



Sea ice concentration decline in an important Adélie penguin molt area

Annie E. Schmidt^{a,1} , Amélie Lescroël^a, Simeon Lisovski^b , Megan Elrod^a, Dennis Jongsomjit^a , Katie M. Dugger^c , and Grant Ballard^a

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Unlike in many polar regions, the spatial extent and duration of the sea ice season have increased in the Ross Sea sector of the Southern Ocean during the satellite era. Simultaneously, populations of Adélie penguins, a sea ice obligate, have been stable or increasing in the region. Relationships between Adélie penguin population growth and sea ice concentration (SIC) are complex, with sea ice driving different, sometimes contrasting, demographic patterns. Adélie penguins undergo a complete molt annually, replacing all their feathers while fasting shortly after the breeding season. Unlike most penguin species, a majority of Adélies are thought to molt on sea ice, away from the breeding colonies, which makes this period particularly difficult to study. Here, we evaluate the hypothesis that persistent areas of high SIC provide an important molting habitat for Adélie penguins. We analyzed data from geolocating dive recorders deployed year-round on 195 adult penguins at two colonies in the Ross Sea from 2017 to 2019. We identified molt by detecting extended gaps in postbreeding diving activity and used associated locations to define two key molting areas. Remotely sensed data indicated that SIC during molt was anomalously low during the study and has declined in the primary molt area since 1980. Further, annual return rates of penguins to breeding colonies were positively correlated with SIC in the molt areas over 20 y. Together these results suggest that sea ice conditions during Adélie penguin molt may represent a previously underappreciated annual bottleneck for adult survival.

climate change | Ross Sea | geolocation | *Pygoscelis adeliae* | Antarctica

Polar regions are experiencing the most rapid and severe impacts of climate change, including dramatic changes in sea ice in some areas (1). Unlike the well-documented declines in Arctic sea ice concentration (SIC), duration, and extent, sea ice trends in Antarctica have varied by region, with some regions like the Ross Sea experiencing increasing sea ice extent and longer sea ice seasons (2, 3), although that trend may have ended recently (see below). The Ross Sea is home to ~33% of the global Adélie penguin population (4, 5). Adélie penguin populations around Antarctica and in the Ross Sea tend to reflect changes in sea ice at larger temporal and spatial scales (5–7), with populations in the Ross Sea stable or increasing over the last several decades (5). However, attempts to link sea ice change to growth of individual colonies or specific Adélie penguin vital rates have met with variable success, and provided complex, sometimes contradictory results. Both positive and negative effects have been described depending on which sea ice characteristic (e.g., concentration or extent), time period (e.g., nonbreeding or breeding season), which response examined (e.g., population growth, survival, or breeding success), and in which region the study occurred. For example, a negative effect of increasing winter sea ice extent on breeding population size (with a multiyear lag) has been reported for Ross Island populations (8) and Adélie Land (9), while a continent-wide analysis showed moderate mean winter SIC near breeding colonies was associated with higher long-term population growth (6). Adult survival was not associated with SIC in the summer breeding season at Ross Island colonies (10, 11) but was related to winter sea ice extent (12). While there is consensus that Adélie penguins require some amount of sea ice during all phases of their life cycle (13), a better understanding of the pathways by which sea ice impacts Adélie penguin populations is necessary for predicting their response to future sea ice changes.

On the basis of projections from climate modeling and existing knowledge, the Ross Sea is expected to remain suitable as a penguin habitat for longer than many other regions around Antarctica (14). However, a recent string of years with anomalously low sea ice extent and concentration (15–17) raises the possibility that the positive trend has already ended, increasing the urgency to understand how reductions in sea ice might affect this stronghold of Antarctic penguin populations. Adélie penguins fall in the middle of the “slow-fast” life history continuum for seabirds (18, 19); they have delayed maturity (20, 21), produce a maximum clutch size of 2 eggs annually (20, 22), and exhibit moderate to high

Significance

Adélie penguins rely on sea ice throughout their annual cycle but may face particularly challenging conditions during their annual molt, a 19-d period when they replace all their feathers. We identify areas with high sea ice concentration (SIC) that provide critical molting habitat for Adélie penguins in the Ross Sea. SIC during the molt period was unusually low during the study and has decreased since 1980, in contrast with regional trends, potentially creating a previously unrecognized bottleneck for adult survival. These findings emphasize the importance of preserving sea ice habitats crucial to the survival of this iconic species and the need for continued efforts to understand the impacts of changing sea ice conditions on Adélie penguin population dynamics.

Author affiliations: ^aPoint Blue Conservation Science, Antarctica Program, Petaluma, CA 94954; ^bAlfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Polar Terrestrial Environmental Systems, Potsdam 14473, Germany; and ^cUS Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Corvallis, OR 97331

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¹To whom correspondence may be addressed. Email: aschmidt@pointblue.org.

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annual survival (63 to 99%; 10, 11). Environmental factors that affect annual survival will directly impact population growth, thus are of particular interest in population projections. While relationships between Adélie penguin survival and SIC and extent have been documented in several studies (noted above), the effect of sea ice variability during the molting period is essentially unknown.

Molt in birds is the process of replacing worn or damaged feathers. Most species replace their feathers at least once a year, but penguins are somewhat unusual in that they rapidly replace all their feathers at once in a condensed complete, or “catastrophic”, molt, typically just after the breeding season. During their approximately 3-wk molt, Adélie penguins are not able to enter the water to forage, resulting in a loss of ~45% of their body mass (23, 24). Most (>75%) are thought to molt on sea ice (22, 23, 25–27) while a smaller proportion molt on land (28). In previous work, we presented initial evidence that the molting area for Adélie penguins from Ross Island was associated with pack ice in the Eastern Ross Sea (26). In the present study, we test the hypothesis that persistent areas of high SIC provide important molting habitat for Adélie penguins.

To do this, we analyzed data from 195 geolocating dive recorders (GDRs) deployed on adult penguins at the same two colonies previously studied, Cape Crozier (77°27'S, 169°14'E, ~300,000 breeding pairs) and Cape Royds (77°33'S, 166°10', ~2,500 breeding pairs, Fig. 1), over 3 y, covering molt periods in 2017 to 2019. These are two colonies of the four-member metapopulation (including Cape Bird and Beaufort Island) in the southwest Ross Sea (10). Using the geolocation and diving data, we identified the most highly used molting areas and assessed the sea ice conditions for those areas. We used mark-resighting data from a long-term study that began in 1996 at these two colonies to estimate adult return rates to the breeding colonies and evaluated the relationship between annual return rates of individuals to breeding colonies

(an index of apparent survival) to SIC in molt areas. Finally, we assess how molt areas correspond to the existing protection of the Ross Sea Region Marine Protected Area (RSRMPA).

Results

We recovered 242 (60%) of 403 GDRs that had been deployed on Adélie penguins at Cape Crozier and Cape Royds during the 3 y of this study. We used the recovered dive logs to identify periods when the penguins were not diving to estimate molt dates for 208 individuals with sufficient data (the remainder had gaps in the GDRs' archives), 159 from Cape Crozier, and 49 from Cape Royds. Mean date of molt initiation was February 21, starting as early as January 31 and as late as March 23 (SE = 0.68 d). Molt lasted for an average of 19.3 d (range = 13 to 26, SE = 0.124 d), consistent with previous findings of between 17 and 20 d (23, 27, 29).

Molt Locations. During the breeding season, 24-h daylight and lack of twilight at the breeding colony prevents light levels and twilight times from being used to estimate locations. The date of the first postbreeding locations we were able to estimate from light-level data each year ranged from February 13 to March 7. After filtering to remove locations near the autumnal equinox, molting locations were estimated for 195 tracks (119 unique individuals, $n = 1$ to 50 molt locations per track) between February 13 and March 26 with most individuals (93%) completing molt prior to the equinox cutoff of March 26th. Of the 208 tracks with estimated molt dates, there were 13 (4 in 2018, 9 in 2019) for which we were unable to estimate any molting locations, largely because these individuals completed molt early, between February 17 and March 11, prior to the first geolocation estimate for each track (one device malfunctioned). Molting location density estimates showed two distinct molting areas, with most individuals (175 of 195 = 89.7%) molting in the eastern Ross Sea. A smaller number of birds (20 of 195 = 10.3%) molted along the western Ross Sea coastline (Fig. 2). Penguins from both colonies used eastern and western molt locations but individuals from Cape Crozier were more likely to molt in the eastern Ross Sea (95.3% overall, range 88.6 to 100% each year) compared to penguins from Cape Royds where up to 41.2% used the western molt region (71.1% overall used the eastern region, range 58.8 to 81.2% each year). The 50% core areas of all molting locations were largely contained within the boundaries of the RSRMPA general protection zone (Fig. 2). Molt locations showed high consistency between years within the 95% contours (Fig. 3 and *SI Appendix, Table S1*): the proportion of overlap between years ranged from 0.43 to 0.57 in the east and 0.40 and 0.70 in the west. The core 50% area was more variable, with the proportion of overlap ranging from 0.03 to 0.25 in the east, and 0.12 to 0.43 in the west (*SI Appendix, Table S1*). A small number of penguins (8 out of 63 with multiple years of molt locations) switched molt areas between years.

SIC in Molt Areas. SIC (the percent of the area covered in sea ice) in the annual core (50%) molt areas ranged from 2.9 to 24.1% during the 3 y of the study (February 13 to March 26, 2017 to 2019, Figs. 3A and 4). For comparison, the broader Ross Sea region encompassed by the combined nonbreeding range polygon, averaged 4.2 to 6.7%. SIC was typically higher in the west than in the east during this study (Figs. 3A and 4). However, the long-term sea-ice data indicated that the eastern molt area historically had much higher SIC than the west and was also higher than the combined nonbreeding range (Fig. 3). SIC from 1980 to 2021 showed a significant decline in the eastern molt area in both the 50% core area ($y = 1388.1 - 0.67x$, R^2 (Adj) = 0.15, $P = 0.007$)

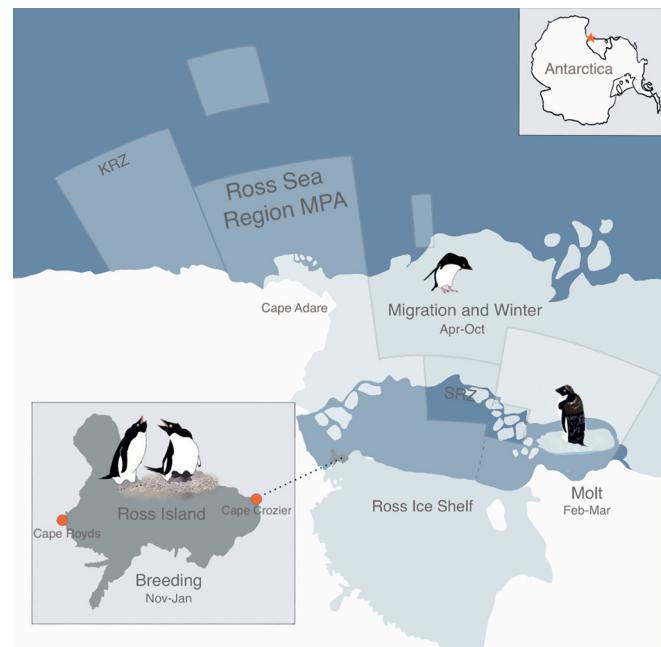


Fig. 1. Maps of study area in the Ross Sea sector of the Southern Ocean. Orange star in Antarctica inset indicates the location of Ross Island. Ross Island Inset shows a zoomed in view of Ross Island and the locations of two study colonies, Cape Crozier and Cape Royds as orange points. Light gray area shows boundaries of the RSRMPA, with the krill research zone (KRZ) and special research zones (SRZ) labeled.

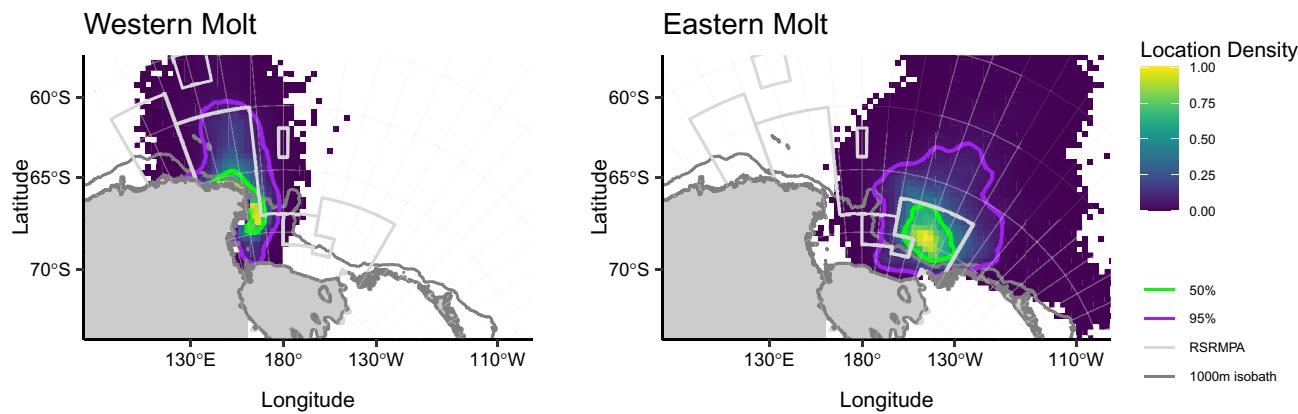


Fig. 2. Maps showing two distinct molting areas in the western and eastern portions of the Ross Sea region. Location densities were estimated after first assigning a molt location to east or west based on whether an individual's median location during molt was east or west of Longitude 180. Green lines indicate the 50% density contour, purple lines indicate the 95% density contour. The boundary of the RSRMPA is shown in light gray and the Ross Sea shelf break is the 1,000 m isobath shown in dark gray.

and the larger 95% molt region ($y = 856 - 0.41x$, $R^2(\text{Adj}) = 0.16$, $P = 0.005$, Fig. 3B). In contrast, there was a weak positive trend in SIC in the western area (50% trend: $y = -643.5 + 0.33x$, $R^2(\text{Adj}) = 0.05$, $P = 0.08$, 95% trend: $y = -477.4 + 0.25x$, $R^2(\text{Adj}) = 0.08$, $P = 0.04$, Fig. 3B). There was no trend in the SIC for the broader Ross Sea region in the combined nonbreeding range during the molt period (Fig. 3B).

Effect of SIC in Molt Areas on Return Rates. Banded bird return rates at Cape Crozier were best modeled with a linear effect of SIC in the eastern 95% molt region ($y = 59.7 + 0.24x$, $R^2(\text{Adj}) = 0.29$, Fig. 5 and Tables 1 and 2), and no other models were competitive (i.e., none with $\Delta\text{AIC}_c \leq 2$). For Cape Royds, the top model also included a linear effect of SIC in the western 95% molt region ($y = 49.08 + 0.48x$, $R^2(\text{Adj}) = 0.20$, Fig. 5; Tables 1 and 2). Models including a linear effect of SIC in the broader Ross Sea Region and in the western 50% molt region were also competitive ($\Delta\text{AIC}_c \leq 2$). The top models for both Cape Crozier and Cape Royds colonies found a positive relationship between SIC in the Adélie penguin molt region and return rates of adult penguins to the breeding colonies. Specifically, a 10-percentage point increase in SIC in the eastern molt region resulted in a 2.4 percentage point increase in banded bird return rates to Cape Crozier, while a 10-percentage point increase in the western molt region of Cape Royds led to 4.8 percentage point increase in return rates to Cape Royds.

Discussion

We identified two distinct areas of high use by molting Adélie penguins from two colonies on Ross Island. Specifically, we found that the vast majority of study penguins molted in the eastern Ross Sea sector although an area in the western Ross Sea also appears to be an important molting area, particularly for penguins from the smaller Cape Royds colony. These two areas were used persistently over the 3 y of this study and were consistent with results from the 2003 to 2005 tracking study (26) as well as ship-based observations in the 1980s (30, 31) that noted high densities of Adélie penguins in the eastern Ross Sea sector at a similar time of year. The addition of time-depth recorders to location trackers in the present study enabled us to accurately define both timing and location of molt. The eastern Ross Sea sector, where the majority of the study birds molted, has historically been an area of high SIC relative to the entire migratory range of Ross Island Adélie

penguins, consistent with the hypothesis that persistent areas of high SIC provide important molting habitat for Adélie penguins. Concerningly, this important molt area in the eastern Ross Sea sector has experienced a decline in SIC since 1980, with SIC in this area reaching a record low in the first year of the study (Fig. 3). We found that return rates of penguins at both colonies were related to SIC in the dominant molt areas, which raises important questions about the impact that future sea ice decline may have on these populations.

The Adélie penguin is well known as a sea ice obligate, it is found only in areas with sea ice and is declining in areas where sea ice is declining (6, 7, 32, 33). While the mechanisms that drive this dependence on sea ice are complex, previous studies have offered numerous hypotheses linking Adélie penguin population size and growth rates to SIC and sea ice extent at various geographic and temporal scales (5, 8, 34–37). The relative importance of different mechanisms through which sea ice impacts penguin demographics is still unclear and may vary by population, geographic region, and time series under consideration. Here, we present initial evidence that sea ice conditions on a relatively limited spatial and temporal scale (molt location and period) may provide an important additional constraint on Adélie penguin population growth. We hypothesize that the molt period may function as a bottleneck in annual adult survival for Southern Ross Sea, and possibly other, Adélie penguin populations, with low sea ice availability inducing higher mortality and/or immigration rates.

Previous research reported high sensitivity of Ross Island Adélie penguin population growth to fluctuations in adult survival, with a reported elasticity value of 0.81 indicating that small reductions have proportionally large effects on population growth rates, all other vital rates remaining constant (8). For example, a 10% reduction in adult survival, which is within the range of variation that has been reported for Adelie penguins (9, 10, 12), could lead to an 8.1% decrease in the population growth rate. Thus, even a moderate decrease in adult survival could potentially trigger significant shifts in population dynamics. From 1981 to 2018, the number of breeding pairs at Cape Crozier increased according to aerial survey estimates (5, 38). Despite recent low return rates after poor molt SIC conditions, the population size hasn't yet declined significantly. However, population estimates for the years after the most recent severe sea ice conditions (2019 to 2022) are not yet available. We found that SIC in molt areas predicted 20 to 29% of the variation in adult return rates. While this is substantial for a single variable, there are clearly other factors influencing return

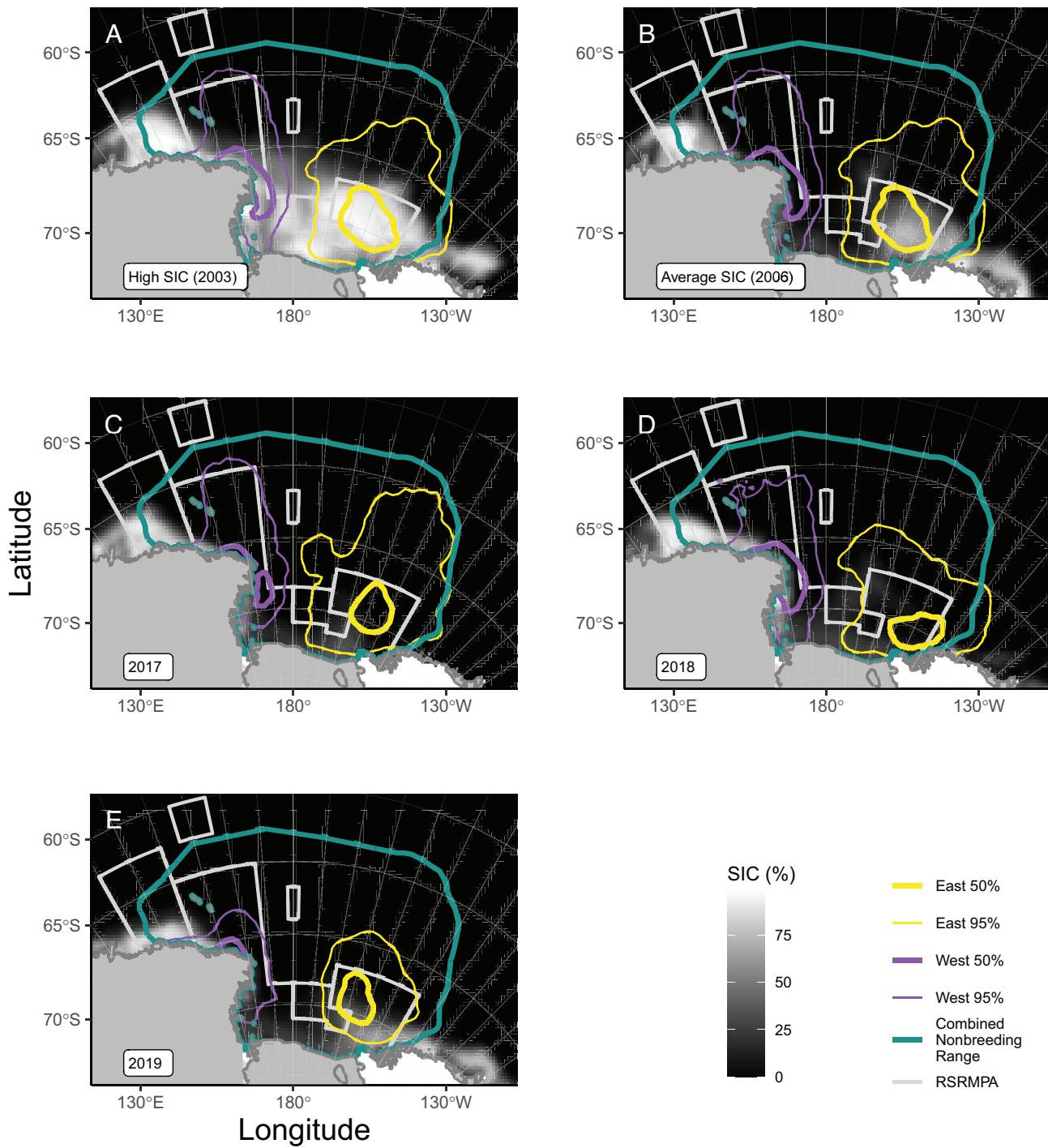


Fig. 3. Maps of molt regions with SIC using SSMI data during the molt period February 13 to March 26 each year. (A) An example year with very high SIC (2003) along with the boundaries of the combined 3-y molt regions, west in purple, east in yellow and the total combined nonbreeding range in turquoise. (B) An example year with “average” SIC (2006). (C–E) SIC during the 3 y of the study with molt contours estimated separately for each year.

rates and population rate of change that should be evaluated. The interaction of vital rates affecting population change for a species with a complex life history means that changes in adult survival may not immediately affect breeding population numbers, particularly if other demographic variables such as high reproduction, juvenile survival, or breeding propensity can compensate. In particular, juvenile survival has been proposed as a critical factor driving Adélie penguin population fluctuations (8). Because juveniles do not molt during their first year at sea, they may not be as affected by sea ice changes during the adult molting period.

Recognizing this complexity, it will be valuable to develop a comprehensive population model that can provide a deeper understanding of the impact of SIC changes during molt on the overall population trajectory.

Several other studies have highlighted the potential significance of sea ice in the molting process of Adélie penguins. Adélie penguins tracked from Signy Island, north of the Antarctic Peninsula (27, 39), all molted in the pack ice in areas with very high SIC (>80%). Both studies note this dependence on sea ice for molt could make populations vulnerable if sea ice declines.

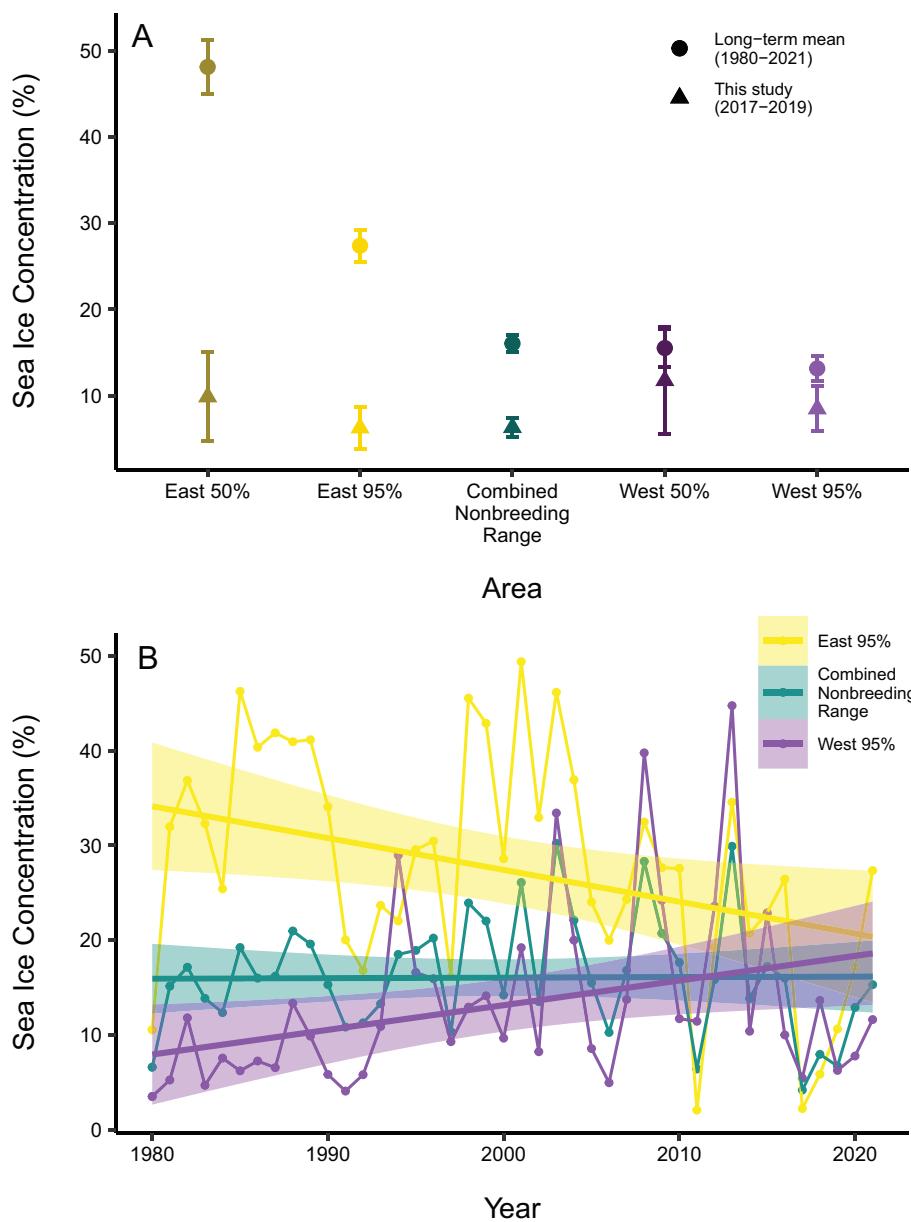


Fig. 4. (A) Points show long-term mean (with SE) SIC during the molt period, February 13 to March 26 each year (calculated from SMMR and SSM/I-SSMIS data; NASA Team algorithm) by molt region. Triangle symbols show mean and SE in the same regions during the 3 y of the study (2017 to 2019). (B) Time series of SIC in molt regions during the molt period with linear trend by region. Combined nonbreeding range refers to the area encompassing all known nonbreeding locations for Ross Island Adélie penguins during this study as well as in Ballard et al. (26).

From the West Antarctica Peninsula, birds moved into the Weddell Sea post-breeding to molt where more reliable sea ice can be found (40). In East Antarctica, Adélie penguins spent the postbreeding period between February and April in areas of higher than average SIC, possibly due to the need for ice floes on which to molt (41).

There may be multiple important consequences of not having sufficient sea ice available in the right places and at the right time for molting penguins. For example, if penguins are forced to travel long distances in search of suitable molting habitat, they may incur higher energy costs, which may force them to delay or curtail molt (42). Delaying molt might force penguins to molt quicker which could have consequences for plumage quality that may affect survival (43) or breeding propensity. Penguins rely on their tails, which grow in after the primary body feather molt (44), for maneuvering, controlling pitch, and yaw (45, 46). Reduced plumage quality, including the loss or reduction of tail feather length, could hinder their ability to make quick turns while pursuing prey, significantly impacting foraging ability for significant portions of

the year (47). When sea ice is reduced or limited, the density of molting penguins on the remaining ice may be increased, putting individuals at a higher risk of predation or spread of disease. Furthermore, lower SIC conditions may result in more frequent wave overwash of ice floes (48). This could increase the likelihood of penguins being washed into the water, where their underdeveloped plumage would leave them vulnerable to hypothermia (24). Finally, while SIC serves as a widely used metric, there is no distinction in the SIC dataset between first-year or multi-year ice or between landfast and pack ice, differences that may be important for molting Adélie penguins. Multiyear pack ice is thicker and more likely to have ridges and hummocks that penguins prefer to shelter behind during molt (49). Therefore, it may be necessary to consider not only SIC but also the specific type of ice when assessing ecological impacts of declining ice cover.

Evidence for molt as a period of increased mortality has been found for little penguins (*Eudyptula minor*) (50, 51), yellow-eyed penguins (*Megadyptes antipodes*) (52), and Galapagos penguins [*Spheniscus mendiculus*; (53)]. In most cases, mortality appears to

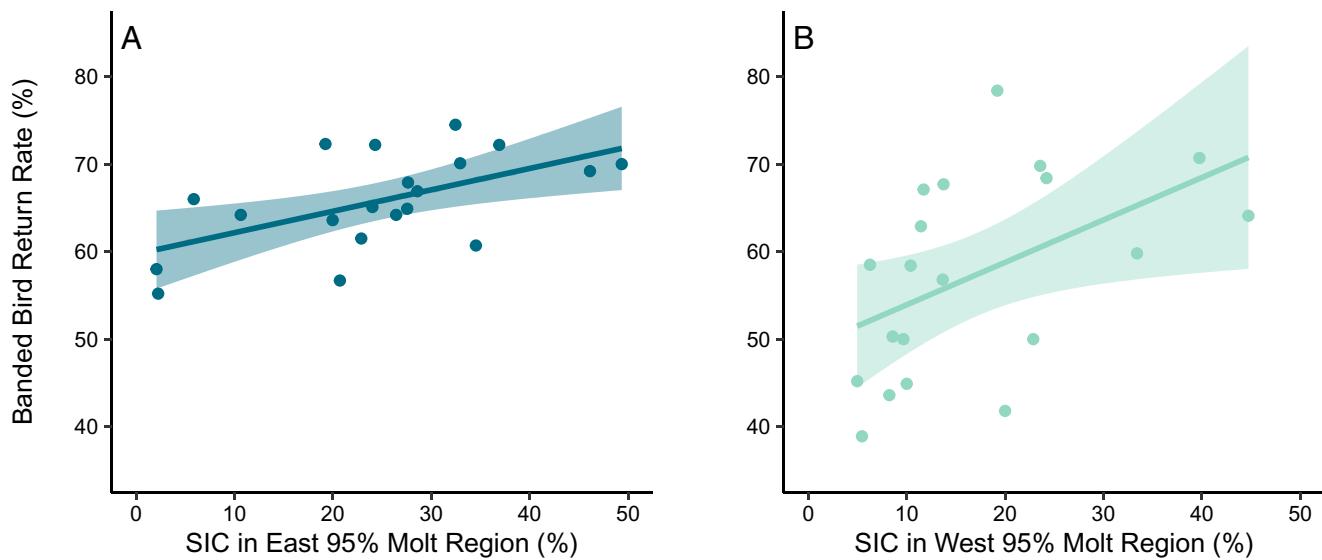


Fig. 5. Results of top models showing the relationship between banded bird return rates and SIC during the molt period (February 13 to March 26 each year) at (A) Cape Crozier and (B) Cape Royds. The top models were fitted with linear regression and are depicted with shaded 95% CIs.

have been the result of starvation. Adélie penguins are at their heaviest weight of the year just prior to molt (23), and pre-molt energy expenditure has been estimated at nearly 2x energy expenditure during chick rearing (54). Macaroni penguins were also found to have the highest daily prey consumption during the premolt period (55). This implicates the premolt foraging period as a critical phase that may determine molt mortality rates, meaning that penguins need to be in an area of high prey concentration just prior to molt to prepare for the molt fast, and just after molt to recover. Although very few direct observations of prey density in the eastern Ross Sea exist, particularly in ice covered areas, high densities of Adélie,

Emperor, and other predators in the region (56) suggest abundant prey is available.

Adélie penguins can and do molt on land, although it is not well-established what proportion of the global population does so. Existing evidence suggests that this phenomenon constitutes a minor fraction, estimated at ~10 to 25% (22, 23, 49). Their ability to molt on land may give Adélie penguins the capacity to adapt to changing sea ice conditions and shift to land when SIC is reduced, although that shift is likely to come at some cost. The negative association between SIC in the molt areas and return rates to Ross Island breeding colonies suggests that

Table 1. Model selection results including ΔAICc (the difference in AICc between each candidate model and the model with the lowest AICc value), model degrees of freedom (df), Akaike weights (AICc wt), $-2\log\text{likelihood}$ ($-2\log\text{Lik}$), rms error (rmse), and adjusted R^2 for models relating return rates of banded birds at Cape Crozier and Cape Royds to linear or quadratic effects of SIC (February 13 to March 26 each year) in different regions

Cape Crozier

SIC region	ΔAICc^*	df	AICc wt	$-2\log\text{Lik}$	rmse	R^2 (Adj)
East 95	0	3	0.38	115.56	4.35	0.29
Ross Sea Region	2.04	3	0.14	117.60	4.58	0.22
Ross Sea Region + Ross Sea Region ²	2.40	4	0.11	114.70	4.26	0.28
East 95 + East 95 ²	2.62	4	0.10	114.92	4.28	0.27
East 50	2.74	3	0.10	118.30	4.66	0.19
West 50	4.05	3	0.05	119.62	4.81	0.13
West 95 + West 95 ²	4.89	4	0.03	117.20	4.53	0.19
Intercept only	5.17	2	0.03	123.58	5.31	0
Cape Royds						
West 95	0	3	0.28	147.17	9.59	0.20
Ross Sea Region	0.85	3	0.18	148.02	9.79	0.16
West 95 + West 95 ²	1.2	4	0.15	145.11	9.11	0.23
West 50	1.97	3	0.1	149.13	10.07	0.11
West 50 + West 50 ²	2.26	4	0.09	146.17	9.35	0.19
Intercept only	2.63	2	0.08	152.65	10.99	0

Only models with variables performing better than the null (intercept only) model are shown.

*Lowest AICc for Cape Crozier = 123.16; lowest AICc for Cape Royds = 154.77.

Table 2. Effect size estimates, SEs and 95% CIs from the top models explaining banded bird return rates at Cape Crozier and Cape Royds

Cape Crozier

Term	Estimate	SE	95% CI
Intercept	59.72	2.28	54.94 to 64.50
East 95	0.24	0.08	0.07 to 0.42
Cape Royds			
Intercept	57.36	2.27	0.53 to 0.62
West 95	0.48	0.20	0.05 to 0.91

there is some constraint, perhaps the need to move outside the prey depletion halo, particularly near large breeding colonies (57–60), that prevents most penguins from molting at the breeding colonies. The handful of individuals that switched molting regions between years indicate that the molt region is not fixed within individuals and populations may be able to shift and adapt in response to changing conditions. Although the eastern region has had higher SIC historically, concentrations were similar between regions during the study and the western region shows some indication of being more resilient to sea ice declines [Fig. 3B; (17, 61)] which may make this area a more significant molting location in the future.

The RSRMPA includes the core molt areas used by the penguins in this study, so molting penguins may derive some benefit from reduced interactions with vessels within those boundaries. However, the entire area used extends well beyond the MPA boundaries and includes “special research zones” within the MPA that are open to certain kinds of fishing. Additionally, increasing visitation by tourist vessels (62), that are likely to visit the Ross Sea during the low sea ice/mol season, may become more of an issue and specific guidance offered to tour companies who are not restricted from entering the MPA may be helpful for protecting penguins (i.e., molting penguins should be avoided). Unfortunately, the main threat to the penguins in this context is climate-driven sea ice reduction, which the marine protected area does not directly address.

Conclusion

Our study provides quantitative evidence that sea ice conditions during Adélie penguin molt may affect the return of adults to breeding colonies, with implications for demographic variability. Further investigation is needed to fully understand the relationship between SIC in the molt areas and vital rates of Adélie penguins, while considering other, potentially correlated, environmental drivers. In addition, studies synthesizing molt location and habitat data from throughout the species' range, assessing the prey escape before and after molt using biologging and gliders, and making direct observations of molting penguin and predator behavior in years with varying sea ice availability will be important. The recent decrease in SIC during the molt period in the eastern Ross Sea Sector, the largest molt hotspot in our study, underscores the urgency of this research.

Methods

Study Sites. The study was conducted at two colonies on Ross Island, Cape Crozier (77°27'S, 169°14'E, ~300,000 breeding pairs) and Cape Royds (77°33'S, 166°10', ~2,500 breeding pairs, Fig. 1). Breeders arrive at Ross Island in late October/early November, build a nest out of pebbles, and lay a maximum of two eggs by mid-November. Chicks hatch about 35 d after egg laying and are fed by both parents from mid-December to early February before fledging. After the breeding season, adults undergo a condensed complete annual molt, replacing

all of their feathers at once (23) [except tail feathers which grow in over a period of months (44)].

Biologging. During the austral summers of 2016 to 2018, we equipped 403 Adélie penguins at both colonies with GDRs (“LUL” tags, 22 × 21 × 15 mm, weight = 4 g, from Atesys, Strasbourg, France, hereafter referred to as GDRs). These devices recorded light every 60 s, temperature (with a precision of ±0.5 °C) every 30 s, and pressure (with a precision of ±0.3 m) every second for 12 to 15 mo. The GDRs were encapsulated in transparent flexible heat-shrink tubing shaped into a leg strap and attached to the tibiotarsus of each bird in the field using a polyester-coated stainless-steel zip tie to secure the ends of the strap together such that the tag could rotate freely around the leg but not slip over the tarsus joint. Devices were left in place for 1 y and recovered the following year. Individuals that returned were reequipped with a new device for up to two additional years. Devices that were deployed during the breeding season recorded molt locations for the following calendar year (e.g., devices deployed during the 2016 to 2017 breeding season record molt locations in early 2017) so we refer to years by calendar year throughout.

Estimating Molt Dates. All analyses were conducted in R [v. 3.6.0–4.1.1; (63)]. The pressure data underwent various processing steps that were adapted from the diveMove package [v. 1.4.5–1.6.0; (64)]. To correct for instrument drift and noise, pressure data were zero offset corrected using the “filter” method in the calibrateDepth function (64). We used a depth threshold of 3 m to qualify as a dive. Adélie penguins typically molt in February to March (22, 23, 39, 65) each year. To estimate the molt period for each bird, we quantified the number of dives per day for each individual and assumed that the bird was molting if the 7-d rolling mean of the number of dives was less than 15 dives per day. This criterion resulted in a well-defined molt period for all except two individuals. For these two individuals, there was still a noticeable period with fewer dives, but it did not meet the <15 per day criterion. After visual inspection of the raw data, it was clear that most of the “dives” recorded during this period resulted from noisy pressure data. For these two individuals, the molt period was determined manually by examining the total dive time as well as the number of dives per day to generate an informed estimate of the molt period. An additional third individual had slightly noisy dive data and the estimated molt period was manually extended by several days to a point when daily dives obviously started increasing (see *SI Appendix*, Fig. S1 for example dive and molt period estimation).

Molt Locations. We calculated two positions per day per penguin using the light level data collected by the GDR's following previously established geolocation methods (66). Sunrise and sunset times were defined using a light level threshold set to 1 log lux. Devices were calibrated by leaving them at a known location to record sunsets and sunrises for a few days post deployment to enable an estimation of clock drift. An initial path was then estimated with the “SGAT” package (67, 68), then further refined in a Bayesian framework, using Markov chain Monte Carlo (MCMC) simulations informed by the twilight events, their error distribution, the information on the last and first date at the colony, and a movement model. We ran 2,000 simulations and used the last 500 MCMC chains of all estimated positions during the molt period for each penguin to generate year and region-specific polygons representing the 50% and 95% probability contour of molt locations. Locations near the equinoxes, which are known to be prone to error (26, 66, 69), were truncated by identifying the date range that contained the 25% least certain positions as determined by the width of the 95% credible interval around the estimated median position. The truncated periods where no positions were estimated fell between March 27 to April 19 and August 17 to September 26 each year. After truncating, locations were binned into 50-km grid cells and scaled so that the highest density cells had a value of one (i.e., range 0 to 1) prior to calculating the 50% and 95% density quantiles. When initial density contours were calculated, a distinct break along Longitude 180 was apparent that divided a western region from an eastern region (*SI Appendix*, Fig. S2). Individuals were then assigned to a region based on whether their median molt location was east or west of 180° and a density contour estimated separately for birds molting in east and west regions. We evaluated molt location consistency by calculating the proportion (by area) of the molt regions that overlapped between years using the formula:

$$\text{ProportionOverlap} = \text{Aoverlap} / (\text{A1} + \text{A2} - \text{Aoverlap}),$$

where *Aoverlap* = the area of intersection between the two polygons being compared (intersection calculated using the function *gIntersect* in the R package

rgos v0.5-9), A1 = the area of the first polygon, and A2 = the area of the second polygon. We calculated the proportion overlap for each molt region (East 50%, East 95%, West 50%, and West 95%) and each pair of years (2017 and 2018, 2018 and 2019, 2017 and 2019).

To define the broader Ross Sea region used by the penguins during the nonbreeding season, we first selected individuals that had data for a complete year and again used the last 500 MCMC chains of estimated positions for these tracks. After truncating around the equinoxes, locations were again binned into a 50 km grid, scaled 0 to 1, and the 95% density contour for the entire nonbreeding season calculated [$n = 185$ tracks from 111 unique individuals, 62,715 (x500 estimates) positions; *SI Appendix, Fig. S3*]. We then combined this polygon with the estimated area used by Adélie penguins in the nonbreeding season from a prior study (26). The polygon used by penguins in the prior study overlapped the area used in this study by 89%. As in the prior study, the intent in this was to use the best available data to reflect the range of places where an Adélie penguin from Cape Crozier or Cape Royds might be found during the nonbreeding period. With 6 y of study in widely differing sea ice conditions and a total sample of 152 (41 previous + 111 current) individuals, we believe that this combined information represents a robust approximation of the total range of these populations.

SIC. SIC (percent area covered by sea ice) data were downloaded from the National Snow and Ice Data Center as collected by the SMMR and SSM/I-SSMIS [1980 to 2021; NASA Team algorithm (70)]. To estimate SIC in the molt areas, we first calculated a comprehensive molt period encompassing the earliest and latest molt locations observed over the three-year study. We combined molt locations from all three years to calculate the cumulative 50% and 95% contours for east, west, and Ross Sea regions and then calculated mean SIC within these contours during the comprehensive molt period annually from 1980 to 2021. A trend was estimated by fitting a linear model to the annual mean SIC values by contour region. Residuals were checked for normality and autocorrelation to assess whether assumptions of linear models were met.

Return Rates of Banded Birds. Between 1996 and 2019, a total of 7110 chicks near fledging were banded at Cape Royds (range 70 to 450, median 200 per year) and 19,709 (range 100 to 1,000, median 1,000 per year) at Cape Crozier. Bands were attached to the bird's left flipper and were engraved with a 5-digit number that is legible through binoculars (71). Extensive searches at each of these colonies were made annually for banded recruits. To calculate return rates of banded birds, we tallied the number of individuals sighted each year, and the percent of these individuals that were resighted the following year. Adélie penguins in our study do not recruit until they are at least 3 y old [range 3 to 14 y; (20, 21)]. Thus, we calculated band return percentage beginning with data in 2001 to ensure that we had a reasonable sample of birds aged three or older. Flipper bands can reduce annual survival and it is not clear to what extent that effect varies by year (71). Lacking evidence to the contrary, we

assume that the effect of flipper bands is uniform across the study population and across years. We excluded all individuals that had GDRs attached in case there was any bias in return rate due to GDR attachment. This calculation of annual band return rates does not account for variability in detection probability or immigration and is thus an index to annual adult survival. However, as previous analyses showed that annual detection probabilities were consistently very high (10) and immigration rates are very low (<1% for breeders; 10), we consider return rates of banded birds a reasonable index of annual survival. We evaluated whether the return rates of banded individuals to each colony were related to SIC in eastern or western molt areas, as well as the larger Ross Sea region, during the molt period using linear regression (stats package v4.2.1). We tested for linear and quadratic effects between SIC and return rates for each colony and included an intercept-only model for comparison. We evaluated models using Akaike's Information Criterion corrected for small sample sizes (AICc, $n = 20$ y). We used the difference in AICc between each candidate model and the model with the lowest AICc value (ΔAICc) and Akaike weights (AICc wts) to rank models (72). Models within $2 \Delta\text{AICc}$ of the top model were considered competitive and we calculated the adjusted R^2 to estimate the amount of variation in band return rates explained by model covariates. The quadratic effect was considered uninformative if it did not reduce the AICc score compared to the model with linear term only (73).

All penguin survey, capture, and handling methods used for data collection were performed following all relevant guidelines and regulations under the approval and oversight of the Institutional Animal Care and Use Committees of Oregon State University and Point Blue Conservation Science. Additionally, all work was approved and conducted under Antarctic Conservation Act permits issued by the US NSF and the US Antarctic Program.

Data, Materials, and Software Availability. [10.15784/601482](https://doi.org/10.15784/601482) Code used in this analysis available on GitHub (74, 75). Data available from the US Antarctic Program Data Center (76).

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