Ecological change in the Southern Ocean – Insights from Antarctic seabirds

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Abstract of the Dissertation

Ecological change in the Southern Ocean – Insights from Antarctic seabirds

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Substantial changes in environmental conditions have been observed over the past century, with profound impacts on ecological systems. However, despite considerable efforts to understand how ecosystems are responding to these changes, much remains unknown. Using Antarctic seabirds as a focal study group, I explored several ways in which ecological systems might be changing at the population and community levels, namely, phenology, population dynamics, and food web interactions. I approached this work using a combination of hierarchical statistical modeling, quantitative remote sensing, and laboratory techniques. Findings show that nuance in these ecological processes may have been heretofore ignored, and that previous assumptions regarding how ecological systems respond to environmental change may be unfounded. Phenological dynamics appear to differ substantially from those seen in better-studied temperate systems, and large fluctuations among species within a seabird community suggest that even closely related species may be responding largely independently to environmental fluctuations. No shift in Antarctic food dynamics, as they pertain to the Adélie penguin, is apparent despite abiotic change over the past several decades. Dietary patterns do appear to have implications for penguin population dynamics and provide insight on the impacts of historical resource exploitation in the Southern Ocean. Results highlight the complex and heterogeneous responses of ecological processes to global change, and emphasize the need to synthesize information across time, space, species, and ecosystem to develop a holistic understanding of ecological change.

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To Shyamie

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1 – Introduction

Substantial changes in abiotic environmental conditions have been observed across the globe over the last century (Pachauri et al. 2014). Increasing global temperatures have resulted in a series of cascading effects, ranging from altered precipitation patterns (Dore 2005) to large-scale changes in oceanographic dynamics (Thornalley et al. 2018) to an increase in extreme weather events (Rahmstorf and Coumou 2011). These rapid changes have had profound ecological impacts for a diverse range of taxa in both terrestrial and marine ecosystems (Walther et al. 2002). Range shifts (Pounds et al. 1999, Thomas and Lennon 1999), declines in abundance (Both et al. 2006), and altered species interactions (Chapin III et al. 2000, Suttle et al. 2007) have all been attributed to changes in the abiotic environment. Despite considerable efforts within the ecological community to understand how ecosystems are responding to environmental change, much remains unknown due to the complexity (May 2001) and heterogeneity (Walther et al. 2002) inherent in both ecological systems and the abiotic changes themselves.

Given the regional differences in abiotic change in Antarctica and the surrounding Southern Ocean over the last century (Turner et al. 2005) and the underrepresentation of ecological studies outside temperate systems (Martin et al. 2012), the Antarctic ecosystem represents a key opportunity to better understand the nature of ecological change. The western region of the Antarctic continent is undergoing rapid warming. Mean winter temperatures in some areas have increased more than 5°C over the past 60 years and have been coupled with declines in sea ice. East Antarctica, however, has experienced little change in temperature and an overall increase in sea ice (Mayewski et al. 2009). Changes to atmospheric, oceanic, and cryospheric conditions in the Antarctic are expected to continue into the near future. These will likely substantially modify regional habitat structure (Arrigo and Thomas 2004, McNeil and Matear 2008, Doney et al. 2012), which in turn will impact biological components in the Antarctic system.

Predator species, such as seabirds are often used to better understand the nature of ecological change, as they integrate a large suite of environmental conditions and are relatively easy to monitor (Gaston 2004). In a food web characterized by few trophic levels and relatively low prey diversity (Laws 1985), seabirds represent a key predator group in the Southern Ocean. Throughout the work presented in this dissertation, I used Antarctic seabirds as a focal study group. Particular attention was paid to the responses of the Adélie penguin *Pygoscelis adeliae* to environmental change, though other *Pygoscelis* spp. penguins and some flying Antarctic seabirds were also addressed. The Adélie penguin provided a particularly important perspective into Antarctic ecosystem dynamics as the circumpolar population of 6 million breeding pairs (Che-Castaldo et al. 2017) represents a substantial portion of the seabird biomass in Antarctica (Croxall and Prince 1980).

While there are many ways in which ecological change may be assessed, I took a population- and community-level perspective with this work. Efforts were particularly focused on how the timing of key ecological events (phenology), demographic fluctuations (population dynamics), and trophic interactions (food web processes) are responding to environmental change in the Antarctic. From an abiotic perspective, I focused principally on changes in temperature and sea ice dynamics, given their importance in driving physical processes in this system. I approached these questions using a range of techniques, from hierarchical Bayesian modeling to quantitative remote sensing, applied to data over large spatial and/or temporal scales. The large (often continental, multidecadal) scale at which this work was conducted is critical to making robust inferences on ecological responses to environmental change, particularly given the nonlinearity and multidimensionality of these changes.

In seasonal environments, the timing of ecological events plays a critical role in ecosystem functionality. In recent years, however, ‘phenological mismatches’ have been observed across a number of systems – the result of phenological shifts attributed to changes in the abiotic environment (Visser et al. 2010). These mismatches arise when one element of a system is not temporally ‘in sync’ with another (the result of differences in the rates of phenological change among trophic levels [Thackeray et al. 2010]), resulting in negative fitness consequences. For instance, if periods of high energy requirements for a given organism do not coincide with periods of high energy availability, depressed breeding success may be observed (Kerby et al. 2012). While numerous examples of phenological change exist (Edwards and Richardson 2004, Parmesan 2007), little attention has been paid to phenology or the consequences of a potential mismatch for species in the Antarctic ecosystem. Potential for climate change driven phenological mismatch in the Antarctic ecosystem is apparent, due to the highly synchronized and highly seasonal nature of life history events across multiple trophic levels (Lynch et al. 2012a, Chambers et al. 2013).

Using a circumpolar database of Adélie penguin breeding phenology and satellite-derived data on Antarctic environmental timing, I examined long-term changes in the breeding phenology of the Adélie penguin and assessed the degree to which phenological mismatch is playing a role in demographic processes (Chapter 2). I further examined the role of large inter-annual fluctuations in environmental phenology (sea ice and phytoplankton dynamics) in driving mismatch dynamics in this system and assessed whether the circumpolar comparison of phenological mismatch revealed contrasting impacts of climate change around the Antarctic continent.

In trying to understand how phenology is changing through time and whether a mismatch exists between components of the ecosystem, it is important to assess the degree of phenological variability in the absence of environmental forcing. Studies often attribute phenological variability to extrinsic factors, such as fluctuations in temperature and precipitation (Sparks and

Yates 1997, Tryjanowski, et al. 2003, Parmesan 2007). However, intrinsic factors, such as fixed differences among individuals, and the role of stochasticity in the timing of ecological events are often ignored. A null model of the degree of interannual variability in phenology is needed before proper attribution of phenological drivers can be made. Captive animal populations kept under controlled environmental conditions provide one way of controlling for fluctuating environmental conditions, while individual-level data provides a way of assessing intrinsic differences. Using data from both captive and wild populations of Adélie penguins, I assessed the relative contributions of extrinsic, intrinsic, and stochastic factors in driving penguin breeding phenology, and evaluated what implications these findings have for interpreting phenological variability (Chapter 3).

Ecologists often rely on a subset of physical and biological measures of the environment to attempt to understand the underlying dynamics in complex ecological systems and how these may be changing through time. Demographic measures, such as population size and breeding productivity are several such metrics that are widely used in the ecological research community (Spellerberg 2005). They might provide information on a variety of ecological aspects of interest such as habitat quality and population health (Landres et al. 1988, Landres 1992, Johnson 2007), and are consequently well entrenched in environmental management and conservation. However, these metrics may be chosen based on convenience rather than some set of optimal ecological characteristics (Caro and O'Doherty 1999). It is often not asked how appropriate these metrics are for assessing ecological change. Are indicator metrics actually representative of the ecosystem processes of interest? Demographic metrics, some of the most commonly used measures in ecology, might be indicative of the population status of a species, the population status of other species in the same ecological community, or abiotic or biotic environmental conditions that a given species is experiencing. Using more than three decades of data on breeding success and abundance derived from six Antarctic seabird species, I assessed the generality of demographic measures as indicators (Chapter 4). I evaluated how these measures changed through time, what role environmental factors played in driving these processes, and the degree of synchrony among species in this community.

One of the 'major scientific challenges involving Southern Ocean ecosystems' (Murphy et al. 2012) is addressing how food webs will respond to both changes in the physical environment and growing pressures from direct human pressures, such as a burgeoning Antarctic krill *Euphausia superba* (a principal food resource for Antarctic predators) fishery (Nicol et al. 2012). Antarctic krill dominate the Antarctic marine food web, representing the most connected prey species in the trophic network (de Santana et al. 2013). Because of the limited number of linkages between primary producers and top predators in the Antarctic system, krill provide an efficient pathway of energy transfer throughout the food web. They represent a taxonomic bottleneck in the system, creating a 'wasp-waist' food-web topology – so called due to its resemblance to the body of the insect of the same name (Flores et al. 2012) – in which both predator and primary producer diversity is high, but diversity at intermediate trophic levels is restricted. Due to the high degree of connectivity and relative abundance exhibited by krill, this key industry species is of considerable importance to many Antarctic predators, including penguins (Polito et al. 2011).

Changes in dietary patterns of predator species, such as the Adélie penguin, might indicate a shift in the state of the lower trophic levels of the ecosystem, including krill availability. Because of the intensive nature of many dietary sampling techniques and logistical difficulties, information on Adélie penguin diet is only available for a limited period of time, over limited areas of the Antarctic. While the harsh Antarctic environment presents logistical challenges for research efforts, the unvegetated landscape makes it possible to study seabird dynamics over large spatial and temporal scales from satellite-based sensors (Lynch and LaRue 2014, Schwaller et al. 2018). To assess recent changes in Antarctic food web dynamics, I developed a novel method combining remote sensing, spectroscopy, and stable isotope analysis to monitor Adélie penguin diet over the past 34 years at a continental spatial scale using satellite-derived data (Chapter 5). I explored the role that physical factors such as bathymetry and sea ice have on penguin diet, and the relationship between penguin population growth rates and penguin diet over the entirety of the species' global range.

2 – Circumpolar analysis of the Adélie penguin reveals the importance of environmental variability in phenological mismatch

2.1 – ABSTRACT

Evidence of climate change-driven shifts in plant and animal phenology have raised concerns that certain trophic interactions may be increasingly mismatched in time, resulting in declines in reproductive success. Given the constraints imposed by extreme seasonality at high latitudes and the rapid shifts in phenology seen in the Arctic, it might also be expected that Antarctic species would be highly vulnerable to climate change-driven phenological mismatches with their environment. However, few studies have assessed the impacts of phenological change in Antarctica. Using the largest database of phytoplankton phenology, sea-ice phenology, and Adélie penguin breeding phenology and breeding success assembled to date, I find that while a temporal match between penguin breeding phenology and optimal environmental conditions sets an upper limit on breeding success, only a weak relationship to the mean exists. Despite previous work suggesting that divergent trends in Adélie penguin breeding phenology are apparent across the Antarctic continent, I found no such trends. Furthermore, I found no trend in the magnitude of phenological mismatch, suggesting that mismatch is driven by interannual variability in environmental conditions rather than climate change-driven trends, as observed in other systems. I propose several criteria necessary for a species to experience a strong climate change-driven phenological mismatch, of which several may be violated by this system.

2.2 – INTRODUCTION

The phenological response of biological systems to climate change has received much attention in the scientific literature in recent years (Edwards and Richardson 2004, Parmesan 2007). Of particular concern is the role that climate change may play in altering synchrony among trophic levels, a process structured over millennia of coexistence. Differential rates of change in the phenology of consumers and resources may create a scenario in which peak energy requirements of an organism become temporally uncoupled with peak resource availability. This 'phenological mismatch' may result in decreased fitness (Cushing 1974, Visser and Both 2005) and have long-term repercussions for population dynamics (Ludwig et al. 2006, Miller-Rushing et al. 2010). Impacts associated with phenological mismatch have been observed in a variety of systems (Kerby et al. 2012 and references therein) in a diverse range of taxa including birds (Both et al. 2009, Visser et al. 2012), invertebrates (Winder and Schindler 2004, Both et al. 2009), fish (Durant et al. 2005), and mammals (Post and Forchhammer 2008).

The consequences of phenological mismatch may be exacerbated in high latitude systems by the strong seasonality of the environment, which often necessitates close synchrony among ecological components. At high latitudes a narrow window for reproduction and growth (driven by seasonality) means that even a slight temporal uncoupling between consumers and resources may be detrimental to survival and/or reproductive success (e.g., Ji et al. 2013). While latitude *per se* explains only a small degree of variation in phenological shifts among species, these shifts are generally larger in magnitude at high latitudes (Parmesan 2007). The elevated prevalence of migratory species at high latitudes, also increases the risk of mismatch (Both 2010, Jones and Cresswell 2010). A number of studies have demonstrated the importance of phenological coupling for reproductive success in the Arctic (Post and Forchhammer 2008, Burthe et al. 2012, McKinnon et al. 2012, Clausen and Clausen 2013, Kerby and Post 2013, Doiron et al. 2015). In Antarctica, while the potential for climate-change driven phenological mismatch has generated concern (Forcada and Trathan 2009), few studies have directly addressed this issue.

Within the limited body of literature focused on the phenology of Antarctic species, much attention has been paid to the Adélie penguin (*Pygoscelis adeliae*), a well-studied, circumpolar species that is known to be highly sensitive to anomalous weather and long-term changes in climate (reviewed in Ainley 2002, Ainley et al. 2010). Adélie penguins are colonially breeding seabirds with strong breeding synchrony within a breeding colony (Ainley 2002). Diet of this species during spring and summer is dominated by krill (*Euphausia* spp.), Antarctic silverfish (*Pleuragramma antarctica*), and several other species of fish, the relative proportions of which vary by region and year (Ainley 2002, Trathan and Ballard 2013). Both the spatio-temporal availability and the quality of these prey may be affected by the availability of phytoplankton, which is influenced by the spring phytoplankton bloom (Atkinson et al. 2008, Saba et al. 2014), though seasonal and interannual changes in phytoplankton community composition add complexity to that relationship (cf. Smith et al. 2014, Ainley et al. 2015)12/10/18 9:43:00 PM. Fish prey species commonly eat krill and other crustaceans (La Mesa and Eastman 2012), suggesting that the distribution of fish eaten by penguins may also be related to that of krill (Ainley et al. 1991). Adélie penguin population trends in the Antarctic Peninsula region of West Antarctica have been previously associated with Chlorophyll *a*, a proxy for phytoplankton bloom magnitude (Lynch et al. 2012b). Adélie penguin colony locations in East Antarctica have also been associated with phytoplankton blooms located in coastal polynyas, within which Arrigo and van Dijken (2003) demonstrate an association between colony size and phytoplankton bloom magnitude. The timing of phytoplankton blooms may thus influence the availability and quality of food resources. The timing of sea-ice break-out near breeding grounds can affect penguin access to prey, as too much sea-ice may obstruct access to suitable foraging habitat (Ainley 2002, Olmastroni et al. 2004, Massom et al. 2006, Dugger et al. 2014, Emmerson et al. 2015, Wilson et al. 2016) and too little provides inadequate prey habitat (Atkinson et al. 2008, La Mesa and Eastman 2012, Sailley et al. 2013). Both prey availability and prey quality likely influence

Adélie penguin reproductive success (Ainley 2002, Chapman et al. 2011, Whitehead et al. 2015, Jennings et al. 2016).

Previous studies focusing on patterns in penguin breeding phenology have focused on the possible role that climate change may play in any observed trends (e.g., Barbraud and Weimerskirch 2006, Hinke et al. 2012, Lynch et al. 2012a). Barbraud and Weimerskirch (2006) found a delay (later breeding) in Adélie penguin reproductive phenology in the eastern sector of East Antarctica, which they attributed to changes in sea-ice extent (defined as distance of large scale ice edge from the colony during spring). These findings contrast with trends found in most other organisms, particularly those at high latitudes (Parmesan 2007). Later work, however, indicated that Adélie penguin breeding phenology was, in fact, either not changing (Emmerson et al. 2011; western sector of East Antarctica) or advancing (earlier breeding) over time (Lynch et al. 2012a; Antarctic Peninsula). These disparate trends were attributed to spatial variation in climate change in Antarctica, namely changing wind patterns contributing to rapid warming and declining winter sea-ice coverage on the Antarctic Peninsula and increasing sea-ice coverage in the East Antarctic and Ross Sea sectors of the Southern Ocean (Stammerjohn et al. 2008, 2012, Mayewski et al. 2009, Holland and Kwok 2012). Here I assess the impact of phenological mismatch on Adélie penguin reproductive success using data spanning a significant portion of the global distribution of this species. This provides a unique circumpolar comparison between penguin populations currently experiencing divergent environmental responses to climate change across Antarctica (i.e., decreasing populations on the northern Antarctic Peninsula [Lynch et al. 2012b, Lynch and LaRue 2014], but increasing elsewhere in East and West Antarctica [Ainley et al. 2010, Lyver et al. 2014, Lynch and LaRue 2014, Southwell et al. 2015]).

I assembled a circumpolar database of Adélie penguin breeding phenology and satellite-derived data on the timing of phytoplankton blooms and sea-ice retreat. My aim was to address the following questions: (1) is there evidence for a long-term shift in the timing of key phenological events in the Antarctic marine ecosystem?; (2) is there evidence that a phenological mismatch with environmental conditions causes a decrease in Adélie penguin breeding success (the match-mismatch hypothesis)?; and (3) does the circumpolar comparison of phenological mismatch reveal contrasting impacts of climate change around the Antarctic continent?

2.3 – METHODS

Description of data

The penguin reproductive cycle involves several key events, including arrival at the nest site, initiation of courtship behavior, egg laying, and subsequent hatching of those eggs to produce chicks. For my analysis, I used the mean clutch initiation date (CID – date the first egg was laid in the nest) in each year to characterize the timing of breeding in each of the following populations (see Appendix 1 for details): Admiralty Bay (62.21°S, 58.42°W) and Humble Island (64.77°S, 64.05°W) on the northern Antarctic Peninsula; Cape Crozier (77.45°S, 169.20°E), Cape Bird (77.22°S, 166.43°E), and Cape Royds (78.55°S, 166.17°E) in the Ross Sea sector of Antarctica; and Point Géologie (67.17°S, 140.00°E) and Béchervaise Island (67.58°S, 62.82°E) in the Indian Ocean sector of Antarctica (Figure 2-1). Data collection methods for breeding phenology and breeding success were similar across sites (Appendix 1). Periods of data collection differed among sites, ranging from 13 years (Humble Island) to 34 years (Point Géologie) (see Appendix 1 for details). Breeding phenology data (CID) were accompanied by data on breeding success, defined here as the number of chicks to reach the crèche stage (pre-fledging but chicks independent of parents) per breeding pair. Breeding success data were not available for all years in which phenology data were available (Appendix 1).

To understand how both the biological and physical Southern Ocean environments might influence the breeding phenology and success of Adélie penguins, I also assembled data on phytoplankton-bloom onset and sea-ice retreat (the decrease of sea-ice during spring-summer). Together, these metrics represent the principle measures by which one might define the arrival of spring in this system. Phytoplankton-bloom timing and sea-ice phenology were thought to impact penguin resource availability/quality and the accessibility to these resources, respectively (see above).

As reliable, continuous, regional-scale data on phytoplankton-bloom phenology (ocean color) are not available prior to 1997, I used sea-ice adjusted light as a proxy for the spring phytoplankton-bloom onset (microwave data to assess sea-ice cover are available since 1979). This is calculated by taking the Julian day in which a particular light threshold is reached within a 250 km radius of the colony of interest, and applying a correction for light blocked by local sea-ice (see Li et al. 2016). Previous work has shown this metric to be highly correlated with phytoplankton-bloom phenology, as deduced from ocean color, near penguin breeding colonies (Li et al. 2016). I calculated bloom onset using a 250 km radius, which incorporates the size of most coastal polynyas (Arrigo and van Dijken 2003, Arrigo et al. 2015) and the Adélie penguin foraging areas, as I was interested in a regional indicator of bloom onset. While foraging behavior, including foraging trip distance, differs among sites and years (Ballance et al. 2009), 100-200 km is typically the maximum range at which Adélie penguins forage from breeding colonies during the breeding season (Ainley 2002, Lyver et al. 2011, Oliver et al. 2013, Emmerson et al. 2015). I followed methodology outlined by Li et al. (2016) and used a 10-hour light threshold (see Appendix 1 for details). Sea-ice observations for the correction were obtained from the satellite-based Nimbus 7, SMMR, and SSM/I-SSMIS passive microwave sensors from 1979-2013, processed by the NASA Team algorithm (Cavalieri et al. 1995) at 25 km resolution via the National Snow and Ice Data Center (Cavalieri et al. 1996).

The date of sea-ice retreat around each penguin breeding site was calculated using the aforementioned sea-ice data following the approach of Stammerjohn et al. (2012) (Appendix 1). Date of sea-ice retreat was defined as the first day in which the average sea-ice concentration within a 250 km radius of the breeding site fell below 15%.

Phytoplankton-bloom phenology and sea-ice retreat were used to calculate a ‘Bloom Mismatch Index’ and ‘Sea-ice Mismatch Index’ to represent the magnitude of the phenological mismatch between Adélie penguins and biological (timing of bloom onset) and physical (timing of sea-ice retreat) oceanographic conditions, respectively. The Bloom Mismatch Index was defined as the standardized difference (see Equation 2-1 below) between penguin CID and the phytoplankton-bloom onset at each particular site in a given breeding season (during the austral summer). The Sea-ice Mismatch Index was likewise defined as the standardized difference between penguin CID and the date of sea-ice retreat. Positive (negative) values for the mismatch indices represent a clutch initiation date that is later (earlier) than the long-term average relative to the phenology of the environment. A mismatch index of zero represents no difference from mean mismatch, but does not imply an optimal degree of synchrony (Reed et al. 2013). The timing of the physical and biological environments are intrinsically linked (i.e. non-zero covariance) though the correlation between the Bloom Mismatch Index and Sea-ice Mismatch Index was relatively weak (Pearson’s correlation coefficient = 0.62), prompting the inclusion of both variables in this analysis. I assumed the importance of bloom phenology and sea-ice phenology lies in its relationship to breeding phenology. For this reason, I included Bloom Mismatch Index and Sea-ice Mismatch Index rather than phytoplankton-bloom onset and sea-ice retreat in my analysis.

CID, breeding success, Bloom Mismatch Index, and Sea-ice Mismatch Index (each represented as x_{ij}) were normalized across years (i) and within site (j), using the mean and standard deviation at each site, to create a standardized variable (S) that allows for more meaningful inter-site comparisons:

$$S_{ij} = \frac{x_{ij} - \bar{x}_j}{sd(x_j)} \tag{2-1}$$

Estimating response of breeding success to phenology and environment

The impact of 1) mismatch with the phytoplankton-bloom, 2) mismatch with sea-ice retreat, and 3) penguin breeding phenology on Adélie penguin breeding success were modeled using a quantile regression approach (Koenker and Bassett Jr 1978). While originally developed for econometrics, quantile regression has seen increased use in the field of ecology in recent years (Sankaran et al. 2005, Fujita et al. 2013). Rather than estimating the rate of change in the mean of the response variable distribution as a function of the predictor variables (as in traditional regression), quantile regression estimates the rate of change in a particular quantile of the response variable distribution (Cade and Noon 2003). This holds particular utility for complex relationships in which multiple factors are thought to control or limit a response variable, as is the case with penguin reproductive success. In this way, I sought to determine whether phenological and environmental factors were setting an upper limit on breeding success.

An 85th quantile regression was implemented in a Bayesian framework (see Yu and Moyeed 2001) with the ‘bayesQR’ package (Benoit and Van den Poel 2017) in the R statistical environment (R Core Team 2016). Appendix 2 provides a brief overview of interpreting results derived from Bayesian analyses, but more details can be found in Gelman and Hill (2006). I used the 85th quantile as it is near the upper boundary of breeding success and approximately one standard deviation away from the mean. I used a quadratic polynomial function to model the effect of phenological and environmental predictor variables on penguin breeding success, as I hypothesized the response variable would be maximized at a particular set of parameters. Standardized breeding success z was modeled as:

$$z = \alpha + \beta_1 * X + \beta_2 * X^2 + \varepsilon \tag{2-2}$$

where X is the predictor variable and the error term ε is distributed such that the 85th quantile is zero. Data from all years and sites were used to fit the model. Uninformative normal priors were used for α, β_1, and β_2. Inferences were derived from 10,000 samples drawn following a 'burn-in' period of 40,000 draws using 3 chains. Model convergence was assessed through a visual analysis of the posterior chains, in addition to the use of the Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998). All models unambiguously converged.

Statistical analysis of trends in phenology and Mismatch Index

Temporal trends in the Bloom Mismatch Index, Sea-ice Mismatch Index, and penguin breeding phenology were modeled individually using a hierarchical Bayesian approach, which allowed me to treat missing data in times series as latent states to be sampled and allowed me to better assess parameter estimate uncertainty (Gelman and Hill 2006). Each response variable (y – Bloom Mismatch, Sea-ice Mismatch, and breeding phenology) was modeled as normally distributed with a mean μ_{ij} that is a linear function of year (i) with location (j)-specific slope and intercept. The coefficients of the linear model for μ_{ij} were themselves modeled as normally distributed.

$$\begin{gathered} y_{ij} \sim N(\mu_{ij}, {\sigma_j}^2) \\ \mu_{ij} = \alpha_j + \beta_j * Year_i \\ \alpha_j \sim N(\mu_\alpha, {\sigma_\alpha}^2) \\ \beta_j \sim N(\mu_\beta, {\sigma_\beta}^2) \end{gathered} \tag{2-3}$$

The precision ($1/{\sigma_j}^2$) was given an uninformative gamma prior. The coefficients for mean intercept (μ_α) and slope (μ_β) were given uninformative normal priors, and the associated precisions ($1/{\sigma_\alpha}^2$ and $1/{\sigma_\beta}^2$) given uninformative gamma priors (Appendix 1). Models were fitted using the R package 'R2jags' (Su and Yajima 2015), to interface with JAGS (Plummer 2003) in the R statistical environment (R Core Team 2016). Inferences were derived from 50,000 samples drawn following a 'burn-in' period of 1,900,000 draws using 3 chains and a thinning rate of 2. Model convergence was assessed through a visual analysis of the posterior chains, in addition to the use of the Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998). All models unambiguously converged. For each variable of interest, the differences in β (slope) parameter estimates between each pair of sites were calculated for each iteration of the Markov Chain Monte Carlo. Posterior distributions of these differences were then analyzed to investigate whether trends differed among sites.

2.4 – RESULTS

The Bloom Mismatch Index, Sea-ice Mismatch Index, and penguin breeding phenology showed a robust relationship with the upper limit (85th quantile) of breeding success (Figure 2-2) but explained little variation in the mean response (Table A2-1). The degree of mismatch and breeding phenology each appear to set an upper limit for Adélie penguin breeding success but are poor absolute predictors of breeding success at any one point in time and space (Figure 2-2). Breeding success was maximized in years with slightly earlier breeding phenology and near zero to negative Bloom Mismatch Index and Sea-ice Mismatch Index (Figure 2-2, Appendix 2).

With the exception of Humble Island, I found little evidence of a temporal trend in either Bloom Mismatch Index or Sea-ice Mismatch Index (Figures 2-1, 2-3, Appendix 2). At all sites, the estimated rates of change in the mismatch indices were substantially smaller than the magnitude of interannual variability. Even where trends were greatest (i.e., Humble Island), the estimated rates of change for the Bloom Mismatch and Sea-ice Mismatch Indices were small compared to their interannual standard deviation. Interannual variation in the Bloom Mismatch and Sea-ice Mismatch indices appears to be driven predominantly by phytoplankton-bloom phenology and sea-ice phenology, respectively, rather than by breeding phenology. This is evidenced by: 1) larger interannual variation in both phytoplankton ($\bar{\sigma} = 10.9$ days) and sea-ice phenology ($\bar{\sigma} = 15.7$ days) compared to penguin breeding phenology ($\bar{\sigma} = 2.7$ days); 2) high degrees of correlation between both mismatch indices and their associated non-penguin phenological components (Pearson's correlation coefficients = -0.97, -0.98 for Bloom and Sea-ice respectively); and 3) the weak relationship between penguin breeding phenology and both phytoplankton-bloom phenology (Pearson's correlation coefficient = 0.23) and sea-ice phenology (Pearson's correlation coefficient = 0.19).

I also found large inter-annual variations but no robust temporal trends in Adélie penguin breeding phenology at all seven breeding locations (Figure 2-1, Figure 2-3). Despite previous suggestions of an east-west dichotomy in breeding phenology (through comparison of Barbraud and Weimerskirch [2006] with Lynch et al. [2012a]), resulting from the spatially heterogeneous impacts of climate change in Antarctica, I found no difference in phenology among sites/regions (Appendix 2).

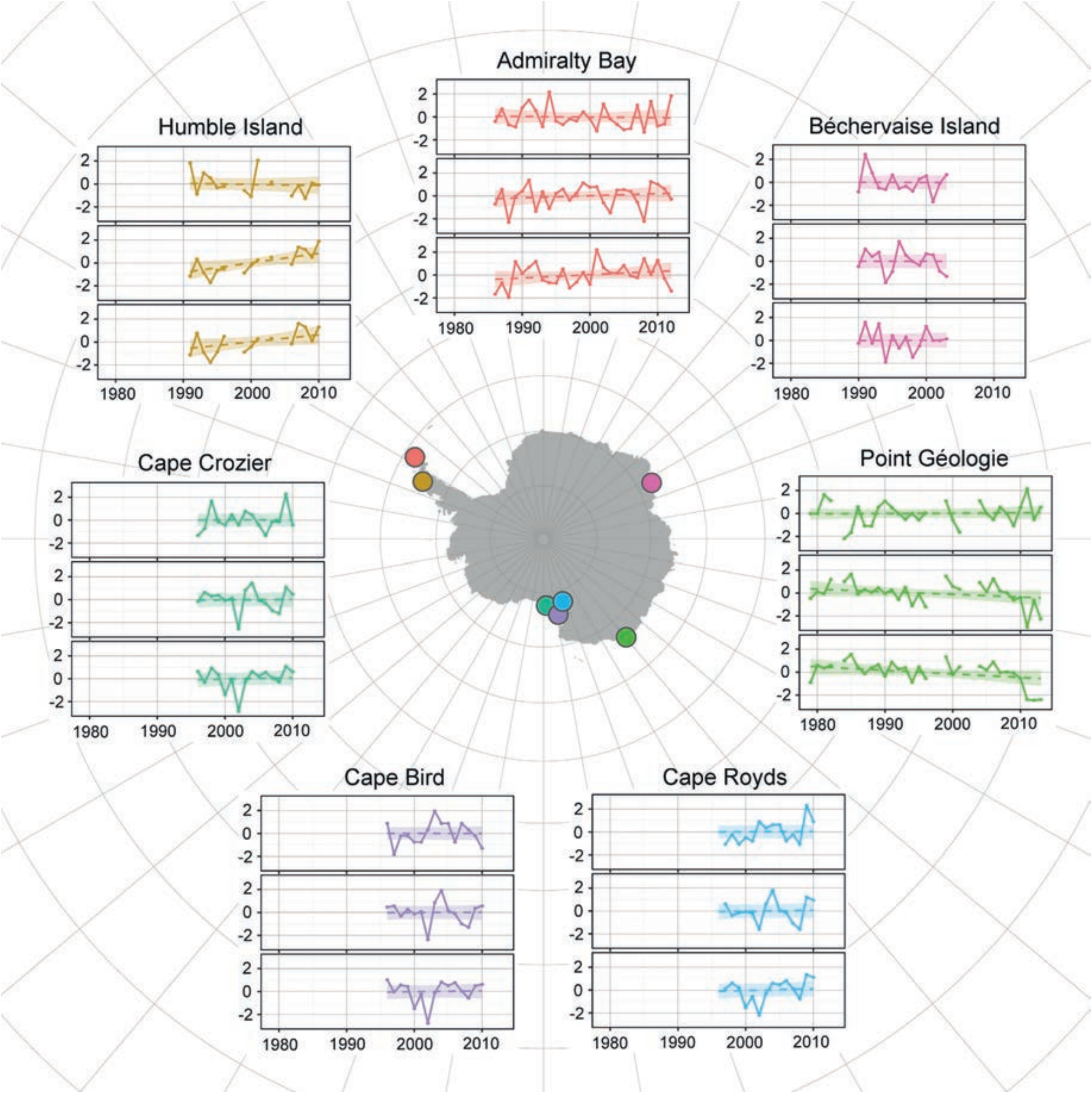

Figure 2-1: Time series for normalized penguin breeding phenology (top panels), Bloom Mismatch Index (middle panels), and Sea-ice Mismatch Index (bottom panels) for each study site. Dashed lines represent model fit. Credible intervals (95%) are denoted by the shaded regions in each plot. Note year *t* represents the austral summer spanning years *t* and *t+1*. Site locations are represented on the map as colored dots.

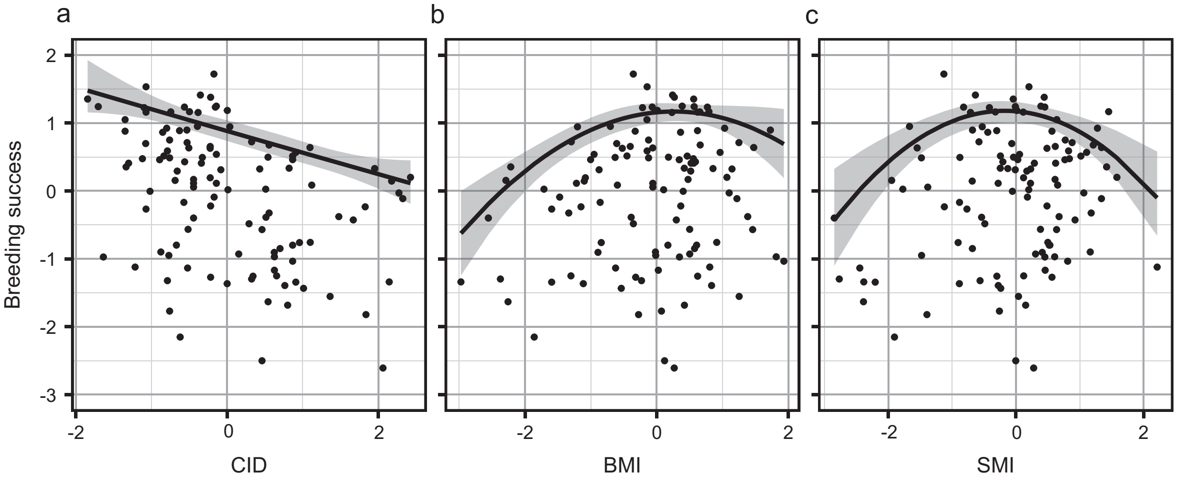

Figure 2-2: Breeding success as a function of a) penguin breeding phenology, b) Bloom Mismatch Index, and c) Sea-ice Mismatch Index. Model fit for 85th quantile regression shown in black with credible intervals (95%) shown in grey. All measures are normalized. Data points from all sites are shown and were used to conduct the analyses.

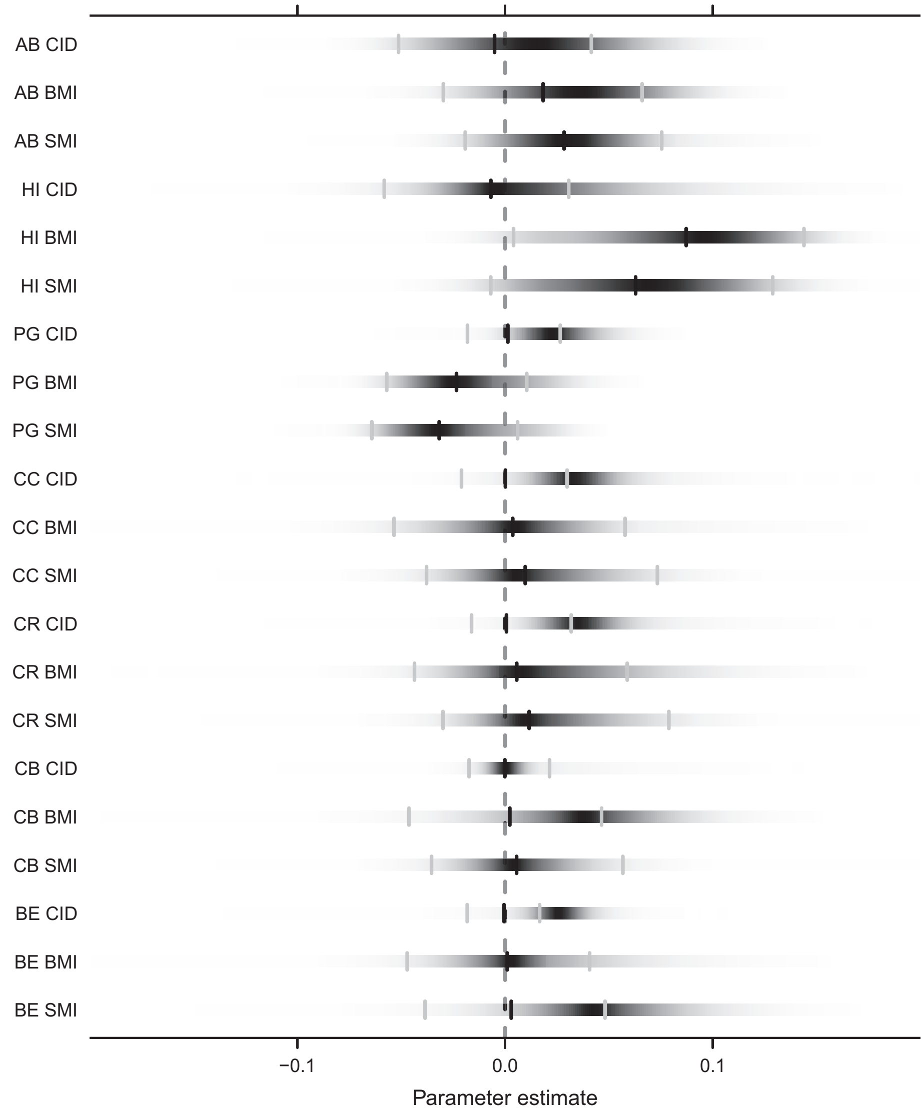

Figure 2-3: Posterior distributions of β (slope) parameters for penguin breeding phenology (CID), Bloom Mismatch Index (BMI), and Sea-ice Mismatch Index (SMI). Posterior means are indicated by black ticks. Credible intervals (95%) are indicated by grey ticks. The dashed line represents 0. Letter codes represent each of the 7 study sites: AB = Admiralty Bay, HI = Humble Island, PG = Point Géologie, CC = Cape Crozier, CR = Cape Royds, CB = Cape Bird, BE = Béchervaise Island.

2.5 - DISCUSSION

In contrast to my initial expectations, and despite contrasting impacts of climate change in Antarctica as a function of region, I found no evidence of a trend in Adélie penguin breeding phenology in any region. I found that while both breeding phenology and phenological mismatch set an upper limit on Adélie penguin breeding success neither had a strong relationship to the mean. The magnitude of phenological mismatch has not changed over the last several decades in this species. I found that phenological mismatch is driven by large interannual and spatially localized variability (i.e., Ainley 2002, Massom et al. 2006, Emmerson and Southwell 2008, Wilson et al. 2016), rather than the climate change-driven environmental trends found in a number of other systems (Kerby et al. 2012 and references therein). I propose several criteria that may be necessary for a strong climate change-driven phenological mismatch, of which several may be violated in the Southern Ocean system.

Trends in phenology and consequences for breeding success

While previous work showed contrasting responses in Adélie penguin breeding phenology between the Antarctic Peninsula and East Antarctica (Barbraud and Weimerskirch 2006, Lynch et al. 2012a), I found no trends in breeding phenology at any site. These results are particularly interesting, as updated and extended versions of the same time series used by Barbraud and Weimerskirch (2006) and Lynch et al. (2012a) are analyzed here (Appendix 1). I attribute the contrast with Lynch et al. (2012a) to the use of an extended time series and different methodology (considering population mean data and only one species) in this analysis (Appendix 3). I attribute the contrast with Barbraud and Weimerskirch (2006) to a differing period of analysis. Breeding phenology at Point Géologie is stable after the late 1970s (Barbraud and Weimerskirch 2006) with a distinct shift in the 1970s/1980s. I hypothesize this change-point may be due to a large-scale regime shift, rather than a continuous trend from the 1950s to the present

(Jenouvrier et al. 2005; Appendix 3). I cannot assess the effect of such a regime shift on penguin breeding phenology at other locations due to lack of phenological data during this time period.

In accordance with previous studies on both the Adélie penguin (Ainley 2002, Smiley and Emmerson 2016) and closely-related gentoo penguin (*Pygoscelis papua*; Hinke et al. 2012), I find that breeding success is maximized when penguins breed earlier (Figure 2-2a), relative to the site average, while later breeding results in a lower ceiling on breeding success. Several mechanisms may explain why the timing of breeding appears to set an upper limit on breeding success. Adélie penguins may breed earlier in years with favorable environmental conditions (e.g., less ice cover close to the colony), which could lead to higher breeding success. Later breeding may result in a shorter period of time in which to raise offspring to sufficient body condition before the molt period and winter migration, a pattern that may be especially true of highest latitude colonies (Ainley et al. 1983, Ainley 2002). Interspecific competition for prey resources among penguins, whales, and seals, may also play a role, but has been little studied and therefore likely under-appreciated (Ainley et al. 2007, Trathan et al. 2012; but see Trivelpiece et al. 2011). While Hinke et al. (2012) suggest declines in food availability in the northern Antarctic Peninsula region did not significantly contribute to a decrease in breeding success observed with delayed breeding (see also Sailley et al. 2013), previous work has demonstrated that the presence of competitors for prey resources may lead to an increase in foraging trip duration (which has been linked to decreased breeding success [Ainley et al. 2006, 2015, Emmerson and Southwell 2008, Emmerson et al. 2015, Wilson et al. 2016]) and prey-switching behavior in the Adélie penguin (Ainley et al. 2006, 2015). Earlier breeding may decrease temporal overlap with prey competitors, many of which are migrants and present only in summer. More information is needed to determine what factors drive the arrival of competitors such as whales and seals, as well as the relationship between competitor and penguin phenology and its effect on penguin breeding success.

Trends in phenological mismatch: the role of environmental variability

As with breeding phenology, a phenological match with the environment appears to be a necessary but not sufficient condition for peak Adélie penguin reproductive success (Figure 2-2b, Figure 2-2c), suggesting that a combination of factors, rather than one in isolation, is required for successful breeding. In this way, Adélie penguins are bound to the Anna Karenina Principle – success does not require that a single condition be met, but rather requires that many conditions of failure be avoided (McClay and Balciunas 2005). It should be noted that the scale at which the environmental variables are measured does weakly influence these results but not my resulting conclusions (Appendix 4).

I found little evidence of trends in the magnitude of phenological mismatch. While marginally non-zero slopes were estimated at some sites (Admiralty Bay and Humble Island), the mean rates of change in phenological mismatch through time are small compared to the large interannual variations observed in this system – any trend in mismatch is unlikely to be biologically significant. The trend observed at Humble Island should additionally be interpreted with caution. Missing data may be related to environmental conditions (heavy sea-ice preventing access to the colony; e.g., Massom et al. 2006) and thus may not be 'missing at random' (Appendix 1). The high degree of ‘noise’ in these time series leads me to conclude that robust trends are not apparent at these sites.

It appears that Adélie penguins do not match the large interannual variations in environmental timing in the Southern Ocean. Rather, it is these year-to-year fluctuations that drive phenological mismatch in this system. This contrasts with the scientific community’s understanding of phenological mismatch in other systems, in which differential shifts in long-term mean phenology are the principal drivers of phenological mismatch (Visser and Both 2005, Durant et al. 2007). Phenological mismatch appears to be the historical condition for Adélie penguin life history, similar to the patterns observed in one insect-host plant system (Singer and Parmesan 2010).

Although I have shown that a mismatch is apparent, it is not the principal driver of reproductive dynamics. Several not-mutually exclusive hypotheses may explain why this might be the case.

1) Adélie penguins (similar to emperor penguins) arrive at breeding colonies with large deposits of body fat (Ainley 2002), which may provide a buffer during mismatched periods. These penguins subsist largely on these reserves during periods of food scarcity (especially early season when extensive sea ice often inhibits ocean access), somewhat exemplifying a 'capital' breeding strategy (Drent et al. 2006).
2) Changes in phytoplankton community composition within a given season may result in the main phytoplankton bloom being uncoupled with penguin prey resources. In the Ross Sea – a region characterized by high-latitude coastal, latent heat polynyas – early phytoplankton blooms tend to be dominated by colonial *Phaeocystis antarctica*, owing to its ability to persist in low light levels (Smith et al. 2014). Blooms of colonial *P. antarctica* generally lead to food webs that do not involve penguin prey resources (Smith et al. 2014; but see Haberman et al. 2003), which may weaken the relationship between the Bloom Mismatch Index and penguin reproductive success in some regions.
3) Adélie penguins feed on prey (krill and several species of fish) that are several years old (Ainley et al. 2003, Fraser and Hofmann 2003, La Mesa and Eastman 2012), which may buffer the response of breeding success to phenological mismatch. Most other systems in

which phenological mismatch has been observed are populated by consumers that feed on annual resources (Miller-Rushing et al. 2010) (e.g., mammals on vegetation, passerines on larval insects, alcids on first year herring, *Clupea* spp.). Unlike these systems, the timing of prey reproduction in a particular year may not seriously affect overall penguin-accessible prey abundance in that same year. While the timing of the phytoplankton bloom and sea-ice retreat may regulate the spatio-temporal availability and quality of prey, overall prey abundance also plays a role in reproductive success (Emmerson et al. 2015).

4) Density-independent processes for the Adélie penguin may mask the effects of phenological coupling. Increased precipitation and unusually high concentrations of sea-ice unrelated to seasonality (such as large tabular icebergs) have both been shown to significantly impact penguin breeding success (Olmastroni et al. 2004, Massom et al. 2006, Bricher et al. 2008, Fraser et al. 2013, Dugger et al. 2014, Barbraud et al. 2015, Wilson et al. 2016) and are largely decoupled from any mismatch with spring phenology.
5) The importance of breeding synchrony among individuals at a breeding site may outweigh the importance of synchrony with the environment, as suggested by Hinke et al. (2012) (see also Young 2005). Penguins may wait for some collective cue among conspecifics to initiate courtship, copulation, and clutch initiation, as strong social facilitation may provide a reprieve from predators or facilitate foraging efforts, which may lead to increased breeding success (Darling 1938, Emlen and Demong 1975, Young 2005). This idea is supported by an analysis of breeding success and breeding synchrony at Admiralty Bay (Appendix 5), where decreased breeding success is observed in years with less synchronous breeding. This suggests that colonial breeding may both hamper

individuals’ capacity to track the environment and reduce the relative importance of doing so.

It is also worth noting that phenological mismatch may exist at the individual level, yet is masked at the population level (Reed et al. 2013, McLean et al. 2016). Some individuals have a tendency to breed early while others have a tendency to breed later (Ainley et al. 1983, Hinke et al. 2012). Years in which environmental timing is particularly late (or early) may benefit some individuals while being disadvantageous for others. Since younger birds tend to breed slightly later than older birds (Ainley 2002), age structure may also influence population level phenology in a way that is uncoupled from environmental conditions.

Conclusion

Evidence presented here suggests that phenological mismatch in Adélie penguins is driven by interannual environmental variability rather than by climate-change driven trends in environmental conditions – a surprising conclusion given the significant rate of environmental change in the Southern Ocean (Jacobs 2006, Stammerjohn et al. 2008). I suggest that mismatch might represent the historical condition in other highly variable systems and that further study is needed in this area. However, much as ‘mountain passes are higher in the tropics’ (Janzen 1967), species that inhabit environments characterized by high interannual variability are likely able to cope with significant asynchrony between life history events and the timing of favorable environmental conditions, effectively diluting the effects of mismatch. This same reasoning suggests that species in these highly variable environments, all else being equal, will be less susceptible to climate change-driven mismatch than species in environments with lower interannual variability.

My findings suggest a set of conditions exists under which strong phenological mismatch is more likely. Populations most vulnerable to mismatch are those that are unable to track the timing of favorable environmental conditions, have rates of reproductive success that are strongly regulated by food availability (strong density-dependence), have an ‘income’ breeding strategy, and use resources characterized by a narrow window of temporal availability (as highlighted by Miller-Rushing et al., 2010). In the face of rapid climate change, phenological change and associated mismatch has garnered much attention. I suggest that the null hypothesis for studies of phenological mismatch should not necessarily be one of no mismatch but should reflect the underlying variability that may be a natural component of the system. The role of phenological mismatch in population processes, the driving forces behind such phenomena, and how these patterns may persist into the future are likely more nuanced than currently accepted by the ecological community.

3 – Rethinking 'normal': The role of stochasticity in the phenology of a synchronously breeding seabird

3.1 – ABSTRACT

Phenological changes have been observed in a variety of systems over the past century. There is concern that, as a consequence, ecological interactions are becoming increasingly mismatched in time, with negative consequences for ecological function. However, substantial spatial heterogeneity (inter-site) and temporal variability (inter-annual) can make it difficult to separate intrinsic, extrinsic, and stochastic drivers of phenological variability. The goal of this study was to understand the timing and variability of breeding phenology of Adélie penguins under fixed environmental conditions, and to use those data to identify a 'null model' appropriate for disentangling the sources of variation in wild populations. Data on clutch initiation were collected from both wild and captive populations of Adélie penguins. Clutch initiation in the captive population was modeled as a function of year, individual, and age to better understand phenological patterns observed in the wild population. Captive populations displayed as much inter-annual variability in breeding phenology as wild populations, suggesting that variability in breeding phenology is the norm and thus may be an unreliable indicator of environmental forcing. The distribution of clutch initiation dates was found to be moderately asymmetric (right skewed) both in the wild and in captivity, consistent with the pattern expected under social facilitation. The role of stochasticity in phenological processes has largely gone unaddressed. However, these results suggest that inter-annual variability in breeding phenology can arise independent of any environmental or demographic drivers and that synchronous breeding can enhance inherent stochasticity. This complicates efforts to relate phenological variation to environmental variability in the wild. This is particularly true for colonial species where breeding

synchrony may outweigh each individual's effort to time breeding with optimal environmental conditions.

3.2 – INTRODUCTION

There is concern that ecological interactions are becoming increasingly mismatched in time as a result of climate change-driven shifts in the timing of key life history events such as migration, foraging, and breeding (Thackeray et al. 2016). Such mismatches may result in decreased fitness (Cushing 1974, Visser and Both 2005) with long-term repercussions for population dynamics (Ludwig et al. 2006, Miller-Rushing et al. 2010, McLean et al. 2016). These asynchronies have been observed in a diverse range of taxa, including arthropods (Winder and Schindler 2004, Both et al. 2009), birds (Both et al. 2009, Visser et al. 2012), fish (Durant et al. 2005), and mammals (Post and Forchhammer 2008) and in a variety of ecological systems (Kerby et al. 2012 and references therein). To better understand and predict how phenological change might impact ecological systems, it is important to recognize what factors drive the timing of these life-history events.

Photoperiod has been identified as a proximate driver of the timing of key life history events in both plants and animals (e.g., animal breeding, animal migration, plant flowering; Hay 1990, Temte and Temte 1993, Bradley et al. 1999, Helm 2009, Zerbe et al. 2012). Studies of phenological variation (inter-annual variation and/or long-term trends), however, have focused on abiotic environmental factors such as temperature and precipitation (Visser et al. 2009, Thackeray et al. 2016), or biotic factors such as body condition, which may reflect environmental conditions and/or prey availability (Bêty et al. 2003; see review in Dawson 2008). Variability in population-level phenology arises by some combination of three factors: (1) extrinsic drivers: changes in environmental (both abiotic and biotic) conditions, including changes in other components of the ecological community (e.g., prey, predators, mutualists); (2)

intrinsic drivers: fixed differences among individuals coupled with demographic turnover within the population; and (3) stochastic variation: seemingly random variation in the timing of breeding of individuals (unrelated to known intrinsic or extrinsic factors) that propagates up to population-level metrics of phenology. Consistent with usage by Lande et al. (2003), I define stochasticity in this context as variability that is either truly random or appears random with respect to factors relevant to the question of interest. While numerous studies have focused on intrinsic and extrinsic drivers of phenology, there has been relatively little attention paid to the role of stochasticity. This lack of attention to stochastic factors is due, in part, to the fact that wild populations are subject to fluctuating environmental conditions, making it difficult to identify forces independent of measureable extrinsic and intrinsic factors.

The scale on which data are collected (i.e., population-level vs. individual-level) also contributes to the challenge of identifying stochasticity. Most studies of phenology in wild populations use population-level summary statistics (such as first or mean timing of a life-history event in a population) due to difficulties associated with collecting individual-level data. Metrics that capture the first instance of an event of interest are known to be problematic due to their sensitivity to population size and sampling frequency (Miller-Rushing et al. 2008). While more robust to these influences, population mean metrics can be affected by other factors such as age (Ainley et al. 1983, Ainley 2002) and random variation among individuals (Crawley and Akhteruzzaman 1988) that, through shifts in demographic composition, can impact population-level statistics. For instance, if older individuals breed earlier, an aging population will display an apparent trend towards earlier breeding (Lewis et al. 2012). Similarly, any random subset of individuals may, by chance, have an earlier or later average phenology than another such random subset of individuals.

Individual-level data, in either wild or captive populations, allows for the assessment of the role of demographic turnover (age and individual effects) on phenological response. An even more comprehensive understanding of the role for stochastic factors in driving phenological variability can be developed by paring studies of wild populations with studies of populations under fixed environmental conditions (Lambrechts et al. 1999, Dunne et al. 2003, Visser et al. 2009). Phenological variability in captive populations kept under fixed conditions represents a null model against which interannual variability in wild populations can be compared. Without such a control group, it may be difficult to determine the extent to which phenological variability is driven by environmental variability or, alternatively, inherent stochasticity. An estimate of inter-annual variation under fixed environmental conditions is, therefore, of value when interpreting phenological studies of wild populations and may be particularly important for colonially breeding species that rely on social cues to synchronize breeding (Ims 1990a).

Here I used long-term data collected from both wild (representing naturally variable environmental conditions) and captive (representing fixed environmental conditions) populations of Adélie penguins *Pygoscelis adeliae*, to identify the role of stochastic factors in driving breeding phenology. Adélie penguins are a site faithful, highly colonial species that inhabit the Antarctic continent and surrounding islands. Several studies (Barbraud and Weimerskirch 2006, Emmerson et al. 2011, Hinke et al. 2012, Lynch et al. 2012a, Youngflesh et al. 2017) have sought to understand the conditions associated with breeding phenology in Adélie penguins. However, despite considerable effort to collect and analyze long-term phenological data, the scientific community's understanding of what drives phenology in this species and the potential role that stochastic factors might play, is limited. My aim was to address three principal questions with this study: 1) how variable is Adélie penguin breeding phenology in the absence of environmental variability; 2) can variation in breeding phenology under fixed environmental conditions be explained by individual variation and age structure, or is there substantial residual random variation that remains unexplained; and 3) what implications do these findings have for interpreting variability in wild populations of synchronously breeding colonial species? Answering these questions will help determine to what degree the scientific community has been overemphasizing the role of exogenous environmental forcing in the phenological variability of some wild populations.

3.3 – METHODS

Description of data

Individual-level data on clutch initiation date (CID – the date in which the first egg is laid in each nest) were obtained for all individuals in a captive Adélie penguin population at SeaWorld San Diego from 1992 - 2015 (89 penguins in total). The number of breeding females in each year varied from 12 to 37 throughout the course of the study. The youngest birds to breed were 2 years of age, while the oldest were 45 years of age. Most penguins (67 of the 89) were born in captivity – individuals born before 1984 were taken as chicks from wild populations in the Ross Sea region of Antarctica in 1976.

All captive penguins were associated with unique identifiers, and metrics for each individual were tracked through time. Temperature at the facility was kept at a constant -4°C to -2°C year-round. Feeding regime of the captive birds did not change over the study period. Nesting materials (stones) were provided on the same date each year. Photoperiod for the exhibit lighting mimicked that of 77°S latitude (though minimal exhibit lighting is required during the winter period), representative of the southern limit of the Adélie penguin breeding range, for each year of the study. The viewing area is setup in such a way to minimize light exposure to the penguin enclosure. The penguin exhibit at SeaWorld underwent a 6-month renovation in 2005. The captive penguin population used in this study was kept in a separate enclosure during this renovation, which may have impacted breeding phenology in that year.

Data on CID were also obtained for a unique set of 100 individuals each year in a wild population of Adélie penguins located at Admiralty Bay, Antarctica (62.2°S, 58.4°W) from 1986-2012 using methodologies outlined in Hinke et al. (2012). Individual-level data across years was not available for the wild population. Wild penguins are typically younger than those in captivity, generally less than 20 years of age (Ainley et al. 1983, Ainley 2002).

Statistical analysis of individual phenology in marked captive penguins

For the captive Adélie penguin time series, a hierarchical Bayesian approach was used to model CID (y_{ij}), with year (i) and individual (j) as random effects (α and β, respectively) and age as a fixed effect (γ):

$$y_{ij} = \mu + \alpha_i + \beta_j + \gamma * AGE_{ij} + \varepsilon_{ij} \tag{3-1}$$

$$\alpha_i \sim N\left(0, {\sigma^2}_{year}\right)$$

$$\beta_j \sim N(0, {\sigma^2}_{individual})$$

$$\varepsilon_{ij} \sim N(0, {\sigma^2}_{model})$$

where μ represents the intercept, AGE represents the age of the female, and ε represents the error term. This model was used to determine whether variation in y_{ij} was driven by the α parameter (variance attributed to a colony-wide effect that varies among years), the β parameter (variance attributed to fixed differences between individuals), the AGE covariate, or the error term (ε). Individual data used in this statistical framework allowed me to account for potential confounding factors related to differences in phenology due to individual identity (or quality) and age, and provide a more complete understanding of these processes than is possible using population-level summary statistics.

Models were fit using the R package ‘rjags’ (Plummer 2016), an interface to JAGS (Plummer 2003), in the R statistical environment (R Core Team 2016). Normal priors were used for α, β, γ, and ε. Broad Gamma priors were used for all precision $\left(\tau = \frac{1}{\sigma^2}\right)$ parameters (shape = 0.01, rate = 0.01). Posterior distributions were derived from three chains with 5,000 samples (after thinning every other draw) following a ‘burn-in’ period of 40,000 draws and an adaptation period of 5000 draws. Model convergence was assessed through a visual analysis of the posterior chains, in addition to the use of the Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998). All models unambiguously converged. Parameter estimate plots were generated using the ‘MCMCvis’ package (Youngflesh 2018) while other plots were generated using the ‘ggplot2’ package (Wickham 2009) in the R statistical environment.

Statistical analysis of population-level phenology in captive and wild penguins

No information on individual phenology across years was available for the wild population (i.e., no information on the β parameter or AGE covariate), leaving it ambiguous as to which component was contributing to the variability in y_{ij} (CID of individual j in year i). Therefore, to directly compare the captive and wild Adélie populations, I considered population-level aggregate summaries of phenology in both populations. The median colony CID in each year (median across individuals; denoted $y_{i\cdot}$) was calculated for both the captive and wild Adélie penguin populations. Between year variation in median phenology, $\sigma^2_{between} = var(y_{i\cdot})$, included variation from all sources (year, individual, age, and unexplained variance as captured by ε). Note that in contrast to ${\sigma^2}_{model}$ in Equation 3-1, $\sigma^2_{between}$ includes variation due to age and individual identity as well as residual stochastic variation unrelated to these factors. For both the captive and wild populations, variation within year i, $\sigma^2_{i,within} = var(y_{ij})$, was used as a measure of year-specific, within-population breeding synchrony. While differences in (simulated) latitude may have generated a fixed difference in photoperiod between the captive and wild populations, this analysis examined only within-site inter-annual variability in breeding phenology.

To investigate whether individual breeding dates within a colony were distributed symmetrically around a population mean, as might be expected *a priori* if individuals were acting independently, CID values in each year were standardized $\left(z_{i\cdot} = \frac{y_{i\cdot} - \bar{y}_{i\cdot}}{sd(y_{i\cdot})}\right)$ and aggregated across years to be analyzed for skewness using a D'Agostino skewness test (D'Agostino 1970). All analyses were performed in the R statistical environment (R Core Team 2016).

3.4 – RESULTS

Inter-annual and intra-annual variance in CID

Inter-annual variance of median colony CID was similar between the captive ($\sigma^2_{between-captive} = 15.8\ [SE = 4.7]$) and wild ($\sigma^2_{between-wild} = 13.5\ [SE = 3.7]$) populations (Figure 3-1). This degree of phenological variability is comparable to that seen in other taxa (Both et al. 2009, Valtonen et al. 2017; Appendix 6). Within year, individual birds were relatively synchronous in both populations, with greater synchrony among individuals in the wild population compared to the captive population ($E[\sigma^2_{within-wild}] < E[\sigma^2_{within-captive}]$; Welch two-sample t-test, t= 4.99, df = 28.5, p < 0.001) (Figure 3-1; Appendix 6).

Individual phenology in marked captive penguins

A strong year effect (α) on CID was apparent for the captive penguin population (Figure 3-2a; $median(\sigma^2_{year})$ = 13.81 [Appendix 6]). Significant year to year variation was found, even when accounting for the effects of age and individual. Inter-annual variation was still substantial when accounting for first-order autocorrelation (Appendix 7). Random effects due to individual (β) were notable (as evidenced by the spread of β parameter estimates), with some individuals breeding consistently earlier/later than other individuals (Figure 3-2b; $median(\sigma^2_{individual})$ = 13.66 [Appendix 6]). Over the 24-year study period, 16 different individuals were the first to lay eggs in a particular year (in 3 of these years, multiple individuals laid eggs on the same day). No biologically significant effect of age (γ) on CID was found (median posterior estimate = 0.06 days/year); the 95% credible interval overlapped 0 (Figure 3-2c). Variance unaccounted for by the model is represented by $median(\sigma^2_{model})$ = 34.96 (Appendix 6).

Intra-annual variance in CID

The distributions of CID for both captive and wild populations (Figure 3-3) had a small but statistically significant right skew ($g_1^{captive}$ = 0.54 [SE = 0.10]; g_1^{wild}= 0.79, [SE = 0.04]; D'Agostino test, $p < 0.001$).

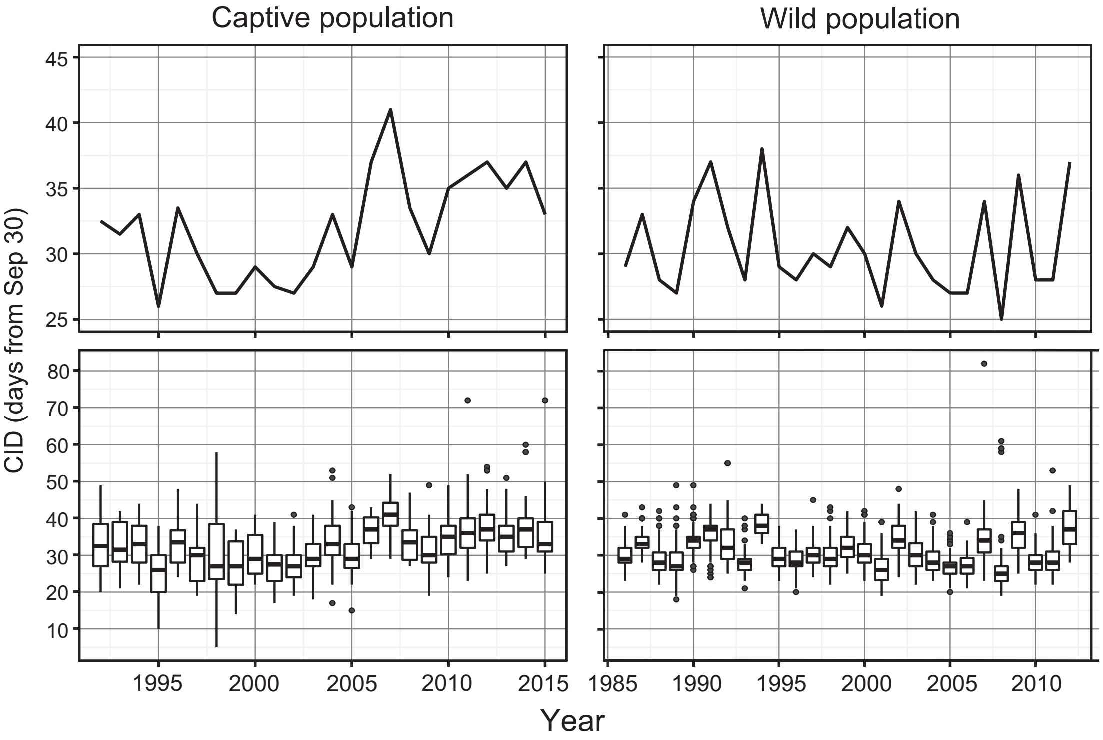

Figure 3-1: Mean colony breeding phenology (top panels) and distribution of individual CID in each year (bottom panels). The bold lines in the box-and-whisker plots represent the median CID while boxes represent the 25th and 75th quantiles. The top and bottom of the whiskers are 1.5 × IQR (inter-quartile range) from the upper and lower boxes, respectively. Data beyond this range are plotted as points. The number of data points per year in the captive population ranged from 13 to 38. One hundred data points were collected for each year in the wild population.

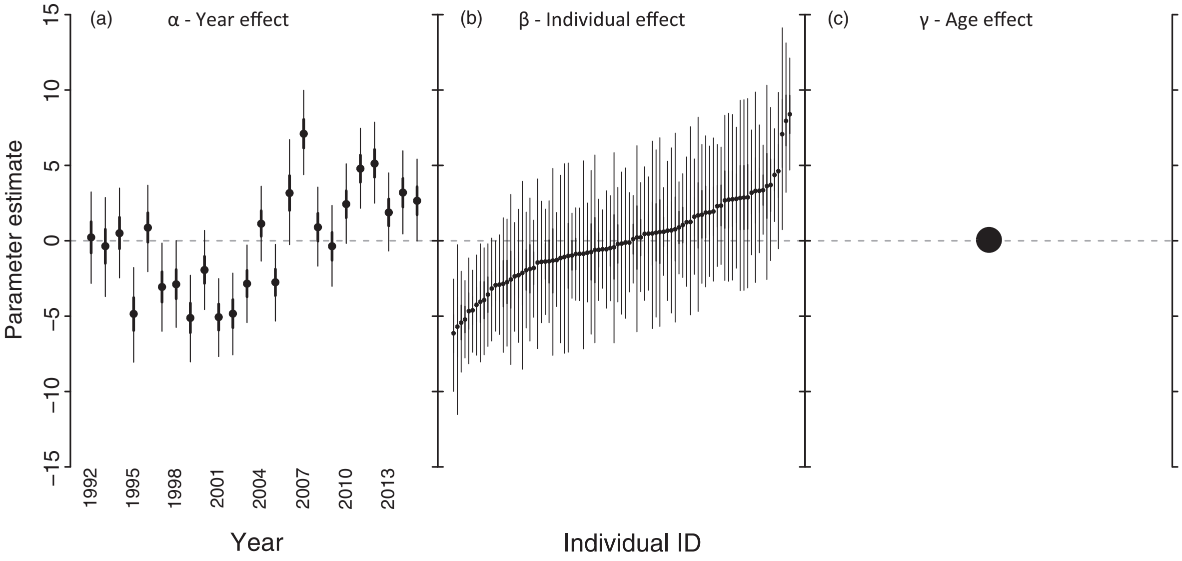

Figure 3-2: Posterior estimates for the captive population parameters: (a) year effect – α; (b) individual effect – β; and (c) age effect – γ parameters (see Equation 3-1). Black circles represent posterior medians. Thicker lines represent 50% credible intervals while thinner lines represent 95% credible intervals. Error bars for the γ parameter are obscured by the point itself.

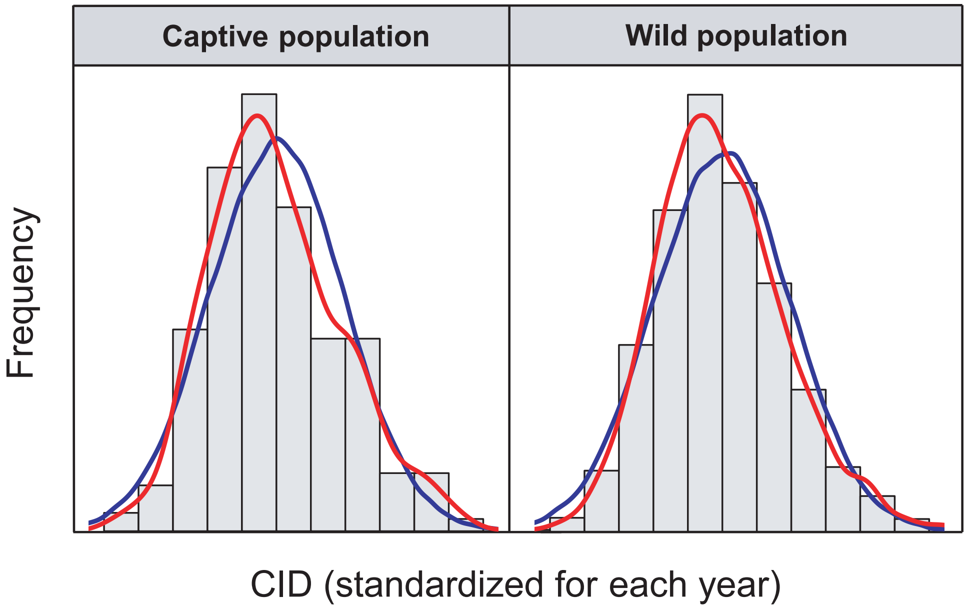

Figure 3-3: Distribution of CIDs for the captive (left) and wild (right) populations. Data were standardized and aggregated across years. Colored lines depict the kernel density estimates on the distribution. Red lines represent the actual distributions of CID, while the blue lines represent the normal distributions generated using the actual mean and variance of the CID distribution.

3.5 - DISCUSSION

Despite prior expectations of lower inter-annual variance in breeding phenology under fixed environmental conditions, I found that both the captive and wild Adélie penguin populations exhibit a similar degree of inter-annual fluctuation in breeding phenology. Stochasticity appears to play a substantial role in determining the timing of Adélie penguin breeding within the window of time dictated by biological and physical constraints. I suggest that stochasticity at the individual level is amplified by the importance of breeding synchrony among individuals, producing the observed inter-annual variance.

Inherent inter-annual variation

Previous studies have suggested that photoperiod (Dawson 2008), abiotic conditions such as rainfall (Leitner et al. 2003, Deviche et al. 2006) and temperature (Both et al. 2004, Torti and Dunn 2005, Visser et al. 2009), biotic conditions such as food availability (Reynolds et al. 2003), or some combination of these factors, are important in regulating phenology in a number of bird species. While these conditions may define a larger envelope of time in which successful breeding may occur, my analysis of a captive Adélie penguin population shows that external drivers neither explain nor are required to generate substantial inter-annual variability in breeding phenology (i.e., a large year effect). Inter-annual fluctuations are apparent even under constant environmental conditions and after accounting for the effects of individual variation and age (Figure 3-2a). Other potential factors that might have influenced penguin breeding phenology, such as number of breeders in a given season, the timing of nesting material availability, and potential effects of the 2005 captive population exhibit renovation, were investigated but ultimately determined to have only minor effects (Appendix 7).

Beyond the random effect of year, some fixed differences in the timing of breeding among individuals in the captive population do exist – that is, some individuals breed earlier than others on average (Figure 3-2b). However, the relatively minor shifts in the composition of the population each year cannot explain the inter-annual fluctuations in the breeding phenology of captive individuals. While previous work has suggested that age plays a role in determining Adélie penguin breeding phenology in the wild (Ainley et al. 1983, Ainley 2002), the effect of age on breeding phenology was minimal in the captive population studied here (Figure 3-2c). This is not surprising, given that one hypothesized mechanism by which age might impact breeding phenology is through an individual's ability to navigate back to the breeding colony following the overwintering period. Older individuals, being more experienced, are thought to be able to find their way back to the breeding colonies more quickly, particularly through substantial sea ice (Ainley et al. 1983). With no migration in a captive population, it might be expected that age and experience have a substantially smaller impact on breeding phenology.

Interplay between synchrony and stochasticity

Adélie penguins are highly synchronous breeders within a population in a given season (Figure 3-1; see also Ainley 2002), and previous work has shown that increased synchrony among individuals leads to increased breeding success (Youngflesh et al. 2017). Where colonial breeding is driven by predator avoidance, individuals that breed not only in the same area but also at the same time as others in the population would be at an advantage (Darling 1938, Young 2005). Penguins breeding during the same time period in the same location can more easily defend nests against aerial predators, a principal threat to Adélie penguin chicks (Emslie et al. 1995, Young 2005). Synchronous breeding also results in an overwhelming influx of potential prey resources for species that prey on penguins; such 'predator-swamping' can facilitate higher breeding success (Ims 1990b). I hypothesize that the fitness consequences of breeding in synchrony with conspecifics may outweigh the importance of matching optimal environmental conditions within the environmentally-driven time envelope in which reproduction can occur successfully (as suggested in Hinke et al. 2012, Youngflesh et al. 2017). I suggest that the importance of this phenomenon for any given species reflects a balance between the expected fitness advantages of synchronous breeding among conspecifics and the fitness advantages of breeding during some (environmentally-determined) optimal period of time – the latter of which may be more difficult to assess for an individual with limited information.

In this way, predators indirectly influence the breeding phenology of Adélie penguins – a top-down process. Abiotic (e.g., photoperiod, temperature) and/or bottom-up processes (e.g., resource availability, which might affect organism physiological condition) are typically the focus of phenological studies. However, top-down forcing (via antagonists such as predators and pathogens) has been identified as an important process in the regulation of a number of phenological processes, including absolute phenology (Elzinga et al. 2007, Galloway and Burgess 2012), phenological synchrony (Hatchwell 1991, Sinclair et al. 2000), and the rate at which offspring develop (Vonesh 2005). These processes often operate in concert with abiotic and/or bottom-up processes (as suggested by Varpe et al. 2007, Burr et al. 2016), painting a complex picture of multiple ecological determinants of phenological processes. While the mechanisms for top-down control on phenology are diverse, these patterns may be more common among colonial breeders given the importance of phenological synchrony for predator avoidance in many species (Ims 1990a).

While the precise mechanism that regulates this highly synchronous behavior in Adélie penguins is unknown, social cues have been found to drive courtship and copulation (Waas 1988, 1991, 1995, Waas et al. 2000), and result in more synchronized breeding patterns (Setiawan et al. 2007). This has been demonstrated in a number of birds (Burger 1979, Danchin 1988, Waas et al.

2005), including other species of penguins, as well as in mammals (McClintock 1978, Scott 1986, Berger 1992). Vocalizations (Clark et al. 2012), exposure to courtship displays (Lehrman and Friedman 1969), and chemical cues (McClintock 1978) have all been demonstrated as proximate behavioral mechanisms by which this social facilitation occurs.

For both the wild and captive populations in this study, slightly right skewed distributions of CID are apparent within each year – very late breeders in this right skewed distribution contribute to a relatively large residual variance in my model. This skew is also consistent with, though by no means proves a role for social facilitation in the timing of breeding. Even a simple model in which breeding is accelerated proportional to the number of pairs that have recently initiated breeding creates a right skewed distribution for clutch initiation (Appendix 6). This notion of facilitation is further supported by the strong relationship (70% of variance explained) between first CID (the first breeders in each year) and median CID in both the captive and wild populations (Appendix 6). Right skewed distributions of phenological events are apparent in many species of both birds and plants (Thomson 1980, Sparks et al. 2005, Wilson 2013) at magnitudes similar to those observed here (Appendix 6). Environmental factors may play a role in driving this pattern for many species, a hypothesis difficult to exclude when only wild data are available. In this case, however, both a right skewed distribution and a strong relationship between first breeding and median breeding are apparent under controlled conditions, despite inter-annual variability in the overall timing of breeding.

It should be noted that the captive penguin population in this study exhibited less synchrony among individuals in a given year than did the wild population (Figure 3-1; Appendix 6). One possible explanation for this relates to colony size; larger populations in the wild may, through increased colony noise, better facilitate the transmission of social cues (Waas et al. 2000). Other possibilities include the notion that the degree of synchrony is a plastic trait that may be relaxed under the predator-free conditions of captivity. Future work, including manipulative experiments, is required to understand the precise behavioral mechanisms regulating synchrony in this species.

Synchronous breeding is not necessary to observe the impacts of stochastic factors on breeding phenology at the individual level. Rather, the importance of synchrony in colonial species may facilitate the propagation of stochasticity from the individual-level to that of the population. Social cues that facilitate synchrony (see above) may encourage individuals to initiate breeding once other individuals in the colony have done so. This cascading effect of synchronous breeding may drive a shift in the average phenology of the population that is largely uncoupled from any environmental trigger.

By not considering the role of stochasticity, have we been modeling noise?

In the search for causal drivers for phenology, the role of inherent stochasticity has generally not been considered in the existing phenological literature. The work presented here has important implications for studying patterns of phenology across all animal systems as it highlights the difficulty of teasing apart the extent to which the environment may, or may not, be driving variation in phenology. The observed levels of inter-annual variability under fixed environmental conditions are of a similar magnitude as those seen in the wild (Figure 3-1; Appendices 6, 7) – a surprising result. Previous studies of Adélie penguin phenology at Admiralty Bay found October mean air temperature (thought to be related to snow melt and nest site availability) to be the most important environmental determinant of CID in a model selection framework (Hinke et al. 2012, Lynch et al. 2012a). My analyses of the same CID data (with additional years beyond those used in the original studies) do not contradict these original findings, but suggest that environmental drivers, such as temperature, are layered on top of substantial ‘built in’ variability. Put another way, the null model for phenological studies should not, by default, be one of stasis.

Whether the drivers that influence a pair's 'decision' to breed are unknown, or unknowable, the implication is that phenological variability of the magnitude observed in this study can be generated in the absence of environmental variability. This finding is of practical importance, as it highlights the difficulty in identifying external causal drivers of phenological events. This study shows that stochastic variation in penguin breeding phenology, with respect to the environmental factors addressed here, may be the rule rather than the exception and does not require external forcing from the environment. This is similar to stochastic patterns observed for individuals, whereby identical individuals, experiencing identical conditions, will differ with respect to lifespan and fecundity (Caswell 2011). This role of stochasticity may partially explain previous findings of a relatively weak relationship between Antarctic seabird breeding phenology and environmental forcing (Barbraud and Weimerskirch 2006).

One way to address the inherent convolution of environmental variability and inherent stochasticity is through the study of captive populations in controlled conditions. While studies focusing on plants more often include experiments in controlled environments to distinguish the role of multiple factors on phenology (Cleland et al. 2007), there are fewer studies elucidating inter-annual changes in phenology in captive animals (but see Lambrechts et al. 1999, Visser et al. 2009). Captive animal populations are not, of course, perfect replicas of wild populations. For instance, penguins in captive populations are kept in enclosed spaces and do not undergo an overwinter migration. Captive populations are also limited in size, often smaller than what might be observed in the wild. Accordingly, caution must be taken not to overextend the analogy between captive and wild populations. Nevertheless, studies focusing on populations in controlled conditions can provide a wealth of information on phenology in the absence of all environmental factors deemed potentially important in wild populations. Identification and tracking of individual animals further allows for straightforward estimation of age effects and random individual variation. Ultimately these studies can provide a reasonable null model against which to assess factors contributing to variation in wild populations. Studies involving experimental manipulation and/or transplantation of organisms to new environments (e.g., Helm 2009) may provide additional power to disentangle the factors controlling breeding phenology. This study highlights the challenges of understanding the factors driving phenology in wild populations and serves as a reminder to take caution in ascribing causality when the degree of inherent variation in the response variable of interest is unknown.

4 – Divergent trends and unsynchronized dynamics in a seabird community – the challenge in finding effective ecological proxies

4.1 - ABSTRACT

Indicator metrics are often used to understand the underlying dynamics of complex ecological systems, but the efficacy and generalizability of these measures is often taken for granted. Using long-term data from six Antarctic seabird species, I assessed the generality of demographic indicators by assessing trends in breeding productivity and abundance, the role of environmental forcing in driving these trends, and the degree to which these demographic parameters fluctuate in synchrony across the community. I found discordance between abundance and breeding productivity when considering both short-term and long-term association and little evidence for synchrony in breeding productivity among species. Surprisingly, however, some similarity in long-term trends among species was apparent. These results suggest the use of demographic information as indicators for population health or environmental conditions is limited, though long-term trends in conjunction with community-wide extreme events may provide some indication of how ecological dynamics are fluctuating over time. This work demonstrates the challenges in finding effective ecological proxies, and the need for sustained monitoring aggregating data over multiple species if robust inference is to be made.

4.2 – INTRODUCTION

Ecological systems are characterized by complex webs of interacting components. This inherent complexity makes it difficult to understand how ecosystems function and how they are changing in response to rapid changes in the abiotic environment occurring over the past half-century (Walther et al. 2002, Pachauri et al. 2014). Given these difficulties, researchers must often rely on a subset of physical and biological metrics to infer changes in underlying ecological processes.

Measures of individual species are often used as surrogates, or indicators, for measures of ecological systems that cannot, or simply are not, measured directly (Landres et al. 1988). These indicators can provide information on habitat quality (Johnson 2007), ecosystem health (McClanahan et al. 1996), and population dynamics (Landres et al. 1988, Landres 1992, Montevecchi 1993). Consequently, the use of indicators is commonplace (Siddig et al. 2016) and well entrenched in the practices of feedback management and conservation. While some theoretical basis for the selection of indicator species and surrogate metrics often exists, in practice, the degree to which these species or metrics might be indicative of broader ecological dynamics is often not fully assessed (Niemeijer and de Groot 2008, Hilborn et al. 2017). Logistical constraints (e.g., cost, accessibility) often drive the final selection of ecological indicators (Caro and O’Doherty 1999).

Demographic measures, such as population size and breeding productivity, are commonly used indicator metrics across a number of systems, as they are biologically meaningful, easily compared across time and space, and relatively easy to collect (Spellerberg 2005). These demographic measures may be indicative of: 1) population status of a particular species; 2) population status of some other species in the same ecological community; or 3) abiotic and biotic environmental conditions (Landres et al. 1988, Spellerberg 2005).

Here I used a long-term (36 year) dataset of population size and breeding productivity for six sympatrically breeding Antarctic seabird species (Adélie penguin *Pygoscelis adeliae*, emperor penguin *Aptenodytes forsteri*, southern fulmar *Fulmarus glacialoides*, cape petrel *Daption capense*, snow petrel *Pagodroma nivea*, and south polar skua *Stercorarius maccormicki*) to evaluate the degree to which species-level metrics might be appropriately used as indicators of ecological dynamics. Seabirds have been extensively used as environmental indicators from the tropics to the poles (Gaston 2004), particularly in the Antarctic where they represent some of the most easily studied components of the food web. As one example, abundance and breeding success of Adélie penguins are formally used as one species in the Convention for the Conservation of Antarctic Marine Living Resources Ecosystem Monitoring Program (CCAMLR 2014). The seabird species considered here are highly site faithful and feed on prey items found in the marine environment near the breeding colony (e.g., krill, fish, and squid), with the exception of south polar skua, which preys primarily upon Adélie penguin young during the breeding season at this site (Ridoux and Offredo 1989).

My aim was to improve the scientific community's understanding of the generality of demographic indicator metrics by addressing the following ecological questions: 1) how are population size and breeding productivity in this Antarctic seabird community changing through time?, 2) what role does environmental forcing play in driving these demographic processes?, and 3) to what degree are species responding in synchrony to year-to-year environmental variation? This information is not only important for evaluating the generality of indicator metrics, but also contributes to the scientific community's understanding of how Antarctic communities are responding to variability and change in the environment.

4.3 – METHODS

Description of data

Data were collected on six sympatrically breeding seabird species at breeding sites at Pointe Géologie, Antarctica (67.17°S, 140.00°E) during the Antarctic summer (December – February). The number of breeding pairs and number of chicks fledged were recorded from 1980-2016, although data are not available for every species in all years (see (Barbraud et al. 2015) for detailed data collection protocols; Appendix 8). While data for some species exist as far back as 1952, community-wide information is not available prior to 1980.

Sea ice data from both the austral summer (December – February) and austral winter (June – November) were derived from the satellite-based Nimbus 7, SMMR, and SSM/I-SSMIS passive microwave sensors from 1980 – 2016, processed by the NASA Team algorithm (Cavalieri et al. 1995) via the National Snow and Ice Data Center (Cavalieri et al. 1996). Mean sea ice concentration (fraction of water covered by sea ice) within a 150 km radius of Pointe Géologie was calculated, coincides with the primary foraging areas for these species during summer (Delord et al. 2014, Barbraud et al. 2015).

Long-term trends in Abundance and Breeding Success

Temporal trends in Abundance (defined as the log number of breeding pairs in a given year for a given species) and Breeding Success (defined as the number of fledged chicks/pair in a given year for a given species) were modeled separately using a hierarchical Bayesian approach. This approach naturally accommodates missing data in time series analyses, as latent states are sampled from a probability density function, and allows for a straightforward assessment of parameter uncertainty in the model (Gelman and Hill 2006). Each response variable (y: Abundance or Breeding Success) was modeled as Normally distributed with mean μ_{ij} that is a linear function of year (i) with species (j)-specific slope and intercept.

$$y_{ij} \sim N(\mu_{ij}, \sigma_j^2) \tag{4-1}$$

$$\mu_{ij} = \alpha_j + \beta_j * YEAR_i$$

$$\begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} \sim N\left(\begin{pmatrix} \overline{\alpha} \\ \overline{\beta} \end{pmatrix}, \Sigma\right)$$

The α (intercept) and β (slope) parameters were modeled jointly from a multivariate normal distribution, to accommodate correlation between these parameters (Gelman and Hill 2006). The variance term of the multivariate normal distribution is represented by a 2 x 2 covariance matrix – variance for α and β on the diagonals, and the covariance between the two on the off-diagonals. All variance terms were given broad uniform priors following Gelman and Hill (Gelman and Hill 2006) (Appendix 8). Models were fit using the R package 'rjags' (Plummer 2016), to interface with JAGS (Plummer 2003) in the R statistical environment (R Core Team 2016). Inferences were obtained from 60,000 samples drawn from three chains with a thinning rate of 500, following a 'burn-in' period of 30,000,000 draws and an adaptation phase of 8000 draws. Convergence of the model was assessed via a visual analysis of the posterior chains, in addition to the use of the Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998). All models unambiguously converged. Parameter estimates and plots of the posterior distributions were generated using the 'MCMCvis' (Youngflesh 2018) package, while all other plots were created using the 'ggplot2' package (Wickham 2009) in the R statistical environment.

Relationship between Abundance and Breeding Success

To assess the relationship between population size and breeding productivity, the Pearson correlation coefficient between Abundance and Breeding Success was calculated from lag 0 to lag 8 (to account for the time it takes chicks to recruit into the breeding population (Ainley et al. 1990, Jenouvrier et al. 2003, 2005b, 2005c, Brooke 2004)), excluding comparisons with missing values for one or both metrics. Data were detrended prior to analysis to remove the effect that long-term trends may have on correlation coefficients. Following Bjørnstad et al. (Bjornstad et al. 1999), 95% confidence intervals for the correlation coefficient at each lag point were calculated by resampling with replacement (n = 10,000) paired values for Abundance and

Breeding Success from the original dataset and calculating the correlation coefficient for each resampled set of time series.

Community synchrony in breeding productivity

Seabird breeding productivity was modeled across the six seabird species to assess synchrony in reproductive dynamics. Using a framework developed by Lahoz-Monfort et al. (Lahoz-Monfort et al. 2013), the number of chicks F in year i for species j was modeled as binomially distributed, where E is the total number of eggs laid that season (i.e., number of trials), and p is the probability that a particular egg survives the breeding season (i.e., probability of success).

$$F_{ij} \sim Binom(E_{ij}, p_{ij}) \tag{4-2}$$

$$logit(p_{ij}) = \mu_j + \delta_i + \epsilon_{ij}$$

$$\delta_i \sim N(0, \sigma_\delta^2)$$

$$\epsilon_{ij} \sim N(0, \sigma_{\epsilon_j}^2)$$

I will refer to this modeling framework as the L-M model. The total number of eggs was determined by multiplying the number of pairs (in a given year) by the number of eggs laid per pair, a species-specific trait that is highly conserved (two eggs for Adélie penguin and south polar skua, one egg for all other species).

The logit of p is a function of a species-specific intercept (μ), year effect (δ), and residual error term (ϵ). δ and ϵ were modeled as normally distributed with variance σ_δ^2 (representing the variance in the year effect) and σ_ϵ^2 (representing the variance of each species while accounting for the year effect), respectively. Only years in which data were available for all species were used (1994, 1996, 1998-2016). Extreme years were defined as any year in which the 95% credible intervals for the year effect (δ) did not overlap 0.

The effect of anomalous events on community-level synchrony was assessed by fitting a model identical to the L-M model above (Equation 4-2) but excluding data from these extreme years. All models unambiguously converged. For each of the models, estimates of variance were partitioned to calculate Synchrony Indices (I),

$$I_j = \frac{\sigma_\delta^2}{\sigma_\delta^2 + \sigma_{\epsilon_j}^2} \tag{4-3}$$

which represent the fraction of total variance for each species explained by the year effect (i.e., to what extent the variability in productivity for that species is synchronous with the other seabird species (Lahoz-Monfort et al. 2013)). Mean Synchrony Indices ($\bar{I}$) were calculated by taking the arithmetic mean of the median posterior estimates for each species at each iteration of the model.

Effect of environmental factors on community synchrony

Finally, to evaluate the impact of sea ice concentration on breeding productivity and synchrony, an L-M model identical to those above was fit, using data from all years, with the addition of covariates on the logit of p.

$$F_{ij} \sim Binom(E_{ij}, p_{cov_{ij}}) \tag{4-4}$$

$$logit\left(p_{cov_{ij}}\right) = \mu_{cov_j} + \sum_{k=1}^{4}\left(\beta_{k_j} * c_{k_i}\right) + \delta_{cov_i} + \epsilon_{cov_{ij}}$$

$$\beta_{k_j} \sim N(0, \sigma_{\beta_k}^2)$$

$$\delta_{cov_i} \sim N(0, \sigma_{\delta_{cov}}^2)$$

$$\epsilon_{cov_{ij}} \sim N(0, \sigma_{\epsilon_{cov_j}}^2)$$

where β_{k_j} is the effect of covariate c_k (summer sea ice, summer sea ice on a one year lag, winter sea ice, and winter sea ice on a one year lag) on the breeding productivity of species j. Lagged sea ice was included to account for any potential carry-over effect on year i breeding productivity from the previous year. β parameters were modeled as normally distributed, with variance $\sigma^2_{\beta_k}$.

The median posterior variance estimates were compared from the models with and without covariates to calculate the proportion of synchronous variation explained by the covariates, C_δ (Lahoz-Monfort et al. 2013):

$$C_\delta = 1 - \frac{\widehat{\sigma^2_{\delta_{cov}}}}{\widehat{\sigma^2_\delta}} \tag{4-5}$$

Note that the numerator ($\widehat{\sigma^2_{\delta_{cov}}}$) is derived from Equation 4-4, while the denominator ($\widehat{\sigma^2_\delta}$) is derived from Equation 4-2.

4.4 – RESULTS

Long-term trends in Abundance and Breeding Success

Abundance of Adélie penguin, emperor penguin, and south polar skua showed unambiguous positive trends over time. Abundance of southern fulmar and snow petrel also exhibited positive trends over time. Abundance of cape petrel showed no trend over time. Trends in Breeding Success were similar among species – either no trend was detected or slightly negative trends were apparent despite primarily increasing trends in Abundance (Figures 4-1, 4-2).

Interannual fluctuations in Abundance and Breeding Success

Year-to-year fluctuations in Abundance were uncoupled from fluctuations in Breeding Success, even when accounting for the delayed impact that Breeding Success may have on future

Abundance. When controlling for multiple comparisons, no statistically significant relationships were found between these metrics (Appendix 9). In fact, in some cases (e.g., snow petrel lags 4-6, 8) results were suggestive of a negative relationship (i.e., high Breeding Success in year t is associated with low Abundance in year $t + x$, where x is the duration of the lagged effect).

Community synchrony in breeding productivity

Baseline productivity values (chicks per pair: $\overline{p_J} * E_j$), as determined from the initial L-M model (all years), were estimated as: 0.672 [95% CI: 0.670 – 0.675] for Adélie penguin, 0.558 [95% CI: 0.555 – 0.561] for emperor penguin, 0.660 [95% CI: 0.627 – 0.692] for southern fulmar, 0.665 [95% CI: 0.656 – 0.675] for cape petrel, 0.475 [95% CI: 0.462 – 0.488] for snow petrel, and 0.656 [95% CI: 0.619 – 0.692] for south polar skua. One community-wide extreme year (2013) was identified (Figure 4-4a). This was excluded in the fitting of the second L-M model. A dampened year effect was apparent when excluding the identified extreme year (Figure 4-4a).

Synchrony Indices (I), which reflect the proportion of year-to-year variation in breeding productivity that is explained by fluctuations among all six species, were altered substantially by the removal of the extreme year. Community-level fluctuations explained relatively little of the interannual fluctuations for any given species when excluding 2013 (Figure 4-4b, Table 4-1).

Effect of environmental factors on community synchrony

The effect of sea ice concentration in year t (both summer and winter) on breeding success in that same year was negligible, except for summer sea ice for the Adélie penguin. Sea ice concentration in year $t - 1$ (both summer and winter) showed no effect on breeding success in year t (Figure 4-5). C_δ was estimated to be 0.28, suggesting that between one-fourth and one-third of the community-wide synchrony in breeding success was explained by sea ice concentration.

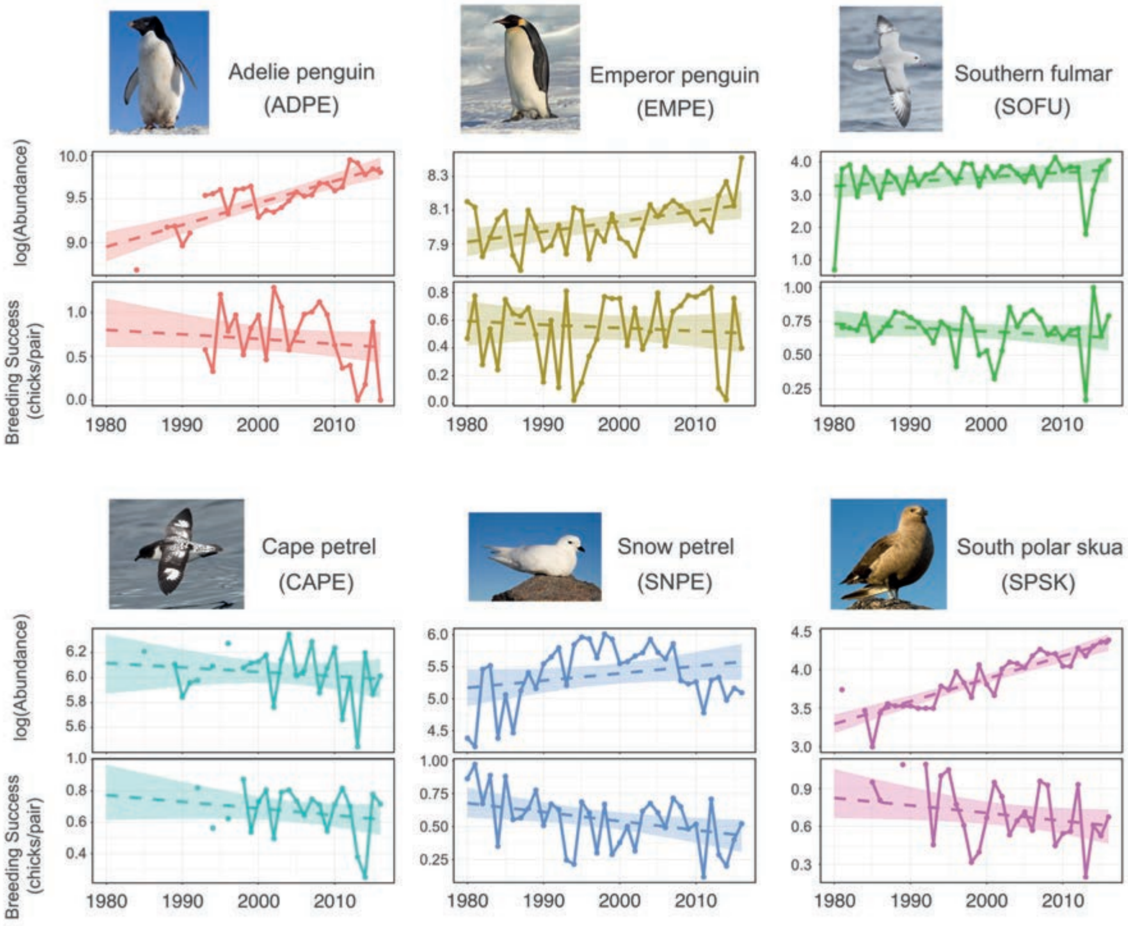

Figure 4-1: Trends in Abundance (top panels) and Breeding Success (bottom panels) for the six study species. Dotted lines represent model fit, while shaded bands represent 95% credible intervals.

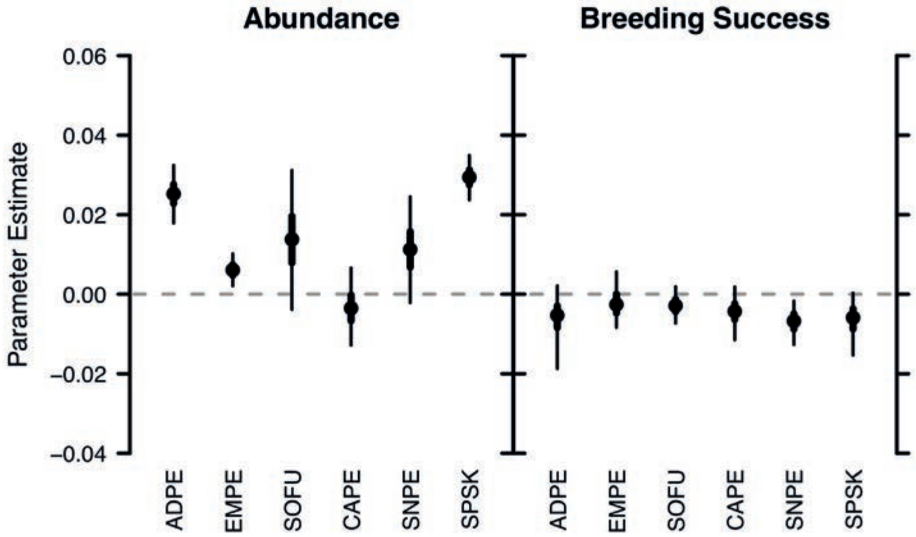

Figure 4-2: Posterior estimates for trends in Abundance and Breeding Success (change per year) for the six study species. Black circles represent posterior medians. Thicker lines represent 50% credible intervals while thinner lines represent 95% credible intervals. ADPE – Adélie penguin; EMPE – emperor penguin; SOFU – southern fulmar; CAPE – cape petrel; SNPE – snow petrel; SPSK – south polar skua

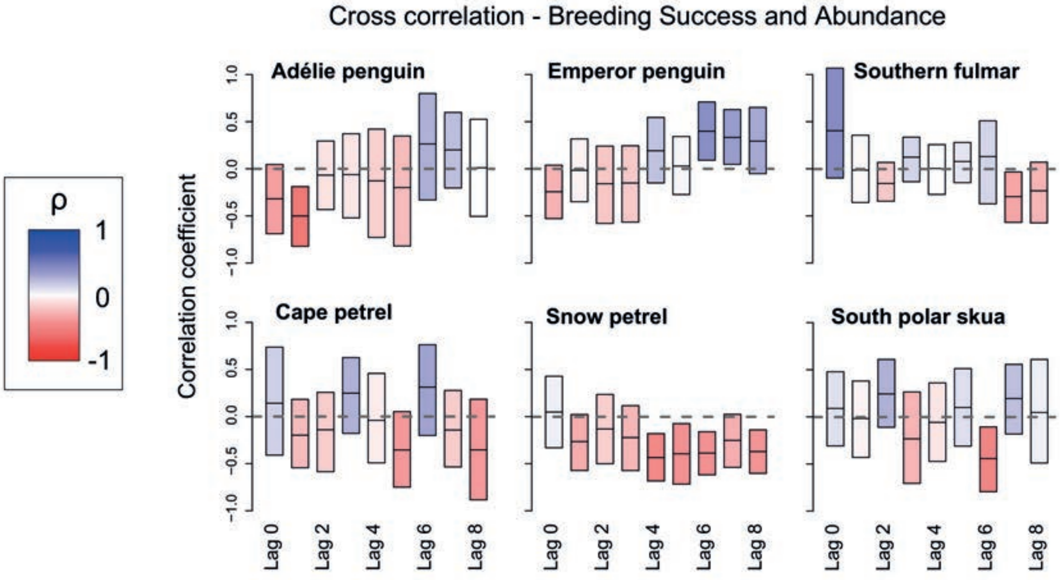

Figure 4-3: Pearson correlation coefficients between Breeding Success and Abundance from Lag 0 to Lag 8. The line bisecting each bar represents the calculated correlation coefficient – the color of each bar corresponds to this value and represents the strength of the correlation. The ends of the bars represent 95% confidence intervals. Dashed lines represent 0.

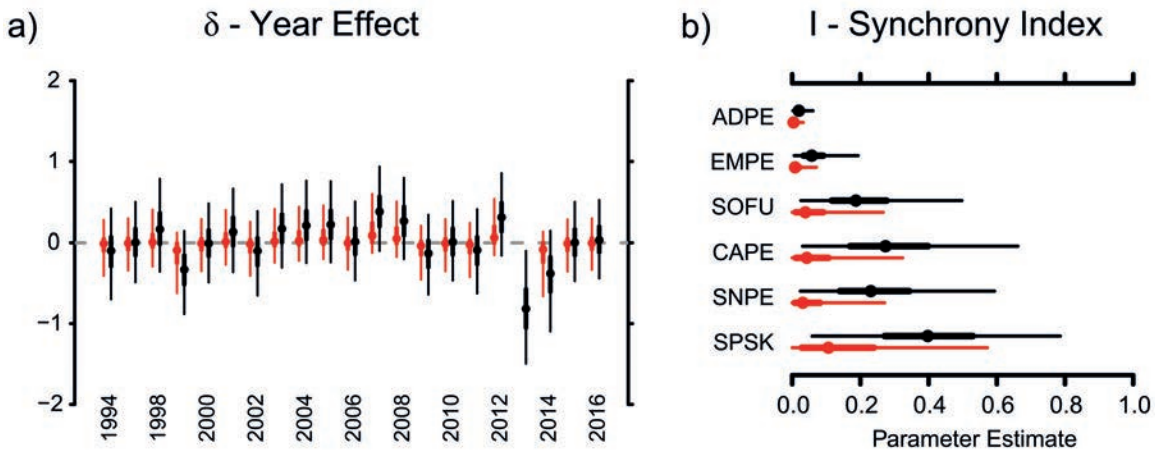

Figure 4-4: a) Posterior estimates for δ (year effect) and b) I (Synchrony Indices for breeding productivity). Synchrony Indices reflect the proportion of year-to-year variation in breeding productivity that is explained by fluctuations among all six species. Results are shown for models including (black) and excluding (red) the identified extreme year (2013). In both cases, circles represent posterior medians. Thicker lines represent 50% credible intervals while thinner lines represent 95% credible intervals. ADPE – Adélie penguin; EMPE – emperor penguin; SOFU – southern fulmar; CAPE – cape petrel; SNPE – snow petrel; SPSK – south polar skua.

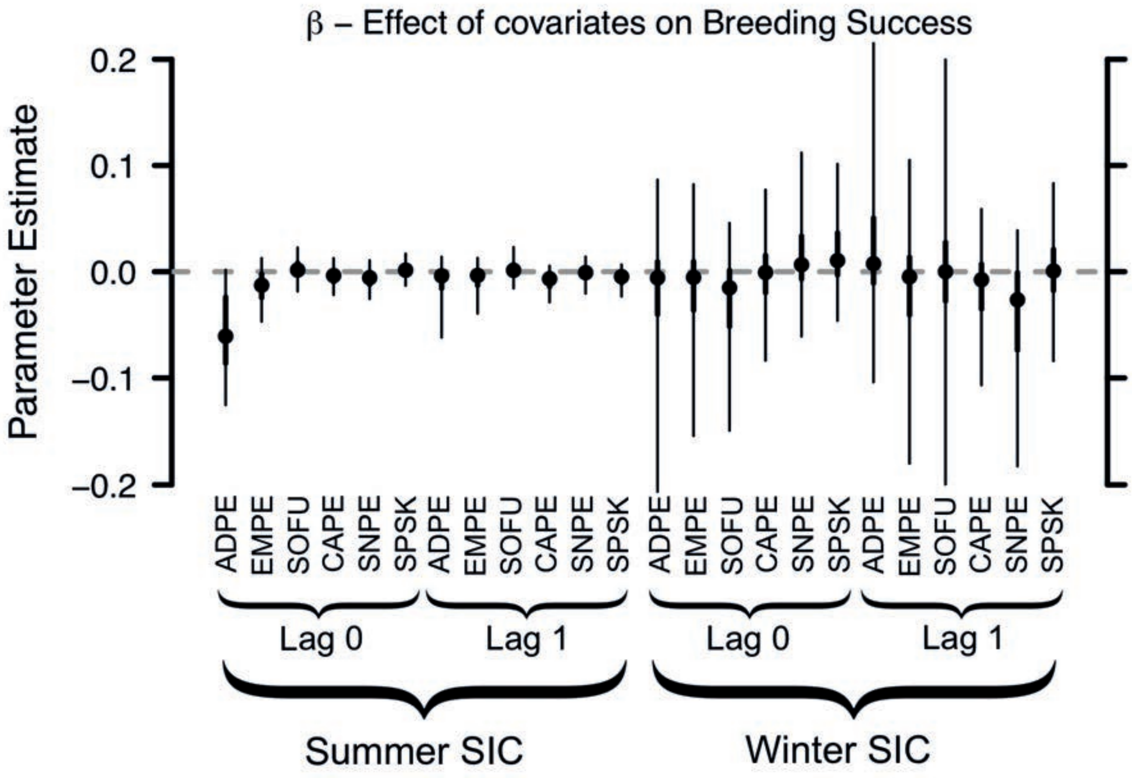

Figure 4-5: Estimates for β (effect of sea ice concentration on breeding productivity). Circles represent posterior medians. Thicker lines represent 50% credible intervals while thinner lines represent 95% credible intervals. ADPE – Adélie penguin; EMPE – emperor penguin; SOFU – southern fulmar; CAPE – cape petrel; SNPE – snow petrel; SPSK – south polar skua

Table 4-1: Estimates for Synchrony Indices (*I*) (for each species, the proportion of interannual variation in breeding productivity explained by community-level fluctuations) as well as the mean synchrony index calculated across all species. Removal of the extreme year resulted in a drop in estimated synchrony across the community.

Species	With extreme year	Without extreme year
Adélie penguin	0.02	0
Emperor penguin	0.06	0.01
Southern fulmar	0.19	0.04
Cape petrel	0.27	0.04
Snow petrel	0.23	0.03
South polar skua	0.4	0.1
$\bar{I}$	0.21	0.04

4.5 – DISCUSSION

Despite their intrinsic linkage, measures of observed population size are largely independent of breeding productivity in this community of Antarctic seabirds. Measures of productivity were also largely unsynchronized across species, though rare community-wide extreme events apparently synchronizing the community did exist. However, some similarity in long-term trends among species was apparent for demographic measures for the species examined. These results demonstrate the complexity of demographic fluctuations and highlight the challenges in finding effective proxies of ecological dynamics, particularly in the face of global change.

Discordance between Abundance and Breeding Success

Breeding success necessarily impacts abundance in any given population. However, as observed in this seabird community and consistent with earlier theoretical work (Adahl et al. 2006), other contributing factors may mask this relationship, leading to seemingly independent fluctuations in these two metrics. While long-term trends in abundance at this breeding site are unambiguously increasing for three of these species (with suggestive increases for two others), trends in breeding success are relatively stable or slightly decreasing over time for the entire community (Figures 4-1, 4-2). While these patterns are consistent with density dependent effects on breeding success, little support for this notion exists, except for the Adélie penguin (Appendix 9). Short-term interannual fluctuations in breeding success are additionally not strongly correlated with abundance (Figure 4-3).

Given the life history characteristics of these birds (long-lived, late-maturing, low annual reproductive output), tightly correlated short-term dynamics between breeding success and abundance may not be expected (McLean et al. 2016). However, the degree to which uncoupling of these two parameters exists on long-term time scales is surprising. Changes in juvenile survival, recruitment, and adult breeding probabilities are likely largely responsible for these opposing trends, as adult survival for long-lived seabirds generally varies little over time (e.g., Adélie penguins (Jenouvrier et al. 2006, Hinke et al. 2007), southern fulmars (Jenouvrier et al. 2003), snow petrels (Jenouvrier et al. 2005b), south polar skua (Ainley et al. 1990)). Changes in mortality rates of juveniles across years may themselves be linked to fluctuations in environmental conditions (Oro et al. 2010, Fay et al. 2015). For example, for Adélie penguins, increased sea ice following the fledging period may provide more favorable conditions for young birds, as these penguins rely on pack ice during the overwinter period (Ballard et al. 2010) (Appendix 9).

Factors such as individual quality of breeders may also contribute to the observed pattern. Population increases may result in birds of lower quality accumulating in greater numbers, depressing breeding productivity (Jenouvrier et al. 2015, 2017). Increased breeding frequency over time might also result in increased abundance independent of an increase in breeding success (Jenouvrier et al. 2005a).

Low community synchrony in productivity

While previous studies have identified community synchrony in other ecological systems (Reid and Croxall 2001, Frederiksen et al. 2007, Keitt 2008, Hansen et al. 2013), I found no such evidence here (quantitative comparisons of synchrony in these studies are difficult due to differences in methodology). Fluctuations in breeding productivity are not well synchronized across this community of seabirds (i.e., productivity does not vary collectively; Figure 4-4b, Table 4-1). This result is surprising, particularly considering the high degrees of both abiotic (Clarke and Harris 2003) and biotic (Che-Castaldo et al. 2017, Youngflesh et al. 2018) variability in the Antarctic system, which might be thought to synchronize community dynamics.

Initial estimates of community synchrony were largely driven by one extreme year (2013), in which exceptionally poor breeding success was observed for all species (Figure 4-4a). This previously documented event was hypothesized to be due to high sea ice coverage at the breeding site (Barbraud et al. 2015). Large disturbances such as this may lead to a synchronized response in a community (Keitt 2008), as community dynamics may be more likely to exhibit a shared response in exceptionally poor years as opposed to exceptionally favorable years. However, not all exceptionally poor years for a given species are shared across the community (i.e., the worst year in terms of breeding productivity for a given species may be an average year for all other species). For instance, Adélie penguin had a near complete breeding failure in 2016 at this site, while other species exhibited a relatively average year for breeding productivity (Appendix 9).

South polar skua showed a modest, but increased, degree of synchrony with community-level productivity in comparison to the other species (Figure 4-4b). This is likely due to the fact that this species preys upon the young of other species in the community, most notably Adélie penguins (Young 2005). Dynamics of predator prey systems may be more likely to exhibit synchrony (Vasseur and Fox 2009) than species occupying the same trophic level.

Unsynchronized demographic dynamics are likely driven by niche separation among these species. While all species forage and nest in similar locations, they employ different foraging strategies, rely on different proportions of similar prey items, and utilize different nesting habitats (Ridoux and Offredo 1989). Each species may also be buffered from environmental variability in different ways, such as through chick provisioning and skipped breeding (see also (Grémillet and Charmantier 2010, Youngflesh et al. 2017)). Stochastic factors, including demographic stochasticity (Lande et al. 2003), heterogeneity in the quality of individuals within each of these populations (Vindenes et al. 2008, Jenouvrier et al. 2015), and small-scale stochastic variation in the distribution of prey (Weimerskirch 2007), may also play a role. Irrespective of the underlying drivers, however, divergent trends between population size and breeding productivity and unsynchronized dynamics in breeding productivity are apparent in this seabird community.

Impact of sea ice dynamics on productivity and synchrony

The effects of both summer and winter sea ice concentration on breeding success were determined to be relatively small for all species except the Adélie penguin (though I highlight the uncertainty in this estimate; Figure 4-5). For this species, years with greater summer sea ice concentration were associated with lower breeding success. These findings, however, do not preclude a more complex relationship between sea ice and breeding productivity (see (Barbraud et al. 2015)). Favorable environmental conditions may be a necessary but not sufficient condition for high productivity (Youngflesh et al. 2017). While overall community synchrony was low (Figure 4-4b, Table 4-1), sea ice dynamics accounted for one third of the total variability in community productivity that did exist (though when the extreme year is excluded, no additional variability is explained by the sea ice covariates; Appendix 8).

Generality of demographic indicators

The primary purpose of indicator metrics is to better understand latent ecological dynamics and infer how ecosystems are fluctuating over time. Of the ways in which demographic indicators might be informative, the population status of a species is the most straightforward. Successful breeding is a necessary though not sufficient condition for population maintenance which has led to the hope that tracking breeding productivity will serve as an effective monitoring strategy for assessing population status. Breeding productivity has a clear advantage of being a faster and possibly more responsive early-warning system than long-term population trends. These results show, however, that breeding productivity may be largely uncoupled from changes in abundance (Figures 4-1, 4-2) and therefore not a useful indicator of population health. In fact, I found that breeding success was largely stable or declining even as population sizes increased.

Demographic metrics have also been used as indicators of the population dynamics of other species in an ecological community (Severinghaus 1981, Landres et al. 1988). A general lack of synchrony in the breeding productivity of this seabird community, however, suggests that it cannot be assumed that inter-annual dynamics of one species are informative of dynamics of another species. Long-term changes in demographic measure may be more useful and reliable than inter-annual fluctuations, though in a qualitative, rather than quantitative sense.

Finally, demographic metrics may be used to infer abiotic or biotic environmental conditions. The lack of synchrony in breeding productivity suggests that interannual environmental fluctuations impact each species differently, or that the effect of these fluctuations is masked by the importance of other factors. This notion is supported by earlier work which shows that substantial noise and heterogeneous responses may exist between demographic parameters and biotic conditions, such as prey availability (Cairns 1987, Furness and Camphuysen 1997, Cury et al. 2011, Hilborn et al. 2017). As noted above, however, long-term trends may serve more utility in qualitative assessments. Community-wide extreme events (such as 2013 in this study) may also serve to identify anomalous environmental conditions, though these events are rare and require the monitoring of entire communities over long periods of time.

Conclusions

Identifying appropriate metrics to better understand complex ecological systems in a changing world is a challenging task. The utility of demographic information as robust indicators in the ways outlined above, appears limited (and should not be assumed *a priori*). In the face of substantial ecological ‘noise’, aggregation may provide a solution, whether that be aggregation over time and space (Che-Castaldo et al. 2017), or over multiple species (Reid et al. 2005, Durant et al. 2009). For instance, long-term trends from multiple species may result in more robust trends, and community-wide extreme events may indicate substantial changes in ecosystem state (which may be increasingly useful as the frequency of anomalous climate events continues to grow (Rahmstorf and Coumou 2011, van de Pol et al. 2017)). Unfortunately, effective approaches require sustained monitoring over long periods of time, with data aggregated over multiple species within ecological communities.

5 – Satellite-based monitoring of Antarctic food-web dynamics

5.1 – ABSTRACT

Rapid global change is driving a multitude of ecological shifts around the earth. In Antarctica, changes are apparent in both the distribution and abundance of organisms throughout the food web. However, despite these observations, a holistic understanding of changes in the underlying dynamics of the Antarctic ecosystem is lacking. Drawing inference on such processes requires research efforts on large spatial and/or temporal scales, which is often logistically difficult in polar systems. Using a novel approach combining remote sensing, field spectroscopy and stable isotope analysis, I characterized changes in Antarctic food web dynamics as reflected in the diet of an Antarctic predator, the Adélie penguin, *Pygoscelis adeliae*, over nearly three decades at a continental scale. Using a hierarchical Bayesian approach to account for model uncertainty, I found that Adélie penguin diet has not changed substantially in recent years, suggesting that, despite recent changes in the physical Antarctic environment, food web dynamics have not shifted substantially over the period analyzed. Results show that diet does, however, vary spatially and is linked to population trends at penguin breeding colonies across the Antarctic. These patterns may be reflective of past resource exploitation in the region. This work represents a general framework for assessing future ecological change in Antarctic food web dynamics at unprecedented spatial and temporal scales and has important implications for our understanding of ecological responses to global change.

5.2 – INTRODUCTION

The impacts of both direct and indirect anthropogenic factors on ecological systems are apparent around the world (Walther et al. 2002, Parmesan and Yohe 2003). In the Antarctic system, this is principally exemplified by changes in oceanographic and atmospheric dynamics (Mayewski et al. 2009), and the commercial exploitation of marine resources (Leaper and Miller 2011, Nicol et al. 2012). These pressures have coincided with shifts in the distribution and abundance of a wide variety of Antarctic organisms ((Moline et al. 2004, Montes-Hugo et al. 2009, Lynch et al. 2012b). Despite these observations, however, a holistic understanding of changes in food web dynamics through time and space and the associated demographic consequences, is lacking.

Given the complexities of ecological interactions and the difficulties in monitoring food web processes, predator species, such as the Adélie penguin, *Pygoscelis adeliae*, are often used to make inference on latent ecological dynamics. Measurable ecological responses of these birds may integrate a large number of physical and biological environmental variables (Ainley 2002, Boersma 2008), providing a means to understand change in this system. However, monitoring these processes on the large spatial and/or temporal scales necessary to make robust inference, is often logistically difficult in polar systems. Satellite-based sensors provide one solution to this problem of scale, having been used to monitor penguin populations in the Antarctic using the large guano deposits at breeding colonies (Schwaller et al. 2013, Lynch and LaRue 2014). Recent work has additionally suggested that the spectral properties of penguin guano may be linked to penguin diet (Fretwell et al. 2015, Rees et al. 2017), though these linkages has not, as of yet, been demonstrated.

Using a novel, multi-tiered approach incorporating quantitative remote sensing, field spectroscopy, and stable isotope analysis, I characterized changes in Antarctic food web dynamics as reflected in the diet and demographic processes of the Adélie penguin over a 29-year period on a continent-wide scale. I sought to determine: 1) whether Adélie penguin diet has shifted in trophic level over time and space, 2) what role environmental factors such as sea ice concentration and bathymetry play in driving diet, and 3) what implications diet has for Adélie penguin population dynamics.

5.3 – METHODS

Relationship between penguin diet and guano spectra

I collected a total of 108 guano samples (~10 g) from 16 *Pygoscelis* spp. breeding colonies in the Antarctic Peninsula region during the 2014 and 2015 austral summers (Dec 5 – Dec 23). During the breeding season, these penguins rely principally on a diet of Antarctic krill (*Euphausia superba*), Antarctic silverfish (*Pleuragramma antarctica*), and several other species of krill and fish, though diet varies by region and year (Ratcliffe and Trathan 2012). Samples were derived from three species in the genus *Pygoscelis* (Adélie penguin, *P. adeliae*, gentoo penguin, *P. papua*, and chinstrap penguin, *P. antarctica*) to increase the dietary breadth and overall number of samples used to derive a quantitative relationship between guano spectra and diet (Appendix 10). Samples were collected from the ground adjacent to penguin nests at each breeding colony.

I homogenized each guano sample inside the sampling bag before spreading evenly on wax paper in preparation for spectral analysis. Spectral properties of each guano sample were characterized by obtaining high spectral-resolution reflectance measurements in a laboratory environment using a full range (350 – 2500 nm) field-portable spectroradiometer (Analytical Spectral Devices FieldSpec 4) in a bench top configuration, with the fiber (and attached 18° optic) positioned at a 45° angle to the sample. A full-spectrum light source (Analytical Spectral Devices Illuminator) illuminated samples for spectral analysis. Following spectral analysis, samples were dried in a commercial food dehydrator at 43° C for 10 hours and checked for desiccation. All samples were stored at room temperature before undergoing additional analyses.

I used stable isotope analysis (SIA) to measure the ratios of naturally occurring isotopes ($\delta^{15}N$) in each dried guano sample. While applications of the method vary widely, SIA is accepted as a robust, relatively low-cost, minimally invasive way of quantifying penguin diet

(Emslie and Patterson 2007, Polito et al. 2011, Huang et al. 2013). $\delta^{15}N$ values are commonly used to indicate at which trophic level an organism is feeding (Polito et al. 2011). This metric should be interpreted as a relative measure of dietary trophic level, as isotopic discrimination factors needed to link true prey proportions to isotopic signatures were unavailable (Polito et al. 2009). Given the lower trophic level occupied by krill (Emslie and Patterson 2007, Polito et al. 2011), lower $\delta^{15}N$ values indicate larger proportions of krill, while higher $\delta^{15}N$ values reflect larger proportions of fish in penguin diet. Approximately 0.8 mg of dried guano was loaded into tin cups before being flash-combusted and analyzed for $\delta^{15}N$ through a Thermo Delta V Plus continuous-flow stable isotope ratio mass spectrometer. Raw δ values were normalized using USGS-40 and USGS-41 standards. All δ values are reported in per mille notation (‰), relative to atmospheric N_2.

I convolved laboratory-obtained, high spectral-resolution reflectance measurements for each sample to the relevant spectral bands of the Landsat 4 TM, Landsat 5 TM, and Landsat 7 ETM+ satellite-based sensors, spanning the visible, near infrared, and short wave infrared portions of the electromagnetic spectrum (Appendix 10). Convolved spectra simulate how these satellite sensors detect the spectral reflectance of each guano sample. The ‘hsdar’ package (Lehnert et al. 2018) in the R statistical environment (R Core Team 2016), which additionally accounts for the spectral response curve of each sensor, was used to perform spectral convolutions (Appendix 10).

I used a partial least-squares regression (PLSR) modeling approach, implemented using the ‘pls’ package (Mevik and Wehrens 2007) in the R statistical environment (R Core Team 2016), to associate $\delta^{15}N$ (dietary proxy used here) to the convolved spectra. This approach decomposes predictor variables (reflectance values) into a set of uncorrelated ‘principal components’, which are then fit to predict a response variable ($\delta^{15}N$ values obtained from SIA). This method is commonly used to associate plant traits to spectral characteristics (Serbin et al. 2014). As PLSR is sensitive to outliers (Hubert and Branden 2003), and the goal was to develop the best predictive model possible, Cooks distance was used to eliminate those samples with anomalous spectra properties (Bollen and Jackman 1990; Appendix 10). Based on this procedure, 4 samples were removed from the dataset. Following Serbin et al. (2014), the data were split into calibration (80%) and independent validation (20%) sets to validate the derived relationship between spectra and δ^{15}N values. I selected the appropriate number of principal components by determining whether additional principal components significantly reduced the predicted sum-of-squares (PRESS) statistic, as determined using a t-test (Serbin et al. 2014). Variable Importance Factors (VIP) were calculated to determine which portion of the spectra most strongly contributes to the derived relationship to δ^{15}N.

Relationships between spectra and δ^{15}N values were derived for each sensor (Landsat 4 TM, Landsat 5 TM, and Landsat 7 ETM+) to account for differences in the spectral curves and bandwidths. Model fit was assessed using the coefficient of determination (R^2), the root mean square error (RMSE), and model bias. Further model validation was conducted by calculating error distributions and model coefficients through further subsetting of the calibration set through permutation (Appendix 10). Residual variance from each of the models was calculated to propagate the uncertainty in δ^{15}N values in further analyses.

Landsat retrievals

I retrieved reflectance values for Adélie penguin breeding colonies using cloud-free satellite scenes (images) from the Landsat 4 TM, Landsat 5 TM, and Landsat 7 ETM+ satellite-based multispectral sensors (30 m resolution) during December and January (the peak of the Adélie penguin breeding season), from 1984/1985 – 2012/2013. The spatial extent of this analysis represents nearly the entirety of the species’ global range (Lynch and LaRue 2014). While this methodology could be applied to any satellite-based or airborne sensor, the Landsat program was chosen based on the long time series that it provides. Adélie penguin colonies were identified from Landsat scenes using an algorithm developed by Schwaller et al. (2013).

Using the retrieved reflectance values and the quantitative relationships derived from the PLSR analyses (above), δ^{15}N values were predicted for each 30 m pixel identified as Adélie penguin breeding colony. It is important to note that each pixel is not composed entirely of guano, and other factors (including the penguins themselves) impact the spectra measured by satellite sensors. As δ^{15}N values are interpreted as a relative marker of trophic level, this does not change the interpretation of predicted values. Data were processed in such a way that each 30m pixel at a breeding colony was assigned a unique ID that remained consistent through time. Data availability varied over time due to the acquisition schedule of the Landsat instruments and cloud cover. In total, 998 unique acquisitions (satellite sampling events at a penguin colony) were obtained (Appendix 10). Multiple scenes were often available for a given site in a given year.

Statistical analyses

I modeled predicted δ^{15}N values using a hierarchical Bayesian approach, which allowed missing data in time series to be treated as latent states to be sampled, and formally accounted for the uncertainty in parameter estimates (Gelman and Hill 2006). Predicted δ^{15}N (y_{ijks}, where i is season id, j is breeding colony id, k is unique pixel id for each j, and s is the scene number for each ijk) was modeled as normally distributed with mean $z_{scene_{ijks}}$, with a fixed variance of 2.35, which was derived from the residuals of the PLSR analysis (to account for the uncertainty in δ^{15}N prediction). In this way, z_{scene} represents the true state of the variable of interest (true δ^{15}N), while y represents the observed state (observed δ^{15}N).

$$y_{ijks} \sim N(z_{scene_{ijks}}, 2.35) \tag{5-1}$$

$z_{scene_{ijks}}$ (predicted δ^{15}N for a given scene/pixel/site/year) was modeled as normally distributed with mean $z_{pix_{ijk}}$ (mean predicted δ^{15}N for a given pixel/site/year), which is normally distributed with mean $z_{year_{ij}}$ (mean predicted δ^{15}N for a given site/year).

$$z_{scene_{ijks}} \sim N(z_{pix_{ijk}}, \sigma^2_{pix}) \tag{5-2}$$

$$z_{pix_{ijk}} \sim N(z_{year_{ij}}, \sigma^2_{site})$$

To assess dietary change over time, $z_{year_{ij}}$ was then modeled as normally distributed with mean $\mu_{z_{ij}}$, which is a function of year, with colony-specific slope and intercept.

$$z_{year_{ij}} \sim N(\mu_{z_{ij}}, \sigma^2_z) \tag{5-3}$$

$$\mu_{z_{ij}} = \alpha_j + \beta_j * X_i$$

$$\begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} \sim N\left(\begin{pmatrix} \overline{\alpha} \\ \overline{\beta} \end{pmatrix}, \Sigma\right)$$

The α (intercept) and β (slope) parameters were modeled jointly from a multivariate normal distribution, to accommodate correlation between these parameters (Gelman and Hill 2006). The variance term of the multivariate normal distribution is represented by a 2 x 2 covariance matrix – variance for α and β on the diagonals, and the covariance between the two on the off-diagonals. All variance terms were given broad uniform priors following Gelman and Hill (2016). Models were fit using the R package ‘rjags’ (Plummer 2016), to interface with JAGS (Plummer 2003) in the R statistical environment (R Core Team 2016). Inferences were obtained from 50,000 samples drawn from six chains with a thinning rate of 20, following a ‘burn-in’ period of 30,000 draws and an adaptation phase of 8000 draws.

I used mean posterior estimates for $z_{year_{ij}}$ (mean predicted δ^{15}N for a given site/year) from the above to assess the relationship between penguin diet and both average sea ice concentration during the penguin breeding season (December – January; Cavalieri et al. 1995) and area of continental shelf (defined as ocean floor less than 1000m depth; Clarke et al. 1998) within 150 km of the breeding colonies (the typical maximum foraging range for the Adélie penguin; Ainley 2002, Emmerson et al. 2015; Appendix 10). Both have been suggested to play a role in the diet of Adélie penguins (Ainley et al. 1998, Ratcliffe and Trathan 2012). $z_{year_{ij}}$ was modeled as normally distributed, with mean z_{site_j} (mean predicted δ^{15}N for a given site) and variance $\sigma^2_{z_{year_{ij}}}$.

$$z_{year_{ij}} \sim N(z_{site_j}, \sigma^2_{z_{year_{ij}}}) \qquad (5\text{-}4)$$

Posterior variance estimates for $z_{year_{ij}}$ were used for $\sigma^2_{z_{year_{ij}}}$ to account for the uncertainty in the estimate of these parameters. z_{site_j} was modeled as normally distributed with mean μ_{m_j}, which is a function of sea ice concentration (SIC) and continental shelf area (SA), and variance σ^2_m.

$$z_{site_j} \sim N(\mu_{m_j}, \sigma^2_m) \qquad (5\text{-}5)$$

$$\mu_{m_j} = \alpha_m + \beta_{m_1} * SIC_j + \beta_{m_2} * SA_j$$

α_m represents the intercept term while $\beta_{m_1}$and β_{m_2} represent the effect of SIC and SA, respectively. The model was fit using the above procedure, with inferences obtained from 10,000 samples drawn from three chains, with a burn-in period of 10,000 draws, and an adaptation phase of 8000 draws.

I explored regional differences in penguin diet by calculating regional mean predicted δ^{15}N values using the posterior chains from z_{site_j}. At each iteration of the posterior chain, mean predicted δ^{15}N was calculated for all breeding sites in Western Antarctica (defined as any breeding colony between -180° and 0° longitude; $WA_{\delta^{15}N}$) and all breeding sites in Eastern Antarctica (defined as any breeding colony between 0° and 180° longitude; $EA_{\delta^{15}N}$). These chains were differenced to produce an estimate (with associated uncertainty) of the regional differences in predicted δ^{15}N values.

Finally, to explore the association between penguin diet and population processes, I modeled estimates of population growth rate at each Adélie penguin breeding colony (derived from Che-Castaldo et al. 2017) as a function of z_{site_j}. Posterior variance estimates for g_j, which represents the posterior mean for population growth rate for a given site, were used for $\sigma^2_{g_j}$ to account for uncertainty in these parameters.

$$g_j \sim N(\mu_{p_j}, \sigma^2_{g_j}) \tag{5-6}$$

Likewise, z_{site_j} represents the posterior mean for mean predicted δ^{15}N for a given site. Posterior variance estimates for z_{site_j} were used for $\sigma^2_{z_{site_j}}$. Both $\sigma^2_{g_j}$ and $\sigma^2_{z_{site_j}}$ were provided values and were not estimated parameters in the model. In this way, uncertainty in estimates of the population growth rates and predicted δ^{15}N values were taken into account.

$$z_{site_j} \sim N(\mu_{c_j}, \sigma^2_{z_{site_j}}) \tag{5-7}$$

$$\mu_{p_j} \sim N(\mu_{f_j}, \sigma^2_f)$$

$$\mu_{f_j} = \alpha_p + \beta_p * \mu_{c_j}$$

α_p represents the intercept term while β_p represents the slope of the relationship between population growth rate and mean predicted δ^{15}N. The model was fit using the above procedure, with inferences obtained from 10,000 samples drawn from three chains, with a burn-in period of 10,000 draws, and an adaptation phase of 8000 draws.

Convergence for all models was assessed via a visual analysis of the posterior chains, in addition to the use of the Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998). All models unambiguously converged and all parameters showed a low degree of prior posterior overlap (Appendix 10). Parameter estimates and plots of the posterior distributions were generated using the ‘MCMCvis’ (Youngflesh 2018) package, while all other plots were created using the ‘ggplot2’ package (Wickham 2009) in the R statistical environment.

5.4 – RESULTS

Relationship between spectra and $\delta^{15}N$

Using Cook’s distance, four guano samples were determined to have anomalous spectra compared to other samples (Appendix 10). This resulted in 104 samples being used to derive a quantitative relationship between $\delta^{15}N$ and spectra using PLSR. Laboratory analysis revealed a range of $\delta^{15}N$ values from 1.43 – 14.22‰ with a mean of 6.13‰ (sd = 2.44‰; Appendix 10).

Spectral analysis of penguin guano revealed peaks in the near infrared (NIR), and shortwave infrared (SWIR) regions of the electromagnetic spectrum (Figure 5-1). PLSR results showed that spectra binned to the spectral responses of the Landsat sensor can predict $\delta^{15}N$ values with some accuracy, though some uncertainty exists, which was accounted for in the modeling framework (Table 5-1). VIP results indicate that the NIR portion of the spectrum was the most important for predicting $\delta^{15}N$ values (Appendix 10).

Spatial and temporal variation in diet

Model results suggest that predicted $\delta^{15}N$ values changed little, if at all, over time (Figure 5-2). Mean predicted $\delta^{15}N$ values varied across the range of the Adélie penguin (Figure 5-3). Western

Antarctica exhibited lower mean predicted $\delta^{15}N$ values than Eastern Antarctica. The mean difference between the two regions was 3.65‰ (95% credible interval: 3.54 - 3.75‰; Figure 5-3).

Diet, environment, and demographics

Model results suggest that sea ice concentration has a relatively small effect on mean colony predicted $\delta^{15}N$ values, while shelf area was negatively associated with mean predicted $\delta^{15}N$ values (Figure 5-4). Results show that population growth rate had a negative relationship with predicted $\delta^{15}N$ values (Figure 5-5). The mean posterior estimate for β_p was 0.007 (95% credible interval: 0.005 – 0.009; Appendix 10).

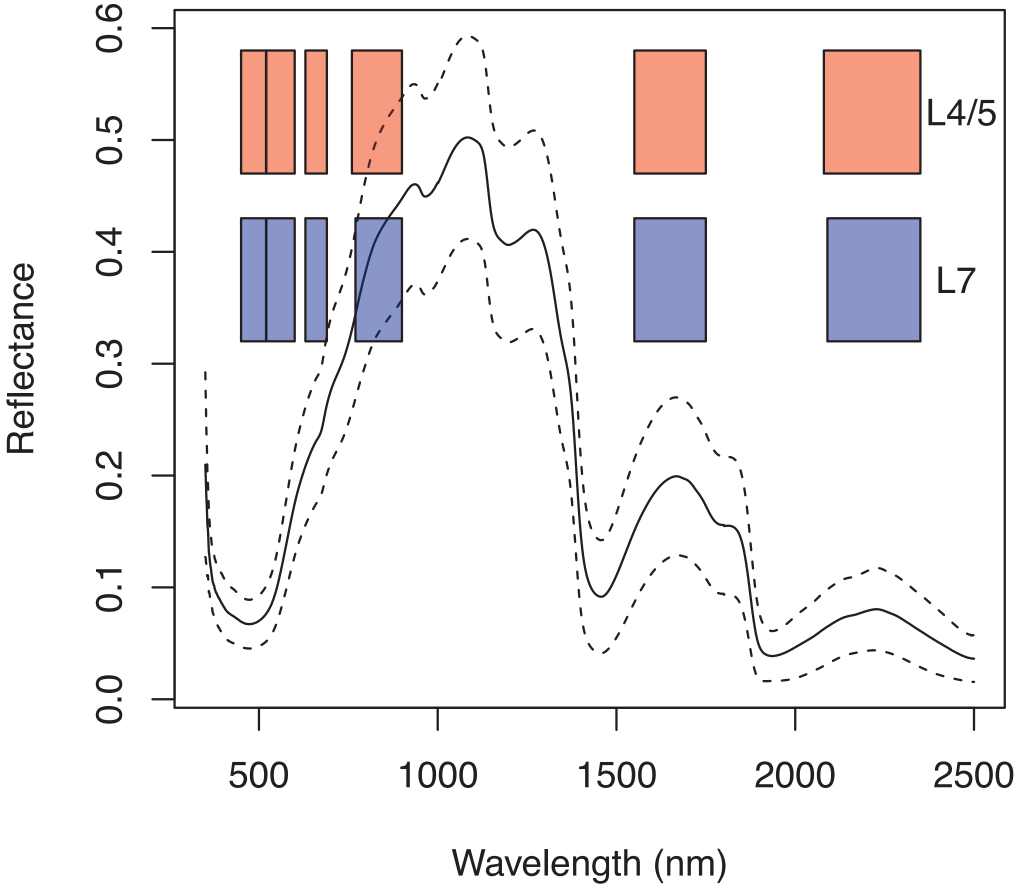

Figure 5-1: Spectral reflectance of penguin guano samples used in analyses. The solid black line represents the mean spectra of all samples, while dotted lines represent 95th quantiles. Colored boxes represent the bandwidths for the Landsat 4 TM and Landsat 5 TM (red), and Landsat 7 ETM+ (blue) sensors. Note that the Landsat 4 TM and Landsat 5 TM sensor have identical bandwidths.

Table 5-1: PLSR model results for each satellite sensor.

Sensor	No. components	R^2	RMSE
Landsat 4 TM	5	0.47	1.73
Landsat 5 TM	5	0.47	1.74
Landsat 7 ETM+	5	0.46	1.75

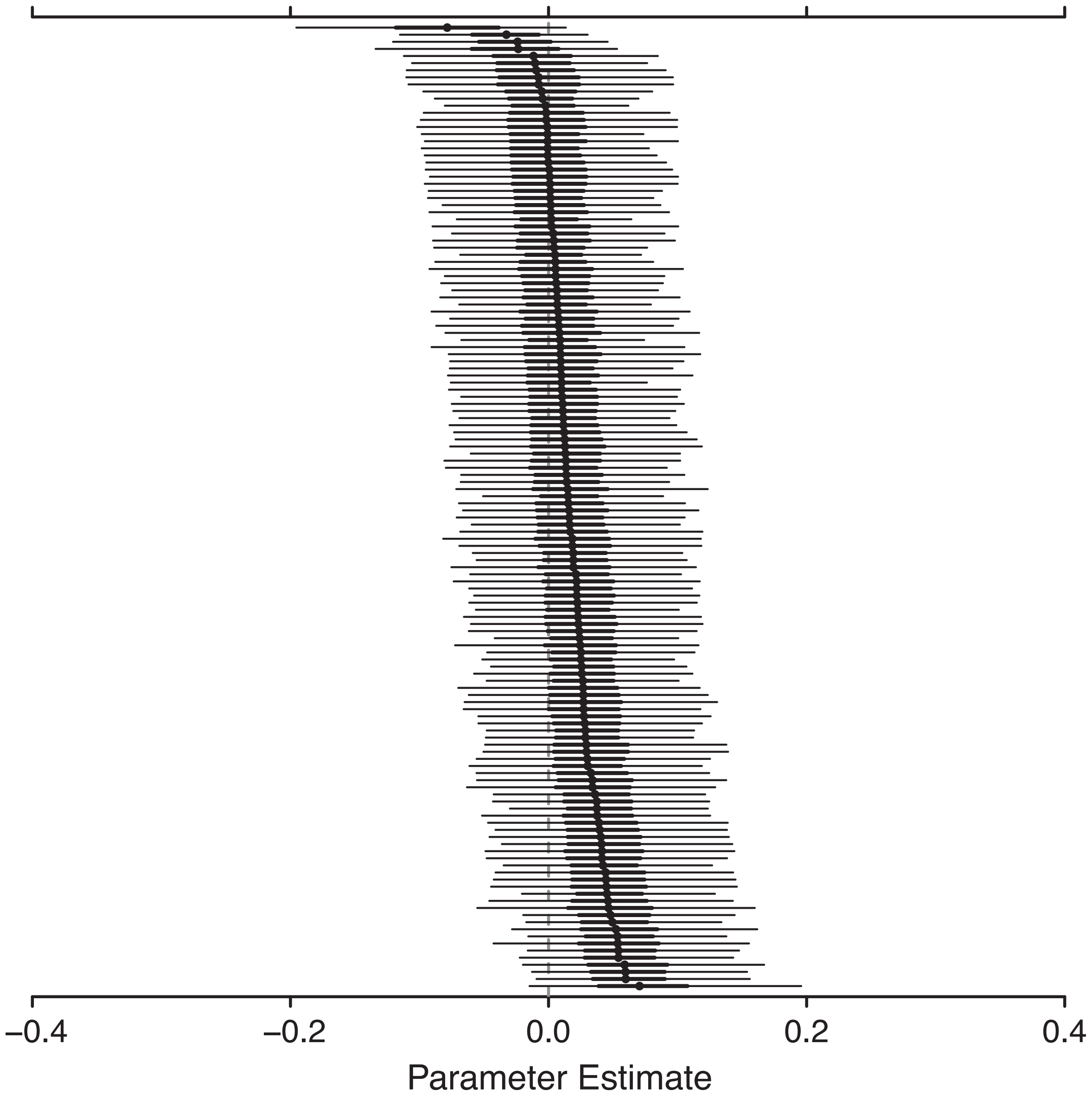

Figure 5-2: Posterior estimates for β parameters from Equation 5-3, representing the change in predicted $\delta^{15}N$ values over time. Black circles represent posterior medians. Thicker lines represent 50% credible intervals while thinner lines represent 95% credible intervals.

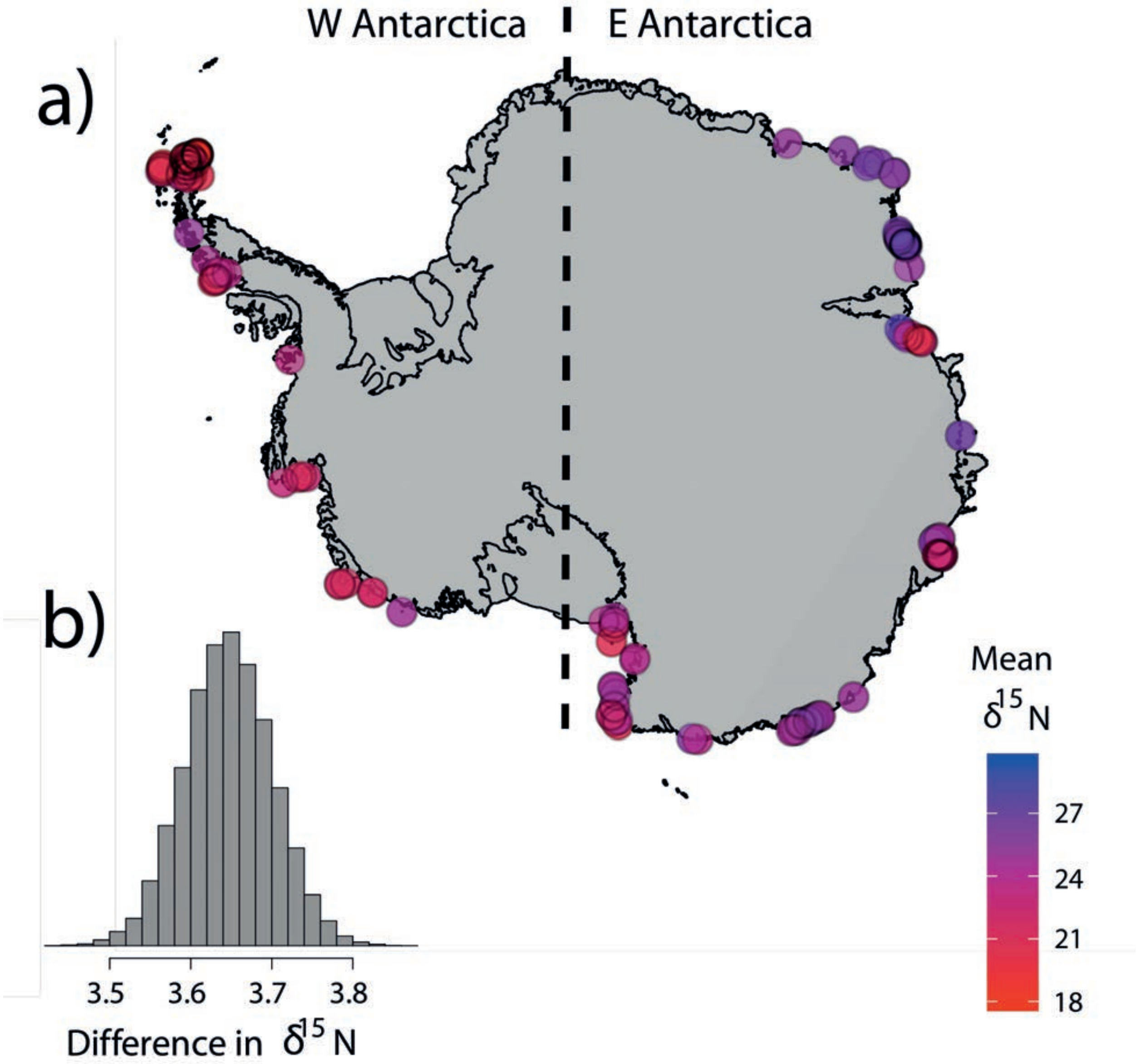

Figure 5-3: a) Estimated mean predicted $\delta^{15}N$ values at each Adélie penguin breeding colony where data were available for this study. The dashed line represents the boundary between West and East Antarctica. b) Posterior estimate for difference in predicted $\delta^{15}N$ between East Antarctica and West Antarctica.

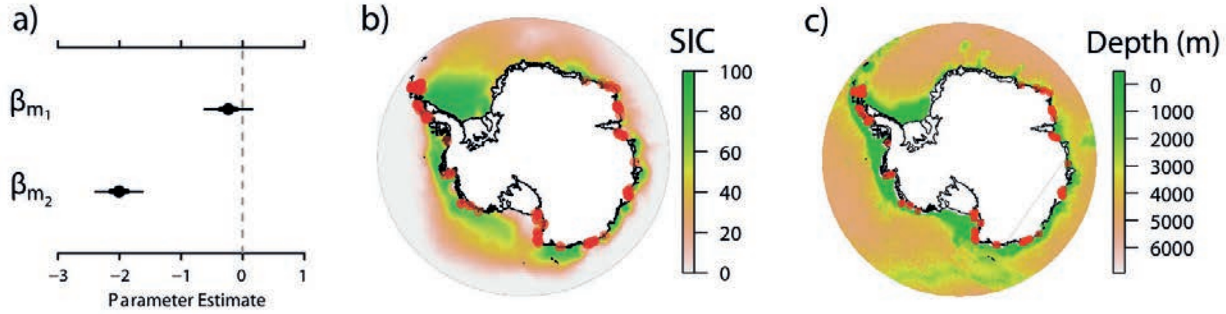

Figure 5-4: a) Parameter estimates for β_{m_1} (effect of SIC on $\delta^{15}N$ values) and β_{m_2} (effect of shelf area on predicted $\delta^{15}N$ values). Black circles represent posterior medians. Thicker lines represent 50% credible intervals while thinner lines represent 95% credible intervals. b) Sea ice concentration (percent sea surface covered with ice). c) Sea floor depth (m). Red dots represent Adélie penguin colonies for which data were available for this study.

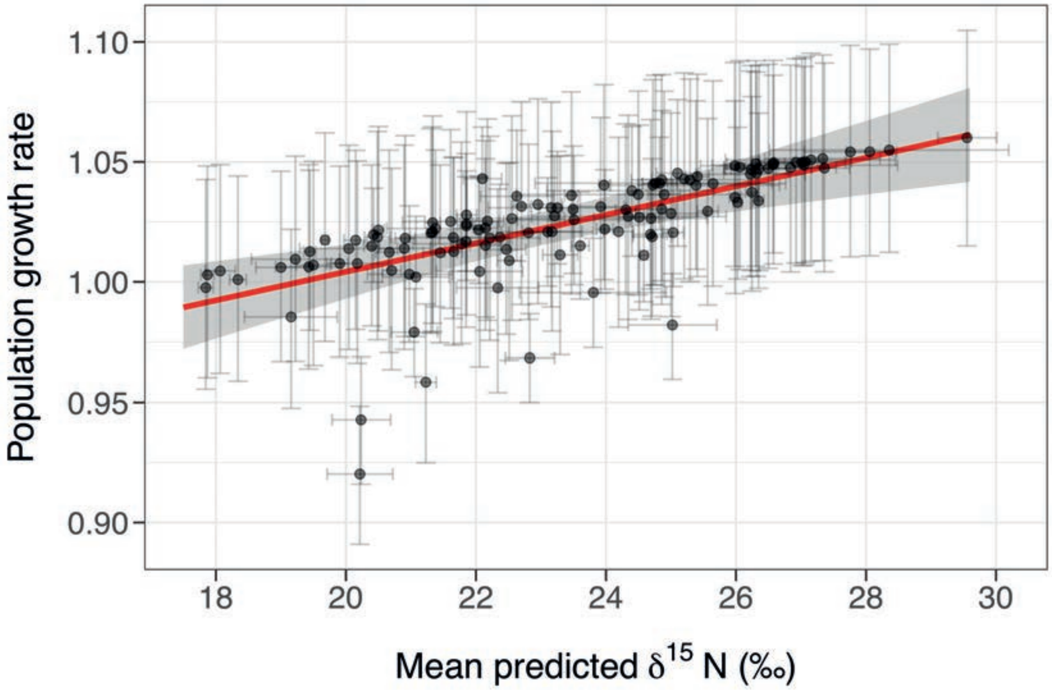

Figure 5-5: Estimated penguin colony population growth rates plotted against mean site predicted δ^{15}N values for each breeding colony. Error bars represent 95% credible intervals for growth rate and predicted δ^{15}N values. The red line represents the model fit, while the gray band represents the model 95% credible interval.

5.5 - DISCUSSION

Using a derived quantitative relationship between guano spectra and stable isotopes, in conjunction with a long-term archive of satellite imagery, I characterized Antarctic food web dynamics, as reflected by the diet of the Adélie penguin, over unprecedented temporal (decadal) and spatial (continental) scales. To my knowledge, this is the first example of the use of remote sensors to quantify food web dynamics, and the first effort to characterize dietary changes over nearly the entire global range of a species. Despite recent changes in abiotic environmental conditions in Antarctica, I found no evidence for a shift in food web dynamics over the 29-year study period. Penguin diet did however vary spatially and was linked to penguin population changes around the Antarctic continent, which may be reflective of past resource exploitation, and a declining (though taxonomically unchanging) prey base in some regions.

No evidence of dietary shift over time

While abiotic conditions in the Antarctic system are changing heterogeneously around the continent (rapid warming and declining in sea ice in West Antarctica, no change in temperature and increasing sea ice in East Antarctica; Mayewski et al. 2009), I found no robust evidence of a shift in the trophic level of Adélie penguin diet in either the Eastern or Western region over the 29-year study period (Figure 5-2; Appendix 10). Given the importance of sea ice in driving ecosystem dynamics in the Antarctic ecosystem, this is somewhat surprising (Loeb et al. 1997, Arrigo and Thomas 2004, Doney et al. 2012). This lack of dietary shift suggests that the taxonomic diversity of prey available to Adélie penguins has not changed over this study period.

Spatial patterns of diet

Spatial differences in diet were apparent across the Antarctic continent, with breeding colonies in West Antarctica showing a lower trophic level diet, compared to breeding colonies in East

Antarctic (Figure 5-3). Previous studies have shown that Adélie diet can differ across space and time, both across and within years (Ainley et al. 1998, 2003, Jarman et al. 2013). Dietary patterns in this study are also consistent with previous work, with more krill-centric (lower trophic level) diets in West Antarctica, and more fish-centric (higher trophic level) diets in East Antarctica (Ainley et al. 1992, Watanuki et al. 1997, Jarman et al. 2002, Fraser and Hofmann 2003, Nicol et al. 2008, Cherel 2008).

While differences in sea ice have been shown to influence dietary composition within sites (Ainley et al. 1998, Ratcliffe and Trathan 2012), I found no evidence that average sea ice conditions during the penguin breeding season influenced average penguin diet (Figure 5-4). Sea ice conditions may have a stronger impact on diet at inter- or intra-annual time scales. Shelf area was found to be negatively associated with average dietary trophic level, a pattern driven by the large continental shelf regions in West Antarctica, and relatively small shelf regions in East Antarctica (Figure 5-4). Previous studies have suggested that Antarctic krill are generally preyed upon when penguins are foraging beyond the continental shelf (Ainley et al. 1998, Ratcliffe and Trathan 2012), which is not the case in West Antarctica. Within sites, on inter- and intra-annual time scales, the influence of shelf area on diet may be more apparent.

Diet and population trends

Compared to breeding colonies with higher predicted $\delta^{15}N$ values (more fish-centric diets), Adélie penguin populations with lower predicted $\delta^{15}N$ values (more krill-centric diets) are growing more slowly (or declining more rapidly; Figure 5-5). This notion suggests that while the taxonomic composition of the Adélie penguin prey base has not changed over the past 30 years (Figure 5-2), the overall availability of food resources in some regions, namely West Antarctica, has.

Previous work has shown that Adélie penguins relied largely on higher trophic level prey, such as fish, across their continental range in the deep past, and have moved to a lower trophic level diet within the last several hundred years (Emslie and Patterson 2007). A ‘krill surplus’ was proposed to be the mechanism by which this shift occurred – a predatory release of krill predators from commercial sealing and whaling efforts resulted in higher krill availability (Laws 1985). However, following this period of exploitation, a systematic ‘fishing down’ of Antarctic fish stocks began, particularly in West Antarctica, which greatly reduced the number of fish available for penguins (Kock 1992, Pauly 1998, Ducklow et al. 2007, Ainley et al. 2007). With depleted fish availability, Adélie penguins in West Antarctica now rely principally on krill resources. While some disagreement exists regarding the rate of change in krill abundance in the Southern Ocean (Atkinson et al. 2004, Steinberg et al. 2015), there is little debate that increased competition for krill resources now exists from a growing krill fishery (Hinke et al. 2017), and recovering fur seal (Hucke-Gaete et al. 2004, Trathan et al. 2012) and baleen whale populations (Nowacek et al. 2011, Leaper and Miller 2011), principal krill consumers. This decrease in krill availability, coupled with a lack of suitable alternative prey items (e.g., fish) is likely to be driving the regional decline of Adélie penguin populations in parts of West Antarctica (Trivelpiece et al. 2011). Increasing temperatures negatively impacting krill populations might further contribute to the lack of krill availability into the future (Klein et al. 2018).

The lack of dietary change in Adélie diet and decrease in penguin populations in some areas further indicates that Antarctic fish stocks likely have not recovered substantially in some regions. A ‘surplus’ of krill functionally no longer exists as resources are being divided amongst increasing numbers of consumers. While often considered one of the least impacted marine ecosystems on the planet (Halpern et al. 2008), this system currently exists in a state unlike that seen before the onset of industrialized resource extraction in the Antarctic, with clear demographic responses to these changes.

Next steps

The methodology presented here, quantifying penguin diet from satellite sensors using spectra and stable isotopes, represents an important first effort in quantifying Antarctic food web dynamics on large temporal and spatial scales. Remotely sensed data from a number of additional sensors, including Landsat 8 OLI could extend this time series from 2013-present. However, differing spectral bandwidths (e.g., a narrow NIR band on the Landsat 8 OLI sensor), make comparisons across some sensors difficult (Holden and Woodcock 2016). A correction factor could potentially be created using a third sensor (such as World View 2) to calibrate predictions across sensor eras. Further field sampling of guano over the circumpolar range of the Adélie penguin may also improve the relationship between guano spectra and diet (Appendix 10). Careful field validation using satellite-derived spectra, near surface spectra, dietary samples derived from multiple techniques, and δ^{15}N isoscapes could also be used to link δ^{15}N values predicted from remote sensors to actual dietary proportions, rather than relative proportions used here. Incorporation of information on other isotopic measures, such as δ^{13}C, may be also help in this way, and allow for the detection of prey shifts within the same trophic level.

Conclusions

This work represents a general framework for assessing ecological change in Antarctic food web dynamics at unprecedented spatial and temporal scales and represents a novel application of satellite imagery to key questions facing ecology today. Large-scale research efforts such as this may prove useful for environmental management efforts, particularly in the face of novel climate likely to be experienced in the near future (Cimino et al. 2016), and increased interest in resource extraction in the region.

6 – Conclusion

This body of work represents my efforts to better understand how changes in the abiotic environment might be impacting ecological processes in the Antarctic ecosystem, using seabirds as a lens to explore these concepts. These findings contribute not only to the scientific community's understanding of Antarctic ecosystem dynamics, but also to the larger body of knowledge regarding how ecosystems are responding to global change, particularly from the perspective of population- and community-level processes. Much of this work highlights the idiosyncratic nature of responses to global change and explores nuances in these ecological processes that have been heretofore unexplored in the literature.

While phenology and phenological mismatch have been the subject of extensive research, not much was previously known about these processes in the Antarctic. Results show that phenology is changing little if at all in this system, and that mismatch dynamics have a relatively small influence on demographic processes for the Adélie penguin (Chapter 2). This differs substantially from other systems, where large changes in phenology have led to an increase in the degree of phenological mismatch, with negative consequences for populations (Kerby et al. 2012). These findings suggest that phenology-independent factors may outweigh the importance of breeding during an optimal period of time, a notion supported by the long-term persistence of these penguin populations in the face of frequent mismatch.

Surprising patterns of phenological variability were also apparent for the Adélie penguin (Chapter 3). A strong stochastic component in Adélie penguin breeding phenology was apparent. Phenological variability in a captive Adélie penguin population kept under constant conditions was as great as that seen in wild populations. This point, coupled with additional evidence, suggests that breeding in synchrony with conspecifics is more important than breeding at some optimal point in time. While these findings focus on the Adélie penguin, they have relevance for any colonially breeding species.

Taking a community approach, I showed that each species in an Antarctic seabird community responds largely independently to fluctuations in the environment, perhaps due to a substantial degree of niche partitioning (Chapter 4). While large amounts of environmental variability might be expected to synchronize dynamics across an ecological community (as has been found in some systems), this is contrary to observations here. Making inference regarding the population status of other species in a given community or inferring changes in the abiotic environment may thus be difficult. Previous work has suggested that aggregation of demographic measures across time and space is often needed to draw robust conclusions (Che-Castaldo et al. 2017). I extend this idea by suggesting that aggregating across species may also be necessary if we are to truly develop a holistic understanding of ecological change through demographic information.

Finally, efforts to characterize large-scale dietary patterns showed that Adélie penguin diet has not changed substantially over time, despite changes in the physical environment (Chapter 5). Dietary patterns did vary by region, however, and were linked to population growth rates. Evidence suggests that past resource extraction may have driven these dietary patterns and that current food web dynamics are critical for understanding Antarctic predator demographics. Extractive factors may have as large an impact on ecosystems as environmental change, with substantial consequences for ecosystem function.

Much in the way that ‘mountain passes are higher in the tropics’ (Janzen 1967), systems exhibiting high degrees of variability may result in them being more robust to environmental change, when compared to systems that exhibit less temporal variability (when considering the same degree of change in each system). In this way, the Antarctic system (exhibiting high interand intra-annual variability) may be less susceptible to abiotic changes than systems that exhibit lower levels of variability. However, while determining which systems are more susceptible to these changes and why is a key question moving forward in ecology, the nuances and idiosyncrasies of ecological responses to a given environmental factor greatly complicates efforts for understanding. A need exists to sample a greater portion of the ‘ecological parameter space’ to enhance this understanding. This work demonstrates the importance of exploring these questions of ecological change across space, time, species, and ecosystems. The way in which ecological processes operate in well-studied (e.g., temperate North American and European) systems may be quite different when compared to systems that receive less attention from the research community. It is necessary to explore these questions from a great many directions if we are to synthesize this information and truly grasp how the natural world is shifting over time.

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