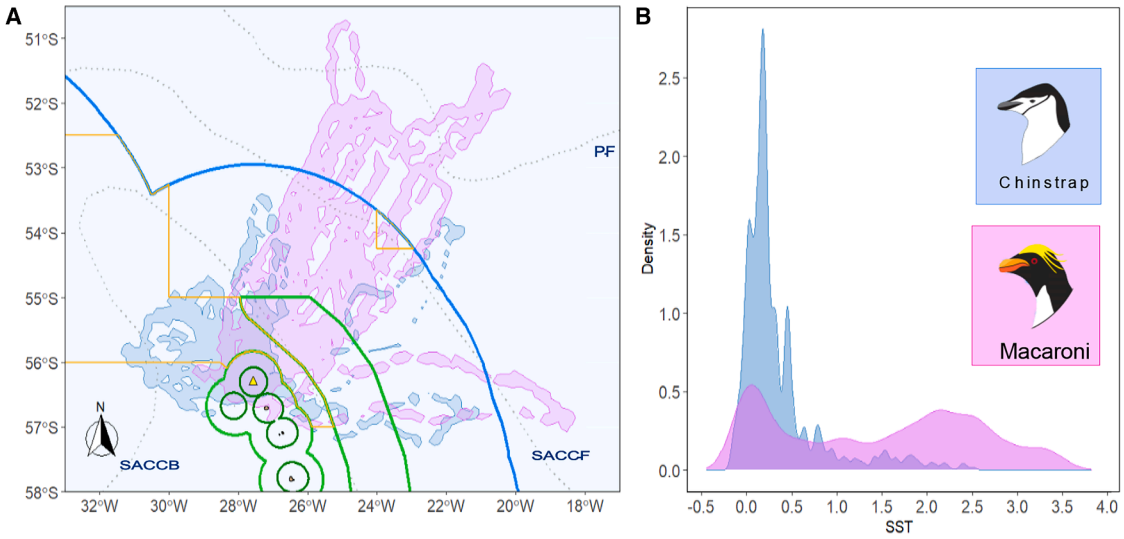


Figure 5. At-sea distributions of satellite-tagged penguins

Birds were tracked from Zavodovski Island (yellow triangle) during the breeding season.

(A) Spatial distribution based on 95% isopleths of kernel density distributions overlaid on features of the MPA (blue line: MPA boundary; dark green, light green, and ochre are the incrementally extending closed areas following reviews in 2013, 2018, and 2025, respectively). Dotted lines are the average locations of oceanic fronts (PF, Polar Front; SACCF, South Antarctic Counter Current Front; and SACCB, South Antarctic Counter Current Boundary).

(B) Kernel density of the frequency distributions of sea surface temperatures (SSTs in °C) at the hourly sampled locations occupied by each species.

expected for an eruption-induced mass mortality event.[25,27] Penguins consistently avoid nesting on Asphyxia Plain, downwind of Mount Curry's crater (Figure 2), which probably minimized the impacts of the eruption. Nonetheless, eruptions of greater magnitude can have devastating impacts upon penguin populations. For example, a paleoecology study revealed that a large eruption extirpated gentoo penguins from Ardley Island, in the South Shetlands, which remained abandoned for several centuries afterward.[28]

Krill fisheries have the potential to compete with penguins for food,[5] which has led to calls for the whole of the SGSSI MPA lying within CCAMLR Subarea 48.4 to be declared a no-take zone for krill fishing.[29] The SGSSI MPA has extended closed areas around colonies following successive MPA reviews,[12] and our findings show that these have improved protection for penguin foraging areas over the period that chinstrap penguins declined. Moreover, fishing effort for krill in Subarea 48.4 has always been sparse and ceased altogether in the early 1990s owing to wider regulations across the SGSSI MPA.[12] The available evidence therefore suggests that the evolution of MPA regulations has ensured krill fishing has played a negligible role in the decline of chinstraps on Zavodovski, and current management makes such impacts unlikely in the future. Nonetheless, current flows connect SSI to South Georgia and the Antarctic Peninsula, where krill fishing occurs,[10] and the effects of this harvesting upon the availability of food to predators foraging downstream are poorly understood.

Table 1. Proportions of time penguins spend at sea within management units

Species	Area	Overlap
Chinstrap	SGSSI MPA	0.987
Chinstrap	closed area 2013	0.137
Chinstrap	closed area 2018	0.422
Chinstrap	closed area 2025	0.798
Macaroni	SGSSI MPA	0.742
Macaroni	closed area 2013	0.087
Macaroni	closed area 2018	0.342
Macaroni	closed area 2025	0.457

SGSSI MPA is the South Georgia and South Sandwich Islands Marine Protected Area, and the closed areas are areas in which fishing for krill is prohibited during intervals between the given years.

Climate-induced changes in competitive dominance have the potential to result in niche displacement,[30] so increasing competition from the growing number of macaronis on Zavodovski may have exacerbated the chinstrap decline. However, the total area occupied by nesting penguins on Zavodovski has shrunk massively, and extensive abandoned areas are evident around chinstrap colonies, indicating that nesting habitat is not limiting. The two species show differences in marine distribution and habitat use, as also observed at Bouvet Island (54.42°S, 3.36°E), which may reduce potential competition for food via niche partitioning.[31] The observed community shift on Zavodovski is therefore best explained by changes in the spatial projection of the two species' fundamental niches, without the need to invoke competitive exclusion.

An alternative potential competitor for krill prey is humpback whales, *Megaptera novaeangliae*, whose western Atlantic population has recovered to pre-exploitation levels in recent decades.[32] Humpback whales show preference for habitats to the northeast of Zavodovski,[33,34] where they consume an estimated 19%–29% of the CCAMLR Subarea 48.4 standing krill stock.[33] The overharvesting of whales in the 20th century is hypothesized to have created a krill surplus that allowed penguin

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numbers to grow, so a recovery in whale numbers could conceivably lead to the reverse effect.[35] However, krill stocks were in decline prior to the recovery of whale numbers due to falling primary production associated with climate forcing and possibly also a breakdown of the positive feedback loop from nutrient subsidies by whale feces.[35,36] This has led to humpback whales, in common with penguins, experiencing bottom-up regulation of vital rates[37] and potentially future population declines, based on model projections.[38] The recovery of whales is therefore unlikely to be the sole driver of penguin population declines, but it is plausible that they compete for dwindling krill resources at local scales.[39] However, the more nearshore habitat preferences of breeding penguins, compared with whales (Baines[33] and Bamford[34] vs. Clucas[40]), may reduce the risk of such competition arising via spatial niche partitioning.[41]

Our study reveals worrying changes in the penguin community on Zavodovski, but surveys across SSI are required for wider spatial context, particularly at Candlemas Island, Visokoi, and Saunders, which each hosted huge colonies (>150,000 pairs) of chinstraps in 2011.[8] Further research into drivers of change should leverage SSIs' potential as a natural experiment, in which powers of inference are enhanced through replicated sampling across eleven islands that span a sensitive climatic gradient.[10] Achieving these goals at this hostile geographic frontier will be challenging but stands to provide valuable insights into ecosystem function in this neglected region of the Southern Ocean.

RESOURCE AVAILABILITY

Lead contact

Requests for further information should be directed to and will be fulfilled by the lead contact, Norman Ratcliffe (notc@bas.ac.uk).

Materials availability

The study did not generate any new, unique reagents.

Data and code availability

The datasets generated during this study are available from the NERC Polar Data Centre: chinstrap tracking data (https://doi.org/10.5285/529808a4-3967-49fe-abf6-fdb4fe5a7e5e), macaroni tracking data (https://doi.org/10.5285/459597b2-ca0c-4110-b59c-62490867f348), aerial survey imagery (https://doi.org/10.5285/e2f65907-7aaa-4a45-917c-6f31ca644ad6), colony boundary and AON shapefiles (https://doi.org/10.5285/7220dc6b-2f52-4160-a6c0-e57c50963308), and 2011 chinstrap nesting densities (https://doi.org/10.5285/96febb5d-1821-4f49-9b5f-32e489ae3839). Code to reproduce the values and figures presented in the paper from these data is available on GitHub (https://github.com/Norman-Ratcliffe/Zavodovski-code).

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AUTHOR CONTRIBUTIONS

N. Ratcliffe designed the study with input from T.H., C.C., K.P., P.C., P.F., and M.B. J.D., G.C., E.M., C.C., and N. Richter conducted the fieldwork. N. Ratcliffe, N.F., and P.F. analyzed the data. N. Ratcliffe wrote the manuscript with input from all coauthors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2026.09.010.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Colony mapping and penguin tracking data	NERC Polar Data Centre	https://doi.org/10.5285/529808a4-3967-49fe-abf6-fdb4fe5a7e5e; https://doi.org/10.5285/459597b2-ca0c-4110-b59c-62490867f348; https://doi.org/10.5285/e2f65907-7aaa-4a45-917c-6f31ca644ad6; https://doi.org/10.5285/7220dc6b-2f52-4160-a6c0-e57c50963308; https://doi.org/10.5285/96febb5d-1821-4f49-9b5f-32e489ae3839; https://github.com/Norman-Ratcliffe/Zavodovski-code
Software and algorithms		
Pix4D	Pix4D, Lausanne, Switzerland https://www.pix4d.com	Pix 4D 4.9.0
ArcGIS Desktop	ESRI, Redlands, USA	ArcGIS Desktop 10.6
RStudio	RStudio Team https://www.rstudio.com/	RStudio 4.4.1
R package car	Fox and Weisberg[42]	https://cran.r-project.org/web/packages/car/index.html
R package CRAWL	Johnson et al.[43]	https://cran.r-project.org/web/packages/crawl/index.html
R package adehabitatHR	Calenge et al.[44]	https://cran.r-project.org/web/packages/adehabitatHR/index.html
Other		
Multi-rotor drone	DJI, Shenzen, China, https://www.dji.com	Mavic 3 Themal with CMOS ½ inch 48 mega pixel sensor and 24 mm lens
Satellite tags (platform terminal transmitters)	Wildlife Computers, Redmond, USA, https://wildlifecomputers.com/	SPOT 367A

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Handling and equipping of birds were conducted under a permits issued by the Government of South Georgia and the South Sandwich Islands (Ref 2023/022) and the British Antarctic Survey's Animal Welfare and Ethics Review Board (Ref 1089).

METHOD DETAILS

Aerial surveys

A six-person expedition landed and camped on Zavodovski Island between 10th and 16th December 2023, with support from the yacht *Vinson of Antarctica* (Pelagic Expeditions, Southampton, UK). To estimate population size, a Mavic 3T quadcopter (DJI, Shenzhen, China) with a CMOS ½ inch 48 mega pixel sensor and 24 mm lens was used to collect aerial imagery of penguin colonies across almost the whole island on 14th December 2023, which coincided with the incubation period of both species. The flight plan was programmed in the DJI Pilot application to provide 70% image overlap at an altitude of 70m – 100 m above ground level, resulting in a ground sampling distance of 1.9 - 2.7 cm. The drone survey achieved almost complete coverage of the penguin-occupied area of the island, with the exception of chinstrap colonies on the southwestern plateau and at Stench Point. Two overflights of the island were made in the Royal Air Force (RAF) Airbus A400M Atlas aircraft, operating from Mount Pleasant in the Falkland Islands, on the 12th and 20th December 2023, during which oblique photographs of the penguin colonies around the entire coast were taken with a Canon R5 digital camera with a 35mm sensor and 100-500m EFS lens. Vantor or Airbus satellite images of the entire island (excluding cloud covered areas) were obtained from December 2010, January 2011, 2016 and 2025, and February 2020 and 2022 (Supplement S1; Table S1).

Drone image processing

Drone images were processed into orthomosaics using the Pix4D 4.9.0 package (Lausanne, Switzerland) in three spatial blocks covering the north, east and south sectors of the island. The imagery was imported and an initial image alignment undertaken to

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determine the exterior orientation (x, y, z, omega, phi, kappa). Image alignment was undertaken at full image scale (1:1), finding common points between the images, while also using the spatial information collected by the onboard Global Navigation Satellite System (GNSS) receiver. Once the alignment of the images had been completed, a dense point cloud was produced, representing a 3D surface of the target area. Due to the size of the area, to minimise processing requirements, the dense point cloud was produced at half-image scale. The dense point cloud was then transformed into a raster to produce a digital elevation model (DEM), which was then used to produce an orthorectified mosaic. This removed the geometry of the terrain from the imagery (along with any image distortion), allowing the images to be mosaiced together, without overlapping each other and ensuring each penguin only appears once in the final mosaic. Both the DEM and orthorectified mosaic were then exported as tif files, with the projection UTM 26S and EGM2008 geoid (EPSG 32726).

Polygons were drawn around the sub-colony boundaries on the orthomosaic for each species (Figure S1) in ArcGIS Desktop 10.6 (Esri, Redlands, USA). Chinstraps have blue-toned backs, lower nesting density and guano rings around their nests[45] which allows their sub-colonies to be distinguished from those of the black-backed, denser nesting macaronis (Figure S2). The census unit was an apparently occupied nest (AON; analogous to counts of nesting pairs) defined as a bird or pair of birds occupying suitable nesting habitat and showing a prone or hunched posture consistent with incubation or brooding. Other breeding species were manually counted from the drone imagery (Antarctic fur seal pups, southern giant petrel AON and king penguin apparently incubating adults or crèche-stage chicks).

Satellite Image Processing

The drone survey represents an accurate baseline for future comparisons but is not comparable with the previous census from 2011, which was based on direct observations of nesting densities multiplied by colony areas measured from satellite images. Satellites from two platforms were tasked to acquire images of the island from 1 December to 28 February of both 2023/4 and 24/25, but, owing to persistent cloud cover, only a single image was obtained (on 12 January 2025) in which all penguin sub colonies were clearly visible. The imagery available for analysis in previous years experienced some degree of cloud cover over penguin-occupied areas. In January 2011, a small patch of cloud, and its shadow obscured an area near Pacific Point that contained three medium-sized macaroni penguin sub-colonies. These were omitted in the estimates presented in Lynch et al.[8] but we used imagery from December 2010 and March 2011 to fill this gap. In 2016, a small section southeast of Pungent Point (c. 3% of the total sub colony area) was obscured by cloud, which was filled using imagery from 2020. In 2020 and 2022 a large portion of the north and south sections of the island, respectively, were obscured and so digitization of three images were combined to provide complete coverage representative of a 2021 mid-point. This produced a time-series of satellite imagery for the whole of the penguin-occupied areas of Zavodovski at approximately quintennial intervals.

Sub-colony outlines were digitized manually by drawing polygons around colonized areas that were recognized by their unique stippled appearance (Figure S3). Macaroni sub-colonies show a darker shade than chinstraps on satellite images owing to their higher densities and hunched posture, allowing identification to species level.[8] In their study, Lynch et al.[8] digitized colony boundaries based on the area of guano which may produce overestimates of the occupied area following declines owing to remaining areas of old, weathered guano in abandoned areas.[46] We therefore re-digitized the 2011 polygons around our revised definition of colony boundaries to ensure comparability through the time series. Linear regression of the natural log of area in relation to time was used to estimate the annual rate at which the extent of chinstrap colonies contracted.

Penguin tracking

To evaluate the potential for competition between the two penguin species and with fisheries, twelve breeding chinstrap penguins and eight macaroni penguins were equipped with Wildlife Computers SPOT 367A satellite tags (45g, 107 x 18 x 21 mm) that were attached to the back feathers using epoxy resin and waterproof tape.[47] These transmitted locations throughout the breeding periods of both species.

QUANTIFICATION AND STATISTICAL ANALYSIS

Automated nest counting

A semi-automated classifier was developed that counted AON only within the clipped boundaries of the colony polygons[48] (Figure S4), which reduced the area requiring analysis and the number of false positives (dark rocks, penguins roosting or walking outside colonies). A brightness threshold was applied to the blue band of the orthomosaic to discriminate the dark penguins from the background using a ''setnull'' process. The remaining pixels were converted to polygons. This identified penguins as small dark dots, that were converted to points and buffered at a 17 cm radius to combine partners standing together at their nest into a single AON unit. Identification to species level was achieved using an automated analysis based on blueness of the penguin dots. The species assignments of the classified points and the sub-colony polygons that enclosed them showed good agreement.

The classifier counts were validated against manual counts within 114 quadrats of 5 x 5 m dimension. Linear regression was used to estimate the slope between manual and classifier counts, within species, using the lm function in the base R package version 4.5.2. The linearHypothesis function from the car package was used to test whether slopes differed significantly from unity.[42] The classifier counts were divided by the slope of the regression line to produce adjusted estimates, with confidence limits being calculated as the 2.5 and 97.5 percentiles of bootstrapped slope values (i.e. slope estimates from 10,000 resamples of *n* raw data values, with

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replacement) to allow for uncertainty around the regression model. Areas where the classifier performed poorly due to haze or rocky ground were counted manually, while the small gaps in drone coverage of the chinstrap occupied area were filled using photographs from the A400M survey (Stench Point) or January 2025 satellite imagery (southwestern plateau).

Estimation of population status and trends

Total nesting densities were calculated by dividing the summed calibrated number of nests by the summed sub-colony area, based on the classifier counts and boundary polygons derived from the December 2023 drone survey. Confidence intervals were estimated using bootstrapping at the sub-colony scale, after removing those occupying less than 25 m^2, which caused long tails in their frequency distributions. These tails were to the right for chinstraps (owing to boundaries being drawn too close to single, isolated AONs) and left for macaronis (owing to small colonies tending to occur on rough terrain, where suitable nesting habitat was patchy). The bootstrapped density values were each adjusted with the n^{th} value of the bootstrapped calibration estimates. Values were centered on the total density estimate and multiplied by the colony area before calculating the 2.5 and 97.5 quantiles. This produces 95% confidence intervals of population size that include uncertainty from both the spatial variation in density and sampling error around the calibration regression line.

The greater resolution of drone images allows polygons to be drawn more tightly to the colony edge than for satellite images. Using drone-derived densities will therefore tend to overestimate numbers when extrapolated to more coarsely drawn, and hence larger, satellite-derived areas. Satellite areas were therefore adjusted by the proportional difference between the Jan 2025 satellite and Dec 2023 drone imagery.

For the 2011 census, Lynch et al.[8] used density estimates of 0.66 for chinstrap and 1.07 for macaroni penguins. The chinstrap estimate was taken from ground and manual counts of drone images within measured sub-colony areas at Zavodovski in January 2011. Confidence intervals were estimated by bootstrapping the 49 density measures collected by Lynch et al.[8] No calibration adjustment was made to these values as the counts were made manually on the ground or from drone images. The macaroni density estimate for the 2011 survey of 1.05 AON m^{-2} was from Bird Island in South Georgia[49] where birds nest among boulders that impose wider spacing between nests. The macaroni nesting density from the Dec 2023 drone survey was therefore used to estimate the population size in 2011 as it is more representative of the more even nesting substrate found on Zavodovski.

The overall percentage change in population size between 2011 and 2025 and annual population multiplication rates (λ), with confidence limits, were estimated (Equation 1).

$$\lambda = \frac{N_{t2}}{N_{t1}}^{\left(\frac{1}{(t2-t1)}\right)} \quad \text{Equation 1}$$

Where N is the population estimate and t is the year if the count.[50] Confidence intervals were taken by randomizing the order of the 10,000 bootstrapped population estimates for 2011 and 2025 and calculating the 2.5 and 97.5 quantiles of the calculated percentage change and λ. Projected rates of change for chinstraps over 3 generations (28 years[16]) based on λ estimates from SSI and those for rest of the Scotia Sea (based on penguin counts from the MAPPD database[51] modelled using Supplement 6 of Oosthuizen et al.[52]) were weighted by the regional population sizes[9] and summed to produce a frequency distribution of global population change. Proportions of the possible change values falling within the IUCN categories of Critical (>-80%), Endangered (-80% to -50%) and Vulnerable (-50% to -30%) for criteria A2 (i.e. population reduction observed, estimated, inferred or suspected in the past, where the causes of reduction may not have ceased OR may not be understood OR may not be reversible, based on (a) direct observation[53] were then calculated.

Penguin tracking data analysis

The R package CRAWL[43] was used to estimate penguin locations at hourly intervals at a precision of < 5km, accounting for uncertainty based on the ARGOS error ellipses of the raw fixes and the movement process of the birds.[54] Time spent within a 5 km buffer of the island's coastline was classed as ashore and removed. For each species the proportion of at-sea time spent within the SGSSI MPA, and the time-varying closed areas therein (where krill fishing is prohibited) were quantified. The spatial overlap of the 95% isopleth of the utilisation distributions of the two species was estimated using Bhattacharyya's Affinity, where a value of zero equates to no overlap and unity to complete overlap.[44] The sea surface temperature (SST) at each penguin location was sampled from a NOAA OISST V2 raster (averaged for Dec 2023 to Feb 2024) and the proportional overlap of the kernel density of the frequency distributions of the two species in environmental space was estimated.[55]