LOCAL- AND LARGE-SCALE EFFECTS OF CLIMATE CHANGE
ON PYGOSCELIS PENGUIN HABITAT AND DEMOGRAPHY

by

Megan A. Cimino

A dissertation submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Oceanography

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ABSTRACT

Climate change around Antarctica is coincident with shifts in the distribution and abundance of *Pygoscelid* penguins, understanding this link between penguins and climate is the motivation behind this dissertation. I conducted two studies at Palmer Station, located along the rapidly warming West Antarctic Peninsula (WAP). First, I examined foraging behaviors of tagged Adélie and gentoo penguins while an autonomous underwater vehicle simultaneously measured Antarctic krill (penguins’ main prey) distributions. We detected krill aggregations within the horizontal and vertical foraging ranges of both species. Adélie and gentoo penguins had spatially and vertically segregated foraging habitats, a strategy that may limit competition for food. This reveals that these recently sympatric penguin species were unlikely competing for food, which agrees with recent studies showing that krill biomass is not in decline. This is a notable finding because past studies hypothesized that WAP penguin population declines are mainly driven by increased competition and decreased krill biomass, related to large-scale changes in sea ice concentration (SIC) and sea surface temperature (SST). Second, I found that interannual variability in Adélie penguin chick fledging mass was related to large-scale climate and local weather; chicks weighed less in cold, wet and windy years, suggesting there could be increased thermoregulatory costs for wet chicks. The mass of a chick before fledging the colony is thought to be an important indicator because heavier chicks are more likely to recruit into the breeding population. This direct impact of climate on chicks
illustrates that climate change may affect penguins through pathways that are unrelated to sea-ice influenced food webs.

I also conducted two continent-wide studies to understand spatiotemporal changes in Adélie, gentoo and chinstrap penguin breeding habitats throughout each species entire geographic range using SIC and SST from past satellite observations (1981-2010), and for Adélie penguins, I also used global climate model projections (2011-2100). During the contemporary period, predicted habitat suitability largely agreed with population trends and declining Adélie penguin populations experienced more years with warm sea surface temperature compared to populations that are increasing. An ensemble of global climate models suggests one-third of current Adélie penguin colonies may be in decline by 2060 but refugia may exist in parts of the continent beyond 2099, especially in the Ross and Amundsen Seas. I was not able to determine the mechanism relating austral-summer SST and SIC to penguins. SIC and SST may be an indicator of the quality of terrestrial nesting habitats and chick mass, through the high covariation between oceanic and atmospheric conditions, or related to the availability or quality of food resources. This dissertation demonstrates that local and large-scale studies can provide insights into species habitat use, indicators of penguin population trends and ultimately, a greater understanding of the consequences of climate change in the Southern Ocean.
INTRODUCTION

The contribution of climate change to a species distribution and abundance can shape biodiversity and ecosystem function. However, understanding and projecting the ecological response of a species to change is a major challenge in ecology, which is becoming increasingly critical for conservation and management. During the late 1970s or early 1980s, a regime shift occurred in the Southern Hemisphere (Reid et al. 2015; Weimerskirch et al. 2003; Ekaykin et al. 2014) causing an abrupt change from one steady climate state to another (Hare & Mantua 2000). In the Antarctic, the regime shift is associated with asymmetric climate change, with cooling in parts of the continent and warming along the West Antarctic Peninsula (WAP) (Ducklow et al. 2013; Stammerjohn et al. 2008; Vaughan et al. 2003; Meredith & King 2005). This warming affects the entire ecosystem from phytoplankton to top predators and appears to be having positive impacts on some species in specific locations and negative impacts on others (Moline et al. 2004; Montes-Hugo et al. 2009; Quetin & Ross 2009; Reid & Croxall 2001; Weimerskirch et al. 2003), perhaps making climate change ‘winners’ and ‘losers’ (LaRue et al. 2013; Clucas et al. 2014).

The ice-obligate Adélie (Pygoscelis adeliae), ice-intolerant chinstrap (P. antarctica) and gentoo (P. papua) are Pygoscelis penguins that occupy different geographic ranges in the Southern Ocean with their breeding range overlapping in the northern WAP (Ainley 2002; Forcada et al. 2006). In general, Pygoscelis penguins have declining populations in their northernmost range and increasing populations in their southernmost range (Lynch et al. 2012; Woehler et al. 2001). Climate change is
coincident with the southward shift in these penguins’ breeding habitats where Adélie penguins are contracting their range while gentoo and chinstrap penguins are expanding their range. The paleoclimate record shows that climate has long influenced the distribution patterns of penguins where colony abandonment and occupation correspond to cooling periods with extensive sea ice and warming periods with sea ice declines (Clarke et al. 2007). With the recent regime shift, warming has disparate effects on penguins compared to geologic records, which calls into question the major drivers of their population shifts.

Population control can be influenced by biotic factors from the bottom-up (food resources), top-down (predation), and through competition, or from abiotic factors (habitat suitability, thermal tolerances, etc.). The classic hypothesis used to explain shifting penguin populations is through climate change effects on bottom-up forcing where biophysical couplings influence Antarctic krill (Euphausia superba) abundance (Atkinson et al. 2004; Schofield et al. 2010), a major food source for penguins. Increased sea surface temperature (SST) and decreased sea ice concentration (SIC), hypothesized to cause declines in krill abundance and increased competition for food resources, were often used to explain changes in penguin populations (Trivelpiece et al. 2011; Parmesan 2006; Forcada et al. 2006). However, more recent studies suggest other factors may also be important. The Antarctic food web is indeed tightly coupled, where sea ice, wind, and water column stability impact phytoplankton and Antarctic krill recruitment (Saba et al. 2014; Venables et al. 2013), but there is no long-term change in WAP krill biomass from 1993-2013 (Steinberg et al. 2015). In 1993, there were 12,232 breeding pairs of Pygoscelis penguins at Palmer Station, WAP, (12,004 were Adélie) and in 2010, a total of 5,098 breeding pairs (2,338
were Adélie). While prey quality or availability could be contributing factors to penguin population changes (Ruck et al. 2014), the substantial decrease in breeding penguins at Palmer Station and no evidence of krill biomass declines suggests bottom-up effects through the food web cannot be the sole driver. This thesis is motivated by the need to investigate alternative explanations for penguin population shifts on local- and large-scales, including interspecific competition (Chapter 1), drivers of chick fledging mass (Chapter 2), and habitat suitability (Chapter 3 & 4). To completely understand the mechanistic effects of climate change on a species, I believe it is necessary to study a species lifecycle on fine spatiotemporal scales and throughout a species entire geographic range to make synoptic projections of a species’ response to a changing ecosystem.
Study Site and Dissertation Structure

The Adélie, gentoo and chinstrap penguin are ideal species to study in relation to recent climate shifts because they are closely related but have contrasting habitat preferences and life history strategies. All three species co-exist at Palmer Station, a Long-Term Ecological Research (LTER) site in the WAP, which makes Palmer Station a prime location to test how species are responding to a changing environment. For this research, I utilized long-term biological and physical data collected as part of the LTER, and remote-sensing technologies that allowed for short-term, meter-scale measurements (animal-borne tags, autonomous underwater vehicle) and multi-decadal, kilometer-scale observations (satellites). Understanding local-scale processes at Palmer Station (Chapter 1 & 2) was useful for interpreting continental-scale habitat predictions (Chapter 3 & 4).

This dissertation is a compilation of three published manuscripts (Chapter 1-3) and one manuscript that is currently under review for publication (Chapter 4). Therefore, there is some redundancy in the text, and results from one chapter are often cited in other chapters. The chapters are not organized by chronology of publication date, but rather are arranged by the spatial and temporal scale under study. Chapters 1 and 2 investigate local-scale effects of climate change on Pygoscelis penguins breeding at Palmer Station while Chapters 3 and 4 provide a continental view of changes in penguin chick-rearing habitat suitability in the past and into the future. Over the course of my dissertation, there have been some shifts in way this system is typically understood, especially regarding the major mechanism relating
penguin demographics to climate change and a greater appreciation for alternative drivers, as discussed above. This does not change the results presented here but only the interpretation of the results. This is particularly evident in Cimino et al. (2013) (Chapter 3), where we suggest changes in SST and SIC are solely related to krill declines. We have rectified this in Chapter 3 by altering the published text, and in Chapter 4, where similar analyses to Chapter 3 were conducted, by giving an updated explanation of possible mechanisms driving penguin population shifts.
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Chapter 1

CLIMATE-DRIVEN SYMPATRY MAY NOT LEAD TO FORAGING COMPETITION BETWEEN CONGENERIC TOP-PREDATORS

Climate-driven sympatry may lead to competition for food resources between species. Rapid warming in the West Antarctic Peninsula (WAP) is coincident with increasing gentoo penguin and decreasing Adélie penguin populations, suggesting that competition for food may exacerbate the Adélie penguin decline. On fine scales, we tested for foraging competition between these species during the chick-rearing period by comparing their foraging behaviors with the distribution of their prey, Antarctic krill. We detected krill aggregations within the horizontal and vertical foraging ranges of Adélie and gentoo penguins, and found that krill selected for habitats that balance the need to consume food and avoid predation. In overlapping Adélie and gentoo penguin foraging areas, four gentoo penguins switched foraging behavior by foraging at deeper depths, a strategy that may limit competition with Adélie penguins. This suggests that climate-driven sympatry does not necessarily result in competitive exclusion of Adélie penguins by gentoo penguins. Contrary to a recent theory, which suggests that increased competition for krill is one of the major drivers of Adélie penguin population declines, we suggest that declines in Adélie penguins along the WAP are more likely due to direct and indirect climate impacts on their life histories.
1.1 Introduction

Climate directly influences species by affecting their physiology and life history (Walther et al. 2002). Species’ distributions can be indirectly affected by new biotic interactions between species; for example, climate-driven sympatry can lead to niche displacement through competitive interactions (Sinervo 2010; Finstad et al. 2011; Mooney & Cleland 2001). Along the West Antarctic Peninsula (WAP), a climate migration from polar to subpolar conditions decreased the sea ice extent and coverage duration (Meredith & King 2005) and altered the food web (Atkinson et al. 2004). Coincidently, there has been an abrupt decline in the ice-obligate Adélie penguin (Pygoscelis adeliae) breeding population and an abrupt increase in the ice-intolerant gentoo penguin (P. papua) breeding population around Palmer Station, Anvers Island, WAP (Bestelmeyer et al. 2011). The competitive exclusion principle suggests that Adélie penguins could be displaced if they compete with gentoo penguins for the same food resources (Hardin 1960). A recent hypothesis suggested that the decrease in Adélie penguin abundance in the WAP is due to increased competition between krill predators and a long-term decline in Antarctic krill (Euphausia superba), the penguins’ main prey (Trivelpiece et al. 2011). If competitive interactions typically govern species distributions, climate-based projections of penguin populations will not be informative (Araujo & Luoto 2007). Therefore, rapid climate change along the WAP provides a unique opportunity to study the outcome of new climate-driven sympatry and to evaluate the importance of interspecific competition for common resources in a rapidly changing polar marine system.

Species competing for the same resources can coexist if they occupy different niches and find adequate resources within their niche (MacArthur 1958). In long-established colonies, previous studies demonstrate that penguin species avoid
competition by using different foraging habitats horizontally (Wilson 2010), vertically (Blanchet et al. 2013), and temporally (Miller et al. 2010). However, it is not clear if habitat partitioning occurs for newly established sympatric interactions due to recent climate changes. Although conspecifics or heterospecifics may occupy different niches with minimal foraging overlap, competition may still exist if the prey are highly mobile or sparse (Wilson 2010). Antarctic krill are highly mobile because they are capable of directed movements over small (Hamner 1984) and large spatial scales (Kanda et al. 1982), and are rapidly transported by winds (Warren et al. 2009) and oceanographic conditions (Bernard & Steinberg 2013). Therefore, studying penguin foraging behavior and the prey distribution within the foraging range is vital to identify resource competition between penguin species.

Penguins do not experience or feed on the average concentration of prey in their foraging domain, but rather use directed searching and different foraging behaviors to find rare, high concentrations of prey in the environment (Fauchald 2009). Therefore, to understand the marine environment as a penguin experiences it, it is necessary to sample on similar spatiotemporal scales of a foraging penguin. Traditional sampling methods using net tows or profiling equipment do not typically provide nearshore, concurrent, continuous, and high-resolution oceanographic data of multiple factors. However, autonomous underwater vehicles (AUVs), travelling at similar speeds, depth ranges and endurance as a foraging penguin, can sample the dynamic marine environment as experienced by a penguin (Moline et al. 2005; Ainley et al. 2015). These AUV’s navigate in nearshore coastal environments, and can simultaneously measure multiple trophic levels and physical properties of the water column. Near Palmer Station, congeneric Adélie and gentoo penguins are central
place foragers and breed synchronously on nearby colonies during the austral summer. We focused on the chick-feeding phase of the breeding cycle when adults are provisioning chicks and parental foraging ranges of both species overlap. This period is a critical time for chick growth as fledglings with a higher body mass are more likely to survive (Chapman et al. 2010). We deployed an AUV informed by real-time positions of foraging penguins outfitted with satellite transmitters to measure the prey field and ocean properties. Using these innovative methods, we investigate the existence of competitive exclusion between sympatrically breeding Adélie and gentoo penguins.

1.2 Methods

1.2.1 Penguin tracking and swimming behavior

From January 4 to 31, 2011, we studied Adélie and gentoo penguin foraging ecology near Palmer Station, Anvers Island, Antarctica (64° 46′ S, 64° 03′ W). We deployed satellite transmitters on Adélie penguins (5 female, 5 male) from Humble Island (64° 46′ S, 64° 06′ W) and gentoo penguins (5 female, 3 male) from Biscoe Point (64° 49′ S, 63° 46′ W) (Fig. 1.1AC). All protocols were carried out in accordance with the approved guidelines of the Marine Biological Laboratory Institutional Animal Care and Use Committee, Assurance #A3070-01. The penguin location and depth data were filtered to remove inaccurate locations and corrected for drift in depth sensors (Appendix A). We classified penguin dive behaviors into transit, search and foraging dives (Fig. A.4). Foraging dives consisted of wiggles, plateaus or bottom time (Halsey et al. 2007) where penguins pursue or consume prey. The depth of foraging or most frequent depth was calculated using a kernel density estimate (Scott 1992).
We determined the proportion of each foraging behavior (bottom time, wiggles or plateaus) for each individual and then each species (mean ± SD). We tested for differences in the presence and absence of different foraging behaviors in Adélie and gentoo penguins using GLMMs fit by maximum likelihood using glmer in the lme4 package (Bates et al. 2011) in R (R Development Core Team 2014). Mixed models are useful when repeated measurements are made on an individual or related clusters because it takes the correlation of these repeated measures into account. Previous studies show that diurnal tides aggregate krill (Bernard & Steinberg 2013) and correspond to shorter distance penguin foraging trips (Oliver et al. 2013). We accounted for a tidal effect on penguin foraging behavior by classifying each day as diurnal or semidiurnal (Oliver et al. 2013). We treated the individual as a random effect and included maximum dive depth, tide and sex as covariates. We used a binomial error structure because our dependent variable was the presence or absence of each behavior. We also tested for significant differences in foraging dive duration and dive frequency (number of dives/hr) using LMMs treating the individual as a random effect using the nlme package (Pinheiro et al. 2010). The residuals of the LMMs were normal. Results were considered to be statistically significant when p < 0.05 and marginally significant when 0.05 < p < 0.10.

1.2.2 AUV data collection

A propeller-driven REMUS-100 AUV (Moline et al. 2005) was deployed for 11 days between January 12 to 31, 2011, within the foraging regions of penguins near Palmer Station (Fig. 1.1AC). The REMUS was equipped with sensors to measure temperature, density, CHL, PAR and relative acoustic backscatter (Sv) (Appendix A). Zooplankton and fish are known to aggregate in groups of various densities, which
has an unknown effect on predators’ acquisition of prey. To investigate differences between aggregation types, we identified dense aggregations from SV measurements, likely consisting of densely grouped krill, fish and other zooplankton, and diffuse aggregations, likely consisting of less densely aggregated groups of zooplankton (Appendix A). Data from the project can be found here (http://gcmd.nasa.gov/getdif.htm?NSF-ANT10-19838).

The REMUS undulated in a seesaw pattern and we treated each vertical undulation as a vertical profile of the water column. We characterized each profile by determining the CHL$_{\text{max}}$, integrated CHL in the upper 50m, depth of the CHL$_{\text{max}}$, MLD (the depth of the maximum change in density), density at the MLD, surface PAR (mean of the upper 2m), depth of the 1 W/m$^2$ isolume, thermocline depth, and the mean temperature above/below the thermocline. The depth of the CHL$_{\text{max}}$ was not affected by non-photochemical quenching (NPQ) (Müller et al. 2001), and integrated CHL was highly correlated to integrated CHL with regions affected by NPQ removed. We also created profiles of the background SV by removing all aggregations and taking 1m depth averages of SV within 3m of the REMUS. We found that profiles of background SV were highly correlated to CHL profiles, which suggests that zooplankton were either highly coupled with CHL distributions or we were actually detecting larger chain-forming or aggregated diatoms (ex. Fig. A.5).

We tested for significant differences between physical and biological properties associated with dense and diffuse aggregations using a LMM. We treated each sampling day as a random effect in order to account for repeated measurements taken each day and for spatiotemporal variability. We also tested for relationships between the mean depths of aggregations, tide and water column
properties using LMMs, treating day as a random effect. We square-root transformed mean depth to achieve normality.

1.2.3 Presence/absence modeling of aggregations

We predicted the presence/absence of a dense or diffuse aggregation given water column properties. We used the information-theoretic model comparison (ITMC) approach to test multiple hypotheses, compare a suite of candidate models, and to select a small set of best approximating models (Johnson & Omland 2004; Stephens et al. 2005). We tested multiparameter candidate models using different combinations of explanatory variables, based on our hypotheses and existing knowledge on the system. We fit presence-absence GLMMs with glmer, included a random intercept term for sampling day and a binomial error structure. The Akaike Information Criteria (AIC) allowed us to choose the most parsimonious model that accounts for the most variation with the fewest terms, and we considered models with ∆AIC < 2 to have substantial support (Burnham & Anderson 2002). We tested for multicollinearity between predictor variables using variance inflation factors, but values < 4 indicated multicollinearity was not present in our models (O'brien 2007). Prior to modeling, all predictor variables were standardized (Zuur et al. 2009).

To validate our models, we used the package PresenceAbsence (Freeman & Moisen 2008) to preform a 10-fold cross-validation resampling procedure. We repeated this procedure 10 times and calculated predictive accuracies with Cohens’s kappa statistic (Cohen 1960), sensitivity (true positive rate), specificity (true negative rate), PCC, and AUC, which estimates receiver-operating characteristics (Fielding & Bell 1997). The kappa statistic measured the proportion correctly classified after accounting for probability of chance agreement. The AUC is a measure of accuracy
that is prevalence and threshold independent, and evaluates the false and true positive error rate (McPherson et al. 2004). An AUC of 1 represents perfect model performance and values below 0.5 are no better than random. To demonstrate model performance, we report the mean ± SD of 10 iterative runs from cross-validated estimates.

1.2.4 Overlap between penguins and aggregations

We focused on the spatiotemporal overlap of foraging penguins and the detection of dense and diffuse aggregations (see Table A.2 for details on aggregation detections). The spatial region occupied by penguins and aggregations was determined using two-dimensional kernel density estimations with an axis-aligned bivariate normal kernel (Venables & Ripley 2002) (Fig. 1.1BD).

We compared the depth distributions of penguin dives and aggregations within Adélie and gentoo penguin foraging regions (Fig. 1.2). We used a two-sample Kolmogorov–Smirnov K-S) test, which is a nonparametric test that compares two one-dimensional probability distributions and quantifies the distance between two distribution functions (Venables & Ripley 2002). We performed a two-sided K-S test to determine if there was a significant difference (p < 0.05) between distributions, if so we used an alternative K-S test to determine if a distribution was greater or less than the other distribution. We used a simpler K-S test instead of a complex mixed model because the Intra Class Correlations (ICCs) were low (<30%). ICC represents a measure of reliability or dependence among individuals (Conover 1971). A low ICC suggests there is a low correlation among observations within the same cluster and that no random effect is present in the data. Within the Adélie, gentoo, and overlapping foraging regions, we tested for a day effect on diffuse and dense
aggregation depths. We used LMM to test for differences in penguin dive depths within different foraging regions. If necessary, dependent variables were log10 or square root transformed to achieve normality.

1.3 Results

1.3.1 Habitat space of foraging penguins and prey aggregations

We studied the spatial habitat of foraging penguins and prey aggregations during diurnal and semidiurnal tidal regimes because it has been shown that tidal regime influences krill aggregation characteristics (Bernard & Steinberg 2013) and Adélie penguin foraging location (Oliver et al. 2013). Adélie and gentoo penguins had spatially segregated foraging habitats (Fig. 1.1, A.1). Their core foraging areas, within the 50% contour of the kernel densities of foraging locations, were generally located near each of the penguin species’ respective colonies, with no foraging overlap between them (Fig. 1.1BD). However, the area of the overlap in the overall foraging range was 17.18 km² and 72.10 km² during diurnal and semidiurnal tides, respectively. The Remote Environmental Monitoring UnitS (REMUS) AUV acoustically detected dense and diffuse aggregations within both species’ foraging ranges (Fig. 1.1BD), which likely consisted mostly of densely and diffusely grouped krill, the dominant zooplankton species in the region and the driver of penguin foraging behavior. There were no differences between the depth, length or length-to-height ratio of dense or diffuse aggregations, but dense aggregations were significantly taller, larger in area and produced higher acoustic scattering ($S_v$) within the aggregation (Table 1.1). These krill aggregation dimensions were similar to previous
studies around Palmer Station (Bernard & Steinberg 2013) and along the WAP (Lascara et al. 1999).

Figure 1.1: During diurnal and semidiurnal tides, the REMUS AUV detected prey aggregations within the foraging ranges of tagged penguins, near Palmer Station (yellow diamond), Antarctica. (A) The tracks of gentoo penguins breeding on Biscoe Point (green diamond) and Adélie penguins breeding on Humble Island (blue diamond), and areas sampled by the REMUS during 7 day-long missions during diurnal tides. (B) Kernel density estimates of foraging locations for Adélie and gentoo penguins, and dense and diffuse aggregations detected acoustically by the REMUS during diurnal tides. (C) Penguin tracks and areas sampled by the REMUS during 4 day-long mission and (D) the associated kernel density estimates during semidiurnal tides. The 50% contour lines (B, D) represent the core foraging areas of penguins, and the primary area with aggregation detections. For individual maps of kernel density estimates see Fig. A.1. The maps were produced in R (R Development Core Team 2014).
In the upper 100 m of the water column, the depth distributions of diffuse and dense aggregations were generally very similar within different penguin foraging locations and tidal regimes. There were significantly deeper distributions of diffuse

Table 1.1: Differences in size and acoustic return between dense and diffuse aggregations detected by the REMUS AUV.

<table>
<thead>
<tr>
<th></th>
<th>Dense Aggregation</th>
<th>Diffuse Aggregation</th>
<th>Mann-Whitney U-test Z</th>
<th>Mann-Whitney U-test p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>148</td>
<td>227</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Depth (m)</td>
<td>30.25 ± 16.24</td>
<td>30.91 ± 17.44</td>
<td>-0.19</td>
<td>0.85</td>
</tr>
<tr>
<td>Height (m)</td>
<td>5.91 ± 7.34</td>
<td>2.8 ± 2.61</td>
<td>-3.47</td>
<td>0.00049</td>
</tr>
<tr>
<td>Length (m)</td>
<td>40.44 ± 59.02</td>
<td>19.61 ± 21.09</td>
<td>-1.33</td>
<td>0.18</td>
</tr>
<tr>
<td>Area (m²)</td>
<td>198.14 ± 543.05</td>
<td>19.91 ± 20.2</td>
<td>-4.23</td>
<td>2.02 x 10⁻⁵</td>
</tr>
<tr>
<td>Length: Height ratio</td>
<td>6.58 ± 3.17</td>
<td>8.32 ± 8.34</td>
<td>1.65</td>
<td>0.099</td>
</tr>
<tr>
<td>S, of aggregations</td>
<td>-61.90 ± 4.53</td>
<td>-66 ± 2.72</td>
<td>-12.62</td>
<td>&lt; 2.2e-16</td>
</tr>
</tbody>
</table>

and dense aggregations in the Adélie penguin region than the gentoo penguin region (Fig. A.2AC; K-S test, D=0.46, p=0.018; Fig. A.2BD; K-S test, D=0.47, p=0.032).

Additionally, within the Adélie penguin foraging region, dense aggregations were significantly deeper during diurnal tides than semidiurnal tides (Fig. 1.2B, K-S test, D=0.43, p=0.0078). Due to the small sample size of aggregation detections during diurnal tides (only ~20% of patch detections occurred during diurnal tides), it is
difficult to determine if this was a real effect. Overall, the depth of all dense and diffuse aggregations was not affected by tides when ignoring location (LMM, Dense p=0.51; Diffuse p= 0.61). Therefore, we grouped aggregations together between the two tidal regimes (Fig. 1.2). We found no significant differences between the depth distributions of dense and diffuse aggregations within the same foraging region or between diffuse/dense aggregations in different foraging regions. The depth of diffuse and dense aggregations peaked near the mixed layer depth (MLD) and chlorophyll maximum (CHL$_{max}$) at ~ 20 m and there was often a secondary peak near the 1 W/m$^2$ isolume at ~ 40 m.

Penguin foraging dive distributions were also compared between tidal regime and location (Fig. 1.2). Notably, tidal regime had no affect on Adélie or gentoo penguin dive depths but there were some small differences in behavior during different tides. Sex had no affect on penguin dive depths or behavior. Gentoo penguin maximum dive depth was significantly deeper than Adélie penguins by 34.64% (Fig. 1.2 CDGH;
Figure 1.2: The vertical kernel density distribution of penguin dive and aggregation depths, and physical and biological properties of the water column within the Adélie penguin foraging habitat (top panel), gentoo penguin foraging habitat (middle panel) and the overlapping region where both species foraged (bottom panel) during diurnal and semidiurnal tides. The horizontal lines represent the mean depth of the CHL$_{\text{max}}$, the 1 W/m$^2$ isolume and mixed layer depth (MLD) within profiles with diffuse or dense aggregations and within each respective penguin foraging contour (Fig. 1.1BD). (A) The kernel density estimate of the depth of diffuse and (B) dense aggregations within the Adélie foraging habitat that were measured during different tidal regimes were combined because there was no difference in their overall depth distributions between the tidal regimes (See Fig. A.2 for separation between tidal regimes). (C) The kernel density estimate of Adélie penguin foraging and maximum dive depths during diurnal and (D) semidiurnal tides. (E) The kernel density estimate of the depth of diffuse and (F) dense aggregations within the gentoo penguin foraging habitat during both tidal regimes. (G) The kernel density estimate of gentoo foraging and maximum dive depths during diurnal and (H) semidiurnal tides. (I) The kernel density estimate of the depth of diffuse and (J) dense aggregations within the overlapping region where both species forage during both tidal regimes. (K) The kernel density estimate of Adélie (n=3) and gentoo penguin foraging (n=2) and maximum dive depths within the region that both species utilized during diurnal tides, (L) the overlapping region between Biscoe Point and Humble Island during semidiurnal tides (Adélie n=4, gentoo n=2). The 95% confidence interval is shown around each kernel density estimate. Sample size (n) in each panel represents the number of aggregations or penguin dives.

LMM t-statistic= 5.31, p = 1.00x10$^{-4}$. Generally, Adélie penguins did not dive below the average 1 W/m$^2$ isolume (Fig. 1.2CD) while gentoo penguin foraging and maximum dive depths were often below this depth (Fig. 1.2GH). During diurnal and semidiurnal tides, four different gentoo penguin (2 per tidal regime) foraging ranges overlapped with those of Adélie penguins (Fig. 1.1CD). In this area of overlap, gentoo
penguins dove deeper than Adélie penguins during both tidal regimes (Fig. 1.2K; LMM $t$-statistic$_{\text{max_depth}}$ = 7.74, $p=0.0045$; $t$-statistic$_{\text{forage_depth}}$=7.90, $p=0.0042$;)

![Graph showing depth distribution of penguin dives](image)

**Figure 1.3:** Comparison of gentoo penguin foraging dive depth distributions in areas that overlap and don't overlap with Adélie penguins during diurnal and semidiurnal tides. (A) The kernel density estimate of gentoo penguin (n=2) foraging and maximum dive depths in the area of non-overlap and (B) the area that overlaps with Adélie penguins during semidiurnal tides. (C) The kernel density estimate of gentoo penguin (n=2) foraging and maximum dive depths in the area of non-overlap and (D) the area that overlaps with Adélie penguins during diurnal tides. The 95% confidence interval is shown around each kernel density estimate. Sample size (n) represents the number of penguin dives.

Fig. 1.2L $t$-statistic$_{\text{max_depth}}$ = 3.73, $p=0.020$; $t$-statistic$_{\text{forage_depth}}$=3.35, $p=0.029$).

Additionally, in both cases, gentoo penguin foraging and maximum dive depths were
significantly deeper in the area of overlap compared to the area of non-overlap (Fig. 1.3AB, LMM t-statistic_{max_depth} = 5.00, p=0; t-statistic_{forage_depth} = 4.85, p=0; Fig. 1.3CD; t-statistic_{max_depth} = 4.12, p=0; t-statistic_{forage_depth} = 4.31, p=0). During diurnal tides, one Adélie penguin entered the foraging domain of gentoo penguins (Fig. 1.1D). Here, the Adélie penguin foraging and maximum dive depths were not significantly different from gentoo penguins within the same region (Fig. A.3A) but the Adélie penguin dive depths were significantly deeper in the area of overlap compared to the area of non-overlap (Fig. A.3AB, linear regression t-statistic_{max_depth} = 7.21, p=5.95x10^{-12}; t-statistic_{forage_depth} = 6.18, p=1.71x10^{-9}).

Adélie and gentoo penguins had similar and different proportions of foraging dive types. On average, 83.75 ± 8.07% of Adélie penguin foraging dives had bottom time, 16.70 ± 7.00% had vertical undulations or wiggles and 16.35 ± 10.10% had plateaus (ex. Fig. A.4). In comparison, 73.70 ± 8.06% of gentoo dives had bottom time, 27.75 ± 12.07% had wiggles and 16.73 ± 10.18% had plateaus. Using generalized linear mixed models (GLMMs), we found bottom time occurred less in gentoo foraging dives, and was positively related to the maximum dive depth (z_{species} = -3.55, p = -3.08x10^{-4}; z_{max_depth} = -3.85, p = 1.12x10^{-4}). There was no difference in the presence of wiggles between species but wiggles were more likely to be present in deeper dives (z_{max_depth} = 19.01, p = 2.60x10^{-16}). Plateaus occurred more in the foraging dives of gentoo penguins than Adélie penguins, and were positively related to semidiurnal tides and negatively related to dive depth (z_{species} = 2.74, p = 6.24x10^{-3}; z_{max_depth} = -21.54, p = 2.60x10^{-16}; z_{tide} = 3.50, p = 4.67x10^{-4}). The foraging dive durations of gentoo penguins were significantly longer than Adélie penguins by 39.23 s and foraging dive durations were significantly shorter during semidiurnal tides by
6.34 s (gentoo: 113.98 ± 14.70 s, Adélie: 74.75 ± 10.41 s, LMM t-statistic_{species} = 5.97, p = 0; t-statistic_{tide} = -3.44, p = 6.00 \times 10^{-4}), but Adélie penguins had a marginally higher dive frequency than gentoo penguins (Adélie: 17.67 ± 11.14 dives/hr, gentoo: 13.25 ± 7.24 dives/hr, LMM t = -2.05, p=0.060).

\subsection*{1.3.2 Presence/absence modeling of prey aggregations}

We related the presence/absence of dense and diffuse aggregations to physical and biological properties associated with the vertical water column, all measured concurrently with the AUV (Table A.1). Nearly all of the models with substantial support (ΔAIC < 2) showed the presence of dense and diffuse aggregations were associated with a deeper CHL$_{max}$, lower integrated CHL and a shallower 1 W/m$^2$ isolume. About half of these models showed a relationship between aggregation presence with a lower density at the MLD, which can be indicative of the strength of water column stratification and was related to a shallower MLD. Additionally, one or two models showed that aggregation presence was related to higher temperatures above the thermocline, deeper MLD, shallower thermocline, and lower surface photosynthetically available radiation (PAR). In general, the strongest predictor of both dense and diffuse aggregation presence was the 1 W/m$^2$ isolume. These models were informative with an area under the curve (AUC) > 0.70 and with a moderately-high kappa value (~0.56), where a high kappa is > 0.60. The percent correctly classified (PCC) was high (~ 92), but the models had low sensitivity (~ 50) and high specificity (~98). This suggests the models over predicted the number of absences. Notably, we found no significant differences between individual vertical profile characteristics associated with dense and diffuse
aggregations from LMMs. This suggests the two aggregation types may be keying off similar water column properties, which our GLMMs also suggest.

Similarly, the mean depth of dense aggregations was positively related to depth of CHL$_{\text{max}}$ (LMM t-stat=1.98, p=0.048), negatively related to surface PAR (LMM, t-stat= -2.22, p=0.029), and marginally related to the isolume (LMM t-stat= 1.85, p=0.067). The depth of diffuse aggregations was only marginally related to the density at MLD (LMM, t-stat=1.74, p=0.085).

1.4 Discussion

Climate shifts can increase the intensity of sympatry between species and lead to interspecific competition, which has strong implications for understanding population trajectories and ecosystem structure (Hardin 1960). In this study, we used a combination of penguin satellite telemetry, time-depth recorder and AUV data collected at the scale of the top predator to map the dynamic food resources used by both the Adélie and gentoo penguins. Sympatrically breeding Adélie and gentoo penguins had spatially segregated foraging habitats and mainly utilized the upper 100m of the water column in regions of low interspecific competition (Fig. 1.2) but gentoo penguins foraged at deeper depths in areas of foraging overlap (Fig. 1.3). Subantarctic gentoo penguins, rather than Adélie penguins, switched behavior and vertically partitioned their foraging habitat to potentially avoid direct competition, even though shallow prey resources were available in the upper water column and both species are capable of deep dives. These species often employed different foraging strategies, which could be related to different interspecific dive strategies or prey aggregation characteristics. We detected two types of prey aggregations, dense and diffuse, at similar depths in the water column but without further study, it is
unclear how these aggregation types influence penguin behavior. In the upper 100 m, the distribution of prey aggregations within penguin foraging regions were mainly associated with CHL and light and without observation of deeper prey aggregations, this could not explain the vertical segregation between species. Furthermore, both penguin species were provisioning chicks during satellite tracking, implying adults were returning to the nest with enough food, which also suggests that competition was not limiting food resources.

Krill are an important prey item in the Southern Ocean (Nicol 2006) because they form large aggregations and have high nutritional value. Krill are a highly patchy and mobile resource; therefore, it is critical to study their distribution patterns to detect possible competition between top predators. We detected prey aggregations within the horizontal and upper vertical foraging ranges of Adélie and gentoo penguins (Fig. 1.1, 1.2). In contrast to Bernard & Steinberg (2013), we did not detect a large tidal effect on krill aggregation depth, which could be attributed to our observations being <100 m deep. We also did not detect differences in penguin dive depths between diurnal and semi-diurnal tides (Fig. 1.2), suggesting tide does not affect aggregation depths within the penguin foraging range. We detected fewer aggregations during diurnal tides, but with only 11 sampling days our inference is small. Aggregations were mainly found in areas that had a deeper CHL$_{max}$, lower integrated CHL and shallower isolume (1 W/m$^2$). Prey aggregations were likely selecting for habitats that balance the need to consume food and avoid predation, which is consistent with habitat choice theory (Fossheim & Primicerio 2008). Similar uncoupling between krill depth and chlorophyll was seen in the Ross Sea, which further highlights the trade-off between predator avoidance and food acquisition.
(Ainley et al. 2015). Light influences a species’ distribution because the pelagic environment offers few refuges from visual predators. High resource availability (i.e., high CHL) and predation are often correlated, suggesting high resource habitats are riskier (Brown 1998) and may lead to a negative relationship between aggregations and their food (Folt & Burns 1999). Each aggregation may select for different habitats based on individual variations in sex, age class, and conflicts between maximizing food intake and minimizing predation (Fossheim & Primicerio 2008; Widder & Frank 2001). Nevertheless, our models suggest these aggregations had information about the availability of food or nearby ocean conditions (Benoit-Bird et al. 2010) and chose optimal habitats for increased survival.

Penguins are highly effective at finding food resources in a dynamic marine environment and can adjust their behavior to local foraging conditions (Ropert-Coudert et al. 2002). Penguin foraging strategies can also change according to dietary preference, location, morphology, physiology, or oceanographic conditions, which may aid in explaining the different foraging dive types in Adélie and gentoo penguins. In our study, the main foraging dive type for Adélie and gentoo penguins was bottom time, but more Adélie penguin foraging dives had bottom time while more gentoo penguin foraging dives had plateaus. Plateaus may allow a penguin to silhouette its prey against a bright background when observed from below (Ropert-Coudert et al. 2000) and attack prey with minimal warning. Bottom time in Adélie penguins is thought to be a successful strategy to obtain krill (Bost et al. 2007). Gentoo penguins dove deeper and for longer durations, a likely result of their greater oxygen stores and body size (Boyd & Croxall 1996). Interestingly, near Palmer Station, Adélie penguins generally foraged in the upper 50 m (Fig. 1.2CD) but are capable of much
deeper dives to depths >150 m (Watanuki et al. 1997) while gentoo penguins generally foraged in the upper 100 m but foraged as deep as 150 m (Fig. 1.2GH). These species may have ideal foraging depths based on where they achieve neutral buoyancy, likely deeper for the larger-bodied gentoo penguin (Sato et al. 2009), or preferences for how they attack krill aggregations (skimming off the top, mean aggregation depth, depth of maximum krill density, or behavioral strategies based on aggregation characteristics, etc.). The Adélie penguins’ small foraging range and shallow foraging depths suggest food resources were adequate in the nearshore waters around Palmer Station and they didn’t need to exploit deeper prey resources, or perhaps deeper prey were not equally available as in the gentoo penguin foraging region. For example, when one Adélie penguin entered the gentoo penguin foraging domain, it dove deeper in this area than when it did not overlap with gentoo penguins (Fig. A.3). This could indicate that shallower prey aggregations were less available or deeper prey aggregations are typically more available in the gentoo penguin foraging region, which could potentially explain the generally deeper foraging dives of gentoo penguins. Additional penguin foraging locations and prey observations below 100 m are necessary to decipher if differences in prey availability exist between the two species’ foraging domains. The one Adélie penguin foraging in the gentoo penguin domain was also likely competing for the same prey as gentoo penguins and highlights the possible inflexibility of Adélie penguins to alter their behavior to buffer against direct competition.

Adélie and gentoo penguin foraging habitats were spatially and vertically segregated, which should minimize competition and allow for coexistence (Trivelpiece et al. 1987). Competition was low near each species’ respective colony
and both species utilized the upper water column (Fig. 1.2). It is more efficient to forage near the surface for air-breathing marine predators because it allows the time spent feeding to be maximized (Kooymen et al. 1992). Interestingly, in regions of foraging overlap, gentoo penguins shifted their foraging dives to deeper depths below the foraging range of Adélie penguins (Fig. 1.2KL, 1.3). Here, the gentoo penguins utilized a habitat that was not utilized by Adélie penguins, which may be a successful behavioral strategy to acquire food. During this season, both species consumed krill of similar size classes (Fig. A.6) with <1% of their diet (wet mass weights) consisting of fish. Similar diets between species suggests they exploited the same prey field and diets did not change by foraging depth, which further supports that this change in behavior is not due to prey differences but rather, to buffer against competition. Admittedly, our sample size is small (four individuals), but all of the gentoo penguins in this study that entered the Adélie penguin foraging region displayed this behavioral switch (Fig. 1.3). This vertical segregation agrees with previous studies demonstrating spatiotemporal niche partitioning between gentoo and other Pygoscelid penguins (Wilson 2010; Miller et al. 2010), and suggests this is a common strategy of gentoo penguins even in new sympatric interactions. The plasticity of gentoo penguin foraging behaviors to buffer against competition may be advantageous as climate changes and prey distributions are uncertain (Lescroël & Bost 2005).

Other factors could be important in driving and interpreting penguin foraging behavior in our study. Our sample size was small and it is possible that the foraging ranges and overlap between the two species would be larger if we tracked more individuals (Soanes et al. 2013) over a longer time period encompassing different
breeding stages (Cottin et al. 2012). Although, the overall Adélie penguin spatial foraging distribution from 2002-2011 (Oliver et al. 2013) is very similar to this study. This suggests that we are adequately representing the Adélie penguin foraging domain (Fig. 1.1) and tracking more individuals during the same breeding phase may not be more informative. Additionally, previous studies showed that larger penguin colonies had larger foraging areas, potentially due to the deletion of prey resources over time by more individuals (Ballance et al. 2009; Ainley et al. 2004). Therefore, given the relatively small penguin breeding populations (<10,000 pairs) at Palmer Station, we may expect that the foraging range and overlap between species is also small. In addition, the availability of prey can be influenced by other physical factors. For example, the head of a large submarine canyon near Palmer Station (between the Adélie and gentoo penguin foraging regions) is recognized as an area of higher primary production that supports higher trophic levels (Kahl et al. 2010), but details on the role of the local topography on ocean currents, prey distributions and penguin foraging ecology is lacking.

Limited krill availability and competition from rebounding krill predators were hypothesized to explain the decline in Adélie penguin populations in the WAP and Scotia Sea, (Trivelpiece et al. 2011) but this study ignored increasing, krill-dependent, gentoo penguin populations in the same regions (Lynch et al. 2012). Furthermore, contrary to previous analyses showing large-scale krill declines along the WAP (Atkinson et al. 2004), a new long-term krill study shows that krill populations are not declining in response to a changing WAP climate (Steinberg et al. 2015). Taken with our analysis, if similar foraging segregation is a characteristic of WAP colonies, we hypothesize that the declining Adélie penguin populations in the
WAP are unlikely solely driven by competition or krill limitation. Further research is needed to support this hypothesis but in light of recent studies, we want to point out that other possible drivers should not be ignored. Population trajectories may be affected by different life history strategies, foraging behavior or wintering habitats, which can be influenced by climate and sea ice conditions. Therefore, the “sea ice hypothesis” cannot be discounted due to the direct and indirect effects of sea ice on the availability of wintering habitats and krill (Fraser et al. 1992).

In a warming climate, it is expected that species better suited to a northern subantarctic climate will displace ice-obligates (Walther et al. 2002). Our results suggest that foraging competition may not always cause displacement, especially for penguins that are known to partition their habitat with competitors or have the behavioral flexibility to cope with competition. Sympatrically breeding Adélie and gentoo penguins exhibited different foraging strategies and had segregated foraging habitats, suggesting that food resources are not limiting and competitive exclusion may not be a main driver of opposing population trends. Foraging competition needs to be compared between multiple years and information on deep prey aggregations is necessary to understand differences in dive depth distributions between species. Previous studies near Palmer Station demonstrate how climate and weather influence penguin breeding habitats (Fraser et al. 2013), the marine foraging environment (Cimino et al. 2013), foraging trip duration (Fraser & Hofmann 2003) and chick mass (Cimino et al. 2014). We suggest future studies focus on wintering habitats and life history strategies, which are also likely affected by large-scale climate forcing. In particular, we must look outside the breeding season to fully understand ecological structure and the vulnerability of a species to dynamic marine
environments. A balance of small and large-scale studies can provide insights into habitat use of keystone species, drivers of top predator population trends and ultimately, a synoptic understanding of the consequences of climate shifts in the Southern Ocean.
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Chapter 2

LARGE-SCALE CLIMATE AND LOCAL WEATHER DRIVE INTERANNUAL VARIABILITY IN ADÉLIE PENGUIN CHICK FLEDGING MASS

The fledging mass of penguin chicks can be an indicator of food availability and environmental conditions at a penguin colony. From 1989 to 2011, we analyzed predictor variables of environmental and food resource factors acting on multiple spatial scales near Palmer Station, Antarctica, that may influence the interannual variability in Adélie penguin chick fledging mass (CFM). To understand the influence of parental Adélie penguin diet on CFM, we modeled the energy density and krill demographics of penguin diet samples. We found a weak positive, but significant relationship between the proportion of immature krill in adult penguin diets and CFM, which may indicate that krill recruitment and prey availability to adults influences CFM. However, the impact of large-scale climate and local weather outweighed the impact of parental diet characteristics on CFM. CFM was negatively associated with a positive Antarctic Oscillation (or Southern Annular Mode) and increased westerly winds, and positively associated with increased air temperature. The mechanistic relationship between climate, local weather and CFM could include direct and indirect impacts, such as increased thermo-regulative costs for unattended chicks, decreased chick feeding frequency, and smaller meal mass for chicks driven by the geophysical transport of krill by climate and wind events.
2.1 Introduction

Chicks with a high body mass at fledging have enhanced post-fledging survival and recruitment into the breeding population due to larger energy reserves that provide a buffer against energetic and environmental stresses (Chapman et al. 2010, Naef-Daenzer et al. 2001, Saraux et al. 2011, Morrison et al. 2009). It has been shown that seabirds are affected by many environmental, weather and climatic factors acting on different scales (Ainley et al. 2005, Smith et al. 1999, Wilson et al. 2001).

The West Antarctic Peninsula (WAP) is a region of high climate variability and rapid climate change (Vaughan et al. 2003), where sea ice concentration, extent and duration have decreased (Massom & Stammerjohn 2010, Stammerjohn et al. 2012) and ocean temperatures have increased (Meredith & King 2005). Primary producer and consumer abundance and community structure have been altered (Montes-Hugo et al. 2009, Moline et al. 2004, Atkinson et al. 2004) and Pygoscelis penguin populations have shown different responses to these changes (Forcada & Trathan 2009, Ducklow et al. 2007). For example, Adélie penguins (Pygoscelis adeliae) are a circum-Antarctic, sea-ice-dependent species whose populations have declined precipitously throughout the northern WAP (Ainley 2002). The hypothesized main drivers of the trends in Adélie penguin populations and demographics include large-scale climate shifts, local weather and food availability (Patterson et al. 2003, Forcada & Trathan 2009, Trivelpiece et al. 2011, Emmerson et al. 2011). To gain insight into Antarctic ecosystem function in a region of rapid change, we must elucidate not only the long-term trend, but also the drivers of interannual ecosystem variability. Changes in climate variability are a major expected component of climate projections (Suppiah et al. 2007). Here, we aimed to understand the interannual variability in mean chick fledging mass (CFM) at a penguin colony, which is an annual integrator of
large-scale climate, local weather, and food resources, and represents the investment of the colony as a whole to the next generation.

Large-scale climate forcing is often associated with local atmospheric and oceanic conditions at penguin-breeding colonies. The main modes of climate variability in the Southern Ocean are the El Nino-Southern Oscillation (ENSO), which reflects ocean-atmosphere interactions in the Tropical Pacific, and the Antarctic Oscillation (AAO; also known as the Southern Annular Mode), which reflects atmospheric dynamics and a meridional shift in the position and intensity of the westerly winds (Carleton 2003). Along the WAP, low sea ice conditions have been associated with warmer sea surface temperature from La Nina (Yuan 2004), and warm winds from a positive austral spring AAO (Stammerjohn et al. 2008). The ENSO has been associated with penguins breeding in the Falkland Islands (Baylis et al. 2012), Scotia Sea (Forcada et al. 2006, Trathan et al. 2006), Indian Ocean sector (Le Bohec et al. 2008, Jenouvrier et al. 2005) and Ross Sea (Wilson et al. 2001). The AAO has been related to opposing population trends between growing colonies in the Indian Ocean and Ross Sea and declining colonies along the WAP (Ainley et al. 2005). The Antarctic Dipole (ADP) is associated with the oscillation of air temperature, sea ice extent, and sea level pressure between the Pacific and Atlantic sectors (Yuan & Martinson 2001). The ADP may be a possible driver of the interannual variability in Adélie demographics through the influence of sea ice on phytoplankton and zooplankton (Fraser & Hofmann 2003, Clarke et al. 2002). These climate indices are hypothesized to be associated with penguin population dynamics, breeding success, and other life history traits through direct and indirect pathways, including food.
availability, prey quality, marginal ice zone, ice cover, polynya size, and terrestrial effects (Forcada & Trathan 2009).

Nest sites offer little protection from extreme temperature, wind, and precipitation, therefore local weather conditions at a penguin colony can impact chick growth (Chappell et al. 1990, Fraser et al. 2013). During the guard stage, adult Adélies alternate between providing protection, food and warmth for chicks as they develop their thick, downy plumage (Bucher et al. 1990, Ainley 2002). Once plumage is developed, chicks are left unattended and gather in crèches for protection and warmth while adults simultaneously forage to meet the energetic demands of their chicks (Davis 1982, Lawless et al. 2001). Adélie chicks can cope with severe weather and maintain their body temperature within a wide range of air temperatures and wind speeds (Chappell et al. 1989). However, intense storms, blizzards, or continued exposure to precipitation can increase cold stress, thermoregulatory costs, and ultimately reduce growth and survivorship (Schreiber 2002, Muller-Schwarze 1984, Olmastroni et al. 2004, Patterson et al. 2003, Demongin et al. 2010). Adélie chicks are also affected by heat stress (Murrish 1983), such as prolonged periods of temperatures > 7°C on sunny days with low winds (Chappell et al. 1990). Hyperthermia can create high metabolic costs due to panting and behaviors that increase the flux of heat away from the chick. Chicks can regulate their energetic consumption and metabolic demands by changing their level of activity (Salihoglu et al. 2001), but in general, chicks have few strategies to avoid weather induced environmental stress.

Parental care is critical to chick survivorship because parents are the sole providers of food resources and provide protection from avian predators. Prey
quality, abundance, availability, and provisioning rate influence chick growth and mass (Clarke et al. 2002, Chapman et al. 2011). Adults can mediate environmental stress by providing chicks with a higher quantity and quality of prey (Chapman et al. 2011); however, this strategy is not possible when prey choices are limited. Therefore, mean CFM for a colony represents the integrated investment made by the parents to the next generation given environmental and food resource constraints. Here we test the sensitivity of mean colony CFM to interannual variability of environmental and food resource factors acting on both large- and local-scales. We aim to understand the relative importance of parental diets (food quality) against the direct (temperature stress) and indirect (prey availability) effects of environmental conditions on CFM.

2.2 Methods

2.2.1 Adélie Penguin Chicks

Prior to fledging, Adélie penguin chicks gather along two beaches on Humble Island (64° 46’ S, 64° 03’W), which is located a few kilometers from Palmer Station, Anvers Island, Antarctica (Fig. 2.1). Approximately 54 days after hatching, the mass of a chick was recorded prior to entering the water, which is the fledging mass. We considered a fledgling to be a chick that was independent of their colony, standing on a fledging beach and in full juvenal plumage (fully feathered, free of any downy plumage). Before weighing, all potential fledglings on the beach were censused and we weighed 30% of the total number of fledglings. Chicks were herded together, captured with hand nets and weighed in a bag (to the nearest 50 g). Weather permitting, chicks were weighed every 2 days during the fledgling period, which
Figure 2.1: The Antarctic Peninsula (inset) and the location of an Adélie penguin-breeding colony on Humble Island near the US Research Base, Palmer Station, Anvers Island. Regional sea ice observations were measured within the Palmer LTER grid (gray box, inset).

began when the first group of chicks arrived and ended when the last chick fledged. Each chick was color-marked to avoid repeat weighing. From color-marking studies, fledglings on a fledging beach departed within ~2 days. From 1987 to 2011, 90 to 400 (mean of 250) individual CFM were recorded each year. We calculated the mean CFM for each season. In our study, we could not control for clutch size or significant differences that may exist between single-chick broods and that of twins (Jarvis 1974, Ainley & Schlatter 1972), so we focused on the interannual variability of mean CFM.

After departing from the colony, Adélie fledglings do no return to their natal breeding site until about 3-4 years later (Ainley 2002). From 1987 to 2004, a fledgling
resighting study on Humble Island showed that resighted birds had a significantly higher mean CFM (3.152 ± 0.352 kg) compared to birds that were not resighted (3.035 ± 0.258 kg; Chapman et al. 2010). Birds that were not resighted were never seen again. The chicks apart of the resighting study were from the same beaches as our study, making our study comparable to Chapman et al. (2010). We refer to the mass of “resighted” and “not resighted” birds as “survivors” and “non-survivors”.

2.2.2 Environmental Data

We used large-scale climate and local weather data during the chick-rearing period (Dec-Feb) because all climate and weather events during this time have the potential to influence chick growth and mass. Climate indices may affect CFM through the remote forcing of atmospheric teleconnections on the local environment, which can directly influence chicks terrestrial environment and change thermo-regulative costs or alter marine conditions and thus, food availability. Monthly values for the austral summer (Dec-Feb) Antarctic Oscillation (AAO), Southern Oscillation Index (SOI) and El Niño 3.4 (N3.4) were obtained from the NOAA National Weather Service, National Centers for Environmental Prediction, Climate Prediction Center (http://www.cpc.ncep.noaa.gov/). The AAO is the periodic strengthening and weakening of the circumpolar vortex in the Southern Hemisphere, where a strong vortex/positive AAO is associated with stronger westerly winds around 60°S and warmer/wetter conditions along the WAP (Oshima & Yamazaki 2004, van den Broeke & van Lipzig 2004). The SOI is the difference in the air pressure anomaly between the Tahiti Islands and Darwin, Australia and represents fluctuations in air pressure between the Western and Eastern Tropical Pacific during ENSO events. The Niño 3.4 is the departure of sea surface temperature from the long-term mean in
the Eastern Tropical Pacific at 5°N-5°S and 170-120°W. SOI and Nino 3.4 reflect warm El Nino (negative SOI; high Nino 3.4) and cold La Nina (positive SOI; low Nino 3.4) conditions in the equatorial Pacific (Carleton 2003; Kwok and Comiso 2002). The Antarctic Dipole (ADP) is the difference between the mean ice edge anomaly from the Pacific center at 150°W-120°W and the Atlantic center mean ice edge anomaly at 50°W-20°W (Xiaojun Yuan, pers. comm.), where a positive ADP signifies higher ice conditions along the WAP. Chick-rearing habitat (CRH) suitability is a spatially explicit, large-scale index from satellite-derived sea surface temperature, sea ice concentration and bathymetry (Cimino et al. 2013, see next Chapter), which describes the marine habitat suitability for Adélie penguins around Antarctica (25 x 25 km resolution). We used average CRH suitability within 75 km of Palmer Station to incorporate the Adélie penguins’ potential foraging range. For all climate indices, we created seasonal averages for the austral summer (Dec-Feb) to match with the timing of the chick-rearing period for the Adélie penguin colony on Humble Island.

2.2.3 Local Environment

The daily local atmospheric environment around Palmer Station is influenced by air temperature, precipitation, and wind, which were measured as part of the Palmer Long-Term Ecological Research (LTER) program from 1989-2012 (http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets). These atmospheric conditions can affect chick’s thermo-regulative costs, and winds can alter ocean currents, water column mixing and prey availability. Wind speeds were attenuated from 10m to the height of a chick following the methods of Chapman et al. (2011), which does not account for small elevation changes at Humble Island. We calculated u and v wind vector components from wind speed and direction (+u is a
westerly wind, +v is a southerly wind). We determined the number of days with high winds, cold and high temperatures, heat stress, chill factor, zero precipitation (Table B.1) and mean wind chill. Daily averages were computed from hourly

Table 2.1: Linear and linear quadratic regression models relating mean Adélie chick fledging mass (CFM) to environmental and prey quality predictor variables at Humble Island 1989-2011. The model formulas are described by the number of estimated parameters (k), Adjusted $R^2$, $\Delta AIC_c$ for small sample size, $\Delta AIC_c$ (difference from the lowest $AIC_c$; amount of information lost), relative likelihood (strength of evidence) and Akaike weight representing relative model support or probabilities. The intercept is chick mass in grams. Models are sorted by ascending $\Delta AIC_c$ and only models with a $\Delta AIC_c < 10$ are shown (models with a $\Delta AIC_c > 10$ have little support). * Indicate models with substantial support ($\Delta AIC_c < 2$). The bolded variables in the models include: Antarctic Oscillation (AAO), air temperature (Temp), u wind component (Uwind), wind speed, number of days with zero precipitation (NoPrecip), krill wet-mass energy density (WED), and the proportion of immature krill (Imm).

<table>
<thead>
<tr>
<th>Model Formula</th>
<th>k</th>
<th>$R^2$</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>Relative Likelihood</th>
<th>Akaike Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. $-37.46$AAO + $175.67$Temp - $113.30$Uwind + $194.87$AAO*Temp + $3082.8$</td>
<td>5</td>
<td>0.60</td>
<td>260.01</td>
<td>0.00</td>
<td>1.00</td>
<td>0.35</td>
</tr>
<tr>
<td>B. $-59.68$AAO + $189.77$Imm - $90.78$Uwind + $4.30$NoPrecip + $2964.7$</td>
<td>5</td>
<td>0.58</td>
<td>261.18</td>
<td>1.18</td>
<td>0.56</td>
<td>0.19</td>
</tr>
<tr>
<td>C. $-496.61$AAO + $139.07$WED - $112.61$Uwind + $306.01$Temp + $91.99$AAO$^2$ + $3626.7$</td>
<td>6</td>
<td>0.62</td>
<td>261.59</td>
<td>1.58</td>
<td>0.45</td>
<td>0.16</td>
</tr>
<tr>
<td>D. $357.96$AAO + $199.66$Temp - $82.15$Uwind - $4.23$WindSpeed - $165.04$AAO*WindSpeed + $71.71$AAO$^2$ + $67.50$Uwind$^2$ + $3065.6$</td>
<td>8</td>
<td>0.72</td>
<td>261.61</td>
<td>1.61</td>
<td>0.45</td>
<td>0.15</td>
</tr>
<tr>
<td>E. $-97.84$AAO - $90.91$Uwind + $228.31$Temp + $61.14$AAO$^2$ + $3060$</td>
<td>5</td>
<td>0.54</td>
<td>263.22</td>
<td>3.22</td>
<td>0.20</td>
<td>0.07</td>
</tr>
<tr>
<td>F. $468.33$AAO + $4.04$WindSpeed + $1903.7$Temp - $199.79$AAO<em>WindSpeed - $611.85$Temp</em>WindSpeed + $77.27$AAO$^2$ + $3031.2$</td>
<td>7</td>
<td>0.54</td>
<td>269.15</td>
<td>9.15</td>
<td>0.01</td>
<td>0.00</td>
</tr>
</tbody>
</table>

measurements. Seasonal averages or counts were computed for the chick-rearing period from Dec 19 to Feb 10, which corresponds to mean hatch and fledge dates (Chapman et al. 2010). The mean value does not always represent short periods (hours) of extremes or storm events (days) that affect chick growth.
Sea ice extent, duration and day of retreat in the Palmer LTER grid (Fig. 2.1) was measured by the Scanning multichannel microwave radiometer–Special Sensor microwave/imager (SMMR-SSM/I) by the National Snow and Ice Data Center and analyzed by Stammerjohn et al. (2008). From 1987 to 2011, we classified each year as having early, late or average ice retreat by calculating the standard deviate (Quetin & Ross 2001), where the long-term time series mean was subtracted from each annual value and then divided by the standard deviation for the long-term time series. A value less than -0.5 was considered a year of early ice retreat, greater than 0.5 was late and a value between -0.5 to 0.5 was average. We also calculated mean sea ice extent during Sept-Nov. We used sea ice classifications in our Antarctic krill (Euphausia superba) energetics calculations (see next section and Appendix B) and tested the impact of ice conditions on CFM. High sea ice can act as a barrier to foraging and alternatively, low sea ice has been associated with decreased krill availability (Atkinson et al. 2004).

The tides near Palmer Station oscillate between semidiurnal and diurnal tidal regimes. Diurnal tides aggregate krill (Bernard & Steinberg 2013) and allow penguins to forage at shorter distances (Oliver et al. 2013). At Palmer Station, a tidal prediction model reported hourly water level predictions relative to mean sea level (Amos 1993; pers. comm.). Following Oliver et al. (2013), we counted the number of high tides per day to determine tidal regime, where one high tide per day was classified as diurnal and more than one high tide was classified as semidiurnal. We then determined the fraction of diurnal tides during the chick-rearing period, which may be an indicator of prey availability, biomass and thus, Adélie foraging behavior.
2.2.4 Converting Antarctic krill size classes into energy density and sex/maturity stages

During our study, Adélie penguins at Humble Island almost exclusively preyed upon krill, generally > 98% krill by mass. The stomach contents of Adélie penguin adults with chicks were sampled using the lavage method (Wilson 1984). Individual krill were measured at 5-mm intervals from 16-65 mm to obtain size frequency distributions but the sex was not determined. The total number and proportion of krill in each class were determined for each year during the chick-rearing period. Based on annual sea-ice conditions (referred to as the dynamic scenario in the Appendix B), these size class frequency distributions were then used to estimate the proportion of each sex/maturity stage and the mean wet-mass energy density (WED) of krill consumed by chicks each year according to the methods of Chapman et al. (2010), which is summarized in Appendix B. It was necessary to convert krill size classes into sex/maturity stages and WED because krill size does not necessarily dictate energy content. Generally, during the chick-rearing period, the lipid content of immature krill is greater than mature males and spent females but less than gravid females (Chapman et al. 2010). Using this methodology, we investigated the total energy content of the annual krill cohort in parental diets and also, the energy content and proportion of the krill population associated with each life stage (immature krill, mature males, gravid and spent females).

2.2.5 Linear and Polynomial Regression

We used forward and backward stepwise regression to determine the predictor variables that were most related to CFM (MATLAB and Statistics Toolbox Release R2013a, The Mathworks, Inc., Natick, Massachusetts, United States). We used linear and quadratic models that allowed for interactions between predictor
variables. The predictor variable that contributes most to a model’s fit of observed data has the largest absolute value of the t-statistic (Kuhn & Johnson 2013). Models in Table 2.1 did not have outliers, their residuals were normal and each term in the models listed were significant at the $p = 0.05$ level. Additionally, the sign of the regression coefficient of a predictor variable, interaction or quadratic term had to be ecologically plausible and consistent between various models (Graf et al. 2005). Akaike’s information criterion for small sample size ($AIC_c$) was used to identify models that account for the most variation with the fewest terms ($k$), select the model with the best balance between bias and precision, and avoid over fitting (Burnham & Anderson 2002). We considered models with a $\Delta AIC_c < 2$ to have substantial support and models with $\Delta AIC_c > 10$ to have no support. Therefore, we only reported models with a $\Delta AIC_c < 10$ (Table B.1). We also reported the Adjusted $R^2$, relative likelihood and Akaike weight.

Prior to modeling, all predictor variables were detrended if they exhibited a significant linear or quadratic trend over time ($p < 0.05$) to isolate the meaningful variability in the time series. Predictor variables that were not normally distributed were transformed to achieve normality using log or square-root transformations (Table B.2). Multicollinearity, the significant correlation between predictor variables, can be problematic in regression models because information in one predictor variable is contained in its correlate. Our approach was to use predictor variables that were uncorrelated, or at least those that had a level of multicollinearity that could be ignored. To test for multicollinearity in our predictor variables before running regression models, we computed cross-correlation coefficients using Spearman’s rank correlation ($\rho$; Fig. B.1). Because we examined a large suite of
variables (Fig. B.1), it was necessary to eliminate variables that were collinear and less related to CFM to reduce the possible number of regression models. Using a stringent threshold for $p$ of 0.5, we eliminated correlated variables that had a less direct influence on CFM (Graf et al. 2005). The large-scale variables that were eliminated using the above criteria include: SOI, N3.4, and CRH. ADP was not included in our models because the time series only extends to 2007. The local-scale variables that were eliminated include: number of days with high winds, number of days with cold temperatures, number of days with high temperatures, number of days with heat stress, number of days with chill factor, mean solid precipitation and mean wind chill. Therefore, the suite of models we tested included all combinations of: the AAO, $u$ and $v$ wind component, days with no precipitation, mean wind speed, mean air temperature, sea ice extent, fraction of diurnal tides, WED and the proportion of immature krill. Subsequent to our regression models, we again tested for multicollinearity using Variance Inflation Factors (VIFs) for predictor variables in each model (Allison 1999). VIFs provide an index to measure how much the variance of an estimated regression coefficient is increased because of collinearity in predictors included in any given model. Multicollinearity was not a problem in our models (Table B.1) because VIF values were less than 4 (O’Brien 2007).

### 2.3 Results

#### 2.3.1 Interannual variation in CFM and krill quality

We investigated the interannual variability in Adélie CFM from 1987 to 2011 (Fig. 2.2). CFM was normally distributed each year and varied from ~1.5 to ~4.5 kg. At
Figure 2.2: The mean mass of surviving and non-surviving Adélie penguin chicks was taken from a fledgling resighting study (Chapman et al. 2010). Mean CFM oscillates between the mass of survivors (CFM > 3.152 kg; closed circles) and non-survivors (CFM < 3.035 kg; squares) from 1987 to 2011. Open circles represent CFM between the mass of survivors and non-survivors. Interannual variability in the 25th and 75th quartile of mean CFM. Years represent the austral summer field season, ex. 1987 = Dec. 1987 and Jan, Feb 1988.

least 25% of the CFMs were above and below the mean mass that is descriptive of surviving and non-surviving chicks each year (Chapman et al. 2010). Mean CFM varied by only 0.35 kg (2.835 to 3.180 kg), but were generally significantly different between years that differed by > 0.05 kg. There were 11 years with mean CFM below the mean mass of non-survivors and five years with mean CFM above the mean mass of survivors.
Using krill size-class frequency distributions from Adélie penguin diets from 1987 to 2011, we estimated the interannual variation in WED and the proportion of each sex/maturity stage using the methods of Chapman et al. (2010) (Fig. 2.3).

Estimates of WED were not correlated to CFM (ρ < 0.1). The range of WED was comparable to previous studies, which show WED varies from 3.5 to 5.0 kJ/g (Davis et al. 1989, Janes & Chappell 1995, Nagy & Obst 1992). CFM was not correlated to the proportion of mature males, mature females, gravid females or larger krill in the diet, but it was moderately correlated to the proportion of immature krill (ρ = 0.33, p = 0.11).

![Figure 2.3: Interannual variability in WED (black) and the proportion of immature krill (grey).](image)
2.3.2 **Individual large- and local-scale predictors of CFM**

CFM was related to individual large-scale indices and local environmental factors (Fig. 2.4, 2.5). Mean CFM was significantly higher in years with a negative AAO index, positive ADP and low CRH suitability (p < 0.05, Fig. 2.4). There was no

![Probability density of mean CFM between negative (-) and positive (+) or high (H) and low (L) Antarctic Oscillation (AAO) from 1987-2011, Antarctic Dipole (ADP) from 1987-2007, El Nino 3.4 (N3.4) from 1987-2011, Southern Oscillation Index (SOI) from 1987-2011 and chick-rearing habitat suitability (CRH) from 1987-2010. Blue and gray colors indicate higher and lower mean CFM. Significant differences between the means were computed using a t-test. Stars denote significant differences in the mean between – and + or H and L indices (** P < 0.05; * P < 0.1) while no stars signify non-significant differences. The dashed horizontal line represents surviving CFM while dotted horizontal line represents non-surviving CFM. The thick black box specifies the interquartile range, the thinner black lines are the upper and lower adjacent values, the points are the median, and x’s are the mean.](image-url)
relationship between CFM and N3.4 or the SOI. In addition, CFM was marginally higher in years with warmer air temperature and lower wind speeds ($p < 0.1$, Fig. 2.5). There was no significant relationship between CFM and the u or v wind component, the number of days with zero precipitation, WED or the proportion of immature krill.

![Figure 2.5: Probability density of CFM between high (H) and low (L) air temperature (temp), u wind component (Uwind), v wind component (Vwind), wind speed, number of days with zero precipitation (No precip), krill wet-mass energy density (WED), and the proportion of immature krill (Imm). The weather data spans 1989 to 2011 and the krill data spans 1987 to 2011 during the chick-rearing period. The lone point in the WED and immature krill boxes represents the year of lowest CFM in 2001, which was affected by anomalous weather events and thus, was excluded from significance testing. See Fig. 2.4 caption for more details.](image-url)
2.3.3 Predictor variables of CFM from Linear and Polynomial Regression

Using stepwise regression, we related CFM to different environmental and prey predictor variables simultaneously (Table B.1). The four best models (A-D) performed well and explained most of the variance ($R^2 = \sim 0.6$ to 0.7) using 5 to 8 predictor variables in quadratic and linear combinations. Model A explained the most variance using the fewest predictor variables and had the highest Akaike weight of 35%, which was roughly double that of Models B, C, and D. In comparison to models B and C, model D had a similar AICc (within 0.5 units), relative likelihood ($\sim 50\%$) and Akaike weight ($\sim 15\%$) but explained $\sim 10\%$ more variance using 2-3 more predictor variables.

We compared measured CFM with estimated CFM from models A-D from 1989 to 2011 (Fig. 2.6). The model estimates of CFM were generally in good agreement with the data. We created an ensemble of models A-D, where the contribution of each model to the ensemble was weighted by the Akaike weights (Table B.1). The ensemble was on average within $\sim 0.03$ kg of measured CFM, but ranged from 0.006 to 0.103 kg. The ensemble had the greatest deviance from measured values in 2001, 2005 and 2011 by 0.079, 0.103, and 0.082 kg, respectively. Conversely, model D was able to more accurately estimate CFM in 2001 and 2011 but no model accurately estimated CFM in 2005.

There were eleven unique terms in models A-D with varying importance to model performance. These included seven linear predictor variables, two interactions between predictor variables and two quadratic predictor variables (Fig. 2.7). The AAO and u wind component were the only predictor variables used in all models A-D. Additionally, AAO appeared in all reported models (Table B.1). The u wind
Figure 2.6: Comparison of mean CFM and modeled CFM from models A-D, which had substantial support (Δ AIC < 2). The ensemble is the mean of models A-D, where the contribution of each model to the ensemble was weighted by the Akaike weights. The dashed horizontal line represents surviving CFM while dotted horizontal line represents non-surviving CFM.

Component ranked the highest being either the first or second most important variable in models A-D. The AAO also ranked high in models B and C, but ranked fourth and fifth in models A and D. However, in models A and D, the interaction between air temperature and wind speed with AAO ranked third and first. Air temperature ranked second in model A and ranked third in models C and D. The quadratic predictor variables were moderately important: AAO$^2$ ranked fourth in models C and D and U wind$^2$ ranked sixth in model D. The number of days with zero precipitation ranked third in Model B. Lastly, the three least important linear
predictor variables to the models were wind speed, WED and the proportion of immature krill, which all ranked last in their respective models.

Figure 2.7: The frequency that each predictor variable appeared in models that were substantially supported (Δ AIC <2). Each variable was ranked in order of highest to lowest t-statistic for individual models with 1 being the most predictive variable and 7 being the least. The letters (A-D) correspond to that respective model. The variables include: Antarctic Oscillation (AAO), air temperature (temp), U wind component (U wind), wind speed, number of days with zero precipitation (No Precip), krill wet-mass energy density (WED), and the proportion of immature krill (Imm).

The effects of each predictor variable on CFM were compared between models in a sensitivity test (Fig. 2.8). Increasing AAO, u wind, air temperature and precipitation individually had the greatest effect on CFM, confirming the parameter ranks in Fig. 2.7. A positive change in AAO and u wind decreased CFM by ~0.2 kg
while a positive change in air temperature and the number of days with zero precipitation increased CFM by ~0.2 kg. Increased wind speed and WED decreased CFM by ~0.1 kg and a higher proportion of immature krill increased CFM by ~0.1 kg. Parameters in models A-D had a similar effect on CFM, confirming the consistency of different model predictions.

Figure 2.8: Predicted effects on CFM when individual variables were increased in Models A-D. Each point represents the mean predicted effect on CFM and the horizontal line is the 95% confidence interval from the prediction. The variables in the models include: Antarctic Oscillation (AAO), air temperature (Temp), u wind component (U wind), wind speed, number of days with zero precipitation (NoPrecip), krill wet-mass energy density (WED), and the proportion of immature krill (Imm).
To understand the synergistic effects of wind speed and air temperature with AAO, we compared the sensitivity of CFM to wind speed and air temperature during a highly negative, low, and highly positive AAO index. During a negative AAO index, increased wind speed increased CFM, but during a positive AAO, increased wind speed decreased CFM (Fig. 2.9a). When the AAO was low, wind speed had little to no effect on CFM. In addition, during a negative AAO, increased air temperature had little to no effect on CFM, but increased temperature in a positive and low AAO increased CFM (Fig. 2.9b).

![Figure 2.9](image)

**Figure 2.9:** Interactive effects on CFM between (a) wind speed and the Antarctic Oscillation (AAO) in Model A and (b) air temperature and AAO in Model D. Each line represents a positive, low or negative AAO index.

### 2.4 Discussion

High interannual variability is characteristic of the Antarctic ecosystem, but the relative contribution of large-scale and local processes in generating interannual
variation in this ecosystem is largely unknown. In this paper, we examined the relative importance of large-scale and local processes on the interannual variation in Adélie penguin CFM. Mean CFM at a colony represents the integrated investment of adults to the next generation and is the balance between seasonally integrated food resources and metabolic demand, both of which could be linked to large-scale and local processes in complex ways. To elucidate the major drivers of this variability, we tested environmental and prey factors acting on multiple spatial scales from 1987 to 2011. Our approach emphasizes the importance of uncorrelated predictor variables and quantifies the impact of interactions between these predictor variables on mean CFM. Our model results demonstrate that the large-scale AAO, local westerly winds and air temperature were the dominant predictor variables of CFM in our models (Fig. 2.7). These predictor variables caused a change in mean CFM by ~0.2 kg (Fig. 2.8), which is greater than the difference between the mean masses of surviving and non-surviving chicks (Chapman et al. 2010, Fig. 2.2). Our model results also show that the local mean wind speed, number of days with zero precipitation, dietary proportion of immature krill, and WED were less important predictor variables of mean CFM (Fig. 2.8). This highlights the importance of large-scale and local weather conditions at a penguin colony, relative to krill resources (Fig. 2.3). In the remainder of the discussion, we will provide the major interpretations of our model results as they relate to large-scale climate, local weather, their potential interactions and food resource quality.

2.4.1 Large-scale Climate Predictors of CFM

The implicit assumption of large-scale climate correlates to local biological measurements is that the climate index is associated with multiple local-scale
oceanographic conditions or weather phenomena that directly affect a biological system. We examined five different climate indices that have been hypothesized to influence ecosystem variability along the WAP (Fig. 2.4). Of the five indices we examined, three (AAO, ADP and CRH) have significant relationships with CFM. The AAO has been positively correlated to a western wind anomaly, air temperatures, precipitation, and moisture along the WAP (Oshima & Yamazaki 2004, van den Broeke & van Lipzig 2004), and may represent a synergy between many local climate forces that could subsequently affect penguin chicks. Multiple studies have suggested that the austral winter ADP (once referred to as the Antarctic Circumpolar Wave) impacts Adélie penguins (Ainley et al. 2005, Fraser & Hofmann 2003, Clarke et al. 2002) through the influence of winter sea ice on krill reproductive output and survival (Quetin & Ross 2003) and thus, food availability for penguins. In this study, we provide the first preliminary results indicating that CFM covaries with the austral summer ADP index (Fig. 2.4); however, the mechanisms between austral summer ADP and CFM are unknown. CRH suitability is an index that incorporates sea surface temperature, sea ice and bathymetry that is indicative of the suitability of Adélie penguin chick-rearing habitats (Cimino et al. 2013, more details in Chapter 3). CRH suitability was originally developed to predict whether or not Adélie penguin colonies were growing or shrinking. Surprisingly, low CRH suitability was significantly related to high CFM (Fig. 2.4). During years of low CRH suitability, the air temperature was warmer (Fig. B.1), which suggests that while a warming environment has a negative effect on Adélie populations (Cimino et al. 2013) the warmer air temperature may decrease thermoregulatory costs for chicks.
In our best performing regression models (Table B.1), the AAO was a leading, and only large-scale climate index predictor for CFM. All other climate indices except ADP were rejected prior to modeling because they were highly collinear with other environmental predictor variables and likely detect similar climate signals (Fig. B.1). ADP was rejected because the record was incomplete (available only through 2007). Although the AAO has been implicated in driving local weather patterns along the WAP, we found only a moderate correlation between AAO and mean wind speed ($\rho = 0.41$, $p = 0.05$) and days with zero precipitation ($\rho = -0.37$, $p = 0.08$) but found no correlation between westerly winds ($+u$) or air temperature (Fig. B.1). The AAO is linked by remote forcing of atmospheric teleconnections to the local environment, which may not be manifested in mean local weather conditions at Palmer Station. This suggests that the significance of the AAO as a predictor of CFM is not because it correlates to any one weather signal, but represents an integrated but unknown mixture of climate forces as they relate to interannual variability in CFM. For instance, austral winters of high sea ice extent and spring physical processes (low wind and high salinity-driven density gradients in the upper water column), modulated by negative July and spring (Sept-Oct-Nov) AAO events, promote high phytoplankton biomass at Palmer Station (Saba et al. 2014). Summers with high chl-$a$ anomalies were in turn significantly correlated with the start of a new krill cohort, which was evident in penguin diets the following summer. This demonstrates a tight coupling within the food web (Saba et al. 2014) and the varying impact of climate and weather forces on different trophic levels.
2.4.2 Local Weather Predictor of CFM

We tested the effects of multiple local weather conditions on CFM using different metrics for air temperature, wind and precipitation (Fig. 2.4, Table B.1). Individually, these parameters did not have a strong relationship with CFM (Fig. 2.5). However, results from our stepwise regressions (Table B.1) indicate that the wind component and air temperature were major predictor variables of CFM, causing ~0.2 kg change, while wind speed and days with zero precipitation were minor predictor variables, causing ~0.1 kg change in CFM (Fig. 2.7, 2.8). The negative effect of low air temperature alone does not provide a mechanistic link to CFM because chicks can withstand a wide range of temperatures (Chappell et al. 1989) but we will discuss this negative effect further in the next section in relation to the statistical interaction with other predictor variables. Although precipitation was not a key predictor variable in our models, it can cause chicks plumage to become damp or wet and is generally a major factor causing egg and chick mortality, and slow growth due to hypothermia (Thyen & Becker 2006, Konarzewski & Taylor 1989). For example, Boersma and Rebstock (2014) found more chicks died when rainfall was high and air temperature was low. Wetness decreases the insulating properties of feathers and this disruption likely increases heat loss (McCafferty et al. 1997, Wilson et al. 2004). Therefore, more days with no precipitation have a positive effect on CFM likely due to lower thermoregulatory costs.

Local winds were a strong predictor of CFM in our models. Onshore westerly winds and to a lesser extent wind speeds could indirectly affect a parent’s foraging domain and directly affect a chick’s terrestrial habitat. In the Falkland Islands, strong westerly winds were hypothesized to aggregate prey and were correlated to Rockhopper penguin mass gain (Dehnhard et al. 2013). Prey distributions may be...
affected by regional ocean circulation, fronts, eddies, current velocities, and water mass distributions (Trivelpiece & Fraser 1996), which can be affected by strong winds. Over small spatial (10’s km) and temporal (days) scales, a near gale can alter nearshore hydrography in the upper 100 m of the water column, decrease krill biomass and change the foraging distribution of krill predators (Warren et al. 2009). Alternatively, wind is hypothesized to have adverse effects on CFM and seabird survival (Chapman et al. 2011, Finney et al. 1999) in locations with little shelter from the prevailing wind or onshore wind component (Frederiksen et al. 2008, Harris & Wanless 1996). Winds can influence where snowfall will accumulate or which locations will receive the most wind scour (Fraser et al. 2013).

2.4.3 Climate and Weather Interaction Predictor Variables of CFM

Interactions between our predictor variables provide insight into how CFM is synergistically affected by the large and local-scale environment (Fig. 2.9). During summers of a positive AAO index with high wind speeds (Fig. 2.9a) and low air temperatures (Fig. 2.9b), CFM was lower. As previously discussed, the AAO is likely a synergy between many local weather factors at Palmer Station. However, the AAO is positively correlated to the number of days with precipitation and is likely an indicator of humidity. Our interpretation of these interactions is that chicks are more likely to become wet during a positive AAO, and incur higher thermoregulative costs during wet, cold and windy years (Lustick & Adams 1977). When the AAO is negative, or near zero, the effect of air temperature on CFM is eliminated or reduced. Additionally, when the AAO is negative, wind speed is positively related to CFM. The reasons for this particular relationship are unknown. This interaction relationship points to the importance of local wind speed on either food resources or nest site
conditions. A previous study on Adélie penguins in East Antarctica also linked interannual variation in breeding phenology to the AAO, air temperature, wind speed and direction (Emmerson et al. 2011). This suggests our predictor variables are not unique to Adélie chicks at Humble Island and can impact many parts of the Adélie life cycle.

2.4.4 Food Resource Predictors of CFM

We examined the impact of interannual variability in krill WED and demography on CFM because krill is the main food source for Adélie penguins on Humble Island during our study period. In our regression models (Table B.1), we found the proportion of immature krill and WED had a minor contribution to model predictions, causing a change in CFM by ~0.1 kg (Fig. 2.7, 2.8). It was counterintuitive to find that increased WED corresponded to lower CFM (Fig. 2.8) because high-energy prey should increase chick growth (Drent & Daan 1980, Litzow et al. 2002). However, finding higher energy prey could pose a greater time cost to the parent and reduce the frequency or amount of food delivered to the chick. The negative relationship between WED and CFM suggests that a diet of high-energy content does not necessarily produce chicks with a higher mass. Therefore, it may be plausible for a chick to attain the same amount of energy from a diet of gravid females and immature krill. Other studies suggest krill biomass (Trivelpiece et al. 2011) or meal mass (Clarke et al. 2002) is the dominant driver of demographic changes or chick survival in Adélie penguins.

Determining the dietary proportion of each sex and maturity stage of krill from shifting size class frequency distributions (Ducklow et al. 2013) required fewer assumptions compared to WED (Equations 1-2). A higher proportion of immature krill
had a positive effect on CFM (Fig. 2.8). A higher proportion of small krill may be indicative of a higher level of krill recruitment (Lynnes et al. 2004) and increased encounter rates for penguins, making foraging trips shorter and chicks provisioned at more frequent intervals (Fraser and Hofmann 2003). Hinke et al. (2007) showed that recruitment of Adélie penguins was positively related to small krill, which could suggests that small krill influences CFM. Hinke et al. (2007) did not detect this relationship because they looked at mean krill size in Adélie diets, which they found was not correlated to CFM. Lynnes et al. (2004) also found Adélies exhibited stronger recruitment in years with a higher proportion of smaller krill. Alternatively, a diet of immature krill may be easier for chicks to digest and result in high assimilation efficiencies. For example, penguins digest fish quicker than squid (van Heezik and Seddon 1989, Wilson et al. 1985) and digest smaller otoliths faster than larger otoliths (van Heezik and Seddon 1989). Therefore, the small carapace of juvenile krill may be digested more rapidly than the thicker and more developed carapace of mature krill. Recently at Palmer Station, other krill-consuming penguin species have established breeding colonies with growing populations and similar foraging distributions to Adélies, which suggests krill are not a limiting resource and should not be a dominant predictor variable of CFM. Although krill energy content and demography are not main drivers in our models, this should not underscore the importance of krill in this ecosystem. In general, regional declines in krill biomass and variability in recruitment (Siegel & Loeb 1995, Loeb et al. 1997) have indications for negative density dependence and juvenile mortality even if chicks reach a surviving mass.
2.4.5 Potential sources of unexplained model variance and non-significant predictor variables

The accuracy of our CFM models was generally supported by the data (Fig. 2.6) but 30-40% of variability in CFM remains unexplained (Table B.1), which shows our approach did not account for all processes or interactions involved in parental care or chick growth. We did not directly account for all factors affecting a parent’s ability to forage efficiently due to inter/intraspecific competition (Siniff et al. 2008, Ducklow et al. 2007), foraging duration/behavior (Takahashi et al. 2003, Watanuki et al. 2002), barriers (such as, thick ice cover), food availability, parent age/experience (Ainley 2002, Ainley & Schlatter 1972) and parent body condition (Tveraa et al. 1998, Ballard et al. 2010). Notably, we found few indications of heat stress during the chick-rearing period. Heat stress is known to cause behavioral changes in penguins around Palmer Station (Fraser pers. obs.), which suggests the effects of heat operate at finer temporal scales than our daily mean weather observations can detect. We also tested for the effect of the tidal regime as a predictor variable of CFM. It has been suggested that tides are active aggregators of krill in the region (Oliver et al. 2013, Bernard & Steinberg 2013) but the seasonal fraction of diurnal tides were a non-significant predictor of CFM. However, our treatment of the tides as seasonal fractions may be overly simplistic.

Within our study period, the documented effects of atmospheric events on Adélie penguins point to overlooked predictor variables in our models. In 2001, an anomalous blocking-high pattern coincided with a positive summer AAO, the lowest mean CFM in our time series, low reproductive success, the largest between season population decline and deferred breeding by many birds at Palmer Station (Massom et al. 2006). This was triggered by strong and persistent north-northwesterly flow of
mild and moist air across the WAP, extreme ice compaction, high snowfall, thick snow cover and subsequent high temperatures that caused snowmelt to flood nests and drown eggs and small chicks. A similar event occurred in 2005, coincident with a near neutral AAO (Massom et al. 2008). Although atmospheric anomalies on this scale are extremely rare (Turner et al. 2002), it is unknown if blocking-high episodes will become more prevalent in future climate scenarios.

2.5 Conclusions

Understanding the interannual variability in Adélie mean CFM using large and local-scale predictor variables is fundamental to gaining a more robust understanding of the Adélie penguins’ response to environmental variability in Antarctica. We expected krill predictor variables to play a larger role in predicting CFM, however, large-scale climate and local weather were more important. It is unclear how general our results are with respect to the rest of the Antarctic continent. Along the WAP, a positive austral summer AAO produces warm, windy and humid conditions, while cold, calm and dry conditions occur in East Antarctica. Therefore, opposing effects of the AAO around the continent may explain the opposing patterns in Adélie demography and population trends (Hindell et al. 2012, Ainley et al. 2005, Emmerson et al. 2011). Our results suggest that climate and weather are dominant drivers of mean CFM, however, there is still a significant amount of variance in CFM that we could not explain. We suggest that a more detailed analysis of overwintering conditions and parental foraging behavior during the chick-rearing period are important for understanding the variation in mean CFM.
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Chapter 3

SATELLITE DATA IDENTIFY DECADAL TRENDS IN THE QUALITY OF *PYGOSCELIS* PENGUIN CHICK-REARING HABITAT

*Pygoscelis* penguins are experiencing general population declines in their northernmost range while 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 to 2010. Generally, 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.
3.1 Introduction

The success of *Pygoscelis* penguin populations is strongly linked to chick survival (Forcada and 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. Due to the short food web and the ability of climate to directly impact penguins (Chapter 2), 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 and 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 and 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 West Antarctic Peninsula (WAP) and Bellingshausen Sea, sea ice concentration (SIC) declined precipitously over the last few decades (Massom and 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 has increased (Meredith and King 2005), and 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 and 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 and Ross 2009). Due to the short food web, high CHL has been related to krill recruitment events and greater krill abundance (Saba et al. 2014), and thus could be directly related to the availability of food for penguins (Atkinson et al. 2004).

Increased SST can decrease SIC and alter prey distributions, quality and availability, which has been linked to penguin population declines (Cunningham and Moors 1994; Guinard et al. 1998; Le Bohec et al. 2008; Ruck et al. 2014). 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. 3.1). Using this data, we developed distribution models that define and predict suitable CRHs for each species. We show that 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.
3.2 Methods

3.2.1 Colony Location Data

Adélie, gentoo, and chinstrap penguin breeding colony locations were obtained from Woehler and Croxall (1997) and Woehler (1993). Colonies with populations fewer than 100 pairs were excluded and data collected prior to 1970 were excluded to decrease influence of small or transient colonies. These historical

Figure 3.1: 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 3.2.
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 penguins could inhabit a specific breeding site for 100s to 1000s of years (Emslie 2001; Emslie and McDaniel 2002). We refer to these historic colony locations as penguin chick-rearing habitats (CRHs) and these locations were matched with the corresponding environmental data (Fig. 3.1). Information on environmental data processing is located in the appendix.

3.2.2 Characterizing Penguin Colonies

Penguin colonies were matched to records of sea surface temperature (SST; 1981-2010), sea ice concentrations (SIC; 1978-2010), chlorophyll concentrations (CHL; 1978-1986, 1997-2010) and bathymetry during their chick-rearing season (Dec-Feb). 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 West Antarctic Peninsula (WAP) separately from the continental Adélie penguin colonies for two reasons (Fig. 3.1). 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 and Patterson 2007; Goodwin 1993). Since the environmental data was not normally distributed, we used a non-parametric 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.

3.2.3 Penguin CRH Models

We used a presence-only modeling technique to estimate penguins’ CRH distributions. In presence-only modeling, non-observations 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 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 and 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 and 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 and 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 (McPherson 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 anti-correlated, 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 there is unique information in SST and SIC variables that aid in predicting a species distribution. The
CRH models were trained with a Dec-Feb average climatology from 1978-1984 (Fig. C.2). We assumed that between the years of 1978-1984, penguins CRHs reflected their preferences. Using a multi-year 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 (Dec-Feb) for SIC, SST, and bathymetry from 1985-2010. 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 while 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.

3.2.4 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 3.2). Estimated population trends were based on the cited references in Table 3.2. 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 75km of each penguin colony
between the years that a particular penguin population was documented. The mean and twice the standard deviation of CRH suitability were calculated for each colony (Table 3.2). 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.

3.3 Results

3.3.1 Large Scale Trends in Satellite Data

The 30-year satellite record of penguin chick-rearing seasons (Dec-Feb) allowed us to estimate the magnitude of environmental change near penguin colonies. Since the onset of the modern satellite era, sea ice concentration (SIC), sea surface temperature (SST) and chlorophyll concentration (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 West Antarctic Peninsula (WAP) while areas in the Ross Sea, Weddell Sea and Indian Ocean have increased by up to 2% per year (Fig. 3.2a) which agrees with previous, year-round trends in SIC (Massom and 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. C.5c and f. Significant changes in \( \log_{10} \) CHL concentrations during chick-rearing seasons were evident but were patchy and irregular (Fig. 3.2b). Significant changes in CHL were within ±1.3 mg m\(^{-3}\) per year. It should be noted that the CHL record from 1978-2010 has a 10-year gap from 1987 to 1996. From 1997-2011, SeaWiFS and MODIS Aqua show continuous measurements of CHL within our
polar projection (Fig C.5b) and within 200 km from land (Fig. C.5e). 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 is more variable due to missing data, poor quality measurements or changes occurring between the

![Figure 3.2: Significant environmental changes around Antarctica during the austral summer (Dec-Feb): (a) sea ice percent from 1978-2011, (b) log10 CHL concentration from 1978-1986 and 1997-2011, (c) and SST from 1981-2011. Black areas indicate non-significant trends at the 0.05 level.](image)

large time gap from CZCS and SeaWiFS measurements. This should be considered when interpreting Fig. 3.2b. From 1997-2011, significant changes in log$_{10}$ CHL were also calculated without CZCS data (Fig. C.6). 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. 3.2b. For chick-rearing seasons 1981 to 2010, SST in the Weddell Sea, and areas extending from the WAP into the northern Ross Sea have increased up to 0.1°C per year (Fig. 3.2c). Northern latitudes around the continent had patchy decreases in SST up to 0.1°C per year. Similarly, Meredith and King (2005) described up to a 0.05°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 1981-2011, we found comparable mean SST within our polar projection (Fig. C.5a) and within 200km from land (Fig. C.5d), which indicated 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 changes occurring on the WAP are uncharacteristic of the Antarctic continent as a whole (Massom and Stammerjohn 2010).

Figure 3.3: Probability density of (a) sea ice percent from 1978-2011, (b) SST from 1981-2011, (c) CHL concentration from 1978-1986 and 1997-2011, 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 non-parametric Kruskal-Wallis test and a multiple comparison test after Kruskal-Wallis. Letters denote non-significant 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.
3.3.2 Characterizing Penguin CRH

Mean SIC and SST conditions were significantly different among these penguin colonies (Fig. 3.3ab). Adélie penguin colonies were found in higher SICs and lower SSTs compared to 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 15% greater than WAP Adélie penguins. In addition, mean SST at continental colonies were about 1.5°C lower than 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. 3.3c). Similar mean CHL was seen without CZCS CHL data (Fig. C.7). Mean bathymetry was not significantly different among species (Fig. 3.3d).

We visualized the intersection of SIC, SST and bathymetry for each penguin species chick-rearing habitats (CRHs; Fig. 3.4,C.3). 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 compared to WAP Adélie penguins. Compared to Adélies and gentoos, chinstraps had a very narrow and well-defined predictor space.

3.3.3 MaxEnt Model Performance

The area under the curve (AUC) calculations showed the CRH models performed well, with the mean AUC for each species models above 90% (Table 3.1).
Figure 3.4: 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.

AUC values have a tendency to be higher for species with a narrow range in relation to the amount of environmental data input (McPherson et al. 2004); thus, chinstraps had an AUC of 99%. CHL was omitted from these models because its inclusion decreased 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 the Adélie CRH models at about 70% while SST had a mere 2% contribution. For gentoo penguins, SIC contributed 55% and SST contributed 18%. Lastly, SST contributed 51% to the chinstrap CRH model while SIC contributed 24%.
Table 3.1: Mean AUC for CRH models for each species and mean percent contribution for each environmental variable in the model.

<table>
<thead>
<tr>
<th></th>
<th>Adélie</th>
<th>Gentoo</th>
<th>Chinstrap</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean AUC</strong></td>
<td>0.91 ± 0.001</td>
<td>0.92 ± 0.001</td>
<td>0.99 ± 0.0002</td>
</tr>
<tr>
<td><strong>SST Percent Contribution</strong></td>
<td>2.0 ± 0.25</td>
<td>18.2 ± 1.17</td>
<td>51.3 ± 1.25</td>
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<tr>
<td><strong>Sea Ice Percent Contribution</strong></td>
<td>69.8 ± 0.43</td>
<td>54.6 ± 1.41</td>
<td>23.9 ± 0.98</td>
</tr>
<tr>
<td><strong>Bathymetry Percent Contribution</strong></td>
<td>28.2 ± 0.36</td>
<td>27.2 ± 0.91</td>
<td>24.7 ± 0.74</td>
</tr>
</tbody>
</table>

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 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. C.4b). Comparing the training data for WAP and continental Adélie models showed SST was warmer and SIC were generally lower on the WAP (Fig. C.2). 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 C.1). 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 C.1). To eliminate the influence of a warming environment on Adélie penguin preferences, our final model was trained on only continental colony locations.
3.3.4 Mean CRH Suitability

From 1982 to 2010, Adélie, chinstrap and gentoo penguins had geographically different mean CRH suitability (Fig. 3.5 abc). The penguins’ CRH suitabilities were consistent with their colony location as well as the associated

![Image](image_url)

**Figure 3.5:** Top panel: Mean CRH suitability from each CRH model output from 1982-2010 for (a) Adélie, (b) gentoo and (c) chinstrap penguins. Red areas indicate suitable conditions while dark blue areas are unsuitable conditions. Bottom panel: Significant changes in CRH suitability from 1982-2010 for (a) Adélie, (b) gentoo, and (c) chinstrap penguins. Warm colors indicate an increase in suitability while cool colors display regions with decreases in suitability. Black areas indicate non-significant 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. C.8-13).
environmental parameters (Fig. 3.1, 3.4). 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 3.5a). Their most suitable CRHs were located in Ross Sea where populations are growing (Wilson et al. 2001). In contrast, gentoo and chinstrap penguins had high CRH suitability predominately in the northern WAP (Fig. 3.5 bc). Gentoo penguins’ suitable ranges also extended to outlying islands, into the southern tip of South America and a few regions in East Antarctica.

3.3.5 Large-Scale Trends in CRH Suitability

Significant changes in CRH suitability from 1982-2010 were mostly located along the WAP (Fig. 3.5) coinciding with regions of environmental change (Fig. 3.2). 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. 3.5d). Intermittent regions extending from Marguerite Bay southward to the Amundsen Sea increased more than 50% in suitability for Adélie penguins while 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. 3.5ef). 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. 3.5ef). The southern WAP became more suitable for gentoo
chick rearing compared to 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 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. Because 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 (Fig. 3.4, 3.5e). 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 (Fig. 3.4, 3.5f).

3.3.6 Comparison of Population Trends and CRH Suitability

We matched modeled CRH suitabilities to penguin colonies with documented penguin population trends (Table 3.2). 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. 3.6a). Increasing Adélie penguin populations had a mean habitat suitability that was 0.25 higher than the mean of decreasing populations (Fig. 3.6a). The mean CRH suitability at increasing Adélie colonies was about 0.3 ± 0.2 (Fig. 3.6a, Table 3.2). In comparison, the significantly different lower CRH suitability (approximately 0.05 ± 0.1) at decreasing Adélie colonies indicated conditions were not suitable for Adélie penguin chick rearing. Gentoo penguins had more similar CRH suitabilities between increasing and
Figure 3.6: 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.

decreasing colonies (Fig. 3.6b). Mean CRH suitability at increasing gentoo colonies was only ~0.2 higher than at decreasing colonies (Table 3.2). This also indicates increasing gentoo populations were in regions of higher CRH suitability compared to decreasing gentoo populations and shows conditions at increasing colonies along the WAP may be suitable for gentoo population growth (Table 3.2). In our literature search, we found one population of chinstrap penguins with an increasing population. CRH suitability was about 0.07 units higher at increasing colonies than the mean CRH suitability at decreasing colonies (Fig. 3.6c). 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 estimated (Table 3.2). 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 while 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 non-significant trends in CRH suitability.

### 3.4 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 for 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 and 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) while chinsstraps migrate north of the pack ice into open water habitats (Fraser *et al.* 1992; Wilson *et al.* 1998). While
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* penguin ecology (Pearson and 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 (Fig. 3.3, 3.4). The partitioning of their niche spaces is consistent with the general latitudinal segregation of *Pygoscelis* colonies.

Sea ice concentration (SIC) and sea surface temperature (SST) during the austral summer season show significant changes over the last three decades. The largest changes in SIC and SST are in the West Antarctic Peninsula (WAP), but there are also significant changes in the Ross Sea region. The WAP is warming while areas in the Ross Sea region appear to be mostly cooling during the chick-rearing season (Fig. 3.2). Generally, we found valid and continuous measurements between long-term records of different CHL and SST satellite sensors in the Southern Ocean (Fig C.6, C.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. 3.5).

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 penguins censuses, there are enough non-continuous populations counts that allow us to distinguish increasing and decreasing
populations at different locations. Generally, predicted mean and significant trends in CRH suitability for *Pygoscelis* penguins were in agreement with documented population trends. However, while 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 3.2). This is because CRH suitability has high inter-annual 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. 3.6a). Adélie penguin populations largely declined at sub-Antarctic islands and along the WAP while populations increased or remained stable in the Ross Sea and East Antarctica (Fig. 3.1, Table 3.2). 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 over-winter 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 prey populations for penguin colonies (Jenouvrier *et al.* 2006; Kato *et al.* 2002).
In general, increasing gentoo penguin populations have slightly higher CRH suitability compared to shrinking gentoo penguin populations but there was no significant difference (Fig. 3.6b). 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 and Korczak 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 3.6c.). Chinstrap population declines are potentially influenced by changes in food resources or increased competition, 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. 3.5f).

There is a southward shift in suitable CRHs along the WAP for all Pygoscelis species (Fig. 3.5). 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. 3.5ef) may be explained by fewer cold years and the consequent decrease in sea ice (Fraser et al. 1992). This suggests increased warming events will cause conditions to become less suitable for Adélie penguins compared to 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 and Trathan 2009). In East Antarctica, there was evidence for increasing CRH suitability for chinstrap and gentoo penguins, which suggests 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 to chinstrap penguins (Fig. 3.5bc). 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 and 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.
Table 3.2: 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. 3.1.

<table>
<thead>
<tr>
<th>Species</th>
<th>General Location</th>
<th>Specific Location</th>
<th>Population Trend</th>
<th>CRH Suitability Trend</th>
<th>Years</th>
<th>CRH Suitability</th>
<th>Reference</th>
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<tbody>
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<td>Adélie</td>
<td>South Shetland Islands</td>
<td>Penguin Island (1)</td>
<td>-</td>
<td>0.00011 (p=0.88)</td>
<td>1982-2003</td>
<td>0.02 ± 0.04</td>
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<td>Adélie</td>
<td>South Shetland Islands</td>
<td>King George Island, Stranger Point, Isla 25 de Mayo (1)</td>
<td>-</td>
<td>6.8e-05 (p=0.91)</td>
<td>1995-2006</td>
<td>0.02 ± 0.01</td>
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<td>0.02 ± 0.03</td>
<td>Hinke et al. 2007; Chwedorzew ska and Korczak 2010</td>
<td></td>
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<tr>
<td>Adélie</td>
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<td>-</td>
<td>0.0015 (p=0.54)</td>
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<td>0.31 ± 0.23</td>
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Table 3.2 continued,

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<th>Species</th>
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<th>Year Period</th>
<th>Sample Size</th>
<th>Significance</th>
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<td>0.03 ± 0.01</td>
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<td>Location</td>
<td>Species</td>
<td>Site Name</td>
<td>Change</td>
<td>Year Duration</td>
<td>Trend ± SE</td>
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<tr>
<td>Adélie 108</td>
<td>Adélie</td>
<td>Pointe Geologie Archipelago (9)</td>
<td>+</td>
<td>1982-2003</td>
<td>0.26 ± 0.25</td>
<td>Jenouvrier et al. 2006</td>
</tr>
<tr>
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<td>Adélie</td>
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<td>+</td>
<td>1982-1997</td>
<td>0.39 ± 0.24</td>
<td>Wochler et al. 2001; Wilson et al. 2001</td>
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<td>Adélie</td>
<td>Cape Royds (5)</td>
<td>+</td>
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<td>Wochler et al. 2001; Jenouvrier et al. 2006</td>
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<td>King George Island, Stranger Point, Isla 25 de Mayo (1)</td>
<td>+</td>
<td>1998-2003</td>
<td>0.26 ± 0.24</td>
<td>Carlini et al. 2009</td>
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<td>Gentoo</td>
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<td>King George Island, Admiralty Bay (1)</td>
<td>-</td>
<td>1982-2008</td>
<td>0.41 ± 0.17</td>
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<td>0.43 ± 0.18</td>
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<td>South Orkney Islands</td>
<td>Signy Island (2)</td>
<td>+</td>
<td>1982-2007</td>
<td>0.18 ± 0.24</td>
<td>Forcada et al. 2006, 2009</td>
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<tr>
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<td>Bird I (4)</td>
<td>-</td>
<td>1982-1999</td>
<td>0.54 ± 0.08</td>
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<td>WAP</td>
<td>Anvers Island, Palmer Station region (3)</td>
<td>+</td>
<td>1993-2010</td>
<td>0.57 ± 0.27</td>
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<td>Petermann Island (3)</td>
<td>+</td>
<td>1982-2007</td>
<td>0.48 ± 0.39</td>
<td>Lynch et al. 2010</td>
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Chapter 4

ASYMMETRIC RESPONSE OF ADÉLIE PENGUINS TO ANTARCTIC CLIMATE CHANGE

The contribution of climate change to shifts in a species’ geographic distribution is a critical and often unresolved ecological question. Climate change in Antarctica is asymmetric, with cooling in parts of the continent and warming along the West Antarctic Peninsula (WAP). The Adélie penguin (*Pygoscelis adeliae*) is a circumpolar meso-predator exposed to the full range of Antarctic climate and is undergoing dramatic population shifts coincident with climate change. We used true presence-absence data on Adélie penguin breeding colonies to estimate past and future changes in habitat suitability during the chick-rearing period (CRHS) based on historic satellite observations and future climate model projections. During the contemporary period, declining Adélie penguin populations experienced more years with warm sea surface temperature compared to populations that are increasing. Based on this relationship, we project that one-third of current Adélie penguin colonies, representing ~20% of their current population, may be in decline by 2060. However, climate model projections suggest refugia may exist on continental Antarctica beyond 2099, buffering species-wide declines. Climate change impacts on penguins in the Antarctic will likely be highly site specific based on regional climate trends, and a southward contraction in the range of Adélie penguins is likely over the next century.
4.1 Introduction

Climate has influenced the distribution patterns of penguins for millions of years (Clarke et al. 2007). The Adélie penguin has intermittently occupied the WAP for ~6,000 years (Emslie 2001), East Antarctica for at least 14,000 years (Younger et al. 2015), and the Ross Sea for ~45,000 years (Emslie et al. 2007). The paleoclimate record suggests that periodic colony abandonment corresponds to glacial expansion or extensive permanent sea ice while reoccupation corresponds to warming periods marked by deglaciation or sea ice declines that allow access to rocky nesting habitats (Emslie 2001; Emslie et al. 2007; Younger et al. 2015). On the other hand, late 20th century climate warming along the WAP is coincident with Adélie population declines (Ducklow et al. 2013) while stable or cooling conditions around the remainder of the continent generally correspond to stable or increasing populations (Lynch & LaRue 2014) (Fig. 4.1). This contrast highlights that the effect of environmental drivers on penguin distributions are relative to the climate regime under consideration.

Climate change can have profound effects on penguins’ terrestrial nesting sites and marine food resources. Adélie penguins construct nests on ice- and snow-free terrain with pebbles to keep eggs and chicks dry and out of any water. Precipitation and snowmelt can cause nest site flooding that drowns eggs and small chicks (McClintock et al. 2008), influences chick mass and survival (Cimino et al. 2014), and has been linked to population declines (Fraser et al. 2013). Tight coupling in the Antarctic food web, where sea ice, wind, and water column stability impact phytoplankton and Antarctic krill (Euphausia superba) recruitment (Saba et al. 2014), has lead to concerns that climate change will cause a decrease in krill abundance, a major food source for Adélie penguins. However, recent studies show no long-term (1993-2013) change in WAP krill biomass (Steinberg et al. 2015) and current krill
biomass should support Adélie penguin breeding colonies (Sailley et al. 2013).
Although changes in, or competition for, krill may not be the main driver of WAP population declines (Cimino et al. 2016), we cannot discount the negative effects of warm waters on krill quality (Ruck et al. 2014), or the availability of krill to penguins. Antarctic silverfish (*Pleuragramma antarcticum*), another component of Adélie penguin’s diet, have declined coincident with WAP climate changes (Ducklow et al. 2007; Ruck et al. 2014) and could also influence penguin demographics such as breeding success, chick mass and survival.

Multi-decadal satellite observations provide continuous spatiotemporal measurements of sea surface temperature (SST) and sea ice concentration (SIC) in the Southern Ocean, which are essential for a continental-scale view of Adélie penguin chick-rearing habitats (Cimino et al. 2013). The high covariance between atmospheric (e.g., air temperature, wind, sea level pressure) and oceanic conditions (Fan et al. 2014) suggest that SST and SIC may be good proxies for the quality of penguins’ terrestrial nesting habitats that can be impacted by weather, and/or indicators of food resources. Here, we develop austral-summer CRHS models that simulate the quality of coastal habitats using true presence-absence Adélie penguin colony locations (Fig. 4.1) and satellite-derived information on SIC, SST, and bare-rock locations. We used this model to project the quality of penguin habitats in the future using global climate models assessed by the Intergovernmental Panel on Climate Change (IPCC) and a prototype, high-resolution global climate model developed by the Geophysical Fluid Dynamics Laboratory (GFDL). To understand the sensitivity of our results, we compared two species distribution models (MaxEnt and Generalized
Additive Models [GAMs]) and used presence and absence data from different portions of the Adélie penguin's range.

Figure 4.1: Adélie penguin breeding colonies and population status across Antarctica. Each colored circle represents a colonies’ current population trend. The black dashed line separates West Antarctic Peninsula (WAP) from continental Adélie penguin colonies. Bare rock (■) locations around the coastline and light to dark blue represents shallow to deep bathymetry reproduced from Cimino et al. (2013).

4.2 Methods

4.2.1 Adélie penguin colony information

We obtained Adélie penguin breeding colony abundance, distribution, (Lynch & LaRue 2014) and population trends (Lynch et al. 2012). These datasets provided true presence and true absence locations throughout the entire Adélie penguin
breeding range (Fig. 4.1). Population observations and agreement between regional scale population trends provides confidence in individual colony trends (Lynch et al. 2012). We considered present locations to be all colonies present in the late 70s/early 80s that had a colony status of present or presumed present. All analyses and statistics were carried out in R (www.r-project.org, R Development Core Team, 2004).

4.2.2 Environmental variables

We used satellite-derived SIC, SST, and bare-rock locations to estimate the suitability of penguin chick-rearing habitats in Antarctica (See Appendix D). Years represent the austral summer field season, e.g. 1978 = Dec 1978 - Feb 1979.

Historical and future climate projections of SST and SIC were obtained from the IPCC’s fifth assessment (Representative Concentration Pathway 8.5) via the Coupled Model Intercomparison Project Phase 5 (CMIP5) archive and two additional NOAA GFDL global climate models (see Appendix D, Table D.1; more information on the global climate models can be found at http://cmip-pcmdi.llnl.gov/cmip5/).

Satellite-derived and climate model projections of SST and SIC are available on different spatial scales and were interpolated to a 25 x 25 km polar stereographic grid surrounding Antarctica (Cimino et al. 2013). Yearly climatologies were created for each parameter for the austral summer chick-rearing period from December to February (DJF). To understand, compare and account for climate model biases, we computed differences in the mean and standard deviation between DJF satellite observations (1978-2004) and climate model historical runs, using the historical runs from the CMIP5 models (1978-2004) and from the GFDL 1990 control simulations (years 101-140, global atmospheric CO$_2$ was fixed at year 1990 concentration; CM2.1,
CM2.6). We created climate model deltas by subtracting the mean of historical runs from the CMIP5 models (1978-2004) and the control simulation for GFDL models from their respective climate model projection for each year. The projections from GFDL models CM2.1 and CM2.6 were a transient climate response experiment such that CO$_2$ in the atmosphere increased by 1% per year until it doubled by year 70. Further details on these models and experiments can be found in Saba et al. (2015). Using the delta approach to bias correct the mean, we added climate model SST and SIC deltas to the satellite climatologies to create annual climatologies of climate model conditions. Due to poor coastal resolution, we interpolated climate model projections to land (except for GFDL-CM2.6 which has high coastal resolution) and evaluated model biases based on the 200-km surrounding Antarctica and sub-Antarctic islands. From SST and SIC mean biases (Fig. D.18), we considered the best models to have average projections within ± 1ºC and ± 20% SIC. All models had a relatively low bias in SIC and SST variability (Fig. D.19). This resulted in seven global climate models and we also used GFDL-CM2.6 because it is a high-resolution model, which may more accurately represent dynamics in the coastal ocean.

Our study focused on the coastline around sub-Antarctic islands and Antarctica. Each coastline pixel was classified as having bare-rock present or absent. For the satellite record and climate projections, we spatially averaged SIC and SST within 75 km of each coastline pixel for each year to incorporate the ocean environment within the penguins foraging range.

4.2.3 Models for penguin habitat suitability during the chick-rearing period

We modeled the suitability of Adélie penguin chick-rearing habitats using two species distribution models, a maximum entropy approach (MaxEnt) and generalized
additive models (GAMs, see Appendix D). Both approaches estimate the habitat suitability, ranging from 0 (least suitable) to 1 (most suitable). The CRHS models were trained with bare rock locations, and average SST and SIC climatologies from 1978–1984 (Cimino et al. 2013). This multiyear average smoothed the high interannual variability characteristic of Antarctic marine environments. The model trained on 1978–1984 was then projected onto annual climatologies for SIC, SST, and bare-rock locations from 1981 to 2010. Bare rock locations were static for all years. Our approach does not account for possible changes in bare-rock locations due to sea level rise, or coastal glacial collapse exposing new nest sites. We compared models trained on different combinations of all presence-absence and only continental presence-absence data (Fig. 4.1) to compare model performance and spatial variability in CRHS (Fig. D.20). We also projected the model onto future climate scenarios from our eight best performing models using GAMs and all presence-absence locations. We created CRHS maps for each year and used linear regression across time to identify locations of significant change in CRHS. We also identified areas with novel climate using multivariate environmental similarity surfaces in MaxEnt, which measures the similarity between the environment in the model training dataset and the new environment in the projection years.

4.3 Results

Adélie penguin CRHS models show the spatial distribution of novel climate and changes in CRHS compared to historic observations (Fig. 4.2). In this study, novel climate is SST or SIC outside the range of average SST and SIC observations from 1978-1984, which corresponds to CRHS model training data (see methods). The WAP experienced the greatest number of novel climate years, with up to seven years of
novel climate from 1981-2010 and over 40 years of novel climate using an ensemble of global climate model projections from 2011-2099 (Fig. 4.2a, see Fig. D.1-8 for individual climate model output and Fig. D.9 for variability). Marguerite Bay appears to be on a slower warming trajectory compared to the WAP (Fig. 4.2a), which is also evident in the high-resolution GFDL-CM2.6 projections (Fig. D.8). While both the WAP and Ross Sea regions have been characterized by high CRHS in the recent past (Fig. 4.2b), our model projects a substantial decrease in CRHS along the WAP and an increase in CRHS in the Ross Sea over the next century (Fig. 4.2c). The northeastern Antarctic Peninsula appears to be a more favorable environment than the southwestern Antarctic Peninsula (Fig. 4.2a,b). From 1981-2010, the South Shetland Islands and the WAP had a similar number of novel climate years and mean CRHS (Fig. 4.2ab) but CRHS improved in the South Shetland Islands (Fig. 4.2c). During this time, the more northerly South Sandwich and South Orkney Islands experienced no years with novel climate, higher mean CRHS and improved CRHS compared to southerly islands and the WAP. Comparing two species distribution modeling approaches and two spatial subsets of the presence-absence data, we found the modeling methods (MaxEnt vs. GAMs) produced similar results but varied more when presence or absence data was incomplete. Model output was most sensitive to incomplete absence data, especially when true presence data was included, perhaps because absence data was missing within a specific environmental niche and Adélie penguins do not occupy all available habitats (Appendix D Results).

We determined whether each penguin colony experienced novel climate from 1981 to 2010, and tested for significant differences between the number of years with novel climate at decreasing, increasing and stable populations (Fig. 4.3). Over
Figure 4.2: Novel climate and Adélie penguin habitat suitability during the chick-rearing period (CRHS) from past satellite observations and in the future using an ensemble of global climate models. (a) The number of years with novel climate, which is data outside the range of the model training data, in the past and future. (b) Mean CRHS and (c) trends in CRHS in the past and future (See Figs. D.1-8 individual climate models). In the past, black outlines represent significant changes over time ($p < 0.05$) and in the future, black outlines show regions where all climate models project changes in the same direction. PS = Palmer Station and MB = Marguerite Bay.
50% of decreasing penguin colonies experienced novel climate as a result of warm SST (Fig. 4.3a). Only ~15% of increasing and stable populations had novel climate related to warm SST, cool SST, or high SIC. Almost 25% of populations with an unknown trend had novel climate due to warm SST and are located along the WAP, suggesting these population may be in decline. Colonies with decreasing populations experienced significantly more years with novel climate than populations that were increasing in abundance (nonparametric Krustal-Wallis test and multiple comparisons test after Krustal-Wallis, p < 0.05), suggesting recent warming effects are detrimental to Adélie penguin populations. Penguin colonies near Palmer Station, which have declined by 80% since the 1970s (Ducklow et al. 2013), experienced the most novel climate years (seven) (Fig. 3b). About 47% of decreasing populations did not experience novel climate, which may partially be due to inaccuracies in the population trends themselves as it is challenging to estimate continent-wide populations from satellite imagery (also noted by Southwell et al. 2015). There are also many other factors that influence population trends that we could not account for, such as predation (Young 1990), competition (Trivelpiece et al. 2011), wintering habitat (Emmerson and Southwell 2011), weather impacts on nest sits with specific geomorphology (Fraser et al. 2013), phenological shifts that result in a mismatch between predators and prey (Durant et al. 2007), and human impacts including tourism, pollution and fishing (Trivelpiece et al. 2011, Ellis et al. 1998, Chwedorzewska and Korczak 2010).

Eight Adélie penguin colonies failed between 1980 and 2010 (Fig. 4.1). In Enderby Land, six extirpations were concurrent with 2-3 years of novel climate due to high SIC. Within two adjacent 25 x 25 km grid cell pixels, there were three colony
extirpations while three other colonies had increasing or stable populations, suggesting that penguins from failed colonies joined these nearby colonies located in a more suitable habitat (similar to other emigrations: LaRue et al. 2013; Dugger et al. 2010). Two of eight documented extirpations located in the Ross and Amundsen Seas did not experience any novel climate. Additional factors, either at finer scales than captured by our datasets, or factors not included in our analysis, likely contribute to extirpations and population declines. It is also possible that Adélie penguins are sensitive to climate that is not considered to be novel. This may explain why, despite good model performance (Appendix D Results), 45% of declining populations did not experience novel climate as measured by the environmental variables considered (Fig. 4.2). Because individual colonies may be impacted by idiosyncratic factors operating on fine-scales independent of large-scale climatic influences, patterns of occupancy and trend at regional and continental-scales are required to understand the role of changing climate on habitat suitability.
Figure 4.3: Proportion of colonies with novel climate and number of years with novel climate for each population status from 1981-2010. a) The proportion of colonies for each population status that have no novel climate (none) or the leading cause of novel climate is due to warm sea surface temperature (SST), cool SST or high sea ice concentration. b) Probability density of the number of years with novel climate at colonies that experienced at least one year of novel climate for populations that are decreasing, increasing, stable and unknown. The thick black box represents the interquartile range, thinner black lines represent upper and lower adjacent values and the white points are the median.

Climate projections from global models assessed by the IPCC and from GFDL’s high-resolution CM2.6 reveal similar trends in the cumulative number of years with
Figure 4.4: The cumulative number of years with novel climate at Adélie penguin colonies in different Antarctic sectors. Location map of Adélie penguin colonies and bare rock locations. Each line represents the mean of all colonies in that sector colored by the climate model used for the projection. Satellite observations of novel climate are in red from 1981-2010, IPCC models from 2006-2099 and GFDL-CM2.6 from year 1-79 where atmospheric CO₂ increases by 1% per year and atmospheric CO₂ doubles at year 70 in the model simulation. The IPCC ensemble mean shows the average trend for all IPCC models in a sector (not including GFDL-CM2.6). See Figs. D.10-17 for individual models.

novel climate in various Antarctic sectors (Fig. 4.4). The southern WAP, sub-Antarctic islands, and northern WAP regions, which are already experiencing population declines, are projected to experience the greatest frequency of novel climate in this century due to warm SST (Fig. 4.4, see Figs. D.10-17 for colony projections from each
climate model). Adélie penguin colonies in East Antarctica and Enderby Land are projected to experience < 10 years of novel climate by 2099 while colonies in the Ross and Amundsen Seas are projected to experience < 5 years of novel climate.

![Image](image_url)

**Figure 4.5**: Percent of Adélie penguin breeding colonies experiencing different rates of novel climate, accounting for different colony sensitivity. Each line is the average of satellite observations from 1981-2010 and the global climate model ensemble from 2011-2099.

We determined the rate that novel climate will occur at Adélie penguin colonies using satellite observations (1981-2010) and the global climate model ensemble (2011-2099) (Fig. 4.5). During 1981 to 2010, decreasing populations had a minimum of one, an average of four, and a maximum of seven years of novel climate over 30 years of observation (Fig. 4.2) illustrating differential sensitivity of colonies to novel climate. This corresponds to a rate of 3.3%, 13.3% and 23.3% of novel climate per annum associated with colony decline. By 2060, our projections suggest 58%,
36% and 25% of colonies could experience population declines, containing 43%, 21% and 9% of the currently known Adélie penguin abundance, respectively. Similarly, by 2099, our projections suggest 78%, 58% and 51% of colonies could experience declines, containing 64%, 46% and 39% of the current abundance.

4.4 Discussion

On geologic timescales, Adélie penguin populations were positively affected by warming and negatively affected by cooling (Emslie 2001; Emslie et al. 2007; Younger et al. 2015) but the rapid response of penguin populations to multi-decadal warming events (similar to population shifts from 1980-2010, Fig. 4.1) cannot be assessed in the geologic record because of its coarse temporal frequency. Our study suggests that in many regions of Antarctica climate warming has tipped past peak suitability so that further warming is no longer beneficial to Adélie penguins. Warm SSTs may drive a substantial decline in the suitability of chick-rearing habitats at northerly latitudes but several refugia, particularly in the more stable Ross and Amundsen Seas, may buffer species-wide declines under climate change projections. Interestingly, northern sub-Antarctic islands appear to be more favorable chick-rearing habitats, with fewer years of novel climate, than southern islands and the WAP. WAP Adélie penguin populations may have undergone similar population boom and busts in the geologic past because the current rate of warming, while highly unusual, is not unprecedented (Mulvaney et al. 2012). Over the past two millennia, the WAP had high climate variability (Mulvaney et al. 2012) that could makes it an unstable chick-rearing site for Adélie penguins with more sporadic occupancy than seen elsewhere. The WAP appears disproportionately vulnerable to projected climate change compared to other regions. Contemporary warming on the
WAP is related to both atmospheric changes (Ding et al. 2011) and the delivery of warmer upper circumpolar deep water onto the continental shelf (Martinson 2012). The direct or indirect effects of this warming are detrimental to Adélie penguin populations and could lead to population declines at ~30% of colonies by 2060 and ~60% of colonies by 2099 (Fig. 4.5). With continued warming, new bare rock nesting habitats may become available as glaciers disintegrate but colonization will likely be limited to southern localities (Ainley et al. 2010).

Many Adélie penguin population declines were associated with novel climate due to warm SSTs, which may be associated with inadequate food resources or weather that impacts the quality of nest sites. For example, reduced prey availability or quality may inhibit penguins from meeting their energetic demands (Ruck et al. 2014) while blizzards and unprecedented snow accumulation in West Antarctica (Thomas et al. 2015) can have catastrophic impacts on penguins (Massom et al. 2006; Ducklow et al. 2007). Adélie penguins are considered to be highly philopatric (Ainley & DeMaster 1980), but there is surprisingly little genetic differentiation among Adélie penguin populations at the continental scale (Roeder et al. 2001). It is unknown if warming prompts Adélie penguin emigration, but repeated colony abandonment and recolonization over millennia confirm this possibility. In this study, we suggest climate novelty is detrimental to Adélie penguins. While we cannot yet establish the specific mechanism for this relationship, our study focuses attention on areas where climate change is likely to create a high frequency of unsuitable conditions during the 21st century and, by contrast, suggests several refugia are likely to persist.
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Chapter 5

CONCLUDING REMARKS

The rate of current climate warming in the WAP is not unprecedented (Mulvaney et al. 2012), but the direct impacts of this warming are concerning and reversing these effects could take thousands of years. Penguins are known to repeatedly abandon and recolonize nest sites as the climate changed over millennia, and thus, are bio-indicators of environmental change. This dissertation focused on the response of *Pygoscelis* penguins to recent climate shifts in the Southern Ocean. Long-term measurements by the Palmer Station LTER and remote sensing observations provided massive volumes of high quality data that span many time and space scales, and allowed for innovative links between climate signals and penguins. These studies point to biotic and abiotic factors that may be more important to population control than previous thought and other factors that may not be as important. The general paradigm of climate change effects rippling up through a tightly coupled food web to impact larger predators does not appear to be the only way that climate can influence penguin demographics and population shifts as direct climate action can impact each trophic level independently. While I was not able to test for food web interactions on a scale fine enough to reject these interactions as population drivers, direct climate impacts on penguins appear important in the WAP. This dissertation contributes to our understanding of the fate of *Pygoscelis* penguins and provides approaches for evaluating other species persistence in a changing environment.
In Chapter 1, foraging patterns of Adélie and gentoo penguins were evaluated in relation to the distribution of krill (their prey) and vertical water column properties measured from a REMUS autonomous underwater vehicle at Palmer Station. These species generally had spatially segregated foraging areas but within overlapping foraging regions they vertically partitioned their habitat, a strategy that could limit competition. Gentoo penguins, the newcomer to the Palmer Station region, do not appear to be interacting or competing with Adélie penguins in a way that could contribute to the Adélie penguin population decline. Furthermore, prey biomass does not appear to be in decline (Steinberg et al. 2015) and krill aggregation structure in the upper 100 m (depth range of REMUS) of the water column was not different in the two species foraging ranges. For a greater understanding of local prey effects on penguin foraging behaviors, we need simultaneous observations of prey structure and variability within both species foraging ranges throughout the entire water column. In general, it is expected that species better suited to a northern sub-Antarctic climate will displace ice-obligate species, but as shown here climate-driven sympatry may not always cause displacement.

In Chapter 2, large-scale climate and local weather were related to Adélie penguin chick fledging mass over 25 years at Palmer Station. The fledging mass of a chick is thought to be an important indicator of prey availability and environmental conditions during the chick-rearing period as well as survival and recruitment into the breeding population (Chapman et al. 2010). During krill recruitment years, when a high proportion of immature krill were found in Adélie penguin diets, chicks had a higher mass. However, local weather had a greater impact on chicks, where wet, windy and cold weather likely increased thermoregulatory costs for chicks without
waterproof feathers. Many other studies also show catastrophic impacts of increased storms and rain events on penguin nesting habitats and chick health (Massom et al. 2006; Ducklow et al. 2007; Boersma & Rebstock 2014; Fraser et al. 2013; Massom et al. 2008; Chapman et al. 2011). It is possible that Adélie penguins’ historic diet of higher energy fish could buffer the negative effects of weather. Furthermore, a southern WAP rookery at Avian Island, characterized by greater over-winter sea ice, produced heavier Adélie penguin chicks than at Palmer Station; however, Pygoscelis penguin chicks at Palmer were still of sufficient quality at the physiological level (Gorman 2015). Challenging the view that changes in food webs directly influence chick survival and that chick mass is an indicator of survival, Gorman (2015) hypothesized that chicks of a lower mass that were reared under unsuitable conditions may recruit into a different colony, but further study is needed to support this.

In Chapter 3, SST, SIC and bathymetry were used to understand changes in the quality of Pygoscelis penguin chick-rearing habitats in the Southern Ocean from 1980-2010. In general, chick-rearing habitat suitability at colony locations agreed with documented population trends over the same time period. Interestingly, these factors also identified the transition zone from suitable to unsuitable habitats along the WAP that corresponded to Pygoscelis penguin population shifts. Non-significant trends in habitat suitability in the northern WAP and on some sub-Antarctic islands may suggest factors unrelated to direct climate impacts might also be important in these regions (such as competition). Habitat suitability was also negatively related to chick fledging mass, where low suitability corresponded to warmer temperature years, and suggests that although a warming environment appears to have an overall
negative effect on populations, warmer weather may decrease thermoregulatory costs for chicks.

Similarly, in Chapter 4, SST, SIC and bare rock locations were used to understand changes in the quality of coastal Adélie penguin chick-rearing sites in the past (1980-2010) and into the future (2011-2099). During the historic period, declining Adélie penguin populations experienced more years with novel climate due to warm SST compared to increasing populations. This suggests the detrimental effects of warming may be increased when warming has tipped into a novel condition. As warming continues, a contraction in the range of Adélie penguins is likely over the next century, especially along the WAP, but refugia may exist in continental Antarctica beyond 2099. The specific mechanisms relating SST, SIC and novel climate (warm SST) to penguins is unknown, but the quality or availability of food resources or weather impacts on nest sites could be important correlated factors. It is also possible that novel climate leads to dispersal, which is supported by the low genetic diversity in WAP Adélie penguin colonies (Gorman 2015, Clucas et al. 2014). Furthermore, gentoo penguin colonies show high genetic differentiation while chinstrap penguin colonies have lower genetic diversity (Clucas et al. 2014). Gene flow may also be facilitated by wintering behaviors where resident species (gentoo) generally have higher population structure than migratory species (Adélie, chinstrap) that disperse during the winter (Friesen et al. 2007).

Recent Antarctic climate changes have been attributed to a Southern Hemisphere regime shift occurring in the late 1970s or early 1980s (Reid et al. 2015; Weimerskirch et al. 2003; Ekaykin et al. 2014). Natural climate regime shifts occur on decadal timescales and alternate between warm and cool periods. Along the WAP,
the colder period in the 1970-1980s corresponded to more fish in penguin diets while the warmer period in ~1990-2010 corresponded to mostly krill in penguin diets (William Fraser, unpublished). The near disappearance of fish in the warmer regime could have severe consequences for adult penguins and their chicks. For example, chick fledging masses in the colder regime (prior to the study period in Chapter 2) were higher (William Fraser, unpublished). Chicks that are fed a diet of higher energy fish may be able to tolerate local weather extremes more so than chicks that are feed a diet of lower energy krill. Foraging for fish as a parent penguin could be more profitable resulting in shorter foraging trips and allowing chick provisioning to occur more frequently. A fish-based diet could also result in lower competition for food with krill specialists. If multi-decadal regime shifts are the main driver of warm and cool periods in the WAP, it is possible that we will soon enter another cold period and perhaps, the return of fish could have positive effects on penguin demographics.

This dissertation provides a robust understanding of some local and large-scale environmental influences on *Pygoscelis* penguins. It is particularly challenging to decipher the effects of SST and SIC on penguins because many oceanic and atmospheric parameters are highly correlated. To elucidate how SST and SIC are mechanistically related or correlated to penguins, further study is necessary. First, utilizing the LTER’s record of Adélie penguin breeding success, it would be informative to determine the percent of the breeding population that rears a chick to fledging each year, the environmental factors that drive interannual variability in breeding success and how this relates to chick fledging mass. Second, it is important that future studies consider divergent overwintering strategies and locations of *Pygoscelis* penguin to fully understand the ecological structure and regional
vulnerability of penguins to dynamic WAP environments. Winter conditions could contribute to adult and chick survival, adult body condition at the beginning of the breeding period and may help explain colony-level responses to change. Third, a greater understanding of how penguins locate their prey and individual predator-prey dynamics are necessary to elucidate the effects of variable prey resources on penguins and differences in Adélie and gentoo penguin foraging depths and strategies. Finally, with recent and projected increases in storm frequency, future studies should test for influences of wind on water column stability, krill distributions, and penguin dive depth/location, which could influence chick mass and survival through the quantity of food delivered to a chick and provisioning rates. Many factors that we consider to be characteristic of Adélie penguins (ex. philopatry, inflexible behaviors) may hold true under stable climate conditions but disturbance or climate shifts may lead to uncharacteristic responses of Adélie penguins (ex. dispersal, behavioral adaptations). Understanding climate-induced changes in behavior could be important to understanding penguin responses and change the way we think about climate-species relationships.
REFERENCES

Boersma PD, Rebstock GA (2014) Climate change increases reproductive failure in magellanic penguins. PLOS one 9: e85602


Appendix A

CHAPTER 1 SUPPLEMENTAL MATERIALS

A.1 Methods

A.1.1 Penguin satellite transmitter deployment details

We instrumented penguins with satellite transmitters based on a custom SPLASH tag configuration (Wildlife Computers Redmond, WA, USA). Satellite transmitters had a pressure sensor to measure dive depths (resolution of 0.05m and accuracy of 2m) and dive data was recorded at 1 Hz. Penguins selected for instrumentation were paired and had brood-stage nests containing two chicks. Satellite transmitters were attached to the anterior body feathers using waterproof tape and small plastic cable ties. The transmitters had a sloped frontal area of 17×18 mm (306 mm²), weighed 55 g, had an antenna length of 12 cm and tag length of 86 mm. The transmitters represented < 2% of the penguins body mass and were rotated to new penguins every 3-5 days depending on weather conditions.

A.1.2 Penguin dive behavior analysis

The penguin location data were filtered following the methods of (Oliver et al. 2013) to remove inaccurate location data due to erroneous terrestrial positions, unreasonable locations based on maximum sustained swimming speed (8 km/hr) (Ainley 2002) and coastal geometry. We corrected for drift in TDR depth sensors using recursive filtering and a diving threshold in the diveMove package (Luque 2007)
in R (R Development Core Team 2014). We time-matched dive records to location data and linearly interpolated between Argos locations to have an approximate location for all depth data. Penguin diving behavior varies between day and night (Miller et al. 2010). Therefore, we removed all dives that occurred during civil twilight (when the sun is less than 6° below the horizon) (Pütz & Cherel 2005) because few dives occurred during this time and dives were generally shallower. In addition, the REMUS did not sample during civil twilight.

We classified penguin dives into transit, search and foraging dives (Fig. A.2). A transit dive is a near-surface traveling behavior with a duration < 20s (Chappell et al. 1993) or a maximum depth < 5m (Kokubun et al. 2010; Takahashi et al. 2003). The dive duration was the time span between the start and end of the dive between the first and last surfacing (Rodary et al. 2000).

Foraging dives were longer dives with wiggles, bottom time or plateaus (Fig. A.4). Wiggles are vertical undulations in the dive profile that reflect prey pursuit or encounters (Bost et al. 2007; Kirkwood & Robertson 1997). A wiggle was defined as a deviation in depth > 2 m (error range on tag) with the vertical speed getting through 0 (Bost et al. 2007; Rodary et al. 2000). The number of wiggles was likely underestimated because many wiggles had a vertical depth change of < 2m (Bost et al. 2007). Bottom time occurred during the flat part of a dive or near the maximum depth (Wilson 1995; Chappell et al. 1993). Bottom time was the amount of time spent within 85% of the maximum depth (also known as the ledge) (Wienecke et al. 2007; Pütz & Cherel 2005; Kirkwood & Robertson 1997). We calculated the time spent below the ledge and considered foraging to occur if the time spent below the ledge was greater than 25% of the total dive duration. At depths shallower than the
ledge, plateaus were events that were relatively long (temporal) and horizontal (spatial), and often consisted of wiggles (Halsey et al. 2007; Ropert-Coudert et al. 2000). Plateaus can occur during the descent, ascent, or can be a long and horizontal phase between two deep diving periods (Halsey et al. 2007; Ropert-Coudert et al. 2000). We defined a plateau as a period having an overall variation in depth of less than 10% of the maximum dive depth (Halsey et al. 2007) and occurring for more than 25% of the dive duration. Previous studies have used a more lenient threshold of 10% (Halsey et al. 2007) but we found a higher threshold to be more appropriate and allowed us to focus on dives where intense prey pursuit likely occurred. Foraging dives had bottom time, 2 or more wiggles (Wilson et al. 1996), a plateau, or were > 90 seconds (6, 9).

V-shaped dives are typically search or exploratory dives, where the penguin does not spend a significant amount of time at any one depth. These dives consisted of no bottom time, < 2 wiggles, no plateaus and < 90 seconds. We calculated the penguins swimming speed (descent/ascent rate) as the change in depth divided by time. The average rate of descent (ROD) was calculated between the surface and the ledge (85% of the maximum depth). The average rate of ascent (ROA) was after the maximum depth and between the ledge and the surface. If bottom time was present, the average ROD had to be < 0.7 m/s (Rodary et al. 2000) to be considered a search dive. This threshold assumes that a foraging penguin dives at a steeper angle or greater ROD to a foraging depth compared to a traveling or searching penguin.

A.1.3 Dense and diffuse aggregation detection

The REMUS AUV missions ranged from 2 to 9 hrs (mean 6.8 ± 1.8 hr) where the REMUS traveled 13 to 54 km (mean 40.3 ± 10.7 km). The average speed was 1.6 ±
0.07 m/s. The REMUS undulated in a seesaw pattern between the surface and ~60m at a pitch of 6°, while occasionally pausing at the surface for a GPS fix. The REMUS was equipped with a Neil-Brown CTD, Wetlabs ECO-series backscatter/fluorometer, Satlantic downwelling irradiance OCR-5071 sensor and Satlantic upwelling radiance OCR-507R sensor. The wavelengths for the OCR sensors are centered at 412, 442, 490, 532, 555, 669, and 683 nm and were converted into photosynthetically available radiation (PAR) from downwelling irradiance. Data from all these sensors were averaged into 1 m depth bins.

Acoustic backscatter was also measured using an upward- and downward-looking 1200-kHz RD Instruments Workhorse Navigator acoustic Doppler current profilers (ADCP). The ADCPs provided relative acoustic backscatter (S_v) as an estimate of scattering volume, instead of current velocities. The range limits on the ADCP were restricted to 8.75 m (upward-looking ADCP) and 6.75 m (downward-looking ADCP) due to high acoustic noise in the system. S_v measurements were binned vertically into 0.25 m depth bins and horizontally into 8 m bins. All acoustic measurements taken at depths < 5 m were removed due to high surface noise and measurements from the downward-looking ADCP that could have resulted from bottom reflections were eliminated.

From acoustic measurements, we first identified dense aggregations that likely consisted of densely grouped krill, fish or other zooplankton. A running 5 m vertical median was taken for each day (Moline et al. 2010). The points at which a bin crossed above the daily median were used to define the upper and lower edges of the aggregation (Benoit-Bird et al. 2010). The local background value was defined as the average value of these two crossing points (Benoit-Bird et al. 2010). A bin was
considered a dense aggregation when values of the bin exceeded 1.2 times the local background (18). The minimum size of a dense aggregation was a height of at least 1 m (4 vertical bins) or a width of ~16 m (2 horizontal bins). If an aggregation was simultaneously measured on the upward and downward looking ADCP, it was considered one aggregation. All aggregations were visually examined to confirm detection.

Kril, zooplankton and fish can also occur in less densely aggregated groups or layers, which would produce a lower acoustic return. To detect this type of diffuse aggregation, we removed all dense aggregations from the acoustic dataset. We calculated a new median and used the same methodology as described above to identify diffuse aggregations.
Table A.1: Summary of performance parameters for dense and diffuse aggregation presence-absence models using the information-theoretic model comparison approach. (AIC: Akaike Information Criterion, ΔAIC: difference from lowest AIC, Akaike weight representing relative model support or probabilities, AUC: area under the curve, PCC: percent correctly classified). Models with a substantial support (ΔAIC < 2) are in bold. Variables in the models: CHLmax: chlorophyll maximum, depth_CHLmax: depth of the chlorophyll maximum, MLD: mixed layer depth, density_MLD: density at the mixed layer depth, isolume: 1 W/m² isolume, surface_PAR: Photosynthetically available radiation at the surface, integrated_CHL: integrated chlorophyll above 50 m, thermocline: depth of greatest change in temperature, temp_above: mean temperature above the thermocline, temp_below: mean temperature below the thermocline)
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Table A.2: REMUS and aggregation sampling information. The number of dense and diffuse aggregations detected by the REMUS in comparison to total number of profiles sampled. Due to missing data or multiple aggregations detected in one profile, the number of profiles with dense and diffuse aggregations is often less than the number aggregations detected.

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Figure A.1: Kernel density estimates of foraging locations for (A) Adélie penguins breeding on Humble Island (blue diamond), (B) gentoo penguins breeding on Biscoe Point (green diamond), and (C) diffuse and (D) dense aggregations detected acoustically by the REMUS near Palmer Station (yellow diamond). The white or black 50% contour lines represent the core foraging areas of penguins, and the primary area with aggregation detections. The maps were produced in R (R Development Core Team 2014).
Figure A.2: During diurnal (D) and semidiurnal (SD) tides, we measured physical and biological properties within the Adélie penguin foraging habitat (top panel), gentoo penguin foraging habitat (middle panel) and the overlapping region where both species foraged (bottom panel). The horizontal lines represent the mean depth of the CHL_{max}, the 1 W/m^2 isolume and mixed layer depth (MLD) within profiles with diffuse or dense aggregations within each respective penguin foraging contour (Fig. 1BD). The kernel density estimate of the depth of (A) diffuse and (B) dense aggregations within the Adélie foraging habitat, (C) diffuse and (D) dense aggregations within the gentoo foraging habitat, and (E) diffuse and (F) dense aggregations within the overlapping region where both species forage. Due to small sample size during diurnal tides, the depth of aggregations are shown as horizontal lines in EF. The 95% confidence interval is shown around each kernel density estimate. Sample size (n) in each panel represents the number of aggregations during each respective tidal regime.
Figure A.3: Comparison of Adelie dive depth distributions in areas that overlap and don't overlap with gentoo penguins during semidiurnal tides. (A) The kernel density estimate foraging and maximum dive depths within the overlapping region of the gentoo foraging habitat (Adélie n=1, gentoo n=3). (B) The kernel density estimate of the Adélie penguin dive depths in the area of non-overlap. The 95% confidence interval is shown around each kernel density estimate. Sample size (n) represents the number of penguin dives.
Figure A.4: Comparison of search and foraging dive behaviors. Foraging behaviors include plateaus (b, e), wiggles (b, d, e), or bottom time (c, d). The gray horizontal line represents the ledge or 85% of the maximum depth for each dive.
Figure A.5: Comparison of Chlorophyll (CHL, green) and acoustic scattering (black) profiles with depth (R = 0.96). This example shows the high correlation between CHL and acoustic scattering for a profile where an aggregation was not detected.
Figure A.6: Similar krill size class frequency distributions between Adélie and gentoo penguin diet samples during 2011.
REFERENCES


Luque SP (2007) Diving behaviour analysis in r. R news 7:8–14


Appendix B

CHAPTER 2 SUPPLEMENTAL MATERIALS

B.1 Methods

B.1.1 Converting Antarctic Krill size classes into energy density and sex/maturity stages

Below, we review the methodology of Chapman et al. (2010), as well as the exceptions and assumptions that we made, to calculate the mean wet-mass energy density (WED) of krill consumed by chicks each year. We created two scenarios based on average sea ice conditions in the region (static scenario; sWED) and the influence of sea ice on the krill reproduction cycle (dynamic scenario; dWED). First, the length at maturity function (Siegel & Loeb 1994) calculates the proportion of mature males \((m)\) and females \((f; P_{m/f,n})\) in each size class \((n)\):

\[
P_{m/f,n} = \frac{1}{1 + e^{-K_{m/f} (T_L - L_{50,m/f})}} \quad \text{Equation 1}
\]

\(K_{m/f}\) controls the rate of increase in the proportion of sexually mature krill \((k_m = 0.6; k_f = 0.83; \text{Siegel and Loeb 1994})\), \(T_L\) is the mean total length (mm) of krill within each size class \((n)\) and \(L_{50,m,f}\) is the length where 50% of krill reach sexual maturity \((L_{50m} = 42\text{mm}; L_{50f} = 34\text{mm}; \text{Siegel and Loeb 1994})\). Altering these variables had no effect (<0.01 kg) on simulated CFM (Chapman et al. 2010); therefore, these parameters remained fixed.
The total proportion of mature males and females ($T_{m/f}$) in the population from size class distributions for each year:

$$T_{m/f} = \sum_{1}^{N} P_{m/f,n} R_{m/f} SC_n$$

Equation 2

$R_{m/f}$ is the sex ratio in the population ($R_m = 0.5, R_f = 0.5$). We assumed no active selection of female krill over males (Fraser & Hofmann 2003, Salihoglu et al. 2001). $SC_n$ is the proportion of the krill population within each size class, which we measured from Adélie penguin diet samples. The proportion of immature krill is the proportion that was not accounted for by mature males or females.

The proportion of mature males and females that participate in spawning ($SP_{m/f}$):

$$SP_{m/f} = T_{m/f} SP_{m/f}$$

Equation 3

$SP_{m/f}$ is the proportion of mature males and females that spawn. Variability in the percentage of male and female spawners had no effect on CFM (Chapman et al. 2010). Due to the high interannual variability of the region, between 10-100% of mature krill actually spawn (Quetin & Ross 2001, Siegel & Loeb 1995). The intensity of krill reproduction is a function of adequate food availability or primary production during the time of ovarian development, which has been related to spring sea ice extent and timing of ice retreat (Quetin & Ross 2001, Quetin et al. 2007). In the Palmer Station region, average sea ice extent and retreat are ideal for high reproductive output, but late retreat causes a shortage of food during ovarian development and early retreat produces the worst conditions for primary production.
and krill reproduction (Quetin and Ross 2001). For the static scenario, we assumed all
mature krill spawn. For the dynamic scenario, we assumed 90% of krill spawn under
average ice retreat, 70% spawn under late retreat and 50% spawn under early
retreat.

Since gravid female krill lose ~54% of their lipid content during spawning
(Clark 1980), the proportion of gravid females ($P_{\text{gravid}}$) in the diet was calculated for
each day of the chick-rearing period:

$$P_{\text{gravid}}(t) = T_f e^{-(t-s_{pk})^2/S_{dur}}$$

Equation 4

t is time (days). Our simulation began at chick hatching (day 1) and ended at
the beginning of the starvation period (day 50), which occurs 3 to 7 days before
fledging when parents stop feeding their chicks (Trivelpiece et al. 1987, Ainley 2002,
Chapman et al. 2010). $S_{pk}$ is the peak spawning day where the maximum proportion
of gravid mature females occurs, $S_{dur}$ is the spawning duration, i.e. the period in
which >50% of the spawning females are gravid, and $T_f$ is the proportion of spawning
females (Equation 2). Before peak spawning ($S_{pk}$), $P_{\text{gravid}}$ was equal to $T_f$, which
assumed all spawning mature females were gravid. After peak spawning, the
proportion of spent females was the difference between the proportion of spawners
($T_f$) and current proportion of gravid females ($P_{\text{gravid}}$). The average lipid content of a
spawning female was 28% dry mass and a spent female was 18% (Clark 1980, Virtue
et al. 1996, Hagen et al. 1996). For each day, the proportion of gravid/spent females
was multiplied by the corresponding lipid content and then the sum of the product
was taken. After the 50-day simulation, we computed the mean dry-mass lipid
content for mature females. We did not account for interannual variability in the
length of the starvation period or duration of the chick rearing period, which could affect chick mass (Chapman et al. 2010).

According to Chapman et al. (2010), the date of peak spawning and timing of seasonal lipid accumulation had the greatest influence on CFM. For the static ice scenario, $S_{pk}$ was set to January 20 and $S_{dur}$ was 60 days (Quetin & Ross 2001). An early ice retreat associated with a late phytoplankton bloom can delay krill spawning due to slower oöcyte maturation (Quetin et al. 2007). Conversely, a late ice retreat and early bloom promote early spawning. For the dynamic ice scenario, peak spawning ($S_{pk}$) was on January 20 during an average ice retreat, it was 2 weeks later for an early retreat, and 2 weeks earlier for a late retreat.

Variations in $S_{pk}$ and $S_{dur}$ altered the amount of high-lipid gravid and low-lipid spent females in the diet. Delaying or advancing peak spawning by other time intervals (1 or 3 weeks) produced WEDs within ± 0.1 KJ/g for each year and were highly correlated ($\rho > 0.97$) to the 2-week interval. Chapman et al. (2010) noted that changing $S_{dur}$ (17-99 days) had up to a 90 g effect on CFM. Thus, we created static ice scenarios with an $S_{dur}$ of 20 and 100 days; both scenarios produced WEDs that were within ± 0.1 KJ/g per year and highly correlated ($\rho > 0.95$), so $S_{dur}$ for the static ice scenario was held constant at 60 days. To approximate spawning characteristics for the dynamic ice scenario, $S_{dur}$ was 100 days for late retreat, 20 days for early retreat and 60 days for average retreat.

The lipid content of mature males and immature krill typically increases over the austral summer in preparation for over-wintering (Quetin & Ross 1991, Hagen et al. 1996). The lipid content of immature krill is greater than mature males and spent females but less than gravid females. We created a time varying
l lipid content for mature males and immature krill based on average lipid content before and after the peak spawning date. The average lipid content before peak spawning was 10% dry mass for mature males and 16% for immature krill; after peak spawning the average lipid content was 21% for mature males and 24% for immature krill (Clark 1980, Virtue et al. 1996, Hagen et al. 1996). For the static ice scenario ($S_{pk}$ = Jan 20), chicks consumed more krill before peak spawning than after peak spawning (64% time before $S_{pk}$ vs. 36% time after). For the dynamic ice scenario, where peak spawning varied with the timing of ice retreat, the ratio of time (before : after) peak spawning for average, late and early retreat was 0.64:0.36, 0.36:0.64, and 0.92:0.08, respectively. For each year, the proportion of time spent consuming male/immature krill was multiplied by the respective time varying maturity stage lipid content. This value was the mean dry-mass lipid content for mature males and immature krill.

Lastly, dry-mass energy density ($E_{kdm}$, kJ/kg) for the krill population was calculated for each year ($t$):

$$E_{kdm}(t) = \sum_{l=1}^{n} P_{ms}(t)L_{ms}(t)LED$$

Equation 5

$p_{ms}$ is the proportion of each sex/maturity stage in the population ($n$), $L_{ms}$ is the dry-mass lipid content of each sex/maturity stage and LED is the lipid energy density, which converts lipid content to energy density ($LED=0.0395$; (Clark 1980). We converted dry-mass energy density into WED (kJ/g) by dividing $E_{kdm}$ by 0.216 (Ikeda & Mitchell 1982).
In estimating WED, we had to make a number of assumptions in computing the relative proportion of mature male and female krill and the proportion of spawners. Chapman et al. (2010) found CFM was most sensitive to variation in the timing of spawning, which we controlled for in the dynamic ice scenario by changing the timing of spawning dependent on the timing of sea ice retreat. Dynamic WED was higher and more variable than static WED, which largely resulted from changing the proportion of spawning mature krill (Fig. B.2). In contrast, altering spawning duration and peak spawning date had only a small effect on WED (<0.1 kJ/g), making these WED scenarios highly correlated (ρ >0.95, p<0.05). We found that CFM was not correlated to sWED (ρ =0.08) or dWED (ρ =0.07) and was moderately correlated to the proportion of immature krill from the static (ρ =0.36, p = 0.09) and dynamic scenario (ρ =0.33, p = 0.11) when 2001 was eliminated (a year of anomalous weather events). SWED and dWED were not correlated (ρ =0.10) while both scenarios for immature krill were highly correlated (ρ =0.76, p<0.05)(Fig. B.2). Additionally, dWED and the proportion of immature krill from the dynamic scenario were significant predictor variables in our stepwise regression models (Table 2.1). We expected the dynamic ice scenario to be more important because of the known influence of sea ice dynamics on the krill reproduction cycle (Quetin & Ross 2001). Therefore, we focused on the dynamic scenario for WED and the proportion of immature krill throughout this paper.
Table B.1: The number of days with specific weather conditions were determined during the chick-rearing period according to the following criteria. The minimum/maximum air temperature refers to the minimum/maximum recorded on each day.

<table>
<thead>
<tr>
<th>Weather Condition</th>
<th>Threshold</th>
<th>Reference/Justification</th>
</tr>
</thead>
<tbody>
<tr>
<td>High Wind</td>
<td>mean &gt; 6 m/s</td>
<td>Chapman et al. (2011)</td>
</tr>
<tr>
<td>Cold Air Temperature</td>
<td>minimum &lt; 0°C</td>
<td>Chapman et al. (2011)</td>
</tr>
<tr>
<td>High Air Temperature</td>
<td>maximum &gt; 7°C</td>
<td>Chappell et al. (1990)</td>
</tr>
<tr>
<td>Chill factor</td>
<td>minimum temp. &lt; 0°C &amp; mean wind speed &gt; 4 m/s</td>
<td>Chapman et al. (2011); &gt; 4 m/s is a moderately high wind speed</td>
</tr>
<tr>
<td>Heat Stress</td>
<td>maximum temp. &gt; 7°C &amp; mean wind &lt; 1.5 m/s</td>
<td>Chappell et al. (1990); &lt; 1.5 m/s is a low wind speed</td>
</tr>
<tr>
<td>No Precipitation</td>
<td>precipitation = 0 cm</td>
<td>Assumed any precipitation could negatively impact chicks</td>
</tr>
</tbody>
</table>
Table B.2: Variable transformations to remove significant trends over time or to achieve normality.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Transformation</th>
<th>Justification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Air temperature</td>
<td>Detrended; log transformed</td>
<td>Negative linear trend; skewed</td>
</tr>
<tr>
<td>Mean wind chill</td>
<td>Detrended</td>
<td>Negative linear trend</td>
</tr>
<tr>
<td>U wind component</td>
<td>Detrended</td>
<td>Positive linear trend</td>
</tr>
<tr>
<td>Days with zero precipitation</td>
<td>Detrended</td>
<td>Positive linear trend</td>
</tr>
<tr>
<td>V wind component</td>
<td>Square root transformed</td>
<td>Skewed</td>
</tr>
<tr>
<td>Solid precipitation</td>
<td>Square root transformed</td>
<td>Skewed</td>
</tr>
<tr>
<td>High wind</td>
<td>Square root transformed</td>
<td>Skewed</td>
</tr>
<tr>
<td>Chill factor</td>
<td>Log transformed</td>
<td>Skewed</td>
</tr>
<tr>
<td>Cold temperature</td>
<td>Log transformed</td>
<td>Skewed</td>
</tr>
<tr>
<td>CRH suitability</td>
<td>Log transformed</td>
<td>Skewed</td>
</tr>
</tbody>
</table>
Figure B.1: Correlogram showing correlation coefficients using Spearman’s rank correlation rho from 1989 to 2011. For legibility, the values range from -100 to 100 but can be interpreted as Spearman’s rank correlation rho, which ranges from -1 to 1. Each correlation is displayed by color and intensity of shading where warm colors indicate a negative correlation and cool colors indicate a positive relationship. The variables in the correlogram include: chick fledging mass (CFM), Antarctic Oscillation (AAO), El Nino 3.4 (N3.4), Antarctic Dipole (ADP), Southern Oscillation Index (SOI), chick-rearing habitat suitability (CRH), air temperature (Temp), u wind component (Uwind), v wind component (Vwind), wind speed, wind chill, solid precipitation (SolidPrecip), number of days without precipitation (NoPrecip), seasonal fraction of diurnal tides (Tide), sea ice extent (IceExtent), krill wet-mass energy density (WED) from the dynamic (dWED) and static scenario (sWED), and the proportion of immature krill in the dynamic (dImm) and static scenario (sImm). Days with high winds, cold temperatures, high temperatures, heat stress, chill factor, and mean wind chill were not included in the figure because they were collinear, and mean air temperature and mean wind speed had a higher correlation to CFM. Sea ice duration and retreat day were also not included because they are collinear with sea ice extent. Temp, NoPrecip, and Uwind were detrended.
Figure B.2: Interannual variability in (a) WED and (b) the proportion of immature krill as calculated in the static (circles) and dynamic ice scenario (squares).
REFERENCES


Appendix C

CHAPTER 3 SUPPLEMENTAL MATERIALS

C.1 Methods

C.1.1 Environmental Data

To estimate the environmental conditions necessary for successful chick-rearing, we used sea ice concentrations (SIC), sea surface temperatures (SST), chlorophyll concentrations (CHL), and bathymetric data from multiple data sources (Fig. C.1). Since these environmental parameters were measured on different spatial scales, each parameter was interpolated to the same 25 x 25 km polar stereographic grid surrounding the Antarctic continent (ftp://sidads.colorado.edu/pub/DATASETS/seaice/polar-stereo/tools/). Then, we created annual climatologies for each environmental parameter consisting of the penguins’ chick-rearing period (December-February). Using these annual climatologies, we estimated the rate of change during the chick-rearing period for SIC (1978-2010), SST (1981-2010), and CHL (1978-1986, 1997-2010) using the slope of the linear regression over time. Significant changes in these environmental parameters over time were assessed at the 0.05 level (Fig. 3.2). All analyses and statistics were carried out in R (www.r-project.org, R Development Core Team, 2004).

From 1978-2011, SIC were obtained from NSIDC’s Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR) and the Defense Meteorological

CHL data from 1978-1986 were acquired from the Coastal Zone Color Scanner (CZCS) (http://oceandata.sci.gsfc.nasa.gov/CZCS/Mapped/Monthly/4km/chlor/); from 1997-2007 from Sea Viewing Wide Field of View Sensor (SeaWiFS; http://oceandata.sci.gsfc.nasa.gov/SeaWiFS/Mapped/Monthly/9km/chlor/); and from 2008-2011 from the MODIS Aqua sensor (http://oceandata.sci.gsfc.nasa.gov/MODISA/Mapped/Monthly/4km/chlor/). All statistical analyses using CHL data were computed in log_{10} units.

SST data from 1981-1984 was obtained from the NOAA Advanced Very High Resolution Radiometer (AVHRR; ftp://podaac-ftp.jpl.nasa.gov/allData/avhrr/L3/pathfinder_v51/monthly/day/04km/) and from 1985-2009 (ftp://podaac-ftp.jpl.nasa.gov/allData/avhrr/L3/pathfinder_v5/monthly/day/04km). In addition, SST data from 2010-2011 was obtained from NASA’s MODIS Aqua satellite (http://oceandata.sci.gsfc.nasa.gov/MODISA/Mapped/Monthly/4km/SST/).

Bathymetry data was obtained from the International Bathymetric Chart of the Southern Ocean (http://www.ngdc.noaa.gov/mgg/aboutmgg/oceanmapping.html).
**Table C.1:** 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.

<table>
<thead>
<tr>
<th></th>
<th>All Adélie</th>
<th>WAP Adélie</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mean AUC</strong></td>
<td>.89 ± 0.001</td>
<td>.95 ± 0.001</td>
</tr>
<tr>
<td><strong>SST Percent Contribution</strong></td>
<td>14.4 ± 0.39</td>
<td>50.9 ± 0.39</td>
</tr>
<tr>
<td><strong>Sea Ice Percent Contribution</strong></td>
<td>40.5 ± 0.32</td>
<td>7.3 ± 0.25</td>
</tr>
<tr>
<td><strong>Bathymetry Percent Contribution</strong></td>
<td>45.1 ± 0.39</td>
<td>41.8 ± 0.39</td>
</tr>
</tbody>
</table>
FIGURES

Figure C.1: Mean (a) SIC, (b) SST and (c) CHL around Antarctica during the austral summer (Dec-Feb).

Figure C.2: (a) Sea ice percent and (b) SST training data for CRH models for continental Adélie, WAP Adélie, gentoo and chinstrap penguins.
Figure C.3: Alternative view of niche spaces defined by SIC, SST and bathymetry for continental Adélie penguins, WAP Adélie penguins, gentoo penguins and chinstrap penguins similar to Fig. 3.4. Video available: http://bit.ly/1UHI9JX
Figure C.4: 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 C.5: 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 C.6: Significant changes in log_{10} CHL from 1997-2011 around Antarctica during the austral summer (Dec-Feb). Black areas indicate non-significant trends at the 0.05 level.
Figure C.7: Probability density of CHL concentrations from 1997-2011 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 non-parametric Kruskal-Wallis test and a multiple comparison test after Kruskal-Wallis. Letters denote non-significant 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 C.8: Mean CRH suitability for Adélie penguins from each CRH model output from 1982-2010. Red areas indicate suitable conditions while dark blue areas are unsuitable conditions. The WAP, a region of rapid change, is highlighted in the bottom left corner.
Figure C.9: Mean CRH suitability for gentoo penguins from each CRH model output from 1982-2010. Red areas indicate suitable conditions while dark blue areas are unsuitable conditions. The WAP, a region of rapid change, is highlighted in the bottom left corner.
Figure C.10: Mean CRH suitability for chinstrap penguins from each CRH model output from 1982-2010. Red areas indicate suitable conditions while dark blue areas are unsuitable conditions. The WAP, a region of rapid change, is highlighted in the bottom left corner.
Figure C.11  Significant changes in CRH suitability from 1982-2010 for Adélie penguins. Warm colors indicate an increase in suitability while cool colors display regions with decreases in suitability. Black areas indicate non-significant trends at the 0.05 level. The WAP, a region of rapid change, is highlighted in the bottom left corner.
Figure C12: Significant changes in CRH suitability from 1982-2010 for gentoo penguins. Warm colors indicate an increase in suitability while cool colors display regions with decreases in suitability. Black areas indicate non-significant trends at the 0.05 level. The WAP, a region of rapid change, is highlighted in the bottom left corner.
Figure C.13: Significant changes in CRH suitability from 1982-2010 for chinstrap penguins. Warm colors indicate an increase in suitability while cool colors display regions with decreases in suitability. Black areas indicate non-significant trends at the 0.05 level. The WAP, a region of rapid change, is highlighted in the bottom left corner.
Appendix D

CHAPTER 4 SUPPLEMENTAL MATERIALS

D.1 Methods

D.1.1 Environmental variables

Similar to Cimino et al. 2013, from 1978-2011, sea ice concentration (SIC) was obtained from NSIDC’s Nimbus-7 Scanning Multichannel Microwave Radiometer and the Defense Meteorological Satellite Program’s Special Sensor Microwave/Imager. Sea surface temperature (SST) data was obtained from the NOAA Advanced Very High Resolution Radiometer (AVHRR) from 1981-2009 and NASA’s MODIS Aqua satellite from 2010-2011. There was no discontinuity in the SST data when satellite platforms changed from AVHRR to MODIS Aqua (Cimino et al. 2013). Bare rock locations were obtained from Landsat 8; this data is included in the Antarctic Digital Database.

We used climate projections from GFDL climate version 2.1 (CM2.1) because it was considered to be one of four best models for gauging penguin habitat (Ainley et al. 2010) and GFDL climate version 2.6 (CM2.6) is similar to CM2.1 but makes high-resolution projections of Antarctic coastal climate unlike more widely used models assessed by the Intergovernmental Panel on Climate Change (IPCC). GFDL-CM2.1 and CM2.6 are coupled atmosphere-ocean-land-sea ice global models. CM2.1 uses a nominal 1.0º grid spacing and has been widely used as part of the IPCC (Delworth et
CM2.6 is a higher-resolution model that uses a nominal 0.10° grid spacing, with improved representation of the ocean mesoscale and is a more accurate simulation compared to the previous suite of Climate Models in version 2.0–Ocean (Winton et al. 2014; Griffies et al. 2015; Delworth et al. 2012). Only CM2.1 included eddy parameterization in the ocean component.

### D.1.2 Penguin chick-rearing habitat suitability models

We modeled the suitability of Adélie penguin chick-rearing habitats using two species distribution modeling approaches, a maximum entropy approach (MaxEnt version 3.3.3k; Phillips et al. 2006) and generalized additive models (GAMs, BIOMOD package (Thuiller 2003). Both approaches are capable of fitting complex surfaces and non-linear relationships. MaxEnt uses presence-only locations and pseudo-absences from background data to compute the maximum entropy distribution. GAMs predicted habitat suitability using a binomial error structure and presence-absence (PA) locations. Although it is unadvised to use presence-only methods (MaxEnt) when PA data is available, we found it informative to compare results from MaxEnt and GAMs. We excluded duplicate presence records from our training dataset, which resulted from merging colony locations onto our large-scale grid. We fit MaxEnt models with default settings (Cimino et al. 2013), and when necessary, increased the regularization parameter to smooth fitted relationships. When changing the regularization, we chose settings that limited complex fits through visual inspection of response curves and used a multiplier of 2.6 (Elith et al. 2010). The GAMs used smoothing splines as the smoother functions with 3 knots to avoid over-fitting.

For both modeling approaches, we used a cross-validation resampling procedure with four replicate runs that partitioned 75% of the penguin colonies into
the fitting fold and 25% of the colonies into the left out fold (Cimino et al. 2013). This allowed for assessment of predictive performance on the held-out folds using the area under the receiver operating characteristics curve (AUC). The AUC is an indicator of the accuracy of the models, where 1 represents a model with perfect performance and 0.5 indicates a model that is no better than random (Hosmer & Lemeshow 2000). In MaxEnt, jackknife tests were used to quantify which environmental predictors are contributing the most to fitting the model. For GAMs, we estimated the importance of each predictor variable as described by (Thuiller et al. 2009). In all models, the species prevalence was set to 0.147, which is the true prevalence of Adélie penguins in the Southern Ocean on our polar stereographic grid. We compared MaxEnt and GAM predictions (Fig. D.20), fitted response functions (Figs. D.21,D.22), variable importance and AUC (Table D.2).

**D.1.3 Matching novel climate and chick-rearing habitat suitability to penguin colony locations**

From 1981-2010, we matched predicted trends in CRHS from MaxEnt and GAMs to colony locations and compared trends in CRHS in different Antarctic sectors. We also determined the number of years with novel climate for each coastline pixel, which was also matched to documented population trends. If novel climate occurred at a colony with a population status, we determined the main cause for that novel climate: warm SST, cool SST or high SIC (low SIC was not a category because the lowest SIC (zero sea ice) was documented). We used a nonparametric Kruskal–Wallis test to determine if there were significant differences between documented penguin population statuses and the number of years with novel climate. We also used a multiple comparison test after Kruskal–Wallis to determine if the number of years
with novel climate differed between population groups. For future climate projections, we matched novel climate to current colony locations to understand how conditions at those colonies could change in the future.

D.2 Supplemental Results

To verify and understand the sensitivity of species distribution model predictions (Fig. D.2), we tested different combinations of PA datasets (all = full dataset, Cont = only continental locations; Fig. D.1) and used two species distribution model approaches (MaxEnt and GAMs) (Fig. D.20). Mean CRHS from respective GAM and MaxEnt models were highly correlated (Pearson correlations, r > 0.95, p < 0.05). We compared trends in CRHS from respective GAM and MaxEnt models and found ALL PA and Cont P/All A were highly correlated (r > 0.90, p < 0.05), Cont P/A were significantly correlated (r = 0.71, p < 0.05), and All P/Cont A had a lower, yet significant correlation (r = 0.39, p < 0.05). A noticeable difference between MaxEnt and GAMs appears in the Cont P/A example in which MaxEnt produces results more similar to All P/A compared to the respective GAM. In general, the high correlations between MaxEnt and GAM predictions agree with other studies demonstrating the high correlation between presence-only MaxEnt and PA GAM results (Hijmans & Graham 2006) but we also show that model results are more similar when PA data is complete. All models performed well (area under the curve (AUC) > 0.85, Table D.2) and predicted trends in suitability were higher at locations with available bare rock, which is necessary for nesting (Fig. D.23, D.24). The trends in CRHS by Antarctic sector at present, absent, and no bare rock locations highlight how model predictions deviate based on given PA data (Fig. D.24). Predictions can be further explained by response curves (Fig. D.21, D.22) and variable importance (Table D.2).
The WAP is a warmer environment compared to the continent (Fig. 1), and thus, represents a different environmental niche that Adélie penguins occupy. Models that did not include WAP absence or pseudo-absence data over-predicted mean and trends in CRHS in the WAP (ex. Cont P/A and more so for All P/Cont A, Fig. D.20). The response curves show a change in the right hand tail of the SST distribution when WAP absence data was excluded (Fig. D.21, D.22). SST and SIC observations that were outside the range of the model training data, caused the models to extrapolate into novel climate. For All P/Cont A, excluding absence data along the warmer WAP resulted in higher suitability predictions for all WAP locations because the model has information that the penguin colonies are present within this SST and SIC range. Furthermore, losing absence data across part of the range (All P/Cont A) appears more harmful than losing presence data across part of the range (Cont P/All A). This can be seen in the mean CRHS and trends in CRHS in which CRHS did not substantially change when WAP presence data was excluded (All P/A vs. Cont P/All A) while much higher CRHS was seen along the WAP when WAP absence data is excluded (All P/A vs. All P/Cont A) (Fig. D.20 b,d). This highlights the importance of having absence data throughout the entire environmental range that a species occupies and the sensitivity of species distribution models to input PA data (also noted by Elith et al. (2010)). Overall, models varied more based on treatment of PA data than modeling method (as concluded by Elith et al. (2010)).

Similar model output using true absences and pseudo-absences indicates the MaxEnt models and GAMs produced valid results. We are not suggesting that other studies use MaxEnt when PA data are available (also see Guillera-Arroita & Lahoz-Monfort (2014)) but rather, in our case MaxEnt performed similar to GAMs. We also
suggest using caution when solely using the AUC as a metric for determining model performance. In our study, all of our models had an AUC > 0.85 but we know the models extrapolated into novel climate, especially when PA data was incomplete. In ecology, it is rare to have true PA data as in this study, which makes it important to evaluate the distribution of your PA data, and response curves, in relation to your projection environment.
Table D.1: Climate models and groups from the Intergovernmental Panel on Climate Change (IPCC) assessment report (AR5) and two additional NOAA GFDL models that we used in our analyses.

<table>
<thead>
<tr>
<th>Model</th>
<th>Modeling group</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACCESS1-0</td>
<td>CSIRO (Commonwealth Scientific and Industrial Research Organisation, Australia), and BOM (Bureau of Meteorology, Australia)</td>
</tr>
<tr>
<td>ACCESS1-3</td>
<td>CSIRO (Commonwealth Scientific and Industrial Research Organisation, Australia), and BOM (Bureau of Meteorology, Australia)</td>
</tr>
<tr>
<td>CCSM4</td>
<td>National Center for Atmospheric Research</td>
</tr>
<tr>
<td>CESM1-BGC</td>
<td>National Science Foundation, Department of Energy, National Center for Atmospheric Research</td>
</tr>
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<td>CESM1-CAM5</td>
<td>National Science Foundation, Department of Energy, National Center for Atmospheric Research</td>
</tr>
<tr>
<td>CMCC-CESM</td>
<td>Centro Euro-Mediterraneo per I Cambiamenti Climatici</td>
</tr>
<tr>
<td>CMCC-CM</td>
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</tr>
<tr>
<td>CNRM-CM5</td>
<td>Centre National de Recherches Meteorologiques / Centre Europeen de Recherche et Formation Avancees en Calcul Scientifique</td>
</tr>
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<td>GFDL-CM3</td>
<td>NOAA Geophysical Fluid Dynamics Laboratory</td>
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<td>-------------------------------------------------------------------------------------------------</td>
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<td>Institut Pierre-Simon Laplace</td>
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</tr>
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<td></td>
<td>Atmospheric and Ocean Research Institute (The University of Tokyo), and National Institute for</td>
</tr>
<tr>
<td></td>
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<td>MPI-ESM-MR</td>
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<td>GFDL-CM2.6</td>
<td>NOAA Geophysical Fluid Dynamics Laboratory</td>
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</table>
Table D.2: Variable importance (VI, %) and area under the curve (AUC) for Generalized Additive Models (GAMs) and MaxEnt models (mean ± standard deviation) with different combinations of presence-absence (P/A) data (Cont = continental).

<table>
<thead>
<tr>
<th></th>
<th>All P/A Model</th>
<th>Cont. P/ All A Model</th>
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<th>All P/ Cont A Model</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GAM</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VI Bare Rock</td>
<td>54.69 ± 1.97</td>
<td>47.20 ± 1.56</td>
<td>67.5 ± 3.25</td>
<td>68.87 ± 3.23</td>
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<tr>
<td>VI SST</td>
<td>22.38 ± 2.53</td>
<td>26.17 ± 1.64</td>
<td>24.52 ± 8.84</td>
<td>30.07 ± 4.21</td>
</tr>
<tr>
<td>VI Ice</td>
<td>22.93 ± 3.69</td>
<td>26.64 ± 2.49</td>
<td>7.98 ± 6.87</td>
<td>1.06 ± 1.11</td>
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<tr>
<td>AUC</td>
<td>92.12 ± 1.85</td>
<td>95.50 ± 1.41</td>
<td>95.25 ± 1.67</td>
<td>95.94 ± 1.14</td>
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<tr>
<td><strong>MaxEnt</strong></td>
<td></td>
<td></td>
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<tr>
<td>VI Bare Rock</td>
<td>85.85 ± 0.89</td>
<td>77.37 ± 0.53</td>
<td>91.33 ± 0.61</td>
<td>41.5 ± 1.6</td>
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<tr>
<td>VI SST</td>
<td>6.44 ± 0.81</td>
<td>13.07 ± 0.49</td>
<td>4.54 ± 0.86</td>
<td>44.74 ± 1.37</td>
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<tr>
<td>VI Ice</td>
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<td>9.55 ± 0.51</td>
<td>4.12 ± 0.66</td>
<td>13.75 ± 0.69</td>
</tr>
<tr>
<td>AUC</td>
<td>86.6 ± 0.14</td>
<td>91.46 ± 0.15</td>
<td>89.76 ± 0.31</td>
<td>90.71 ± 0.55</td>
</tr>
</tbody>
</table>
FIGURES

ACCESS1-0, 2011–2099

a

b

Mean CRHS

Change in CRHS

Number of Years with Novel Climate
Figure D.1: Novel climate and Adélie penguin chick-rearing habitat suitability (CRHS) according to ACCESS1-0. (a) The number of years with novel climate, (b) mean CRHS and (c) trends in CRHS from General Additive Models using all presence-absence data from 2011-2099. Black outlines represent significant changes over time (p < 0.05).
Figure D.2: Novel climate and Adélie penguin chick-rearing habitat suitability (CRHS) according to ACCESS1-3. (a) The number of years with novel climate, (b) mean CRHS and (c) trends in CRHS from General Additive Models using all presence-absence data from 2011-2099. Black outlines represent significant changes over time (p < 0.05).
Figure D.3: Novel climate and Adélie penguin chick-rearing habitat suitability (CRHS) according to CESM1-BGC. (a) The number of years with novel climate, (b) mean CRHS and (c) trends in CRHS from General Additive Models using all presence-absence data from 2011-2099. Black outlines represent significant changes over time (p < 0.05).
Figure D.4: Novel climate and Adélie penguin chick-rearing habitat suitability (CRHS) according to CESM1-CAM5. (a) The number of years with novel climate, (b) mean CRHS and (c) trends in CRHS from General Additive Models using all presence-absence data from 2011-2099. Black outlines represent significant changes over time ($p < 0.05$).
Figure D.5: Novel climate and Adélie penguin chick-rearing habitat suitability (CRHS) according to CMCC-CM. (a) The number of years with novel climate, (b) mean CRHS and (c) trends in CRHS from General Additive Models using all presence-absence data from 2011-2099. Black outlines represent significant changes over time (p < 0.05).
Figure D.6: Novel climate and Adélie penguin chick-rearing habitat suitability (CRHS) according to MICOC-ESM. (a) The number of years with novel climate, (b) mean CRHS and (c) trends in CRHS from General Additive Models using all presence-absence data from 2011-2099. Black outlines represent significant changes over time ($p < 0.05$).
Figure D.7: Supplemental Figure 7. Novel climate and Adélie penguin chick-rearing habitat suitability (CRHS) according to NORESM1-M. (a) The number of years with novel climate, (b) mean CRHS and (c) trends in CRHS from General Additive Models using all presence-absence data from 2011-2099. Black outlines represent significant changes over time (p < 0.05).
Figure D.8: Novel climate and Adélie penguin chick-rearing habitat suitability (CRHS) according to GFDL-CM2.6. (a) The number of years with novel climate, (b) mean CRHS and (c) trends in CRHS from General Additive Models using all presence-absence data from model runs 1-79. Black outlines represent significant changes over time ($p < 0.05$)
Figure D.9: Variability in novel climate and Adélie penguin chick-rearing habitat suitability (CRHS) from 2011-2099. (a) The standard deviation of number of years with novel climate, (b) standard deviation of CRHS and (c) standard deviation in trends in CRHS from an ensemble of global climate models in Fig. 4.2.
Figure D.10: The cumulative number of years with novel climate from ACCESS1-0 at Adélie penguin colonies in different Antarctic sectors from 2006-2099. Location map of Adélie penguin colonies and bare rock locations. Each climate model time-series is colored by the current population trend. The ensemble mean shows the average number of years with novel climate for all colonies in a sector. Pie charts show the proportion of colonies in each sector that have no novel climate (none) or the leading cause of novel climate is due to warm sea surface temperature (SST), cool SST or high sea ice concentration.
Figure D.11: The cumulative number of years with novel climate from ACCESS1-3 at Adélie penguin colonies in different Antarctic sectors from 2006-2099. Location map of Adélie penguin colonies and bare rock locations. Each climate model time-series is colored by the current population trend. The ensemble mean shows the average number of years with novel climate for all colonies in a sector. Pie charts show the proportion of colonies in each sector that have no novel climate (none) or the leading cause of novel climate is due to warm sea surface temperature (SST), cool SST or high sea ice concentration.
Figure D.12: The cumulative number of years with novel climate from CESM1-BGC at Adélie penguin colonies in different Antarctic sectors from 2006-2099. Location map of Adélie penguin colonies and bare rock locations. Each climate model time-series is colored by the current population trend. The ensemble mean shows the average number of years with novel climate for all colonies in a sector. Pie charts show the proportion of colonies in each sector that have no novel climate (none) or the leading cause of novel climate is due to warm sea surface temperature (SST), cool SST or high sea ice concentration.
Figure D.13: The cumulative number of years with novel climate from CESM1-CAM5 at Adélie penguin colonies in different Antarctic sectors from 2006-2099. Location map of Adélie penguin colonies and bare rock locations. Each climate model time-series is colored by the current population trend. The ensemble mean shows the average number of years with novel climate for all colonies in a sector. Pie charts show the proportion of colonies in each sector that have no novel climate (none) or the leading cause of novel climate is due to warm sea surface temperature (SST), cool SST or high sea ice concentration.
Figure D.14: The cumulative number of years with novel climate from CMCC-CM at Adélie penguin colonies in different Antarctic sectors from 2006-2099. Location map of Adélie penguin colonies and bare rock locations. Each climate model time-series is colored by the current population trend. The ensemble mean shows the average number of years with novel climate for all colonies in a sector. Pie charts show the proportion of colonies in each sector that have no novel climate (none) or the leading cause of novel climate is due to warm sea surface temperature (SST), cool SST or high sea ice concentration.
Figure D.15: The cumulative number of years with novel climate from MIROC-ESM at Adélie penguin colonies in different Antarctic sectors from 2006-2099. Location map of Adélie penguin colonies and bare rock locations. Each climate model time-series is colored by the current population trend. The ensemble mean shows the average number of years with novel climate for all colonies in a sector. Pie charts show the proportion of colonies in each sector that have no novel climate (none) or the leading cause of novel climate is due to warm sea surface temperature (SST), cool SST or high sea ice concentration.
The cumulative number of years with novel climate from NORESM1-M at Adélie penguin colonies in different Antarctic sectors from 2006 to 2099. Location map of Adélie penguin colonies and bare rock locations. Each climate model time-series is colored by the current population trend. The ensemble mean shows the average number of years with novel climate for all colonies in a sector. Pie charts show the proportion of colonies in each sector that have no novel climate (none) or the leading cause of novel climate is due to warm sea surface temperature (SST), cool SST or high sea ice concentration.
Figure D.17: The cumulative number of years with novel climate from GFDL-CM2.6 at Adélie penguin colonies in different Antarctic sectors. GFDL-CM2.6 ranges from year 1-79 where atmospheric CO₂ increases by 1% per year and atmospheric CO₂ doubles at year 70 (gray dashed line) in the model simulation. Location map of Adélie penguin colonies and bare rock locations. Each climate model time-series is colored by the current population trend. The ensemble mean shows the average number of years with novel climate for all colonies in a sector. Pie charts show the proportion of colonies in each sector that have no novel climate (none) or the leading cause of novel climate is due to warm sea surface temperature (SST), cool SST or high sea ice concentration.
Figure D.18: Comparison of CMIP5 and two additional NOAA GFDL models showing austral summer (DJF) sea ice and sea surface temperature (SST) mean bias within 200 km of land around Antarctica. (a) Mean SST bias (model minus observations) and (b) Mean sea ice concentration bias relative to mean observations from the satellite record (1981-2004 SST, 1978-2004 Sea Ice). Mean model output from the CMIP5 models is from the IPCC AR5 historical runs (years 1978-2004). Mean model output from NOAA GFDL’s CM2.1 and CM2.6 is from years 101-140 of the 1990 control simulation (global atmospheric CO$_2$ fixed at the 1990 level). The * symbol indicates the models chosen for further analysis (mean bias within ±1°C and ±20% sea ice, represented by horizontal dashed lines, and GFDL-CM2.6 was chosen because it is a high-resolution model).
Figure D.19: Comparison of CMIP5 and two additional NOAA GFDL models showing austral summer (DJF) sea ice and sea surface temperature (SST) standard deviation bias within 200 km of land around Antarctica. (a) Standard deviation of SST bias (model minus observations) and (b) Standard deviation of sea ice concentration bias relative to mean observations from the satellite record (1981-2004 SST, 1978-2004 Sea Ice). Mean model output from the CMIP5 models is from the IPCC AR5 historical runs (years 1978-2004). Standard deviation of model output from NOAA GFDL’s CM2.1 and CM2.6 is from years 101-140 of the 1990 control simulation (global atmospheric CO₂ fixed at the 1990 level). The * symbol indicates the models chosen for further analysis.
Figure D.20: Comparison of chick-rearing habitat suitability (CRHS) from MaxEnt and Generalized Additive Models (GAM) using different combinations of presence-absence (P/A) data from 1981-2010. Each column specifies which combination of P/A data was used to train the model (Cont = continental). (a) The number of years a pixel had novel climate data, which is data outside the range of the training data. (b) Mean and (c) change in CRHS from MaxEnt models. (d) Mean and (e) change in CRHS from GAMs. Black shading represent significant trends over time (p < 0.05).
Figure D.21: MaxEnt response plot showing the relationship between predicted chick rearing habitat suitability (CRHS) and environmental variables when all other variables were held at their empirical average. Response plot for sea ice, sea surface temperature (SST) and bare rock for models trained on (a) all presence-absence (P/A) data, (b) continental (cont) presence and all absence data, (c) cont presence/absence data, and (d) all presence and cont absence data. The black line is the response curve and the black dashed line is +/- one standard deviation.
Figure D.22: GAM response plot showing the relationship between predicted chick rearing habitat suitability (CRHS) and environmental variables when all other variables were held at their empirical average. Response plot for sea ice, sea surface temperature (SST) and bare rock for models trained on (a) all presence-absence (P/A) data, (b) continental (cont) presence and all absence data, (c) cont presence/absence data, and (d) all presence and cont absence data. The black line is the response curve and the black dashed line is +/- one standard deviation.
Figure D.23: Adélie penguin breeding colonies in the Southern Ocean. The black dashed line separates West Antarctic Peninsula (WAP) from continental Adélie penguin colonies. Bare rock (■) locations along the coastline and light to dark blue represents shallow to deep bathymetry. Penguin colonies were grouped into four Antarctic sectors according to the boxes. AP = Antarctic Peninsula.
Figure D.24: Comparison of trends in chick rearing habitat suitability (CRHS) in four different Antarctic sectors (see map in Supplemental Fig. 7). Trends in CRHS at locations with no bare rock, absent (A) locations, and present (P) locations according to (a) MaxEnt models and (b) Generalized Additive Models (GAMs) trained with different combinations of presence-absence (P/A) data (cont = continental). Note the scale for Maxent trends for All P/Cont A model is different than the other Maxent trends.
REFERENCES


Appendix E

PUBLISHED CHAPTERS OR CHAPTERS SUBMITTED FOR PUBLICATION

Chapter 1, in full, was published:

Climate-driven sympathy may not lead to foraging competition between congeneric top-predators, Cimino, M. A, Moline, M. A, Fraser, W. R., Patterson-Fraser, D. L., and Oliver, M. J. *Scientific Reports*, 6, 2016.

http://www.nature.com/articles/srep18820

Chapter 2, in full, was published (licensed to reproduce):

Large-scale climate and local weather drive interannual variability in Adélie penguin chick fledging mass, Cimino, M.A., Fraser, W.R., Patterson-Fraser, D.L., Saba, V.S., and Oliver, M.J., *Marine Ecology Progress Series*, 513, Copyright©2014, Inter-Research.

http://www.int-res.com/abstracts/meps/v513/p253-268/

Chapter 3, in full, was published:


Chapter 4, in full, was submitted for publication: