

Satellite data identify decadal trends in the quality of *Pygoscelis* penguin chick-rearing habitat

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Abstract

Pygoscelis penguins are experiencing general population declines in their northernmost range whereas there are reported increases in their southernmost range. These changes are coincident with decadal-scale trends in remote sensed observations of sea ice concentrations (SIC) and sea surface temperatures (SST) during the chick-rearing season (austral summer). Using SIC, SST, and bathymetry, we identified separate chick-rearing niche spaces for the three *Pygoscelis* penguin species and used a maximum entropy approach (MaxEnt) to spatially and temporally model suitable chick-rearing habitats in the Southern Ocean. For all *Pygoscelis* penguin species, the MaxEnt models predict significant changes in the locations of suitable chick-rearing habitats over the period of 1982–2010. In general, chick-rearing habitat suitability at specific colony locations agreed with the corresponding increases or decreases in documented population trends over the same time period. These changes were the most pronounced along the West Antarctic Peninsula where there has been a rapid warming event during at least the last 50 years.

Keywords: climate change, MaxEnt, *Pygoscelis* penguins, satellites, Southern Ocean, species distribution models, suitability, West Antarctic Peninsula

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Introduction

The success of *Pygoscelis* penguin populations is strongly linked to chick survival (Forcada & Trathan, 2009), and therefore the quantity and quality of chick-rearing habitats (CRHs). The coastal Antarctic food web is relatively short, where energy is passed from large phytoplankton, to krill to penguins. Trophically, penguins are not far removed from the primary physical processes that drive Antarctic ecosystem productivity; therefore changes in primary physical processes ought to be reflected in the location of penguin CRHs (Ainley, 2002; Smith *et al.*, 1999). Understanding penguins' selection of CRHs in Antarctica is becoming more important as the Antarctic climate and local weather patterns change (Olivier & Wotherspoon, 2006). What is not known is how changes in climate affect the quality and viability of existing CRHs or what the implications are of recent decadal-scale climate trends on the spatial distribution of penguin colonies.

The Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*) and Gentoo (*P. papua*) are *Pygoscelis* penguin species that rear chicks in the Southern Ocean (Fraser *et al.*,

1992; Williams, 1995). Although these penguins have evolved to survive in the harsh environment of the Southern Ocean, each penguin species requires specific environmental parameters for establishing nesting colonies and for successful breeding (Forcada & Trathan, 2009; Kooyman, 2002). Adélie penguins are an ice-obligate, circum-Antarctic species, breeding over an extensive geographic span (Ainley, 2002; Forcada *et al.*, 2006), unlike Gentoo and Chinstrap penguins whose range is largely restricted to the West Antarctic Peninsula (WAP) and sub-Antarctic islands due to their ice-intolerance (Trivelpiece *et al.*, 1987; Forcada *et al.*, 2006). Decreasing sea ice extent may allow Chinstrap and Gentoo penguins to expand their range and colonize shorelines with receding ice.

There have been significant losses and gains in sea ice cover in the Antarctic system. For example, annual sea ice extent and duration has increased in the west Ross Sea, however, along the WAP and Bellingshausen Sea, sea ice concentration (SIC) declined precipitously over the last few decades (Massom & Stammerjohn, 2010; Stammerjohn *et al.*, 2008). The loss of sea ice in the WAP is contemporaneous with a rapid regional warming event on the WAP, where mean winter air temperature has increased 6 °C since 1950 (Ducklow *et al.*, 2007; Vaughan *et al.*, 2003), sea surface temperature (SST) has increased (Meredith & King, 2005), and

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phytoplankton concentration (Montes-Hugo *et al.*, 2009) and community structure (Moline *et al.*, 2004) have been altered. It appears that the historic cold and dry climate of the WAP is being replaced by a northern maritime climate (Ducklow *et al.*, 2007; Smith *et al.*, 1999). Rapid climate change in Antarctica may be altering the distribution and abundance of penguin CRHs, which may cause an expansion or contraction in their range, phenological changes, and alterations in their predator-prey dynamics (Forcada & Trathan, 2009).

Satellite observations offer spatial (kilometers) and temporal (weeks) data around Antarctica and are critical for studying the large-scale physical and biological factors that correlate with penguin breeding colonies (Kooyman, 2002). These observations from polar orbiting satellites allow for historic records of ecologically important ecosystem variables like SIC, SST, and chlorophyll concentrations (CHL) to be studied on large spatial scales, and linked to penguin CRHs. For example, sea ice provides a predictable food source or a range restriction for ice-intolerant penguins (Quetin & Ross, 2009). Due to the short food web, high CHL are directly related to the availability of food for penguins (Atkinson *et al.*, 2004). Increased SST can decrease SIC and alter prey distributions and availability, which has been linked to penguin population declines (Cunningham & Moors, 1994; Guinard *et al.*, 1998; Le Bohec *et al.*, 2008). Antarctic bathymetry, which is a combination of satellite altimetry and ship observations, identifies topographic features that influence the spatial distribution of SIC, SST, and CHL. For example, deep troughs can enhance production by allowing the transport of warm nutrient-rich waters onto the continental shelf influencing the formation of polynyas and biological hotspots (Klinck *et al.*, 2004; Schofield *et al.*, 2010; Sydeman *et al.*, 2006). These ecologically significant hotspots can provide predictable foraging locations for top predators, such as penguins (Sydeman *et al.*, 2006; Valavanis *et al.*, 2004).

We combine satellite-derived SIC, SST, CHL, and bathymetry and historical colony locations of three *Pygoscelis* penguin species around Antarctica (Fig. 1). Using this data, we developed distribution models that define and predict suitable CRHs for each species. We show that the model-predicted CRH suitability correlate with known population trends at specific nesting sites for *Pygoscelis* penguins. Our analysis suggests that there have been significant changes in the location and suitability of CRHs since 1982. The largest changes in CRHs are along the WAP, and are concurrent with a rapid regional warming event. On the WAP, there is a southward shift in the most suitable CRHs for each *Pygoscelis* species.

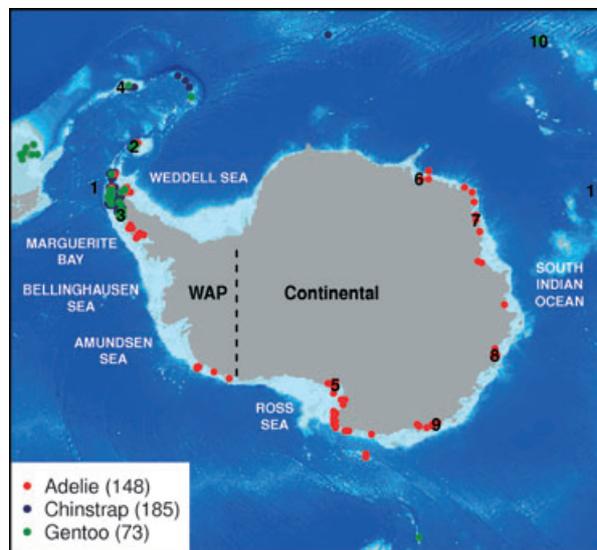


Fig. 1 Location of 406 Antarctic and sub-Antarctic penguin breeding colonies in the Southern Ocean with bathymetry in the background. Light blue represents shallow regions whereas deeper waters are darker blue. The number of unique breeding locations for each species is given in parenthesis. The dotted line separates WAP Adélie colonies from continental Adélie colonies. Numbers 1–11 correspond to breeding colonies with documented population trends given in Table 2.

Materials and methods

Colony location data

Adélie, Gentoo, and Chinstrap penguin breeding colony locations were obtained from Woehler & Croxall (1997) and Woehler (1993). Colonies with populations fewer than 100 pairs were excluded and data collected prior to 1970 were excluded to decrease the influence of small or transient colonies. These historical colonies are likely still in existence because of the high nest-site fidelity of penguins (Ainley *et al.*, 1983; Martinez, 1992). Radiocarbon dating of organic remains at breeding colonies indicated that the penguins could inhabit a specific breeding site for hundreds to thousands of years (Emslie, 2001; Emslie & Mcdaniel, 2002). We refer to these historic colony locations as penguin CRHs and these locations were matched with the corresponding environmental data (Fig. 1). Information on environmental data processing is located in the appendix.

Characterizing penguin colonies

Penguin colonies were matched to records of SST (1981–2010), SIC (1978–2010), CHL (1978–1986, 1997–2010), and bathymetry during their chick-rearing season (December–February). For a particular colony, we spatially averaged our environmental data within 75 km of the colonies. This spatial resolution accommodates the foraging range of the penguins while chick rearing. Then these spatial means were averaged again across

all breeding seasons so that each colony was assigned a characteristic SST, SIC, CHL, and bathymetry during the chick-rearing season.

We treated Adélie colonies located along the WAP separately from the continental Adélie penguin colonies for two reasons (Fig. 1). The first is that Adélie colonies on the WAP have been influenced by a rapid warming event along the WAP (Wilson *et al.*, 2001). The second reason is that the relatively young Adélie populations along the WAP (Emslie *et al.*, 1995, 1998; Tatur *et al.*, 1997) are likely derived from Ross Sea source populations that continue to thrive (Wilson *et al.*, 2001; Emslie & Patterson, 2007; Goodwin, 1993). As the environmental data was not normally distributed, we used a nonparametric Kruskal–Wallis test to determine if environmental parameters associated with each species/group originate from the same distribution. We also used a multiple comparison test after Kruskal–Wallis to determine if environmental predictors differentiated the species groups.

Penguin CRH models

We used a presence-only modeling technique to estimate penguins' CRH distributions. In presence-only modeling, nonobservations do not verify the species is absent (Irwin *et al.*, 2011). However, these techniques have been shown to model the same ecological relationships as presence-absence methods when biases are reduced or eliminated (Elith *et al.*, 2011). We assume that there is a good understanding of the penguins chick-rearing range in Antarctica. Therefore, penguins' CRH distributions were estimated using MaxEnt version 3.3.3k, which represents a species' ecological niche by the environmental variables tested and is useful for presence-only data (<http://www.cs.princeton.edu/~schapire/maxent/>; Phillips *et al.*, 2006). MaxEnt has been shown to be a robust method for estimating species distribution (Reiss *et al.*, 2011) and has been used previously to model the distribution of Antarctic predators (Friedlaender *et al.*, 2010). The maximum entropy approach uses environmental variables that are thought to be predictive of a species habitat selection and species occurrence observations to create a model of the species suitable range by estimating the probability distribution of maximum entropy (or closest to uniform; Phillips *et al.*, 2006). MaxEnt estimates the probability of a species being present (or habitat suitability), ranging from 0, the least suitable, to 1 being the most suitable for a species to be present (Phillips & Dudík, 2008).

For this analysis, we used a cross-validation resampling procedure, which randomly divides colony occurrence locations into a specified number of equally sized groups or folds. We ran the model by leaving each fold out in turn; the model was fit on the preserved data and predicted onto the left out data. The predictions generated from the withheld fold were used to test the performance of the model created on the preserved data (Elith *et al.*, 2011). We used four replicate runs that partitioned 75% of the penguin colonies into the fitting fold and 25% of the colonies into the left out fold (Redon & Luque, 2010). We used jackknife tests to quantify which environmental predictors are contributing the most to fitting the model. The accuracy of the models were validated by the area under

the receiver operating curve (AUC) measurement, where 1 represents a model with perfect performance and 0.5 indicates a model that is no better than a random test (Hosmer & Lemeshow, 2000). In evaluating model predictive performance for species distribution models, it is effective to use the AUC because of its prevalence and threshold independence (Mcpheerson *et al.*, 2004). A similar study that predicted Adélie penguin distributions on the WAP also used a cross-validation procedure, jackknife tests, and the AUC statistic to assess model performance (Friedlaender *et al.*, 2010).

We tested combinations of SIC, SST, CHL, and bathymetry in our CRH model development. However, CHL is extremely irregular in satellite measurements of the Southern Ocean because of recurrent cloud and ice cover. This kept us from using CHL in our final CRH model. In general, SST and SIC are physically anticorrelated, which can make it difficult to interpret how each variable affects the MaxEnt predictions (Phillips *et al.* 2004; Irwin *et al.*, 2011). MaxEnt creates response functions to describe how changes in an environmental variable affect the predicted habitat suitability. The marginal response curves in our CRH models indicated that there is unique information in SST and SIC variables that aid in predicting a species distribution. The CRH models were trained with a December–February average climatology from 1978 to 1984 (Fig. S2). We assumed that between the years of 1978 and 1984, penguins CRHs reflected their preferences. Using a multiyear average for training smoothed the high interannual variability characteristic of Antarctic marine systems (Ducklow *et al.*, 2006). The model trained on 1978–1984 was then projected onto annual averages (December–February) for SIC, SST, and bathymetry from 1985 to 2010. We limited predictions to within 200 km of land to focus on the Antarctic coastal ocean. Adélie penguin CRH models only included landmasses and islands directly around the Antarctic continent whereas Gentoo and Chinstrap CRH models included all land features south of -40° latitude.

Also, we created three separate models for Adélie penguins: continental Adélie only, WAP Adélie only, and all Adélie colonies together to control for the rapid warming event in the WAP. Sensitivity tests were conducted to validate the outcome of the CRH models by adding 5% normally distributed noise to each environmental observation. We computed CRH suitability maps for each species for each year in our study. We then used linear regression across time to identify the location of significant changes in CRHs for each *Pygoscelis* species.

Matching penguin CRH suitability to population trends

We analyzed the results of our CRH models by matching predicted CRH suitability to penguin colony locations that have documented population trends (Table 2). Estimated population trends were based on the cited references in Table 2. Penguin population observations are irregular, often occurring over different years with variable temporal resolution. Therefore, we computed the mean and trend in CRH suitability predicted by our model within 75 km of each penguin colony between the years that a particular penguin population was documented. The mean and twice the standard deviation of

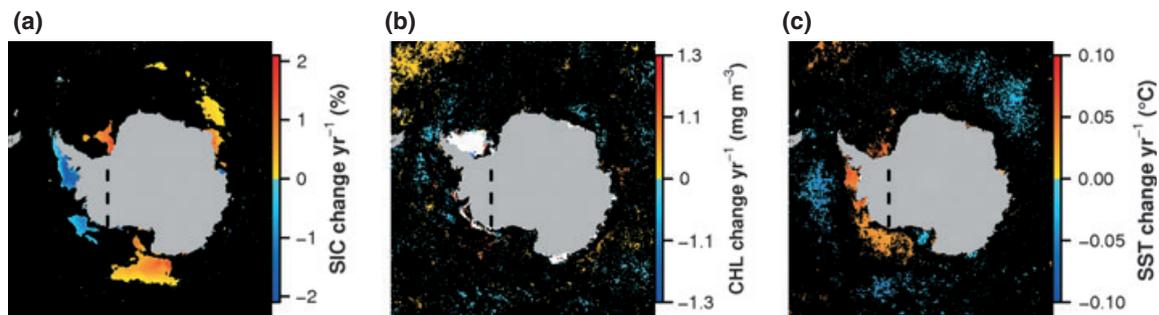


Fig. 2 Significant environmental changes around Antarctica during the austral summer (December–February): (a) sea ice percent from 1978 to 2011, (b) \log_{10} CHL concentration from 1978 to 1986 and 1997 to 2011, (c) and SST from 1981 to 2011. Black areas indicate non-significant trends at the 0.05 level.

CRH suitability were calculated for each colony (Table 2). We used an ANOVA to test for significant differences in CRH suitability between documented increasing and decreasing penguin populations. Using linear regression, we calculated trends in CRH suitability and significance was assessed at the 0.05 level.

Results

Large-scale trends in satellite data

The 30-year satellite record of penguin chick-rearing seasons (December–February) allowed us to estimate the magnitude of environmental change near penguin colonies. Since the onset of the modern satellite era, SIC, SST, and CHL all show significant changes during penguin chick-rearing seasons in different regions of Antarctica. From 1978 to 2010, SIC decreased by about 2% per year along the WAP, whereas areas in the Ross Sea, Weddell Sea, and Indian Ocean have increased by up to 2% per year (Fig. 2a) which agrees with previous, year-round trends in SIC (Massom & Stammerjohn, 2010; Stammerjohn *et al.*, 2008). Mean trends in SIC on our polar stereographic projection and within 200 km from land are shown, respectively, in Fig. S5c and f. Significant changes in \log_{10} CHL concentrations during chick-rearing seasons were evident but were patchy and irregular (Fig. 2b). Significant changes in CHL were within $\pm 1.3 \text{ mg m}^{-3} \text{ yr}^{-1}$. It should be noted that the CHL record from 1978 to 2010 has a 10-year gap from 1987 to 1996. From 1997 to 2011, SeaWiFS and MODIS Aqua show continuous measurements of CHL within our polar projection (Fig. S5b) and within 200 km from land (Fig. S5e). CHL from CZCS was more variable and the images were patchier due to cloud cover and the removal of poor quality data. It is difficult to determine if the CZCS CHL data are more variable due to missing data, poor quality measurements, or changes occurring between the large time gap from

CZCS and SeaWiFS measurements. This should be considered when interpreting Fig. 2b. From 1997 to 2011, significant changes in \log_{10} CHL were also calculated without CZCS data (Fig. S6). Montes-Hugo *et al.* (2009) documented a decrease in CHL concentrations in the northern WAP and a substantial increase to the south, which agrees with trends in Fig. 2b. For chick-rearing seasons 1981–2010, SST in the Weddell Sea, and areas extending from the WAP into the northern Ross Sea have increased up to $0.1 \text{ }^{\circ}\text{C yr}^{-1}$ (Fig. 2c). Northern latitudes around the continent had patchy decreases in SST up to $0.1^{\circ}\text{C yr}^{-1}$. Similarly, Meredith & King (2005) described up to a $0.05 \text{ }^{\circ}\text{C}$ increase per year in SST in the austral summer along the WAP from 1955 to 1998. In the east Ross Sea, increasing SIC coincided with a small patch of decreasing SST, whereas SST increased in the west Ross Sea. From 1981 to 2011, we found comparable mean SST within our polar projection (Fig. S5a) and within 200 km from land (Fig. S5d), which indicated that there isn't a discontinuity in the data when sensors switch from AVHRR to MODIS Aqua. The most noticeable environmental shifts occurred on the WAP and into the Amundsen Sea where there was a significant decrease in SIC and increase in SST. In contrast, conditions were most stable along East Antarctica. This indicates that the changes occurring on the WAP are uncharacteristic of the Antarctic continent as a whole (Massom & Stammerjohn, 2010).

Characterizing penguin CRH

Mean SIC and SST conditions were significantly different among these penguin colonies (Fig. 3a and b). Adélie penguin colonies were found in higher SICs and lower SSTs compared with that of Gentoos and Chinstraps. Also, continental and WAP Adélie penguin chick-rearing sites showed significant differences in SIC and SST. Continental Adélie penguins inhabited regions with the highest SICs, which were on average

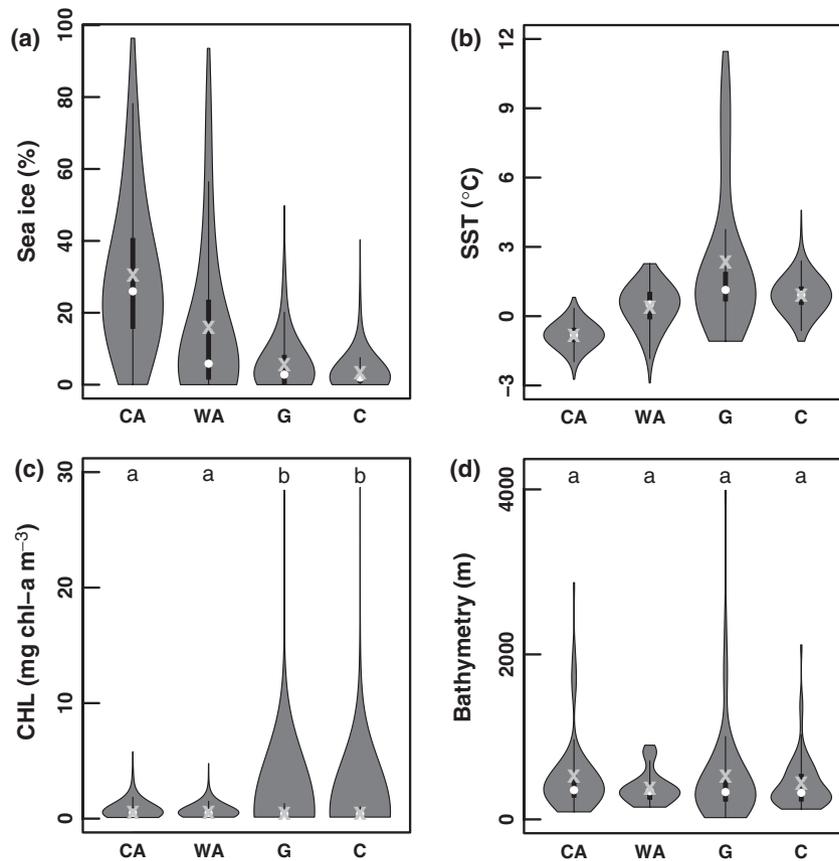


Fig. 3 Probability density of (a) sea ice percent from 1978 to 2011, (b) SST from 1981 to 2011, (c) CHL concentration from 1978 to 1986 and 1997 to 2011, and (d) bathymetry, for continental Adélie penguins (CA), WAP Adélie penguins (WA), Gentoo penguins (G), and Chinstrap penguins (C). Significant differences ($P < 0.05$) were computed using a nonparametric Kruskal–Wallis test and a multiple comparison test after Kruskal–Wallis. Letters denote nonsignificant differences in the mean. The thick black box indicates the interquartile range, the thinner black lines are the upper and lower adjacent values, the white points are the median, and gray 'x's are the mean.

15% greater than that of WAP Adélie penguins. In addition, mean SST at continental colonies was about 1.5 °C lower than that of WAP colonies. Gentoo penguins reared chicks in the warmest waters, but preferred intermediate SICs. Mean CHL was significantly higher for Adélie penguins, but more variable at Gentoo and Chinstrap penguin colonies (Fig. 3c). Similar mean CHL was seen without CZCS CHL data (Fig. S7). Mean bathymetry was not significantly different among species (Fig. 3d).

We visualized the intersection of SIC, SST, and bathymetry for each penguin species CRHs (Fig. 4, S3). Each penguin group is clearly distinguished by an ellipsoid that incorporates 50% of penguin colonies and the ellipsoids are centered on the mean. Using SIC, SST, and bathymetry as predictors, Gentoo penguins occupied a predictor space that was broad in its SST range and small in SIC range. Adélie penguins spanned the widest SIC range with continental Adélie penguins occupying a range with higher SIC and lower SST com-

pared with that of WAP Adélie penguins. Compared to Adélies and Gentoos, Chinstraps had a very narrow and well-defined predictor space.

MaxEnt Model Performance

The AUC calculations showed the CRH models performed well, with the mean AUC for each species models above 90% (Table 1). AUC values have a tendency to be higher for species with a narrow range in relation to the amount of environmental data input (Mcperson *et al.*, 2004); thus, Chinstraps had an AUC of 99%. CHL was omitted from these models because its inclusion decreased the model performance. The jackknife tests confirmed the importance of these environmental variables for penguins CRHs. Notably, each variable had a different mean weight for each penguin species. Bathymetry had the most uniform contribution to the models ranging from about 25% to 28%. SIC was the highest contributor to

Table 1 Mean AUC for CRH models for each species and mean percent contribution for each environmental variable in the model

	Adélie	Gentoo	Chinstrap
Mean AUC	0.91 ± 0.001	0.92 ± 0.001	0.99 ± 0.0002
SST percent contribution	2.0 ± 0.25	18.2 ± 1.17	51.3 ± 1.25
Sea ice percent contribution	69.8 ± 0.43	54.6 ± 1.41	23.9 ± 0.98
Bathymetry percent contribution	28.2 ± 0.36	27.2 ± 0.91	24.7 ± 0.74

the Adélie CRH models at about 70% whereas SST had a mere 2% contribution. For Gentoos, SIC contributed 55% and SST contributed 18%. Lastly, SST contributed 51% to the Chinstrap CRH model whereas SIC contributed 24%.

We trained each CRH model on historic conditions in the beginning of the satellite record and then, projected each penguin species preferences based on this training data onto subsequent years to demonstrate how habitat suitability shifted with environmental changes. In doing this, we assumed that these historic conditions reflect the penguins' preferences and warming trends had not yet affected their habitat suitability. However, training an Adélie model on only WAP colonies produced an inaccurate representation of Adélie penguins' historic CRH range and preferences (Fig. S4b). Comparing the training data for WAP and continental Adélie models showed SST was warmer and SIC were generally lower on the WAP (Fig. S2). This may indicate that warming events began to influence conditions at WAP Adélie colonies. In addition, SIC only contributed ~7% to the creation of the WAP Adélie CRH model (Table S1). A model trained on all Adélie colonies produced similar results to training on only continental Adélie colonies, but the all Adélie model had a lower AUC (Table S1). To eliminate the influence of a warming environment on Adélie penguin preferences, our final model was trained on only continental colony locations.

Mean CRH suitability

From 1982 to 2010, Adélie, Gentoo, and Chinstrap penguins had geographically different mean CRH suitability (Fig. 5a–c). The penguins' CRH suitabilities were consistent with their colony location as well as the associated environmental parameters (Figs 1 and 4). Mean suitable CRHs largely coincided with existing colony locations. For Adélie penguins, suitable CRHs were in the southern WAP, Ross Sea, and intermittent regions in East Antarctica (Fig. 5a). Their most suitable CRHs

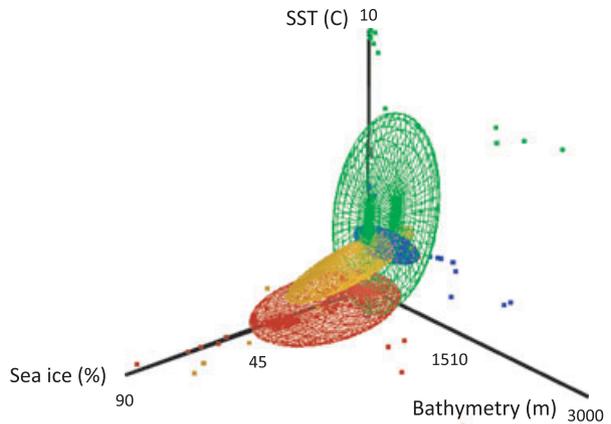


Fig. 4 Niche spaces defined by SIC, SST, and bathymetry for continental Adélie penguins (red), WAP Adélie penguins (orange), Gentoo penguins (green), and Chinstrap penguins (blue). Each point represents mean conditions at a nest site throughout the satellite record. See Fig. S3 for a rotating plot of niche spaces.

were located in Ross Sea where populations are growing (Wilson *et al.*, 2001). In contrast, Gentoo and Chinstrap penguins had high CRH suitability predominantly in the northern WAP (Fig. 5b and c). Gentoo penguins' suitable ranges also extended to outlying islands, into the southern tip of South America and a few regions in East Antarctica.

Large-scale trends in CRH suitability

Significant changes in CRH suitability from 1982 to 2010 were mostly located along the WAP (Fig. 5) coinciding with regions of environmental change (Fig. 2). The probability of finding suitable penguin CRHs along the WAP had similar large-scale trends for all species, with a general decrease in suitability in the northern WAP and increases to the south. This pattern on the WAP is consistent with the migration of the northern, maritime climate southward (Ducklow *et al.*, 2007). North of Marguerite Bay, the probability of finding suitable Adélie CRH decreased more than 50% (Fig. 5d). Intermittent regions extending from Marguerite Bay southward to the Amundsen Sea increased more than 50% in suitability for Adélie penguins whereas intermittent increases and decreases were seen throughout the rest of the continent. In East Antarctica, CRH suitability increased about 25% for Gentoo and Chinstrap penguins and there was a noticeable decline in the Ross Sea for both species (Fig. 5e and f). Along the WAP, changes in Gentoo and Chinstrap penguin CRH suitability displayed a similar pattern with decreased suitability in the northern WAP and outlying islands (Fig. 5e and f). The southern WAP became more

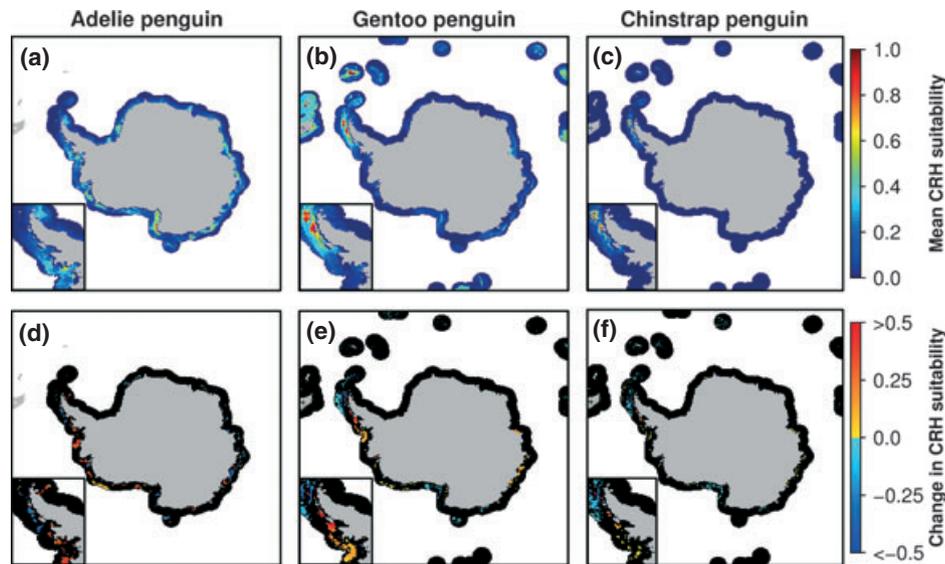


Fig. 5 Top panel: Mean CRH suitability from each CRH model output from 1982 to 2010 for (a) Adélie, (b) Gentoo, and (c) Chinstrap penguins. Red areas indicate suitable conditions whereas dark blue areas are unsuitable conditions. Bottom panel: Significant changes in CRH suitability from 1982 to 2010 for (a) Adélie, (b) Gentoo, and (c) Chinstrap penguins. Warm colors indicate an increase in suitability whereas cool colors display regions with decreases in suitability. Black areas indicate nonsignificant trends at the 0.05 level. The WAP, a region of rapid change, is highlighted in the bottom left corner of each figure. Larger versions of each subpanel can be found in the appendix (Fig. S8–13).

suitable for Gentoo chick-rearing compared with that of Chinstrap chick-rearing. The transition from suitable to unsuitable CRH along the WAP varied between species. For Adélie penguins, the transition between decreasing and increasing CRH suitability was near Marguerite Bay, but the transition region for Gentoo and Chinstrap penguins was ~400 km to the north near Anvers Island. In addition, more regions along the southern WAP and into the Ross Sea increased in suitability for Adélie penguins reflecting the emergence favorable SIC and SST conditions. As Gentoo penguin CRHs spanned a wide SST range and low SICs, sea ice reductions and warming ocean waters increased their CRH suitability along the southern WAP (Figs 4 and 5e). Chinstrap penguins had fewer regions with significant changes in CRH suitability, although the patterns in CRH on the WAP were very similar to Gentoo penguins (Figs 4 and 5f).

Comparison of population trends and CRH suitability

We matched modeled CRH suitabilities to penguin colonies with documented penguin population trends (Table 2). In general, we found that modeled CRH suitability was higher at penguin colonies with increasing population trends. Adélie penguins with increasing colonies had significantly higher CRH suitability compared to colonies with decreasing populations (Fig. 6a).

Increasing Adélie penguin populations had a mean habitat suitability that was 0.25 higher than the mean of decreasing populations (Fig. 6a). The mean CRH suitability at increasing Adélie colonies was about 0.3 ± 0.2 (Fig. 6a; Table 2). In comparison, the significantly different lower CRH suitability ($\sim 0.05 \pm 0.1$) at decreasing Adélie colonies indicated that the conditions were not suitable for Adélie penguin chick-rearing. Gentoo penguins had more similar CRH suitabilities between increasing and decreasing colonies (Fig. 6b). Mean CRH suitability at increasing Gentoo colonies was only ~ 0.2 higher than at decreasing colonies (Table 2). This also indicates that the increasing Gentoo populations were in regions of higher CRH suitability compared to decreasing Gentoo populations and shows that the conditions at increasing colonies along the WAP may be suitable for Gentoo population growth (Table 2). In our literature search, we found one colony of Chinstrap penguins with an increasing population. CRH suitability was about 0.07 units higher at the increasing colony than the mean CRH suitability at decreasing colonies (Fig. 6c). Decreasing Chinstrap populations were in regions of low CRH suitability.

We also computed CRH suitability trends at penguin colonies with documented populations between the time periods of population observations. Most colonies had CRH suitability trends not significantly different than zero during the time interval that populations were

Table 2 Population trends for Adélie, Gentoo, and Chinstrap penguins in comparison to the mean and trends in CRH suitability around those colony locations. Increasing population trends are denoted by (+) and decreasing trends are denoted by a (–). The strength of the CRH suitability trend is given with the *P*-value in parentheses. The mean and trend in CRH suitability was calculated between years that population counts were recorded and twice the standard deviation was calculated around the mean. The number in parenthesis under specific location refers to numbered colony locations in Fig. 1

Species	General location	Specific location	Population trend	CRH suitability trend	Years	CRH suitability	Reference
Adélie	South	Penguin Island (1)	–	0.00011 (<i>P</i> = 0.88)	1982–2003	0.02 ± 0.04	Sander <i>et al.</i> (2007a)
Adélie	Shetland Islands	King George Island, Stranger Point, Isla 25 de Mayo (1)	–	6.8e-05 (<i>P</i> = 0.91)	1995–2006	0.02 ± 0.01	Carlini <i>et al.</i> (2009)
Adélie		King George Island, Admiralty Bay(1)	–	–0.00017 (<i>P</i> = 0.67)	1982–2008	0.02 ± 0.03	Hinke <i>et al.</i> (2007), Chwedorzewska & Korczak (2010)
Adélie	South Orkney Islands	Signy Island (2)	–	0.0015 (<i>P</i> = 0.54)	1982–2007	0.06 ± 0.17	Forcada <i>et al.</i> (2006), Forcada & Trathan (2009)
Adélie	WAP	Anvers Island, Palmer Station region (3)	–	–0.0031 (<i>P</i> = 0.041)	1982–2010	0.06 ± 0.13	W.R. Fraser (unpublished data)
Adélie		Petermann Island (3)	–	–0.0051 (<i>P</i> = 0.11)	1982–2007	0.1 ± 0.22	Lynch <i>et al.</i> (2010)
Adélie	East Antarctic	Béchervaise I, Mawson (7)	+	–0.0049 (<i>P</i> = 0.43)	1982–1999	0.31 ± 0.23	Woehler <i>et al.</i> (2001)
Adélie		Whitney Pt, Casey (8)	+	–0.0055 (<i>P</i> = 0.14)	1982–2005	0.32 ± 0.23	Woehler <i>et al.</i> (2001), Bricher <i>et al.</i> (2008)
Adélie		Lutzow-Holm Bay (6)	+	0.0025 (<i>P</i> = 0.4)	1982–2002	0.03 ± 0.14	Woehler <i>et al.</i> (2001), Kato <i>et al.</i> (2002)
Adélie		Pointe Geologie Archipelago (9)	+	–0.0036 (<i>P</i> = 0.46)	1982–2003	0.26 ± 0.25	Jenouvrier <i>et al.</i> (2006)
Adélie	Ross Sea	Cape Bird (5)	+	–0.0021 (<i>P</i> = 0.79)	1982–1997	0.39 ± 0.24	Woehler <i>et al.</i> (2001), Wilson <i>et al.</i> (2001)
Adélie		Cape Royds (5)	+	0.0084 (<i>P</i> = 0.27)	1982–1999	0.41 ± 0.28	Woehler <i>et al.</i> (2001), Jenouvrier <i>et al.</i> (2006)
Gentoo	South Shetland Islands	King George Island, Stranger Point, Isla 25 de Mayo (1)	+	–0.0015 (<i>P</i> = 0.82)	1995–2006	0.42 ± 0.15	Carlini <i>et al.</i> (2009)
Gentoo		King George Island, Admiralty Bay (1)	–	–0.0047 (<i>P</i> = 0.04)	1982–2008	0.41 ± 0.17	Chwedorzewska & Korczak (2010)
Gentoo		Cape Shirreff, Livingston Island (1)	Stable	–0.017 (<i>P</i> = 0.14)	1996–2004	0.43 ± 0.18	Hinke <i>et al.</i> (2007)
Gentoo	South Orkney Islands	Signy Island (2)	+	–0.0029 (<i>P</i> = 0.42)	1982–2007	0.18 ± 0.24	Forcada <i>et al.</i> (2006); Forcada & Trathan (2009)
Gentoo	South Georgia Island	Bird I (4)	–	0.00056 (<i>P</i> = 0.8)	1982–1999	0.54 ± 0.08	Woehler <i>et al.</i> (2001)
Gentoo	WAP	Anvers Island, Palmer Station region (3)	+	0.0048 (<i>P</i> = 0.46)	1993–2010	0.57 ± 0.27	W.R. Fraser (unpublished data)
Gentoo		Petermann Island (3)	+	0.0063 (<i>P</i> = 0.28)	1982–2007	0.48 ± 0.39	Lynch <i>et al.</i> (2010)
Gentoo		Alice Creek and Damoy Pt,	+	0.0049 (<i>P</i> = 0.64)	1982–1998	0.5 ± 0.35	Woehler <i>et al.</i> (2001)

Table 2 (continued)

Species	General location	Specific location	Population trend	CRH suitability trend	Years	CRH suitability	Reference
Gentoo	South Indian Ocean	Port Lockroy, Wienecke I (3) Marion I (10)	–	0.0021 ($P = 0.052$)	1994–2002	0.16 ± 0.02	Crawford <i>et al.</i> (2003)
Gentoo	Illes Kerguelen	Courbet Peninsula (11)	–	$-4.6e-05$ ($P = 0.83$)	1987–2004	0.03 ± 0.01	Lescroël and Bost (2006)
Chinstrap	South Shetland Islands	King George Island, Admiralty Bay's islets (Shag Island, Chabrier rock) (1)	–	-0.0048 ($P = 0.051$)	1982–2004	0.15 ± 0.14	Sander <i>et al.</i> (2007b)
Chinstrap		Penguin Island (1)	–	-0.004 ($P = 0.08$)	1982–2003	0.13 ± 0.12	Sander <i>et al.</i> (2007a)
Chinstrap		King George Island, Admiralty Bay (1)	–	-0.0029 ($P = 0.1$)	1982–2008	0.15 ± 0.13	Hinke <i>et al.</i> (2007), Chwedorzewska & Korczak (2010)
Chinstrap		Cape Shirreff, Livingston Island (1)	–	-0.013 ($P = 0.2$)	1996–2004	0.16 ± 0.15	Hinke <i>et al.</i> (2007)
Chinstrap	South Orkney Islands	Signy Island (2)	–	-0.0025 ($P = 0.14$)	1982–2007	0.04 ± 0.11	Forcada <i>et al.</i> (2006), Forcada & Trathan (2009)
Chinstrap	WAP	Anvers Island, Palmer Station region (3)	+	-0.00091 ($P = 0.7$)	1982–2010	0.2 ± 0.19	W.R. Fraser (unpublished data)

estimated (Table 2). The Adélie penguin colony near Palmer Station, Anvers Island, along the WAP, was the only Adélie colony that had a significant trend in CRH suitability. From 1982 to 2010, CRH suitability significantly decreased, which agreed with the negative trend in Adélie populations and the low mean CRH suitability of 0.06 ± 0.13 . From 1982 to 2008, a Gentoo penguin colony in Admiralty Bay, King George Island, in the South Shetland Islands, had a negative trend in CRH suitability and population trends whereas the mean CRH suitability was 0.41 ± 0.17 . The Adélie and Gentoo colonies with significant trends in CRH suitability had the longest record of population counts for their species. All Chinstrap penguin colonies had nonsignificant trends in CRH suitability.

Discussion

In this study, we demonstrate how satellite-derived environmental predictors can be used to define the austral summer niche spaces for *Pygoscelis* penguin chick-rearing in the Southern Ocean. The accuracy of these niche spaces is supported by documented penguin population trends. Our approach does not account for all processes or biotic interactions that are involved

in successful chick-rearing events. We could not control factors such as predation, competition for food, or local weather (winds, precipitation, optics), which have been shown to affect the survival of *Pygoscelis* chicks (Ainley *et al.*, 1994). Furthermore, *Pygoscelis* colony persistence is also related to the environmental parameters that occur outside the summer breeding season (Emmerson & Southwell, 2011). During winter months, Gentoos are nonmigratory (Trivelpiece *et al.*, 1987), but Adélie penguins can travel hundreds of kilometers to the ice edge to forage (Ainley, 2002) whereas Chinstraps migrate north of the pack ice into open water habitats (Fraser *et al.*, 1992; Wilson *et al.*, 1998). Although there are a multiplicity of behaviors and environmental forces that act on penguin colonies, we focused on environmental predictors that were available on a synoptic scale during the austral summer. Our approach follows a principle of pragmatic parsimony, where we sought to use synoptic and relatively few environmental predictors that were conceptually related to *Pygoscelis* ecology (Pearson & Dawson, 2003). Despite *Pygoscelis* penguins occupying a similar trophic level that feeds on primary consumers such as Antarctic krill (*Euphausia superba*), their environmental niche spaces were significantly different and well-defined (Figs 3 and 4). The partitioning

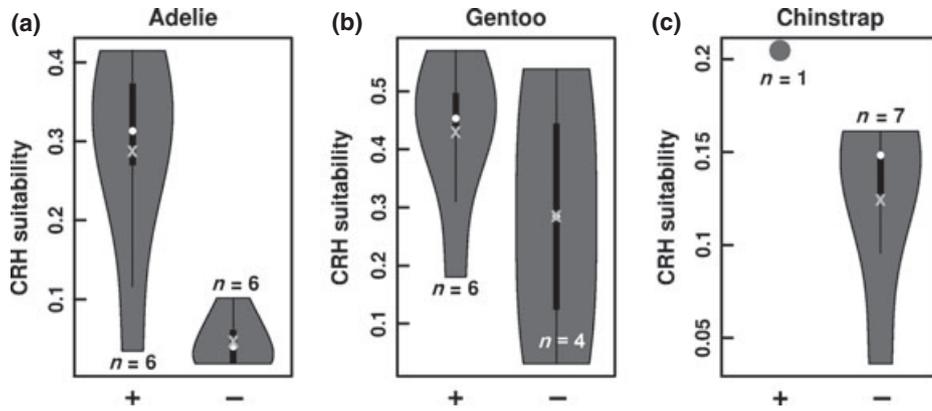


Fig. 6 Mean CRH suitability at penguin colonies with increasing or stable populations (+) and at colonies with decreasing populations (-) for (a) Adélie, (b) Gentoo, and (c) Chinstrap penguins. *N* is the number of penguin breeding colonies matched to the corresponding CRH suitability. Adélie penguin CRH suitability is significantly different at increasing and decreasing colonies.

of their niche spaces is consistent with the general latitudinal segregation of *Pygoscelis* colonies.

Sea ice concentration and SST during the austral summer season shows significant changes over the last three decades. The largest changes in SIC and SST are in the WAP, but there are also significant changes in the Ross Sea region. The WAP is warming whereas areas in the Ross Sea region appear to be mostly cooling during the chick-rearing season (Fig. 2). In general, we found valid and continuous measurements between long-term records of different CHL and SST satellite sensors in the Southern Ocean (Fig S6, 7). Using species distribution models to quantitatively link the *Pygoscelis* niche spaces with climate observations shows how chick-rearing habitat (CRH) suitability is increasing in the south, and decreasing in the north (Fig. 5).

Long-term population studies provide a unique opportunity to compare population trends of *Pygoscelis* penguins with our CRH models. Although, there are not many studies that conduct annual penguin censuses, there are enough noncontinuous populations counts that allow us to distinguish increasing and decreasing populations at different locations. In general, predicted mean and significant trends in CRH suitability for *Pygoscelis* penguins were in agreement with documented population trends. However, although there are large areas of significant CRH suitability change in coastal Antarctic waters, it was difficult to find significant trends in CRH suitability at locations with documented penguin populations. Only two locations with documented penguin populations showed significant trends in suitable CRHs (Table 2). This is because CRH suitability has high interannual variability that we could not account for. Mean CRH suitability may be equally informative of current and future population trends as CRH suitability trends. For

example, populations with a high mean CRH suitability, but a declining CRH suitability trend could still have a growing population if the population response to CRH suitability is a threshold function. Our model showed that Adélie penguin colonies with increasing population trends had a significantly higher mean CRH suitability than colonies with decreasing population trends indicating that the environmental predictors in our Adélie penguin CRH model are sufficient to capture general trends in Adélie penguin populations (Fig. 6a). Adélie penguin populations largely declined at sub-Antarctic islands and along the WAP whereas populations increased or remained stable in the Ross Sea and East Antarctica (Fig. 1; Table 2). Documented declines in the northern WAP are probably related to increasing SST, decreasing SIC during the chick-rearing season (Smith *et al.*, 1999), and possibly due to overwinter mortality (Carlini *et al.*, 2009; Croxall *et al.*, 2002; Hinke *et al.*, 2007; Lynch *et al.*, 2010). In the Ross Sea and East Antarctica, sea ice conditions are favorable for Adélie penguins, and could sustain large krill populations for penguin colonies (Jenouvrier *et al.*, 2006; Kato *et al.*, 2002).

In general, increasing Gentoo penguin populations have slightly higher CRH suitability compared with that of shrinking Gentoo penguin populations, but there was no significant difference (Fig. 6b). Our model did poorly for Gentoo colonies at sub-Antarctic islands, but did well in the WAP and the South Indian Ocean. On the sub-Antarctic South Shetland Islands there were populations that increased and decreased within one model grid cell, which is difficult to predict using our large-scale technique. Some factors that may contribute to the differences in these populations are human impacts or higher concentrations of predators (Chwedorzewska & Korchak, 2010). We are not able to capture

small-scale processes in the sub-Antarctic islands in our CRH models. This indicates that the incorporation of demographic processes, regional approaches, or finer scale models similar to Friedlaender *et al.* (2010) are needed to understand complex changes in Gentoo penguin populations in these island chains.

Compared to Adélie and Gentoo penguins, it is more difficult to determine the accuracy of our model projections for Chinstrap penguins because we found only one study documenting increasing Chinstrap penguin populations. However, we do show that declining populations had very low CRH suitability (Fig 6c.). Chinstrap population declines are likely influenced by diminished food resources, which were affected by the decreased frequency of cold years (Sander *et al.*, 2007b), but it is the decrease in the number of cold years and reduced SICs that is allowing southern populations to grow and migrate further south. Anvers Island, the region of recent Chinstrap population increases, seems to be the transition region from suitable to unsuitable Chinstrap CRH. Assuming climate changes continue in the same fashion, we expect Chinstrap populations to continue increasing in that region and decreasing at northern latitudes (Fig. 5f).

There is a southward shift in suitable CRHs along the WAP for all *Pygoscelis* species (Fig. 5). These trends in CRH suitability may be foretelling about colony persistence, range expansion, or contraction and indicative of an individual penguin's fitness. The expansion of suitable Gentoo and Chinstrap CRH southward (Fig. 5e and f) may be explained by fewer cold years and the consequent decrease in sea ice (Fraser *et al.*, 1992). This suggests that increased warming events will cause conditions to become less suitable for Adélie penguins compared with that of ice-intolerant species (Lynnes *et al.*, 2002). If the warming trend in the WAP continues, we expect the continued southward translation of all penguin CRH locations. Whether or not these new locations are colonized will also depend on small-scale factors such as shoreline availability and a locally abundant food source (Croxall *et al.*, 2002; Forcada & Trathan, 2009). In East Antarctica, there was evidence for increasing CRH suitability for Chinstrap and Gentoo penguins, which suggest that these areas may eventually be colonized by these species if these environmental trends persist. This may be more realistic for Gentoo penguins whose mean CRH suitability was higher in this region compared with that of Chinstrap penguins (Fig. 5b and c). In conclusion, satellite driven CRH models are supported by penguin population counts. This suggests that *Pygoscelis* penguins are important bio-indicators of environmental change in Antarctica (Forcada & Trathan, 2009; Smith *et al.*, 1999). Importantly, SIC and SST are routinely

predicted by climate models, which means that our CRH model can be used to predict the distribution of *Pygoscelis* CRHs under a variety of future climate scenarios.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Mean AUC for CRH models trained on all Adélie penguin colony locations and WAP Adélie penguin colony locations and mean percent contribution for each environmental variable in the model.

Figure S1. Mean (a) SIC, (b) SST, and (c) CHL around Antarctica during the austral summer (December–February).

Figure S2. (a) Sea ice percent and (b) SST training data for CRH models for continental Adélie, WAP Adélie, Gentoo, and Chinstrap penguins.

Figure S3. A rotating plot of niche spaces defined by SIC, SST, and bathymetry for continental Adélie penguins, WAP Adélie penguins, Gentoo penguins, and Chinstrap penguins similar to Fig. 4.

Figure S4. Mean CRH suitability from a MaxEnt model trained (a) on all Adélie penguin colony locations and (b) on WAP Adélie penguin colony locations. Change in the CRH suitability from a MaxEnt model trained (c) on all Adélie penguin colony locations and (d) on WAP Adélie penguin colony locations.

Figure S5. Mean SST (a, d), CHL (b, e), SIC (c, f), within our polar stereographic grid (top row) and within 200 km from land (bottom row) during the chick-rearing period. Measurements were taken from different satellites.

Figure S6. Significant changes in \log_{10} CHL from 1997 to 2011 around Antarctica during the austral summer (December–February). Black areas indicate nonsignificant trends at the 0.05 level.

Figure S7. Probability density of CHL concentrations from 1997 to 2011 for continental Adélie penguins (CA), WAP Adélie penguins (WA), Gentoo penguins (G), and Chinstrap penguins (C). Significant differences ($P < 0.05$) were computed using a nonparametric Kruskal–Wallis test and a multiple comparison test after Kruskal–Wallis. Letters denote nonsignificant differences in the mean. The thick black box indicates the interquartile range, the thinner black lines are the upper and lower adjacent values, the white points are the median, and gray x's are the mean.

Figure S8. Mean CRH suitability for Adélie penguins from each CRH model output from 1982 to 2010. Red areas indicate suitable conditions whereas dark blue areas are unsuitable conditions. The WAP, a region of rapid change, is highlighted in the bottom left corner.

Figure S9. Mean CRH suitability for Gentoo penguins from each CRH model output from 1982 to 2010. Red areas indicate suitable conditions whereas dark blue areas are unsuitable conditions. The WAP, a region of rapid change, is highlighted in the bottom left corner.

Figure S10. Mean CRH suitability for Chinstrap penguins from each CRH model output from 1982 to 2010. Red areas indicate suitable conditions whereas dark blue areas are unsuitable conditions. The WAP, a region of rapid change, is highlighted in the bottom left corner.

Figure S11. Significant changes in CRH suitability from 1982 to 2010 for Adélie penguins. Warm colors indicate an increase in suitability whereas cool colors display regions with decreases in suitability. Black areas indicate nonsignificant trends at the 0.05 level. The WAP, a region of rapid change, is highlighted in the bottom left corner.

Figure S12. Significant changes in CRH suitability from 1982 to 2010 for Gentoo penguins. Warm colors indicate an increase in suitability whereas cool colors display regions with decreases in suitability. Black areas indicate nonsignificant trends at the 0.05 level. The WAP, a region of rapid change, is highlighted in the bottom left corner.

Figure S13. Significant changes in CRH suitability from 1982 to 2010 for Chinstrap penguins. Warm colors indicate an increase in suitability whereas cool colors display regions with decreases in suitability. Black areas indicate nonsignificant trends at the 0.05 level. The WAP, a region of rapid change, is highlighted in the bottom left corner of each figure.

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