Who wins when the competition heats up?
Effects of climate change on interactions among three Antarctic penguin species

Submitted by Harriet Lucy Clewlow to the University of Exeter
as a thesis for the degree of
Doctor of Philosophy in Biological Sciences
in April 2019

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

ABSTRACT

This thesis sought to elucidate the mechanisms driving the large-scale population changes observed in *Pygoscelis* penguins in the Western Antarctic Peninsula (WAP)/Scotia Sea region since the 1970s, with particular focus on the interactions between the species. During this period the climate in this region has changed dramatically, with rapid warming and sea ice declines occurring until the late 20th century to be followed by a pause in the warming. These changes have altered biotic and abiotic conditions in the penguins' ecosystem and researchers widely agree that this is driving their population changes. In order to elucidate the exact mechanisms of population change, we attempted to fill crucial knowledge gaps, including foraging ecology, migration and breeding success, throughout their annual cycle and all with particular focus on the interactions between the three *Pygoscelis* species.

Direct tracking and isotope analysis provided novel insights into foraging behaviour and the role of niche partitioning between the species throughout the annual cycle, and its importance for reducing interspecific competition. During the breeding season, allochrony between Adélie and chinstrap penguins was found to reduce competitive overlap in foraging areas by 54%, compared to synchronous breeding, and to be resilient to climate change. The migration routes and over-winter sites of chinstrap penguins from the South Orkney Islands were identified for the first time and were found to be segregated from birds from the neighbouring South Shetland Islands archipelago. The environmental conditions at the two over-winter sites differed but the population trends at the two archipelagos were similar, suggesting that winter conditions are not likely to be a major driver.

Developing on our findings of contrasting environmental conditions across the chinstrap over-wintering sites, we investigated the effect of multiple environmental variables on population trends in the final two thesis chapters. Sea ice has been shown to be a major driver of Adélie penguin breeding success, and thereby population trends, and birds in our study region experience particularly dramatic seasonal changes in sea ice concentration (SIC), as it is located near the northern extent of winter ice. The three *Pygoscelis* species are widely cited as having different ice tolerances, termed the 'sea ice hypothesis', with Adélies being described as 'ice-loving', chinstraps as 'ice tolerant' and gentoos as 'ice averse'. These differing ice tolerances are thought to be a major factor in the species' contrasting population changes in this region and these hypothesised preferences could theoretically induce a sea ice optima for breeding and forging success. However, no evidence was found for a sea ice optima at the study colony, despite previous studies finding a 20% optima for Adélies in East Antarctica, and SIC was found to have no significant effect on breeding productivity or diet composition but some effect was found for fledging mass and foraging trip duration.

The combined influence of environmental conditions and interspecific interactions on the three species' population trends was investigated for the first time in this system. Data from large and local scale climate and a long time period (more than 25 years) were investigated at the two study archipelagos using a multi-species Gompertz population model. The model failed to identify any of the modelled variables as major drivers of the population variation, suggesting that other factors, such as predation and prey availability were potentially important drivers.

This thesis also identified a number of priorities for future research and identified the need for a greater emphasis on modelling the effects of Antarctic krill biomass, rather than climate variables, upon penguin demographic variables.

ACKNOWLEDGMENTS

Firstly, I would like to thank my main PhD advisor Dr. Norman Ratcliffe for his guidance and for sharing his extensive knowledge. I would also like to thank my collaborators for their generous data-sharing and helpful comments and the fieldworkers who collected much of the data in this project. This work would not have been possible without the financial support of the Natural Environment Research Council (NERC) and the World Wide Fund for Nature (WWF-UK). Last but not least, I would like to thank my family for their encouragement and guidance and give special thanks to my partner, Becs, for her constant support. I would not have been able to do this without you.

Table of Contents

List of Tables and Figures

Chapter 1 – *General introduction*

Figure 3 – Map showing the locations of the two study sites, produced using the package ggmap (Kahle and Wickham, 2016) in R version 3.3.0 (R Core Team, 2015).

Figure 4 – Map showing the monitored breeding sites on Signy Island, South Orkney Islands and the proximity of other islands within the archipelago. Maps were produced by the authors using the package ggmap (Kahle and Wickham, 2016) in R version 3.3.0 (R Core Team, 2015).

Figure 5 – Map showing the four monitored breeding sites on King George Island, South Shetland Islands and the proximity of other islands within the archipelago. Maps were produced by the authors using the package ggmap (Kahle and Wickham, 2016) in R version 3.3.0 (R Core Team, 2015).

Figure 6 – Schematic diagram indicating links between thesis chapters.

Chapter 2 – *Niche partitioning of sympatric penguins by leapfrog foraging appears to be resilient to climate change*

Figure 1 – Utilization distribution kernels of peripheral (95%) (thin line) and core (50%) foraging areas (shaded area with thick line) using raw GPS data of foraging trips during incubation (a), guard (b) and crèche (c) stage for Adélies (blue) and chinstraps (red) overlaid on bathymetry (metres) shown in greyscale shading. The maps were produced by the authors using R version 3.3.0.

Figure 2 – Leapfrog foraging behaviour throughout the breeding season based on Adélie (black line) and chinstrap (grey line) foraging distances. Shaded areas show when one species has leapfrogged the other by foraging further away from the colony. Areas below the dotted line show when Adélies have leapfrogged chinstraps and areas above show when chinstraps have leapfrogged Adélies (difference = daily maximum chinstrap distance – daily maximum Adélie distance).

Figure 3 – Daily (number of days from 1st October) utilization distribution overlap index (UDOI) values, and area under the curve (AUC) values, for with allochrony (top panel) and without allochrony (bottom panel) in core (left column) and peripheral (right column) foraging areas.

Figure 4 – Kernel density estimation curves of vertical overlap in dive depths for core (a), peripheral (b) and no horizontal overlap areas (c) between Adélies (black) and chinstraps (grey).

Figure 5 – Annual laying date for Adélies (black) and chinstraps (grey) against annual mean October air temperatures (°C) over the 20 year study period. Points are marked with years and shading represents 95% confidence intervals.
Appendix S1 – Sampling and variability of tracks among years

Table S1 – GPS/TDR tag deployments summed by breeding stage for all years of deployment

Table S2 – Comparison between years within breeding stages using a Utilisation Distribution Overlap Index (UDOI)

Figure S1 – Utilization distribution kernels of peripheral (95%; thin line) and core (50%; shaded area with thick line) foraging areas using raw GPS data of annual breeding stage foraging trips for Adélies (blue) and Chinstraps (red) overlaid on bathymetry. The maps were produced by the authors using R version 3.3.0.

Animation S1 – Animation illustrating the process of simulating tracks through the breeding season using Adélie penguins on Signy Island, South Orkneys as an example. Blue tracks represent resampled tracks from incubation, green from brood-guard and yellow from crèche. Accessible online - https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2656.12919

Animation S2 – Animation showing overlap in 50% (shaded area with thick lines) and 95% isopleths (thin lines) of Adélie (blue) and chinstrap penguin (red) dive locations derived from the simulation analysis. Accessible online - https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2656.12919

Table S3 – Examples of allochrony in sympatric congeneric seabirds. Definitions of allochrony type: staggered allochrony is a situation where birds breed during the same season but have different peaks in laying; complete allochrony is where birds breed in different seasons (e.g. summer, winter) such that their seasons do not overlap at all; Differences in breeding synchrony is where both species overlap their breeding seasons, but one species activity is more spread out through time than the other. Leapfrog foraging may arise in those species showing staggered allochrony where this is combined with stage-dependent foraging ranges.

Chapter 3 – *Chinstrap penguins display archipelago specific migration routes and strong migratory connectivity*

Table 1 – Sample sizes of geolocator (GLS) tracks and biological samples collected from Signy Island, South Orkney Islands archipelago.

Table 2 – Summary of tail feather and eggshell (2007 only) isotopic values (mean±SD) and Bayesian core niche area estimate (SEA_b) for each sampling year at each archipelago. Values in parentheses are 95% credibility intervals.

Figure 1 – Monthly 95% contours of birds from the South Orkney Islands (dashed lines – colony location at red triangle) and South Shetland Islands (solid line – colony location red circle) with April to November coloured in the following order: red, brown, blue, green, orange, purple and grey. The maps were produced by the authors using R version 3.6.1. and the ggplot2 packages (R Core Team, 2015; Wickham and Chang, 2016).

Figure 2 – Mean near-surface ocean velocity field (2012-2016) for the Southern Ocean, with the colour axis set to a maximum of 0.3 m s^{-1} for clarity of visualisation. Arrows indicate current velocity (larger arrow = faster flow) plotted at every 1° latitude and 2° longitude. Data were obtained from the E.U. Copernicus Marine Service information (Copernicus Marine Environment Monitoring, 2018). South Shetland Islands highlighted with red circle and South Orkney Islands highlighted with red triangle.

Figure 3 – Annual sea-surface temperature values at the over-winter site of each archipelago population during each tracking year.

Figure 4 – Annual chlrophyll-a values at the over-winter site of each archipelago population during each tracking year.

Figure 5 – Total (TA–dashed line) and core isotopic niche area (SEA_c–solid line) and group centroid (cross) for chinstrap penguin biological samples*.* Plot A–All feather samples from both archipelagos–black=South Shetland Islands, red=South Orkney Islands; B–All eggshell samples–black=South Shetland

Islands, red=South Orkney Islands; C–South Shetlands individual years tail feathers–black= 2012, red= 2014; D–South Orkney individual years tail feathers–black= 2013, red= 2015 and grey=2018; E–tail feathers of individual birds sampled on successive years–black= 2016 samples, red=2017 samples.

Chapter 4 – *Investigating the effect of sea ice on breeding and foraging performance metrics of Pygoscelis penguins at the South Orkney Islands*

Figure 1 – Conceptual graph of the sea ice optima for Adélies' (blue), chinstraps' (red) and gentoos' (grey) breeding productivity (ratio chicks to pairs).

Figure 2 – Map showing the monitored breeding sites on Signy Island, South Orkneys and the proximity of other islands within the archipelago. Maps were produced by the authors using the package ggmap in R version 3.3.0.

Figure 3 - Average annual foraging trip duration against average annual sea ice cover for Adélies (blue) and chinstraps (red) with error bars representing the standard error of model prediction values. Note that both species had similar trip durations in 2008 and 2012 but Adélie trips were longer in 2014 and 2016.

Figure 4 – Annual variation in the proportion of krill in diet, fledging mass and breeding success for Adélies (blue) and chinstraps (red) with error bars representing the standard error.

Figure 5 – Annual proportion of krill in diet against average annual sea ice cover for Adélies (blue) and chinstraps (red) with error bars representing the standard error of model prediction values.

Figure 6 – Average annual fledging mass against average annual sea ice cover for Adélies (blue) and chinstraps (red) with error bars representing the standard error of model prediction values.

Figure 7 – Breeding productivity (ratio of chicks per pair) with sea ice cover (SIC) for Adélies (blue), chinstraps (red) and gentoos (grey) with error bars representing the standard error of model prediction values.

Table 1 - Annual variation in trip duration (hours) and the effect of sea ice concentration (SIC), where t is year, s is species, x is SIC, K is the number of

model parameters and ΔAICc is the difference in AICc between the model in question and the best fit model.

Table 2 – Mean annual trip durations and standard deviations for Adélies and chinstraps.

Table 3 - Annual variation in percentage krill in diet samples models and the effect of sea ice concentration (SIC), where t is year, s is species, x is SIC, K is the number of model parameters and ΔAICc is the difference in AICc between the model in question and the best fit model.

Table 4 – Annual variation in fledging mass models and the effect of sea ice concentration (SIC), where t is year, s is species, x is SIC, K is the number of model parameters and ΔAICc is the difference in AICc between the model in question and the best fit model.

Table 5 – Annual variation in breeding productivity models and effect of sea ice concentration (SIC), where t is year, s is species, x is SIC, K is the number of model parameters and ΔAICc is the difference in AICc between the model in question and the best fit model.

Chapter 5 – *Interactions of competition and the environment upon Pygoscelis penguin population trends*

Figure 1 – Maps of (a) the region with the locations of the two study archipelagos, (b) a fine-scale map of the study colonies on Signy Island, South Orkney archipelago and (c) a fine-scale view the study colonies on King George Island, South Shetlands archipelago. Maps were produced by the authors using ggmap and ggrepel in R version 3.3.0 (Kahle and Wickham, 2016; Slowikowski et al., 2018).

Figure 2 – Modelled *Pygoscelis* penguin population trends at (a) Signy Island, South Orkney Islands and (b) King George Island, South Shetland Islands with 95% confidence limits (shaded bands). Note: Signy Island gentoo data is actual number of pairs counted annually in whole island population. Signy Island Adélie and chinstrap data is modelled from numbers of pairs counted annually in selected study colonies.

Figure 3 – First and second Principal Components from the Principal Component Analysis based on environmental variables (SST=sea surface temperature, SIE=Sea ice extent, SAM=Southern Annular Mode, SOI=Southern Oscillation Index, AIR=October air temperature) with the abundance series of each penguin species incorporated as supplementary variables (AP=Adélie penguin, CP=chinstrap penguin, GP=gentoo penguin) for the South Orkney Islands (a) and the South Shetland Islands (b).

Figure 4 – Estimated means and credible intervals (95%) parameters representing the effects of species interactions ($\alpha_{i,j;\ i \neq j}$) on the growth of individual penguin species on the South Orkney Islands (a) and South Shetland Islands (b). A, C and G correspond to Adélie, chinstrap and gentoo penguins respectively so AC denotes Adélie compared to chinstrap.

Figure 5 – Estimated means and credible intervals (95%) for environmental fixed effects denoted by Principal Components (PC1 and PC2) on the growth of individual penguin species at the South Orkney Islands (a) and South Shetland Islands (b). A, C and G correspond to Adélie, chinstrap and gentoo penguins respectively.

Table 1 – Principal Component Analysis results for South Orkney Islands (Dim = principal component axes).

Table 2 – Principal Component Analysis results for South Shetland Islands (Dim = principal component axes).

Table 3 – Model selected environmental variables for South Orkney Islands (Dim = principal component axes).

Table 4 – Model selected environmental variables for South Shetlands (Dim = principal component axes).

Table 5 – Estimates of components of the temporal variance and proportions of the different components with respect to the total temporal variance for the South Orkney Islands.

Chapter 1 – *General introduction*

1 | LITERATURE REVIEW

Global biodiversity is under immense threat from climate change (Sala et al., 2000; Grooten and Almond, 2018), making insights into the effects of climate change a major focus for modern ecologists. Climate change induces far-reaching direct and indirect effects, intensifying many of the global challenges affecting people, species and ecosystems (Blois et al., 2013). Elucidating the mechanisms underlying the observed effects of climate change on species can be complex but it is crucial for accurately predicting potential long-term impacts (Parmesan, 2006).

This research project focuses on a group of species living in one of the most rapidly warming areas globally (Vaughan et al., 2003), utilising long term data sets to investigate the impact of climate change on individual species and the interactions between them, in order to determine the drivers of population change. The study species are the *Pygoscelis* penguins; Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*) and Gentoo penguins (*P. papua ellsworthi*). These congeners breed sympatrically in parts of their range and experience high levels of competitive interactions due to their shared foraging areas and primary prey species.

1.1 | A GLOBAL VIEW OF CLIMATE CHANGE

Climate changes have occurred repeatedly throughout history, however, recent warming rates are far greater than any warming events observed in the past 10,000 years (Blois et al., 2013). Therefore, whilst climate variation is expected, natural causes alone are not enough to explain the scale and rate of the recent changes observed (Intergovernmental Panel on Climate Change, 2014). Anthropogenic factors, particularly greenhouse gas emissions, are thought to play a key role in the observed warming trends and with the ever-growing human population these contributions are only likely to increase

(Solomon et al., 2009). Globally, temperatures have already risen by more than 1°C above pre-industrial levels and world leaders have agreed to try to limit the rise to less than 2°C, as above this level substantial negative impacts are projected (Warren et al., 2011; Intergovernmental Panel on Climate Change, 2014). These large scale temperature changes have already caused global sea levels to rise by up to ~3.2mm annually since 1901 and sea temperatures to warm by 0.11°C per decade between 1971 and 2010 (Intergovernmental Panel on Climate Change, 2014). These changes are magnified in areas of climate extremes, such as at the poles where Arctic sea ice extent has been steadily declining since 1978 (Kirchmeier-Young et al., 2016) and 87% of Antarctic marine glaciers have retreated (Cook et al., 2005).

1.2 | CLIMATE CHANGE IN ANTARCTICA

As the Earth's last great wilderness, Antarctica is key to understanding the Earth's climate and humans' impact upon it. The continent is becoming increasingly more vulnerable to the effects of climate change, which are magnified in areas of climate extremes, such as polar regions or deserts (Walther et al., 2002) where changes have been occurring at a faster and less predictable rate than elsewhere on Earth (Vaughan et al., 2003).

Climate change patterns across the Antarctic continent are highly regional because it spans a wide range of latitudes. East Antarctica has been experiencing temperature declines and increases in sea ice (Turner and Overland, 2009), whilst Western Antarctica is one of three areas of the world experiencing particularly rapid warming (Vaughan et al., 2003; Clarke et al., 2007; Ducklow et al., 2007). The Western Antarctic Peninsula (WAP) has experienced nearly a 3°C rise in average surface temperature since 1951 (Vaughan et al., 2003; Turner et al., 2016), followed by pauses in this warming since 2000 (Turner et al., 2016), which is significantly higher than the mean global average (Intergovernmental Panel on Climate Change, 2014). These dramatic atmospheric temperature changes have caused a 1°C rise in the temperatures of the surrounding oceans as well as increasing salinity levels in the upper-layer (Meredith and King, 2005). In turn, winter sea ice extent has reduced by 10% per decade since the 1950s (Clarke et al., 2007) and almost 90% of glaciers on the Antarctic Peninsula have been retreating since the 1960s (Clarke et al., 2007; Turner, Bindschalder, et al., 2009). This region is currently described as a ‘polar desert’ due to very low annual levels of precipitation but snow fall has been increasing since the start of 20th century (McClintock et al., 2008). This combination of small scale melt and increased snow fall is predicted to be a significant contributor to global sea level rise, even though Antarctic ice sheets are not predicted to melt entirely (Shepherd et al., 2012; Mengel et al., 2016).

The Southern Annular Mode (SAM), the strong westerly wind belt that circles Antarctica (Fig. 1), is thought to be a major factor in determining the contrasting climate observed across the Antarctic continent (Thompson and Solomon, 2002; Ding et al., 2011). Changes in the location, or polarity, of SAM have caused circumpolar westerly winds to increase by ~20% since 1970s directing warm, wet oceanic air to the region from the tropical Pacific; an area also experiencing sea surface warming (Fig. 1; Marshall et al., 2006; Ding et al., 2011; Abram et al., 2014). These westerly winds directly influence seasonal sea ice extent and duration, and this is reflected in the significant negative trends in sea ice observed in the Amundsen and Bellingshausen Seas (Western Antarctica). However, a positive sea ice trend has been observed in East Antarctica and this contrasting sea ice pattern across the continent is called the Antarctic Dipole (Turner, Comiso, et al., 2009). The dipole is highly influenced by the ‘ozone-hole’ above Antarctica and trends are predicted to alter as the hole ‘heals’ towards the end of the 21st century (Turner, Comiso, et al., 2009). Models indicate that as the ‘ozone-hole’ closes sea ice trends will reverse as wind speeds will reduce (Turner, Comiso, et al., 2009). Sea ice levels can also directly drive winter air temperatures, for example the winter temperatures in Western Antarctica are driven by the sea ice extent in the Bellingshausen sea (west of Antarctic Peninsula), meaning regional changes in sea ice may have much wider ranging, long-term effects (Vaughan et al., 2003; Turner et al., 2005). It is important to note, however, that whilst temperatures in the WAP region have increased, the rate of warming has varied greatly and even paused in the late 1990s (Turner et al., 2016).

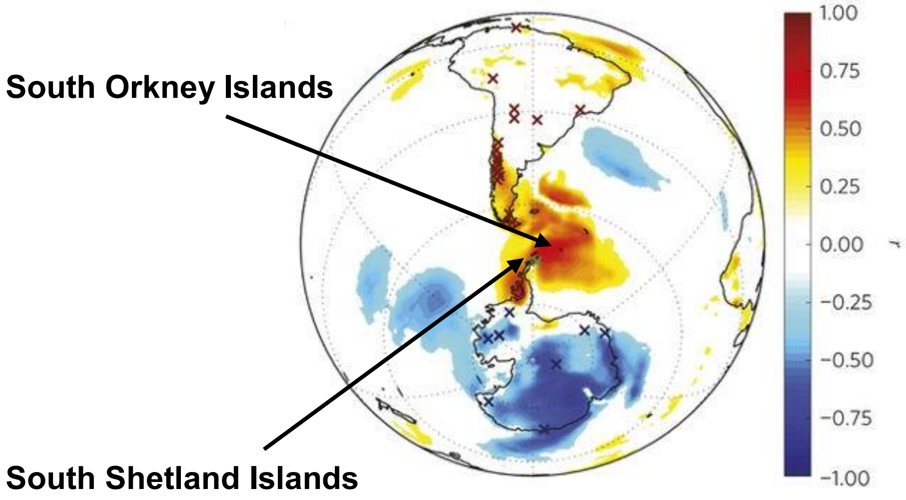


Figure 1 – Figure adapted from Abram et al., 2014 indicating the spatial response of surface air temperatures (°C) to SAM variability across the Antarctic continent from 1979-2012 and the two study sites.

1.3 | INFLUENCES OF CLIMATE CHANGE

Climate change influences individuals, populations and ecosystems through a variety of interconnected mechanisms (Walther et al., 2002; Gilman et al., 2010). These mechanisms can be difficult to disentangle as effects can be direct and/or indirect and positive or negative for the species.

The majority of research has investigated the direct effects of climate change, likely because they are the most immediately apparent and easiest to disentangle, and some biotic alterations in predator-prey interactions, particularly phenological mismatching (Croxall et al., 2002; Hipfner, 2008; Visser et al., 2012; Keogan et al., 2018). However, in doing this most research has ignored the important interactions between climate change (abiotic) and other biotic factors, such as inter- and intraspecific competition (Loreau, 2010), which are crucial in driving key processes in ecosystems (Araújo and Luoto, 2007; Gilman et al., 2010; Helland et al., 2011; Milazzo et al., 2013). Recent studies have indicated the importance of biotic interactions, specifically interspecific competition, in defining a species' response to climate change and that climate conditions can define competitive dominance between species (Helland et al., 2011; Milazzo et al., 2013). Novel climate conditions could, therefore, induce species co-occurrence to shift to competitive displacement, trigger completely novel interspecific interactions or cause breeding cycles to become more synchronised in sympatric breeding areas (termed 'competitor matching' here), with all potentially resulting in food web alterations or species extinctions (Ahola et al., 2007; Blois et al., 2013; Milazzo et al., 2013).

Further to this, in line with global climate change, extreme weather events are becoming increasingly common (Easterling et al., 2000) and can trigger dramatic biological responses at all trophic levels (Parmesan et al., 2000). In Antarctica, a desert ecosystem, storms and rainfall are becoming increasingly common and are predicted to become ever more frequent (IPCC, 2007). Such events have already caused entire seabird colony breeding failures in East Antarctica (Ropert-Coudert et al., 2015, 2018).

1.3.1 | Geographical range expansion and contraction

Climate change has caused some species to shift their geographical range in an attempt to track tolerable climate conditions (Parmesan, 2006) and this is only predicted to become more common with continued warming (Krosby et al., 2015). However, not all species are able to shift their range easily meaning they are open to novel competitive interactions with species who are induced to migrate into their geographic range by climate change (Milazzo et al., 2013; Robillard et al., 2015).

Climate change can induce species to alter their geographical range for a number of reasons but at the most basic level an organisms' physiology only allows them to physically tolerate a specific thermal range and any temperature outside of that may negatively impact their reproductive rate or survival (Barnes et al., 2009; Milazzo et al., 2013). Species who are unable to adapt to novel climate conditions can be forced to contract their geographical range, usually because conditions are outside their thermal tolerance, their preferred habitat is no longer available and/or prey availability is reduced. For example, Ethiopian bush crows (*Zavattariornis stresemanni*) only occupy a very narrow area just of 16,000km^2 that lies within an altitude-related isotherm despite there being extensive areas of suitable habitat, in terms of land-use, available (Donald et al., 2012).

A meta-analysis of 434 species, including plants, birds, mammals, insects, reptiles, fish and marine invertebrates, determined that climate change had caused 80% to shift their geographic range (Parmesan and Yohe, 2003). Polar species generally displayed range contractions (Parmesan and Yohe, 2003) such as Arctic shelf fish communities who have contracted their range northwards (Fossheim et al., 2015) and Antarctic krill (*Euphausia superba*; referred to as krill hereafter) who have contracted their range southwards (Atkinson et al., 2019). However, some polar species have displayed range expansions, such as gentoo penguins (Lynch, Naveen, et al., 2012). In causing such a high percentage of species to alter their range, climate change has the potential to bring previously isolated species into contact with others and for closely related species to come into contact with one another for the first time. This generates novel communities termed ‘non-analogue communities’ that are likely to have particularly high levels of inter and intra-specific competition (Urban et al., 2012) and in extreme cases species hybridisation may occur, leading to long-term negative consequences (Krosby et al., 2015). Therefore, understanding a species’ specific thermal range is integral for accurately predicting a species’ potential geographical range under future climate scenarios.

1.3.2 | Altered Species Interactions

Indirect effects of climate change, such as altered species interactions, are often overlooked but recent studies have shown that they can dramatically influence the response of a species to climate change (Gilman et al., 2010). For example, climate change in Norway has lengthened ice-cover duration altering interactions between Brown Trout (*Salmo trutta*) and Arctic Charr (*Salvelinus alpines*). Brown Trout numbers have not been directly impacted by the environmental changes, except in lakes shared with Arctic Charr where they have experienced population declines (Helland et al., 2011; Ulvan et al., 2012). This demonstrates how climate change can dramatically alter species interactions, causing pre-existing interactions to be intensified, causing co-occurrence, such as sympatric breeding, to switch to competitive displacement (Blois et al., 2013; Milazzo et al., 2013). In fact, every interaction type is believed to be influenced by climate change in some way as a cascade of effects induced by species’ thermal sensitivity (Helland et al., 2011).

In the Antarctic food web, in addition to climate-induced changes in interactions, populations of previously hunted species, such as whales and seals, are recovering (Tulloch et al., 2019). This means that interactions between these species and other predators for their shared prey resource, krill, are increasing and many studies suggest that this is a factor in the krill population reduction (Trivelpiece et al., 2011; Atkinson et al., 2019) and in some areas has forced other predators, penguins, to switch prey type (Ainley et al., 2006).

At a basic level, animals and plants display seasonal activity patterns to ensure they time reproduction and growth with the most optimal environmental conditions and incur fitness and survivorship costs if these demanding activities occur outside of this optimal window (Cotton, 2003; Visser and Both, 2005). The timing of reproduction (phenology) is driven by the interaction of internal physiological and behavioural factors and external environmental influences (Emmerson et al., 2011). For example, breeding is initiated by hormones, and the timing of their release is influenced by photoperiod length and variable environmental factors such as prey availability and the presence of optimal climate conditions (Frederiksen et al., 2004; Emmerson et al., 2011; Ouyang et al., 2011). Climate change has triggered some species to shift their phenology to maintain the coordination with the optimal temperatures they require (Cotton, 2003; Parmesan and Yohe, 2003; Visser and Both, 2005) but this, in turn, has caused the phenology of some predator species to become asynchronous with peaks in their prey species (see section below).

Migratory species, especially birds, are experiencing the greatest levels of reproductive mistiming due to the ever increasing disconnection between the climate in over-wintering areas and those in summer breeding areas (Cotton, 2003; Visser et al., 2004). They must use large-scale environmental cues to determine timing, meaning they are at a disadvantage compared to resident species who are able to use local cues at the breeding sites to more accurately determine when to begin breeding (Wittwer et al., 2015). This difference induces further mismatch in communities containing both resident and migratory species (Frederiksen et al., 2004; Ahola et al., 2007; Emmerson et al., 2011; Lynch, Fagan, et al., 2012; Wittwer et al., 2015). Overall, the phenological response to climate change appears to be highly variable both between species and within populations of the same species (Walther et al., 2002; Visser et al., 2004). A meta-analysis found that 62% of 677 species, including plants, birds, mammals, insects, reptiles, fish and marine invertebrates, have advanced the timing of their phenology (Parmesan and Yohe, 2003), but some processes such as leaf fall, are now occurring later than previously for the majority of tree species (Cotton, 2003).

1.3.2.1 | Effects of climate on food abundance

Climate change impacts are felt throughout the food web and in marine ecosystems these impacts are generally manifested via bottom-up effects (Durant et al., 2007). Meaning that primary and secondary productivity is altered by climate change, usually via changes in ocean circulation, which in turn negatively impacts the reproduction and survival of higher trophic species such as seabirds (Gremillet and Boulinier, 2009). The fitness of organisms in higher trophic levels is entirely dependent upon primary production and therefore the decoupling of the food web in this manner will have a significant negative impact upon the functioning of the entire ecosystem (Behrenfeld et al., 2006; Burthe et al., 2012). These large-scale changes have already been observed in the marine ecosystem of the North Sea, where climate change induced temperature changes have induced a mismatch between primary (dinoflagellates) and secondary producers (copepods), which is negatively affecting higher predators reliant on these productivity peaks (Edwards and Richardson, 2004). The mismatch between predators and prey is believed to be the most prevalent climate-induced alteration across ecosystems. However, it is important to note that responses are highly species specific meaning not all have been negatively impacted (Visser and Both, 2005; Burthe et al., 2012).

Primary production in Antarctica is highly dependent upon sea ice and both are influenced by temperature (Arrigo et al., 1997). The Antarctic food web is centred on krill, a species which is highly reliant on sea ice throughout its lifecycle for breeding and foraging (Atkinson et al., 2008). Therefore, the substantial shifts in sea ice in the Scotia Sea/WAP region, in terms of the timing of extent and advance and the overall duration of the sea ice season (Stammerjohn et al., 2008; Murphy et al., 2014), have all impacted the abundance and distribution of krill (Atkinson et al., 2004, 2019). Krill is the dominant component of many Antarctic penguins’ diet throughout much of their range, particularly Adélies and chinstraps, (Ratcliffe and Trathan, 2012) and in the absence of sufficient food seabird breeding attempts can be delayed, likely to ensure chick provisioning is timed as close as possible to the peak in prey availability (Vinuela et al., 1996; Kowalczyk et al., 2014), or abandoned, particularly if there is a lack of prey resources before the onset of breeding (Hamer et al., 1993; Barrett and Krasnov, 1996; Croll et al., 2006; Kowalczyk et al., 2014). The window of ideal weather conditions for polar species, however, is generally smaller than for temperate/tropical species and as such delaying breeding may mean individuals do not breed successfully that season (Martin and Wiebe, 2004). Entire colony breeding failures have been observed in some penguin species (Ropert-Coudert et al., 2015, 2018).

1.4 | NICHE PARTITIONING

Seabirds are commonly used as model species to investigate niche partitioning because their coloniality and central-place foraging strategy have the potential to create high levels of interspecific competition within their shared foraging ranges (Ballance et al., 2009; Elliott et al., 2009). This competition shapes community structure, species distribution and induces large-scale population changes (Hardin, 1960; Carrete et al., 2005), with foraging competition appearing to be the most influential of all (Chase et al., 2002; Ainley et al., 2004; Wisz et al., 2013). Species sharing limited food resources experience particularly intense competition and will be unable to exist sympatrically, according to the ‘Competitive Exclusion Principle’ of Hardin (1960), if the level of competition is too great. In order to reduce this competition species differentiate along multidimensional niche axes (MacArthur and Levins, 1967); including allochrony (defined as differences in breeding time (phenology) between conspecific individuals) (Trivelpiece et al., 1987), diet (Croxall et al., 1997), timing of foraging behaviour (Harris et al., 2013) and, most commonly observed, core foraging location (MacArthur, 1958; Wilson, 2010; Thiebot et al., 2012). This partitioning can also be defined by intraspecific niches, such as individual differences (Anderson et al., 2009; Ratcliffe et al., 2013), sex (Harris et al., 2013), age (Catry et al., 2004) and/or physical size (Field et al., 2005; Lu et al., 2009).

Competition for food is potentially very high during the breeding season unless segregation occurs along one of the above niche axes, according to niche theory (Croxall and Prince, 1980; Croxall et al., 1997), or prey is superabundant (Forero et al., 2004). Segregation among congeners is predicted to occur along habitat boundaries and within habitats for conspecifics (Ratcliffe et al., 2014; Quillfeldt et al., 2015). This segregation can be in the form of different foraging habitats, areas or depths, differing food resources and/or differing peak resource usage (Quillfeldt et al., 2015). This can be determined by a species' physical abilities, such as size and thermal tolerance (Wilson, 2010; Donald et al., 2012), and species habitat preference (MacArthur, 1958; Fraser et al., 1992). A number of seabird species display foraging behaviour that varies among breeding stages, meaning they access different foraging areas during different breeding phases (Wilson et al., 1995; Weimerskirch, 2007). The three species of *Pygoscelis* penguins have become a classic case study for niche partitioning due to their particularly high potential for competition induced by colonial, sympatric breeding and central-place foraging for shared prey (Trivelpiece et al., 1987).

Colonially breeding seabirds experience different levels of inter- and intra-specific competition throughout their annual cycle (Ratcliffe et al., 2014; Hinke et al., 2015). During the non-breeding period birds no longer have to return to the colony to feed their chick (central-place foraging) and, thus, are able to migrate to reach other foraging areas, which are often occupied by birds from other colonies during the breeding season (González-Solís et al., 2007). The non-breeding period has been studied less extensively than the breeding period due to this change and the migration behaviour of many species is currently unknown. In the studied species, spatial segregation, across multiple niche axes, has been observed during the non-breeding season (Masello et al., 2010; Ratcliffe et al., 2014). However, there is some mixing between birds from the same archipelago but different breeding colonies (Hinke et al., 2015). This combination of segregation and mixing may be driven by a similar competitive process as during the breeding season or it may be induced by factors such as habitat boundaries, genetics or social learning (Hjeljord, 2001; Pomilla and Rosenbaum, 2005; Liechti, 2006).

1.5 | ALLOCHRONY

Allochrony, defined as differences in breeding time (phenology) between conspecific individuals, has been hypothesised by many to be an important differentiating axis for competition reduction. Seasonal allochrony occurs in a range of taxa and is a potential mechanism for sympatric speciation (Taylor and Friesen, 2017). There are three main types of allochrony; complete allochrony in which species breed in non-overlapping periods (Friesen et al., 2007), staggered allochrony where species breed in the same season and overlap but with temporal offsets in their peaks of reproduction (Birkhead and Nettleship, 1987; Trivelpiece et al., 1987), and allochrony in synchrony where two species overlap but one species' breeding season is more spread out through time than that of the other (Stonehouse, 1962). Staggered allochrony is most prevalent at higher latitudes where cold winters impose constraints on the flexibility in breeding seasons (Martin and Wiebe, 2004), while the other two strategies are more commonly found in tropical and sub-tropical latitudes (see global species summary in Supporting Table S8 in Chapter 2). Sympatrically breeding congeneric seabirds, from both the tropics and poles, commonly display allochrony (Robertson et al., 2014 and see Supporting Table S8 in Chapter 2).

In areas of sympatric breeding, *Pygoscelis* penguins begin breeding in sequence over a ~3 week period (Trivelpiece et al., 1987), with Adélies starting first, followed by gentoos and finally chinstraps (Black, 2015), meaning each species reaches the high-prey-demanding chick rearing stage at a different time (Lynch, Fagan, et al., 2012). Climate change could potentially disrupt these carefully timed systems, effectively removing niche partitioning and potentially causing species to move elsewhere (Wilson, 2010; Hinke et al., 2015). Ecologically similar species may alter their breeding phenology in response to warming at different rates (Chadwick et al., 2006; Lynch, Fagan, et al., 2012) and, where breeding cycles become more synchronised, increases in competitive interactions may arise (Ahola et al., 2007), which we termed "competitor matching."

Changes in temperature, sea ice cover and prey availability are influencing *Pygoscelid* penguin breeding (Emmerson et al., 2011; Lynch, Fagan, et al., 2012; Black, 2015). One of the few studies making direct comparisons between the species, studying penguins breeding on the South Shetland Islands, found that gentoo penguins have advanced their phenology at a different rate to the other two species (Lynch, Fagan, et al., 2012). This has caused the interval separating species onset of breeding to decrease between gentoos and chinstraps in particular, whereas the interval between Adélies and chinstraps remained similar (Lynch, Fagan, et al., 2012). The likely reason for this discrepancy is that gentoos differ from the other two species on a range of niche axes such as diet, foraging range, diving ability and they do not migrate over winter (Trivelpiece et al., 1987). Resident species are able to use local cues to determine the onset of breeding, whereas migratory species, such as Adélies and chinstraps, must use large scale cues (Tanton et al., 2004). The importance of allochrony for these three species is often referred to in terms of reducing competition during the crucial chick provisioning period (Trivelpiece et al., 1987; Lynnes et al., 2002; Wilson, 2010), allowing maximal resource availability for both species (Miller et al., 2010; Black, 2015), but it's effects in spatial segregation of foraging areas has not been documented. Previous attempts to describe the spatial segregation between these species' foraging distributions (Lynnes et al., 2002; 110 Wilson, 2010) were confined to the chick-rearing period and will have overestimated the degree of overlap as they assumed that the observed behaviours occurred simultaneously, when in reality they occurred three to four weeks apart.

Many sympatrically breeding seabirds exhibit allochrony in some form (See Table S3 in Chapter 2 for a global summary) and another Antarctic seabird example is the two species of Giant petrels, Northern Giant Petrel (*Macronectes halli*) and Southern Giant Petrel (*Macronectes giganteus*). They have a circumpolar distribution in the southern hemisphere and have overlapping ranges, causing them to breed sympatrically in some locations (Hunter, 1984). The two species have the same prey preferences, generally feeding on carrion, and as such must compete for the limited prey available (Granroth-Wilding and Phillips, 2018). Allochrony appears to be an important way to mitigate this competition for these species too, with Northern Giant Petrels breed up to 6 weeks earlier than Southern Giant Petrels (Hunter, 1984; Granroth-Wilding and Phillips, 2018).

1.6 | STUDY SPECIES – Genus *Pygoscelis* (The Brush-tailed penguins)

This project focused on three Antarctic penguin species; Adélie (*Pygoscelis adeliae*), chinstrap (*Pygoscelis antarctica*) and gentoo penguins (*Pygoscelis papua ellsworthi*), because they breed sympatrically in the WAP/Scotia Sea region and are congeneric species. Sympatrically breeding congeneric species, such as these, have the potential to experience particularly high levels of competition, due to shared prey and breeding and foraging areas, meaning they must partition their niches, and thus any small alterations induced by climate change may have a particularly large impact (Hardin, 1960; MacArthur and Levins, 1967; Carrete et al., 2005).

The three species do not have identical breeding ranges but there is overlap across the sub-Antarctic islands (Fig. 2; Borboroglu and Boersma, 2013; Black, 2015). Adélie penguins breed between 60° and 77° south, chinstrap penguins breed between 54° and 64° south and gentoo breed between 45° and 65° south (Carlini et al., 2005; Borboroglu and Boersma, 2013). Therefore, the WAP is an area of extensive overlap for these three species and penguins constitute the vast majority of avian biomass in Antarctica, with populations of chinstrap and Adélie penguins accounting for 90% of avian biomass in the Scotia Sea region (excluding South Georgia) (Lynnes et al., 2002; Black, 2015).

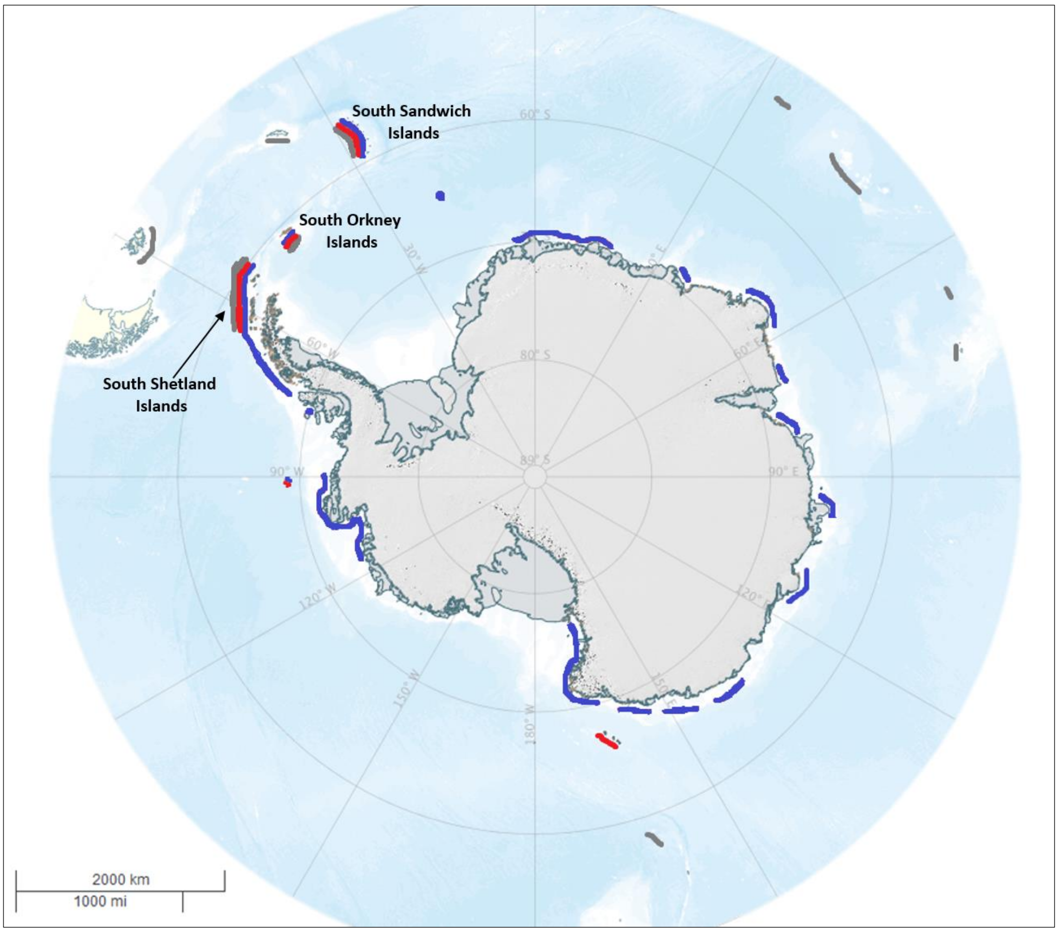


Figure 2 – Approximate breeding ranges of Adélie penguins in blue, chinstrap penguins in red and gentoo penguins in grey. Adapted from figures in Borboroglu and Boersma, 2013 using a basemap from SCAR Antarctic Digital Database Map Viewer (https://www.add.scar.org/).

Increasing temperatures in the region appear to be favouring the less cold-tolerant gentoo penguin (Trathan et al., 1996; Lynnes et al., 2002). Gentoos appear to be more able to react to the changing temperatures by shifting their breeding initiation date by almost twice as much as the other species in sympatric populations on the South Shetland Islands (Lynch, Fagan, et al., 2012) and by being more generalist in their prey preferences (Ratcliffe and Trathan, 2012). This has led to rapid population increases while populations of Adélies and chinstraps have declined (Lynch, Fagan, et al., 2012; Dunn et al., 2016).

1.6.1 | Adélie penguin (*Pygoscelis adeliae)*

Image 1 – An adult Adélie penguin stretches their wings in front of a crèche of chicks.

The Adélie penguin is one of only two truly Antarctic penguin species, the other being the Emperor Penguin (*Aptenodytes forsteri*), and is the most widely distributed penguin species in the Southern Ocean, despite it being the smallest (Borboroglu and Boersma, 2013). Adélie penguins migrate to the pack ice on completion of breeding where they moult and remain throughout the austral winter (Trathan et al., 1996; Clarke et al., 2003; Hinke et al., 2014). Globally, there are c.3.79 million breeding pairs (Lynch and LaRue, 2014), but the global population is predicted to decline at a rate of 20-29% over the next three generations and may even experience a ~46% population decline by 2099 due to interacting impacts of climate change (Ainley et al., 2010; IUCN, 2012; Cimino et al., 2016). Their diet is dominated by Antarctic krill and fish, with the location of their colony defining the proportions of each (Ratcliffe and Trathan, 2012). Their foraging habitat also varies depending on their colony location and they generally forage within pack-ice or in open water (Ratcliffe and Trathan, 2012).

The majority of Adélie penguins are found in Western Antarctica but populations in East Antarctica are faring much better, with some experiencing population increases (Croxall et al., 2002), justifying their classification as Least Concern by the IUCN (IUCN, 2012). The highly regional population trends implicate the significant influences of climate change and the Antarctic Dipole on Adélie penguins (Forcada and Trathan, 2009; Turner, Bindschalder, et al., 2009). The Adélie population on Signy Island have experienced declines of 43% (-1.5% annually) over the last 38 years (Dunn et al., 2016) and there are now c.2,200 breeding pairs of Adélie penguin across the island, with the majority breeding in the large colony on Gourlay Peninsula (Lishman, 1985; Dunn et al., 2016).

1.6.2 | Chinstrap penguin (*Pygoscelis antarctica)*

Image 2 – A chinstrap penguin incubating their chick on Signy Island, South Orkney islands.

Chinstrap penguins are the most abundant penguin in Antarctica with a population of c.8 million pairs (IUCN, 2012) but they are almost entirely confined to the WAP and islands in the Scotia arc (Forcada et al., 2006). They are classified as Least Concern by the IUCN (IUCN, 2012) due to the huge population, consisting of around 1.3 million birds, at the South Sandwich Islands being stable (Lynch et al., 2016) but many other colonies further south are experiencing large population declines (Lynch et al., 2016). Their diet consists of nearly 100% krill across their geographic range and they tend to forage benthically in open water (Takahashi et al., 2003; Ratcliffe and Trathan, 2012). The chinstrap population on Signy has experienced an almost continual population decline since 1979 reducing numbers by 68% (-3.6% annually) and there are now c.1,400 breeding pairs, with the majority breeding on Gourlay Peninsula (Lishman, 1985; Dunn et al., 2016).

1.6.3 | Gentoo penguin (*Pygoscelis papua ellsworthi*)

Image 3 – A gentoo penguin protecting their chicks on Signy Island, South Orkneys.

Gentoo penguins are physically larger than their congeners, weighing up around 2kg more, and are the third largest of all penguin species (Borboroglu and Boersma, 2013). There are two subspecies of gentoo penguin, *P. papua ellsworthi* and *P. papua papua* (Stonehouse, 1970). The *P. p. ellsworthi* subspecies breeds on the Antarctic peninsula, South Shetland, South Orkney and South Sandwich Islands and *P. p. papua* breeds further north on the Falkland Islands, South Georgia and other sub-Antarctic islands (Stonehouse, 1970; Williams, 1995). They are, however, the least abundant Antarctic penguin species with only c.387,000 breeding pairs globally (Borboroglu and Boersma, 2013). Unlike the other *Pygoscelis* species, gentoos are usually resident at their breeding grounds all year around and preferentially breed near warm water upwellings or fast currents to ensure sea ice does not prevent foraging during the austral winter (McClintock et al., 2008). Their diet consists of a smaller proportion krill than the other *Pygoscelis* species, up to 86% of their diet, depending on colony location, compared to up to 100% in the other two species (Ratcliffe and Trathan, 2012), and they consume a variety of fish, crustaceans and squid (Ratcliffe and Trathan, 2012). Gentoo penguins are classified as Least Concern by the IUCN (IUCN, 2012) because most breeding populations are stable or even increasing and their southerly range is expanding (Lynch, Naveen, et al., 2012; Borboroglu and Boersma, 2013). The gentoo population on Signy has experienced dramatic population increases over the last 38 years of 255% meaning there are now c.1,300 pairs breeding on Signy with the entire population breeding at North Point (Dunn et al., 2016).

1.7 | STUDY SITES

The main study sites for this project (Fig. 3) were breeding colonies located on Signy Island, South Orkney Islands (60°42’S, 45°36’W) and on King George Island, South Shetland Islands (62°17’S, 108 58°45’W). These study sites were selected as the three *Pygoscelis* species breed in sympatry at these locations and they are both in the WAP region, which, as discussed above, is an area experiencing extensive climate changes – making them ideal study sites to investigate climate-induced changes in interactions between the species.

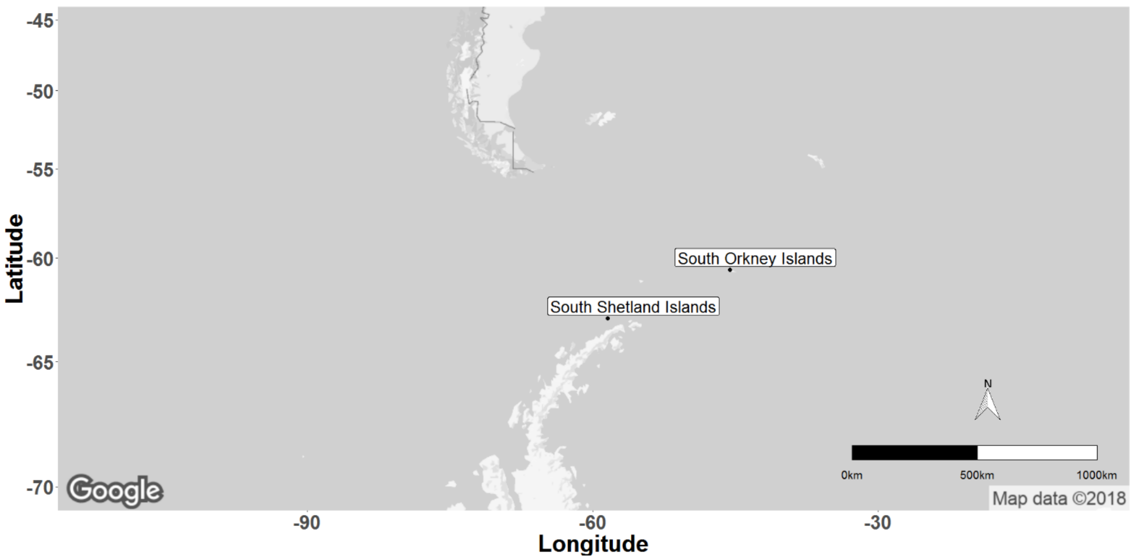


Figure 3 – Map showing the locations of the two study sites, produced using the package ggmap (Kahle and Wickham, 2016) in R version 3.3.0 (R Core Team, 2015).

1.7.1 | Signy Island, South Orkney Islands

Signy Island (referred to as Signy hereafter) is located about 500 kilometres from the other study site on the South Shetland Islands (Fig. 3) and is part of a group of four islands called the South Orkney Islands. Sealers discovered the South Orkney Islands in 1821 and a whaling station was established on Signy in 1907. A research station was founded in Factory Cove, above the old whaling station, in 1947 and scientists have worked on the island ever since. The island itself is only 6.5 kilometres long and less than 4.5 kilometres wide with approximately half of the island covered by a permanent ice-cap (British Antarctic Survey, 2015; BirdLife International, 2019).

The small island is very exposed to weather systems because when moving westerly or easterly at the same latitude from Signy, there is no landfall until the South Orkneys are re-encountered, having travelled all the way around the globe. Signy was designated as an Important Bird and Biodiversity area by BirdLife International due to the exceptional diversity of seabird and seal species living there (Harris et al., 2015). The largest Adélie and chinstrap penguin colonies are located on the Gourlay Peninsula (Fig. 4; Lynnes et al., 2002), whereas gentoo penguins are only found at the North Point of the island (Fig. 4) and are resident at the South Orkney Islands archipelago all year round

(Waluda et al., 2014; Hinke et al., 2017). These colonies have been monitored continuously since the 1970s (British Antarctic Survey, 1973).

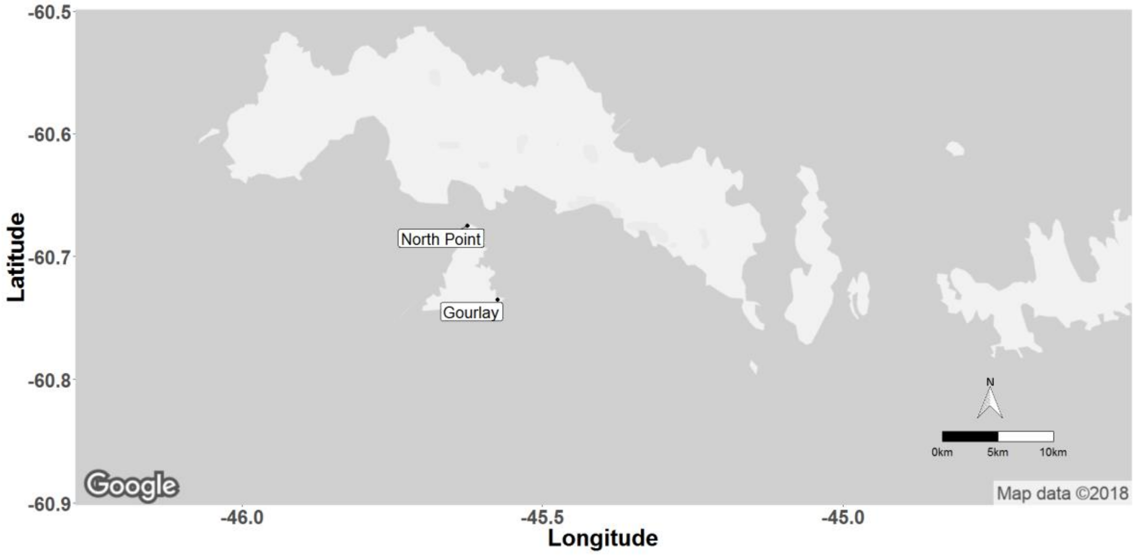


Figure 4 – Map showing the two monitored breeding sites on Signy Island, South Orkney Islands and the proximity of other islands within the archipelago. Maps were produced by the authors using the package ggmap (Kahle and Wickham, 2016) in R version 3.3.0 (R Core Team, 2015).

1.7.2 | King George Island, South Shetland Islands

The South Shetland Islands are located about 120 kilometres from the Antarctic Peninsula and consist of 11 major islands, with King George Island being the largest. During the 19th and 20th centuries the islands were used for sealing and whaling but now this archipelago is highly concentrated with research stations, maintained by countries from across the globe, and is regularly visited by tourism cruises (Encyclopaedia Britannica, 2019).

The vast majority of land is covered by a permanent ice-cap and the elevation varies greatly between the islands, reaching over 2,000 metres above sea level at its peak. All three Pygoscelis species breed sympatrically here and these penguin colonies have been monitored continually since the late 1980s (United States Antarctic Program, 1990).

This study uses data collected on King George Island (62°17’S, 58°45’W) at multiple breeding colonies (Fig. 5). Additional samples were collected from colonies on Livingstone Island (62°47’S, 60°78’W) for Chapter 3.

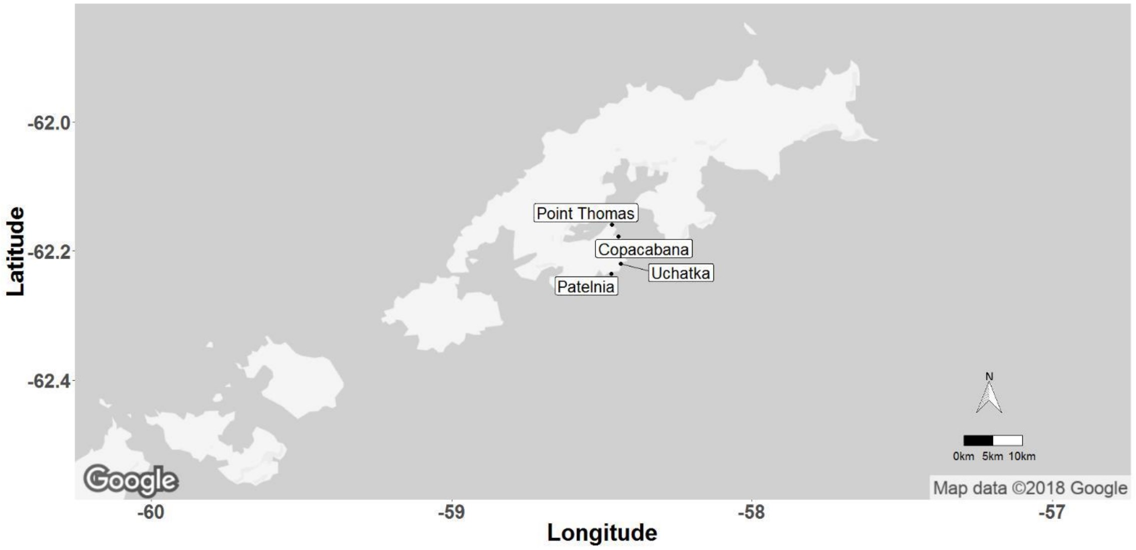


Figure 5 – Map showing the four monitored breeding sites on King George Island, South Shetland Islands and the proximity of other islands within the archipelago. Maps were produced by the authors using the package ggmap (Kahle and Wickham, 2016) in R version 3.3.0 (R Core Team, 2015).

2 | AIMS, OBJECTIVES AND RESULTS

The overall aim of the thesis was to determine how changing environmental conditions are altering interactions between sympatrically breeding Antarctic penguin communities, thereby facilitating understanding of the possible impacts of future climate (see Figure 6 for a schematic linking the thesis chapters). This study focused on the three *Pygoscelis* penguin species; Adélie, chinstrap and gentoo penguins breeding on Signy Island, South Orkney Islands and, for some chapters, on King George Island, South Shetlands during both summer (breeding season) and winter (migration). All three species were not investigated in each thesis chapter as datasets for some species, gentoo penguins in particular, were not available. Long-term data sets were used for analysis throughout the thesis and, depending on the data available/analyses undertaken, covered at least seven years, up to a maximum of forty years.

The objective of the Chapter 2 was to investigate niche partitioning during the breeding season, as we currently have limited knowledge of the mechanisms underlying this. Specifically, the role of allochrony, defined as differences in breeding time (phenology) between conspecific individuals, in foraging niche partitioning during the breeding season and its potential to be influenced by climate change was investigated. Interactions, both inter- and intra-specific, have the scope to induce high levels of competition during the breeding season as all species are central-place foragers they are constrained by the need to regularly return to the colony to incubate eggs or feed growing chicks. The level of competition is potentially increasing due to climate change-induced declines in their primary prey source, krill. Using data from GPS tagged breeding adult Adélie and chinstrap penguins we quantified, for the first time, the integral roles of allochrony and leapfrog foraging in reducing this high competition. Within breeding stages (incubation, guard and crèche) foraging areas used were similar, but the observed allochrony of 28 days resulted in birds leapfrogging each other through the breeding season such that they were exploiting different foraging locations on the same calendar dates. Allochrony reduced spatial overlap between the species by 54.0% over the breeding season compared to a scenario where the two species bred synchronously. If allochrony is reduced by just a single day, spatial overlap was found to increase by an average of 2.1%. However, both species advanced their laying dates in relation to increasing October air temperatures at the same rate, preserving allochrony and niche partitioning. Niche partitioning between the two species by allochrony is therefore resilient to climate change and so competitor matching cannot be implicated in the observed population declines of the two penguin species across the Western Antarctic Peninsula.

The objectives of Chapter 3 were to describe the migration routes and overwintering areas of chinstrap penguins from the South Orkney Islands archipelago for the first time and to assess the spatial segregation between birds originating from the South Orkney Islands archipelago, specifically Signy Island, and the South Shetland Islands archipelago, specifically King George Island, and quantify migratory connectivity across the populations. Chapter 2 highlighted the importance of spatial segregation, defined by the allochrony induced temporal segregation, for reducing competition during the breeding season and we predicted that spatial segregation would also be an important factor during winter. Geolocator tags were used to track adult chinstrap penguins from both archipelagos during their non-breeding period and results showed strong niche partitioning with individuals from the two archipelagos taking completely divergent migration paths. The majority of individuals from the South Shetland Islands headed directly west into the South Pacific region of the Southern Ocean, travelling against the prevailing ocean current, whereas all individuals from the South Orkneys headed north-east towards the South

Sandwich Trench utilising the Antarctic Circumpolar Current. The two archipelago populations occupied separate overwintering areas, which is consistent with migratory connectivity. There was evidence for fidelity as birds from each population consistently followed similar migration routes to similar wintering areas across years. These spatially segregated areas resulted in birds from the two archipelagos experiencing different climate conditions, which has the potential to affect survival and subsequent population trends – this was tested in Chapter 5. Birds from the South Shetlands experienced warmer sea surface temperatures and lower chlorophyll-a levels in their overwintering areas than the South Orkney birds experienced. Stable isotope ratio analysis of tail feathers supported the geolocator findings, showing that birds from the two colonies occupied different locations and isotopic niches. However, there was significant interannual variation in isotope ratios, contradicting the high site fidelity found by the geolocator tags. It is likely that much of this variation was a result of interannual variation in isotopic baselines, which are driven by the dynamic marine biogeochemical cycles (McMahon et al., 2013), and we could not control for using this bulk isotope analysis technique.

The objectives of Chapter 4 were to test the widely cited sea-ice hypothesis, which classifies Adélies, chinstraps and gentoos as ice-loving, ice-tolerant and ice-intolerant, respectively, by quantifying their sea ice optima for foraging and breeding performance. This is a highly cited hypothesis, but studies have only directly quantified the species' ice tolerances in East Antarctica, a region experiencing significantly different climate conditions. The presumed ice tolerance classifications for the three species lead us to predict that Adélies will have a sea ice optima as quantified by previous papers (~20%) (Barbraud et al., 2015; Le Guen et al., 2018), chinstrap performance should remain level before decreasing at moderate levels of sea ice, likely well below Adélies' reported optima, and gentoos performance will decline steeply as sea ice concentration increases. We tested this by analysing the breeding productivity of Adélie, chinstraps and gentoos breeding sympatrically on Signy Island during a 19-year period. Breeding productivity was compared to annual sea ice concentrations during the guard period of breeding and diet composition, foraging trip duration and fledging mass were also monitored to determine the mechanism of sea ice influence on breeding productivity. Sea ice was not found to have a direct influence upon breeding productivity for any of the three species and it was not found to act indirectly by significantly influencing their diet composition or breeding productivity. Fledging mass and foraging trip duration were found to be influenced by sea ice but the species reacted in parallel, which would not occur if the species' ice tolerance differed as their classifications suggest. Our findings do not support the widely asserted Sea Ice Hypothesis and no optima for any of the *Pygoscelid* populations breeding at Signy Island was identified. Sea ice conditions differ greatly between East, where all previous studies were undertaken, and West Antarctica, meaning the birds in the two systems are utilising and reacting to the sea ice differently, likely driving the divergent findings.

The objective of Chapter 5 was to determine the role of competition and the environment upon historic *Pygoscelis* penguin population trajectories. To date, many studies have modelled the direct effects of environment upon species' population trends, but none have included competition, an important driver, in their models. A multi-species population model, based on a Gompertz function, was used to elucidate the effect of interspecific competition, environmental variables and the interactions of these two factors on historical population trajectories, collected over a 40 year period, of *Pygoscelis* penguins from the South Shetlands and South Orkney Islands. This approach was based on the work of Mutshinda et al., 2011. Environmental variables were investigated at multiple scales, local and large atmospheric, and at multiple time lags to provide insight into all drivers of penguin demography. The main modelled components of intra/interspecific competition, environmental variables and the interaction between these two variables were found to have very little effect on the three species' population trajectories at both archipelagos. In fact, environmental variation not directly driven by the variables included in the model accounted for more than 80% of population variation at both archipelagos. This is possibly due to the selected environmental variables not sufficiently representing the availability of key prey species such as Antarctic krill. The lack of support for density dependence and interspecific competition in the model may be due to these processes being unimportant in this system, or due to limitations in this modelling framework for detecting these processes in declining populations.

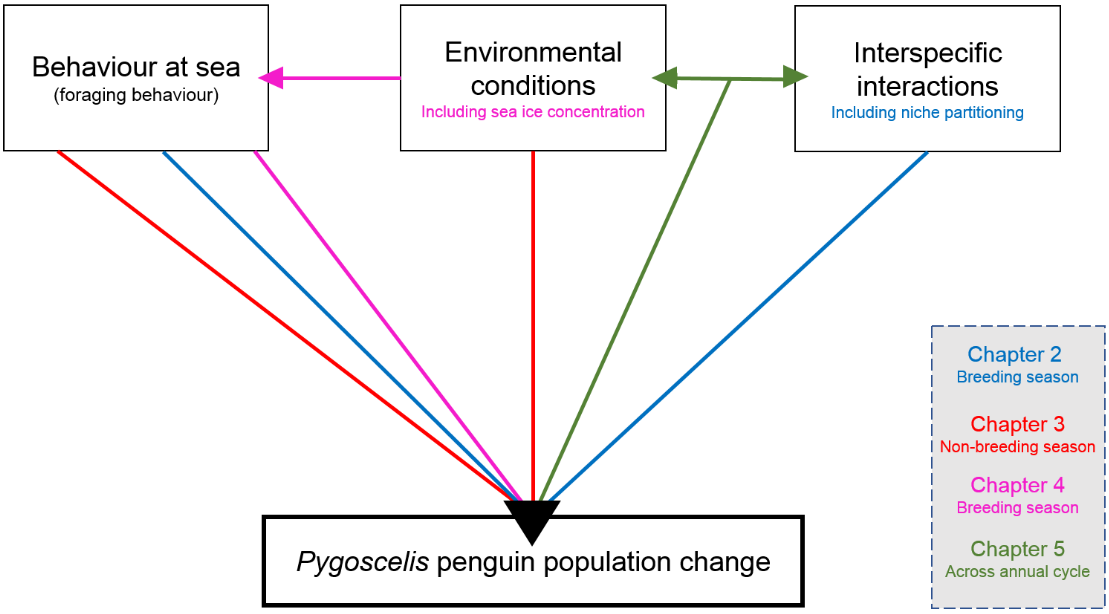


Figure 6 – Schematic diagram indicating links between thesis chapters.

3 | CONTRIBUTION OF PUBLISHED PAPERS TO THE FIELD

Chapter 2 – published as: Clewlow, H. L., A. Takahashi, S. Watanabe, S. C. Votier, R. Downie, and N. Ratcliffe. 2019. Niche partitioning of sympatric penguins by leapfrog foraging is resilient to climate change. Journal of Animal Ecology 88: 223–235. The framework for the study was developed by N.R. and H.L.C. Fieldwork was conducted by N.R., H.L.C., A.T. and S.W. with H.L.C. processing and analysing all data. H.L.C. wrote the paper with contributions from all the other authors, and all authors gave final approval for publication. Tracking data from 2008 was collected and initially processed by A.T and S.W.

4 | REFERENCES

Abram, N. J., R. Mulvaney, F. Vimeux, S. J. Phipps, J. Turner, and M. H. England. 2014. Evolution of the Southern Annular Mode during the past millennium. *Nature Climate Change* 4: 564–569.

Ahola, M. P., T. Laaksonen, T. Eeva, and E. Lehikoinen. 2007. Climate change can alter competitive relationships between resident and migratory birds. *Journal of Animal Ecology* 76: 1045–1052.

Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the Western Ross Sea, Antarctica. *Ecology* 87: 2080–2093.

Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, K. Barton, et al. 2004. Geographic structure of Adelie Penguin populations: overlap in colony-specific foraging areas. *Ecological Monographs* 74: 159–178.

Ainley, D., J. Russell, S. Jenouvrier, E. Woehler, P. O. Lyver, W. R. Fraser, and G. L. Kooyman. 2010. Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels. *Ecological Monographs* 80: 49–66.

Anderson, O. R. J., R. A. Phillips, R. F. Shore, R. a. R. McGill, R. A. McDonald, and S. Bearhop. 2009. Diet, individual specialisation and breeding of brown skuas (*Catharacta antarctica lonnbergi*): an investigation using stable isotopes. *Polar Biology* 32: 27–33.

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16: 743–753.

Arrigo, K. R., D. L. Worthen, M. P. Lizotte, P. Dixon, and G. Dieckmann. 1997. Primary Production in Antarctic Sea Ice. *Science* 276: 394–397.

Atkinson, A., S. L. Hill, E. A. Pakhomov, V. Siegel, C. S. Reiss, V. J. Loeb, D. K. Steinberg, et al. 2019. Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nature Climate Change* 9: 142–147.

Atkinson, A., D. A. Siegel, E. Pakhomov, and P. Rothery. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100–103.

Atkinson, A., V. Siegel, E. A. Pakhomov, P. Rothery, V. Loeb, R. M. Ross, L. B. Quetin, et al. 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series* 362: 1–23.

Ballance, L. T., D. G. Ainley, G. Ballard, and K. Barton. 2009. An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin Pygoscelis adeliae. *Journal of Avian Biology* 40: 279–288.

Barbraud, C., K. Delord, and H. Weimerskirch. 2015. Extreme ecological response of a seabird community to unprecedented sea ice cover. *Royal Society Open Science* 2: 140456.

Barnes, D. K. A., H. J. Griffiths, and S. Kaiser. 2009. Geographic range shift responses to climate change by Antarctic benthos: where we should look. *Marine Ecology Progress Series* 393: 13–26.

Barrett, R. T., and Y. V. Krasnov. 1996. Recent responses to changes in stocks of prey species by seabirds breeding in the southern Barents Sea. *ICES Journal of Marine Science* 53: 713–722.

Behrenfeld, M. J., R. T. O'Malley, D. A. Siegel, C. R. McClain, J. L. Sarmiento, G. C. Feldman, A. J. Milligan, et al. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444: 752–755.

BirdLife International. 2019. Important Bird Areas factsheet: Signy Island. Website http://datazone.birdlife.org/site/factsheet/signy-island-iba-antarctica [accessed 29 June 2019].

Birkhead, T. R., and D. N. Nettleship. 1987. Ecological relationships between Common Murres, *Uria aalge*, and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador. I. Morphometrics and timing of breeding. *Canadian Journal of Zoology* 65: 1621–1629.

Black, C. E. 2015. A comprehensive review of the phenology of *Pygoscelis* penguins. *Polar Biology*: 1–28.

Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate Change and the Past, Present, and Future of Biotic Interactions. *Science* 341: 499–504.

Borboroglu, P., and P. Boersma. 2013. Penguins: natural history and conservation. Samuel and Althea Stroum Book.

British Antarctic Survey. 1973. British Antarctic Survey - LTMS at Signy Island. Website https://www.bas.ac.uk/project/higher-predators-long-term-science/ [accessed 14 March 2018].

British Antarctic Survey. 2015. British Antarctic Survey - Signy Research Station. Website https://www.bas.ac.uk/polar-operations/sites-and-facilities/facility/signy/ [accessed 13 October 2018].

Burthe, S., F. Daunt, A. Butler, D. Elston, M. Frederiksen, and D. G. Johns. 2012. Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Marine Ecology Progress Series* 454: 119–133.

Carlini, A. R., N. R. Coria, M. M. Santos, and S. M. Bujan. 2005. The effect of chinstrap penguins on the breeding performance of Adèlie penguins. *Folia Zoologica* 54: 147–158.

Carrete, M., J. A. Sánchez-Zapata, J. F. Calvo, and R. Lande. 2005. Demography and habitat availability in territorial occupancy of two competing species. *Oikos* 108: 125–136.

Catry, P., A. Campos, V. Almada, and W. Cresswell. 2004. Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size. *Journal of Avian Biology* 35: 204–209.

Chadwick, E. A., F. M. Slater, and S. J. Ormerod. 2006. Inter- and intraspecific differences in climatically mediated phenological change in coexisting Triturus species. *Global Change Biology* 12: 1069–1078.

Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, et al. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* 5: 302–315.

Cimino, M. A., H. J. Lynch, V. S. Saba, and M. J. Oliver. 2016. Projected asymmetric response of Adélie penguins to Antarctic climate change. *Scientific Reports* 6: 1–9.

Clarke, A., E. J. Murphy, M. P. Meredith, J. C. King, L. S. Peck, D. K. A. Barnes, and R. C. Smith. 2007. Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 362: 149–166.

Clarke, J., K. Kerry, C. Fowler, R. Lawless, S. Erberhard, and R. Murphy. 2003. Post-fledging and winter migration of Adélie penguins *Pygoscelis adeliae* in the Mawson region of East Antarctica. *Marine Ecology-progress Series - MAR ECOL-PROGR SER* 248: 267–278.

Cook, A. J., A. J. Fox, D. G. Vaughan, and J. G. Ferrigno. 2005. Retreating Glacier Fronts on the Antarctic Peninsula over the Past Half-Century. *Science* 308: 541–544.

Copernicus Marine Environment Monitoring. 2018. Global Ocean Gridded Sea Surface Heights and Derived Variables (1993-Ongoing).

Cotton, P. A. 2003. Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences* 100: 12219–12222.

Croll, D. A., D. A. Demer, R. P. Hewitt, J. K. Jansen, M. E. Goebel, and B. R. Tershy. 2006. Effects of variability in prey abundance on reproduction and foraging in chinstrap penguins (Pygoscelis antarctica). *Journal of Zoology* 269: 506–513.

Croxall, J. P., and P. A. Prince. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biological Journal of the Linnean Society* 14: 103–131.

Croxall, J. P., P. A. Prince, and K. Reid. 1997. Dietary segregation of krill-eating South Georgia seabirds. *Journal of Zoology* 242: 531–556.

Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and Antarctic seabird populations. *Science* 297: 1510–1514.

Ding, Q., E. J. Steig, D. S. Battisti, and M. Küttel. 2011. Winter warming in West Antarctica caused by central tropical Pacific warming. *Nature Geoscience* 4: 398–403.

Donald, P. F., K. Gedeon, N. J. Collar, C. N. Spottiswoode, M. Wondafrash, and G. M. Buchanan. 2012. The restricted range of the Ethiopian Bush-crow *Zavattariornis stresemanni* is a consequence of high reliance on modified habitats within narrow climatic limits. *Journal of Ornithology* 153: 1031–1044.

Ducklow, H. W., K. Baker, D. G. Martinson, L. B. Quetin, R. M. Ross, R. C. Smith, S. E. Stammerjohn, et al. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 362: 67–94.

Dunn, M. J., J. A. Jackson, S. Adlard, A. S. Lynnes, D. R. Briggs, D. Fox, and C. M. Waluda. 2016. Population Size and Decadal Trends of Three Penguin Species Nesting at Signy Island, South Orkney Islands. *PLOS ONE* 11: e0164025.

Durant, J. M., D. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33: 271–283.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate Extremes: Observations, Modeling, and Impacts. *Science* 289: 2068–2074.

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* 430: 881–884.

Elliott, K. H., K. J. Woo, A. J. Gaston, S. Benvenuti, L. Dall'Antonia, and G. K. Davoren. 2009. Central-Place Foraging in an Arctic Seabird Provides Evidence for Storer-Ashmole's Halo. *The Auk* 126: 613–625.

Emmerson, L., R. Pike, and C. Southwell. 2011. Reproductive consequences of environment-driven variation in Adelie penguin breeding phenology. *Marine Ecology Progress Series* 440: 203–216.

Encyclopaedia Britannica. 2019. South Shetland Islands | British Antarctic Territory. *Encyclopaedia Britannica*. Website https://www.britannica.com/place/South-Shetland-Islands [accessed 23 June 2019].

Field, I. C., C. J. A. Bradshaw, H. R. Burton, M. D. Sumner, and M. A. Hindell. 2005. Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals (Mirounga leonina). *Oecologia* 142: 127–135.

Forcada, J., and P. N. Trathan. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology* 15: 1618–1630.

Forcada, J., P. N. Trathan, K. Reid, E. J. Murphy, and J. P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* 12: 411–423.

Forero, M. G., G. R. Bortolotti, K. A. Hobson, J. A. Donazar, M. Bertelloti, and G. Blanco. 2004. High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. *Journal of Animal Ecology* 73: 789–801.

Fossheim, M., R. Primicerio, E. Johannesen, R. B. Ingvaldsen, M. M. Aschan, and A. V. Dolgov. 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change* 5: 673–677.

Fraser, W. R., W. Z. Trivelpiece, D. G. Ainley, and S. G. Trivelpiece. 1992. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biology* 11: 525–531.

Frederiksen, M., M. P. Harris, F. Daunt, P. Rothery, and S. Wanless. 2004. Scale-dependent climate signals drive breeding phenology of three seabird species. *Global Change Biology* 10: 1214–1221.

Friesen, V. L., A. L. Smith, E. Gómez-Díaz, M. Bolton, R. W. Furness, J. González-Solís, and L. R. Monteiro. 2007. Sympatric speciation by allochrony in a seabird. *Proceedings of the National Academy of Sciences* 104: 18589–18594.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. *Trends in Ecology & Evolution* 25: 325–331.

González-Solís, J., J. P. Croxall, D. Oro, and X. Ruiz. 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment* 5: 297–301.

Granroth-Wilding, H. M. V., and R. A. Phillips. 2018. Segregation in space and time explains the coexistence of two sympatric sub-Antarctic petrels. *Ibis* 12584: 1–16.

Gremillet, D., and T. Boulinier. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. *Marine Ecology Progress Series* 391: 121–137.

Grooten, M., and R. E. A. (Eds) Almond. 2018. WWF Living Planet Report - 2018: Aiming Higher. WWF, Gland, Switzerland.

Hamer, K. C., P. Monaghan, J. D. Uttley, P. Walton, and M. D. Burns. 1993. The influence of food supply on the breeding ecology of Kittiwakes Rissa tridactyla in Shetland. *Ibis* 135: 255–263.

Hardin, G. 1960. The Competitive Exclusion Principle. *Science* 131: 1292–1297.

Harris, C. M., K. Lorenz, L. D. C. Fishpool, B. Lascelles, J. Cooper, N. R. Corla, J. P. Croxall, et al. 2015. Important Bird Areas in Antarctica 2015. *BirdLife International and Environmetal Research Ltd, Cambridge*.

Harris, S., A. R. Rey, R. A. Phillips, and F. Quintana. 2013. Sexual segregation in timing of foraging by imperial shags (Phalacrocorax atriceps): is it always ladies first? *Marine Biology* 160: 1249–1258.

Helland, I. P., A. G. Finstad, T. Forseth, T. Hesthagen, and O. Ugedal. 2011. Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology* 80: 539–547.

Hinke, J. T., A. M. Cossio, M. E. Goebel, C. S. Reiss, W. Z. Trivelpiece, and G. M. Watters. 2017. Identifying Risk: Concurrent Overlap of the Antarctic Krill Fishery with Krill-Dependent Predators in the Scotia Sea. *PLOS ONE* 12: e0170132.

Hinke, J. T., M. J. Polito, M. E. Goebel, S. Jarvis, C. S. Reiss, S. R. Thorrold, W. Z. Trivelpiece, and G. M. Watters. 2015. Spatial and isotopic niche partitioning during winter in chinstrap and Adélie penguins from the South Shetland Islands. *Ecosphere* 6: 1–32.

Hinke, J. T., S. G. Trivelpiece, and W. Z. Trivelpiece. 2014. Adélie penguin (*Pygoscelis adeliae*) survival rates and their relationship to environmental indices in the South Shetland Islands, Antarctica. *Polar Biology* 37: 1797–1809.

Hipfner, J. M. 2008. Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Marine Ecology Progress Series* 368: 295–304.

Hjeljord, O. 2001. Dispersal and migration in northern forest deer - are there unifying concepts? *Alces* 37: 353–370.

Hunter, S. 1984. Breeding biology and population dynamics of giant petrels *Macronectes* at South Georgia (Aves: *Procellariiformes*). *Journal of Zoology* 203: 441–460.

Intergovernmental Panel on Climate Change. 2014. Climate change 2014: Synthesis report. Contribution of working groups I, II and III to fifth assessment report of the Intergovernmental Panel on Climate Change. *Intergovernmental Panel on Climate Change*: 154.

IPCC. 2007. Climate change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

IUCN. 2012. IUCN red list of threatened species (ver. 2012.1). *IUCN*. Website https://www.iucnredlist.org/.

Kahle, D., and H. Wickham. 2016. ggmap - Spatial Visualization with ggplot2. R package version 2.6.1.

Keogan, K., F. Daunt, S. Wanless, R. A. Phillips, C. A. Walling, P. Agnew, D. G. Ainley, et al. 2018. Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nature Climate Change* 8: 313–318.

Kirchmeier-Young, M. C., F. W. Zwiers, and N. P. Gillett. 2016. Attribution of Extreme Events in Arctic Sea Ice Extent. *Journal of Climate* 30: 553–571.

Kowalczyk, N. D., A. Chiaradia, T. J. Preston, and R. D. Reina. 2014. Linking dietary shifts and reproductive failure in seabirds: a stable isotope approach. *Functional Ecology* 28: 755–765.

Krosby, M., C. B. Wilsey, J. L. McGuire, J. M. Duggan, T. M. Nogeire, J. A. Heinrichs, J. J. Tewksbury, and J. J. Lawler. 2015. Climate-induced range overlap among closely related species. *Nature Climate Change* 5: 883–886.

Le Guen, C., A. Kato, B. Raymond, C. Barbraud, M. Beaulieu, C.-A. Bost, K. Delord, et al. 2018. Reproductive performance and diving behaviour share a common sea-ice concentration optimum in Adélie penguins (Pygoscelis adeliae). *Global Change Biology* 24: 5304–5317.

Liechti, F. 2006. Birds: blowin' by the wind? *Journal of Ornithology* 147: 202–211.

Lishman, G. S. 1985. The comparative breeding biology of Adelie and Chinstrap Penguins Pygoscelis adeliae and P. antarctica at Signy Island, South Orkney Islands. *Ibis* 127: 84–99.

Loreau, M. 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 49–60.

Lu, X., D. H. Ke, X. H. Zeng, and T. L. Yu. 2009. Reproductive ecology of two sympatric Tibetan snowfinch species at the edge of their altitudinal range: Response to more stressful environments. *Journal of Arid Environments* 73: 1103–1108.

Lynch, H. J., W. F. Fagan, R. Naveen, S. G. Trivelpiece, and W. Z. Trivelpiece. 2012. Differential advancement of breeding phenology in response to climate may alter staggered breeding among sympatric *Pygoscelid* penguins. *Marine Ecology Progress Series* 454: 135–145.

Lynch, H. J., and M. A. LaRue. 2014. First global census of the Adélie Penguin. *The Auk* 131: 457–466.

Lynch, H. J., R. Naveen, P. N. Trathan, and W. F. Fagan. 2012. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93: 1367–1377.

Lynch, H. J., R. White, R. Naveen, A. Black, M. S. Meixler, and W. F. Fagan. 2016. In stark contrast to widespread declines along the Scotia Arc, a survey of the South Sandwich Islands finds a robust seabird community. *Polar Biology* 39: 1615–1625.

Lynnes, A. S., K. Reid, J. Croxall, and P. Trathan. 2002. Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap penguins. *Marine Biology* 141: 1165–1174.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39: 599–619.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101: 377–385.

Marshall, G. J., A. Orr, N. P. M. van Lipzig, and J. C. King. 2006. The impact of a changing Southern Hemisphere Annular Mode on Antarctic Peninsula summer temperatures. *Journal of Climate* 19: 5388–5404.

Martin, K., and K. L. Wiebe. 2004. Coping Mechanisms of Alpine and Arctic Breeding Birds: Extreme Weather and Limitations to Reproductive Resilience. *Integrative and Comparative Biology* 44: 177–185.

Masello, J. F., R. Mundry, M. Poisbleau, L. Demongin, C. C. Voigt, M. Wikelski, and P. Quillfeldt. 2010. Diving seabirds share foraging space and time within and among species. *Ecosphere* 1: art19.

McClintock, J., H. W. Ducklow, and W. Fraser. 2008. Ecological Responses to Climate Change on the Antarctic Peninsular. *American Scientist* 96: 302–310.

McMahon, K. W., L. L. Hamady, and S. R. Thorrold. 2013. A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnology and Oceanography* 58: 697–714.

Mengel, M., J. Feldmann, and A. Levermann. 2016. Linear sea-level response to abrupt ocean warming of major West Antarctic ice basin. *Nature Climate Change* 6: 71–74.

Meredith, M. P., and J. C. King. 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophysical Research Letters* 32: L19604.

Milazzo, M., S. Mirto, P. Domenici, and M. Gristina. 2013. Climate change exacerbates interspecific interactions in sympatric coastal fishes. *Journal of Animal Ecology* 82: 468–477.

Miller, A. K., M. A. Kappes, S. G. Trivelpiece, and W. Z. Trivelpiece. 2010. Foraging-Niche Separation of Breeding Gentoo and Chinstrap Penguins, South Shetland Islands, Antarctica. *The Condor* 112: 683–695.

Murphy, E. J., A. Clarke, N. J. Abram, and J. Turner. 2014. Variability of sea-ice in the northern Weddell Sea during the 20th century. *Journal of Geophysical Research: Oceans* 119: 4549–4572.

Mutshinda, C. M., R. B. O'Hara, and I. P. Woiwod. 2011. A multispecies perspective on ecological impacts of climatic forcing. *Journal of Animal Ecology* 80: 101–107.

Ouyang, J. Q., P. J. Sharp, A. Dawson, M. Quetting, and M. Hau. 2011. Hormone levels predict individual differences in reproductive success in a passerine bird. *Proceedings of the Royal Society of London B: Biological Sciences* 278: 2537–2545.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669.

Parmesan, C., T. L. Root, and M. R. Willig. 2000. Impacts of Extreme Weather and Climate on Terrestrial Biota. *Bulletin of the American Meteorological Society* 81: 443–450.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.

Pomilla, C., and H. C. Rosenbaum. 2005. Against the current: an inter-oceanic whale migration event. *Biology Letters* 1: 476–479.

Quillfeldt, P., Y. Cherel, K. Delord, and H. Weimerkirch. 2015. Cool, cold or colder? Spatial segregation of prions and blue petrels is explained by differences in preferred sea surface temperatures. *Biology Letters* 11: 20141090.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. *URL https://www.R-project.org/*.

Ratcliffe, N., S. Crofts, R. Brown, A. M. M. Baylis, S. Adlard, C. Horswill, H. Venables, et al. 2014. Love thy neighbour or opposites attract? Patterns of spatial segregation and association among crested penguin populations during winter. *Journal of Biogeography* 41: 1183–1192.

Ratcliffe, N., A. Takahashi, C. O’Sullivan, S. Adlard, P. N. Trathan, M. P. Harris, and S. Wanless. 2013. The Roles of Sex, Mass and Individual Specialisation in Partitioning Foraging-Depth Niches of a Pursuit-Diving Predator. *PLOS ONE* 8: e79107.

Ratcliffe, N., and P. Trathan. 2012. A review of the diet and at-sea distribution of penguins breeding within the CAMLR Convention Area. *CCAMLR Science* 19: 75–114.

Robertson, G. S., M. Bolton, W. J. Grecian, L. J. Wilson, W. Davies, and P. Monaghan. 2014. Resource partitioning in three congeneric sympatrically breeding seabirds: Foraging areas and prey utilization. *The Auk* 131: 434–446.

Robillard, C. M., L. E. Coristine, R. Soares, and J. Kerr. 2015. Facilitating climate-change-induced range shifts across continental land-use barriers. *Conservation Biology* 29: 1586–1595.

Ropert-Coudert, Y., A. Kato, X. Meyer, M. Pellé, A. J. J. MacIntosh, F. Angelier, O. Chastel, et al. 2015. A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. *Ecography* 38: 111–113.

Ropert-Coudert, Y., A. Kato, K. Shiomi, C. Barbraud, F. Angelier, K. Delord, T. Poupart, et al. 2018. Two Recent Massive Breeding Failures in an Adélie Penguin Colony Call for the Creation of a Marine Protected Area in D’Urville Sea/Mertz. *Frontiers in Marine Science* 5: 1–7.

Sala, O. E., F. S. Chapin III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, et al. 2000. Global Biodiversity Scenarios for the Year 2100. *Science* 287: 1770–1774.

Shepherd, A., E. R. Ivins, G. A, V. R. Barletta, M. J. Bentley, S. Bettadpur, K. H. Briggs, et al. 2012. A Reconciled Estimate of Ice-Sheet Mass Balance. *Science* 338: 1183–1189.

Slowikowski, K., A. Schep, S. Hughes, S. Lukauskas, J.-O. Irisson, Z. N. Kamvar, T. Ryan, et al. 2018. ggrepel - Provides text and label geoms for ‘ggplot2’ that help to avoid overlapping text labels. Labels repel away from each other and away from the data points. R package version 0.8.0.

Solomon, S., G.-K. Plattner, R. Knutti, and P. Friedlingstein. 2009. Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences* 106: 1704–1709.

Stammerjohn, S. E., D. G. Martinson, R. C. Smith, and R. A. Iannuzzi. 2008. Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research Part II: Topical Studies in Oceanography* 55: 2041–2058.

Stonehouse, B. 1970. Geographic Variation in Gentoo Penguins Pygoscelis Papua. *Ibis* 112: 52–57.

Stonehouse, B. 1962. The Tropic Birds (*Genusphaethon*) of Ascension Island. *Ibis* 103B: 124–161.

Takahashi, A., M. J. Dunn, P. N. Trathan, K. Sato, Y. Naito, and J. P. Croxall. 2003. Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. *Marine Ecology Progress Series* 250: 279–289.

Tanton, J. L., K. Reid, J. P. Croxall, and P. N. Trathan. 2004. Winter distribution and behaviour of gentoo penguins Pygoscelis papua at South Georgia. *Polar Biology* 27: 299–303.

Taylor, R. S., and V. L. Friesen. 2017. The role of allochrony in speciation. *Molecular Ecology* 26: 3330–3342.

Thiebot, J.-B., Y. Cherel, P. N. Trathan, and C.-A. Bost. 2012. Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. *Ecology* 93: 122–130.

Thompson, D. W. J., and S. Solomon. 2002. Interpretation of Recent Southern Hemisphere Climate Change. *Science* 296: 895–899.

Trathan, P. N., J. P. Croxall, and E. J. Murphy. 1996. Dynamics of Antarctic penguin populations in relation to inter-annual variability in sea ice distribution. *Polar Biology* 16: 321–330.

Trivelpiece, W. Z., J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences* 108: 7625–7628.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. J. Volkman. 1987. Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology* 68: 351–361.

Tulloch, V. J. D., É. E. Plagányi, C. Brown, A. J. Richardson, and R. Matear. 2019. Future recovery of baleen whales is imperiled by climate change. *Global Change Biology* 25: 1263–1281.

Turner, J., R. Bindschalder, P. Convey, G. dl Prisco, E. Fahrbach, D. Hodgson, J. Gutt, et al. eds. . 2009. Antarctic Climate Change and the Environment. *Scientific Committee on Antarctic Research: Cambridge*.

Turner, J., S. R. Colwell, G. J. Marshall, T. A. Lachlan-Cope, A. M. Carleton, P. D. Jones, V. Lagun, et al. 2005. Antarctic climate change during the last 50 years. *International Journal of Climatology* 25: 279–294.

Turner, J., J. C. Comiso, G. J. Marshall, T. A. Lachlan-Cope, T. Bracegirdle, T. Maksym, M. P. Meredith, et al. 2009. Non-annular atmospheric circulation change induced by stratospheric ozone depletion and its role in the recent increase of Antarctic sea ice extent. *Geophysical Research Letters* 36: L08502.

Turner, J., H. Lu, I. White, J. C. King, T. Phillips, J. S. Hosking, T. J. Bracegirdle, et al. 2016. Absence of 21st century warming on Antarctic Peninsula consistent with natural variability. *Nature* 535: 411–415.

Turner, J., and J. Overland. 2009. Contrasting climate change in the two polar regions. *Polar Research* 28: 146–164.

Ulvan, E. M., A. G. Finstad, O. Ugedal, and O. K. Berg. 2012. Direct and indirect climatic drivers of biotic interactions: ice-cover and carbon runoff shaping Arctic char *Salvelinus alpinus* and brown trout *Salmo trutta* competitive asymmetries. *Oecologia* 168: 277–287.

United States Antarctic Program. 1990. LTER Palmer - Antarctica. Website https://lternet.edu/site/palmer-antarctica-lter/ [accessed 23 June 2019].

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society of London B: Biological Sciences* 279: 2072–2080.

Vaughan, D. G., G. J. Marshall, W. M. Connolley, C. Parkinson, R. Mulvaney, D. A. Hodgson, J. C. King, et al. 2003. Recent Rapid Regional Climate Warming on the Antarctic Peninsula. *Climatic Change* 60: 243–274.

Vinuela, J., J. Moreno, L. M. Carrascal, J. J. Sanz, J. A. Amat, M. Ferrer, J. Belliure, and J. Cuervo. 1996. The effect of hatching date on parental care, chick growth, and chick mortality in the chinstrap penguin Pygoscelis antarctica. *Journal of Zoology* 240: 51–58.

Visser, M., C. Both, and M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. *Advances in Ecological Research* 35: 89–110.

Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society of London B: Biological Sciences* 272: 2561–2569.

Visser, M. E., L. te Marvelde, and M. E. Lof. 2012. Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology* 153: 75–84.

Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. Fromentin, et al. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.

Waluda, C. M., M. J. Dunn, M. L. Curtis, and P. T. Fretwell. 2014. Assessing penguin colony size and distribution using digital mapping and satellite remote sensing. *Polar Biology* 37: 1849–1855.

Warren, R., J. Price, A. Fischlin, S. de la N. Santos, and G. Midgley. 2011. Increasing impacts of climate change upon ecosystems with increasing global mean temperature rise. *Climatic Change* 106: 141–177.

Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography* 54: 211–223.

Wickham, H., and W. Chang. 2016. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. R package version 2.2.1. *https://cran.r-project.org/web/packages/ggplot2/index.html*.

Williams, T. D. 1995. The Penguins: Spheniscidae. Oxford University Press, Oxford.

Wilson, R. P. 2010. Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Functional Ecology* 24: 646–657.

Wilson, R. P., J. A. Scolaro, G. Peters, S. Laurenti, M. Kierspel, H. Gallelli, and J. Upton. 1995. Foraging areas of Magellanic penguins *Spheniscus magellanicus* breeding at San Lorenzo, Argentina, during the incubation period. *Marine Ecology Progress Series* 129: 1–6.

Wisz, M. S., J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C. F. Damgaard, C. F. Dormann, et al. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biological Reviews* 88: 15–30.

Wittwer, T., R. B. O'Hara, P. Caplat, T. Hickler, and H. G. Smith. 2015. Long-term population dynamics of a migrant bird suggests interaction of climate change and competition with resident species. *Oikos* 124: 1151–1159.

Chapter 2 - *Niche partitioning of sympatric penguins by leapfrog foraging appears to be resilient to climate change*

This paper has been published as: H. L. Clewlow, A. Takahashi, S. Watanabe, S. C. Votier, R. Downie, and N. Ratcliffe. 2019. Niche partitioning of sympatric penguins by leapfrog foraging is resilient to climate change. Journal of Animal Ecology 88: 223–235.

Author contributions

The framework for the study was developed by N.R. and H.L.C. Fieldwork was conducted by N.R., H.L.C., A.T. and S.W. with H.L.C. processing and analysing all data. H.L.C. wrote the paper with contributions from all the other authors, and all authors gave final approval for publication. Tracking data from 2008 was collected and initially processed by A.T and S.W.

Abstract

1. Interspecific competition can drive niche partitioning along multidimensional axes, including allochrony. Competitor matching will arise where the phenology of sympatric species with similar ecological requirements respond to climate change at different rates such that allochrony is reduced.
2. Our study quantifies the degree of niche segregation in foraging areas and depths that arises from allochrony in sympatric Adélie and chinstrap penguins and explores its resilience to climate change.
3. Three-dimensional tracking data were sampled during all stages of the breeding season and were used to parameterise a behaviour-based model that quantified spatial overlap of foraging areas under different scenarios of allochrony.
4. The foraging ranges of the two species were similar within breeding stages, but differences in their foraging ranges between stages, combined with the observed allochrony of 28 days, resulted in them leapfrogging each other through the breeding season such that they were exploiting different foraging locations on the same calendar dates. Allochrony reduced spatial overlap in the peripheral utilisation distribution of the two species by 54.0% over the entire breeding season, compared to a scenario where the two species bred synchronously.

5. Analysis of long-term phenology data revealed that both species advanced their laying dates in relation to October air temperatures at the same rate, preserving allochrony and niche partitioning. However if allochrony is reduced by just a single day, the spatial overlap of the core utilisation distribution increased by an average of 2.1% over the entire breeding season.
6. Niche partitioning between the two species by allochrony appears to be resilient to climate change and so competitor matching cannot be implicated in the observed population declines of the two penguin species across the Western Antarctic Peninsula.

Keywords: allochrony, climate change, competition, foraging ecology, tracking, leapfrog foraging, niche partitioning, penguin.

1 | INTRODUCTION

Competition within and between species exerts strong influences over population dynamics, community structure and species distributions (Hardin, 1960; MacArthur, 1968). The potential for competition is particularly intense in communities where closely related species breed sympatrically at high densities and share limited food resources (MacArthur, 1968). Interspecific competition may be reduced by differentiating niche space along multidimensional axes such as diet (Croxall et al., 1997), foraging distribution (MacArthur, 1958; Wilson, 2010) and allochrony (i.e. differences in the timing of activity among species). Allochrony in breeding phenology has been documented for a wide range of taxa (Taylor and Friesen, 2017) and can partition niches by offsetting the timing of peak resource use by competing species (Trivelpiece et al., 1987).

Animals’ breeding phenology is often timed to coincide with optimal environmental conditions, but the timing of these events is being influenced by climate change (Blois et al., 2013). The sensitivity of breeding phenology to warming may vary between species, and the resultant uncoupling in the timing of predator demands and prey availability (“predator-prey mismatching”) have become central to our thinking about climate change impacts upon ecosystems (Parmesan and Yohe, 2003; Visser and Both, 2005). The alteration of competitive interactions by climate change has received less attention, although a growing body evidence demonstrates that the presence of competitors may have substantial effects on the magnitude and form of a species' response to climate change. Examples include barnacles (Poloczanska et al., 2008), insects (Bulgarella et al., 2014), fish (Helland, Finstad, Forseth, Hesthagen, & Ugedal, 2011; Milazzo, Mirto, Domenici, & Gristina, 2013), and birds (Sætre et al., 1999; Stenseth et al., 2015; Wittwer et al., 2015). Ecologically similar species may alter their breeding phenology in response to warming at different rates (Chadwick et al., 2006; Lynch, Fagan, et al., 2012) and, where breeding cycles become more synchronised, increases in competitive interactions may arise (Ahola et al., 2007), which we hereafter term as "competitor matching".

Seabirds are frequently used as models for the study of inter-specific competition (Pulliam, 2000; Polito et al., 2015; Rosciano et al., 2016), since their coloniality and central-place foraging strategy often creates high levels of competition within their shared foraging ranges (Ballance et al., 2009; Elliott et al., 2009). Allochrony is known to reduce inter-specific competition by offsetting the peak period of food demand (Barrett et al., 1997) but also has the potential to affect spatio-temporal overlap in foraging areas. Most families of seabird show seasonal variation in foraging ranges (incubation trips are generally longer than chick rearing ones: e.g. Kitaysky et al., 1999; Barlow and Croxall, 2002; Ito et al., 2010, which, when combined with allochrony, will give rise to leapfrog foraging. Leapfrog foraging has been described in high-shore nesting oystercatchers that overfly low-shore nesters to reach estuarine feeding habitat (Ens et al., 1992), but in the case of colonial seabirds it would arise from the whole population of a late-nesting species performing long incubation trips beyond the foraging range of an earlier nesting species that is performing shorter chick-rearing trips. This is analogous to leapfrog migration where populations living at high latitudes overfly a mid-latitude, resident population of conspecifics to reach their lower latitude wintering areas (Newton, 2008), albeit on smaller spatio-temporal scales. Such behaviour has the potential to produce substantial reductions in the spatial overlap of two species' foraging ranges compared to a situation where both species breed synchronously (Granroth-Wilding and Phillips, 2018).

Adélie (*Pygoscelis adeliae*) and chinstrap (*P. antarcticus*) penguins (hereafter Adélies and chinstraps) are congeners that breed sympatrically across the Scotia Arc and Western Antarctic Peninsula (WAP). Here, the diets of both species are dominated by Antarctic krill *Euphausia superba,* constituting more than 95% of both species' diet (unpublished data; British Antarctic Survey annual monitoring), and they have similar foraging behaviour (Ratcliffe and Trathan, 2012), which has prompted several studies of how niche partitioning might facilitate their coexistence (Lynnes, Reid, Croxall, & Trathan, 2002; Trivelpiece et al., 1987; Wilson, 2010). They exhibit pronounced seasonal allochrony, with Adélies initiating breeding in mid-October and chinstraps following three to four weeks later (Black, 2015; Trivelpiece et al., 1987; see Lynnes et al. 2002 for diagram of phenology). This reduces competition among the two species by staggering peaks of prey demand of the two species in time (Trivelpiece et al., 1987), but its effect on partitioning foraging areas via leapfrog foraging is undocumented. Previous attempts to describe the spatial segregation between these species' foraging distributions (Lynnes et al., 2002; Wilson, 2010) were confined to the chick-rearing period and will have overestimated the degree of overlap as they assumed that the observed behaviours occurred simultaneously, when in reality they occurred three to four weeks apart.

The WAP is one of the most rapidly warming areas on the planet (Clarke et al., 2007; Vaughan et al., 2003), resulting in changes to chinstrap and Adélie breeding phenology (Lynch, Fagan, et al., 2012; Black, 2015) and declines in breeding numbers (Forcada and Trathan, 2009; Lynch, Naveen, et al., 2012; Dunn et al., 2016). These studies ascribed the population declines to a reduction in their preferred prey, Antarctic krill, in response to a range of factors including climate change, sea ice loss, overfishing and recovery of marine mammal populations. However, increased competition among the two penguin species for this diminishing prey resource may have further contributed to population declines, and competitor matching has been proposed as a possible mechanism for this (Lynch, Fagan, et al., 2012). An improved understanding of niche partitioning, the role allochrony plays in this and the sensitivities of these processes to climate change are therefore fundamental to understanding the drivers of population change in *Pygoscelis* penguins.

In this study, we present a behaviour-based model of penguin foraging distributions to explore how allochrony contributes to spatial segregation in the two species. The advantage of this approach is that it takes a mechanistic approach to examining responses to changing environments, including those that have not yet been encountered by the study species (Norris, 2004). This enabled us to explore how competitive overlap might alter if the two species became more synchronous as a theoretical exercise. We then used a 20-year time series of breeding phenology data in order to anchor the behaviour-based model's predictions in a real-world context and determine how niche partitioning by leapfrog foraging might be affected by climate change. We tested the following hypotheses: (1) foraging behaviour differs between breeding stages; (2) staggering of this behaviour by allochrony will give rise to leapfrog foraging which will partition spatial niches; (3) this niche partitioning will be reduced as the degree of allochrony is shortened; (4) in areas of spatial overlap, niches will diverge along other axes such as dive depth and (5) the two species' phenology will advance in parallel in relation to temperature, maintaining allochrony and hence niche partitioning.

2 | MATERIALS AND METHODS

2.1 | Study site and tag deployments

This study was conducted at the Gourlay Peninsula on Signy Island, South Orkney Islands (60°42'S, 45°36'W) where Adélie and chinstraps breed sympatrically. Penguins were captured in a net, after being observed leaving the nest at the end of an incubation/brooding shift or after feeding their chick. This avoided exposing eggs or chicks to predation by brown skuas (*Stercorarius antarcticus*) and ensured that all birds were breeding at the time of tag deployment. Birds were tagged between December and February of the 2007/08, 2011/12, 2013/14 and 2015/16 breeding seasons, meaning tracks were obtained from all stages of the breeding cycle (incubation, guard and crèche). Birds were fitted with both GPS loggers and time-depth recorder (TDR) tags for between two and fourteen days in order to log their three-dimensional foraging trips. The number of Adélie foraging trips tracked were 5 during incubation, 44 during guard and 18 during crèche, while those for chinstraps were 21, 89 and 7, respectively. Details of sample sizes according to species, stage and year are provided in Supporting Information Appendix S1, along with justification for the relatively small samples for Adélies during incubation and chinstraps during crèche.

Specifically, devices were combined GPS-TDR loggers (Little Leonardo GPL-380DT, Tokyo, Japan during 2007/08 and Fastloc2 GPS loggers (Sirtrack, Havelock, New Zealand) paired with CEFAS G5 TDRs (CEFAS Technology Ltd, Lowestoft, UK) whose clocks were synchronised in other years. Two-part epoxy resin and waterproof tape (Tesa, Hamburg, Germany) were used to attach the GPS tags to the central back feathers and the TDR to the feathers on the rump. G5 TDRs weigh 2.7g and have a diameter of 8mm and length of 31mm, Fastloc2 GPS weigh 39.9g and measure 65mm long, 28mm wide and 15mm deep and Little Leonardo tags weigh 92g and measure 58 mm long, 28 mm wide and 20 mm deep. The average weight of penguins fitted with devices was 3.84 kg (SD = 0.44) so device loads represented 2.4% (Little Leonardo) and 1.1% (F2 + G5) of their body mass. Tags of this size and placement appear to have negligible effects on the foraging behaviour of *Pygoscelis* penguins (Ratcliffe et al., 2018).

TDRs were initialised to record temperature and pressure every second in all years, while GPS tags recorded positions every second during the 2007/08 season and every three minutes in other seasons. Interruption of GPS fix acquisition by immersion resulted in actual time intervals between positions being greater than those programmed into the devices.

2.2 | GPS and dive data processing

Dive statistics were extracted using the R package diveMove (Luque, 2016). The ‘filter’ method of zero offset correction within diveMove (Luque and Fried, 2011) was used to define the sea-surface and a depth threshold of 5m was used to exclude any non-foraging dive events (Kokubun et al., 2010). Maximum depth and dive start time data were then extracted for each diving event. Foraging trips were demarcated by visualisation of tracks in ArcGIS 10.4.1 (ESRI, Redlands, CA, USA) to determine the approximate times birds left and returned to the colonies. These times were further refined to the nearest minute using the temperature data from the TDR tags: a fast sharp decline in temperature indicated submersion and the reverse pattern indicated haulout.

The spatial distribution of foraging activity was examined using the locations of dives rather than using locations of raw GPS fixes, which would include positions where birds were commuting or resting at sea. We used the R package CRAWL (Johnson, 2015) to interpolate dive locations along the track based on the time at which the dive was initiated. CRAWL uses a correlated random walk model to produce predictions of the location of an animal along the simulated track at user-defined time points. This avoids the unrealistic assumption of linear travel between GPS points and also generates error around the dive locations based on variability in the paths followed on successive simulations. We drew 100 simulated locations for each of the dives and combined these for all individuals within species and stage groupings.

Owing to small sample sizes of tracks within years we pooled data for all years for further analysis. Annual variability in distributions and explanation of the implications of this for our findings are presented in Appendix S1. We used adehabitatHR (Calenge, 2015) to generate kernel densities of dive locations along with their 50% and 95% isopleths. A smoothing (h) parameter of 0.06 was used in the kernel analysis, as this value was found to achieve an optima between constraining the 95% isopleth to the area that birds actually visited whilst smoothing their distributions within it. A utilization distribution overlap index (UDOI) was used to quantify the overlap between species because it provides the best single measure of the degree to which two species share space by presuming that the species use space independently (Fieberg and Kochanny, 2005). It is calculated using the following formula defined by Fieberg and Kochanny, 2005, where UˆD*i*,*p* represents the estimated conditional utilisation distribution (UD) for animal *i* (i.e. the probability distribution for animal *i* given that it is in the area associated with its home range as defined by the *p*th probability contour of UD*i*).

$$\mathrm{UDOI} = A_{1,2} \iint_{-\infty -\infty}^{\infty\ \infty} \hat{\mathrm{UD}}_1\ (x,y) \times \hat{\mathrm{UD}}_2\ (x,y)\, dxdy$$

Therefore, the resulting UDOI value would be 0 if there is no overlap, 1 if there is 100% overlap and the utilisation distributions are uniform, equal distribution across the area, and >1 if overlap is high and the utilisation distributions are non-uniformly distributed (Fieberg and Kochanny, 2005). Meaning value of <1 would suggest less overlap between the two populations than would expected from simple uniform space use and values >1 would suggest higher than normal overlap relative to uniform space use.

2.3 | Statistical analysis of tracking data

Variation in foraging behaviour among species and breeding stages was investigated using the processed GPS dive locations and TDR dive depth data. The maximum distance from the colony reached during each trip was calculated using the R package move (Kranstauber and Smolla, 2016). Linear mixed effects models, fitted using the R package nlme (Pinheiro, 2016), were used to investigate differences in the average maximum distances from colony and average maximum dive depths between breeding stages and species. Models were fitted with an identity link and normal errors, and model selection was conducted using backward-stepwise deletion and likelihood ratio (LR) tests. The global model consisted of maximum distance or maximum dive depth as the response variable, the interaction of breeding stage (incubation, guard or crèche) and species (Adélie or chinstrap) as the fixed factors and individual (with trip nested within it in the case of dive depths) as random intercept effects. Overlap of the two species maximum dive depths were quantified based on the overlap in the kernel densities of their frequency distributions (Mouillot et al., 2005).

2.4 | Behaviour-based model of foraging areas

Assessing the effects of allochrony on spatial overlap of the two species necessitates quantifying overlap in distributions at a daily resolution. It was not possible to design the field sampling of foraging trips in a manner that allowed this due to logistical constraints and availability of equipment. Instead, we created a virtual colony in which a pre-defined number of successfully breeding pairs of each species proceeded through their breeding season, making foraging trips with the frequency and characteristics for the given stage of the breeding season.

The foraging trips we collected were accurate representations of the paths those birds followed during the period of tracking, but these birds on other occasions, or other birds in the colony, would have made trips of similar characteristics (in terms of start and end points, duration, speed and tortuosity) but these would have followed different paths. Rather than sampling tracks from those observed (which would underestimate variation in paths), we generated random tracks around the observed ones using the CRAWL model. For each track we allowed observation error (SD = 3.5 km during long incubation trips, 2.5km during short chick-rearing trips) around each GPS fix (except the start and end points which were fixed at the colony location). We then fitted the CRAWL model and generated 50 correlated random walk tracks for each observed trip and saved the locations of dives along each of these to an array.

For each breeding pair we selected a date for the completion of the clutch from a distribution defined by the mean and standard deviation taken from the Results section. Birds would then complete a fixed number of long incubation trips (two for Adélies, three for chinstraps) and would then perform short incubation trips until hatching (Williams, 1995), each resampled from the appropriate array. After hatching, birds would make repeated brood-guard trips (resampled from the brooding array) until the chicks crèched (after which trips would be resampled from the crèche array). Once the chicks reached fledging age, the simulations would begin for the next pair. This was repeated for 500 Adélie and 750 chinstrap penguin pairs, which preserved the ratio of abundance of these two species on the Gourlay Peninsula. The modelled number of pairs had no influence over estimates and was selected to optimise computing time, whilst ensuring the repeatability of estimates on consecutive runs. An animated visualisation of the model's process of track simulation through the breeding season is shown for Adélie penguins in Animation S1.

We calculated the daily kernel density of dive locations for each species and their UDOI as described previously. The daily overlap values were plotted against date and the area under curve (AUC) was calculated as an index of the amount of spatial overlap between the two species through the entire season.

The simulation model was used to investigate the degree of overlap between the two species' kernels at the observed level of allochrony and in the absence of allochrony (by having chinstraps breed synchronously with Adélies). We also investigated changes in overlap resulting from reducing the level of allochrony in daily increments from the observed difference of 28 days to complete synchrony.

Overlap in dive depths of the resampled dive depths were investigated using kernel density analysis as for the observed data, but dives were grouped according to their degree of overlap horizontally. The horizontal groupings were overlap in 50% isopleths (core), in 95% isopleths (peripheral) and areas outside the 95% isopleth overlap (no overlap). These areas were exclusive of one another (e.g. the peripheral overlap area did not include the core overlap area contained within it).

2.5 | Analysis of breeding phenology data

Long-term patterns in the phenology of both species were investigated by modelling their mean annual laying dates on Signy in relation to October air temperatures. Mean October temperature was selected as the explanatory variable as it is strongly correlated with the laying dates of Adélies and chinstraps elsewhere owing to a link between air temperature, snow melt and the exposure of nesting substrates (Lynch, Fagan, et al., 2012). Temperature data were sourced from the nearest long-running weather station (1903 to present) at Laurie Island, South Orkney Islands (60°44′S 44°44′W) (British Antarctic Survey, 2018), which is 46 km to the east of Signy and at sea level. Trends in October air temperature with time were investigated using linear regression.

Annual mean hatching date was calculated using nest observation data collected during the breeding seasons of 1996 – 2015 (excluding 2010, when no data were collected). During each year, observers recorded the contents of 100 marked nests of each species every three days through to crèche. A binomial model was fitted using the proportion of nests containing one or more chicks as the response variable and the date in days after 1 Oct as the explanatory variable. This model was fitted for each species and year separately. The dose.p function in the MASS package in R (Ripley et al., 2017) was used to derive the day when 50% of nests contained one or more chicks to produce the mean hatching date for each species-year combination. Mean laying dates were back-calculated from the mean hatching dates by subtracting the average incubation periods for each species (35 days for Adélies and 36.4 days for chinstraps, which are relatively constant between years (Williams, 1995; Lynch, Fagan, et al., 2012).

Changes in mean laying dates (expressed as number of days after 1st October) were modelled using Analysis of Covariance (ANCOVA), with laying date as the response variable, species as a factor and mean October temperature as a covariate. The annual residuals from the ANCOVA model were calculated for each species and a Pearson correlation was used to test whether their residuals from the trends with October temperature were related. An ANCOVA was also used to model time trends in laying dates of the two species over the 20-year study period, using year as a linear covariate.

3 | RESULTS

3.1 | Trip and dive metrics

Incubation stage trips ranged furthest from the colony and were directed to and beyond the shelf break in a SSW direction (Fig. 1a), whilst those during guard and crèche were shorter and occurred over the shelf within a quadrant delimited by southerly and westerly bearings from the colony (Fig. 1b and Fig. 1c). Both species' foraging patterns were broadly similar within breeding stages, particularly during the guard stage: overlap of the 95% and 50% isopleths of the two species (according to naïve UDOI statistics that do not account for allochrony) were 0.493 and 0.082 during incubation, 1.968 and 0.265 during guard, and 0.227 and 0.075 during crèche (respectively).

The maximum distances that birds travelled from their colony during a foraging trip varied according to the interaction between breeding stage and species (linear mixed effects model; likelihood ratio test $LR_2 = 13.4$, $P < 0.005$). Adélie trips ranged to 75.9 km ± 19.7 during incubation then shortened to 24.6 km ± 4.8 during brood before increasing again to 95.6 km ± 11.4 during crèche. Those of chinstraps were longer than Adélies' during incubation (135km ± 9.2) and guard (40.9 km ± 7.8) but shorter during crèche (35.9 km ± 20.21). The random between-individual effect explained 43% of the variability in the intercept.

Dive depths were not significantly affected by the interaction of species and breeding stage (linear mixed effects model; $LR_2 = 0.53$, $P > 0.7$) nor an additive effect of breeding stage ($LR_2 = 5.38$, $P > 0.05$), but that of species alone was highly significant ($LR_1 = 11.37$, $P < 0.0001$). Chinstraps dived deeper on average (39.4m ± 2.6) than Adélies (25.35m ± 3.19). The between-individual random effect explained 33.7% of the variability in the intercept and foraging trip within individuals just 7.9%. The overlap in the frequency distributions of the two species' dive depths across all stages was 0.77.

3.2 | Simulated effects of allochrony on spatial overlap

The behaviour-based model revealed that allochrony, in concert with the variation in trip characteristics among breeding stages, caused the two species to leapfrog each other over the course of the breeding season. Chinstraps leapfrogged Adélies by performing long incubation trips whilst the latter were performing short incubation and brood guard trips. As chinstraps began shorter brood guard trips, Adélies leapfrogged back over them to perform long crèche trips. Chinstraps continued short trips through the remainder of their breeding season as Adélies completed chick rearing and departed south to moult (Fig. 2, Animation S2).

Theoretical scenarios showed that, in the absence of allochrony, the overlap in the AUC of all the daily UDOI values was 44.4% higher in core foraging areas and 54.0% higher in peripheral foraging areas over the entire breeding season (Fig. 3). Interestingly, the level of overlap observed at the midpoint of the breeding season if birds bred synchronously was approximately double that for the observed level of allochrony: this corresponds to the guard period when parents are constrained to perform short trips that provide frequent meals for their rapidly growing chicks. We also found that if allochrony decreased by a single day, competitive overlap increased by an average of 2.1% in core foraging areas and 1.8% in peripheral foraging areas over the entire breeding season.

The kernel overlaps in dive depth frequency distributions differed according to the degree of horizontal overlap. Overlap values were 0.75 and 0.77 in areas of peripheral and no horizontal overlap, but were lower at 0.67 in core foraging areas due to Adélies performing a greater proportion of their dives at shallower depths (Fig. 4).

3.3 | Timing of breeding phenology in relation to October air temperature

October air temperatures in the South Orkneys have increased significantly over the last 114 years from an intercept of -4.25°C ± 0.35 in 1903 at a rate of 0.017°C ± 0.005 per annum (linear regression: $F_{1,112} = 11.28$, $P < 0.005$). However, there was considerable annual variability around the trend (SD of model residuals = 1.87) and the adjusted r^2 showed that the time trend explained just 8.3% of the variance. There was no significant trend over the 20-year period for which penguin phenology data were available (linear regression: $F_{1,19} = 0.30$, $P > 0.5$), although the last five years of the time series were among the eight coldest on record, suggesting a recent shift to cooler temperatures (Fig. 5).

Modelling of the long-term time series of phenology data revealed that the interactive effect of species and October air temperature on laying date was not significant (ANCOVA; $F_{1,30} = 0.68$, $P > 0.4$) but the slope of temperature

($F_{1,31} = 9.04$, $P < 0.01$) and difference in the intercept between the two species ($F_{1,31} = 734.04$, $P < 0.001$) were significant. Both species advanced laying dates with temperature at the same rate of 1.02 ± 0.34 days for a 1°C increase in temperature (Fig. 5). The mean Adélie penguin laying date when October temperature was 0° C was 1st November ± 1.02 days and that of chinstraps was 27.89 ± 1.03 days later (Fig. 5). We found that the annual residuals from this model were correlated between the two species (Pearson correlation, $r = 0.767$, $t_{15} = 4.64$, $P < 0.0005$), suggesting a common phenological response to variables other than October air temperature. Allochrony was therefore conserved because the two species advanced their phenology in relation to environmental variability at the same rate. Laying dates of both species became significantly later between 1996 and 2015 at a rate of 0.37 ± 0.08 per annum ($F_{1,31} = 20.8$, $P < 0.001$) owing to the higher incidence of cool October temperatures in recent years.

4 | DISCUSSION

Seabirds may experience high levels of inter-specific competition due to their coloniality and central-place foraging strategy (Polito et al., 2015; Rosciano et al., 2016) and reduce this by partitioning their niches along multidimensional axes such as dietary, spatial or temporal segregation (Navarro et al., 2013; Polito et al., 2015; Pratte et al., 2017). The three species of *Pygoscelis* penguins have become a classic case study in this regard (Trivelpiece et al., 1987). Studies of spatial overlap have mostly been directed at comparing either Adélie or chinstrap penguins with gentoo penguins *Pygoscelis papua*, which occupy a distinctive niche characterised by shorter foraging ranges, deeper dives and a more fish-based diet (Kokubun et al., 2010; Miller et al., 2010; Cimino et al., 2016). Only two have studied the spatial overlap of the ecologically similar Adélie and chinstrap penguins, both of which were confined to the chick-rearing period (Lynnes et al., 2002; Wilson, 2010). Our study builds upon previous work by analysing tracking data from the entire breeding period and quantifying how allochrony gives rise to spatial segregation via leapfrog foraging. Further to this, we tested the resilience of this niche partitioning to climate change, which has the potential to alter the phenology of ecologically similar species at differing rates (Blois et al., 2013), resulting in competitor matching (Ahola et al., 2007). Reduced allochrony in response to climate change has been hypothesised to induce competitor matching among *Pygoscelis* penguins (Lynch, Fagan, et al., 2012) and our study quantifies this over a range of hypothetical and real-world scenarios.

4.1 | Stage-dependent foraging distribution

We found that foraging distribution and the maximum range of trips differed significantly between breeding stages, which supports Hypothesis 1. Trips were longest during incubation compared to brood guard and tended to increase from guard to crèche for Adélie but not chinstrap penguins, as found in previous studies (Clarke, Emmerson & Otahal, 2006; Jansen, Russell & Meyer, 2002; Lynnes et al., 2002; Ratcliffe & Trathan 2012). Longer incubation trips and increasing trip length with chick age is a common pattern found across seabird families (Kitaysky et al., 1999; Barlow and Croxall, 2002; Ito et al., 2010) *and are related to the different energetic and time constraints that incubating eggs and feeding chicks place upon parents.*

4.2 | Allochrony and leapfrog foraging

Allochrony has long been recognised as an axis along which niche partitioning can arise for sympatric species that are otherwise ecologically similar (Birkhead and Nettleship, 1987). Adélie penguins at Signy Island initiated breeding 28 days earlier than chinstrap penguins, a degree of allochrony which is identical to another site, Laurie Island, in the South Orkneys (Carlini, Coria, Santos & Bujan, 2005) but greater than the 21 days observed in the South Shetlands and WAP (Lynch, Fagan, et al., 2012).

The behaviour-based model revealed that leapfrog foraging is an important mechanism for reducing foraging competition among the two species: chinstraps performed long incubation trips while Adélies were performing short incubation and brood-guard trips. Adélies subsequently extended their foraging ranges during crèche as chinstraps switched to short chick-rearing trips for the remainder of the season. Stage-dependent foraging ranges, combined with allochrony, therefore produced two instances of leapfrogging during the breeding season, which supports Hypothesis 2. A similar pattern of leapfrog foraging has been documented for northern and southern giant petrels *Macronectes halli* and *giganteus* (Granroth-Wilding and Phillips, 2018) breeding sympatrically and asynchronously on South Georgia. We postulate that leapfrog foraging will arise wherever two colonial, central place foraging species display a combination of allochrony and stage-dependent foraging ranges, and present 16 further examples of where this might arise for seabirds in Table S3.

Theoretical simulations showed that if the two penguin species were to breed synchronously, their peripheral spatial overlap would increase by 54.0% over the entire breeding season, which supports Hypothesis 3. Previous studies of foraging distributions in Adélie and chinstrap penguins during chick-rearing alone (Lynnes et al., 2002; Wilson, 2010) did not adequately account for the effects of allochrony and therefore overestimated the degree of spatial overlap. Previously, allochrony was shown to offset the timing of peak energetic demands associated with chick-rearing for sympatric Adélie and chinstrap penguins and for Brünnich's and common guillemots *Uria lomvia* and *U. aalge* (Trivelpiece et al., 1987; Barrett et al., 1997). Our results demonstrate that allochrony can additionally reduce overlap in the foraging areas where those demands are met, further partitioning niches.

4.3 | Partitioning of dive depths

Vertical niche partitioning has been found in a range of diving (Mori and Boyd, 2004; Kokubun et al., 2010, 2016; Cimino et al., 2016) *and arboreal* (MacArthur, 1958; Mansor & Ramli, 2017; Slagsvold, 1975) *species where they occur in sympatry. We found that, while dive depths overlapped considerably, chinstraps dived to significantly deeper depths than Adélies. Wilson (2010) found a similar level of overlap in dive depths between these species in the South Shetland Islands, but there chinstraps dived to shallower depths than Adélies, showing that patterns of vertical partitioning among species may vary geographically. We also found evidence that the degree of overlap in dive depths was dependent on the degree of horizontal overlap in foraging areas, which supports Hypothesis 4. Vertical overlap in dive depths was reduced in core foraging areas compared to areas of peripheral or no horizontal overlap. This arose from Adélies diving on average three metres shallower in core foraging areas, which are mostly found in shallow waters close to Signy Island. Here, chinstraps are known to perform benthic dives* (Takahashi et al., 2003)*, whereas Adélies generally rarely do so* (Ropert-Coudert et al., 2002)*, so it possible that Adélies perform shallower pelagic dives when foraging in shallow water with high densities of benthic-feeding chinstraps. Similarly, Cimino et al.*

(2016) found that gentoo penguins performed deeper dives in areas of overlap with Adélie penguins compared to areas of no overlap, presumably to avoid competition with the shallower diving species.

4.5 | Phenology, climate change and competitor matching

Climate change has significantly influenced species interactions and ecosystem functioning on a global scale (Cotton, 2003; Parmesan and Yohe, 2003; Visser and Both, 2005). Avian phenology is particularly sensitive to warming temperatures (Visser et al., 2012) and rates of change can vary among sympatric species with similar ecological requirements, resulting in competitor matching. For example, nest site competition between great tits *Parus major* and pied flycatchers *Ficedula hypoleuca* was greatest when environmental conditions synchronised their breeding phenology (Ahola et al., 2007). Analysis of long-term monitoring data revealed that both Adélie and chinstrap penguins advanced their laying phenology at the same rate of 1.02 days per 1^{o}C increase in October air temperature, supporting Hypothesis 5. This rate of change is lower than the rate of 1.7-1.8 found for the same two species by Lynch et al. (2012) at colonies in the South Shetlands and Western Antarctic Peninsula. Importantly, phenological responses to October air temperature and residual variability around this relationship occurred in parallel for the two species, such that allochrony was preserved in the face of environmentally-induced change. Similarly Lynch et al. (2012) found allochrony between these two species was preserved in relation to October temperature within sites though time, while Black (2015) found it was preserved across sites situated over a wide latitudinal gradient.

The ecological causes of this marked resilience of allochrony to environmental variability warrants further exploration. Adélies occur around the whole of Antarctica and only overlap with chinstraps in a small fraction of their range in the WAP and islands of the Scotia Sea (Williams, 1995). As such, avoidance of competition with chinstraps will not have been be an important selective pressure upon the evolution of Adélie phenology across their range. Rather, their early phenology is believed to have evolved to allow them to exploit peaks in food availability following the spring bloom, avoid competition with migrant baleen whales and complete the breeding and moult cycle prior to the onset of the Antarctic winter (Trivelpiece et al., 1987; Youngflesh et al., 2017). Breeding success of Adélies has a tendency to be lower when laying is delayed (Hinke et al., 2012; Smiley and Emmerson, 2016; Youngflesh et al., 2017), such that there will be a selective pressure for Adélie penguins to lay as early as snow and sea ice conditions at a site allow.

Chinstrap phenology may be constrained by environmental conditions in the same way as that of Adélies, except that their phenology is delayed to a greater degree as their adaptation to the milder conditions of maritime Antarctica results in them being less cold-tolerant than Adélies (Trivelpiece et al., 1987). Alternatively, chinstraps may arrive at a site and adjust their laying phenology according to the stage of the Adélies' breeding season with the aim of minimising foraging competition. Our simulation model shows that spatial overlap in core foraging ranges increased by an average of 2.1% over the entire breeding season for each day of reduction in allochrony, which creates a strong selective pressure for chinstraps to maintain allochrony by adjusting their own breeding season relative to that of Adélie penguins. Separating these competing explanations for maintenance of allochrony will require comparisons of chinstrap phenology across multiple sites where they breed in sympatry and parapatry with Adélies.

Variation in the abundance of Antarctic krill (Ratcliffe and Trathan, 2012), both species' primary prey, may also influence competitive interactions, and thus the resilience of allochrony to environmental variability. However, current knowledge on seasonal prey abundance in this region is limited so it was not possible to investigate the role of this factor in this study.

5 | CONCLUSIONS

Our combined analytical approach has allowed important insights into competitive interactions among the two penguin species. The behaviour-based model reveals that niche partitioning by leapfrog foraging is reduced as the degree of allochrony between the two species is reduced but the analysis of long-term phenology data shows that allochrony is preserved as air temperatures warm and penguin laying dates advance. We conclude that competitor matching due to differing rates of phenological response to environmental change is unlikely to arise among the two species, and will not be a significant contributing factor to the population declines observed for these two species across the WAP and Scotia Sea (Trivelpiece et al., 2011; Lynch, Naveen, et al., 2012; Dunn et al., 2016). These declines are more likely to be driven by changes in recruitment rates of Antarctic krill, recovery of the populations of other competitors such as baleen whales or direct weather effects upon penguin breeding success (Trivelpiece et al., 2011; Lynch, Naveen, et al., 2012).

6 | FIGURES

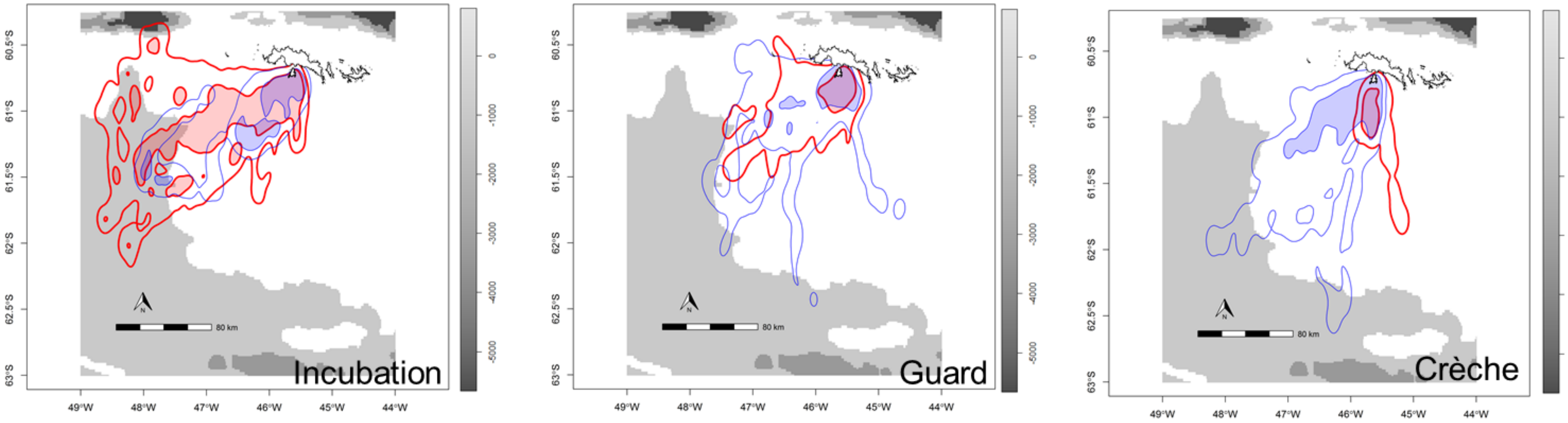


Figure 1 - Utilization distribution kernels of peripheral (95%) (thin line) and core (50%) foraging areas (shaded area with thick line) using raw GPS data of foraging trips for Adélies (blue) and chinstraps (red) overlaid on bathymetry (metres) shown in greyscale shading. The maps were produced by the authors using R version 3.3.0.

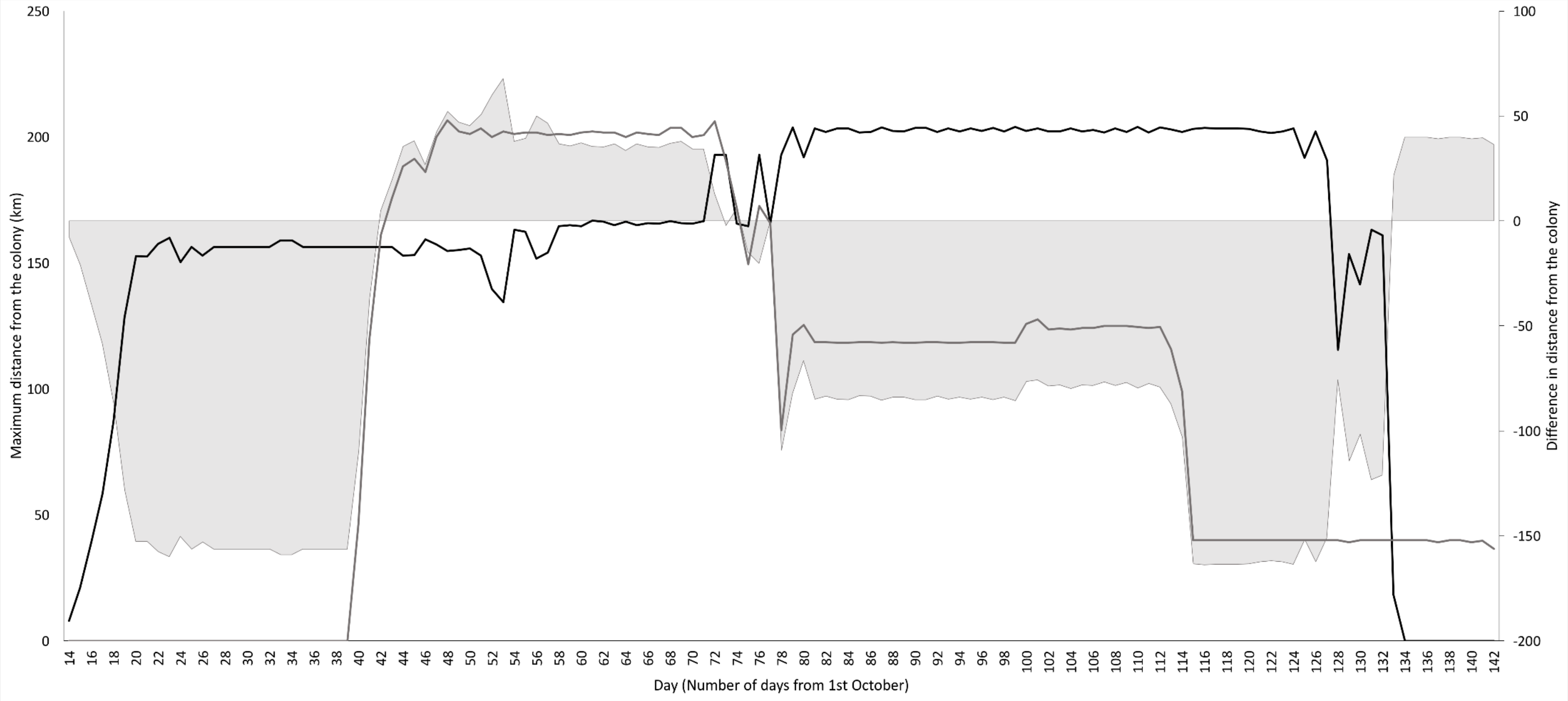


Figure 2 – Leapfrog foraging behaviour throughout the breeding season based on Adélie (black line) and chinstrap (grey line) foraging distances. Shaded areas show when one species has leapfrogged the other by foraging further away from the colony. Areas below the dotted line show when Adélies have leapfrogged chinstraps and areas above show when chinstraps have leapfrogged Adélies (difference = daily maximum chinstrap distance – daily maximum Adélie distance).

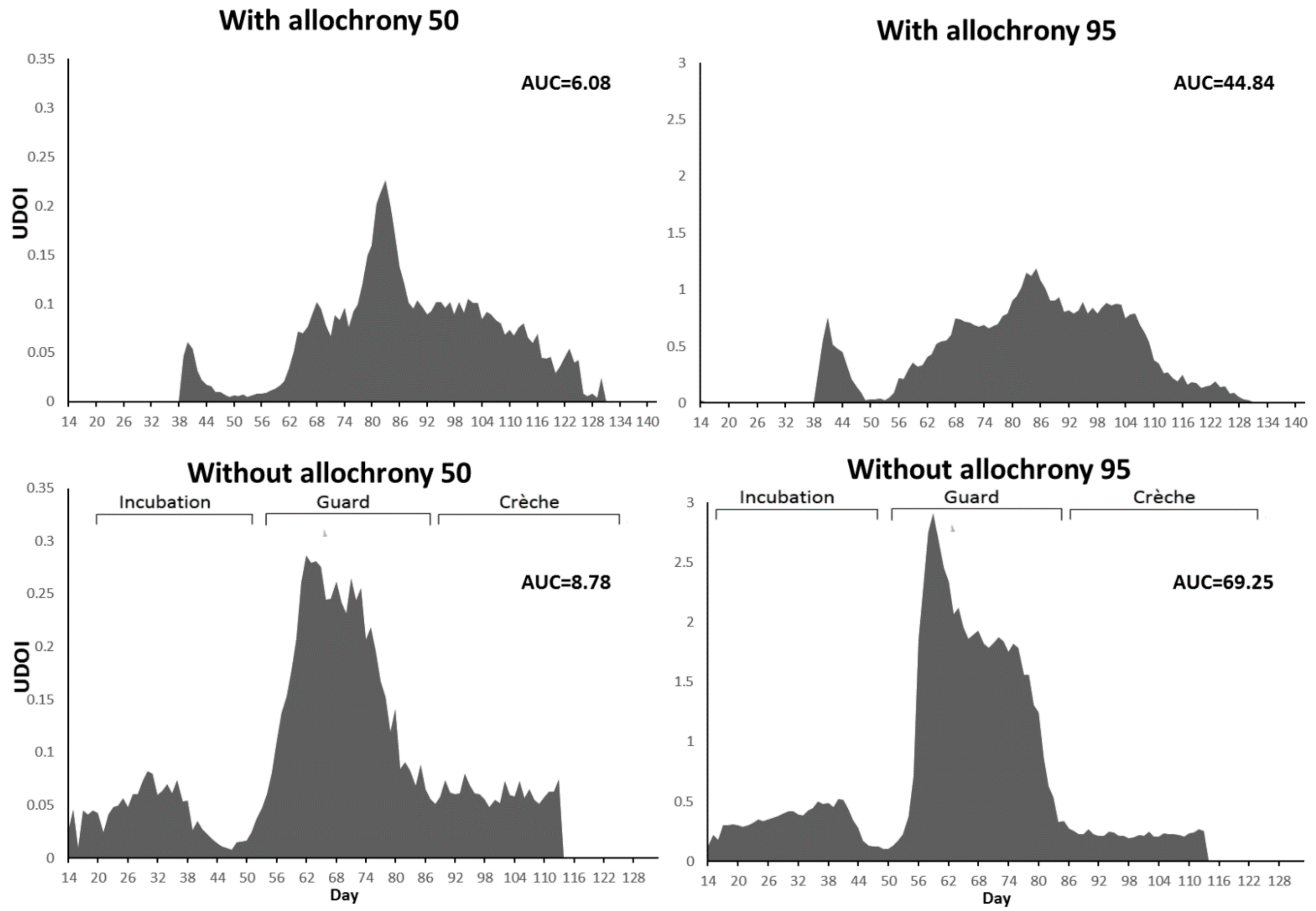


Figure 3 – Daily (number of days from 1st October) utilization distribution overlap index (UDOI) values, and area under the curve (AUC) values, for with allochrony (top panel) and without allochrony (bottom panel) in core (left column) and peripheral (right column) foraging areas.

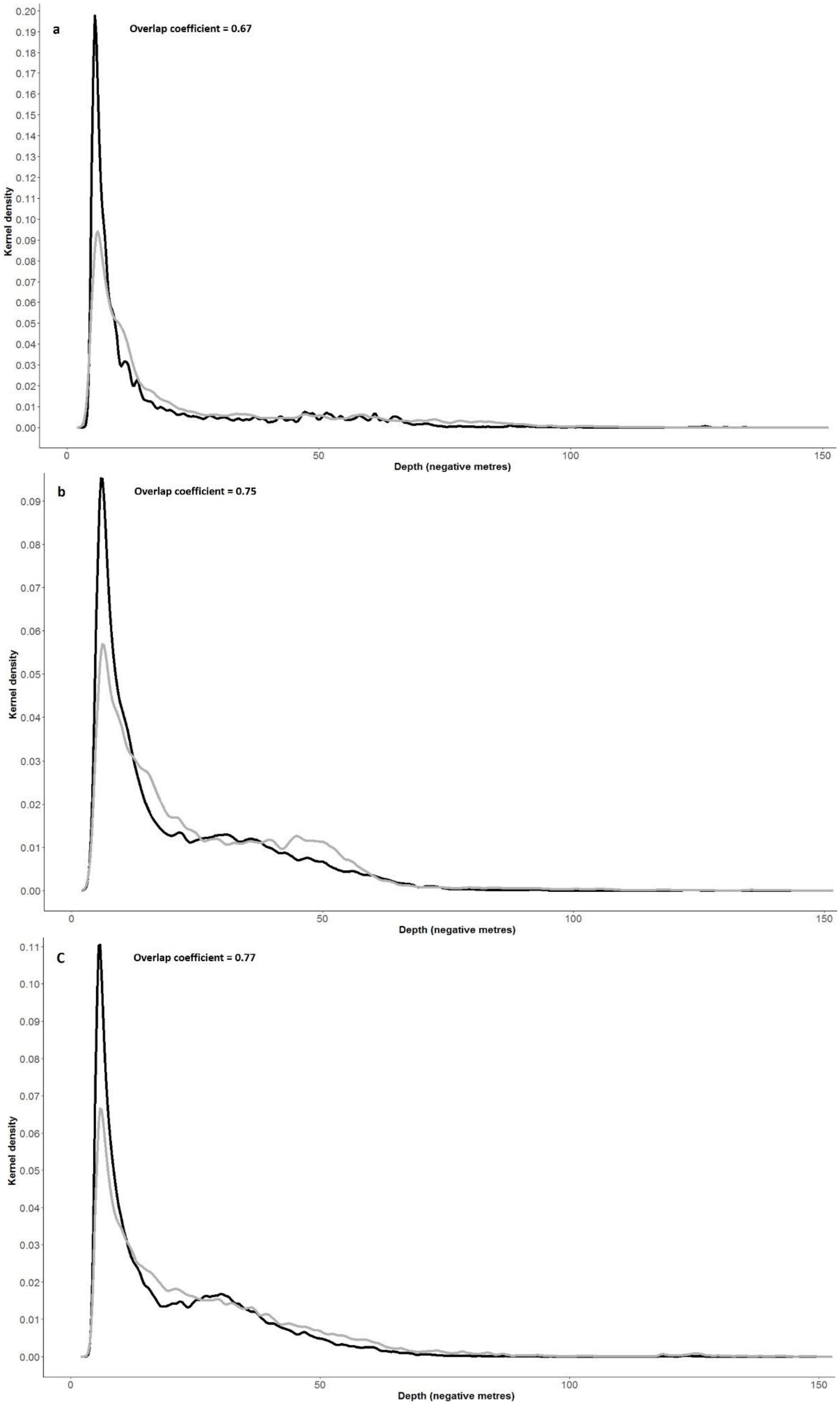


Figure 4 – Kernel density estimation curves of vertical overlap in dive depths for core (a), peripheral (b) and no horizontal overlap areas (c) between Adélies (black) and chinstraps (grey).

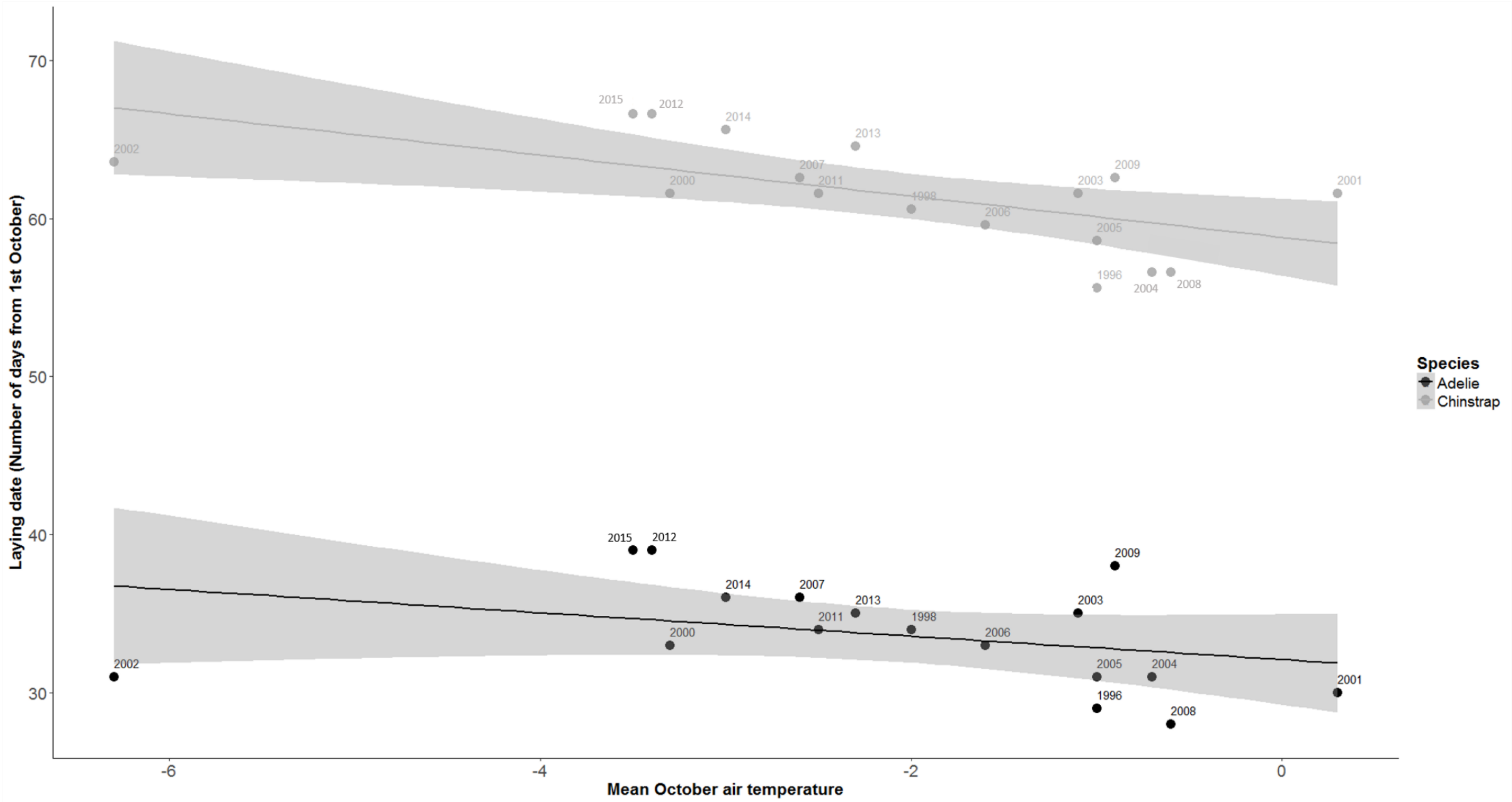


Figure 5 – Annual laying date for Adélies (black) and chinstraps (grey) against annual mean October air temperatures (°C) over the 20-year study period. Points are marked with years and shading represents 95% confidence intervals.

7 | SUPPORTING INFORMATION

Appendix S1 – Sampling and variability of tracks among years

Owing to the high expense of tracking devices and the logistical challenges of maintaining field teams in Antarctica, the sample sizes of tracks within years were relatively small (Table S1), which necessitated pooling of samples across years. Furthermore, obtaining samples from all stages of the penguin breeding cycle can be challenging at Signy Island since it is a summer-only base and input and uplift dates often prevent work during the early and late season. This resulted in sample sizes being particularly small, and sampling occurring in single years, for Adélies during incubation and chinstraps during crèche (Table S1). It is important to assess how this sampling pattern might affect our conclusions about leapfrog foraging.

The small sample sizes during the Adélie incubation stage and chinstrap crèche stage does not create uncertainty in overlap statistics under the observed level of allochrony owing to the complete absence of the competing species from the focal species' foraging range at these times of year. When Adélie penguins are incubating, all chinstraps are courting and nest building on land (Lynnes et al., 2002), whereas when chinstraps are entering crèche, Adélies are migrating south to the Weddell Sea (Dunn et al., 2011).

To investigate annual variability in foraging patterns across years within stages we performed kernel analysis, calculated core and peripheral isopleths and plotted these for each species-stage-year combination for which data were available (for Methods see main article). Figure S1 shows that incubation trips of chinstraps had broadly similar offshore ranges and distributions during 2014 and 2016. During brood guard, ranges were relatively short during all years except for 2016 for both species, when trips extended further offshore, and 2014 for Adélies when trips were of an intermediate range. Importantly, the ranges of both species during brood guard extended in tandem during 2016, and so would not confound sampling of leapfrog foraging across species and stages in the pooled data. Crèche trips for Adélies were broadly similar in 2014 and 2016, but short in 2012, although the latter is likely due to a single trip being sampled immediately after brood guard, before the crèche stage foraging ranges had reached their full extent (Lynnes et al., 2002). Utilisation Overlap

Distribution Indices for pairs of years within stages and species (for Methods see main article) confirms that foraging distributions were similar within stages across years, apart from those during brood guard during 2016 that were anomalous (Table S2).

The areas used in our study are similar to those described in a satellite tracking study of penguin foraging at Signy Island during chick-rearing in 2000 and 2001 (Lynnes et al., 2002). This study also found that Adélie penguins increased their foraging ranges from brood guard to crèche while those of chinstrap penguins remained similar during both stages. More broadly, the species-stage variability in foraging ranges, specifically Adélies performing medium-range incubation trips, short guard trips and long crèche trips and chinstraps performing long incubation trips and short guard and crèche trips, are typical of these species throughout their range (see Clarke et al., 2006; Ratcliffe and Trathan, 2012 for reviews). We therefore conclude that, despite the small sample sizes for some species-stage combinations and uneven sampling across years, our results characterise the stage-specific foraging patterns that are typical of both species and our inferences about leapfrog foraging are supported.

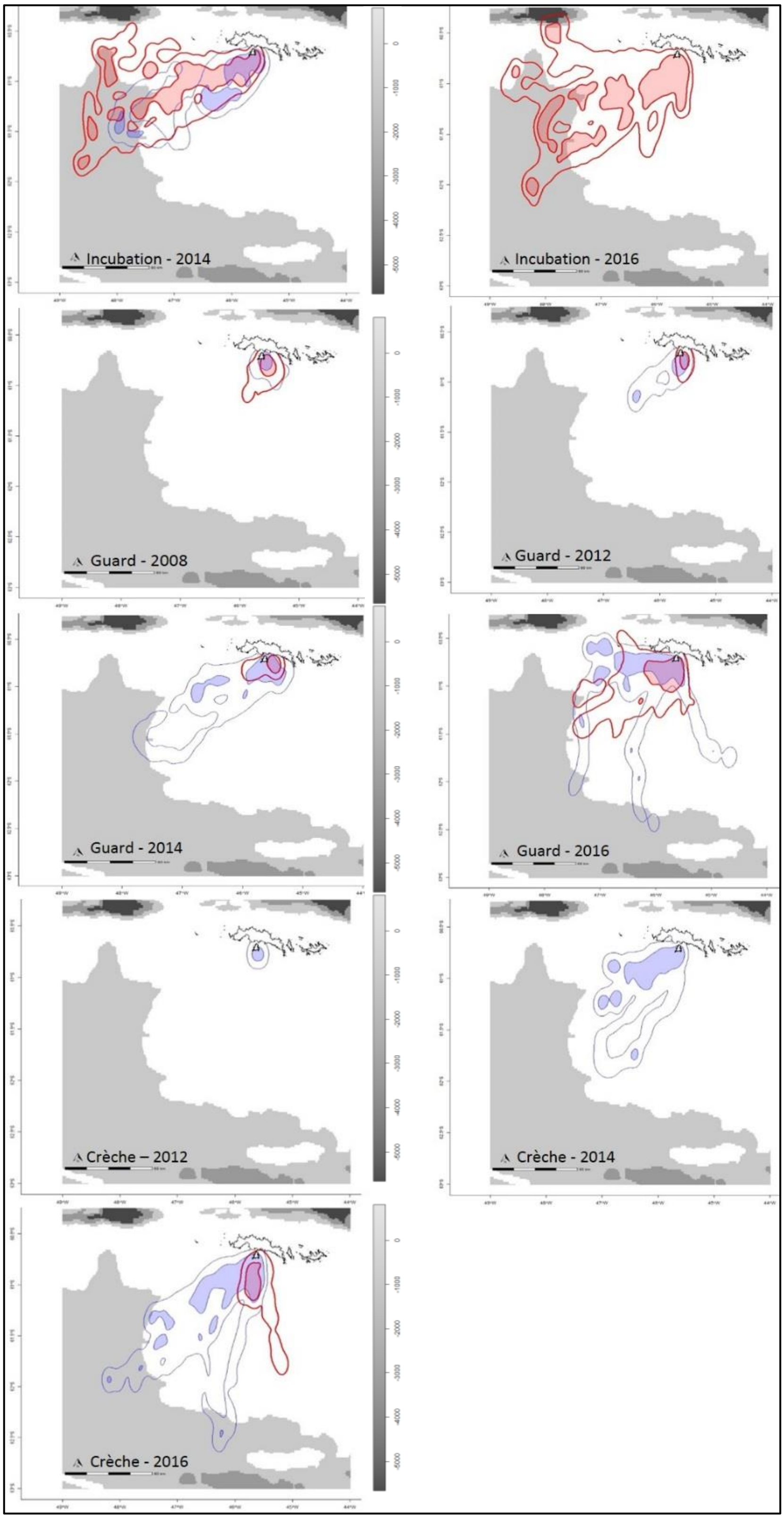
Table S1 – GPS/TDR tag deployments summed by breeding stage for all years of deployment.

Species	**Stage**	**Total equipped birds**	**Total foraging trips**	**Total dives**	**Sampling years (number of birds tagged)**
Adélie	Incubation	4	5	7,799	2014 (4)
	Guard	33	44	30,780	2008(19), 2012(3), 2014(7), 2016(4)
	Crèche	12	18	28,764	2012(1), 2014(6), 2016(5)
Chinstrap	Incubation	19	21	44,313	2014(10), 2016(9)
	Guard	60	89	34,447	2008(36), 2012(3), 2014(3), 2016(18)
	Crèche	4	7	2,848	2016(4)

Table S2 Comparison between years within breeding stages using a Utilisation Distribution Overlap Index (UDOI).

Stage	**Years**	**chinstrap UDOI 50**	**chinstrap UDOI 95**	**Adélie UDOI 50**	**Adélie UDOI 95**
Incubation	2014 - 2016	0.08	0.53	-	-
Guard	2008 - 2012	0.22	0.96	0.09	0.53
Guard	2008 - 2014	0.16	0.91	0.11	0.63
Guard	2008 - 2016	0.05	0.37	0.02	0.10
Guard	2012 - 2014	0.09	0.64	0.11	0.76
Guard	2012 - 2016	0.05	0.23	0.04	0.25
Guard	2014 - 2016	0.01	0.19	0.06	0.37
Guard	Average of all years	0.10	0.55	0.07	0.44
Crèche	2014 - 2016	-	-	0.13	0.62

Figure S1 – Utilization distribution kernels of peripheral (95%; thin line) and core (50%; shaded area with thick line) foraging areas using raw GPS data of annual breeding stage foraging trips for Adélies (blue) and Chinstraps (red) overlaid on bathymetry. The maps were produced by the authors using R version 3.3.0.



Animation S1 – Animation illustrating the process of simulating tracks through the breeding season using Adélie penguins on Signy Island, South Orkneys as an example. Blue tracks represent resampled tracks from incubation, green from brood-guard and yellow from crèche. Accessible online - https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2656.12919

Animation S2 – Animation showing overlap in 50% (shaded area with thick lines) and 95% isopleths (thin lines) of Adélie (blue) and chinstrap penguin (red) dive locations derived from the simulation analysis.

Table S3 – Examples of allochrony in sympatric congeneric seabirds. Definitions of allochrony type: staggered allochrony is a situation where birds breed during the same season but have different peaks in laying; complete allochrony is where birds breed in different seasons (e.g. summer, winter) such that their seasons do not overlap at all; Differences in breeding synchrony is where both species overlap their breeding seasons, but one species activity is more spread out through time than the other. Leapfrog foraging may arise in those species showing staggered allochrony where this is combined with stage-dependent foraging ranges.

Species	**Allochrony type**	**Broad region**	**Allochrony**
Northern (NGP) (*Macronectes halli*) and Southern Giant Petrel (SGP) (*M. giganteus*)	Staggered allochrony and differences in breeding synchrony	Polar	NGPs breed ~6 weeks earlier (Hunter, 1984) and their brooding and guarding is 11 days longer (Hunter, 1984) and display dietary partitioning (Gonzalez-Solis et al., 2000).
Common Murres (*Uria aalge*) and Thick-billed Murres (*U. lomvia*)	Staggered allochrony	Sub-Polar	Common murres breed ~15 days earlier and display dietary segregation between species in sympatric colonies (Barrett et al., 1997)
Adélie, Chinstrap and Gentoo (*P. papua*) penguins	Staggered allochrony	Polar	Species breed at approximately 2 week intervals – Adélie followed by Gentoo, followed by Chinstrap (Trivelpiece et al., 1987)

Rockhopper (*Eudyptes chrysocome*) and Macaroni (*E. chrysolophus*) penguins	Staggered allochrony	Sub-Polar	Dietary segregation with Macaronis eating at a higher tropic level (i.e. more fish) (Whitehead et al., 2017) and ~3 week difference in onset of breeding (Brown, 1987).
Erect-crested (*E. sclateri*) and Rockhopper penguins	Differences in breeding synchrony	Sub-tropical	Breed in sympatry in New Zealand (Williams, 1995) and display allochrony via hatching asynchrony (St. Clair, 1996).
Common diving (CDP) (*Pelecanoides urinatrix*) and South Georgia diving (SGDP) (*P. georgicus*) petrels	Staggered allochrony	Polar	Competition between species is reduced by SGDP utilising more barren habitats (Fischer et al., 2017) and the species display a ~4 week allochrony offset with CDP breeding first (Payne and Prince, 1979).
Wandering (*Diomedea exulans*) and Amsterdam (*D. amsterdamensis*) albatross	Complete allochrony	Sub-polar	Wandering albatross are biennial breeders and in breeding years are active between December and April, whereas Amsterdam albatross breed from March to January (Weimerskirch et al., 1997)
Black footed (*Phoebastria nigripes*) and Laysan (*P. immutabilis*) albatross	Staggered allochrony	Polar	Species display a ~2 week allochrony offset (Rice and Kenyon, 1962).
Black browed (*Thalassarche melanophris*) and grey headed (*T. chrysostoma*) albatross	Staggered allochrony	Polar	Species breed ~3 weeks apart with grey headed albatross breeding first (Weimerskirch et al., 1986).
Sooty (*Phoebetria fusca*) and light mantled sooty (*P. palpebrata*) albatross	Staggered allochrony	Polar	A ~4 week allochrony offset is displayed with Sooty albatross breeding first (Weimerskirch et al., 1986).
Great-winged (*Pterodroma macroptera*) and white headed (*P. lessoni*) petrel	Complete allochrony	Sub-tropical	White headed petrels breed biennially during the summer and great-winged petrels breed annually during the winter (Chastel, 1995).

Great-winged, Atlantic (*Pterodroma incerta*) and soft plumaged (*P. mollis*) petrel	Complete allochrony	Sub-tropical	The three species breed in sympatry on Gough Island and they have a large allochrony offset. Great-winged petrels breed in July, Atlantic petrels breed in September and soft-plumage petrels breed in December/January (Cuthbert et al., 2013; Dilley et al., 2015).
Murphy's (*Pterodroma ultima*) and Kermadec (*P. neglecta*) petrel	Staggered allochrony	Tropical	Significant breeding offset with most Kermadec petrels chicks hatching before Murphy's petrels begin to lay (Brooke, 1995)
Brown (*Stercorarius antarcticus*) and south polar (S. maccormicki) skuka	Staggered allochrony	Polar	The species are sympatric for part of their ranges and in these areas they segregate their foraging niches. Brown skuas breed ~4 weeks earlier, laying at the end of November (Trivelpiece and Volkman, 1982).
Red-billed (*Phaethon aethereus*) and Yellow-billed tropicbird	Complete allochrony	Tropical	Yellow-billed tropicbirds seem to breed all year round with a peak between December and April. Whereas, red-billed tropicbirds breed in a single period between March and December (Stonehouse, 1962).
Crested (*Aethia cristatella*), least (*A. pusilla*) and whiskered (*A. pygmaea*) auklet	Differences in breeding synchrony	Sub-tropical	All three species arrive at the breeding colonies and begin laying at a similar time but display allochrony in their incubation periods, with Crested auklets having the longest (Knudtson and Byrd, 1982)

8 | REFERENCES

Ahola, M. P., T. Laaksonen, T. Eeva, and E. Lehikoinen. 2007. Climate change can alter competitive relationships between resident and migratory birds. *Journal of Animal Ecology* 76: 1045–1052.

Ballance, L. T., D. G. Ainley, G. Ballard, and K. Barton. 2009. An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin Pygoscelis adeliae. *Journal of Avian Biology* 40: 279–288.

Barlow, K. E., and J. P. Croxall. 2002. Seasonal and interannual variation in foraging range and habitat of macaroni penguins Eudyptes chrysolophus at South Georgia. *Marine Ecology Progress Series* 232: 291–304.

Barrett, R. T., M. Asheim, and V. Bakken. 1997. Ecological relationships between two sympatric congeneric species, Common Murres and Thick-billed Murres, Uria aalge and U. lomvia, breeding in the Barents Sea. *Canadian Journal of Zoology* 75: 618–631.

Birkhead, T. R., and D. N. Nettleship. 1987. Ecological relationships between Common Murres, *Uria aalge*, and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador. I. Morphometrics and timing of breeding. *Canadian Journal of Zoology* 65: 1621–1629.

Black, C. E. 2015. A comprehensive review of the phenology of *Pygoscelis* penguins. *Polar Biology* 39: 405–432.

Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate Change and the Past, Present, and Future of Biotic Interactions. *Science* 341: 499–504.

British Antarctic Survey. 2018. BAS READER Project - MetData. Website https://legacy.bas.ac.uk/met/READER/surface/Orcadas.All.temperature.html [accessed 23 March 2018].

Brooke, M. de L. 1995. The breeding biology of the gadfly petrels Pterodroma spp. of the Pitcairn Islands: characteristics, population sizes and controls. *Biological Journal of the Linnean Society* 56: 213–231.

Brown, C. R. 1987. Traveling Speed and Foraging Range of Macaroni and Rockhopper Penguins at Marion Island (Velocidad de Movimiento y Extensión de las Áreas de Forrajeo de los Pingüinos Eudyptes chrysolophus y E. chrysocome). *Journal of Field Ornithology* 58: 118–125.

Bulgarella, M., S. A. Trewick, N. A. Minards, M. J. Jacobson, and M. Morgan-Richards. 2014. Shifting ranges of two tree weta species (Hemideina spp.): competitive exclusion and changing climate. *Journal of Biogeography* 41: 524–535.

Calenge, C. 2015. adehabitatHR: Analysis of Habitat Selection by Animals. R package version 0.4.1.4. *http://CRAN.R-project.org/package=adehabitatHR*.

Carlini, A. R., N. R. Coria, M. M. Santos, and S. M. Bujan. 2005. The effect of chinstrap penguins on the breeding performance of Adèlie penguins. *Folia Zoologica* 54: 147–158.

Chadwick, E. A., F. M. Slater, and S. J. Ormerod. 2006. Inter- and intraspecific differences in climatically mediated phenological change in coexisting Triturus species. *Global Change Biology* 12: 1069–1078.

Chastel, O. 1995. Influence of reproductive success on breeding frequency in four southern petrels. *Ibis* 137: 360–363.

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

Clarke, A., E. J. Murphy, M. P. Meredith, J. C. King, L. S. Peck, D. K. A. Barnes, and R. C. Smith. 2007. Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 362: 149–166.

Clarke, J., L. M. Emmerson, and P. Otahal. 2006. Environmental conditions and life history constraints determine foraging range in breeding Adélie penguins. *Marine Ecology Progress Series* 310: 247–261.

Cotton, P. A. 2003. Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences* 100: 12219–12222.

Croxall, J. P., P. A. Prince, and K. Reid. 1997. Dietary segregation of krill-eating South Georgia seabirds. *Journal of Zoology* 242: 531–556.

Cuthbert, R. J., H. Louw, J. Lurling, G. Parker, K. Rexer-Huber, E. Sommer, P. Visser, and P. G. Ryan. 2013. Low burrow occupancy and breeding success of burrowing petrels at Gough Island: a consequence of mouse predation. *Bird Conservation International* 23: 113–124.

Dilley, B. J., D. Davies, A. L. Bond, and P. G. Ryan. 2015. Effects of mouse predation on burrowing petrel chicks at Gough Island. *Antarctic Science* 27: 543–553.

Dunn, M. J., J. A. Jackson, S. Adlard, A. S. Lynnes, D. R. Briggs, D. Fox, and C. M. Waluda. 2016. Population Size and Decadal Trends of Three Penguin Species Nesting at Signy Island, South Orkney Islands. *PLOS ONE* 11: e0164025.

Dunn, M. J., J. R. D. Silk, and P. N. Trathan. 2011. Post-breeding dispersal of Adélie penguins (*Pygoscelis adeliae*) nesting at Signy Island, South Orkney Islands. *Polar Biology* 34: 205–214.

Elliott, K. H., K. J. Woo, A. J. Gaston, S. Benvenuti, L. Dall'Antonia, and G. K. Davoren. 2009. Central-Place Foraging in an Arctic Seabird Provides Evidence for Storer-Ashmole's Halo. *The Auk* 126: 613–625.

Ens, B. J., M. Kersten, A. Brenninkmeijer, and J. B. Hulscher. 1992. Territory Quality, Parental Effort and Reproductive Success of Oystercatchers (Haematopus ostralegus). *Journal of Animal Ecology* 61: 703–715.

Fieberg, J., and C. O. Kochanny. 2005. Quantifying Home-Range Overlap: The Importance of the Utilization Distribution. *The Journal of Wildlife Management* 69: 1346–1359.

Fischer, J. H., I. Debski, G. A. Taylor, and H. U. Wittmer. 2017. Nest site selection of South Georgia Diving-petrels Pelecanoides georgicus on Codfish Island, New Zealand: implications for conservation management. *Bird Conservation International*: 1–12.

Forcada, J., and P. N. Trathan. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology* 15: 1618–1630.

Gonzalez-Solis, J., J. P. Croxall, and A. G. Wood. 2000. Foraging partitioning between giant petrels Macronectes spp. and its relationship with breeding population changes at Bird Island, South Georgia. *Marine ecology. Progress series* 204: 279–288.

Granroth-Wilding, H. M. V., and R. A. Phillips. 2018. Segregation in space and time explains the coexistence of two sympatric sub-Antarctic petrels. *Ibis* 12584: 1–16.

Hardin, G. 1960. The Competitive Exclusion Principle. *Science* 131: 1292–1297.

Helland, I. P., A. G. Finstad, T. Forseth, T. Hesthagen, and O. Ugedal. 2011. Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology* 80: 539–547.

Hinke, J. T., M. J. Polito, C. S. Reiss, S. G. Trivelpiece, and W. Z. Trivelpiece. 2012. Flexible reproductive timing can buffer reproductive success of *Pygoscelis* spp. penguins in the Antarctic Peninsula region. *Marine Ecology Progress Series* 454: 91–104.

Hunter, S. 1984. Breeding biology and population dynamics of giant petrels *Macronectes* at South Georgia (Aves: *Procellariiformes*). *Journal of Zoology* 203: 441–460.

Ito, M., A. Takahashi, N. Kokubun, A. S. Kitaysky, and Y. Watanuki. 2010. Foraging behavior of incubating and chick-rearing thick-billed murres Uria lomvia. *Aquatic Biology* 8: 279–287.

Jansen, J. K., R. W. Russell, and W. R. Meyer. 2002. Seasonal shifts in the provisioning behavior of chinstrap penguins, Pygoscelis antarctica. *Oecologia* 131: 306–318.

Johnson, D. S. 2015. crawl: Fit Continuous-Time Correlated Random Walk Models to Animal Movement Data. R package version 1.5. *http://CRAN.R-project.org/package=crawl*.

Kitaysky, A. S., J. C. Wingfield, and J. F. Piatt. 1999. Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. *Functional Ecology* 13: 577–584.

Knudtson, E. P., and G. V. Byrd. 1982. Breeding Biology of Crested, Least, and Whiskered Auklets on Buldir Island, Alaska. *The Condor* 84: 197–202.

Kokubun, N., A. Takahashi, Y. Mori, S. Watanabe, and H.-C. Shin. 2010. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Marine Biology* 157: 811–825.

Kokubun, N., T. Yamamoto, N. Sato, Y. Watanuki, A. Will, A. S. Kitaysky, and A. Takahashi. 2016. Foraging segregation of two congeneric diving seabird species breeding on St. George Island, Bering Sea. *Biogeosciences* 13: 2579–2591.

Kranstauber, B., and M. Smolla. 2016. move: Visualizing and Analyzing Animal Track Data. R package version 2.0.0. *http://CRAN.R-project.org/package=move*.

Luque, S. P. 2016. diveMove: Dive Analysis and Calibration. R package version 1.4.1. *http://CRAN.R-project.org/package=diveMove*.

Luque, S. P., and R. Fried. 2011. Recursive Filtering for Zero Offset Correction of Diving Depth Time Series with GNU R Package diveMove. *PLOS ONE* 6: e15850.

Lynch, H. J., W. F. Fagan, R. Naveen, S. G. Trivelpiece, and W. Z. Trivelpiece. 2012. Differential advancement of breeding phenology in response to climate may alter staggered breeding among sympatric *Pygoscelid* penguins. *Marine Ecology Progress Series* 454: 135–145.

Lynch, H. J., R. Naveen, P. N. Trathan, and W. F. Fagan. 2012. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93: 1367–1377.

Lynnes, A. S., K. Reid, J. Croxall, and P. Trathan. 2002. Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap penguins. *Marine Biology* 141: 1165–1174.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39: 599–619.

MacArthur, R. H. 1968. The theory of the niche. *Population biology and evolution (ed. by R.C. Lewontin), Syracuse University Press, New York.*: 159–176.

Mansor, M. S., and R. Ramli. 2017. Foraging niche segregation in Malaysian babblers (Family: Timaliidae). *PLOS ONE* 12: e0172836.

Milazzo, M., S. Mirto, P. Domenici, and M. Gristina. 2013. Climate change exacerbates interspecific interactions in sympatric coastal fishes. *Journal of Animal Ecology* 82: 468–477.

Miller, A. K., M. A. Kappes, S. G. Trivelpiece, and W. Z. Trivelpiece. 2010. Foraging-Niche Separation of Breeding Gentoo and Chinstrap Penguins, South Shetland Islands, Antarctica. *The Condor* 112: 683–695.

Mori, Y., and I. L. Boyd. 2004. Segregation of foraging between two sympatric penguin species: does rate maximisation make the difference? *Marine Ecology Progress Series* 275: 241–249.

Mouillot, D., W. Stubbs, M. Faure, O. Dumay, J. A. Tomasini, J. B. Wilson, and T. D. Chi. 2005. Niche overlap estimates based on quantitative functional traits: a new family of non-parametric indices. *Oecologia* 145: 345–353.

Navarro, J., S. C. Votier, J. Aguzzi, J. J. Chiesa, M. G. Forero, and R. A. Phillips. 2013. Ecological Segregation in Space, Time and Trophic Niche of Sympatric Planktivorous Petrels. *PLOS ONE* 8: e62897.

Newton, I. 2008. The Migration Ecology of Birds. 1st Ed. Academic Press, Oxford.

Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. *Journal of Applied Ecology* 41: 413–426.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.

Payne, M. R., and P. A. Prince. 1979. Identification and breeding biology of the diving petrels Pelecanoides georgicus and P. urinatrix exsul at South Georgia. *New Zealand Journal of Zoology* 6: 299–318.

Pinheiro, J. 2016. nlme: linear and nonlinear mixed effects models. R package version 3.1-128. *http://CRAN.R-project.org/package=nmle*.

Polito, M. J., W. Z. Trivelpiece, W. P. Patterson, N. J. Karnovsky, C. S. Reiss, and S. D. Emslie. 2015. Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of *Pygoscelis* penguins. *Marine Ecology Progress Series* 519: 221–237.

Poloczanska, E. S., S. J. Hawkins, A. J. Southward, and M. T. Burrows. 2008. Modeling the Response of Populations of Competing Species to Climate Change. *Ecology* 89: 3138–3149.

Pratte, I., G. J. Robertson, and M. L. Mallory. 2017. Four sympatrically nesting auks show clear resource segregation in their foraging environment. *Marine Ecology Progress Series* 572: 243–254.

Pulliam, H. r. 2000. On the relationship between niche and distribution. *Ecology Letters* 3: 349–361.

Ratcliffe, N., S. Adlard, G. Stowasser, and R. McGill. 2018. Dietary divergence is associated with increased intra-specific competition in a marine predator. *Scientific Reports* 8: 6827.

Ratcliffe, N., and P. Trathan. 2012. A review of the diet and at-sea distribution of penguins breeding within the CAMLR Convention Area. *CCAMLR Science* 19: 75–114.

Rice, D. W., and K. W. Kenyon. 1962. Breeding Cycles and Behavior of Laysan and Black-Footed Albatrosses. *The Auk* 79: 517–567.

Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, and D. Firth. 2017. MASS: Functions and datasets to support Venables and Ripley,``Modern Applied Statistics with S'' (4th edition, 2002). R package version 7.3-47.

Ropert-Coudert, Y., A. Kato, K. Sato, Y. Naito, J. Baudat, A. Bost, and Y. Le Maho. 2002. Swim speed of free-ranging Adélie penguins Pygoscelis adeliae and its relation to the maximum depth of dives. *Journal of Avian Biology* 33: 94–99.

Rosciano, N. G., M. J. Polito, and A. R. Rey. 2016. Do penguins share? Evidence of foraging niche segregation between but not within two sympatric, central-place foragers. *Marine Ecology Progress Series* 548: 249–262.

Sætre, G.-P., E. Post, and M. Král. 1999. Can environmental fluctuation prevent competitive exclusion in sympatric flycatchers? *Proceedings of the Royal Society of London B: Biological Sciences* 266: 1247–1251.

Slagsvold, T. 1975. Competition between the Great Tit Parus major and the Pied Flycatcher Ficedula hypoleuca in the Breeding Season. *Ornis Scandinavica (Scandinavian Journal of Ornithology)* 6: 179–190.

Smiley, K. M., and L. M. Emmerson. 2016. A matter of timing: Adélie penguin reproductive success in a seasonally varying environment. *Marine Ecology Progress Series* 542: 235–249.

St. Clair, C. C. 1996. Multiple Mechanisms of Reversed Hatching Asynchrony in Rockhopper Penguins. *Journal of Animal Ecology* 65: 485–494.

Stenseth, N. C., J. M. Durant, M. S. Fowler, E. Matthysen, F. Adriaensen, N. Jonzén, K.-S. Chan, et al. 2015. Testing for effects of climate change on competitive relationships and coexistence between two bird species. *Proc. R. Soc. B* 282: 20141958.

Stonehouse, B. 1962. The Tropic Birds (*Genusphaethon*) of Ascension Island. *Ibis* 103B: 124–161.

Takahashi, A., M. J. Dunn, P. N. Trathan, K. Sato, Y. Naito, and J. P. Croxall. 2003. Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. *Marine Ecology Progress Series* 250: 279–289.

Taylor, R. S., and V. L. Friesen. 2017. The role of allochrony in speciation. *Molecular Ecology* 26: 3330–3342.

Trivelpiece, W. Z., J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences* 108: 7625–7628.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. J. Volkman. 1987. Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology* 68: 351–361.

Trivelpiece, W. Z., and N. J. Volkman. 1982. Feeding Strategies of Sympatric South Polar Catharacta Maccormicki and Brown Skuas C. Lönnbergi. *Ibis* 124: 50–54.

Vaughan, D. G., G. J. Marshall, W. M. Connolley, C. Parkinson, R. Mulvaney, D. A. Hodgson, J. C. King, et al. 2003. Recent Rapid Regional Climate Warming on the Antarctic Peninsula. *Climatic Change* 60: 243–274.

Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society of London B: Biological Sciences* 272: 2561–2569.

Visser, M. E., L. te Marvelde, and M. E. Lof. 2012. Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology* 153: 75–84.

Weimerskirch, H., N. Brothers, and P. Jouventin. 1997. Population dynamics of wandering albatross Diomedea exulans and Amsterdam albatross D. amsterdamensis in the Indian Ocean and their relationships with long-line fisheries: Conservation implications. *Biological Conservation* 79: 257–270.

Weimerskirch, H., P. Jouventin, and J. C. Stahl. 1986. Comparative ecology of the six albatross species breeding on the Crozet Islands. *Ibis* 128: 195–213.

Wenger, S. J., D. J. Isaak, C. Luce, H. M. Neville, K. D. Fausch, J. B. Dunham, D. C. Dauwalter, et al. 2011. Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Science* 108: 14175–14180.

Whitehead, T. O., M. Connan, Y. Ropert-Coudert, and P. G. Ryan. 2017. Subtle but significant segregation in the feeding ecology of sympatric penguins during the critical pre-moult period. *Marine Ecology Progress Series* 565: 227–236.

Williams, T. D. 1995. The Penguins: Spheniscidae. Oxford University Press, Oxford.

Wilson, R. P. 2010. Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Functional Ecology* 24: 646–657.

Wittwer, T., R. B. O'Hara, P. Caplat, T. Hickler, and H. G. Smith. 2015. Long-term population dynamics of a migrant bird suggests interaction of climate change and competition with resident species. *Oikos* 124: 1151–1159.

Youngflesh, C., S. Jenouvrier, Y. Li, R. Ji, D. G. Ainley, G. Ballard, C. Barbraud, et al. 2017. Circumpolar analysis of the Adélie Penguin reveals the importance of environmental variability in phenological mismatch. *Ecology* 98: 940–951.

SUPPORTING INFORMATION

The following Supporting Information is available for this article online:

- **SUPPORTING APPENDIX S1** Sample sizes and annual variability of tracks across years, including; **SUPPORTING TABLE S1** GPS/TDR tag deployments summed by breeding stage for all years of deployment, **SUPPORTING TABLE S2** Comparison between years within breeding stages using a Utilisation Distribution Overlap Index (UDOI), and **SUPPORTING FIGURE S1** Utilization distribution kernels of peripheral (95%) and core (50%) foraging areas using raw GPS data of annual stage foraging trips for both species.
- **SUPPORTING ANIMATION S1** Animation illustrating the process of simulating tracks through the breeding season (blue = incubation trips, green = guard trips and yellow = crèche trips) using Adélie penguins on Signy Island, South Orkneys as an example.
- **SUPPORTING ANIMATION S2** Animation showing overlap in 50% and 95% isopleths of Adélie and chinstrap penguin dive locations derived from the simulation analysis.
- **SUPPORTING TABLE S3** Examples of allochrony in sympatric, congeneric seabirds.

Chapter 3 – *Chinstrap penguins display archipelago specific migration routes and strong migratory connectivity*

Harriet L. Clewlow, Jefferson T. Hinke, Michael J. Polito, Rona A.R. McGill, Sally E. Thorpe, Gabriele Stowasser, Stephen C. Votier, Rod Downie and Norman Ratcliffe

Author contributions

The framework for the study was developed by NR and HLC. Geolocator and isotope data from the South Shetland Islands was collected and initially processed by JTH and MJP. RARM and GS assisted with South Orkneys isotope analysis and SET produced the ocean velocity figure (Fig. 2). HLC processed all geolocator and isotope date from the South Orkney Islands, ran all statistical analyses undertaken in this paper and wrote the paper with contributions from all the other authors. Isotope analysis funded by a Natural Environment Research Council Life Sciences Mass Spectrometry Facility grant (EK281-04/17). MODIS data were obtained from NASA's Ocean Biology Processing Group and the altimetry data were provided by the E.U. Copernicus Marine Service Information.

The eggshell isotope data presented here was previously published in Brasso et al. (2012) and the GLS tracking data collected at the South Shetland Islands in 2012 was previously published in Hinke et al. (2015).

ABSTRACT

Migration, the seasonal movement of individuals between breeding and over-winter sites, is common across a range of taxa. Developing a full understanding of a species' life cycle and migratory connectivity, the linkage between their breeding and over-winter sites, may help to elucidate the mechanisms underlying population change and determine the impacts of environmental variation between over-winter sites on these population trends. This is particularly the case for migratory species experiencing large-scale population declines. Chinstrap penguins (*Pygoscelis antarcticus*) breed across the Scotia Arc on island archipelagos and most populations are experiencing rapid population declines. The mechanisms underlying these declines are poorly understood and is impaired by a limited knowledge of migration routes and wintering areas, from breeding sites other than the South Shetland Islands. This study used geolocation and stable isotope analysis to describe the migration routes, wintering areas and diets of chinstrap penguins from the South Orkney archipelago for the first time and compares these with data from the South Shetland Islands. Birds from both archipelagos were found to display strong migratory connectivity and strong spatial segregation in over-winter sites. Individuals from the South Orkney Islands consistently migrated eastwards and northwards, in line with prevailing currents, to an area to the northeast of the South Sandwich Islands, while most of the individuals from the South Shetland Islands migrated westwards to the Pacific region of the Southern Ocean, apparently against prevailing currents. These migration routes and over-wintering sites were consistent across years (South Orkneys – 3 years, South Shetlands – 2 years). The two discrete wintering areas differed in their long-term sea surface temperature and primary productivity, in terms of their averages, trends, and annual variability. Isotopic analysis of tail feathers supported this, finding significant differences in average $\delta^{13}C$ and $\delta^{15}N$ values between birds from the two archipelagos. Additionally, birds from the two archipelagos experienced different environmental conditions at their over-winter sites, with birds from the South Orkneys experiencing higher concentrations of chlorophyll-a (0.21mg m^{-3} higher on average) across study years, while the South Shetlands birds experienced higher SST (0.81°C higher on average). Our findings provide novel insights into the behaviour of this rapidly declining species during winter, support current marine protected area designations and may prove valuable in elucidating the role of environmental variability during the winter period in breeding population declines.

1 | INTRODUCTION

Long-distance migration is the directed seasonal movement of individuals between widely spaced breeding and non-breeding/ over-winter areas and occurs across a range of taxa globally, including mammals, reptiles, fish, birds and insects (McGuire and Fraser, 2014). Migratory connectivity describes the links between breeding and over-winter sites. Strong connectivity occurs when all individuals from one breeding site migrate to the same over-winter site and weak connectivity occurs when individuals from the same breeding site migrate to multiple over-wintering sites (Webster et al., 2002). Populations displaying weak connectivity, or weak inter-annual site fidelity, are less threatened by localised change as the risk is spread across several sites and individuals may have flexibility to relocate to alternative sites in response to deteriorating conditions. Species exhibiting strong connectivity, and inter-annual site fidelity, are likely highly adapted to their specific regions and conditions meaning they will be impacted by any adverse change that occurs in their single winter site. The occurrence and effects of migratory connectivity are well documented in terrestrial birds, shorebirds and wildfowl (Drent et al., 2007; Trierweiler et al., 2014; Finch et al., 2017), but are less well studied in seabirds (but see González-Solís et al., 2007; Ramos et al., 2015).

During the breeding season many seabirds' foraging areas are constrained by their central-place foraging strategy and spatial segregation arises where colonies exist within travelling distances of one another. This occurs because it is more cost-effective to travel a short distance and compete with high densities of birds from the same colony than to travel a long distance and compete with the same density of birds from a neighbouring one (Wakefield et al., 2013). This results in seabirds from neighbouring colonies exhibiting spatially segregated foraging areas (Wakefield et al., 2013; Masello et al., 2016). Central-place foraging constraints are relaxed in the winter period and birds would be expected to disperse, and potentially mix with individuals from other colonies, particularly where the distance among sites is short comparative to the distances they travel (Frederiksen et al., 2012; Ratcliffe, Crofts, et al., 2014). However, tracking studies have shown that over-winter distribution is strongly defined by the bird's breeding colony of origin, with birds from nearby colonies migrating to spatially segregated sites (Tranquilla et al., 2013; Ratcliffe, Crofts, et al., 2014; Clay et al., 2016) and isotope tracking studies have identified strong regional trends in migratory behaviour (Polito et al., 2017).

Seabirds are long-lived and have low annual reproductive success, such that their population trends are particularly sensitive to small variations in overwinter survival (Frederiksen et al., 2008). The degree of migratory connectivity and spatial segregation during winter can therefore have important implications for population trends. Studies have shown that conditions in wintering areas, such as the environmental variability, food availability or anthropogenic threats, can all influence an individual's fitness in the following breeding season and are often termed ‘carry-over effects’ (Webster et al., 2002; Harrison et al., 2011).

Chinstrap penguins (*Pygoscelis antarcticus*; hereafter chinstraps) are largely confined to the Western Antarctic Peninsula (WAP) and islands of the Scotia Arc (see Figure 2 in Chapter 1 for breeding range), a region experiencing rapid climate change (Forcada and Trathan, 2009) and the target of an industrial fishery for Antarctic krill (*Euphausia superba*; hereafter krill; Nicol et al., 2012). They play an important role in the community in terms of food-web dynamics (Fraser and Trivelpiece, 1996) but are experiencing large-scale population declines (Trivelpiece et al., 2011; Lynch et al., 2012; Dunn et al., 2016). Currently, the role that drivers operating during winter have in explaining this decline are largely unknown. One of the barriers to achieving this is a poor understanding of the migration routes and wintering areas of different populations and the environmental conditions and prey that birds encounter there.

Winter movements and diets of chinstrap penguins have only been studied from the South Shetland Islands (e.g. Hinke et al., 2007, 2015; Trivelpiece et al., 2007; Polito et al., 2017) and data from other important breeding localities in the South Orkney and South Sandwich Islands are lacking. A combination of geolocator tracking (GLS) and stable isotope analysis (SIA) was used to address this knowledge gap by determining the migratory behaviour, over-wintering areas, migratory connectivity and winter isotopic niches, defined by diet and foraging habitat, of chinstrap penguins from the neighboring South Orkney and South Shetland Islands archipelagos (referred to as the two or both archipelagos hereafter). Our objectives are to describe whether; (1) chinstrap penguins display strong migratory connectivity, (2) chinstrap penguins from different archipelagos exhibit spatial segregation in wintering areas (3) populations show fidelity (i.e. are the same locations utilised year after year) to their wintering sites across years, (4) environmental conditions and their patterns of change through time differ between wintering areas, (5) migration routes are influenced by prevailing ocean currents (i.e. consistently observed strong currents) and (6) isotopic niches differ between the two archipelagos and between sampling years within archipelagos.

2 | MATERIALS AND METHODS

2.1 | Geolocator deployment sites and location data processing

GLS technology was used to track , n=106 (Table 1), chinstrap penguins throughout their migration as their long battery life and small size and weight enabled them to function for the entire period, whilst causing minimal impact to the birds (Phillips et al., 2004).

South Orkney Island archipelago (hereafter South Orkneys) chinstrap penguins were captured whilst incubating chicks at Gourlay Peninsula on Signy Island (60°42’S, 45°36’W) during 2012/2013, 2013/2014 and 2015/2016 breeding seasons (Table 1). Each bird was fitted with a Biotrack BAStag Mk9 archival geolocator logger (Biotrack, Wareham, UK), which recorded time, light level and activity (wet/dry using a salt water sensor). Tags were attached to each penguin’s tarsus using the ring design of Ratcliffe, Takahashi, et al. (2014).

South Shetland Island archipelago (hereafter South Shetlands) chinstrap penguins were tagged at Cape Shirreff on Livingston Island (62°47’S, 60°78’W) and at Admiralty Bay on King George Island (62°17’S, 58°45’W) during the 2011/2012 and 2014/2015 breeding seasons (Table 1) and fitted with Lotek Nano-Lat 2900-series archival GLS tags (Lotek Wireless, St. Johns, Newfoundland, Canada) using a Darvic plastic band, as detailed in Hinke et al. (2015). At both archipelagos the GLS tags were attached in December or January and recovered in the following November or December. GLS data collected at the South Shetlands during 2011/2012 have previously been published in Hinke et al. (2015) but data from 2014/2015 have not been published previously.

Bird locations were estimated primarily from the light and time data recorded by the GLS tags using geolocation, which produces up to two locations per day with an accuracy of between 40 km and 150 km depending on a number of factors, including the physical tag and environmental conditions (Phillips et al., 2004). GLS tags deployed at the two archipelagos provided raw data sets in slightly different formats and thus required different processing techniques. Tags used at the South Orkneys provided raw light data and this was processed using the BAStag (Wotherspoon, 2014) and SGAT (Wotherspoon et al., 2016) packages in the statistical analysis program ‘R’ (R Core Team, 2015). SGAT uses a Bayesian approach that estimates possible locations by taking account of an animal’s travelling speed, fixed start and end points of trips (i.e. known locations such as the colony location), masking land masses and comparing tag recorded sea surface temperatures (SST) to weekly mean SST data from NOAA online sources (NOAA/ESRL/PSD Climate Data Repository, 2018). Interpolation was then used to fill any gaps between locations and final processed tracks were provided with estimates of uncertainty. Tags used at the South Shetlands provided a single location estimate per day, with all light processing carried out internally and, thus, were processed using a combination of speed filters and correction factors, as outlined in Hinke et al. (2015). Locations were further refined by eliminating locations falling clearly within the mean maximum winter sea-ice extent as defined by National Snow and Ice Data Center (2018) because previous studies have shown that chinstrap penguins spend the winter to the north of the pack-ice (Ainley et al., 1994; Trivelpiece et al., 2007).

During equinox, it is impossible to accurately determine latitude as the day length is approximately the same across the world (Hill, 1994; Phillips et al., 2004). Chinstrap penguins migrate during the September equinox, and despite additional processing using the SST correction of latitude within the SGAT package (Wotherspoon et al., 2016), the data from this period could not provide location estimates and so are not presented.

2.2 | Spatial segregation and site fidelity

Monthly GLS derived locations for birds from each archipelago were pooled to produce population level kernel densities, estimated using the adehabitatHR package (Calenge, 2015) within the statistical program ‘R‘ (R Core Team, 2015), for April to November, excluding September. These monthly kernel densities were then used to produce 95% isopleths for each archipelago. These isopleths indicate the outer bounds of the population’s distribution, whilst removing any major outliers, thereby allowing the distributions of the two archipelago populations to be compared.

Site fidelity, meaning the tendency to return to a previously occupied location year after year, was estimated by quantifying the overlap of the annual kernel densities, all monthly locations pooled, within archipelago using a utilization distribution overlap index (UDOI). A UDOI was also used to describe overlap between distributions of birds, pooled across years, from each archipelago. The UDOI measures the degree to which two populations share space by presuming that the species use space independently (Fieberg & Kochanny, 2005). If there is no overlap the UDOI value would be 0, it would be 1 if there is 100% overlap and the utilisation distributions are uniform and the UDOI value would be >1 if overlap is high and the utilisation distributions are non-uniformly distributed (Fieberg and Kochanny, 2005). Meaning value of <1 would indicate a smaller degree of overlap between the two populations than expected from uniform space use and values >1 would suggest higher than normal overlap relative to uniform space use (for equation see thesis Chapter 2).

2.3 | Migratory connectivity

The strength of migratory connectivity for the two archipelagos was determined using the R package ade4 (Dray et al., 2018) to calculate the Mantel Correlation Coefficient (r_M). This analysis compares pairwise breeding and winter site locations to determine connectivity within a population. This test has been extensively used to investigate banding (or ringing) deployment/recovery data from terrestrial birds, due to the test's basis in disease research meaning it requires just two "locations" (Mantel, 1967), rather than GLS datasets containing multiple locations for the winter site. Thus, winter site locations for the analysis were produced by averaging all locations recorded for each individual during July, the middle of their core winter period (June - August), when they can be thought of as resident in their winter areas as their location is relatively stable. The significance of the r_M value was determined by running 9,999 random permutations (Dray et al., 2018). The r_M value can fall within a range between -1 to 1 and will be negative when populations move further apart between seasons, low migratory connectivity, positive when populations remain close together between seasons, strong migratory connectivity, and zero when populations have no patterns in distribution between seasons (Ambrosini et al., 2009). Therefore, the closer the value is to 1 the stronger the migratory connectivity.

2.4 | Environmental conditions within wintering sites

Environmental conditions experienced by birds within their wintering areas during June – August were investigated using average chlorophyll-a concentrations and SST recorded by the Moderate-Resolution Imaging Spectroradiometer (MODIS) Aqua satellite (Ocean Biology Processing Group, 2015) at a 4km resolution. These environmental variables were selected as they act as a proxy for of the abundance of krill (Atkinson et al., 2019), which comprise chinstrap penguins' primary prey across the majority of their range during breeding (Lishman, 1985b; Miller et al., 2010; Ratcliffe and Trathan, 2012). Krill are a cold water species and require chlorophyll-a for growth and reproduction (Hill et al., 2013; Murphy et al., 2017). Additionally, SST is thought to have indirect effects on penguin survival by influencing sea ice formation and distribution (Croxall et al., 2002).

Due to MODIS coverage issues arising from sea ice and cloud cover, a common limitation of remote sensing (Marshall et al., 1993), during the austral winter, environmental conditions were estimated using an average of daily fields from September to December. Values were extracted by overlaying the GLS derived locations recorded during the core over-winter period for each study year on the rasterised chlorophyll-a and SST data sets from the same year using the R package raster (Hijmans, 2017). The extracted values were then averaged to produce an annual mean chlorophyll-a and SST value for each archipelago populations' over-winter site. Changes in these environmental variables through time and between archipelagos were modelled using Analysis of Covariance (ANCOVA), with either SST or chlorophyll-a concentration as the response variable, time (Year) as the covariate and archipelago as the factor. To visualise current flows encountered by penguins during migration, we calculated and plotted the annual mean near-surface velocity field over 2012 to 2016 from altimetry-derived daily fields of geostrophic velocity at 0.25^{o} horizontal resolution (Copernicus Marine Environment Monitoring, 2018).

2.5 | Biological sampling for stable isotope analysis

Stable isotope analysis (SIA), was used to infer trophic level at which animals were feeding (from $\delta^{15}N$) and the habitat or latitudes animals exploited (from $\delta^{13}C$) (Hobson and Clark, 1992).

Tail feather samples were used to investigate trophic niches during their outbound migration. Samples, n=116 (Table 1), were collected by plucking (South Shetlands) or clipping a central tail feather as close to the skin as possible (South Orkneys), when deploying or recovering the GLS tags (depending on year and archipelago; Table 1). Within these samples, seven individuals from the South Orkneys were sampled on both deployment and recovery of the GLS tags (2015/2016 and 2017/2018 seasons respectively), allowing consistency in isotope ratios to be investigated between two consecutive years. Adult chinstrap penguins undergo a catastrophic moult after completion of breeding but do not grow the tail feathers until after they depart the colony, meaning the sampled section of tail feather was grown between March and June (59±11 days after the onset of moult) according to growth calculations by Hinke et al (2015). Therefore, we can be confident that the isotopic information contained in the sampled section represents the over-winter period when penguins were migrating to, or already located at, their over-wintering areas (Hinke et al., 2015).

Eggshell samples were used to investigate foraging behaviour and diet at the end of migration, just prior to egg laying. Samples were collected from hatched, predated or abandoned eggs at both archipelagos during the 2006/2007 season. Females fast for 10-19 days prior to egg laying and egg formation, once initiated, occurs over a 24 hour period (Astheimer and Grau, 1985; Lishman, 1985a; Emslie and Patterson, 2007). Therefore, eggshell stable isotope values provide information on foraging locations and diets at the end of winter migration when birds are returning to their colony, though it may also include some foraging close to the colony just prior to fasting and egg formation (Emslie and Patterson, 2007; Polito et al., 2009, 2011). These data have been previously published in Brasso et al. (2012) and are presented here to provide further insight into GLS data and a comparison to winter diet.

2.6 | Stable isotope analysis technique

Tail feather samples were trimmed into 3cm long sections, measured from the end closest to where the feather exited the skin, and cleaned by soaking in 2:1 chloroform:methanol solution for 24 hours. Sections were then rinsed and air-dried to ensure all solvent was removed. A 1cm section of shaft, located closest to where the feather exited the skin, was then sampled for isotopes by trimming off small slices (~0.7mg) with stainless steel scissors from the black area of the shaft only, to ensure the results were not affected by the melanin content of the sample (Michalik et al., 2010). Eggshells from the two archipelagos were processed by removing eggshell membranes, rinsing in distilled water to remove any organic material and then grinding to a powder using an analytical mill. Acidification, through titration with five 20 µl aliquots of 6M HCl, was used to remove carbonates from 10 mg samples of cleaned eggshell.

Feather and eggshell samples were weighed into individual tin capsules and then combusted (Elementar PYRO cube and Costech ECS4010 elemental analyzers) and analysed for $\delta^{15}N$ and $\delta^{13}C$ through interfaced Thermo Scientific Delta PLUS XP and Delta V PLUS continuous-flow stable isotope ratio mass spectrometers. To ensure consistency between instruments and laboratories, raw δ values were normalized on a two-point scale using the same glutamic acid reference materials with low and high values (USGS40, USGS41, US Geological Survey, USA. Laboratory standards (Fluka gelatin, Sigma alanine or Sigma glycine, Sigma-Aldrich Company Ltd, Gillingham, UK) were run between every 4-10 samples. Inter and intra-laboratory sample precision based on duplicate standard and sample materials was 0.1% and 0.2% for $\delta^{13}C$ and $\delta^{15}N$, respectively. Stable isotope abundances are expressed in δ notation in per mill units (‰), according to the following equation:

$$\delta X = [(R_{sample} / R_{standard}) - 1] \cdot 1000$$

Where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C / ^{12}C$ or $^{15}N / ^{14}N$. The $R_{standard}$ values were based on the Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}C$ and atmospheric N_2 (air) for $\delta^{15}N$ values.

2.7 | Isotopic niche analysis

Studies commonly use consumer stable isotope values to delineate the trophic ($\delta^{15}N$) and geographic habitat use ($\delta^{13}C$) axes of their isotopic niche space (Newsome et al. 2007), which is comparable, although not identical, to the ecological niche space defined by Hutchinson (1959). As such, we used a modification of the isotopic niche metrics described by Hinke et al. (2015) to compare stable isotope values between the two archipelagos and within each archipelago. An ANOVA was used to test for differences in mean $\delta^{15}N$ and $\delta^{13}C$ ratios between the two archipelagos, in both tail feathers and eggshells. Inter-annual consistency in isotope ratios was tested using a paired t-test on tail feathers collected in two consecutive years from seven South Orkneys individuals.

The R package SIBER (Jackson and Parnell, 2017) was used to calculate and compare isotopic niches within and between archipelagos and sampling years. The core niche estimate (SEA_c), the Bayesian core niche estimate (SEAb) and the total niche (TA), were calculated for each sampling year within each archipelago and for the archipelago overall by combining all available samples (Layman et al., 2007; Jackson et al., 2011). The centroid of each group's TA was determined and the Euclidean distances between the centroids were calculated, using the methods outlined in (Turner et al., 2010; Bowes et al., 2017), to determine niche similarity. Distances close to 0 indicate high isotopic niche similarity (Turner et al., 2010). Niche similarity was also directly quantified by determining the overlap between each sampling group's isotopic niche area using the nicheROVER package (Lysy et al., 2014). A niche region (Nr) was calculated for each group based on 10,000 Monte Carlo draws of elliptical projections using a 95% threshold (i.e. where there is a 95% probability of finding data from that group) and overlaps calculated, a higher percentage indicating greater overlap. The overlap between niches is defined as the probability that an individual drawn randomly from group A is found in the niche region of group B. Therefore, overlap is not necessarily symmetrical and is dependent upon how evenly a species uses its niche area (Swanson et al., 2015).

3 | RESULTS

3.1 | Migration routes and over-wintering areas

Migration routes from the two archipelagos were directed and targeted to relatively discrete overwintering sites (Fig. 1). The South Orkney birds appeared to use some strong elements of the eastward flowing Antarctic Circumpolar Current (ACC) to migrate towards South Georgia and then across to the northern end of the South Sandwich Islands, pausing in the South Sandwich Trench area just to the north of the average winter maximum sea-ice edge, for the core over-winter period (Fig.1 and Fig.2). They then travelled through relatively slack water on their return to the breeding colony. In contrast, the majority of South Shetland birds initially travelled against the mean flow of the ACC, along routes where the flow is weaker (Fig.2), ultimately occupying the relatively slack waters of the South Pacific region (Fig.2) of the Southern Ocean for their core over-winter period (Fig.1). Their return journey to the colony was in the direction of the ACC flow and therefore potentially assisted their progress. The routes followed by all birds circumvented the region of high current flow found in and to the east of the Drake Passage.

The migration routes undertaken by each population were highly divergent with all individuals from the South Orkneys heading eastwards and northwards, while the majority of individuals from the South Shetlands headed westwards (Fig.1). During each GLS sampling year a single bird from the South Shetlands migrated in the same direction as the South Orkneys birds, although only the bird sampled in 2014 travelled the full distance to the South Orkney over-winter area, while the other bird remained close to the sea-ice edge around the South Orkney Islands for the duration of the core over-winter period. By July both of the South Shetland birds had moved west to join the other individuals in the Pacific. The largely divergent migratory pathways resulted in essentially no overlap between individuals from the two archipelagos (average monthly UDOI=0.0003, pooled across years). Birds from breeding colonies on King George Island and Livingston Island within the South Shetlands archipelago displayed shared routes and over-winter site fidelity between years (UDOI=1.24). Birds from both archipelagos showed strong fidelity to their migration route and over-winter sites across years (South Shetlands: UDOI=1.49; South Orkneys: UDOI=1.00). A UDOI value of 1 or above indicates strong overlap between the groups (Fieberg and Kochanny, 2005). The Mantel correlation coefficient supported this by finding that they displayed strong migratory connectivity, as the value is close to the maximum possible value of 1, between breeding and over-winter areas (rM = 0.76, n = 61, p=0.0001).

In terms of environmental conditions, the South Orkneys over-winter site had consistently higher concentrations of chlorophyll-a (0.21mg m^{-3} higher on average; Fig. 3) than the South Shetlands' site across years, while the South Shetlands over-winter site had consistently higher SST (0.81°C higher on average; Fig. 4) than the South Orkneys' site. An ANCOVA revealed that SSTs and chlorophyll-a concentrations differed significantly between each archipelago's over-wintering site (Chlorophyll-a: $F_{1,9555}$=740.44, p=<0.0001; SST: $F_{1,7164}$=559.91, p=<0.0001) and between sampling years within each archipelago's over-wintering site (Chlorophyll-a: $F_{1,9555}$=3.40, p=0.05; SST: $F_{1,7164}$=523.46, p=<0.0001). Krill growth and reproduction occurs most efficiently in areas with high chlorophyll-a levels and lower temperatures, meaning the conditions at the South Orkneys over-winter area were likely to be more favourable (Hill et al., 2013; Murphy et al., 2017).

3.2 | Isotopic niche overlap between the two archipelagos

Overall, the average $\delta^{13}C$ and $\delta^{15}N$ in tail feathers was significantly different between the two archipelagos (ANOVA: $\delta^{13}C$: $F_{1, 113}=5.50$, p= 0.02; $\delta^{15}N$: $F_{1, 113}=39.18$, p= <0.0001), with South Shetlands individuals displaying higher ratios of both isotopes ($\delta^{13}C=+0.39$ ‰, $\delta^{15}N=+0.84$‰; Table 2). Nonetheless, variation around these means resulted in the isotopic niches of the two archipelagos overlapping extensively (Euclidean distance=0.92; mean overlap of $Nr_{Shetlands/Orkneys}=75.89\%$, Fig.4.A). These results suggest that birds from the two archipelagos occupied somewhat different marine habitats and consumed prey of different trophic levels.

The average $\delta^{13}C$ and $\delta^{15}N$ in eggshells from the two archipelagos were not significantly different (ANOVA: $\delta^{13}C$: $F_{1,43}=1.71$, p=0.20; $\delta^{15}N$: $F_{1,43}=0.03$, p=0.87; Table 2), although sample sizes were smaller than for feathers, and the resulting isotopic niches also overlapped extensively (Euclidean distance=0.27; mean overlap of $Nr_{Shetlands/Orkneys}=77.18\%$; Fig.4.B). In contrast, these results suggest that birds from the two archipelagos were occupying similar marine habitats and consuming prey of a similar trophic level.

Unfortunately, it is not possible to directly compare the two tissue types directly as their levels of isotopic enrichment differ (Polito et al., 2009; Hahn et al., 2012).

3.3 | Annual isotopic niche variation within each archipelago

The average $\delta^{13}C$ and $\delta^{15}N$ in tail feathers differed significantly between years within both archipelagos (South Shetlands: $\delta^{13}C$: $F_{1, 60}=22.80$, p=<0.001; $\delta^{15}N$ $F_{1, 60}=1.21$, p=0.28; Table 2, South Orkneys: $\delta^{13}C$: $F_{1, 51}=10.80$, p= 0.002; $\delta^{15}N$: $F_{1, 51}=16.62$, p=0.0002; Table 2). At the South Shetlands archipelago, the average $\delta^{13}C$ was particularly high in 2014 and at the South Orkneys archipelago, the average $\delta^{13}C$ was particularly high and $\delta^{15}N$ was particularly low during 2013. Overlap between the isotopic niches of the two sampling years at the South Shetlands was high (Euclidean distance=0.84; mean niche $overlap_{2012/2014}=72.23\%$; Fig.4.C), whereas overlap between the three sampling years at the South Orkneys was low (Mean Euclidean distance=1.31; mean overlap of $Nr_{2013/2015/2018}$=32.49%; Fig.4.D). A higher percentage overlap value indicates that the area of overlap between the two archipelagos' isotopic niches is larger and the larger the Euclidean distance the greater the distance between the centroids of the two isotopic niches.

The seven SOI birds sampled in consecutive years, at device deployment and recovery in the subsequent year, displayed consistent average tail feather $\delta^{13}C$ values between years (t= -1.74, df=6, p =0.13) but $\delta^{15}N$ values differed (t= -3.21, df=6, p =0.02). This resulted in relatively low overlap between the two groups' isotopic niches (Euclidean distance=0.96; mean overlap of $Nr_{2016/2017}$=48.75%; Fig.4.E).

4 |DISCUSSION

4.1 | Migratory behaviour and environmental conditions

In this study, we identified the over-winter behaviour of chinstrap penguins from the South Orkney Islands for the first time and then compared their behaviour to the birds from the neighbouring South Shetland Islands. Birds from the two study archipelagos displayed high migratory connectivity, strong spatial segregation and consistent migration routes and over-winter sites across sampling years. This led the two populations to experience differing marine habitat types and occupy different dietary niches, defined by environmental conditions and isotopic values.

Spatial segregation within species among colonies of seabirds (Wakefield et al., 2013; Masello et al., 2016) and between species within colonies (Wilson, 2010; Barger et al., 2016; Clewlow et al., 2019) has been observed during both the breeding season and over-winter period (Thiebot et al., 2011, 2012; Ratcliffe, Crofts, et al., 2014; Hinke et al., 2015). There is discussion around the drivers of this segregation with many hypothesising it to be driven by intra- and interspecific competition for shared prey resources. Chinstrap penguins consume krill almost exclusively during the breeding season (Lishman, 1985b; Takahashi et al., 2003; Lynnes et al., 2004; Ratcliffe and Trathan, 2012; Polito et al., 2015; Niemandt et al., 2016; Dimitrijević et al., 2018). Krill plays a central role in the Antarctic food-web as it links lower-trophic levels to all higher predators in the ecosystem (Barrera-Oro, 2002), meaning the demand, and therefore competition, for this resource is particularly high (Barlow et al., 2002; Ainley et al., 2006). Additionally, climate changes occurring in the

WAP region are causing krill to gradually contract their range southwards, away from these breeding colonies, and their recruitment is declining so fewer krill are available than historically (Atkinson et al., 2019), potentially further increasing competition for this resource.

Birds from the two study archipelagos displayed strong spatial segregation, which is often driven by prey availability (Whitehead et al., 2017; Sánchez et al., 2018), and birds within each archipelago displayed high migratory connectivity. Migration routes are thought to be influenced by a combination of expected prey availability, genetics, social learning and environmental conditions (Hjeljord, 2001; Pomilla and Rosenbaum, 2005; Liechti, 2006; Thiebot et al., 2013). However, genetic studies suggest that intermixing occurs between chinstrap populations in the Scotia Arc and WAP (Clucas et al., 2014, 2018; Freer et al., 2015), which suggests that a genetic driver is unlikely in this case. Therefore, cultural fidelity, defined as behaviour or information shared within a community that is acquired from conspecifics through social learning, may be defining the migration routes, and therefore segregation, based on ancestral knowledge of ocean currents and prey availability (Thiebot et al., 2013). Currents often define long-distance migration routes, as they can facilitate or impair movement depending on the animals' direction of travel relative to the currents. Site faithful species are often travel against currents on at least one leg of their migration and this is not unprecedented for penguin species (Ballard et al., 2010; Thiebot et al., 2013; Sherley et al., 2017). There are no gyres of the appropriate spatiotemporal scale available in the Southern Ocean to assist penguin migration, as used by Atlantic salmon (Dadswell et al., 2010), meaning the only alternative is utilising strong currents when they are in the direction of travel and seek slack currents or travel against weaker currents in the opposite direction (Luschi, 2013). Our results indicate that this method is used by chinstrap penguins from the two archipelagos. The penguins from both archipelagos travel eastwards in the direction of the Antarctic Circumpolar Current (ACC), South Orkney birds on their outward leg and South Shetland birds on their return leg, but when they travel westwards the South Orkney birds travel through relatively slack waters whilst South Shetland birds travel against the prevailing current direction. This means birds from the South Shetlands probably experience higher travel costs on their outward journey (Green et al., 2009), which is just after their annual moult, a 3-week fasting period, meaning their energy reserves are already diminished (Williams, 1995). Therefore, the areas accessed via this more costly travel direction are most likely of particularly high quality for this species and thus worth the risk of high energy expenditure during a time of low energy availability (Bon et al., 2015). Birds from both archipelagos circumvent the very strong currents of the Drake Passage, likely due to the high locomotion costs of maintaining position in this area and the reduced availability of prey (Silk et al., 2016; Atkinson et al., 2019). This may act as a physical barrier between the migration routes and over-wintering areas of the two archipelagos and so may explain the minimal overlap observed.

In terms of environmental conditions, our findings are representative of the long-term trends observed for both SST and chlorophyll-a. A study of a 34 year dataset, 1979–2013, showed that the South Shetland over-winter site has warmed whilst the South Orkneys' over-winter site has cooled slightly (Purich et al., 2016). In terms of chlorophyll-a concentrations, a study of an 11 year time series, 1997–2008, found consistently lower levels at the South Shetland over-winter site in comparison to the South Orkneys' over-winter site (Park et al., 2010). These variables are highly valuable as indicators of primary production, thus providing insights into prey availability and density (Montes-Hugo et al., 2009; Hill et al., 2013; Dehnhard et al., 2016). Chinstrap penguins consume krill almost exclusively during the breeding season (Lishman, 1985b; Takahashi et al., 2003; Lynnes et al., 2004; Ratcliffe and Trathan, 2012; Polito et al., 2015; Niemandt et al., 2016; Dimitrijević et al., 2018), and therefore we assume they would preferentially consume krill during the over-winter season if it is available. Unfortunately, there are no direct diet studies available for this species during the winter period and the isotope data presented here unfortunately cannot not add any knowledge to this. However, krill are stenothermic, meaning their abundance and distribution is strongly influenced by environmental conditions (Atkinson et al., 2008). In general, the environmental conditions at the South Orkney population's over-winter site, lower SST and higher chlorophyll-a concentrations, are more optimal for krill growth and reproduction (Atkinson et al., 2004; Murphy et al., 2017). This is supported by information on the known distribution of krill, which indicates that there are far higher densities of krill in this region than in the South Shetland population's over-winter site (Atkinson et al., 2008, 2019). Moreover, the South Shetland chinstrap penguins occupy a much broader area than the South Orkneys population throughout their migration (Fig.1), despite the breeding population sizes being comparable (Trivelpiece et al., 2011; Dunn et al., 2016). This broader dispersion of South Shetland birds is consistent with a lower krill density in the South Pacific sector and the need to reduce inter-specific competition for the available prey.

The ability to obtain adequate prey availability throughout the annual cycle is critical for survival and reproduction and is particularly crucial during pre-moult, pre-breeding, during egg synthesis and during chick growth (Walsberg et al., 1983; Carey, 2009). Since the 1970s both populations have experienced large-scale population declines with monitored colonies declining by 68% in the South Orkneys and >50% in the South Shetlands (Hinke et al., 2007; Trivelpiece et al., 2011; Dunn et al., 2016). The similar magnitudes of decline between the two populations indicate a common environmental driver and this is further supported by observations of population declines in the closely related Adélie penguin (*Pygoscelis adeliae)* breeding at our study archipelagos, that winter in the marginal ice zone of the Weddell Sea and show low overlap with chinstraps (Trivelpiece et al., 2011; Lynch et al., 2012; Dunn et al., 2016). Therefore, declines in the shared primary prey of these species across the WAP and Scotia and Weddell Seas, rather than local variability at over-winter and breeding locations, could be driving these concurrent population declines. Studies have suggested that regime shifts in primary production, driven by shifts in sea-ice cover and wind, are responsible for the reduction in krill availability across the WAP region (Montes-Hugo et al., 2009; Atkinson et al., 2019).

The migration route from the South Orkneys converged at an over-winter site in the South Sandwich region, where the largest known chinstrap colonies in the world are located, containing roughly half of the global breeding population of chinstrap penguins (Lynch et al., 2016). The over-winter behaviour of the South Sandwich population is currently unknown but it is plausible they are largely resident in this area during the over-winter season as levels of primary production in this region are particularly high and they are not displaced by expansion of sea ice as for sites further south. Evidence from Biuw et al., 2010 showed that a bird from a colony on Bouvet Island travelled to the South Sandwich Islands during a pre-moult trip, suggesting that migrating birds may converge in this high productivity region from both the east and west. Therefore, this area may be able to support birds from multiple colonies but further research is needed to determine the over-winter behaviour of the South Sandwich Islands population. Should this area be utilised by birds from the South Sandwich population as well as that from the South Orkneys it would be an important feature to conserve within the South Georgia and South Sandwich Island Marine Protected Area. Protection of these over-winter sites is particularly crucial for the conservation of this species, as their strong migratory connectivity means they are less able to react to changes at these sites and, thus, are more likely to be negatively impacted.

4.2 | Isotopic niches

4.2.1 | Variation between archipelagos

Nitrogen Isotope ratios from tail feather samples suggested that the South Shetlands birds fed at higher trophic levels during outbound migration/the early wintering period. Across the chinstrap penguin breeding range their diet is almost exclusively krill, except individuals breeding at the South Shetland Islands where fish accounts for up to 45% of their diet during some breeding stages (Ratcliffe and Trathan, 2012). The isotopic analysis of their feather suggests that they also feed on higher level prey, likely fish, during the winter, suggesting a continued lack of krill availability or a socially learnt prey preference. The closely related gentoo penguins (*Pygoscelis papua)* at South Georgia switch to fish during summers when krill abundance is low (Croxall et al., 1999; Waluda et al., 2017) and also during winter (Williams, 1991). Alternatively, the higher δ^{15}N ratios in the South Shetland wintering area might arise from elevated baseline values, higher levels of omnivory by krill (Price et al., 1988) or penguins feeding on carnivorous crustaceans such as amphipods (Negrete et al., 2017). Isotope baselines are defined by physical conditions (e.g., temperature), nutrient availability and the composition of primary producers (Graham et al., 2010), which can all vary greatly between years.

δ^{13}C ratios increase with latitude and are higher in pelagic compared to inshore or benthic habitats (Cherel and Hobson, 2007). Our GLS findings show that South Orkney birds occur at lower latitudes than South Shetlands birds but they display higher δ^{13}C ratios, which is the opposite to the general pattern. These higher ratios may be due to the extensive movement of water masses in this area and how they bend through the Scotia Arc, being forced northwards along the Scotia Trench (Venables et al., 2012), such that the South Orkney over-winter site is in waters from further south than that of the South Shetlands over-winter site. Therefore, the observed differences are most likely due to the differing location of the two populations' over-winter sites; the South Orkney over-winter site is located just downstream of land, whereas the South Shetland over-winter site is pelagic. This discrepancy between the isotope values and the tracking data is likely due to the influence of the inter-annual isotopic baseline shifts, which our bulk isotope analysis technique is unable to account for (Polito et al., 2017; Whiteman et al., 2019). Compound specific isotopic analysis can remove these concerns over baseline influence and a study by Polito et al. (2017) hypothesised that birds from our two study archipelagos wintered in different areas based on this isotopic information alone, which our tracking data supports.

The GLS data show that, at the end of migration, birds are near the colony during the period of egg formation and δ^{13}C ratios suggest that birds from both archipelagos are foraging over the shelf and δ^{15}N ratios indicate that they are feeding on low trophic level prey, most likely krill as they do during the breeding season (Lynnes et al., 2002; Takahashi et al., 2003; Hinke et al., 2007).

4.2.2 | Variation within archipelagos

Interannual variation in the isotopic niche, derived from feather samples, of both populations was high, particularly for the South Orkneys population, with significant differences in average δ^{13}C and δ^{15}N values. In the absence of GLS data, the variation in δ^{13}C might have been interpreted as birds accessing different wintering areas between years, which varied in either latitude and/or distance from land. However, the GLS data showed that they consistently used the same over-winter areas between years and thus the variability in this isotope is likely an artefact of interannual baseline shifts, as discussed above. The bulk isotope analysis method employed in this study has been used extensively to explain differences in isotopic niches among site and year groups in a range of penguin species but it is unable to account for interannual baseline shifts (Polito et al., 2011, 2017; Ceia et al., 2015; Dehnhard et al., 2016; Dimitrijević et al., 2018; Whiteman et al., 2019). Therefore, to account for this, studies require information on annual or spatial baseline interannual variability or need to use compound specific methods, which can account for baseline shifts, to make any conclusions about variation in wintering areas from isotopes alone. Alternatively, tracking birds provides more accurate data but it is more logistically challenging, time consuming and expensive (Polito et al., 2017).

5 | CONCLUSIONS

This study extends our knowledge of winter migratory behaviour of chinstrap penguins, revealing the distribution of birds from the South Orkney Islands, during this period, for the first time. This novel insight into the behaviour of this rapidly declining species during winter, is integral in the development of new, and support of current, marine protected areas (MPAs) to reduce the impacts of the local krill fishery. Additionally, it provides valuable information for elucidating the role of environmental variability during the winter period in breeding population declines.

Comparing the newly identified migration areas and over-winter sites of the South Orkney population with the South Shetlands population showed that birds from the two archipelagos wintered in spatially segregated areas, experiencing different environmental conditions and likely consumed prey at different trophic levels, as is the case during the breeding season. The similar rate of population decline occurring at both archipelagos indicates a large-scale regime shift affecting the region, rather than changes within individual wintering or breeding areas. Interestingly, this possible large-scale regime shift is not currently affecting the huge South Sandwich Islands chinstrap population where numbers are currently stable (Lynch et al., 2016). The winter distribution of this population is currently unknown, meaning that they may share wintering areas with birds from the South Orkney Islands and if so, the differing population trends must arise from factors operating in the summer but if their wintering areas differ it could arise from factors in either the summer, the winter, or both. Therefore, further investigation is required to elucidate the drivers of these contrasting population trends and implement conservation action accordingly.

6 | FIGURES

Table 1 – Sample sizes of geolocator (GLS) tracks and biological samples collected from Signy Island, South Orkney Islands archipelago.

Year	Site	Number of GLS tracks	Number of tail feathers	Number of egg shells
2006/2007	South Orkneys	-	-	15
	South Shetlands (King George Island)	-	-	15
	South Shetlands (Livingstone Island)	-	-	15
2011/2012	South Shetlands (King George Island)	19	16 *(collected on recovery - 2012)*	-
	South Shetlands (Livingstone Island)	33	21 *(collected on recovery - 2012)*	-
2012/2013	South Orkneys	8	-	-
2013/2014	South Orkneys	14	27 *(collected on deployment - 2013)*	-
2014/2015	South Shetlands (Livingstone Island)	26	26	-
2015/2016	South Orkneys	6	19 *(collected on deployment - 2015)*	-
2017/2018	South Orkneys	-	7 *(collected on recovery - 2018)*	-

Table 2 – Summary of tail feather and eggshell (2007 only) isotopic values (mean±SD) and Bayesian core niche area estimate (SEA$_b$) for each sampling year at each archipelago. Values in parentheses are 95% credibility intervals.

		Sample number (n)	**δ^{13}C ‰)**	**δ^{15}N (‰)**	**SEA$_b$ (‰)**
South Orkneys	**All years** (tail feathers)	**53**	**-23.08±1.01**	**8.79±0.66**	2.03 (1.55–2.69)
	2007	15	-24.09±0.40	9.15±0.95	1.12 (0.69–1.98)
	2013	27	-22.42±0.81	8.56±0.58	1.22 (0.84–1.83)
	2015	19	-23.97±0.43	8.81±0.61	0.79 (0.51–1.30)
	2018	7	-23.17±0.95	9.58±0.44	1.00 (0.49–2.47)
South Shetlands	**All years** (tail feathers)	**62**	**-22.69±0.77**	**9.63±0.76**	1.77 (1.38–2.29)
	2007	30	-23.82±0.74	9.19±0.59	1.32 (0.94– 1.95)
	2012	37	-23.02±0.69	9.71±0.82	1.73 (1.26–2.44)
	2014	25	-22.20±0.61	9.50±0.66	1.06 (0.72–1.62)

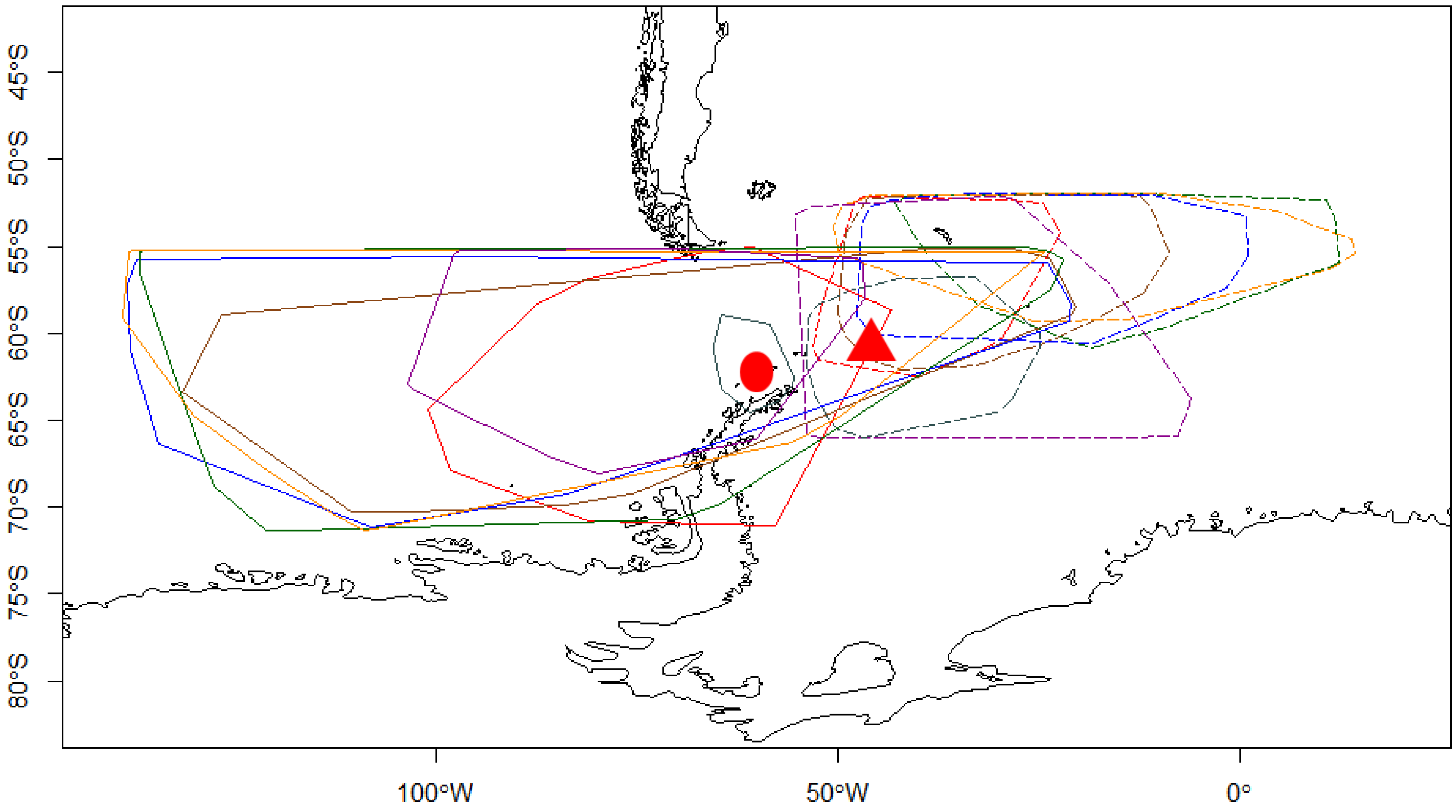


Figure 1 – Monthly 95% contours of birds from the South Orkney Islands (dashed lines – colony location at red triangle) and South Shetland Islands (solid line – colony location red circle) with April to November coloured in the following order: red, brown, blue, green, orange, purple and grey. The maps were produced by the authors using R version 3.6.1. and the ggplot2 packages (R Core Team, 2015; Wickham and Chang, 2016).

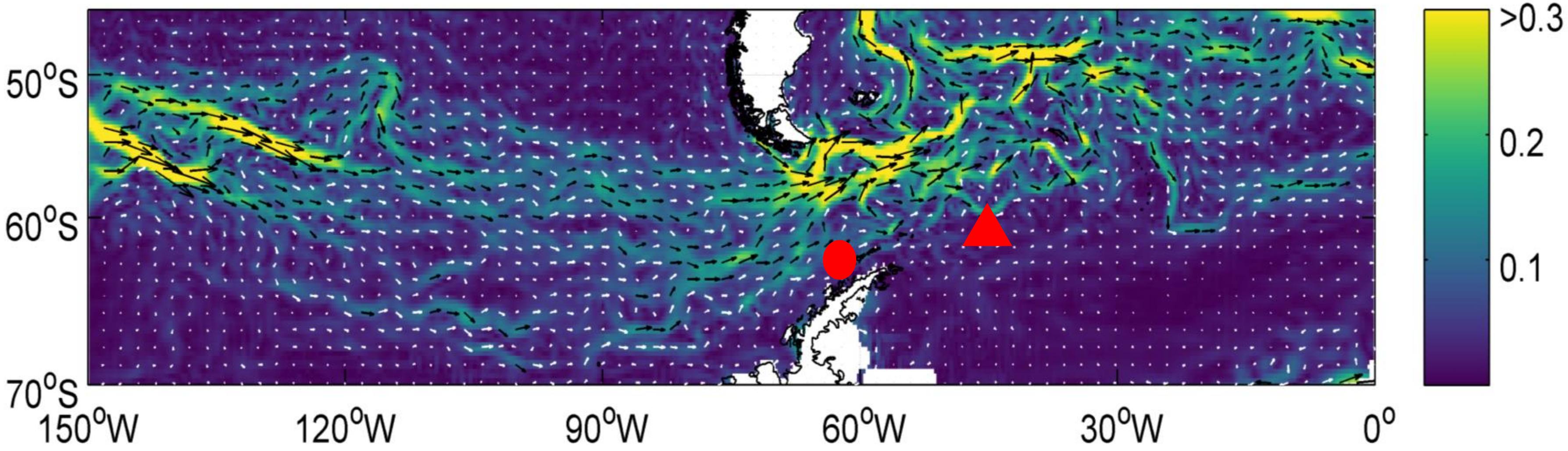


Figure 2 – Mean near-surface ocean velocity field (2012-2016) for the Southern Ocean, with the colour axis set to a maximum of 0.3 m s^{-1} for clarity of visualisation. Arrows indicate current velocity (larger arrow = faster flow) plotted at every 1° latitude and 2° longitude. Data were obtained from the E.U. Copernicus Marine Service information (Copernicus Marine Environment Monitoring, 2018). South Shetland Islands highlighted with red circle and South Orkney Islands highlighted with red triangle.

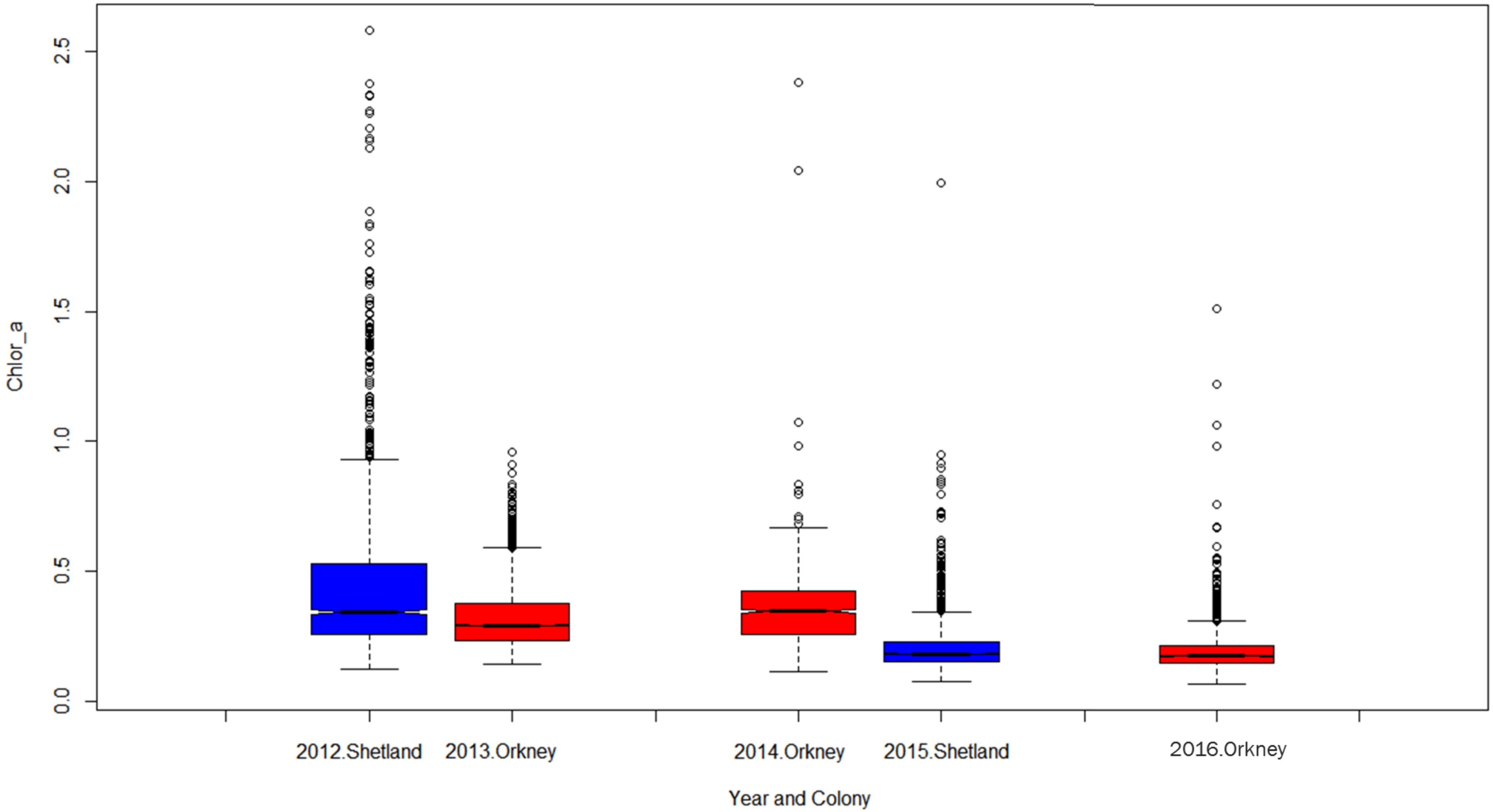


Figure 3 – Annual Chorophyll-a vaues at the over-winter site of each archipelago population during each tracking year.

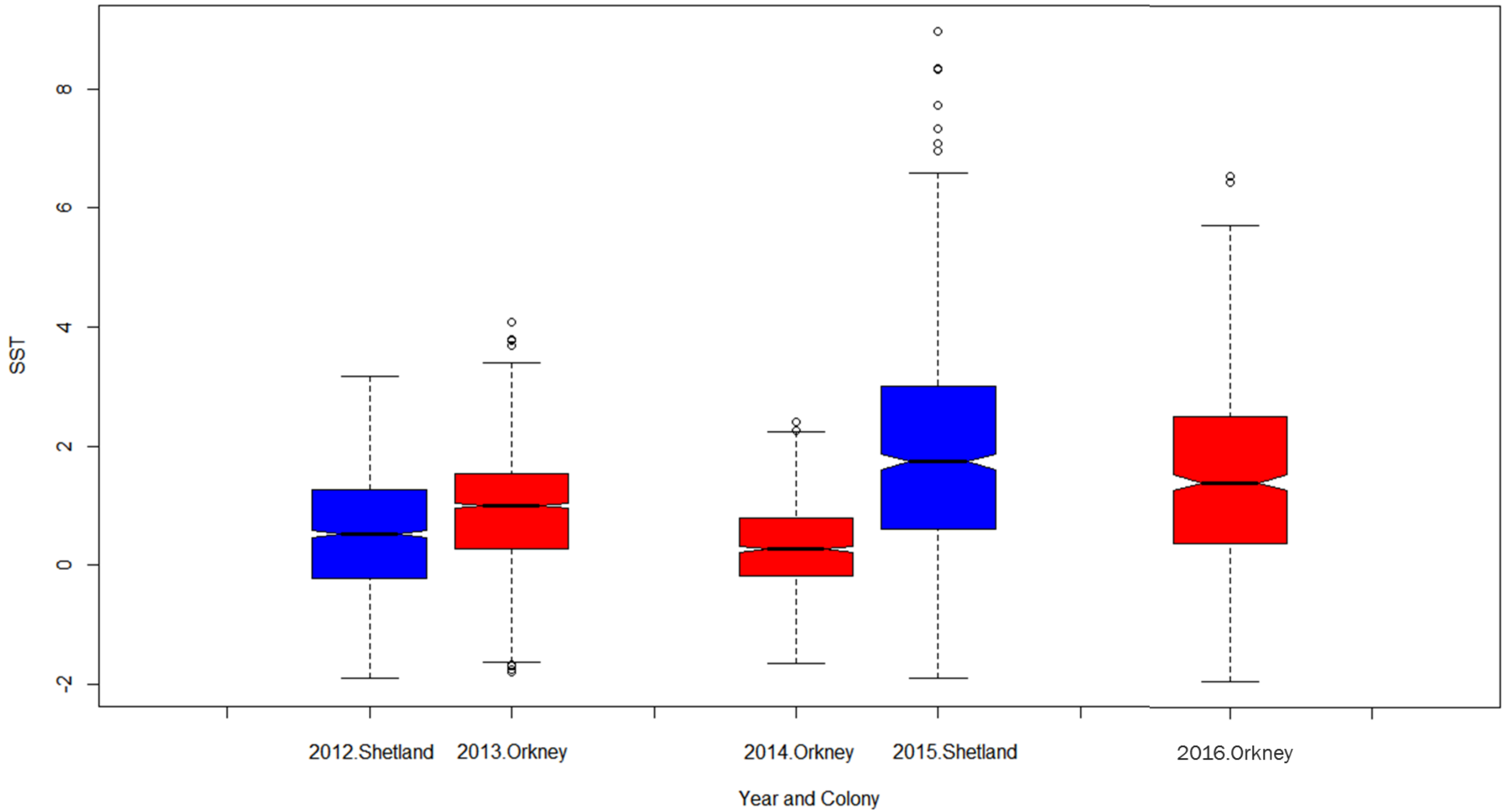


Figure 4 – Annual sea-surface temperature values at the over-winter site of each archipelago population during each tracking year.

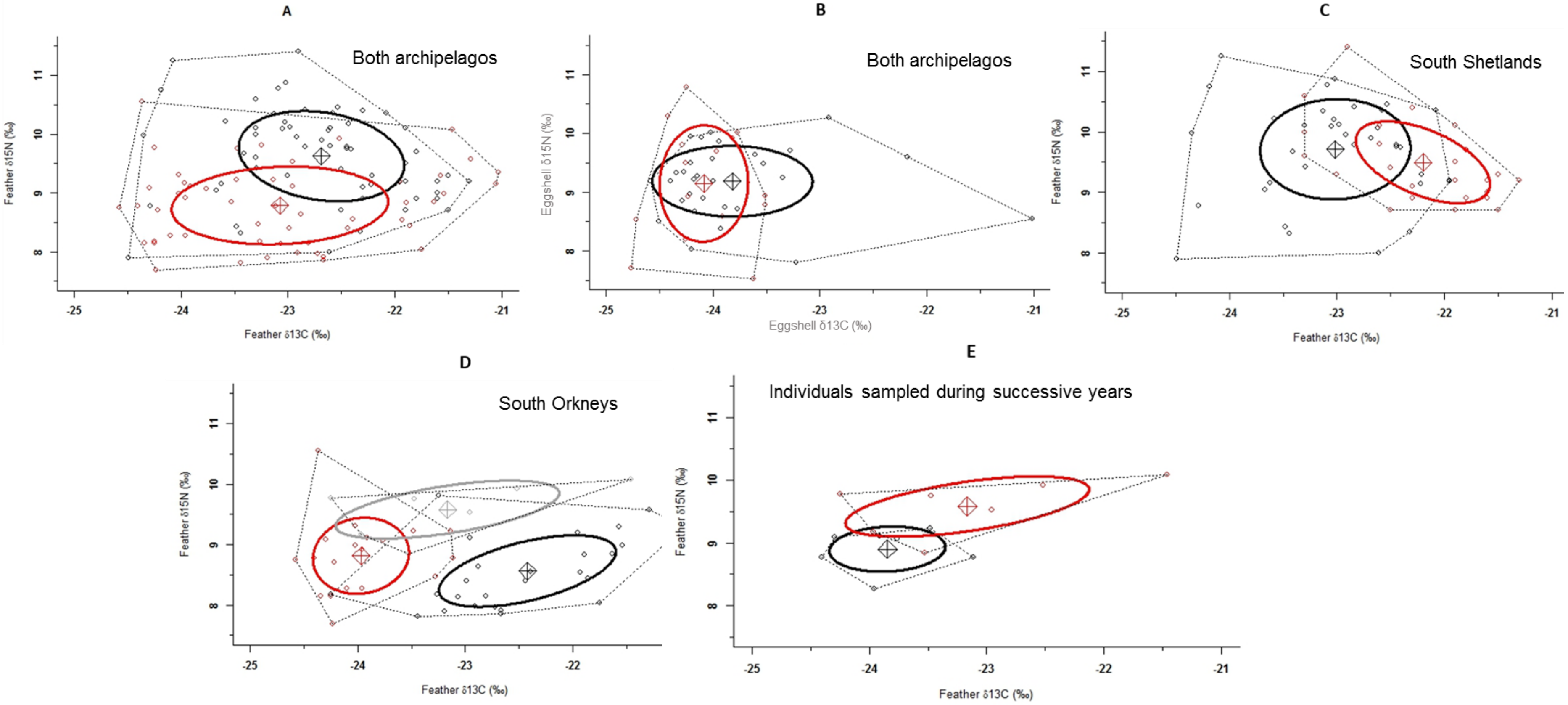


Figure 5 - Total (TA–dashed line) and core isotopic niche area (SEA$_C$–solid line) and group centroid (cross) for chinstrap penguin biological samples. Plot A–All feather samples from both archipelagos–black=South Shetland Islands, red=South Orkney Islands; B–All eggshell samples–black=South Shetland Islands, red=South Orkney Islands; C–South Shetlands individual years tail feathers–black= 2012, red= 2014; D–South Orkney individual years tail feathers–black= 2013, red= 2015 and grey=2018; E–tail feathers of individual birds sampled on successive years–black= 2016 samples, red=2017 samples.

7 | REFERENCES

Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the Western Ross Sea, Antarctica. *Ecology* 87: 2080–2093.

Ainley, D. G., C. A. Ribic, and W. R. Fraser. 1994. Ecological Structure among Migrant and Resident Seabirds of the Scotia--Weddell Confluence Region. *Journal of Animal Ecology* 63: 347–364.

Ambrosini, R., A. P. Møller, and N. Saino. 2009. A quantitative measure of migratory connectivity. *Journal of Theoretical Biology* 257: 203–211.

Astheimer, L. B., and C. R. Grau. 1985. The Timing and Energetic Consequences of Egg Formation in the Adélie Penguin. *The Condor* 87: 256–268.

Atkinson, A., S. L. Hill, E. A. Pakhomov, V. Siegel, C. S. Reiss, V. J. Loeb, D. K. Steinberg, et al. 2019. Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nature Climate Change* 9: 142–147.

Atkinson, A., D. A. Siegel, E. Pakhomov, and P. Rothery. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100–103.

Atkinson, A., V. Siegel, E. A. Pakhomov, P. Rothery, V. Loeb, R. M. Ross, L. B. Quetin, et al. 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series* 362: 1–23.

Ballard, G., V. Toniolo, D. G. Ainley, C. L. Parkinson, K. R. Arrigo, and P. N. Trathan. 2010. Responding to climate change: Adélie Penguins confront astronomical and ocean boundaries. *Ecology* 91: 2056–2069.

Barger, C. P., R. C. Young, A. Will, M. Ito, and A. S. Kitaysky. 2016. Resource partitioning between sympatric seabird species increases during chick-rearing. *Ecosphere* 7: e01447.

Barlow, K., I. Boyd, J. Croxall, K. Reid, I. Staniland, and A. Brierley. 2002. Are penguins and seals in competition for Antarctic krill at South Georgia? *Marine Biology* 140: 205–213.

Barrera-Oro, E. 2002. The role of fish in the Antarctic marine food web: differences between inshore and offshore waters in the southern Scotia Arc and west Antarctic Peninsula. *Antarctic Science* 14: 293–309.

Biuw, M., C. Lydersen, P. J. N. de Bruyn, A. Arriola, G. G. J. Hofmeyr, P. Kritzinger, and K. M. Kovacs. 2010. Long-range migration of a chinstrap penguin from Bouvetøya to Montagu Island, South Sandwich Islands. *Antarctic Science* 22: 157–162.

Bon, C., A. Della Penna, F. d'Ovidio, J. Y.P. Arnould, T. Poupart, and C.-A. Bost. 2015. Influence of oceanographic structures on foraging strategies: Macaroni penguins at Crozet Islands. *Movement Ecology* 3: 32.

Bowes, R. E., J. H. Thorp, and D. C. Reuman. 2017. Multidimensional metrics of niche space for use with diverse analytical techniques. *Scientific Reports* 7: 41599.

Brasso, R. L., M. J. Polito, H. J. Lynch, R. Naveen, and S. D. Emslie. 2012. Penguin eggshell membranes reflect homogeneity of mercury in the marine food web surrounding the Antarctic Peninsula. *Science of The Total Environment* 439: 165–171.

Calenge, C. 2015. adehabitatHR: Analysis of Habitat Selection by Animals. R package version 0.4.1.4. *http://CRAN.R-project.org/package=adehabitatHR*.

Carey, C. 2009. The impacts of climate change on the annual cycles of birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* 364: 3321–3330.

Ceia, F. R., J. A. Ramos, R. A. Phillips, Y. Cherel, D. C. Jones, R. P. Vieira, and J. C. Xavier. 2015. Analysis of stable isotope ratios in blood of tracked wandering albatrosses fails to distinguish a δ13C gradient within their winter foraging areas in the southwest Atlantic Ocean. *Rapid Communications in Mass Spectrometry* 29: 2328–2336.

Cherel, Y., and K. A. Hobson. 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Marine Ecology Progress Series* 329: 281–287.

Clay, T. A., A. Manica, P. G. Ryan, J. R. D. Silk, J. P. Croxall, L. Ireland, and R. A. Phillips. 2016. Proximate drivers of spatial segregation in non-breeding albatrosses. *Scientific Reports* 6: 29932.

Clewlow, H. L., A. Takahashi, S. Watanabe, S. C. Votier, R. Downie, and N. Ratcliffe. 2019. Niche partitioning of sympatric penguins by leapfrog foraging is resilient to climate change. *Journal of Animal Ecology* 88: 223–235.

Clucas, G. V., M. J. Dunn, G. Dyke, S. D. Emslie, H. Levy, R. Naveen, M. J. Polito, et al. 2014. A reversal of fortunes: climate change 'winners' and 'losers' in Antarctic Peninsula penguins. *Scientific Reports* 4.

Clucas, G. V., J. L. Younger, D. Kao, L. Emmerson, C. Southwell, B. Wienecke, A. D. Rogers, et al. 2018. Comparative population genomics reveals key barriers to dispersal in Southern Ocean penguins. *Molecular Ecology* 27: 4680–4697.

Copernicus Marine Environment Monitoring. 2018. Global Ocean Gridded Sea Surface Heights and Derived Variables (1993-Ongoing).

Croxall, J. P., K. Reid, and P. A. Prince. 1999. Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. *Marine Ecology Progress Series* 177: 115–131.

Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and Antarctic seabird populations. *Science* 297: 1510–1514.

Dadswell, M. J., A. D. Spares, J. M. Reader, and M. J. W. Stokesbury. 2010. The North Atlantic subpolar gyre and the marine migration of Atlantic salmon Salmo salar: the ‘Merry-Go-Round’ hypothesis. *Journal of Fish Biology* 77: 435–467.

Dehnhard, N., K. Ludynia, J. F. Masello, C. C. Voigt, R. A. R. McGill, and P. Quillfeldt. 2016. Plasticity in foraging behaviour and diet buffers effects of inter-annual environmental differences on chick growth and survival in southern rockhopper penguins Eudyptes chrysocome chrysocome. *Polar Biology* 39: 1627–1641.

Dimitrijević, D., V. H. Paiva, J. A. Ramos, J. Seco, F. R. Ceia, N. Chipev, T. Valente, et al. 2018. Isotopic niches of sympatric Gentoo and Chinstrap Penguins: evidence of competition for Antarctic krill? *Polar Biology*: 1–15.

Dray, S., A. Dufour, and J. Thioulouse. 2018. ade4: Analysis of Ecological Data: Exploratory and Euclidean Methods in Environmental Sciences. R package version 1.7-11.

Drent, R. H., G. Eichhorn, A. Flagstad, A. J. Van der Graaf, K. E. Litvin, and J. Stahl. 2007. Migratory connectivity in Arctic geese: spring stopovers are the weak links in meeting targets for breeding. *Journal of Ornithology* 148: 501–514.

Dunn, M. J., J. A. Jackson, S. Adlard, A. S. Lynnes, D. R. Briggs, D. Fox, and C. M. Waluda. 2016. Population Size and Decadal Trends of Three Penguin Species Nesting at Signy Island, South Orkney Islands. *PLOS ONE* 11: e0164025.

Emslie, S. D., and W. P. Patterson. 2007. Abrupt recent shift in δ13C and δ15N values in Adélie penguin eggshell in Antarctica. *Proceedings of the National Academy of Sciences* 104: 11666–11669.

Fieberg, J., and C. O. Kochanny. 2005. Quantifying Home-Range Overlap: The Importance of the Utilization Distribution. *The Journal of Wildlife Management* 69: 1346–1359.

Finch, T., S. J. Butler, A. M. A. Franco, and W. Cresswell. 2017. Low migratory connectivity is common in long-distance migrant birds. *Journal of Animal Ecology* 86: 662–673.

Forcada, J., and P. N. Trathan. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology* 15: 1618–1630.

Fraser, W. R., and W. Z. Trivelpiece. 1996. Factors Controlling the Distribution of Seabirds: Winter-Summer Heterogeneity in the Distribution of Adélie

Penguin Populations. Foundations for Ecological Research West of the Antarctic Peninsula, 257–272. American Geophysical Union (AGU).

Frederiksen, M., F. Daunt, M. P. Harris, and S. Wanless. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology* 77: 1020–1029.

Frederiksen, M., B. Moe, F. Daunt, R. A. Phillips, R. T. Barrett, M. I. Bogdanova, T. Boulinier, et al. 2012. Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions* 18: 530–542.

Freer, J. J., B. K. Mable, G. Clucas, A. D. Rogers, M. J. Polito, M. Dunn, R. Naveen, et al. 2015. Limited genetic differentiation among chinstrap penguin Pygoscelis colonies in the Scotia Arc and Western Antarctic Peninsula. *Polar Biology* 38: 1493–1502.

González-Solís, J., J. P. Croxall, D. Oro, and X. Ruiz. 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment* 5: 297–301.

Graham, B. S., P. L. Koch, S. D. Newsome, K. W. McMahon, and D. Aurioles. 2010. Using Isoscapes to Trace the Movements and Foraging Behavior of Top Predators in Oceanic Ecosystems. *In* J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu [eds.], Isoscapes: Understanding movement, pattern, and process on Earth through isotope mapping, 299–318. Springer Netherlands, Dordrecht.

Green, J. A., I. L. Boyd, A. J. Woakes, N. L. Warren, and P. J. Butler. 2009. Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin Eudyptes chrysolophus. *Journal of Avian Biology* 40: 529–538.

Hahn, S., B. J. Hoye, H. Korthals, and M. Klaassen. 2012. From Food to Offspring Down: Tissue-Specific Discrimination and Turn-Over of Stable Isotopes in Herbivorous Waterbirds and Other Avian Foraging Guilds. *PLOS ONE* 7: e30242.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80: 4–18.

Hijmans, R. J. 2017. Raster - R package version 2.6-7. *https://cran.r-project.org/web/packages/raster/vignettes/Raster.pdf*.

Hill, R. D. 1994. Theory of geolocation by light levels. In: Le Boeuf BJ, Laws RM (eds) Elephant seals: population ecology, behvaiour and physiology. *University of California Press, Berkeley, CA*: 227–236.

Hill, S. L., T. Phillips, and A. Atkinson. 2013. Potential Climate Change Effects on the Habitat of Antarctic Krill in the Weddell Quadrant of the Southern Ocean. *PLOS ONE* 8: e72246.

Hinke, J. T., M. J. Polito, M. E. Goebel, S. Jarvis, C. S. Reiss, S. R. Thorrold, W. Z. Trivelpiece, and G. M. Watters. 2015. Spatial and isotopic niche partitioning during winter in chinstrap and Adélie penguins from the South Shetland Islands. *Ecosphere* 6: 1–32.

Hinke, J. T., K. Salwicka, S. G. Trivelpiece, G. M. Watters, and W. Z. Trivelpiece. 2007. Divergent responses of *Pygoscelis* penguins reveal a common environmental driver. *Oecologia* 153: 845–855.

Hjeljord, O. 2001. Dispersal and migration in northern forest deer - are there unifying concepts? *Alces* 37: 353–370.

Hobson, K. A., and R. G. Clark. 1992. Assessing Avian Diets Using Stable Isotopes II: Factors Influencing Diet-Tissue Fractionation. *The Condor* 94: 189–197.

Jackson, A. L., R. Inger, A. C. Parnell, and S. Bearhop. 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* 80: 595–602.

Jackson, A. L., and A. C. Parnell. 2017. SIBER: Stable Isotope Bayesian Ellipses in R. R package version 2.1.3.

Layman, C. A., D. A. Arrington, C. G. Montaña, and D. M. Post. 2007. Can Stable Isotope Ratios Provide for Community-Wide Measures of Trophic Structure? *Ecology* 88: 42–48.

Liechti, F. 2006. Birds: blowin' by the wind? *Journal of Ornithology* 147: 202–211.

Lishman, G. S. 1985a. The comparative breeding biology of Adelie and Chinstrap Penguins Pygoscelis adeliae and P. antarctica at Signy Island, South Orkney Islands. *Ibis* 127: 84–99.

Lishman, G. S. 1985b. The food and feeding ecology of Adélie penguins (Pygoscelis adeliae) and Chinstrap penguins (P. antarctica) at Signy Island, South Orkney Islands. *Journal of Zoology* 205: 245–263.

Luschi, P. 2013. Long-Distance Animal Migrations in the Oceanic Environment: Orientation and Navigation Correlates. *International Scholarly Research Notices Zoology* 2013, Article ID 631839: 23 pages.

Lynch, H. J., R. Naveen, P. N. Trathan, and W. F. Fagan. 2012. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93: 1367–1377.

Lynch, H. J., R. White, R. Naveen, A. Black, M. S. Meixler, and W. F. Fagan. 2016. In stark contrast to widespread declines along the Scotia Arc, a survey of the South Sandwich Islands finds a robust seabird community. *Polar Biology* 39: 1615–1625.

Lynnes, A. S., K. Reid, and J. P. Croxall. 2004. Diet and reproductive success of Adélie and chinstrap penguins: linking response of predators to prey population dynamics. *Polar Biology* 27: 544–554.

Lynnes, A. S., K. Reid, J. Croxall, and P. Trathan. 2002. Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap penguins. *Marine Biology* 141: 1165–1174.

Lysy, M., A. D. Stasko, and H. Swanson. 2014. nicheROVER: (Niche) (R)egion and Niche (Over)lap Metrics for Multidimensional Ecological Niches. R package version 1.0. *https://cran.r-project.org/web/packages/nicheROVER/index.html*.

Mantel, N. 1967. The Detection of Disease Clustering and a Generalized Regression Approach. *Cancer Research* 27: 209–220.

Marshall, G. J., W. G. Rees, and J. A. Dowdeswell. 1993. Limitations imposed by cloud cover on multitemporal visible band satellite data sets from polar regions. *Annals of Glaciology* 17: 113–120.

Masello, J. F., R. Mundry, M. Poisbleau, L. Demongin, C. C. Voigt, M. Wikelski, and P. Quillfeldt. 2016. Diving seabirds share foraging space and time within and among species. *Ecosphere* 1: 1–28.

McGuire, L. P., and E. E. Fraser. 2014. Taxonomic diversity in the biology of migration. *Canadian Journal of Zoology* 92: 463–465.

Michalik, A., R. A. R. McGill, R. W. Furness, T. Eggers, H. J. van Noordwijk, and P. Quillfeldt. 2010. Black and white – does melanin change the bulk carbon and nitrogen isotope values of feathers? *Rapid Communications in Mass Spectrometry* 24: 875–878.

Miller, A. K., M. A. Kappes, S. G. Trivelpiece, and W. Z. Trivelpiece. 2010. Foraging-Niche Separation of Breeding Gentoo and Chinstrap Penguins, South Shetland Islands, Antarctica. *The Condor* 112: 683–695.

Montes-Hugo, M., S. C. Doney, H. W. Ducklow, W. Fraser, D. Martinson, S. E. Stammerjohn, and O. Schofield. 2009. Recent Changes in Phytoplankton Communities Associated with Rapid Regional Climate Change Along the Western Antarctic Peninsula. *Science* 323: 1470–1473.

Murphy, E. J., S. E. Thorpe, G. A. Tarling, J. L. Watkins, S. Fielding, and P. Underwood. 2017. Restricted regions of enhanced growth of Antarctic krill in the circumpolar Southern Ocean. *Scientific Reports* 7.

National Snow and Ice Data Center. 2018. Annual Antarctic Sea Ice Index [Updated daily; accessed on 09/08/2018].

Negrete, P., M. Sallaberry, G. Barceló, K. Maldonado, F. Perona, R. A. R. McGill, P. Quillfeldt, and P. Sabat. 2017. Temporal variation in isotopic composition of Pygoscelis penguins at Ardley Island, Antarctic: Are foraging habits impacted by environmental change? *Polar Biology* 40: 903–916.

Nicol, S., J. Foster, and S. Kawaguchi. 2012. The fishery for Antarctic krill – recent developments. *Fish and Fisheries* 13: 30–40.

Niemandt, C., K. M. Kovacs, C. Lydersen, B. M. Dyer, K. Isaksen, G. J. G. Hofmeyr, F. Mehlum, and P. J. N. de Bruyn. 2016. Chinstrap and macaroni penguin diet and demography at Nyrøysa, Bouvetøya. *Antarctic Science* 28: 91–100.

NOAA/ESRL/PSD Climate Data Repository. 2018. sst.wkmean.1990-present dataset. *https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html*.

Ocean Biology Processing Group. 2015. MODIS Aqua Level 3 Global Daily Mapped 4 km Chlorophyll a v2014.0. Ver. 2014.0. PO.DAAC, CA, USA. Data accessed: 25/01/2018. Website [accessed 25 January 2018].

Park, J., I.-S. Oh, H.-C. Kim, and S. Yoo. 2010. Variability of SeaWiFs chlorophyll-a in the southwest Atlantic sector of the Southern Ocean: Strong topographic effects and weak seasonality. *Deep Sea Research Part I: Oceanographic Research Papers* 57: 604–620.

Phillips, R. A., J. R. D. Silk, J. P. Croxall, V. Afanasyev, and D. R. Briggs. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* 266: 265–272.

Polito, M. J., S. Fisher, C. R. Tobias, and S. D. Emslie. 2009. Tissue-specific isotopic discrimination factors in gentoo penguin (Pygoscelis papua) egg components: Implications for dietary reconstruction using stable isotopes. *Journal of Experimental Marine Biology and Ecology* 372: 106–112.

Polito, M. J., J. T. Hinke, T. Hart, M. Santos, L. A. Houghton, and S. R. Thorrold. 2017. Stable isotope analyses of feather amino acids identify penguin migration strategies at ocean basin scales. *Biology Letters* 13: 20170241.

Polito, M. J., H. J. Lynch, R. Naveen, and S. D. Emslie. 2011. Stable isotopes reveal regional heterogeneity in the pre-breeding distribution and diets of sympatrically breeding Pygoscelis spp. penguins. *Marine Ecology Progress Series* 421: 265–277.

Polito, M. J., W. Z. Trivelpiece, W. P. Patterson, N. J. Karnovsky, C. S. Reiss, and S. D. Emslie. 2015. Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of *Pygoscelis* penguins. *Marine Ecology Progress Series* 519: 221–237.

Pomilla, C., and H. C. Rosenbaum. 2005. Against the current: an inter-oceanic whale migration event. *Biology Letters* 1: 476–479.

Price, H. J., K. R. Boyd, and C. M. Boyd. 1988. Omnivorous feeding behavior of the Antarctic krill Euphausia superba. *Marine Biology* 97: 67–77.

Purich, A., W. Cai, M. H. England, and T. Cowan. 2016. Evidence for link between modelled trends in Antarctic sea ice and underestimated westerly wind changes. *Nature Communications* 7: 10409.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. *URL https://www.R-project.org/*.

Ramos, R., V. Sanz, T. Militão, J. Bried, V. C. Neves, M. Biscoito, R. A. Phillips, et al. 2015. Leapfrog migration and habitat preferences of a small oceanic seabird, Bulwer's petrel (Bulweria bulwerii). *Journal of Biogeography* 42: 1651–1664.

Ratcliffe, N., S. Crofts, R. Brown, A. M. M. Baylis, S. Adlard, C. Horswill, H. Venables, et al. 2014. Love thy neighbour or opposites attract? Patterns of spatial segregation and association among crested penguin populations during winter. *Journal of Biogeography* 41: 1183–1192.

Ratcliffe, N., A. Takahashi, C. Oulton, M. Fukuda, B. Fry, S. Crofts, R. Brown, et al. 2014. A leg-band for mounting geolocator tags on penguins. *Marine Ornithology* 42: 23–26.

Ratcliffe, N., and P. Trathan. 2012. A review of the diet and at-sea distribution of penguins breeding within the CAMLR Convention Area. *CCAMLR Science* 19: 75–114.

Sánchez, S., R. D. Reina, A. Kato, Y. Ropert-Coudert, C. Cavallo, G. C. Hays, and A. Chiaradia. 2018. Within-colony spatial segregation leads to foraging behaviour variation in a seabird. *Marine Ecology Progress Series* 606: 215–230.

Sherley, R. B., K. Ludynia, B. M. Dyer, T. Lamont, A. B. Makhado, J.-P. Roux, K. L. Scales, et al. 2017. Metapopulation Tracking Juvenile Penguins Reveals an Ecosystem-wide Ecological Trap. *Current Biology* 27: 1–6.

Silk, J. R. D., S. E. Thorpe, S. Fielding, E. J. Murphy, P. N. Trathan, J. L. Watkins, and S. L. Hill. 2016. Environmental correlates of Antarctic krill distribution in the Scotia Sea and southern Drake Passage. *ICES Journal of Marine Science* 73: 2288–2301.

Takahashi, A., M. J. Dunn, P. N. Trathan, K. Sato, Y. Naito, and J. P. Croxall. 2003. Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. *Marine Ecology Progress Series* 250: 279–289.

Thiebot, J.-B., Y. Cherel, R. J. M. Crawford, A. B. Makhado, P. N. Trathan, D. Pinaud, and C.-A. Bost. 2013. A Space Oddity: Geographic and Specific Modulation of Migration in Eudyptes Penguins. *PLOS ONE* 8: e71429.

Thiebot, J.-B., Y. Cherel, P. N. Trathan, and C.-A. Bost. 2012. Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. *Ecology* 93: 122–130.

Thiebot, J.-B., Y. Cherel, P. N. Trathan, and C.-A. Bost. 2011. Inter-population segregation in the wintering areas of macaroni penguins. *Marine Ecology Progress Series* 421: 279–290.

Tranquilla, L. A. M., W. A. Montevecchi, A. Hedd, D. A. Fifield, C. M. Burke, P. A. Smith, P. M. Regular, et al. 2013. Multiple-colony winter habitat use by murres Uria spp. in the Northwest Atlantic Ocean: implications for marine risk assessment. *Marine Ecology Progress Series* 472: 287–303.

Trierweiler, C., R. H. G. Klaassen, R. H. Drent, K.-M. Exo, J. Komdeur, F. Bairlein, and B. J. Koks. 2014. Migratory connectivity and population-specific migration routes in a long-distance migratory bird. *Proceedings of the Royal Society of London B: Biological Sciences* 281: 20132897.

Trivelpiece, W. Z., S. Buckelew, C. Reiss, and S. G. Trivelpiece. 2007. The winter distribution of chinstrap penguins from two breeding sites in the South Shetland Islands of Antarctica. *Polar Biology* 30: 1231–1237.

Trivelpiece, W. Z., J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences* 108: 7625–7628.

Turner, T. F., M. L. Collyer, and T. J. Krabbenhoft. 2010. A general hypothesis-testing framework for stable isotope ratios in ecological studies. *Ecology* 91: 2227–2233.

Venables, H., M. P. Meredith, A. Atkinson, and P. Ward. 2012. Fronts and habitat zones in the Scotia Sea. *Deep Sea Research Part II: Topical Studies in Oceanography* 59–60: 14–24.

Wakefield, E. D., T. W. Bodey, S. Bearhop, J. Blackburn, K. Colhoun, R. Davies, R. G. Dwyer, et al. 2013. Space Partitioning Without Territoriality in Gannets. *Science* 341: 68–70.

Walsberg, G. E., D. S. Farner, and J. R. King. 1983. Avian ecological energetics. Avian biology, 161–220. Academic Press, New York.

Waluda, C. M., S. L. Hill, H. J. Peat, and P. N. Trathan. 2017. Long-term variability in the diet and reproductive performance of penguins at Bird Island, South Georgia. *Marine Biology* 164: 39.

Webster, M. S., P. P. Marra, S. M. Haig, S. Bensch, and R. T. Holmes. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17: 76–83.

Whitehead, T. O., M. Connan, Y. Ropert-Coudert, and P. G. Ryan. 2017. Subtle but significant segregation in the feeding ecology of sympatric penguins during the critical pre-moult period. *Marine Ecology Progress Series* 565: 227–236.

Whiteman, J. P., E. A. Elliott Smith, A. C. Besser, and S. D. Newsome. 2019. A Guide to Using Compound-Specific Stable Isotope Analysis to Study the Fates of Molecules in Organisms and Ecosystems. *Diversity* 11: 8.

Wickham, H., and W. Chang. 2016. ggplot2: Create Elegant Data Visualisations Using the Grammar of Graphics. R package version 2.2.1. *https://cran.r-project.org/web/packages/ggplot2/index.html*.

Williams, T. D. 1991. Foraging ecology and diet of Gentoo Penguins Pygoscelis papua at South Georgia during winter and an assessment of their winter prey consumption. *Ibis* 133: 3–13.

Williams, T. D. 1995. The Penguins: Spheniscidae. Oxford University Press, Oxford.

Wilson, R. P. 2010. Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Functional Ecology* 24: 646–657.

Wotherspoon, S. 2014. BAStag: Basic data processing for British Antarctic Survey archival tags. R package: *https://github.com/SWotherspoon/BAStag*.

Wotherspoon, S., M. Sumner, and L. Lisovski. 2016. SGAT: Solar/satellite Geolocation for Animal Tracking - R package version 0.1.3. *https://github.com/SWotherspoon/SGAT*.

Chapter 4 – *Investigating the effect of sea ice on breeding and foraging performance metrics of Pygoscelis penguins at the South Orkney Islands*

H.L. Clewlow, A. Takahashi, S. Watanabe, and N. Ratcliffe

Author contributions

The framework for this study was developed by HLC and NR. HLC processed all data and carried out all statistical analyses. Tracking data from 2008 was collected and initially processed by AT and SW and first published in Clewlow et al. (2019).

ABSTRACT

Rapid warming in West Antarctica is associated large-scale population and extent. The "sea ice hypothesis" states that the loss of sea ice has led to declines in numbers of the "ice-loving" Adélie (*Pygoscelis adeliae*) and "ice tolerant" chinstrap (*Pygoscelis antarctica*) penguins and increases in the numbers and range of the "ice averse" gentoo penguin (*Pygoscelis papua*). Based on this hypothesis and values in published literature, we predicted that Adélies will have a sea ice optima of around 20% for breeding and foraging performance, chinstrap performance will remain constant before decreasing at sea ice concentrations (SIC) below 20% and gentoo performance will decline steeply as SIC increases. We tested these predictions in the WAP region for the first time by modelling penguin performance metrics collected on Signy Island, South Orkney Islands, in relation to concentrations of pack ice within the foraging ranges of each species' during the guard stage. All metrics showed substantial species and interannual variability but SIC only explained a significant amount of the variation in the cases of trip duration and fledging mass. In both cases, the relationships were linear and only in the case of trip duration did the rate of response differ according to species, with the Adélie response being steeper than that of chinstraps. Our findings do not support the hypotheses that the three *Pygoscelis* penguin species have differential tolerances of sea ice, nor that any species have an optimum SIC in this region. Alternative explanations for the contrasting populations trends of the three species here and elsewhere in West Antarctica need to be sought, which are

likely to include regional changes in food availability and environmental conditions.

1 | INTRODUCTION

Over recent decades, ecosystems across the globe have been experiencing large-scale shifts in climate and these shifts are forecast to continue into the next century (Intergovernmental Panel on Climate Change, 1996, 2007). There is abundant evidence that species are responding to these shifts, causing changes to their distributions, phenology and population dynamics (Walther et al., 2002; Parmesan, 2006), contributing to a 60% decrease in global biodiversity since 1970 (Grooten and Almond, 2018). Climate change is highly variable between regions and ecosystems, meaning the type and magnitude of impacts on species differs geographically (Intergovernmental Panel on Climate Change, 2007).

The Polar regions are experiencing some of the most rapid rates of climate change globally, and temperatures here have already increased by twice as much as the global average (Intergovernmental Panel on Climate Change, 2007). These dramatic climate changes have produced concurrent declines in sea ice duration and extent (Stammerjohn, Martinson, Smith and Iannuzzi, 2008; Overland and Wang, 2010), snow and frozen ground layers (Intergovernmental Panel on Climate Change, 2007). Particularly harsh climates and strong seasonality define the Polar Regions, meaning species are highly adapted to a narrow optimal range of environmental conditions and any conditions outside of this range will impact their breeding success and even their survival (Clarke, 1991; Clarke et al., 2007; Milazzo et al., 2013). Therefore, the effects of climate change on species are exacerbated in these regions (Parmesan, 2006; Intergovernmental Panel on Climate Change, 2007).

Sea ice is a significant driver of biogeochemical cycles and thus crucial to the functioning of Polar ecosystems (Post et al., 2013; Wang et al., 2014). The melting of sea ice in spring releases nutrients that trigger phytoplankton blooms and nutrient cycling (Wang et al., 2014). Additionally, sea ice provides a habitat for microalgae and bacteria (Thomas and Dieckmann, 2002), which support pagophilic (ice-loving) fish and crustaceans, including Antarctic krill (*Euphausia superba;* hereafter krill) larvae (Daly and Macaulay, 1988; Atkinson et al., 2004). Air-breathing predators use sea ice as a platform to haul out on, which helps them to reduce energy expenditure and avoid predators (Watanabe et al., 2012), although high coverage of sea ice may negatively affect their foraging by acting as a physical barrier between them and their prey (Clarke et al., 2006; Massom et al., 2009; Ropert-Coudert et al., 2018). These opposing drivers may result in optimal concentrations of sea ice for foraging and demography, whose peaks will vary between species according to their ecological requirements (Kovacs et al., 2011; Post et al., 2013). There is evidence of a sea ice optima in numerous Antarctic seabirds (see Barbraud et al., 2012 for review) and in Arctic seabirds, including, Brünnich's guillemot (*Uria lomvia*) (Gaston, Gilchrist and Hipfner, 2005; Smith and Gaston, 2012) and black-legged kittiwake (*Rissa tridactyla*) (Gaston, Gilchrist and Mallory, 2005) and Arctic marine mammals, including whales, seals and polar bears (*Ursus maritimus*) (Laidre et al., 2008; Moore and Huntington, 2008). This suggests that a sea ice optima for population growth is a widespread phenomenon in high latitude predators (see Barbraud et al., 2012 for review).

The rapid climate changes occurring in West Antarctica are causing the three species of *Pygoscelis* penguins to experience contrasting trends in abundance and range, with Adélie (*Pygoscelis* adeliae; hereafter Adélies) and chinstrap penguins (*Pygoscelis antarctica*; hereafter chinstraps) declining by more than 40% over the last four decades while gentoo penguin (*Pygoscelis papua*; hereafter gentoos) populations increased by more than 255% (Lynch et al., 2012; Dunn et al., 2016). The "sea ice hypothesis" proposes that these patterns are driven by the reduction in sea ice extent across the Western Antarctic Peninsula (WAP), which have benefited the "ice averse" gentoos but caused declines of the "ice loving" Adélies and "ice tolerant" chinstraps (Fraser et al. 1992, Trivelpiece et al. 2011). This hypothesis is based on the different biogeography of the species, with gentoos having a more northerly distribution that includes the ice-free sub Antarctic Islands, Adélies being found around the Antarctic continent including areas with high sea ice concentrations (SIC) and chinstraps being intermediate (Borboroglu & Boersma, 2013). Quantification of chick-rearing habitat within the WAP also finds that Adélie colonies have higher SIC within their foraging ranges compared to the other two species (Cimino et al. 2013), while habitat preferences during the non-breeding period are also consistent with Adélies having a greater affinity for sea ice than chinstraps or gentoos (Hinke et al., 2015, 2017). The responses of Adélie penguins to varying

SIC are well documented and include effects upon foraging performance (Kato et al., 2002; Ballard et al., 2010), breeding success (Clarke et al., 2002; Emmerson and Southwell, 2008; Le Guen et al., 2018) and overwinter survival (Ballerini et al., 2009) with evidence for an optimum value around 20% (Ballard et al., 2010; Barbraud et al., 2015; Le Guen et al., 2018). However, these studies are mostly from east Antarctica and are often confounded by the effects of huge icebergs (Dugger et al., 2014) or weather, so the effects of sea ice loss on Adélies in the WAP region are less clear. Studies of the effects of SIC on chinstrap breeding success are sparse and inconsistent (Lishman, 1985; Trathan et al., 1996; Rombolá et al., 2003) and we are not aware of any that document its effects on that of gentoos. The behavioural and demographic responses of the three species to variations in SIC within the WAP therefore require further investigation in order to test the predictions of the sea ice hypothesis within the region in which it was formulated.

In order to fully understand the mechanisms underlying the influence of SIC on annual breeding productivity, we need to understand its influence on foraging performance metrics including foraging trip duration, diet composition and fledging mass. The metrics link together as follows, long foraging trips combined with small or low-quality meals will reduce food provisioning rate, chick growth and ultimately fledging mass, which in turn will lead to higher chick mortality and therefore, lower breeding productivity. Previous studies on Adélies have found foraging trip duration and distance to increase with increasing SIC, even in the presence of a polynya (Clarke et al., 2006), as the ice impairs access to open water needed for foraging and walking across the ice is slower than swimming (Pinshow et al., 1977). This shift may also be driven by the influence of SIC on krill, the primary prey of all three species in the WAP region (Ratcliffe and Trathan, 2012), abundance and distribution (Atkinson et al., 2008), and thus the proportion of the species in penguins' diet. Obtaining adequate amounts of high calorific prey is crucial for chick survival because it is strongly dependant on them attaining optimal fledging mass (Salihoglu et al., 2001; Croll et al., 2006).

Based on the presumed ice tolerance classifications for the three species, we can make some predictions about their respective sea ice optima for breeding and foraging performance metrics. Adélies will have a sea ice optima as quantified in previous studies (~20%) (Barbraud et al., 2015; Le Guen et al., 2018), chinstrap productivity should remain level before decreasing at low-moderate levels of sea ice, likely well below Adélies' reported optima, and gentoos productivity will decline steeply as sea ice increases (Fig. 1). In this chapter we will test these predictions on Adélie, chinstraps and gentoos breeding sympatrically on Signy Island, South Orkney Islands (60°42'S, 45°36'W), the first direct test of the 'sea ice hypothesis', and attempt to quantify each species' sea ice optima for the first time in this region. This archipelago lies to the north of the marginal ice zone during the austral summer, but persistent southerly winds can result in dense pack ice, originating from the Weddell Sea, collecting on south-facing shorelines during the penguin's breeding season. We monitored breeding productivity, trip duration, diet composition and fledging weights and compared them to annual SIC to determine the influence of SIC on these species in this region.

2 | MATERIALS AND METHODS

2.1 | Sea ice concentration in foraging area

Sea ice concentration (SIC) were obtained from the NOAA/NSIDC passive microwave satellite derived dataset (NOAA OI SST V2) (Reynolds et al., 2018) for each species' guard stage, December to January for Adélies and gentoos and January to February for chinstraps (Black, 2015) (Pers. Obs.), from 1998/1999 to 2016/2017. The 0.25 x 0.25 degree gridded data was rasterised using the raster (Hijmans, 2017) package in the statistical program 'R' (R Core Team, 2015), allowing SIC values to be extracted from a 30km buffer region. This region size was selected based on breeding season foraging ranges (Clewlow et al., 2019), and the findings of Emmerson et al. (2008) that nearshore SIC was the most influential on breeding success, and was centred on the breeding colonies at Gourlay Peninsula for Adélies and chinstraps and on the breeding colonies at North Point for gentoos (Fig. 2). Extracted values, expressed as a percentage of the area covered by sea ice, were averaged for each year.

2.2 | Breeding productivity

The breeding cycle of all three penguin species was monitored annually from the 1998/1999 breeding season to the 2016/2017 breeding season, with data missing for the 2010/2011 season due to logistical issues. Experienced observers carried out direct ground counts of 9 Adélie, 11 chinstrap and 10 gentoo subcolonies using methods standardised by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Programme (CEMP) (CCAMLR, 2014). Breeding productivity was defined as the average number of chicks fledged per breeding pair with eggs, aggregated at the level of sub-colony for Adélie and chinstrap and across all subcolonies for gentoos (since their subcolonies are close together and fledged chicks move among them). The number of breeding pairs was established in November for Adélies and gentoos and in December for chinstraps. The number of fledglings was counted annually in early January for Adélies, late January/early February for gentoos and late February/early March for chinstraps.

2.3 | Diet composition

Adult foraging performance was investigated using diet samples and fledging mass. Diet samples were collected from the 2001/2002 breeding season to the 2016/2017 breeding season and fledging weights were collected from the 1996/1997 breeding season to 2016/2017 breeding season. Data were only available for Adélies and chinstraps as the diet sampling technique is not appropriate for gentoo penguins and their fledging weights were unavailable.

Diet samples were collected each breeding season from adult birds, as soon as they returned from foraging trips, during their respective guard stages of breeding, using the stomach flushing technique (also termed stomach pumping or gastric lavage) as standardised by CCAMLR (2014). Samples were collected from multiple individuals each year (Samples per year – Adélie: 34±9 (mean±SD); chinstrap: 35±6). Information on the proportion of krill was obtained from each diet sample. Results are unlikely to have been affected by digestion before sampling as birds are able to preserve food for their chicks in their stomach for long periods, up to three weeks in some penguin species (Gauthier-Clerc et al., 2000).

Adélie and chinstrap chicks were weighed to the nearest 0.1g using a 5kg Pesola spring-scale (Pesola AG, Feusisberg, Switzerland) just prior to fledging (Samples per year – Adélie: 247±94; chinstrap: 207±78) following the CCAMLR (2014) standardised methods.

2.4 | Foraging trip duration

Breeding Adélie and chinstrap penguins were tagged with GPS loggers (Little Leonardo GPL-380DT, Tokyo, Japan) during 2007/08 and Fastloc2 GPS loggers (Sirtrack, Havelock, New Zealand) during guard stage in four breeding seasons (2007/2008, 2011/2012, 2013/2014 and 2015/2016), totalling 92 Adélies and 42 chinstraps (see Table S1 in Chapter 2 for number of samples per year). Gentoos were not tagged due to the logistical demands of accessing their breeding colonies from the Signy Island Base. GPS tags were attached to the central back feathers using two-part epoxy resin and waterproof tape (Tesa, Hamburg, Germany). Fastloc2 GPS weigh 39.9g and measure 65mm long, 28mm wide and 15mm deep, equating to an estimated surface area of 6430mm^2 and Little Leonardo tags weigh 92g and measure 58 mm long, 28 mm wide and 20 mm deep, equating to an estimated surface area of 6688mm^2. Surface areas are provided for information only and estimates are based on a basic rectangle and thus do not account for the aerodynamic angle of the front of the tags, which differ between the two models. Further details of tagging and processing regime can be found in Chapter 2. The duration of each foraging trip (hours) was calculated using the move package (Kranstauber and Smolla, 2016) in ‘R’ (R Core Team, 2015).

2.5 | Analytical methods

The breeding and foraging performance metrics, specifically foraging trip duration, proportion of krill in diet, fledging mass and breeding productivity, of Pygoscelis penguins were analysed using linear, generalised linear or additive models (GAM), all fitted using the mgcv package (Wood, 2018). Explanatory variables were year and species as factors, sea ice concentration (SIC) as a covariate and, in the case of the model of breeding productivity, sub-colony as a random intercept. The effects of SIC were fitted as a smooth term using a cubic regression spline with three knots: this allowed fitting of the quadratic relationship assumed for optima, whilst providing the flexibility to fit linear or asymptotic relationships of the forms depicted in Fig 1. For productivity, the response variable was the number of fledglings with the natural log of the number of pairs specified as an offset, which expresses the response as a ratio (Crawley, 2002). This was modelled with a negative binomial distribution (owing to over dispersion around the Poisson distribution) and a log link. Fledging mass and trip duration responses were modelled using an identity link and normal errors. The proportion of krill in the diet was modelled with beta errors and a logit link.

For each response, the global time and species dependent model (Year*Species) was simplified by fitting additive time and species effects, removing time and species terms altogether or replacing the time term with the time-dependent covariate of SIC (which could be specific to, or common across, species) to determine the best fit model. We used Akiake's Information Criteria (AIC_c) to guide model selection: the minimum adequate model was that with the lowest AIC score, unless a simpler model differed from this by less than two AIC units. This procedure was followed to identify both the minimum adequate time-dependent model and SIC model.

Where models that included an effect of SIC were supported, analysis of deviance (ANODEV) was used to determine the proportion of the annual variability explained, calculated as $(Dev_c\text{-}Dev_x)/(Dev_c\text{-}Dev_t)$, where c, x, and t indicate models with no time dependence (sampling colony only), with the SIC covariate and full time dependence (sampling year), respectively (Frederiksen et al., 2008).

3 | RESULTS

Overall, SIC during the species' guard stages showed substantial annual variation, ranging from 0 to 69% concentration. Chinstraps experienced 11 ice free years compared to 9 for the other two species, likely due to the former's later breeding phenology. Chinstraps also experienced no years with greater than 50% SIC in comparison to four years for Adélies and three years for gentoos.

3.1 | Trip duration

Modelling of annual variation in trip duration found that the minimum adequate model consisted of the interaction between year and species, as removing either of these variables caused an increase in AIC (Table 1). Trip durations differed between years and between species, with Adélies consistently undertaking longer trips, on average, than chinstraps (Table 2). Trips were relatively short in 2008 and 2012, intermediate in 2014 and longest in 2016. Both species had similar trip durations in 2008 and 2012 but Adélie trips were longer in 2014 and 2016 (Table 2).

Modelling of the effect of SIC on trip duration found that the minimum adequate model was the global model (Year*Species) and removing other variables caused an increase in AIC (Table 1). Both species displayed a linear reduction in trip duration as SIC increased (Fig. 3). No trip duration data were available for Adélies in SIC values under 40% so it is uncertain whether the linear trend continues in years when SIC is low (Fig. 3). ANODEV showed that SIC explained 75% of the annual variability in trip durations across the two species.

Table 1 - Annual variation in trip duration (hours) and the effect of sea ice concentration (SIC), where t is year, s is species, x is SIC, K is the number of model parameters and ΔAICc is the difference in AICc between the model in question and the best fit model.

Model/parameter	**ΔAIC$_c$**	**QDeviance**	**K**
t*s	0	592.86	8
t+s	1.77	607.93	5
s+x+(s*x)	10.66	611.74	8
s+x	11.09	621.11	4
t	20.42	620.78	4
x	26.28	633.63	3
Null model	52.46	648.33	1
s	53.9	645.37	2

Table 2 – Mean annual trip durations and standard deviations for Adélies and chinstraps

Species	**Year**	**Mean±SD**
Adélie	2008	13.3±7.6
chinstrap		8.7±8.1
Adélie	2012	23.0±11.8
chinstrap		10.0±9.4

Adélie	2014	55.8±43.9
chinstrap		9.5±5.3
Adélie	2016	82.4±49.7
chinstrap		36.8±37.4

3.2 | Diet composition

The annual variation in the percentage of krill in diet samples was found to be best explained by the global model, consisting of the interaction between year and species (Table 3). Removing year and species and an additive model of the two caused AIC values to increase. Both species fed on similar diets (Fig. 4), characterised by very high krill composition, up until 2012 with the exception of 2010 (when krill declined in diets of both species). From 2013 diet compositions of the two species uncouple and Adélies start to feed on alternative prey, particularly in 2014, 2016 and 2017 (Fig. 4). The proportion of krill in chinstraps' diets was lower in 2014 and 2017 but not in 2016. Overall, chinstraps consumed a slightly greater proportion of krill on average (0.98±0.08) than Adélies (0.95±0.17; Fig. 4).

There was no support for an effect of SIC on diet composition, as shown by AIC. The AIC for the covariate models were 12.19 units higher than that with the species factor alone. The models including the SIC covariate were a poor fit to annual diet composition estimates and did not explain the low krill composition of diets in 2014, 2016 and 2017 (Fig. 5).

Table 3 - Annual variation in percentage krill in diet samples models and the effect of sea ice concentration (SIC), where t is year, s is species, x is SIC, K is the number of model parameters and ΔAICc is the difference in AICc between the model in question and the best fit model.

Model/parameter	**ΔAIC_c**	**QDeviance**	**K**
t*s	0	-20315.60	32
s+x	1.70	-20303.40	4
s+x+(s*x)	2.86	-20302.90	8
x	15.54	-20297.20	3
t+s	39201.21	-669.39	17

t	39221.84	-662.19	16
s	39309.35	-647.92	2
Null model	39326.32	-642.35	1

3.3 | Fledging mass

The best fit model contained all factors from the global model, as removing species or year increased the model AIC and the interactive model of year and species produced a lower model AIC than the additive interaction between the factors (Table 4). Chinstrap fledglings (3.07±0.48kg) were heavier than Adélies (2.72±0.46kg) throughout the study period, equating to 0.4kg on average. Chinstrap fledglings were lighter in 2005 and 2010 relative to Adélies, and Adélies were heavier relative to chinstraps in 2013 and 2016 (Fig. 4).

The minimal adequate covariate model, comprising an additive effect of species and SIC upon fledging mass was supported by AIC values. The intercept for chinstraps (i.e. fledging mass in the absence of sea ice) was 0.39kg higher than that of Adélies and both species weight increased slightly with increasing SIC (Fig. 6). ANODEV showed that only 11% of the annual variability in fledging mass across both species was explained by SIC.

Table 4 – Annual variation in fledging mass models and the effect of sea ice concentration (SIC), where t is year, s is species, x is SIC, K is the number of model parameters and ΔAICc is the difference in AICc between the model in question and the best fit model.

Model/parameter	**ΔAIC_c**	**QDeviance**	**K**
t*s	0	5472.15	42
t+s	745.86	5820.01	22
s+x+(s*x)	2224.63	6502.12	8
s+x	2291.67	6557.89	4
t	2352.74	6618.96	21
s	2544.86	6681.01	2

x	3817.52	7318.74	3
Null model	3829.86	7320.70	1

3.4 | Breeding productivity

The best fit model contained all factors from the global model, as removing colony increased the model AIC, and the interaction between year and species produced a lower model AIC than the additive one (Table 5). Adélies and chinstraps produced a similar number of chicks until 2007 after which their annual variations differed. Gentoos experienced particularly low productivity in 2010, 2013 and 2016. Chinstrap productivity was also low in 2013 and 2016, and Adélie productivity was low in 2009 and 2010 (Fig. 4). The mean number of chicks produced each year by Adélie pairs was 0.74±0.46 (mean±SD), chinstrap pairs produced 0.73±0.43 and gentoo pairs produced 0.99±0.45.

The smoothed model terms did not provide any support for a significant relationship between productivity and SIC, either across species or within any one of them. The model to the data was a poor fit, with high non-random deviance owing to years of poor productivity that were not explained by SIC (Table 5). The poor fit of the species-specific smooths of SIC to the annual variability in productivity is shown in Fig. 7 and although the smooths show some similarities to the hypothetical relationships in (Fig. 1) we emphasise that these are non-significant and, therefore, could have arisen by chance.

Table 5 – Annual variation in breeding productivity models and effect of sea ice concentration (SIC), where t is year, s is species, x is SIC, K is the number of model parameters and ΔAICc is the difference in AICc between the model in question and the best fit model.

Model/parameter	ΔAIC_c	QDeviance	K
t*s+Colony	0	1517.35	55
t+s+Colony	115.84	1590.14	21
t*s	121.18	1548.35	54
s+x+(s*x)+Colony	143.55	1602.06	12
s+x+Colony	146.89	1604.01	6

x+Colony	146.99	1603.85	4
1+Colony	156.3	1605.47	2

4 | DISCUSSION

Our results highlight the substantial annual variability in breeding productivity, fledging mass, diet composition and foraging trip duration between years for these species. We find little support for our predictions of differing sea ice tolerance between species and no evidence for a sea ice optima in any species. Therefore, we provide compelling evidence that the ‘sea ice hypothesis’ is not applicable to the Pygoscelis species in the WAP region.

4.1 | Links between breeding and foraging performance metrics

Annual breeding productivity has previously been shown to vary depending upon a number of factors including foraging trip duration, meal mass (amount of food) and fledging mass (Clarke et al., 2002; Rombolá et al., 2003). Basically, long foraging trips combined with small or low-quality meals will reduce food provisioning rate, chick growth and ultimately fledging mass, which in turn will lead to higher chick mortality and lower productivity.

Our results show that foraging trip duration differs greatly between years and between species. Longer foraging trips are correlated with a greater mass of krill caught (Rombolá et al., 2003) and this is particularly important during the later stages of breeding as chicks require regular meals of high calorific prey to ensure they attain optimal fledging mass, which greatly increases their chances of survival (Salihoglu et al., 2001; Croll et al., 2006). Therefore, fledging mass can be used as an indicator of the quantity and quality of food available to adults: chicks fed small krill with low calorific value will have a lower weight at fledging than those fed larger krill with higher calorific values (Salihoglu et al., 2001). However, in years of poor food supply, selective mortality of chicks with low body mass can, paradoxically, mean that fledging mass can be higher in years of poor food supply (Williams and Croxall, 1990; Bost and Jouventin, 1991). Adélie fledglings at our study colonies weighed slightly less than the optimal fledging mass (2.8kg-3.2kg) calculated at the highly studied South Shetlands archipelago (Salihoglu et al., 2001), likely contributing to low breeding productivity. Breeding population size has also been identified as a driver of chick mass, with a negative relationship between population size and chick mass, a decrease of 3gr with every 1,000 breeding pair increase in colony size, in multiple Adélie colonies, accounting for 9% of the global population (Dugger et al., 2014). The opposite trend was observed at our study site, but the population sizes are likely too similar, c. 2,200 pairs of Adélies to ~1,400 pairs of chinstraps (Dunn et al., 2016), to induce this density-dependence driven pattern. There were only two years, 2013 and 2016, where chinstrap chicks had a lower average weight than Adélie chicks and during these years the proportion of krill in Adélies diet was lower than average. This may be because Adélies are known to shift prey type when krill quality or abundance is reduced (Ridoux and Offredo, 1989; Ainley et al., 2003) but chinstraps appear to be krill specialists across their range (Lishman, 1985; Takahashi et al., 2003; Lynnes et al., 2004; Ratcliffe and Trathan, 2012; Polito et al., 2015; Niemandt et al., 2016; Dimitrijević et al., 2018).

4.2 | Responses to SIC

We predicted that SIC would be important in explaining the substantial annual variations in the breeding and foraging performance metrics and differences in patterns among the species. Sea-ice variation has been widely cited as the major mechanism mediating the impacts of climate change in the polar regions, influencing marine and terrestrial ecological dynamics (Post et al., 2013). Many studies have identified sea ice as a major driver of penguin demographic change (Spurr, 1975; Lishman, 1985; Barbraud and Weimerskirch, 2001; Clarke et al., 2006; Forcada et al., 2006; Emmerson and Southwell, 2008; Ballerini et al., 2009; Forcada and Trathan, 2009; Barbraud et al., 2015; Le Guen et al., 2018). In contrast to previous work, our models did not find SIC to have any effect on breeding productivity or diet composition, highlighting the complexity of the connections between SIC and penguins. This discrepancy is likely due to differing sea ice conditions between East, where all previous studies were carried out, and West Antarctica, meaning that the way the species utilise and interact with the sea ice is very different. At our study site, the sea ice conditions are largely driven by the seasonal cycle, as the archipelago is located near the northern extent of the winter pack-ice. In spring, pack-ice retreats westwards and southwards away from the islands (Parkinson, 1992) and fast-ice can remain for around 14 days after the pack-ice retreat (Murphy et al., 2014). This fast-ice usually breaks out in mid-October (Murphy et al., 1995), meaning that the sea ice present during the chick rearing period comprises brash-ice blown up from the Weddell Sea, which becomes trapped on the south coast of Coronation Island to form dense pack-ice (Pers. Obs.). A similar situation occurs at other archipelagos in the region (Massom et al., 2008), particularly the South Shetland Islands (Trivelpiece et al., 1987).

Foraging trip duration was found to be strongly influenced by SIC at our study colony, explaining 75% of annual variation, with both species undertaking shorter trips when SIC is high. Sea ice conditions vary greatly across Antarctica, as it is a large continent (Stammerjohn, Martinson, Smith, Yuan, et al., 2008). In East Antarctica fast-ice in summer is more prevalent, whereas in the WAP/Scotia Sea region pack-ice is the dominant type (Stammerjohn et al., 2012). This means that penguins in East Antarctica are highly reliant on polynyas (open water surrounded by sea ice) for foraging (Raymond et al., 2015). Pack-ice is more challenging for penguins to walk across but there are often more holes in the pack, allowing birds to access the water (Pers. Obs.). Most importantly, however, is the distribution of ice in relation to the colony, with high SIC nearshore negatively effecting penguin breeding but the same SIC offshore can be beneficial as it provides penguins with haul outs for predator avoidance and rest and krill is usually more abundant along the ice edge (Brierley et al., 2002; Emmerson and Southwell, 2008). Additionally, sea ice can act as a physical barrier to foraging areas (Massom et al., 2009), forcing adults to undertake longer (Rombolá et al., 2003) and, thus, more energetically demanding foraging trips (Rombolá et al., 2003; Ballance et al., 2009), with fewer, and shorter, foraging trips (Watanuki et al., 1997; Rodary et al., 2000). Sea ice close to breeding colonies, particularly large icebergs, has been linked to lower breeding productivity by a number of previous studies (Dugger et al., 2014; Le Guen et al., 2018). The relationship between SIC and trip duration differs across colonies, with some studies finding duration increases with SIC (Clarke et al., 2002; Watanuki et al., 2002, 2004; Ballard et al., 2010) and others finding a reduction (Watanuki et al., 1997, 2002). It should, however, be noted that our tracking data are limited, and little is available from years with particularly high or particularly low SIC, meaning the shape of the response in trip duration at the extremes of SIC are unknown.

We predicted that diet composition would be influenced by SIC as the lifecycle of the species' main prey, during the breeding season, krill, is closely connected to sea ice (Atkinson et al., 2008). Sea ice acts as a nursey for krill larvae and its abundance and SIC have been linked at a regional scale (Daly and Macaulay, 1988; Atkinson et al., 2004). However, our results showed no relationship between diet composition and SIC. The sea ice during our study is mostly transient and wind-blown, which is not associated with krill larvae in the same way, and the krill caught by the penguins are mostly adults and associated with the shelf breaks (Lynnes et al., 2002; Takahashi et al., 2003; Clewlow et al., 2019), meaning strong relationships between the two are less likely. Recent studies suggest that wind and other large-scale environmental variables may play more of a role than SIC in influencing breeding success (Lowther et al., 2018; Atkinson et al., 2019).

Fledging mass was found to increase with SIC, however this only explained 11% of the annual variation meaning this is a minor driver. The majority of previous studies investigated the effects ice on chick growth rate rather than fledging mass, except see Dugger et al. (2014), as in this study and found it to be negatively impacted by high levels of fast- and pack-ice prior and during breeding (Watanuki et al., 1993; Vinuela et al., 1996), with precipitation (Ropert-Coudert et al., 2018) and region also being highlighted as important factors. The differences, highlighted above, between sea ice conditions across the continent may explain why our findings differ to previous studies, which have all been carried out in East Antarctica. Additionally, there is a large amount of interannual variation, with the two years with particularly low chinstrap fledging mass, 2013 and 2016, having highly contrasting SIC. SIC was particularly high during both chinstrap and Adélie guard in 2013 but very low during chinstrap guard and average during Adélie guard in 2016.

Our results, therefore, find little support for the 20-30% SIC optima for Adélie breeding success (Barbraud et al., 2015; Le Guen et al., 2018), foraging trip duration and meal mass (Ballard et al., 2010) identified by previous studies. In fact, we fail to find any significant relationship between SIC and breeding productivity and only found linear relationships between SIC and foraging trip duration and fledging mass. Importantly, it may be that there is a regional trend influencing the Adélie sea ice optima, as all three of the studies that identified a sea ice optima were carried out in East Antarctica, making direct comparisons between studies invalid. However, whilst these regional differences may impact the value of the sea ice optima, we would still expect to identify an optima and to see differences in sea ice tolerance between the species, as their contrasting sea ice classifications have been used for decades to describe the species. Our findings are in line with a previous study at the South Orkneys for time series prior to the one we analysed (Trathan et al., 1996) which found no relationships between productivity and SIC. No other studies of long time-series of breeding and foraging performance metrics have found any relationship between SIC and gentoo or chinstrap breeding success, although some studies have found lower breeding success and for chinstraps during single years affected by high SIC (Lishman, 1985; Rombolá et al., 2003) compared to ice free ones.

In rejecting this hypothesis, we must consider alternative explanations for the variability observed in the breeding and foraging performance metrics. Breeding productivity was found to vary greatly between years, with recent years having particularly low productivity (Fig. 4). This is reflected in the population declines of Adélies and chinstraps on Signy Island, with chinstraps declining at more than twice the rate of Adélies between 1978/79 to 2015/16, equating to reductions of 68% (-3.6% per annum) compared to Adélie penguin declines of 42% (-1.5% per annum) (Dunn et al., 2016). This suggests that the main driver must be a factor disproportionately impacting chinstraps. The warming temperature trends occurring in the region are not likely to be the driver as Adélies display a preference for cooler temperatures, nesting further south on the Antarctic continent, and therefore would be expected to display the greater population declines. Therefore, shifts in the abundance and availability of chinstraps' primary prey, krill, driven by climate changes (Atkinson et al., 2019), are likely to be the major driver of these population trends. Adélies generally display a preference for krill but appear to be more able to alter their diet based on krill availability. There is little fine scale data available on krill distribution and abundance and it is often temporally mismatched with the penguins' breeding. Therefore, detailed direct sampling of krill targeted in the penguins' foraging areas during the breeding season is required to truly elucidate this as a driver.

5 | CONCLUSIONS

This study represents the first test of the 'sea ice hypothesis' in Western Antarctica and the first attempt to identify a sea ice optima for chinstrap and gentoo penguins. We found that SIC has no direct influence upon breeding productivity for Adélies, chinstraps and gentoos breeding in the South Orkney Islands and that it did not act indirectly on their breeding productivity by significantly influencing all of the important foraging performance metrics. Whilst we did find fledging mass and foraging trip duration to be influenced by SIC, the species reacted in parallel to SIC conditions, which would not occur if the species' ice tolerance differed as their classifications suggest. Therefore, our findings do not support the 'sea ice hypothesis' or the hypothesised optimal SICs for the *Pygoscelid* species breeding at Signy Island. Instead the observed patterns in annual breeding productivity suggest a driver that is disproportionally influencing chinstraps, which is most likely to be krill availability.

6 | FIGURES

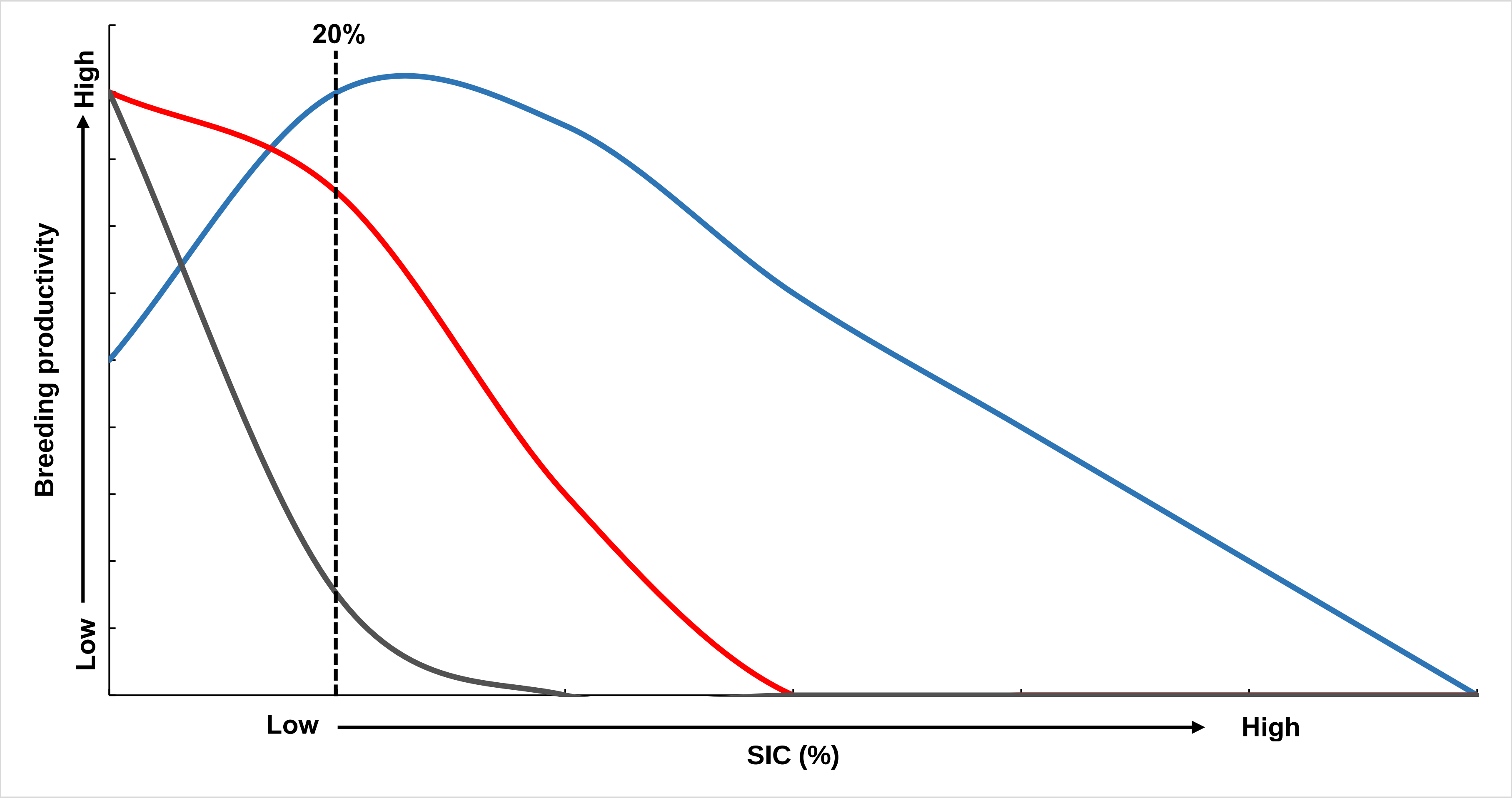


Figure 1 – Conceptual graph of the sea ice optima for Adélies' (blue), chinstraps' (red) and gentoos' (grey) breeding productivity (ratio chicks to pairs).

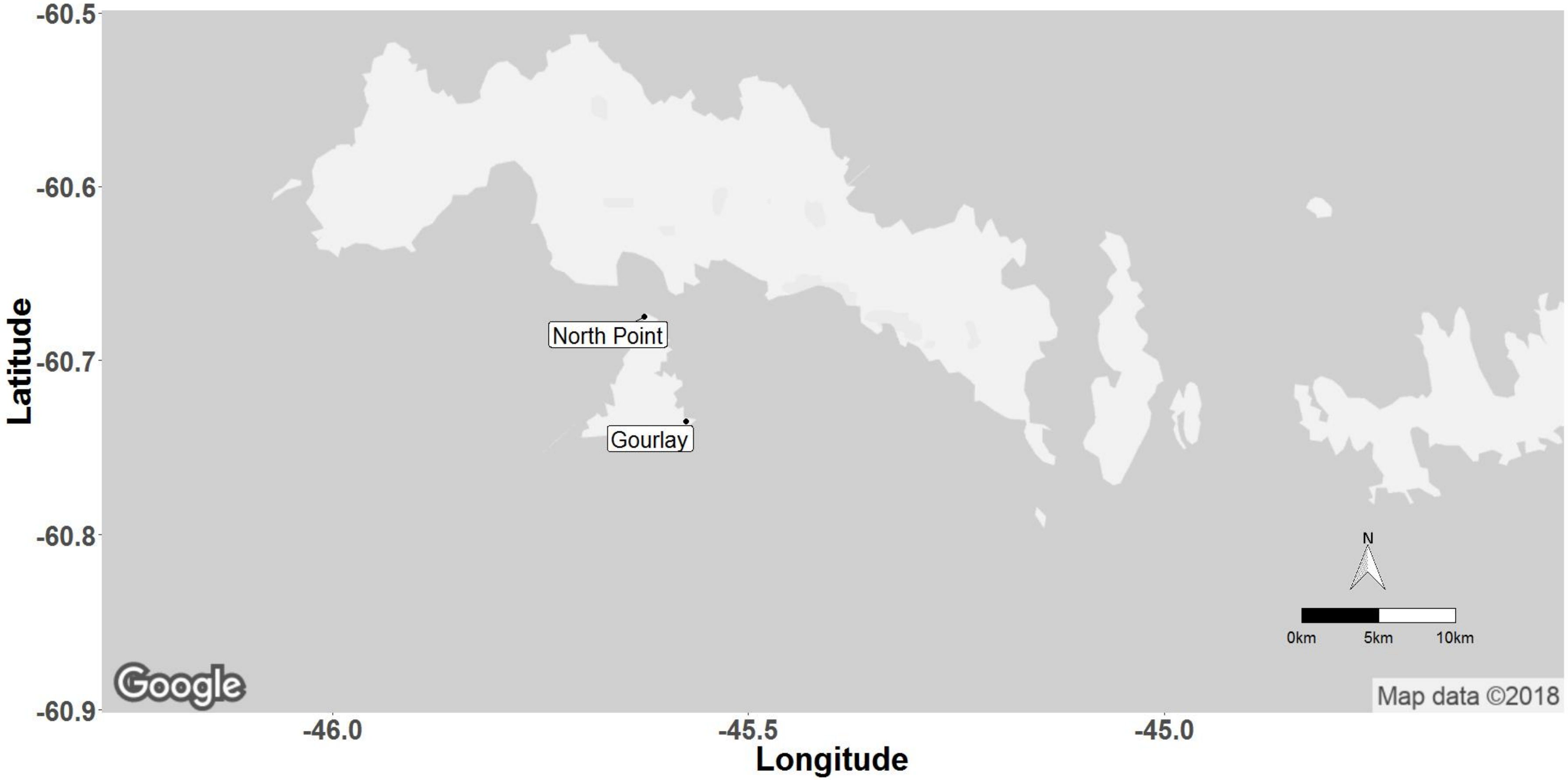


Figure 2 – Map showing the monitored breeding sites on Signy Island, South Orkneys and the proximity of other islands within the archipelago. Maps were produced by the authors using the package ggmap in R version 3.3.0.

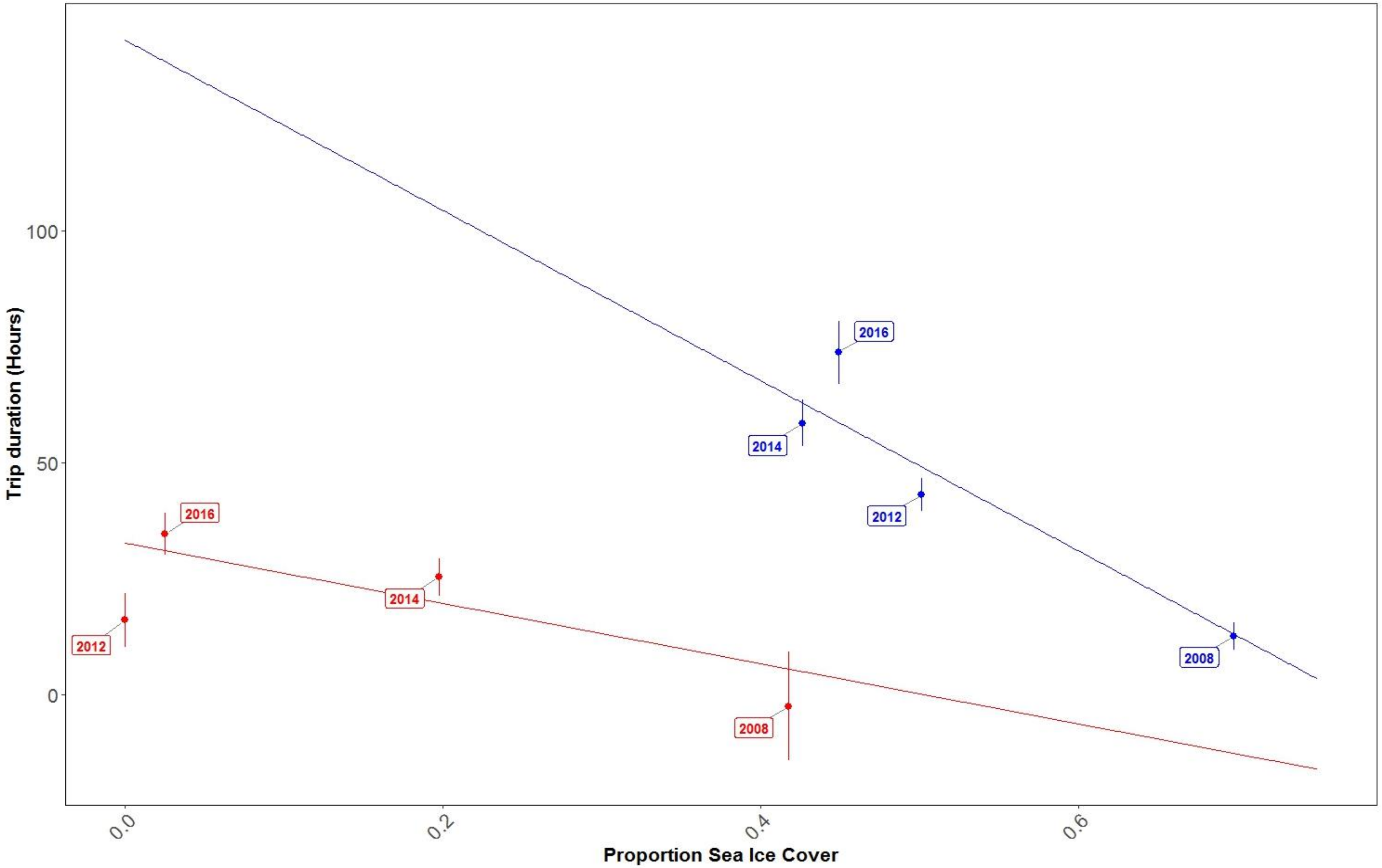


Figure 3 – Average annual foraging trip duration against average annual sea ice cover for Adélies (blue) and chinstraps (red) with bars representing the standard error of model prediction values. Note that both species had similar trip durations in 2008 and 2012 but Adélie trips were longer in 2014 and 2016.

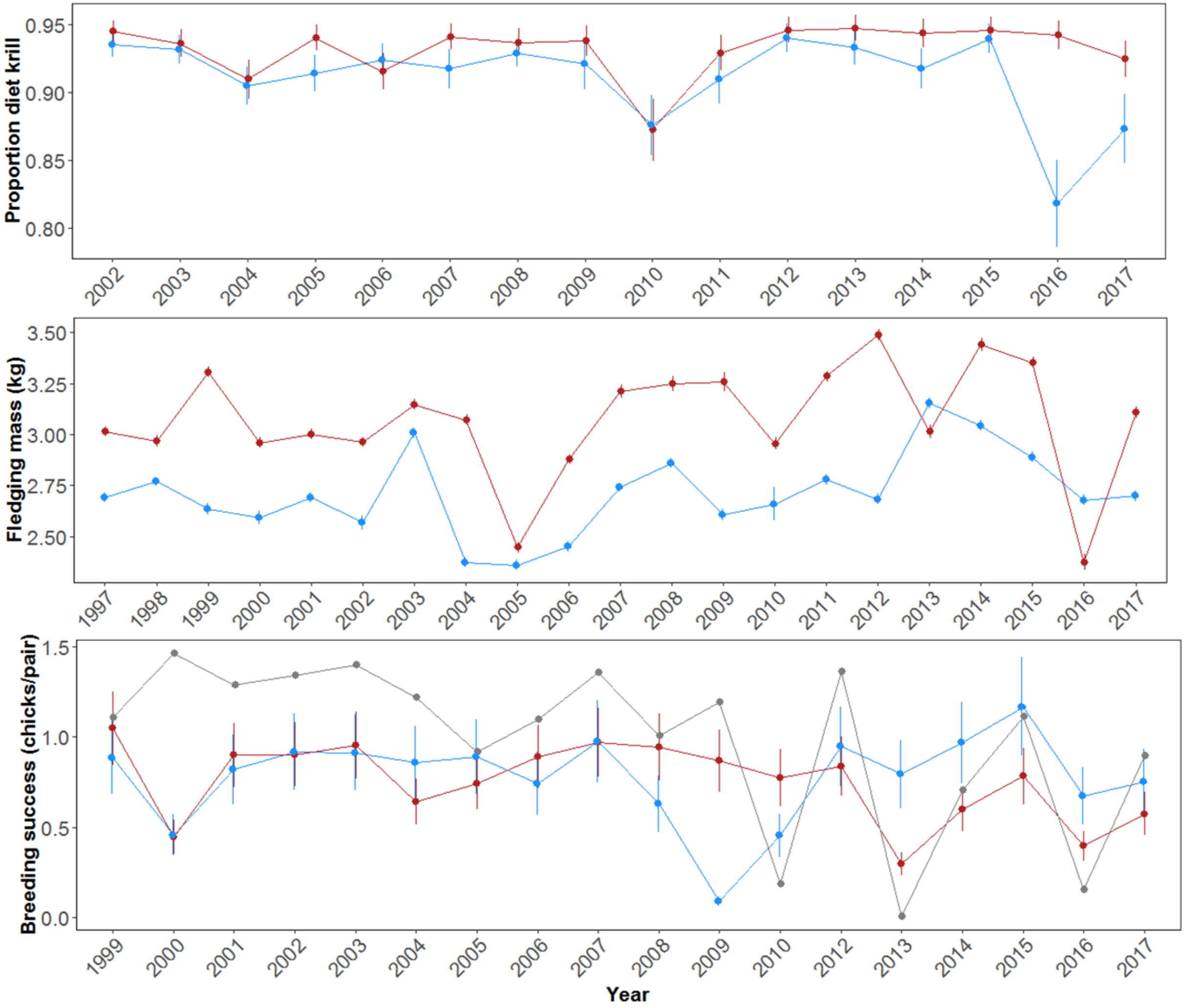


Figure 4 – Annual variation in the proportion of krill in diet, fledging mass and breeding success for Adélies (blue) and chinstraps (red) with error bars representing the standard error.

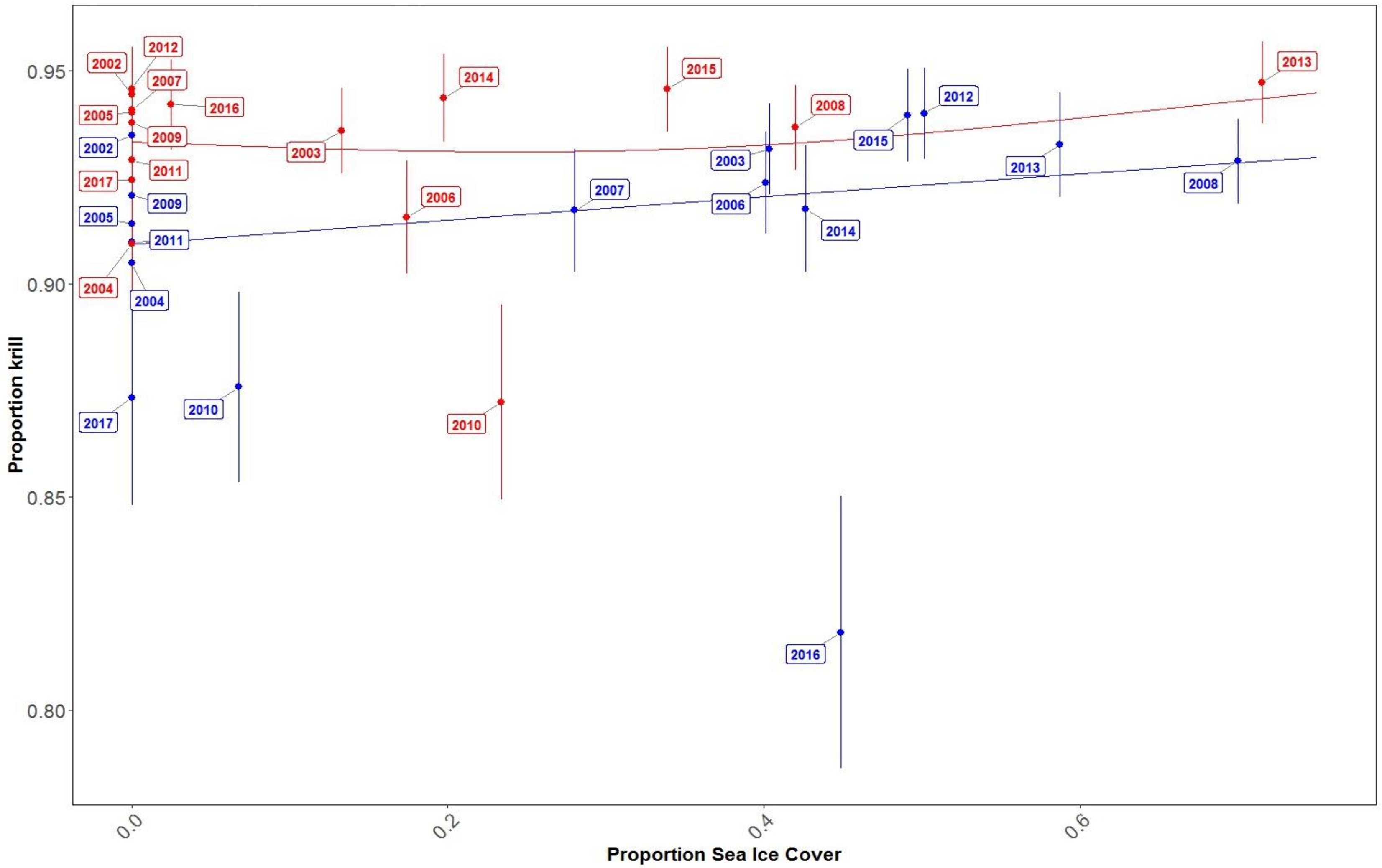


Figure 5 – Annual proportion of krill in diet against average annual sea ice cover for Adélies (blue) and chinstraps (red) with error bars representing the standard error of model prediction values.

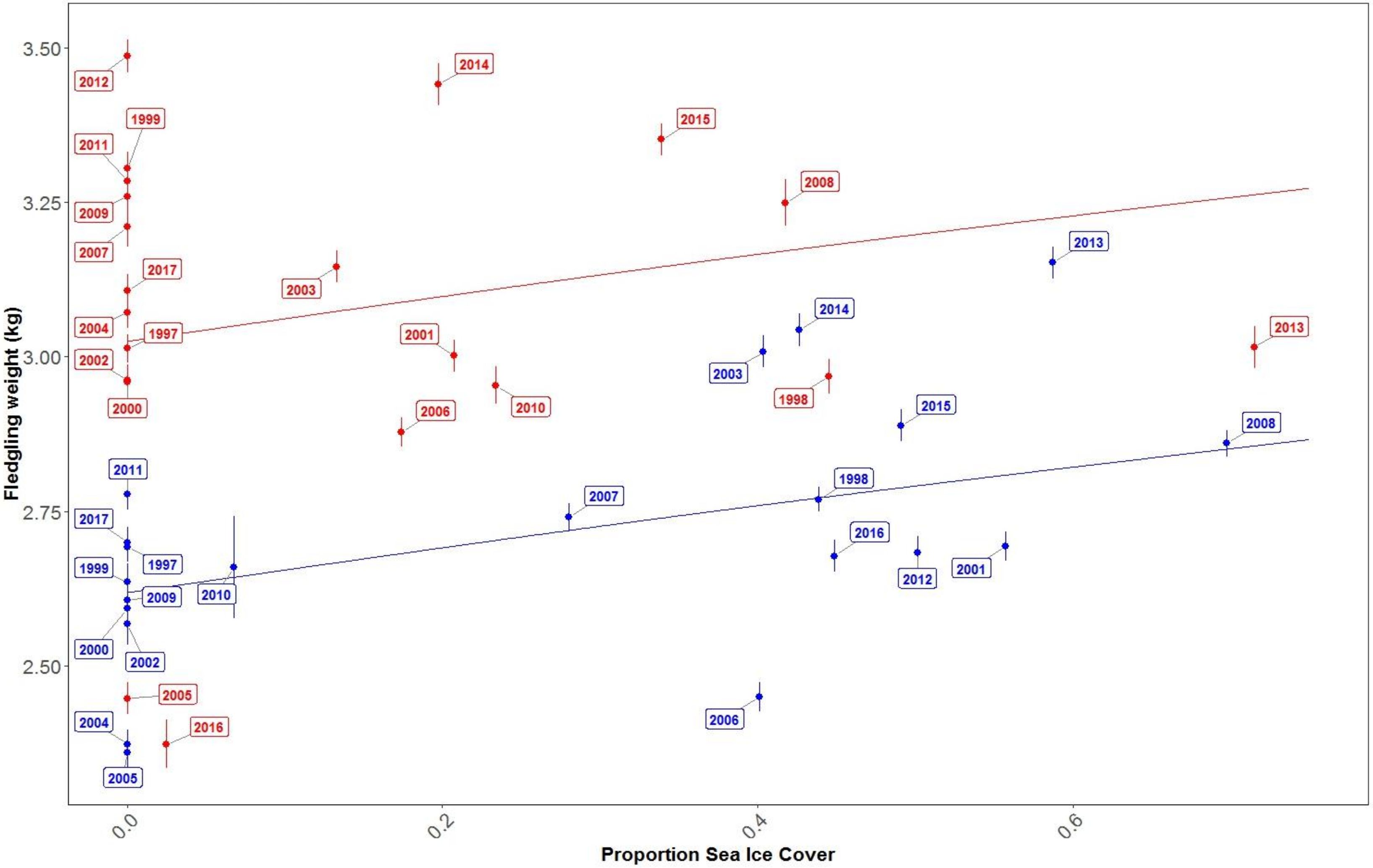


Figure 6 – Average annual fledging mass against average annual sea ice cover for Adélies (blue) and chinstraps (red) with error bars representing the standard error of model prediction values.

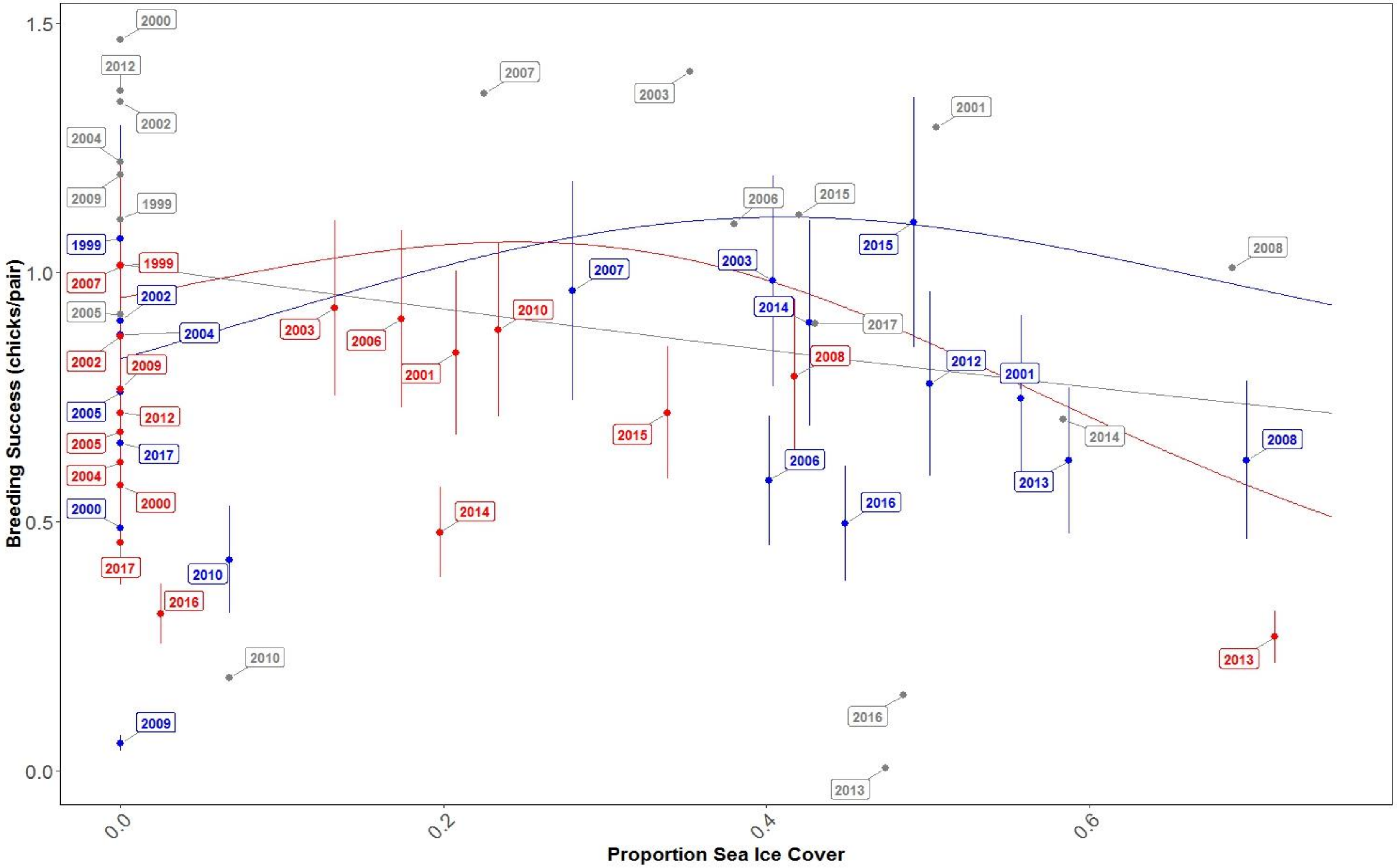


Figure 7 – Breeding productivity (ratio of chicks per pair) with sea ice cover (SIC) for Adélies (blue), chinstraps (red) and gentoos (grey) with error bars representing the standard error of model prediction values.

7 | REFERENCES

Ainley, D. G., G. Ballard, K. J. Barton, B. J. Karl, G. H. Rau, C. A. Ribic, and P. R. Wilson. 2003. Spatial and Temporal Variation of Diet Within a Presumed Metapopulation Of Adélie Penguins. *The Condor: Ornithological Applications* 105: 95–106.

Atkinson, A., S. L. Hill, E. A. Pakhomov, V. Siegel, C. S. Reiss, V. J. Loeb, D. K. Steinberg, et al. 2019. Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nature Climate Change* 9: 142–147.

Atkinson, A., D. A. Siegel, E. Pakhomov, and P. Rothery. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100–103.

Atkinson, A., V. Siegel, E. A. Pakhomov, P. Rothery, V. Loeb, R. M. Ross, L. B. Quetin, et al. 2008. Oceanic circumpolar habitats of Antarctic krill. *Marine Ecology Progress Series* 362: 1–23.

Ballance, L. T., D. G. Ainley, G. Ballard, and K. Barton. 2009. An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin Pygoscelis adeliae. *Journal of Avian Biology* 40: 279–288.

Ballard, G., K. M. Dugger, N. Nur, and D. G. Ainley. 2010. Foraging strategies of Adélie penguins: adjusting body condition to cope with environmental variability. *Marine Ecology Progress Series* 405: 287–302.

Ballerini, T., G. Tavecchia, S. Olmastroni, F. Pezzo, and S. Focardi. 2009. Nonlinear effects of winter sea ice on the survival probabilities of Adélie penguins. *Oecologia* 161: 253–265.

Barbraud, C., K. Delord, and H. Weimerskirch. 2015. Extreme ecological response of a seabird community to unprecedented sea ice cover. *Royal Society Open Science* 2: 140456.

Barbraud, C., V. Rolland, S. Jenouvrier, M. Nevoux, K. Delord, and H. Weimerskirch. 2012. Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. *Marine Ecology Progress Series* 454: 285–307.

Barbraud, C., and H. Weimerskirch. 2001. Contrasting effects of the extent of sea-ice on the breeding performance of an Antarctic top predator, the Snow Petrel Pagodroma nivea. *Journal of Avian Biology* 32: 297–302.

Black, C. E. 2015. A comprehensive review of the phenology of *Pygoscelis* penguins. *Polar Biology* 39: 405–432.

Bost, C. A., and P. Jouventin. 1991. Relationship between Fledging Weight and Food Availability in Seabird Populations: Is the Gentoo Penguin a Good Model? *Oikos* 60: 113–114.

Brierley, A. S., P. G. Fernandes, M. A. Brandon, F. Armstrong, N. W. Millard, S. D. McPhail, P. Stevenson, et al. 2002. Antarctic Krill Under Sea Ice: Elevated Abundance in a Narrow Band Just South of Ice Edge. *Science* 295: 1890–1892.

CCAMLR. 2014. CCAMLR Ecosystem Monitoring Programme, Standarda Methods. Part 1: Standard Methods for Monitoring Parameters of Predator Species; Method A3 - Breeding population size: A Ground count. Hobart, Tasmania.

Clarke, A. 1991. What Is Cold Adaptation and How Should We Measure It? *Integrative and Comparative Biology* 31: 81–92.

Clarke, A., E. J. Murphy, M. P. Meredith, J. C. King, L. S. Peck, D. K. A. Barnes, and R. C. Smith. 2007. Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 362: 149–166.

Clarke, J., L. M. Emmerson, and P. Otahal. 2006. Environmental conditions and life history constraints determine foraging range in breeding Adélie penguins. *Marine Ecology Progress Series* 310: 247–261.

Clarke, J., K. Kerry, L. Irvine, and B. Phillips. 2002. Chick provisioning and breeding success of Adélie penguins at Béchervaise Island over eight successive seasons. *Polar Biology* 25: 21–30.

Clewlow, H. L., A. Takahashi, S. Watanabe, S. C. Votier, R. Downie, and N. Ratcliffe. 2019. Niche partitioning of sympatric penguins by leapfrog foraging is resilient to climate change. *Journal of Animal Ecology* 88: 223–235.

Crawley, M. J. 2002. Statistical Computing: An Introduction to Data Analysis using S-Plus. Wiley.

Croll, D. A., D. A. Demer, R. P. Hewitt, J. K. Jansen, M. E. Goebel, and B. R. Tershy. 2006. Effects of variability in prey abundance on reproduction and foraging in chinstrap penguins (Pygoscelis antarctica). *Journal of Zoology* 269: 506–513.

Daly, K. L., and M. C. Macaulay. 1988. Abundance and distribution of krill in the ice edge zone of the Weddell Sea, austral spring 1983. *Deep Sea Research Part A. Oceanographic Research Papers* 35: 21–41.

Dimitrijević, D., V. H. Paiva, J. A. Ramos, J. Seco, F. R. Ceia, N. Chipev, T. Valente, et al. 2018. Isotopic niches of sympatric Gentoo and Chinstrap Penguins: evidence of competition for Antarctic krill? *Polar Biology*: 1–15.

Dugger, K. M., G. Ballard, D. G. Ainley, P. O. Lyver, and C. Schine. 2014. Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. *Frontiers in Ecology and Evolution* 2: 1–12.

Dunn, M. J., J. A. Jackson, S. Adlard, A. S. Lynnes, D. R. Briggs, D. Fox, and C. M. Waluda. 2016. Population Size and Decadal Trends of Three Penguin Species Nesting at Signy Island, South Orkney Islands. *PLOS ONE* 11: e0164025.

Emmerson, L., and C. Southwell. 2008. Sea Ice Cover and Its Influence on Adélie Penguin Reproductive Performance. *Ecology* 89: 2096–2102.

Forcada, J., and P. N. Trathan. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology* 15: 1618–1630.

Forcada, J., P. N. Trathan, K. Reid, E. J. Murphy, and J. P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* 12: 411–423.

Frederiksen, M., F. Daunt, M. P. Harris, and S. Wanless. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology* 77: 1020–1029.

Gaston, A. J., H. G. Gilchrist, and J. M. Hipfner. 2005. Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (Uria lomvia L.). *Journal of Animal Ecology* 74: 832–841.

Gaston, A. J., H. G. Gilchrist, and M. L. Mallory. 2005. Variation in ice conditions has strong effects on the breeding of marine birds at Prince Leopold Island, Nunavut. *Ecography* 28: 331–344.

Gauthier-Clerc, M., Y. L. Maho, Y. Clerquin, S. Drault, and Y. Handrich. 2000. Penguin fathers preserve food for their chicks. *Nature* 408: 928.

Grooten, M., and R. E. A. (Eds) Almond. 2018. WWF Living Planet Report - 2018: Aiming Higher. WWF, Gland, Switzerland.

Hijmans, R. J. 2017. Raster - R package version 2.6-7. *https://cran.r-project.org/web/packages/raster/vignettes/Raster.pdf*.

Hinke, J. T., A. M. Cossio, M. E. Goebel, C. S. Reiss, W. Z. Trivelpiece, and G. M. Watters. 2017. Identifying Risk: Concurrent Overlap of the Antarctic Krill Fishery with Krill-Dependent Predators in the Scotia Sea. *PLOS ONE* 12: e0170132.

Hinke, J. T., M. J. Polito, M. E. Goebel, S. Jarvis, C. S. Reiss, S. R. Thorrold, W. Z. Trivelpiece, and G. M. Watters. 2015. Spatial and isotopic niche partitioning during winter in chinstrap and Adélie penguins from the South Shetland Islands. *Ecosphere* 6: 1–32.

Intergovernmental Panel on Climate Change. 1996. Climate Change 1995. The Science of Climate Change. Cambridge University Press, Cambridge.

Intergovernmental Panel on Climate Change. 2007. Climate change 2007 synthesis report: Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (104 pp.). *Intergovernmental Panel on Climate Change*.

Kato, A., Y. Ropert-Coudert, and Y. Naito. 2002. Changes in Adelie penguin breeding populations in Lutzow-Holm Bay, Antarctica, in relation to sea-ice conditions. *Polar Biology* 25: 934–938.

Kovacs, K. M., C. Lydersen, J. E. Overland, and S. E. Moore. 2011. Impacts of changing sea-ice conditions on Arctic marine mammals. *Marine Biodiversity* 41: 181–194.

Kranstauber, B., and M. Smolla. 2016. move: Visualizing and Analyzing Animal Track Data. R package version 2.0.0. *http://CRAN.R-project.org/package=move*.

Laidre, K. L., I. Stirling, L. F. Lowry, Ø. Wiig, M. P. Heide-Jørgensen, and S. H. Ferguson. 2008. Quantifying the Sensitivity of Arctic Marine Mammals to Climate-Induced Habitat Change. *Ecological Applications* 18: S97–S125.

Le Guen, C., A. Kato, B. Raymond, C. Barbraud, M. Beaulieu, C.-A. Bost, K. Delord, et al. 2018. Reproductive performance and diving behaviour share a common sea-ice concentration optimum in Adélie penguins (Pygoscelis adeliae). *Global Change Biology* 24: 5304–5317.

Lishman, G. S. 1985. The food and feeding ecology of Adélie penguins (Pygoscelis adeliae) and Chinstrap penguins (P. antarctica) at Signy Island, South Orkney Islands. *Journal of Zoology* 205: 245–263.

Lowther, A. D., P. Trathan, A. Tarroux, C. Lydersen, and K. M. Kovacs. 2018. The relationship between coastal weather and foraging behaviour of chinstrap penguins, Pygoscelis antarctica. *ICES Journal of Marine Science* 75: 1940–1948.

Lynch, H. J., R. Naveen, P. N. Trathan, and W. F. Fagan. 2012. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93: 1367–1377.

Lynnes, A. S., K. Reid, and J. P. Croxall. 2004. Diet and reproductive success of Adélie and chinstrap penguins: linking response of predators to prey population dynamics. *Polar Biology* 27: 544–554.

Lynnes, A. S., K. Reid, J. Croxall, and P. Trathan. 2002. Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap penguins. *Marine Biology* 141: 1165–1174.

Massom, R. A., K. Hill, C. Barbraud, N. Adams, A. Ancel, L. Emmerson, and M. J. Pook. 2009. Fast ice distribution in Adélie Land, East Antarctica: interannual variability and implications for emperor penguins Aptendytes fosteri. *Marine Ecology Progress Series* 374: 243–257.

Massom, R. A., S. E. Stammerjohn, W. Lefebvre, S. A. Harangozo, N. Adams, T. A. Scambos, M. J. Pook, and C. Fowler. 2008. West Antarctic Peninsula sea ice in 2005: Extreme ice compaction and ice edge retreat due to strong anomaly with respect to climate. *Journal of Geophysical Research: Oceans* 113.

Milazzo, M., S. Mirto, P. Domenici, and M. Gristina. 2013. Climate change exacerbates interspecific interactions in sympatric coastal fishes. *Journal of Animal Ecology* 82: 468–477.

Moore, S. E., and H. P. Huntington. 2008. Arctic Marine Mammals and Climate Change: Impacts and Resilience. *Ecological Applications* 18: S157–S165.

Murphy, E. J., A. Clarke, N. J. Abram, and J. Turner. 2014. Variability of sea-ice in the northern Weddell Sea during the 20th century. *Journal of Geophysical Research: Oceans* 119: 4549–4572.

Murphy, E. J., A. Clarke, C. Symon, and J. Priddle. 1995. Temporal variation in Antarctic sea-ice: analysis of a long term fast-ice record from the South Orkney Islands. *Deep Sea Research Part I: Oceanographic Research Papers* 42: 1045–1062.

Niemandt, C., K. M. Kovacs, C. Lydersen, B. M. Dyer, K. Isaksen, G. J. G. Hofmeyr, F. Mehlum, and P. J. N. de Bruyn. 2016. Chinstrap and macaroni penguin diet and demography at Nyrøysa, Bouvetøya. *Antarctic Science* 28: 91–100.

Overland, J. E., and M. Wang. 2010. Large-scale atmospheric circulation changes are associated with the recent loss of Arctic sea ice. *Tellus A: Dynamic Meteorology and Oceanography* 62: 1–9.

Parkinson, C. L. 1992. Interannual variability of monthly Southern Ocean sea ice distributions. *Journal of Geophysical Research: Oceans* 97: 5349–5363.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669.

Pinshow, B., M. A. Fedak, and K. Schmidt-Nielsen. 1977. Terrestrial locomotion in penguins: it costs more to waddle. *Science* 195: 592–594.

Polito, M. J., W. Z. Trivelpiece, W. P. Patterson, N. J. Karnovsky, C. S. Reiss, and S. D. Emslie. 2015. Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of *Pygoscelis* penguins. *Marine Ecology Progress Series* 519: 221–237.

Post, E., U. S. Bhatt, C. M. Bitz, J. F. Brodie, T. L. Fulton, M. Hebblewhite, J. Kerby, et al. 2013. Ecological Consequences of Sea-Ice Decline. *Science* 341: 519–524.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. *URL https://www.R-project.org/*.

Ratcliffe, N., and P. Trathan. 2012. A review of the diet and at-sea distribution of penguins breeding within the CAMLR Convention Area. *CCAMLR Science* 19: 75–114.

Raymond, B., M.-A. Lea, T. Patterson, V. Andrews-Goff, R. Sharples, J.-B. Charrassin, M. Cottin, et al. 2015. Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography* 38: 121–129.

Reynolds, R. W., T. M. Smith, C. Liu, D. B. Chelton, K. S. Casey, and M. G. Schlax. 2018. NOAA OI V2 - High-resolution Blended Analysis of Daily SST and Ice. *Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center.*

Ridoux, V., and C. Offredo. 1989. The diets of five summer breeding seabirds in Adélie Land, Antarctica. *Polar Biology* 9: 137–145.

Rodary, D., B. C. Wienecke, and C. A. Bost. 2000. Diving behaviour of Adélie penguins (Pygoscelis adeliae) at Dumont D'Urville, Antarctica: nocturnal patterns of diving and rapid adaptations to changes in sea-ice condition. *Polar Biology* 23: 113–120.

Rombolá, E., E. Marschoff, and N. Coria. 2003. Comparative study of the effects of the late pack-ice break-off on chinstrap and Adélie penguins' diet and reproductive success at Laurie Island, South Orkney Islands, Antarctica. *Polar Biology* 26: 41–48.

Ropert-Coudert, Y., A. Kato, K. Shiomi, C. Barbraud, F. Angelier, K. Delord, T. Poupart, et al. 2018. Two Recent Massive Breeding Failures in an Adélie Penguin Colony Call for the Creation of a Marine Protected Area in D'Urville Sea/Mertz. *Frontiers in Marine Science* 5: 1–7.

Salihoglu, B., W. R. Fraser, and E. E. Hofmann. 2001. Factors affecting fledging weight of Adélie penguin (Pygoscelis adeliae) chicks: a modeling study. *Polar Biology* 24: 328–337.

Smith, P. A., and A. J. Gaston. 2012. Environmental variation and the demography and diet of thick-billed murres. *Marine Ecology Progress Series* 454: 237–249.

Spurr, E. B. 1975. Breeding of the Adélie Penguin Pygoscelis Adeliae at Cape Bird. *Ibis* 117: 324–338.

Stammerjohn, S. E., D. G. Martinson, R. C. Smith, and R. A. Iannuzzi. 2008. Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research Part II: Topical Studies in Oceanography* 55: 2041–2058.

Stammerjohn, S. E., D. G. Martinson, R. C. Smith, X. Yuan, and D. Rind. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. *Journal of Geophysical Research: Oceans* 113.

Stammerjohn, S. E., R. Massom, D. Rind, and D. Martinson. 2012. Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. *Geophysical Research Letters* 39.

Takahashi, A., M. J. Dunn, P. N. Trathan, K. Sato, Y. Naito, and J. P. Croxall. 2003. Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. *Marine Ecology Progress Series* 250: 279–289.

Thomas, D. N., and G. S. Dieckmann. 2002. Antarctic Sea Ice--a Habitat for Extremophiles. *Science* 295: 641–644.

Trathan, P. N., J. P. Croxall, and E. J. Murphy. 1996. Dynamics of Antarctic penguin populations in relation to inter-annual variability in sea ice distribution. *Polar Biology* 16: 321–330.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. J. Volkman. 1987. Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology* 68: 351–361.

Vinuela, J., J. Moreno, L. M. Carrascal, J. J. Sanz, J. A. Amat, M. Ferrer, J. Belliure, and J. Cuervo. 1996. The effect of hatching date on parental care, chick growth, and chick mortality in the chinstrap penguin Pygoscelis antarctica. *Journal of Zoology* 240: 51–58.

Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. Fromentin, et al. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.

Wang, S., D. Bailey, K. Lindsay, J. K. Moore, and M. Holland. 2014. Impact of sea ice on the marine iron cycle and phytoplankton productivity. *Biogeosciences* 11: 4713–4731.

Watanabe, S., K. Sato, and P. J. Ponganis. 2012. Activity Time Budget during Foraging Trips of Emperor Penguins. *PLOS ONE* 7: e50357.

Watanuki, Y., A. Kato, Y. Mori, and Y. Naito. 1993. Diving Performance of Adélie Penguins in Relation to Food Availability in Fast Sea-Ice Areas: Comparison between Years. *Journal of Animal Ecology* 62: 634–646.

Watanuki, Y., A. Kato, Y. Naito, G. Robertson, and S. Robinson. 1997. Diving and foraging behaviour of Adélie penguins in areas with and without fast sea-ice. *Polar Biology* 17: 296–304.

Watanuki, Y., A. Kato, K. Sato, Y. Niizuma, C. A. Bost, Y. Le Maho, and Y. Naito. 2002. Parental mass change and food provisioning in Adélie penguins rearing chicks in colonies with contrasting sea-ice conditions. *Polar Biology* 25: 672–681.

Watanuki, Y., A. Takahashi, K. Sato, A. Kato, and C. A. Bost. 2004. Inter-colony and sex differences in the effects of parental body condition and foraging effort on the brood growth of Adélie penguins. *Journal of Ethology* 22: 91–98.

Williams, T. D., and J. P. Croxall. 1990. Is Chick Fledging Weight a Good Index of Food Availability in Seabird Populations? *Oikos* 59: 414–416.

Wood, S. 2018. mgcv - Mixed GAM Computation Vehicle with Automatic Smoothness Estimation. R package version 1.8-26. *https://cran.r-project.org/web/packages/mgcv/index.html*.

Chapter 5 – *Investigating the interacting roles of competition and the environment upon long-term Pygoscelis penguin population trends*

H.L. Clewlow, J. Forcada and N. Ratcliffe

Author contributions

The framework for this study was developed by HLC, J.F and NR. All data was processed by HLC, model code was written by J.F, based on the modelling of Mutshinda et al. (2011) and all analyses were carried out by HLC and JF. The data utilised in this chapter were from databases of long-term studies, collected by field workers over many years.

ABSTRACT

The global climate is changing dramatically, particularly at the poles, altering trophic interactions and affecting population trajectories. However, the majority of previous studies have investigated climate change impacts upon single species in isolation, overlooking the potentially important role of species interactions in modifying the response. The three species of *Pygoscelis* penguins in the Western Antarctic Peninsula (WAP) have undergone significant population and range changes over the last few decades which are linked with rapid climate warming in the region. Adélie (*Pygoscelis adeliae*) and chinstrap (*Pygoscelis antarctica*) penguin populations have declined whilst gentoo penguin (*Pygoscelis papua*) populations have increased, leading to speculation that climate change has given the latter a competitive advantage and that the increased competition from gentoos might exacerbate climate impacts on the other two species. To date, the relative roles of environmental drivers and competition upon population trends have not been fully quantified within a single modelling framework for this system. We hypothesised that the population changes experienced by *Pygoscelis* penguins were driven by an interaction of interspecific competition and environmental drivers. This chapter investigated this hypothesis using a multi-species population model to quantify strength of the effects of interspecific competition and environmental variables upon the three *Pygoscelis* penguin species breeding at two colonies in the South Orkney and South Shetland Islands where they nest in sympatry. The models found that stochastic environmental variability was important for driving variability in population trends, but the environmental covariates and competition parameters

fitted in the model only explained a small proportion of the variance. Further research should be directed at identifying the important environmental drivers of the annual variability in the three penguins’ population trends and the demographic rates underpinning these.

1 | INTRODUCTION

Quantifying the effects of climate change on ecosystems is a key focus of contemporary ecological research, and predicting its impacts on biodiversity is of ever-growing importance (Walther et al., 2002; Parmesan and Yohe, 2003). Shifts in species distribution (Parmesan and Yohe, 2003; Svenning et al., 2014), alterations in population dynamics (Saether et al., 2000) and changes in breeding phenology have been widely documented (Thackeray et al., 2016). Interspecific competition may also constrain species distributions and abundance where dominant species exclude subordinate ones from their fundamental niche and confine them to a smaller realised niche (Hutchinson, 1957). Since a species’ thermal tolerance is often an important component of their niche (Hutchinson, 1957; Barnagaud et al., 2012; Donald et al., 2012), it follows that changes in climate may alter competitive dominance among species (Helland et al., 2011; Milazzo et al., 2013). Additionally, the population shifts induced by climate change may also affect the strength of density dependence (i.e. population growth is regulated by the density of the population) (Barbraud and Weimerskirch, 2003). Therefore, the response of a given species to a changing environment will likely depend on the suite of competitors present, or those that colonise as a result of such changes (Araújo and Luoto, 2007; Gilman et al., 2010; Urban et al., 2012). These competitive interactions are often overlooked in the climate impact literature, but there is growing empirical evidence that changes in temperature can alter competitive dominance to such a degree that species’ abundance is affected and there are examples from a wide range of taxa, as discussed in Chapter 2.

Environmental warming events have been magnified at the poles (Walther et al., 2002; Vaughan et al., 2003; Clarke et al., 2007) and the Western Antarctic Peninsula (WAP) is one of the most rapidly warming areas on the planet (Clarke et al., 2007). This region has experienced a 3°C rise in average surface temperature since 1951 (Vaughan et al., 2003; Turner and Overland, 2009; Turner et al., 2016) with associated reduction in sea ice extent (Stammerjohn et al., 2008), although cooling has occurred since 2000 (Turner et al., 2016). In response to these shifts in environmental conditions, species across the ecosystem have displayed shifts in their range, populations and breeding phenology (Lynch, Fagan, et al., 2012; Dugger et al., 2014; Dunn et al., 2016; Clewlow et al., 2019).

The ranges of the three species of *Pygoscelis* penguins, Adélie (*Pygoscelis adeliae*), chinstrap (*P. antarcticus*) and gentoo (*P. papua ellsworthi*) overlap on the WAP and southerly islands of the Scotia Sea and they breed sympatrically at multiple colonies (Woehler, 1995). These species share broadly similar foraging ecology and, in this region, their diets are dominated by Antarctic krill, (*Euphausia superba*; hereafter krill) (Ratcliffe and Trathan, 2012). The species' populations show different responses to climate change in the region: populations of Adélie and chinstrap penguins have declined while gentoos have experienced population growth and range expansions (Lynch, Naveen, et al., 2012; Dunn et al., 2016). The "sea ice hypothesis" attributes the differing population trends to differential tolerances of the species to sea ice concentration directly, in which Adélies are ice loving, chinstraps are ice tolerant and gentoos are ice averse (Fraser et al., 1992; Lynch, Naveen, et al., 2012). Other studies have questioned these classifications and formulated what we call here the "krill habitat hypothesis". The hypothesis proposes that the observed reduction in krill recruitment and range contractions since the 1970s (Atkinson et al., 2019), are due to climate change induced reduction in the sea ice required for krill nursery habitats and increasing sea surface temperatures reducing the amount of suitable marine habitat (Hill et al., 2013; Murphy et al., 2017), which in turn is reducing the amount of prey available for penguins (Trivelpiece et al., 2011; Lynch, Naveen, et al., 2012). Implicit in this hypothesis is the greater ability of gentoos to switch prey preference from krill to fish (Ratcliffe and Trathan, 2012), which would allow their populations to increase even when krill stocks decline. Alternatively, according to the wider predictions of the "competitive exclusion hypothesis" (Hutchinson, 1957), the altered climate conditions may increase gentoos competitive dominance over Adélies and chinstraps allowing them to be displaced in new areas of overlap, likely mediated by gentoos' dietary plasticity and ability to access prey at greater depths (Kokubun et al., 2010; Ratcliffe and Trathan, 2012). An extension of this theory is the “krill surplus” hypothesis”, in which the recovery of krill-eating marine mammals in the 1970s from over exploitation is causing penguin population declines via interspecific competition (Surma et al., 2014). Additionally, the WAP is also the focus of a krill fishery (Nicol et al., 2012; Commission for the Conservation of Antarctic Marine Living Resources, 2019), which could decrease the amount of krill available to penguins, and other krill-feeding predators, but the fishery is closely monitored and controlled by CCAMLR to ensure the krill-feeding predators are impacted as little as possible (Commission for the Conservation of Antarctic Marine Living Resources, 2019). The relative contribution of these drivers upon penguin population trends is a matter of long-running debate, and studies that simultaneously investigate the importance of environmental drivers and competition across species, replicated at different sites, are required to disentangle these complex and inter-related effects.

In this chapter, we use long-term count data collected from two colonies, one in the South Shetland Islands and the other in the South Orkney Islands, where all three species breed in sympatry. These are analysed with a multi-species Gompertz population model that simultaneously estimates the relative importance of interspecific competition and environmental variables upon population trends, whilst controlling for effects of density dependence. We use this framework to test the level of support for the hypotheses discussed above.

2 | MATERIALS AND METHODS

2.1 | Study site and species

Long-term data on Adélie, chinstrap and gentoo penguin population trajectories were obtained from study colonies on the South Orkney Islands (Signy Island: 60°42’S, 45°36’W) and South Shetland Islands (King George Island: 62°17’S, 58°45’W) archipelagos (Fig. 1a). Direct ground counts of active penguin nests were carried out by experienced observers using methods standardised by the CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) Ecosystem Monitoring Programme (CCAMLR, 2014). Counts are conducted during the incubation and guard phases of the breeding season, when observers walk carefully around and through selected study colonies, verifying nest contents and then marking individual nests with temporary, animal-safe, stock marker or a nest marker to avoid double counting or omission.

On Signy Island, nest counts were carried out from 1979 to 2018 in 9 colonies of Adélie penguins, 11 of chinstrap penguins and 10 of gentoo penguins, which were located at Gourlay Peninsula (Adélie and chinstrap), Fyr Channel (chinstrap) and North Point (Gentoo; Fig. 1b). On King George Island, nest counts of the three species were carried out from 1987 to 2013 at Point Thomas for Adélies and gentoos, Copacabana for Adélies and gentoos and Patelnia and Uchatka for chinstraps (Fig. 1c).

2.2 | Modelling annual variation in abundance

Counts of all study colonies were not available for all years, and so these needed to be interpolated from the colonies available to produce complete time series. These were generated by combining count data from all available study sites and inputting them into a generalised linear mixed model framework (Bolker, 2008), where each study site for a given species was treated as a sampling unit. For each species, the count of penguin pairs at site *j* and breeding season *t* was $y_{t,j}$, and it was modelled as $y_{t,j} \sim Poisson(\lambda_{t,j})$, where $\lambda_{t,j}$ was a function of a site fixed effect and random site and random year effects ς_{jt}, $\log(\lambda_{t,j}) = K_j + \varsigma_{jt}$, with $K_j \sim Normal(\mu, \sigma_{\kappa}^2)$ and $\varsigma_{jt} \sim Normal(0, \sigma_{\varsigma}^2)$. This model was fitted using Markov Chain Monte Carlo methods, with BUGS language and program JAGS (Plummer, 2003) and run using package jagsUI in the statistical program ‘R’ (R Core Team, 2015). Diffuse Normal (0, 100) priors were selected on the *K* and placed Uniform (0, 3) priors on the standard deviations. The model ran 500,000 iterations of three Markov chains using dispersed parameter values as starting values and discarded the first 250,000 samples of each chain as burn-in, thinning the remainder to every 50th sample. Convergence was visually assessed using trace plots, through the mixing of the chains and sample autocorrelation plots.

2.3 | Principal Component Analysis selection of environmental variables

A Principal Component Analysis (PCA) was used to select and integrate environmental variables for use as covariates in the Gompertz model. This selection was based on the highest correlation between variables and principal components (PCs), which were new orthogonal variables and uncorrelated to each other. Both local, for each individual archipelago, and large-scale environmental variables were inputted into the PCAs to characterise variables operating at different spatial scales. Local variables were sea ice extent, sea surface temperatures (SST) and air temperature and large-scale variables were the Southern Annular Mode (SAM) and Southern Oscillation Index (SOI).

Annual sea ice extent (SIE) was calculated using passive microwave data from Nimbus-7 SMMR and DMSP SSM/I-SSMIS (Cavalieri et al., 2016), with a grid square being classified as sea ice if there was more than 15% sea-ice coverage, a commonly used threshold in sea ice index products and first used by Parkinson et al. (1987). This data indicated the northern limit of the sea ice edge in February and the limit was taken as the mean of the values between longitudes 46–44°W for the South Orkneys and 62–57°W for the South Shetlands. The SIE for February, when it usually reaches a minimum, was selected as high SIE at this time is indicative of a particularly cold summer season.

Annual SST was calculated using the National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation V2 dataset (NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, 2018). Data was extracted for the summer period, defined as January to March, using the R packages raster (Hijmans, 2017) and ncdf4 (Pierce, 2017) in R (R Core Team, 2015). Locations from GPS tracking of South Orkney *Pygoscelis* penguins, see Clewlow et al., (2019), was overlaid on rasterised annual SST data and values were extracted for each underlying grid square to produce an average annual SST value for the colony. Detailed tracking data was not available from the South Shetlands archipelago to allow values to be extracted for each location so a 25km buffer around each study site was used to extract SST values, which were then averaged to produce a single annual value. This buffer distance was selected based on previously published GPS tracking of *Pygoscelis* penguins from the South Shetlands, which showed that this distance covered both species' entire foraging area (Kokubun et al., 2010).

Air temperature data was obtained from the nearest long-running weather station to each archipelago. Orcadas Station (60°44′S 44°44′W) was selected for the South Orkney Islands, which is located on Laurie Island at 6 metres above sea level and around 40km from the study colonies on Signy

Island (British Antarctic Survey, 2018), and Great Wall Station (62°20′S 58°57′W) was selected for the South Shetland Islands, which is located on King George Island at 10 metres above sea level and around 26km from the study colonies (British Antarctic Survey, 2018). October air temperatures were selected for each year as this is the start of the breeding season and has been shown to correlate with shifts in species' phenology via timing of snowmelt (Lynch, Fagan, et al., 2012; Clewlow et al., 2019) and so has the potential to affect breeding propensity.

The Southern Annular Mode (SAM) is a large-scale atmospheric variable based on the zonal pressure difference between the latitudes of 40°S and 65°S. Positive values of the SAM index correspond with stronger-than-average westerlies over the mid-high latitudes (50°S-70°S) and weaker westerlies in the mid-latitudes (30°S-50°S). Southern Hemisphere atmospheric circulation is strongly influenced by SAM and any variability within SAM has large impacts on Antarctic surface temperatures, ocean circulation, and many other climate variables (Turner, 2004; Stammerjohn et al., 2008). SAM data was obtained from the NERC Polar Data Centre (http://www.nerc-bas.ac.uk/icd/gjma/sam.html) based on the methodology of (Marshall, 2003).

The Southern Oscillation Index (SOI) is another large-scale atmospheric variable, which provides a measure of the development and intensity of El Niño and La Niña episodes. It is calculated by comparing sea-level air pressure between Tahiti and Darwin, Australia. This index provides an indication of fluctuations in SST, precipitation, wind and sea-ice concentration due to El Niño/La Niña episodes (Kwok et al., 2016).

Annual values were produced for all climate variables, but they were investigated at different time lags. This was because the influence of some variables is not evident in life-history events until years later (Guinet et al., 1998; Barbraud et al., 2011) since they are often acting directly on productivity at lower trophic levels than those of penguins (Cullen et al., 2009). Therefore, air temperature and SST were investigated using values from year t (i.e. same year as population data), allowing impacts on breeding propensity to be investigated. SAM and sea ice extent were investigated using values from year t-1, as this could affect overwinter survival from the previous year or have carry over effects on breeding propensity in the focal year (Trathan et al., 1996; Forcada et al., 2006). SOI was analysed using values from year t-2 as this is the lag at which El Nino affects acoustic estimates of krill biomass around the South Shetland archipelago (Richerson et al., 2017) and Signy Island's penguin population trends according to previous analyses (Forcada et al. 2006).

Imputation of missing entries within these environmental data sets was carried out using an iterative procedure developed in R package missMDA (Josse and Husson, 2012). The PCA for each archipelago was performed using R package FactoMineR (Le and Husson, 2008) and penguin abundance data, generated by the population model, were used as supplementary variables in the analysis for a better ecological interpretation of the principal components and their effects on the different species. By including the species in the PCA analysis we could explore how the species' responses differed to one another and their relationships with the environmental variables.

Unfortunately, there are two potentially important factors that we could not directly include in this analysis due to lack of data, the abundance and distribution of krill and predation rates on adults and chicks. Both of these factors have been shown to influence population trends (Trivelpiece et al., 2011; Horswill et al., 2014). Additionally, it is worth noting that krill stocks have been observed to vary cyclically, usually every in cycles of four or five years (Fielding et al., 2014; Richerson et al., 2017) but as our data covers multiple decades, 39 years at the South Orkneys and 26 years at the South Shetlands, and therefore multiple krill cycles, our analysis should not be notably biased by this phenomenon.

2.4 | Multi-species population model

A simplified population dynamics modelling framework, based on the work of Mutshinda et al. (2011), was used to investigate the effects of environmental variables, density dependence and interspecific competition upon population growth rates. A hierarchical Bayesian approach with a state-space formulation (De Valpine and Hastings, 2002) approach allowed flexibility in the incorporation of population count uncertainty, inference on variance components, and quantification of variance explained, carrying over the uncertainty. The state process had a Gompertz formulation at its core, with a similar structure to other multispecies approaches (Loreau and de Mazancourt, 2008; Mutshinda et al., 2011) and well established methods of analysis of environmental variance (Saether et al., 2000; Ripa and Ives, 2003). The

Gompertz formulation was used because it mirrors growth patterns in the real world with a sigmoid growth rate, growth is slowest at the start and end of a given time period (Tjørve and Tjørve, 2017). The number of penguins of species *i* at the study population and breeding season *t*, $N_{i,t}$, was estimated as:

$$N_{i,t} = N_{i,t-1} exp\left[r_i\left(1 - \sum_{j=1}^{S} \alpha_{i,j} logN_{j,t-1}/k_i\right) + \sum \beta_{i,m} Z_{m,t} + \varepsilon_{i,t}\right]$$

where r_i is the intrinsic growth rate and k_i the carrying capacity for species *i*; the interaction coefficient $\alpha_{i,j}$ quantifies the effects of species *j* on growth of species *i*; and the $\beta_{i,m}$ are fixed effects of *m* environmental variables, *Z*. The $\varepsilon_{i,t}$ are error terms represent demographic and unmodelled environmental stochasticity (or variation); they are assumed to be serially independent and normally distributed. Environmental stochasticity consists of un-modelled aspects of the physical and biological environment, such as predation by and of other trophic level species, prey dynamics and other intrinsic dynamics, such as local physiogeography or incidence of disease. In natural logarithmic scale, and using the results of the PCA analysis on environmental variables, the population model was:

$$x_{i,t} = x_{i,t-1} + r_i \left(1 - \sum_{j=1}^{S} \alpha_{i,j} x_{j,t-1}/k_i\right) + \beta_{i,1} PC1 + \beta_{i,2} PC2 + \varepsilon_{i,t}$$

where $x_{i,t}$ is the natural logarithm of $N_{i,t}$, and *PC1* and *PC2* the estimated coordinates of principal components 1 and 2, representing the environmental variables, which were standardized to unit variance. The serially independent vectors of $\varepsilon_{i=1,..,S;t}$ were assumed to be multivariate normally distributed, $\varepsilon_t \sim MVN(0, \Sigma_t)$ with covariance matrix Σ_t, that could be further decomposed as Σ_t = C + D_t, where C is the environmental covariance matrix. This matrix represented the variability not explained by intrinsic dynamics or the environmental covariates; and D_t is the demographic variance affecting species *i* between seasons *t-1* and *t* (Saether et al., 2000), scaled inversely with population size, as $D_t = diag\left(\delta_i^2/N_{i,t-1}\right)$, where *diag* is the diagonal elements of the matrix.

The elements of C, $C_{i,i}$ and $C_{i,j}$, for $i \neq j$, for species *i* and *j* are respectively species-specific and joint species responses to unmodelled environmental factors. From these, $\rho_{i,j} = c_{i,j}/\sqrt{c_{i,i}\, c_{j,j}}$ quantified the correlation between the responses of species *i* and *j* to environmental fluctuations, and the synchrony of the species responses (Loreau and de Mazancourt, 2008) was estimated as

$\varphi_e = \left[1 + (S-1)\overline{\rho_{i,j}}\right]/S$, where $\overline{\rho_{i,j}}$ is the average correlation between species environmental responses. In case there were no interactions between species (all of $\alpha_{i,j}$ were close to zero), the environmental correlations and the correlations in abundance between species ($\varphi_{i,j}$) should be very similar, and this was tested as, $\varphi_{ij} = \theta_{i,j}\rho_{i,j}$, where $\theta_{ij} = \sqrt{\frac{(1-a_{i,i}{}^{2})(1-a_{j,j}{}^{2})}{(1-a_{i,i}{}^{2})(1-a_{j,j}{}^{2})+\left(a_{i,i}-a_{j,j}\right)^{2}}}$ and $a_{i,i}$ was r_i/k_i (Ripa and Ives 2003).

The other quantities were derived following Mutshinda et al. (2011), including total environmental variance for species *i*, $E_i = C_{i,i} + \beta_{i,1}^2 + \beta_{i,2}^2$, where $\beta_{i,1}^2 + \beta_{i,2}^2$ was the part attributable to the environmental covariates; the proportion of this environmental variance was $\left(\beta_{i,1}^2 + \beta_{i,2}^2\right)/E_i$. The environmental covariance between the dynamics of species *i* and *j* was $\beta_{i,1}\beta_{j,1} + \beta_{i,2}\beta_{j,2} + C_{i,j}$; and for $C_{i,j} > 0$ when covariate effects for species *i* and *j* were of the same sign, the proportion of the environmental covariance between species explained by the covariates was $\left(\beta_{i,1}\beta_{j,1} + \beta_{i,2}\beta_{j,2}\right)/\left(\beta_{i,1}\beta_{j,1} + \beta_{i,2}\beta_{j,2} + C_{i,j}\right)$.

The observation process used the modelled estimates of site counts for species *i* in year *t*, $y_{i,t}$, assuming that $y_{i,t}|N_{i,t} \sim Normal\left(n_{i,t},\ \tau_i^2\right)$, where $n_{i,t}$ was $e^{x_{i,t}}$ and τ_i^2were the estimated standard errors of the modelled site counts. This model was fitted using Markov Chain Montel Carlo methods, with BUGS language and program JAGS run from program R using package jagsUI.

The $\alpha_{i,j}$ coefficients of species interactions for spurious values were investigated using stochastic search variable selection (SSVS) (George and McCulloch, 1993), as implemented by (Mutshinda et al., 2011). This method prevented interspecies interactions that were close to zero to affect the model results. A Bernoulli (0.2) prior was specified to the probability of interspecific interactions ($\alpha_{i,j}$). A diffuse Normal (0, 100) prior was used for each of the $\beta_{i,1}$ and $\beta_{i,2}$, and Normal(0, 10) and Normal(0, σ_r^2) for the log-carrying capacities and the intrinsic growth rates of species *i* respectively. An inverse Wishart prior (Gelman and Hill, 2007) with scale matrix Ω was used as the identity matrix and *S*+1 degrees of freedom, where *S* is number of species, for the covariance matrix C. For the standard deviation of δ_i^2 a Uniform (0, 10) prior was selected.

The model ran 200,000 iterations of three Markov chains using dispersed parameter values as starting values and discarded the first 50,000 samples of each chain as burn-in, thinning the remainder to every 10th sample. The convergence was assessed visually using trace plots, through the mixing of the chains and sample autocorrelation plots.

3 | RESULTS

Population models of annual variability in numbers of breeding pairs produced similar broad trends across both study sites, with Adélie and chinstrap populations experiencing overall declines, whilst the gentoo populations increased (Fig. 2). Annual fluctuations around these trends were evident, particularly on Signy Island where periodic dips in numbers occurred across the three species in the same year (1991, 1995, 2000, 2013 and 2017).

At Signy Island, the first two principal components (PC) of the PCA explained 61.36% of the variance in the environmental variables (Fig.3a; Table 1). The first PC axis showed the highest positive correlation with air temperature and the lagged SOI and negative correlation with SST the second PC had highest correlations with the lagged SAM and sea ice extent for Signy Island (Table 3). At King George Island, the first two PC of the PCA explained 50.05% of the variance (Fig. 3b; Table 2). The first PC for King George Island had a positive correlation with lagged SOI, lagged SAM and SST and the second PC was positively correlated with air temperature and negatively correlated with sea ice extent (Table 4).

Interestingly, relationships of local environmental variables (SST, SIE and air temp) to regional climate variables (SAM, SOI) differed among the two archipelagos: SST was positively related to SAM/SOI in the South Shetlands but negatively so in the South Orkneys. SIE and air temperatures at the two sites showed opposite loadings along the two PCA axes. Therefore, in the South Orkneys positive SAM/SOI tended to produce higher SIE and warmer air temperatures but cooler SST, whereas in the South Shetlands they produced lower SIE and cooler air temperatures but warmer SST. The population abundances of the three penguin species showed consistent PCA scores in relation to SAM and SOI across the two archipelagos. Adélie and chinstrap penguin abundances were negatively associated with positive SAM/SOI while that of gentoo penguins was positively related. PCA scores of penguin abundance relative to SIE, SST and air temperatures were inconsistent across sites.

The Gompertz multispecies population models run for each archipelago suggested that the main modelled components of interspecific competition, density dependence and environmental covariates had a modest effect on the three species' population trajectories at both King George and Signy Islands. The influence of interspecific competition accounted for less than 2% of the observed population variance for the South Orkneys population (Table 5) and less than 0.4% for the South Shetlands population (Table 6). Linked to this, density-dependence was also found to have little effect, representing less than 6% of the total population variance respectively for any species at the South Orkneys (Table 5; Fig. 4) and less than 1% at South Shetlands (Table 6; Fig. 4). The modelled environmental variables (PCA axes 1 and 2) only accounted for a small proportion of variance in penguin abundance: between 6 and 13% for the South Orkneys (Table 5; Fig. 5) and 7% for the South Shetlands (Table 6; Fig. 5). The model showed that environmental stochasticity (C) has the greatest influence on species' population trends, explaining between 81 and 93% of the annual variation in penguin numbers at the South Orkneys (Table 5) and between 91 and 92% of variation at the South Shetlands (Table 6).

4 | DISCUSSION

Determining the drivers and mechanisms underlying population trends has been a major focus of climate change researchers for decades. Developing this understanding is crucial for conservation of biodiversity and for elucidating impacts under future climate scenarios. Interspecific competition has been shown to alter species' responses to climate change (Araújo and Luoto, 2007; Helland et al., 2011; Pigot and Tobias, 2013) but has often been overlooked in previous studies. This study has applied the modelling techniques of Mutshinda et al. (2011) to *Pygoscelis* penguin population counts in the rapidly shifting climate of the WAP, which allowed us to investigate the relative importance of environmental variables and interspecific competition as drivers of change. Our study is differs from previous investigations of population trends in that we simultaneously model the effects of environment, interspecific competition and density dependence in a single framework, which provides greater power to disentangle these effects and quantify their relative importance.

4.1 | Patterns of population change among species and archipelagos

The broad patterns of population change that we observed, Adélie and chinstrap penguin populations declined while those of gentoo penguins increased, are typical of these species in a wider analyses across the South Shetlands and WAP (Lynch, Naveen, et al., 2012). Elsewhere in the Antarctic (i.e. south of the Polar Front), *Pygoscelis* population trends differ: at the South Sandwich Islands, populations of Adélie and chinstrap penguins have been relatively stable (Lynch, Naveen, et al., 2012) on South Georgia gentoo populations are fluctuating with no long-term trend (Forcada and Trathan, 2009) while in East Antarctica Adélie populations are increasing (Southwell et al., 2015).

4.2 | Principal component analysis

The PCA analyses showed that Adélie and chinstrap responses to environmental variables were similar whilst gentoos showed an opposing response. At both archipelagos, the three species displayed the same relationship with SOI and SAM: Adélies and chinstraps showed a strong negative relationship, whilst gentoos displayed a strong positive relationship (Fig. 3). However, their responses to SIE differed, which is possibly due to the slightly differing sea ice durations and the type of sea ice at each site (Stammerjohn et al., 2012). The local environmental variables showed differing relationships with SAM and SOI across the two sites, which meant our replicated study design offered power to disentangle these often interrelated effects. Penguin abundances showed consistent patterns with SAM and SOI across the two sites, as indicated by PCA, but their association with local variables differed, which indicates that climate variables operating across the region were more important in driving penguin population trends than local sea ice extent in winter or the air/sea temperatures during the breeding season.

SAM and SOI are large-scale drivers of climate in the Scotia Sea and WAP, influencing environmental variables such as wind, SST, air temperature, precipitation and sea ice (Turner, 2004; Stammerjohn et al., 2008; Kwok et al., 2016). A negative SOI or SAM phase usually produces colder air and sea surface temperatures, higher primary productivity and more extensive sea ice extent during winter which in turn enhance krill recruitment and growth

(Richerson et al., 2017). The warming of the WAP and Scotia Sea region has been associated with a general southward contraction of krill through time (Atkinson et al., 2019) and reductions in Adélie and chinstrap penguin populations (Trivelpiece et al., 2011; Lynch, Naveen, et al., 2012), providing support for the “krill habitat hypothesis”. These region-wide changes in the availability of these species’ main prey explain why large scale climate covariates are more strongly and consistently related to penguin population changes than local covariates.

The increase in gentoo populations in relation to positive SAM and SOI is inconsistent with the krill habitat hypothesis, which might be a result of them being less dependent on krill for prey than the other two species (Ratcliffe and Trathan, 2012). Reduced sea ice extent during winter would be expected to increase the survival rates of gentoos, as they are a resident (Hinke et al., 2017) and thought to be ice intolerant species (Lynch, Naveen, et al., 2012). Therefore, the reduced winter SIE during periods of positive SAM and SOI would be expected to produce increases in gentoo populations, providing support for the “sea ice hypothesis”. The inconsistent effects of local SIE on population trends across the archipelagos contradict this expectation though: gentoos were negatively correlated with local SIE in the South Shetlands but showed a weak positive association the South Orkneys. Further studies of winter movements and overwinter survival of gentoo penguins at the two archipelagos in relation to SIE are required to test the sea ice hypothesis further.

4.3 | Multi-species population model

The population model results, using the environmental variables selected by the PCA, demonstrated that environmental stochasticity was the main driver of the observed population trends and only a small proportion of variance was explained by the specific environmental covariates. Mutshinda et al. (2011) also found that environmental stochasticity explained the greatest amount of variance in long-term population fluctuations. Environmental stochasticity consists of environmental drivers that are not included in the environmental covariates (including the same variables but sampled during different seasons or lags), or biotic variables such as predation, disease and prey availability. The most influential of these is likely to be krill availability, whose stocks tend to be subject to pronounced four or five year cycles that are is only partially explained by environmental covariates such as SAM or SOI (Fielding et al., 2014; Richerson et al., 2017). Local availability of krill to penguins can also be further influenced by its advection in ocean currents and wind, which are inherently unpredictable (Hofmann et al., 1998; Flores et al., 2012). Additionally, predation is likely to be an important factor and has been shown to be an influential driver of penguin population trends in combination with bottom-up environmental effects (Horswill et al., 2014). Penguin population change is a complex outcome of variability in survival rates, fecundity, immigration and emigration, all of which can be affected by multiple drivers operating in varying locations, seasons or lags. It is therefore to be expected that the small suite of covariates fitted in this study did not explain a large proportion of the environmental variance in penguin abundance.

The model found that species interactions explained a trivial proportion of the variation in population changes across species and sites and so did not support the “competitive exclusion hypothesis”. We therefore conclude that the decline of Adélie and chinstrap penguins are due to opposite reactions to the same environmental driver rather than gentoo penguins usurping the other two species from their niches. A similar analysis, found that long-term common guillemot *Uria aalge* population trends were affected by prey abundance but not competition from sympatric and congeneric Brünnich’s guillemot (Durant et al., 2012).

Competition is predicted to increase as shared resources decline (Hutchinson, 1957) and so the southward contraction in krill biomass in the Scotia Sea and WAP region (Atkinson et al., 2019) might be expected to have caused elevated competition among the species. It is likely that niche partitioning among the species has prevented this outcome. During the breeding season Adélie and chinstrap penguin niches are segregated by allochrony (Trivelpiece et al., 1987; Clewlow et al., 2019) and foraging behaviour such as dive depth (Clewlow et al., 2019), while gentoos niches are segregated from the other species by diet, shorter foraging ranges and deeper dives (Kokubun et al., 2010; Wilson, 2010; Herman et al., 2017; Pickett et al., 2018). During winter, the species segregate completely with gentoos being resident (Hinke et al., 2017), chinstraps migrating to open water off the South Sandwich Islands (South Orkneys population) or SE Pacific (South Shetlands population (Chapter 3, Hinke et al. 2015) and Adélies migrating into the pack ice and marginal ice zone of the Weddell Sea from both archipelagos (Dunn et al., 2011; Hinke et al., 2015). Furthermore, despite increases in gentoo penguin populations they are small compared to the other two species in the region (Poncet and Poncet, 1985; Hinke et al., 2007; Dunn et al., 2016) and so would not be expected to exert high levels of competition at anything other than local scales.

While competition among the penguin species was not evident, that from other biota, such as recovering whales and seals, as proposed by the “krill surplus hypothesis” is not addressed. No annual index of whale abundance was available for inclusion as a competitor term in the model, so this variance would have been subsumed into the variance explained by environmental stochasticity. Trivelpiece et al. (2011) proposed that the competition from marine mammals was an important consideration in the decline of penguins at the South Sandwich study colonies, but this was a supposition since no evidence was presented to support this claim. More recently, foodweb simulations indicate that environmental change, rather than whale and seal recovery is more likely to explain the decline of krill stocks and penguins in the Scotia Sea region, which diminishes the support for the krill surplus hypothesis (Surma et al., 2014).

5 | CONCLUSION

Our approach has provided further insight into the role of environmental factors and interspecific interactions in driving *Pygoscelis* population trends and how this varies greatly among conspecifics and archipelagos. The analysis revealed that interspecific competition is likely to be a minor driver of these population trends. We found that the environmental covariates that correlated with penguin population trends in previous studies only explained a small proportion of the variance in population change, with environmental stochasticity being the main driver. The models therefore emphasised the need to explore alternative environmental or biotic drivers of penguin population change rather than continuing to explore those found to be “important” in the past. Food availability is preeminent among these, and time series of acoustic krill biomass off the South Shetlands, South Orkneys and South Georgia are available since 1997 to support such endeavours (Fielding et al., 2014; Richerson et al., 2017) but were not able to be included in this study.

Further investigation should focus on the effects of environmental and biotic changes upon individual demographic rates, such as survival and breeding success, so that environmental data can be sampled from appropriate seasons, locations and time lags. These can then be used to construct an integrated population model which have the power to combine environmental, demographic and count data in order to understand past change in penguin numbers and predict those that might occur in the future (Horswill et al., 2016).

Penguins are a crucial component of the Antarctic ecosystem, linking trophic levels and transporting nutrients between land and sea and enriching both via their faeces. Therefore, their conservation is crucial in maintaining a healthy and fully functioning Antarctic ecosystem for the benefit of both terrestrial and marine species living there.

6 | FIGURES

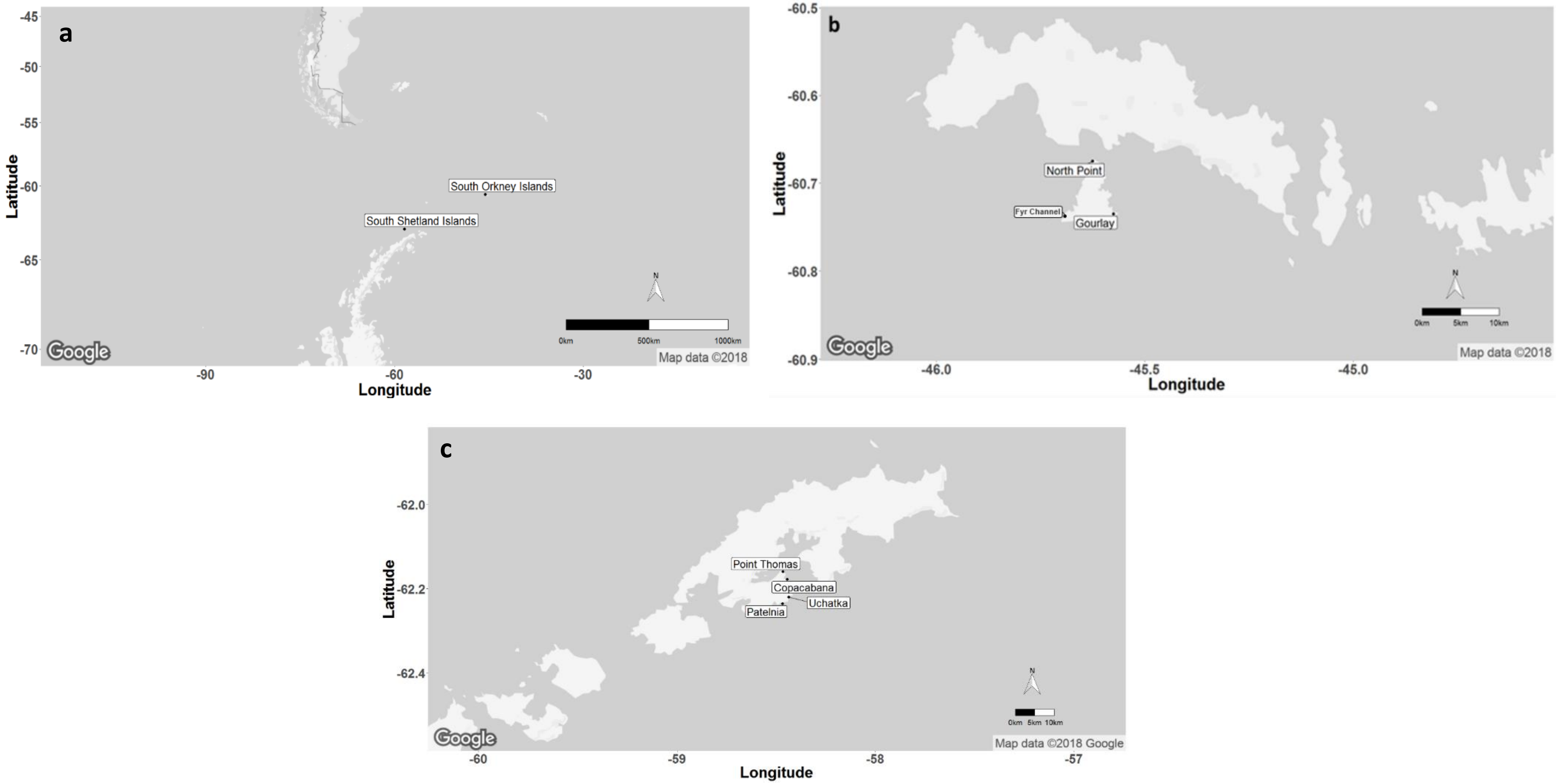


Figure 1 – Maps of (a) the region with the locations of the two study archipelagos, (b) a fine-scale map of the study colonies on Signy Island, South Orkney archipelago and (c) a fine-scale view the study colonies on King George Island, South Shetlands archipelago. Maps were produced by the authors using ggmap and ggrepel in R version 3.3.0 (Kahle and Wickham, 2016; Slowikowski et al., 2018).

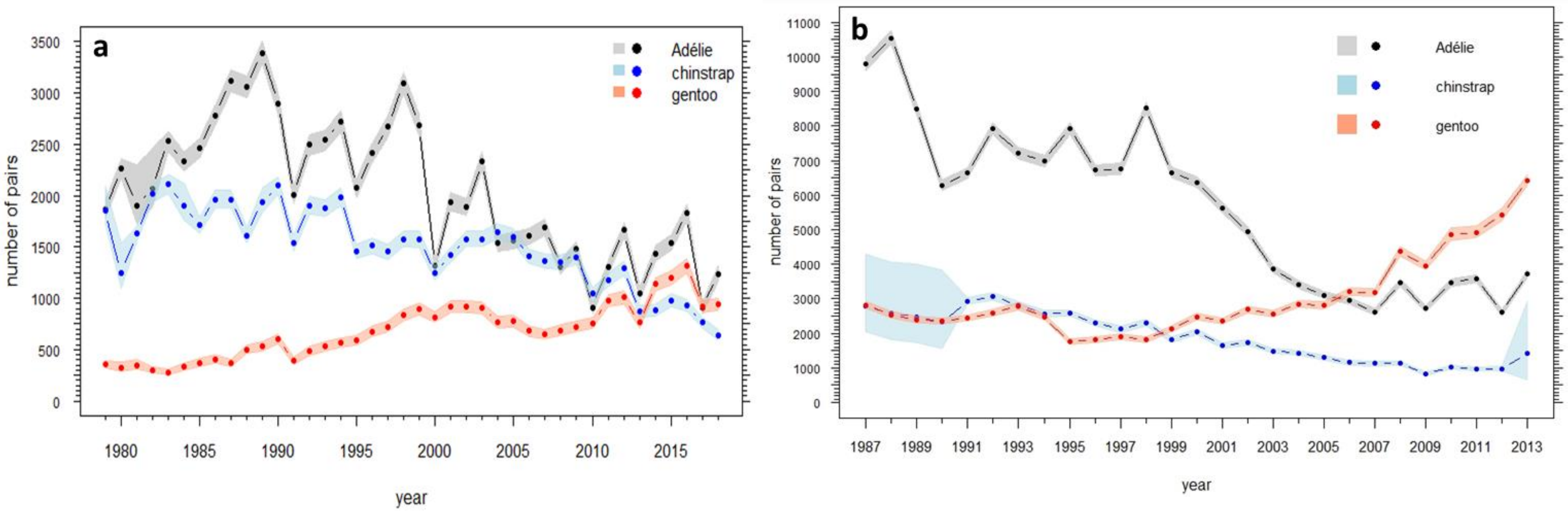


Figure 2 – Modelled *Pygoscelis* penguin population trends at (a) Signy Island, South Orkney Islands and (b) King George Island, South Shetland Islands with 95% confidence limits (shaded bands). Note: Signy Island gentoo data is actual number of pairs counted annually in whole island population. Signy Island Adélie and chinstrap data is modelled from numbers of pairs counted annually in selected study colonies.

Table 1 – Principal Component Analysis results for South Orkney Islands (Dim = principal component axes).

Eigenvalues	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5
Variance	1.63	1.43	0.88	0.56	0.50
% of variance	32.67	28.69	17.58	11.15	9.91
Cumulative % of variance	32.67	61.36	78.932	90.09	100.00

Table 2 – Principal Component Analysis results for South Shetland Islands (Dim = principal component axes).

Eigenvalues	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5
Variance	1.37	1.14	0.96	0.89	0.65
% of variance	27.35	22.70	19.26	17.70	12.99
Cumulative % of variance	27.35	50.05	69.31	87.01	100

Table 3 – Model selected environmental variables for South Orkney Islands (Dim = principal component axes).

Environmental variable	Dim 1	Dim 2	Dim 3	Dim 4	Dim 5
Air temperature	0.67	-0.28	-0.51	0.46	0.03
SAM index	0.43	0.75	0.12	0.08	-0.48
SOI index	0.64	-0.05	0.71	0.15	0.27
SST	-0.74	0.35	0.14	0.55	0.09
Sea Ice Extent	0.20	0.82	-0.30	-0.14	0.43

Table 4 – Model selected environmental variables for South Shetlands (Dim = principal component axes).

Environmental variable	**Dim 1**	**Dim 2**	**Dim 3**	**Dim 4**	**Dim 5**
Air temperature	-0.28	0.79	0.34	0.08	0.41
SAM index	0.78	-0.22	-0.03	-0.21	0.55
SOI index	0.60	0.30	0.55	-0.30	-0.40
SST	0.54	0.23	-0.17	0.78	-0.10
Sea Ice Extent	-0.16	-0.56	0.72	0.36	0.11

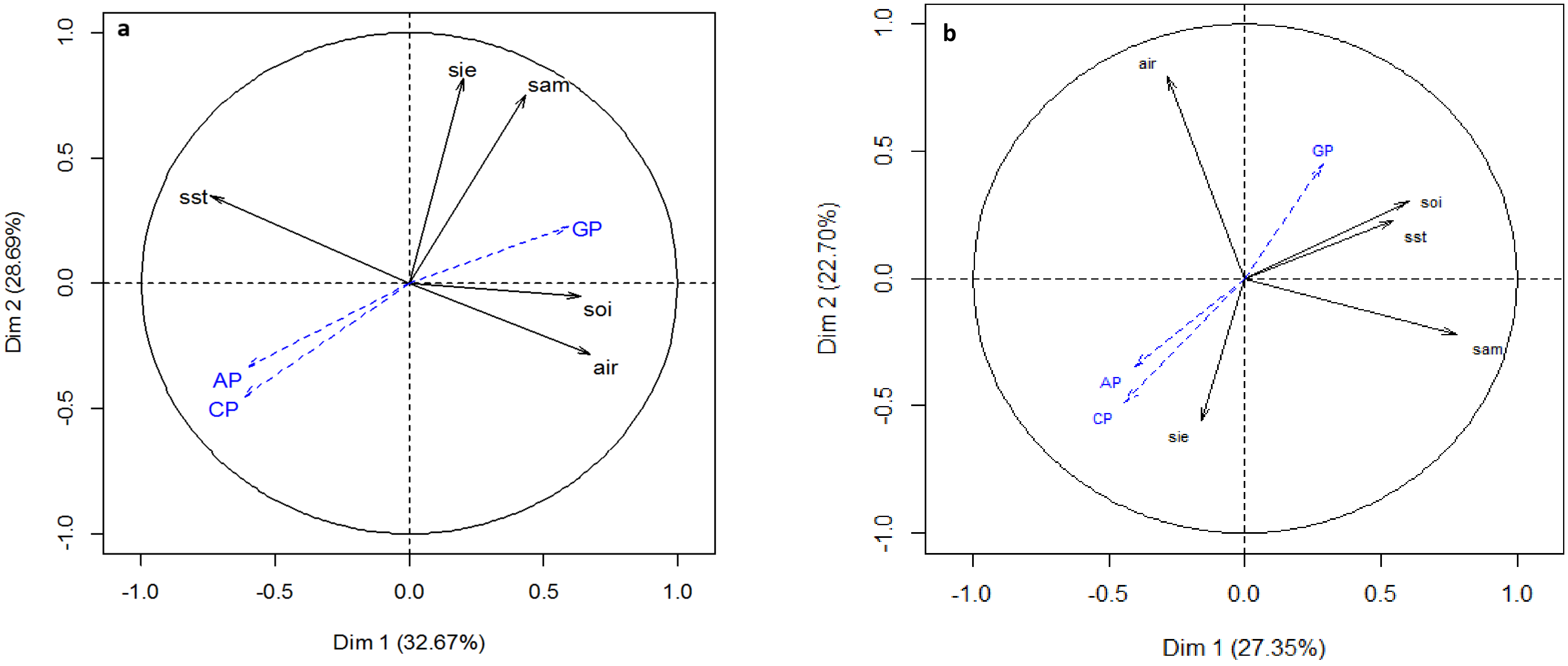


Figure 3 – First and second Principal Components from the Principal Component Analysis based on environmental variables (SST=sea surface temperature, SIE=Sea ice extent, SAM=Southern Annular Mode, SOI=Southern Oscillation Index, AIR=October air temperature) with the abundance series of each penguin species incorporated as supplementary variables (AP=Adélie penguin, CP=chinstrap penguin, GP=gentoo penguin) for the South Orkney Islands (a) and the South Shetland Islands (b).

Table 5 – Estimates of components of the temporal variance and proportions of the different components with respect to the total temporal variance for the South Orkney Islands.

Component	**Adélie penguin**		**chinstrap penguin**		**gentoo penguin**	
	value	**proportion of total**	**value**	**proportion of total**	**value**	**proportion of total**
Total	0.11 (0.06 - 0.18)	-	0.06 (0.04 - 0.09)	-	0.06 (0.04 - 0.10)	-
density-dependence ($\alpha_{i,i}$)	0.0075 (0 - 0.05)	0.06 (0.00001 - 0.31)	0.0007 (0 - 0.01)	0.01 (0 - 0.09)	0.0009 (0 - 0.01)	0.02 (0 - 0.10)
Interspecific competition ($\alpha_{i,j;\, i \neq j}$)	0.002 (0 - 0.02)	0.015 (0 - 0.13)	0.0002 (0 - 0.002)	0.002 (0 - 0.03)	0.00003 (0 - 0.0003)	0.0005 (0 - 0.005)
Environmental covariates ($\beta_{i,PC}$)	0.01 (0.001 - 0.04)	0.11 (0.01 - 0.3)	0.01 (0.001 - 0.02)	0.13 (0.01 - 0.30)	0.003 (0.0001- 0.01)	0.06 (0.002 - 0.18)
Environmental stochasticity (C)	0.10 (0.06 - 0.16)	0.81 (0.47 - 0.98)	0.06 (0.03 - 0.09)	0.86 (0.66 - 0.98)	0.06 (0.04 - 0.10)	0.93 (0.79 – 1.00)

Table 6 – Estimates of components of the temporal variance and proportions of the different components with respect to the total temporal variance for the South Shetland Islands.

Component	**Adélie penguin**		**chinstrap penguin**		**gentoo penguin**	
	value	**proportion of total**	**value**	**proportion of total**	**value**	**proportion of total**
Total	0.08 (0.05- 0.16)	-	0.08 (0.04 - 0.14)	-	0.07 (0.04 - 0.13)	-
density-dependence ($\alpha_{i,i}$)	0.002 (0 - 0.01)	0.01 (0 - 0.12)	0.001 (0 - 0.007)	0.01 (0 - 0.09)	0.0003 (0 - 0.003)	0.004 (0 - 0.03)
Interspecific competition ($\alpha_{i,j;\ i\neq j}$)	0.0006 (0 - 0.005)	0.004 (0 - 0.05)	0.0002 (0 - 0.001)	0.002 (0 - 0.01)	0.00006 (0 - 0.0005)	0.0007 (0 - 0.007)
Environmental covariates ($\beta_{i,PC}$)	0.007 (0.0002 - 0.03)	0.07 (0.002 - 0.24)	0.006 (0.0001 - 0.02)	0.07 (0.002 - 0.22)	0.006 (0.0001 - 0.02)	0.07 (0.002 - 0.24)
Environmental stochasticity (C)	0.09 (0.04 - 0.16)	0.91 (0.70 – 1.00)	0.08 (0.04 - 0.14)	0.92 (0.74 – 1.00)	0.07 (0.04 - 0.13)	0.92 (0.75 – 1.00)

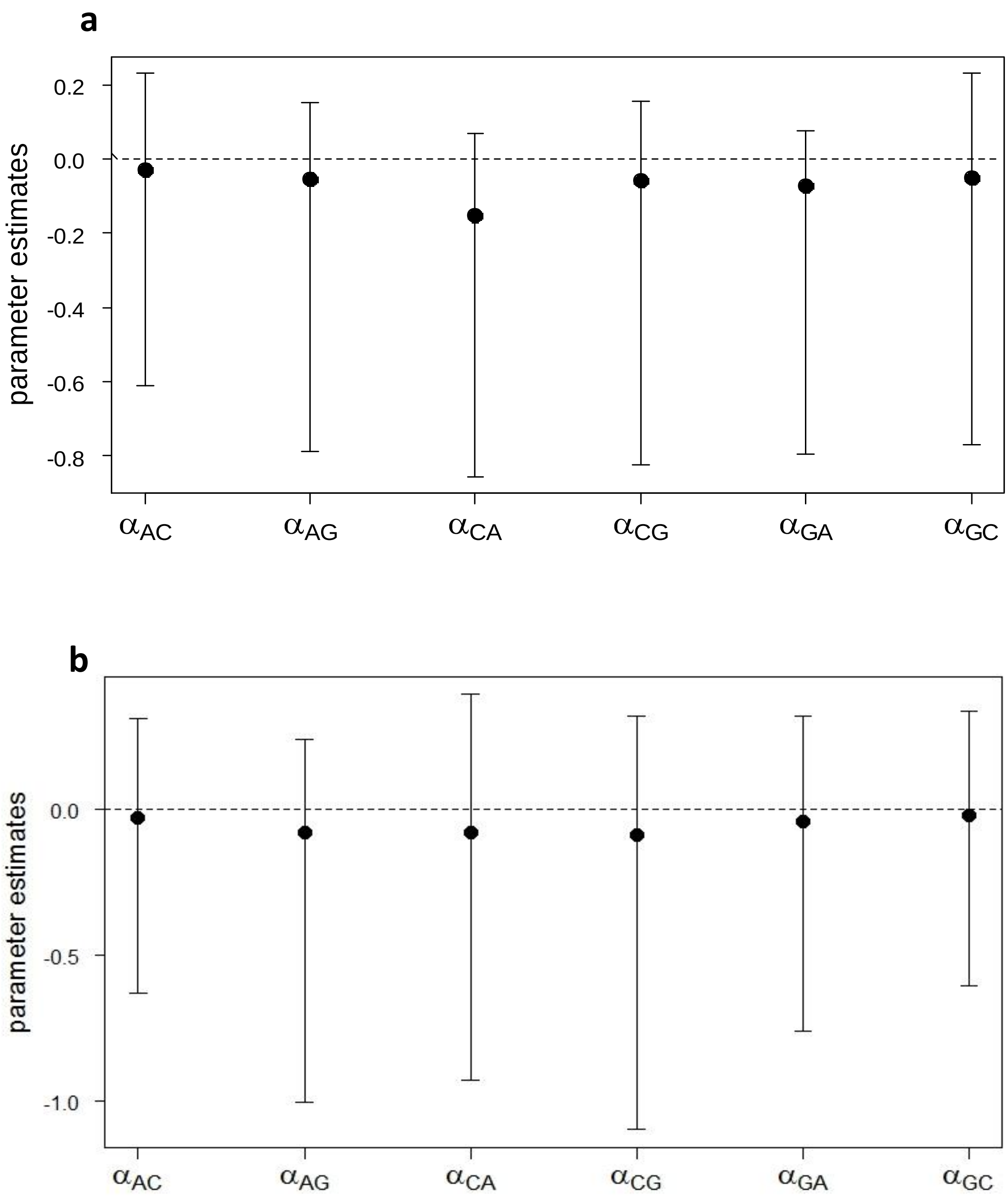


Figure 4 – Estimated means and credible intervals (95%) parameters representing the effects of species interactions ($\alpha_{i,j;\, i \neq j}$) on the growth of individual penguin species on the South Orkney Islands (a) and South Shetland Islands (b). A, C and G correspond to Adélie, chinstrap and gentoo penguins respectively so AC denotes Adélie compared to chinstrap.

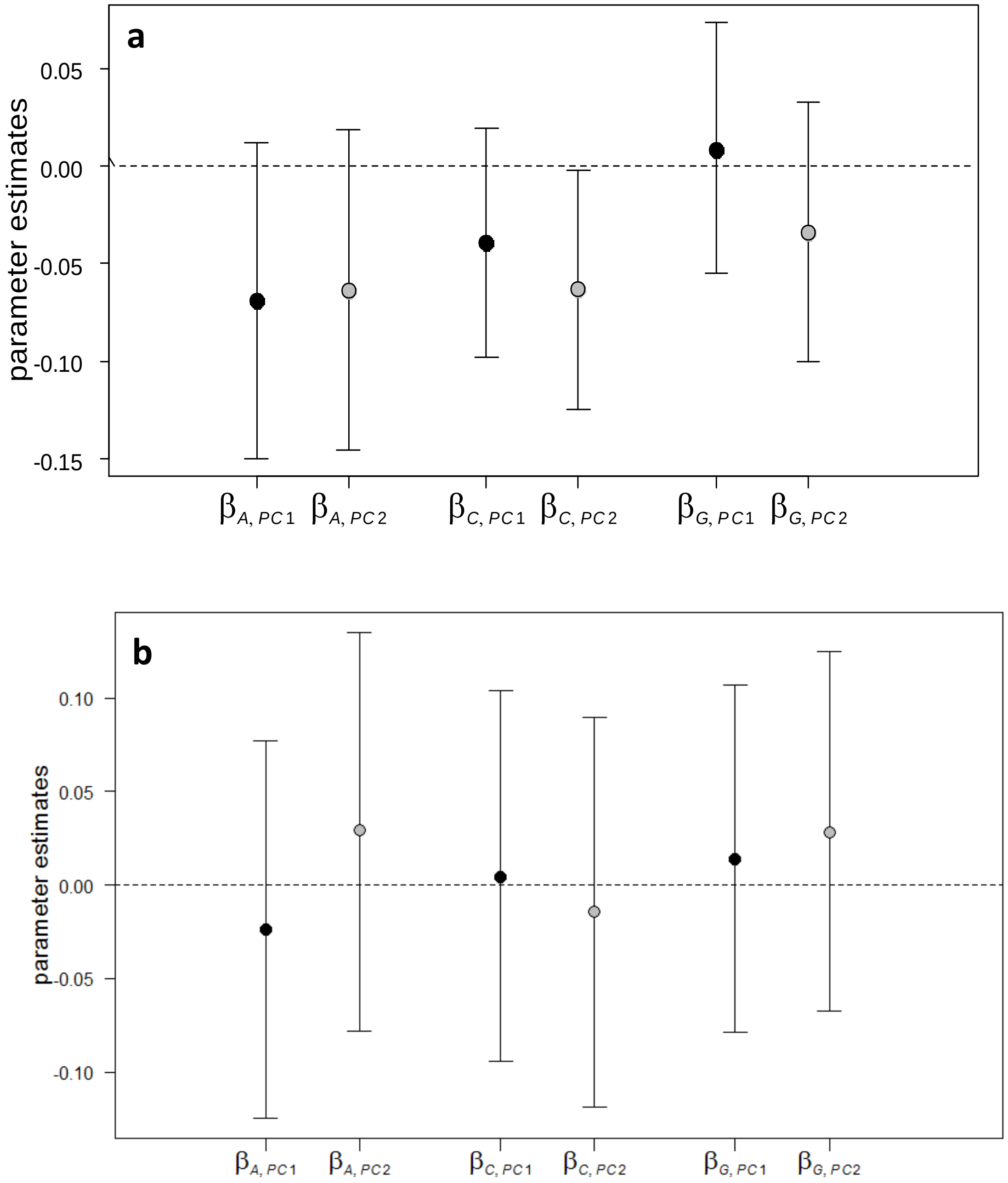


Figure 5 – Estimated means and credible intervals (95%) for environmental fixed effects denoted by Principal Components (PC1 and PC2) on the growth of individual penguin species at the South Orkney Islands (a) and South Shetland Islands (b). A, C and G correspond to Adélie, chinstrap and gentoo penguins respectively.

7 | REFERENCES

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* 16: 743–753.

Atkinson, A., S. L. Hill, E. A. Pakhomov, V. Siegel, C. S. Reiss, V. J. Loeb, D. K. Steinberg, et al. 2019. Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nature Climate Change* 9: 142–147.

Barbraud, C., P. Rivalan, P. Inchausti, M. Nevoux, V. Rolland, and H. Weimerskirch. 2011. Contrasted demographic responses facing future climate change in Southern Ocean seabirds. *Journal of Animal Ecology* 80: 89–100.

Barbraud, C., and H. Weimerskirch. 2003. Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270: 2111–2116.

Barnagaud, J.-Y., V. Devictor, F. Jiguet, M. Barbet-Massin, I. L. Viol, and F. Archaux. 2012. Relating Habitat and Climatic Niches in Birds. *PLOS ONE* 7: e32819.

Bolker, B. 2008. Ecological models and data in R. Princeton University Press, Princeton, N.J.

British Antarctic Survey. 2018. BAS READER Project - MetData. Website https://legacy.bas.ac.uk/met/READER/surface/Orcadas.All.temperature.html [accessed 23 March 2018].

Cavalieri, D. J., C. L. Parkinson, P. Gloersen, and H. J. Zwally. 2016. Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data, Version 1. Boulder, Colorado USA. NASA National Snow and Ice Data Center Distributed Active Archive Center. [Updated yearly, accessed 21/11/2018].

CCAMLR. 2014. CCAMLR Ecosystem Monitoring Programme, Standarda Methods. Part 1: Standard Methods for Monitoring Parameters of Predator Species; Method A3 - Breeding population size: A Ground count. Hobart, Tasmania.

Clarke, A., E. J. Murphy, M. P. Meredith, J. C. King, L. S. Peck, D. K. A. Barnes, and R. C. Smith. 2007. Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 362: 149–166.

Clewlow, H. L., A. Takahashi, S. Watanabe, S. C. Votier, R. Downie, and N. Ratcliffe. 2019. Niche partitioning of sympatric penguins by leapfrog foraging is resilient to climate change. *Journal of Animal Ecology* 88: 223–235.

Commission for the Conservation of Antarctic Marine Living Resources. 2019. Southern Ocean Antarctic krill fishery. Website https://www.ccamlr.org/en/fisheries/krill [accessed 10 July 2019].

Cullen, J. M., L. E. Chambers, P. C. Coutin, and P. Dann. 2009. Predicting onset and success of breeding in little penguins Eudyptula minor from ocean temperatures. *Marine Ecology Progress Series* 378: 269–278.

De Valpine, P., and A. Hastings. 2002. Fitting population models incorporating process noise and observation error. *Ecological Monographs* 72: 57–76.

Donald, P. F., K. Gedeon, N. J. Collar, C. N. Spottiswoode, M. Wondafrash, and G. M. Buchanan. 2012. The restricted range of the Ethiopian Bush-crow *Zavattariornis stresemanni* is a consequence of high reliance on modified habitats within narrow climatic limits. *Journal of Ornithology* 153: 1031–1044.

Dugger, K. M., G. Ballard, D. G. Ainley, P. O. Lyver, and C. Schine. 2014. Adélie penguins coping with environmental change: results from a natural experiment at the edge of their breeding range. *Frontiers in Ecology and Evolution* 2: 1–12.

Dunn, M. J., J. A. Jackson, S. Adlard, A. S. Lynnes, D. R. Briggs, D. Fox, and C. M. Waluda. 2016. Population Size and Decadal Trends of Three Penguin Species Nesting at Signy Island, South Orkney Islands. *PLOS ONE* 11: e0164025.

Dunn, M. J., J. R. D. Silk, and P. N. Trathan. 2011. Post-breeding dispersal of Adélie penguins (*Pygoscelis adeliae*) nesting at Signy Island, South Orkney Islands. *Polar Biology* 34: 205–214.

Durant, J. M., Y. V. Krasnov, N. G. Nikolaeva, and N. C. Stenseth. 2012. Within and between species competition in a seabird community: statistical exploration and modeling of time-series data. *Oecologia* 169: 685–694.

Fielding, S., J. L. Watkins, P. N. Trathan, P. Enderlein, C. M. Waluda, G. Stowasser, G. A. Tarling, and E. J. Murphy. 2014. Interannual variability in Antarctic krill (Euphausia superba) density at South Georgia, Southern Ocean: 1997–2013. *ICES Journal of Marine Science* 71: 2578–2588.

Flores, H., A. Atkinson, S. Kawaguchi, B. A. Krafft, G. Milinevsky, S. Nicol, C. Reiss, et al. 2012. Impact of climate change on Antarctic krill. *Marine Ecology Progress Series* 458: 1–19.

Forcada, J., and P. N. Trathan. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology* 15: 1618–1630.

Forcada, J., P. N. Trathan, K. Reid, E. J. Murphy, and J. P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* 12: 411–423.

Fraser, W. R., W. Z. Trivelpiece, D. G. Ainley, and S. G. Trivelpiece. 1992. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biology* 11: 525–531.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press.

George, E. I., and R. E. McCulloch. 1993. Variable Selection Via Gibbs Sampling. *Journal of the American Statistical Association* 88: 881–889.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. *Trends in Ecology & Evolution* 25: 325–331.

Guinet, C., O. Chastel, M. Koudil, J. P. Durbec, and P. Jouventin. 1998. Effects of warm sea–surface temperature anomalies on the blue petrel at the Kerguelen Islands. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 265: 1001–1006.

Helland, I. P., A. G. Finstad, T. Forseth, T. Hesthagen, and O. Ugedal. 2011. Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology* 80: 539–547.

Herman, R. W., F. C. L. Valls, T. Hart, M. V. Petry, W. Z. Trivelpiece, and M. J. Polito. 2017. Seasonal consistency and individual variation in foraging strategies differ among and within Pygoscelis penguin species in the Antarctic Peninsula region. *Marine Biology* 164: 115.

Hijmans, R. J. 2017. Raster - R package version 2.6-7. *https://cran.r-project.org/web/packages/raster/vignettes/Raster.pdf*.

Hill, S. L., T. Phillips, and A. Atkinson. 2013. Potential Climate Change Effects on the Habitat of Antarctic Krill in the Weddell Quadrant of the Southern Ocean. *PLOS ONE* 8: e72246.

Hinke, J. T., A. M. Cossio, M. E. Goebel, C. S. Reiss, W. Z. Trivelpiece, and G. M. Watters. 2017. Identifying Risk: Concurrent Overlap of the Antarctic Krill Fishery with Krill-Dependent Predators in the Scotia Sea. *PLOS ONE* 12: e0170132.

Hinke, J. T., M. J. Polito, M. E. Goebel, S. Jarvis, C. S. Reiss, S. R. Thorrold, W. Z. Trivelpiece, and G. M. Watters. 2015. Spatial and isotopic niche partitioning during winter in chinstrap and Adélie penguins from the South Shetland Islands. *Ecosphere* 6: 1–32.

Hinke, J. T., K. Salwicka, S. G. Trivelpiece, G. M. Watters, and W. Z. Trivelpiece. 2007. Divergent responses of *Pygoscelis* penguins reveal a common environmental driver. *Oecologia* 153: 845–855.

Hofmann, E. E., J. M. Klinck, R. A. Locarnini, B. Fach, and E. Murphy. 1998. Krill transport in the Scotia Sea and environs. *Antarctic Science* 10: 406–415.

Horswill, C., J. Matthiopoulos, J. A. Green, M. P. Meredith, J. Forcada, H. Peat, M. Preston, et al. 2014. Survival in macaroni penguins and the relative importance of different drivers: individual traits, predation pressure and environmental variability. *Journal of Animal Ecology*: 1057–1067.

Horswill, C., N. Ratcliffe, J. A. Green, R. A. Phillips, P. N. Trathan, and J. Matthiopoulos. 2016. Unravelling the relative roles of top-down and bottom-up forces driving population change in an oceanic predator. *Ecology* 97: 1919–1928.

Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbour Symposia on Quantitive Biology* 22: 415–427.

Josse, J., and F. Husson. 2012. Handling missing values in exploratory multivariate data analysis methods. *Journal de la Société Française de Statistique* 153: 79–99.

Kahle, D., and H. Wickham. 2016. ggmap - Spatial Visualization with ggplot2. R package version 2.6.1.

Kokubun, N., A. Takahashi, Y. Mori, S. Watanabe, and H.-C. Shin. 2010. Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Marine Biology* 157: 811–825.

Kwok, R., J. C. Comiso, T. Lee, and P. R. Holland. 2016. Linked trends in the South Pacific sea ice edge and Southern Oscillation Index. *Geophysical Research Letters* 43: 10,295-10,302.

Le, S., and F. Husson. 2008. FactoMineR: An R package for multivariate analysis. *Journal of Statistical Software* 25: 1–18.

Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. *American Naturalist* 172: E48–E66.

Lynch, H. J., W. F. Fagan, R. Naveen, S. G. Trivelpiece, and W. Z. Trivelpiece. 2012. Differential advancement of breeding phenology in response to climate may alter staggered breeding among sympatric *Pygoscelid* penguins. *Marine Ecology Progress Series* 454: 135–145.

Lynch, H. J., R. Naveen, P. N. Trathan, and W. F. Fagan. 2012. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93: 1367–1377.

Marshall, G. J. 2003. Trends in the Southern Annular Mode from Observations and Reanalyses. *Journal of Climate* 16: 4134–4143.

Milazzo, M., S. Mirto, P. Domenici, and M. Gristina. 2013. Climate change exacerbates interspecific interactions in sympatric coastal fishes. *Journal of Animal Ecology* 82: 468–477.

Murphy, E. J., S. E. Thorpe, G. A. Tarling, J. L. Watkins, S. Fielding, and P. Underwood. 2017. Restricted regions of enhanced growth of Antarctic krill in the circumpolar Southern Ocean. *Scientific Reports* 7.

Mutshinda, C. M., R. B. O'Hara, and I. P. Woiwod. 2011. A multispecies perspective on ecological impacts of climatic forcing. *Journal of Animal Ecology* 80: 101–107.

Nicol, S., J. Foster, and S. Kawaguchi. 2012. The fishery for Antarctic krill – recent developments. *Fish and Fisheries* 13: 30–40.

NOAA/OAR/ESRL PSD, Boulder, Colorado, USA. 2018. NOAA_OI_SST_V2 data. Website https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html.

Parkinson, C. L., J. C. Comiso, H. J. Zwally, D. J. Cavalieri, P. Gloersen, and W. J. Campbell. 1987. Arctic Sea Ice, 1973–1976: Satellite Passive-Microwave Observations. NASA Goddard Space Flight Center; Greenbelt, MD, USA.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.

Pickett, E. P., W. R. Fraser, D. L. Patterson-Fraser, M. A. Cimino, L. G. Torres, and A. S. Friedlaender. 2018. Spatial niche partitioning may promote coexistence of Pygoscelis penguins as climate-induced sympatry occurs. *Ecology and Evolution* 0: 1–15.

Pierce, D. 2017. ncdf4 - R package version 1.16. *https://cran.r-project.org/web/packages/ncdf4/ncdf4.pdf*.

Pigot, A. L., and J. A. Tobias. 2013. Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters* 16: 330–338.

Plummer, M. 2003. JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Samplin. *in* International Workshop on Distributed Statistical Computing (DSC 2003), Vienna, Austria.

Poncet, S., and J. Poncet. 1985. A survey of penguin breeding populations at the South Orkney Islands. *British Antarctic Survey Bulletin* 68: 71–81.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. *URL https://www.R-project.org/*.

Ratcliffe, N., and P. Trathan. 2012. A review of the diet and at-sea distribution of penguins breeding within the CAMLR Convention Area. *CCAMLR Science* 19: 75–114.

Richerson, K., J. A. Santora, and M. Mangel. 2017. Climate variability and multi-scale assessment of the krill preyscape near the north Antarctic Peninsula. *Polar Biology* 40: 697–711.

Ripa, J., and A. R. Ives. 2003. Food web dynamics in correlated and autocorrelated environments. *Theoretical Population Biology* 64: 369–384.

Saether, B. E., J. Tufto, S. Engen, K. Jerstad, O. W. Rostad, and J. E. Skatan. 2000. Population dynamical consequences of climate change for a small temperate songbird. *Science* 287: 854–856.

Slowikowski, K., A. Schep, S. Hughes, S. Lukauskas, J.-O. Irisson, Z. N. Kamvar, T. Ryan, et al. 2018. ggrepel - Provides text and label geoms for ‘ggplot2’ that help to avoid overlapping text labels. Labels repel away from each other and away from the data points. R package version 0.8.0.

Southwell, C., L. Emmerson, J. McKinlay, K. Newbery, A. Takahashi, A. Kato, C. Barbraud, et al. 2015. Spatially Extensive Standardized Surveys Reveal Widespread, Multi-Decadal Increase in East Antarctic Adélie Penguin Populations. *PLOS ONE* 10: e0139877.

Stammerjohn, S. E., D. G. Martinson, R. C. Smith, X. Yuan, and D. Rind. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. *Journal of Geophysical Research: Oceans* 113.

Stammerjohn, S. E., R. Massom, D. Rind, and D. Martinson. 2012. Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. *Geophysical Research Letters* 39.

Surma, S., E. A. Pakhomov, and T. J. Pitcher. 2014. Effects of Whaling on the Structure of the Southern Ocean Food Web: Insights on the “Krill Surplus” from Ecosystem Modelling. *PLoS ONE* 9.

Svenning, J.-C., D. Gravel, R. D. Holt, F. M. Schurr, W. Thuiller, T. Münkemüller, K. H. Schiffers, et al. 2014. The influence of interspecific interactions on species range expansion rates. *Ecography* 37: 1198–1209.

Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helaouet, et al. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535: 241–245.

Tjørve, K. M. C., and E. Tjørve. 2017. The use of Gompertz models in growth analyses, and new Gompertz-model approach: An addition to the Unified-Richards family. *PLOS ONE* 12: e0178691.

Trathan, P. N., J. P. Croxall, and E. J. Murphy. 1996. Dynamics of Antarctic penguin populations in relation to inter-annual variability in sea ice distribution. *Polar Biology* 16: 321–330.

Trivelpiece, W. Z., J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences* 108: 7625–7628.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. J. Volkman. 1987. Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology* 68: 351–361.

Turner, J. 2004. The El Niño–southern oscillation and Antarctica. *International Journal of Climatology* 24: 1–31.

Turner, J., H. Lu, I. White, J. C. King, T. Phillips, J. S. Hosking, T. J. Bracegirdle, et al. 2016. Absence of 21st century warming on Antarctic Peninsula consistent with natural variability. *Nature* 535: 411–415.

Turner, J., and J. Overland. 2009. Contrasting climate change in the two polar regions. *Polar Research* 28: 146–164.

Urban, M. C., J. J. Tewksbury, and K. S. Sheldon. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proceedings of the Royal Society of London B: Biological Sciences* 279: 2072–2080.

Vaughan, D. G., G. J. Marshall, W. M. Connolley, C. Parkinson, R. Mulvaney, D. A. Hodgson, J. C. King, et al. 2003. Recent Rapid Regional Climate Warming on the Antarctic Peninsula. *Climatic Change* 60: 243–274.

Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. Fromentin, et al. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.

Wilson, R. P. 2010. Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Functional Ecology* 24: 646–657.

Woehler, E. J. 1995. Consumption of Southern Ocean marine resources by penguins. In The penguins (eds P. Dann, I. Norman, P. Reilly). 266-295. Surrey Beatty and Sons, Chipping Norton, Australia.

Chapter 6 - *Synthesis chapter*

This thesis sought to elucidate the mechanisms driving the large-scale population changes observed in *Pygoscelis* penguin in the Western Antarctic Peninsula (WAP)/Scotia Sea region since the 1970s (Dunn et al., 2016) using various data collected from penguins breeding on Signy Island, South Orkney Islands, and King George Island, South Shetland Islands. Since the 1970s, the climate in the region has changed dramatically, with rapid warming and sea ice declines occurring until the late 20th century to be followed by a pause in warming (Stammerjohn et al., 2008; Turner et al., 2016). These changes have shifted the prevailing conditions in the penguins' ecosystem and researchers widely agree that this is driving their population changes (Hinke et al., 2007; Forcada and Trathan, 2009; Lynch, Fagan, et al., 2012). However, the exact mechanisms are still poorly understood. In order to elucidate these mechanisms, we attempted to fill crucial knowledge gaps throughout their annual cycle, with particular focus on the interactions between the three *Pygoscelis* species. These species are crucial components of the Antarctic food web, linking trophic levels and conveying nutrients between land and sea, and thus their conservation is important for the functioning of the Antarctic ecosystem.

The breeding season is the most extensively studied period of the species' life cycle because individuals are consistently located at their colonies and are relatively easily accessible. As the three species, Adélie (*Pygoscelis adeliae*; hereafter Adélie), chinstrap (*P. antarcticus*; hereafter chinstraps) and gentoo penguins (*Pygoscelis papua ellsworthi*; hereafter gentoos), breed sympatrically in our study region, share prey resources (Antarctic krill, *Euphausia superba*) and foraging areas, there is scope for high levels of interspecific competition. Therefore, niche partitioning is particularly important in enabling them to obtain the necessary nutrients for successful breeding. The species display pronounced seasonal allochrony, differences in the timing of activity among species, to reduce levels of interspecific competition (Trivelpiece et al., 1987; Lynch, Fagan, et al., 2012). However, allochrony can be impacted by climate change causing timing shifts and it has been interrupted in other species (Parmesan, 2006). The amount of niche partitioning induced by allochrony, and the effect of leapfrog foraging, had not been quantified before our analyses in Chapter 2. We compared data from Adélies and chinstraps, as detailed tracking data for gentoos was not available, to reveal that if the degree of allochrony is reduced, i.e. the number of days offset in the start of breeding between the species, then niche partitioning by leapfrog foraging is reduced. However, analysis of long-term phenology data shows that allochrony is preserved as air temperatures warm and penguin laying dates advance (+1.02 days per 1^{o}C increase in October air temperature). We concluded that competitor matching, due to differing rates of phenological response to environmental change, is unlikely to arise among the two species, and thus will not be a significant contributing factor to the large-scale population declines observed for these two species, as investigated in Chapter 5.

Interspecific competition between these congeneric species is thought to occur throughout their annual cycle and therefore also influence their behaviour throughout the entire period. This means that in order to fully understand the mechanisms underlying the observed population changes we must develop a full understanding of impacts and interactions throughout the species’ life cycle. Adélie and gentoo non-breeding behaviour in the WAP region is relatively well known (Tanton et al., 2004; Dunn et al., 2011; Hinke et al., 2015) but our knowledge of chinstrap behaviour during their non-breeding period is relatively limited (except see Hinke et al. 2015), meaning there is a significant period of influence that is currently not factored into population analyses. In Chapter 3 we addressed this knowledge gap for chinstraps breeding on Signy Island. Utilising geolocator tracking tags, we identified the migration routes and over-winter sites of chinstrap penguins from the South Orkney Islands for the first time and compared it with similar data from the South Shetlands archipelago to determine if niche partitioning also played a role during this period. Birds from the two archipelagos displayed near complete partitioning of over-winter sites, indicating strong migratory connectivity. Ocean currents appeared to play a role in the migration routes of birds from both archipelagos and, possibly due to this, they were faithful to both their migration routes and over-winter sites throughout the multi-year study period. The over-wintering areas of the two archipelago populations differed in their long-term sea surface temperature and primary productivity (chlorophyll-a concentration), in terms of their averages, trends, and annual variability. Stable isotope analysis of tail feathers indicated that birds from the South Shetlands archipelago foraged in different marine habitats and consumed prey at a higher tropic level than birds from the South Orkney Islands. Identifying these over-winter sites will assist in elucidating the role of environmental variability during the winter period, since variables for use in population models can be sampled from appropriate locations. Conditions at over-winter sites have been shown to influence breeding success in the following year, survival and juvenile recruitment (Harrison et al., 2011; Bogdanova et al., 2017). However, the population changes occurring at the two archipelagos are happening at a similar rate, suggesting over-winter conditions are not a major driver. The data from the South Orkneys population identified a previously unknown wintering site that will comprise an important interest feature in the South Georgia and South Sandwich Islands Marine Protected Area (SGSSI MPA) and raises questions about potential interactions/competition with the large number of chinstraps breeding in this area, whose winter behaviour is currently unknown.

Developing on our findings of contrasting environmental conditions across the chinstrap over-wintering sites, we investigated the effect of multiple environmental variables on population trends in the final two thesis chapters. Sea ice is a major component of the Antarctic ecosystem and this region experiences large-scale seasonal changes in sea ice concentration (SIC) as it is located near the northern extent of winter ice. Adélie penguin breeding performance has been shown to be strongly influenced by the level of SIC around breeding colonies because the sea ice has multiple direct, reducing access to foraging areas and increasing foraging trip duration, and indirect effects, impacting prey abundance (Fraser et al., 1992; Trathan et al., 1996; Croxall et al., 2002; Jenouvrier et al., 2012). Studies of the effects of SIC on chinstrap breeding success are sparse and inconsistent (Lishman, 1985; Trathan et al., 1996; Rombolá et al., 2003) and we are not aware of any that document its effects on that of gentoos. The three *Pygoscelis* species are widely cited as having different ice tolerances, termed the ‘sea ice hypothesis’ (Fraser et al., 1992; Trivelpiece et al., 2011), with Adélies being described as ‘ice-loving’, chinstraps as ‘ice tolerant’ and gentoos as ‘ice averse’. These differing ice tolerances are also thought to be a major cause of the species’ contrasting population changes in this region. Previous studies have identified a sea ice optima for Adélie breeding and foraging success of 20% (Le Guen et al., 2018) but no such values are available for chinstraps and gentoos. In Chapter 4 we tested the ‘sea ice hypothesis’ and attempted to identify a sea ice optima for breeding and foraging performance of the three species in this region. Metrics of breeding and foraging performance, including foraging trip duration, diet composition, fledging mass and breeding productivity, were investigated in relation to SIC within each species’ guard breeding stage foraging range. Interspecific and interannual variation was high for all metrics but SIC only explained variation in trip duration and fledging mass. Our findings do not support the ‘sea ice hypothesis’, that the three *Pygoscelis* penguin species have differential tolerances of sea ice, nor do they support a sea ice optimum in any of the species at this location. Alternative explanations for the contrasting populations trends of the three species here and elsewhere in West Antarctica are likely to include regional changes in food availability, changes in the weather conditions experienced at the breeding colonies and carry-over effects from the non-breeding season.

In the final chapter, Chapter 5, we built on previous studies of climate effects (Forcada et al., 2006; Hinke et al., 2007; Lynch, Fagan, et al., 2012) by also investigating the interaction between these environmental drivers and inter- and intra-specific interactions, which has not been undertaken for this system before. These interactions have been observed to alter species responses to climate change and thus are a potentially important driver of population trends (Helland et al., 2011; Stenseth et al., 2015; Wittwer et al., 2015). A multispecies population model, based on the work of Mushinda et al. (2011), was used to quantify the relative contribution of interspecific competition, environmental variables (including sea ice conditions, air temperature, sea surface temperature and atmospheric variables) and specifically test the competing roles of intra- and interspecific competition on long-term population trajectories of the *Pygoscelis* penguin species from the South Shetland and South Orkney archipelagos. The model found that neither the interactions nor any of the fitted environmental covariates explained a substantial proportion of the population variance, with stochastic environmental variability to be identified as the strongest driver. Environmental stochasticity consists of un-modelled aspects of the physical and biological environment, such as predation by and of other trophic level species, prey dynamics and other intrinsic dynamics, such as local physiogeography or incidence of disease. The most influential of these is likely to be krill availability, whose stocks tend to be subject to pronounced four or five year cycles that are is only partially explained by environmental covariates such as SAM or SOI (Fielding et al., 2014; Richerson et al., 2017). Therefore, obtaining detailed data on prey availability during all phases of the annual cycle is crucial in developing a full picture of the effects of both climate change and species interactions on the observed population trends.

Throughout this thesis a combination of techniques have been utilised to provide novel insights into penguin foraging ecology, migration, breeding success and population trajectories. It has also identified a number of priorities for future research into penguins. The study particularly identified the need for a greater emphasis on modelling the effects of krill biomass, rather than climate variables, upon penguin demographic variables and population trajectories in order to test the krill habitat hypothesis for Adélie and chinstrap penguins more robustly. There is also a need for better data on gentoo penguin survival and winter movements in relation to winter sea ice conditions around the South Shetland and South Orkney Islands in order to test the sea ice hypothesis for this species. The migration routes and wintering areas of the enormous chinstrap colonies at the South Sandwich Islands remain a mystery, meaning tracking data are needed to identify important areas and inform marine spatial planning, particularly if these occur outside the current SGSSI MPA. Comparing long-term patterns of environmental change in the wintering areas of the three archipelagos may also help to explain how the South Sandwich chinstrap population has remained stable (Lynch et al., 2016) whilst those in the South Shetlands and South Orkneys have declined (Lynch, Naveen, et al., 2012; Dunn et al., 2016). Therefore, whilst this project has succeeded in filling some important gaps in our understanding of Pygoscelis behaviour and interactions between the three species, it has not been able to fully answer the overall question due to the complexity of the interacting mechanisms driving the system.

REFERENCES

Bogdanova, M. I., A. Butler, S. Wanless, B. Moe, T. Anker-Nilssen, M. Frederiksen, T. Boulinier, et al. 2017. Multi-colony tracking reveals spatio-temporal variation in carry-over effects between breeding success and winter movements in a pelagic seabird. *Marine Ecology Progress Series*.

Croxall, J. P., P. N. Trathan, and E. J. Murphy. 2002. Environmental change and Antarctic seabird populations. *Science* 297: 1510–1514.

Dunn, M. J., J. A. Jackson, S. Adlard, A. S. Lynnes, D. R. Briggs, D. Fox, and C. M. Waluda. 2016. Population Size and Decadal Trends of Three Penguin Species Nesting at Signy Island, South Orkney Islands. *PLOS ONE* 11: e0164025.

Dunn, M. J., J. R. D. Silk, and P. N. Trathan. 2011. Post-breeding dispersal of Adélie penguins (*Pygoscelis adeliae*) nesting at Signy Island, South Orkney Islands. *Polar Biology* 34: 205–214.

Forcada, J., and P. N. Trathan. 2009. Penguin responses to climate change in the Southern Ocean. *Global Change Biology* 15: 1618–1630.

Forcada, J., P. N. Trathan, K. Reid, E. J. Murphy, and J. P. Croxall. 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology* 12: 411–423.

Fraser, W. R., W. Z. Trivelpiece, D. G. Ainley, and S. G. Trivelpiece. 1992. Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? *Polar Biology* 11: 525–531.

Harrison, X. A., J. D. Blount, R. Inger, D. R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology* 80: 4–18.

Helland, I. P., A. G. Finstad, T. Forseth, T. Hesthagen, and O. Ugedal. 2011. Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology* 80: 539–547.

Hinke, J. T., M. J. Polito, M. E. Goebel, S. Jarvis, C. S. Reiss, S. R. Thorrold, W. Z. Trivelpiece, and G. M. Watters. 2015. Spatial and isotopic niche partitioning during winter in chinstrap and Adélie penguins from the South Shetland Islands. *Ecosphere* 6: 1–32.

Hinke, J. T., K. Salwicka, S. G. Trivelpiece, G. M. Watters, and W. Z. Trivelpiece. 2007. Divergent responses of *Pygoscelis* penguins reveal a common environmental driver. *Oecologia* 153: 845–855.

Jenouvrier, S., M. Holland, J. Stroeve, C. Barbraud, H. Weimerskirch, M. Serreze, and H. Caswell. 2012. Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. *Global Change Biology* 18: 2756–2770.

Le Guen, C., A. Kato, B. Raymond, C. Barbraud, M. Beaulieu, C.-A. Bost, K. Delord, et al. 2018. Reproductive performance and diving behaviour share a common sea-ice concentration optimum in Adélie penguins (Pygoscelis adeliae). *Global Change Biology* 24: 5304–5317.

Lishman, G. S. 1985. The food and feeding ecology of Adélie penguins (Pygoscelis adeliae) and Chinstrap penguins (P. antarctica) at Signy Island, South Orkney Islands. *Journal of Zoology* 205: 245–263.

Lynch, H. J., W. F. Fagan, R. Naveen, S. G. Trivelpiece, and W. Z. Trivelpiece. 2012. Differential advancement of breeding phenology in response to climate may alter staggered breeding among sympatric *Pygoscelid* penguins. *Marine Ecology Progress Series* 454: 135–145.

Lynch, H. J., R. Naveen, P. N. Trathan, and W. F. Fagan. 2012. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93: 1367–1377.

Lynch, H. J., R. White, R. Naveen, A. Black, M. S. Meixler, and W. F. Fagan. 2016. In stark contrast to widespread declines along the Scotia Arc, a survey of the South Sandwich Islands finds a robust seabird community. *Polar Biology* 39: 1615–1625.

Parmesan, C. 2006. Ecological and Evolutionary Responses to Recent Climate Change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669.

Rombolá, E., E. Marschoff, and N. Coria. 2003. Comparative study of the effects of the late pack-ice break-off on chinstrap and Adélie penguins' diet and reproductive success at Laurie Island, South Orkney Islands, Antarctica. *Polar Biology* 26: 41–48.

Stammerjohn, S. E., D. G. Martinson, R. C. Smith, and R. A. Iannuzzi. 2008. Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research Part II: Topical Studies in Oceanography* 55: 2041–2058.

Stenseth, N. C., J. M. Durant, M. S. Fowler, E. Matthysen, F. Adriaensen, N. Jonzén, K.-S. Chan, et al. 2015. Testing for effects of climate change on competitive relationships and coexistence between two bird species. *Proc. R. Soc. B* 282: 20141958.

Tanton, J. L., K. Reid, J. P. Croxall, and P. N. Trathan. 2004. Winter distribution and behaviour of gentoo penguins Pygoscelis papua at South Georgia. *Polar Biology* 27: 299–303.

Trathan, P. N., J. P. Croxall, and E. J. Murphy. 1996. Dynamics of Antarctic penguin populations in relation to inter-annual variability in sea ice distribution. *Polar Biology* 16: 321–330.

Trivelpiece, W. Z., J. T. Hinke, A. K. Miller, C. S. Reiss, S. G. Trivelpiece, and G. M. Watters. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences* 108: 7625–7628.

Trivelpiece, W. Z., S. G. Trivelpiece, and N. J. Volkman. 1987. Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology* 68: 351–361.

Turner, J., H. Lu, I. White, J. C. King, T. Phillips, J. S. Hosking, T. J. Bracegirdle, et al. 2016. Absence of 21st century warming on Antarctic Peninsula consistent with natural variability. *Nature* 535: 411–415.

Wittwer, T., R. B. O'Hara, P. Caplat, T. Hickler, and H. G. Smith. 2015. Long-term population dynamics of a migrant bird suggests interaction of climate change and competition with resident species. *Oikos* 124: 1151–1159.