AN ABSTRACT OF THE THESIS OF

Erin Pickett for the degree of Master of Science in Wildlife Science presented on December 1st, 2016.

Title: Foraging Niche Separation of Adélie (*Pygoscelis adeliae*) and Gentoo (*P. papua*) Penguins During the Breeding Season at Palmer Station, Antarctica

Abstract approved:

_____

Ari S. Friedlaender

Climate-induced range overlap can result in novel interactions between similar species and potentially lead to competitive exclusion. The Western Antarctic Peninsula is one of the most rapidly warming regions on Earth and is experiencing a poleward climate migration. This transition from a polar to sub-polar environment has resulted in a range expansion of the ice-intolerant gentoo penguin (*Pygoscelis papua*) and a coincident decline of ice-obligate Adélie penguins (*P. adeliae*) at Palmer Station, Anvers Island (64°46'S, 64°03'W). Ecologically similar species that share a limited prey resource must occupy disparate foraging niches in order to co-exist. Therefore, the aim of this study was to determine the extent of spatial and dietary niche segregation between Adélie and gentoo penguins during the breeding season at Palmer Station. This research was conducted across six austral breeding seasons, from 2010-2015, which allowed for an investigation of the consistency of niche overlap in the context of resource variability. This study was conducted using a twofold methodological approach involving biotelemetry and diet sampling, and little evidence was found to suggest that foraging competition is a primary driver of penguin population trajectories in this region. While substantial overlap was observed in the diets of Adélie and gentoo penguins, who consumed primarily Antarctic krill (*Euphausia superba*), these results show that Adélie and gentoo penguins partitioned this shared prey resource through horizontal and vertical segregation of their core foraging areas. No evidence was found to suggest that Antarctic krill is a limiting resource during the breeding season or that climate-induced sympatry of Adélie and gentoo

penguins has resulted in competition for prey and the subsequent differing population trajectories. Rather, other physical and biological changes to the ecosystem due to the rapidly changing climate around the Antarctic Peninsula may have stronger influences on the current trends of these two species in this region.

Foraging Niche Separation of Adélie (*Pygoscelis adeliae*) and Gentoo (*P. papua*) Penguins
During the Breeding Season at Palmer Station, Antarctica

by
Erin Pickett

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented December 1, 2016
Commencement June 2017

Master of Science thesis of Erin Pickett presented on December 1, 2016

APPROVED:

_____

Major Professor, representing Wildlife Science

_____

Head of the Department of Fisheries and Wildlife

_____

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

_____

Erin Pickett, Author

ACKNOWLEDGEMENTS

Finally, it goes without saying that I am eternally grateful for the support of my family and friends. I've been challenged in many ways over the past two years and your faith in me has always encouraged me to have more faith in myself.

CONTRIBUTION OF AUTHORS

Dr. Bill Fraser made the data available through the Palmer Long-Term Ecological Research Program. Dr. Fraser and Donna Patterson led data collection efforts in the field and Megan Cimino assisted with tag data processing. Dr. Leigh Torres assisted with analytical methods and interpretation of results, and Dr. Ari Friedlaender assisted in project design and interpretation of results.

TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUED)

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1: GENERAL INTRODUCTION

Species interactions play a large role in determining species distribution and community structure and have become increasingly important to understand in the context of climate change (Urban et al. 2016; Zarnetske et al. 2012). By altering the physical environment, climate change directly affects species physiology, phenology and distribution (Hughes 2000; Walther 2002). When trophically interacting or similar species display differential responses to climate change (e.g. dispersal, extinction, and adaptation) altered biotic interactions ensue (Schweiger et al. 2008; Durant et al. 2007). For example, climate-induced range shifts may result in novel or increased competition between species whose ranges didn't historically overlap (Sinervo et al. 2010). Climate-induced range shifts toward higher elevations and higher latitudes have been observed in a wide variety of taxa including plants, butterflies, birds and mammals (Walther et al. 2002). These range shifts have been primarily due to increasing temperatures and have disproportionally affected mountaintop and polar species that already exist near the edge of their range limits (Parmesan 2006). In addition, the effects of climate change are particularly pronounced in Polar Regions, where many species have evolved life history strategies that rely on sea ice (Moline et al. 2008).

The Western Antarctic Peninsula (WAP) is one of the most rapidly warming regions on Earth (Vaughn et al. 2003). Mid-winter atmospheric temperatures along the WAP have increased more than five times faster than the global average and have altered local and large scale climate processes which have in turn transformed this polar marine ecosystem (Schofield et al. 2010; Ducklow et al. 2007; Vaughn et al. 2003). Sea ice is the keystone physical feature that influences the marine ecosystem along the WAP by serving as habitat for ice-dependent species, driving biogeochemical and physical processes like ocean mixing and ultimately, affecting primary and secondary productivity (Massom & Stammerjohn 2010). The overall decline of sea ice along the WAP is primarily due to changes in the timing of its annual fall advance (later) and spring retreat (earlier), resulting in an annual sea ice season that is on average, nearly 100 days shorter than it was in 1978 (Ducklow et al. 2013). This reduction of sea ice, coupled with warmer winds and increased precipitation, have resulted in a southward climate migration on the WAP, from a polar to a sub-polar environment (Schofield et al. 2010; Clarke et al. 2007).

The ongoing poleward climate migration on the WAP has resulted in the expansion of ice-intolerant species and a contraction of ice-obligate species (Fraser et al. 1992). Key life history stages of these ice-obligate (or polar species) have been disrupted as a result of warming-induced habitat shifts and altered trophic interactions, mediated largely by sea ice loss (Moline et al. 2008). For example, Antarctic krill (*Euphausia superba*) are an ice-obligate species whose abundance and distribution are driven primarily by the seasonality of sea ice (Loeb et al. 1997). Due to their crucial role in transferring energy through the food web, Antarctic krill are a key species in the Southern Ocean; they are the dominant grazers as well as a principal prey item for many top predators in this system including seals, seabirds and whales (Ducklow et al. 2007). The reliance of Antarctic krill on sufficient and reliable sea ice cover and primary productivity has made it particularly vulnerable to climate warming (Loeb et al. 1997). Long term declines in krill stocks in some regions of the Southern Ocean (e.g. the Scotia Arc) are correlated with declines in sea ice and primary productivity (Atkinson et al. 2004). Trends in regions such as the central and southern WAP where krill stocks are currently stable are predicted to mirror declines observed farther north as climate warming and sea ice loss continue (Saba et al. 2014).

Similar to krill, the responses of top predators to sea ice loss are mediated by their life history strategies. Along the WAP, the brush-tailed penguins (genus: *Pygoscelis*) have collectively served as the focal species by which to monitor the effects of sea ice change, potential changes in Antarctic krill populations, and the ecological implications of these changes through higher trophic levels. The *Pygoscelis* genus consists of the Adélie (*P. adeliae*), gentoo (*P.papua*) and chinstrap (*P. antarctica*) penguins. A recent global census estimated the number of breeding pairs of Adélie penguins to be 3.79 million, a population 53% larger than the last estimate in 1993 (Lynch & LaRue 2014; Woehler 1993). These numbers stand in stark contrast to those reported for the Antarctic Peninsula region, where Adélie penguins are decreasing at nearly all breeding sites (Lynch et al. 2012). Chinstrap penguins are also in decline at a majority of sites along the WAP, while gentoo penguins are increasing, especially at new breeding sites at their recently expanded southern range (Lynch et al. 2012). These shifts in the community structure of *Pygoscelis* penguins have occurred over the past four decades and provided some of the first evidence that the cascading effects of climate change had reached top predators along

the WAP (Fraser et al. 1992). Since then, the decline of Adélie penguin populations and the simultaneous southward expansion and increase of gentoo penguins on the peninsula have been a central focus of long-term monitoring and research efforts.

Adélie and gentoo penguins are important top predators on the WAP because they represent a large component of the regional avian biomass and require a substantial amount of prey resources (Ducklow et al. 2007). As apex predators, Adélie and gentoo penguins also serve as indicator species, which are animals that provide timely evidence of ecological change, often through some aspect of their foraging behavior or reproductive success (Durant et al. 2009, Piatt et al. 2007). The role of predators as indicator species are especially pronounced in Polar Regions, where trophic systems are less complex and changes in the abundance and distribution of prey are tightly linked to the foraging behavior and reproductive success of predators (Durant et al. 2009). There is great value in monitoring sentinel species at polar latitudes, where the effects of climate change and atmospheric warming are particularly pronounced. The abrupt shifts in the community structure of *Pygoscelis* penguin populations on the WAP have prompted a series of hypotheses that aim to explain the causal mechanisms behind these population trends. Thus far, it has proven difficult to scale up inference beyond studies of regional populations, due to variability in physical and biotic factors affecting penguins along the WAP (Lynch et al. 2012). Integrating a food web perspective with knowledge of physical drivers has also proven challenging (Ducklow et al. 2007).

A key life history difference of Adélie and gentoo penguins is their opposing reliance on sea ice. Adélie penguins are an ice-obligate species, with a circumpolar distribution that is driven by their dependence on sea ice for overwintering habitat (Fraser et al. 1992, Fraser & Trivelpiece 1996). Conversely, due to their affinity for open-water habitat, gentoo penguins are an ice-intolerant species with a sub-Antarctic range (Fraser et al. 1992, Trivelpiece et al. 1987). These life history differences have been cited as one explanation as to why Adélie and gentoo penguins are experiencing shifts in their breeding ranges as the predominant ecosystem type along the WAP moves southward (Fraser et al. 1992). This theory, known as the 'sea ice hypothesis', was challenged by Trivelpiece et al. (2011), who proposed an alternative hypothesis that *Pygoscelis*

populations are driven primarily by the availability of their main prey, Antarctic krill. This theory builds on an earlier 'krill surplus hypothesis' and historical paradigm that the Southern Ocean was structured by top-down forcing and that the depletion of baleen whales in the 20th century caused a significantly increase in the abundance of krill and concomitant increase in smaller krill predators (e.g. penguins) (Laws 1970). Trivelpiece et al. (2011) postulated that increased competition with krill predators and a large-scale decline of krill stocks explain penguin population declines.

Ecological niche theory suggests that species with similar ecological requirements cannot co-exist in a resource limited system unless they differ to some degree in how they utilize these shared resources (Gause 1934; Hutchinson 1957). Species commonly avoid inter-specific competition by differing in their spatiotemporal distributions (Connell 1961; MacArthur 1958) and diets (Pianka 1981). These segregation mechanisms minimize niche overlap, facilitate resource partitioning, and promote stable co-existence among similar species. Similarly, inadequate niche segregation leads to niche displacement and competitive exclusion, whereby one species outcompetes another species for a shared resource (Shoener 1983; Gause 1934). Competitive exclusion has been well documented through studies of invasive species, however less is known about the outcome of species interactions following climate-induced range overlap (Mooney & Cleland 2001). Despite differing tolerances to sea ice, Adélie and gentoo penguins have many similar life history characteristics that promote niche overlap. For example, they are morphologically alike, have similar prey demands and exhibit temporal overlap in their breeding cycles (Croll & Tershy 1998; Trivelpiece et al. 1987). As central-place foragers during the breeding season, both species are spatially constrained and breeding pairs must alternate between guarding nests and making daily foraging trips to feed themselves and their chicks (Croxall & Davis 1999; Williams 1995). Furthermore, on the WAP both species depend primarily on Antarctic krill as a main prey resource (Volkman et al. 1980). A southward expansion of gentoo penguin colonies has led to greater spatial overlap of Adélie and gentoo penguin breeding ranges, thus increasing the potential for competitive interactions between neighboring colonies.

Few studies have investigated the foraging behavior and niche separation of sympatrically breeding Adélie and gentoo penguins (Cimino et al. 2016; Wilson 2010; Trivelpiece et al. 1987). More often the behavior of each of these species has been compared to that of their congener, the chinstrap penguin, whose range overlaps with Adélie and gentoo penguins more often than these two species overlap with each other (Miller et al. 2010, Kokubun et al. 2010, Lynnes et al. 2002). The few studies that have compared the foraging behavior of Adélie and gentoo penguins breeding in the same location have found that these species partition their shared resource in space and time (Cimino et al. 2016; Trivelpiece et al. 1987, Wilson 2010). This separation of space is due largely to differences in dive depth and distance from shore, with Adélie penguins generally foraging farther from shore and at shallower depths than gentoo penguins (Cimino et al. 2016; Wilson 2010; Trivelpiece et al. 1987). Cimino et al. (2016) recently tested for foraging competition between Adélie and gentoo penguins during a single breeding season at Palmer Station, Anvers Island, and did not find evidence to suggest that the two species were competing. Thus far, there has not been a multiyear study that has investigated the stability of the foraging niches of Adélie and gentoo penguins across breeding seasons at Palmer Station, or at any other site where the two species breed sympatrically. As marine predators, Adélie and gentoo penguins rely on spatially and temporally patchy prey, and have adapted flexible foraging strategies as a result. Intraspecific comparisons of Adélie and gentoo penguin foraging behavior have revealed variable dive behavior and diets across breeding sites and seasons.

On the WAP, the population structure of Antarctic krill is a primary determinant of penguin dive behavior, diets and foraging effort during the breeding season. Antarctic krill display high inter-annual variability in recruitment strength, with cyclical patterns of strong krill recruitment occurring every 4-5 years following bursts of phytoplankton production (Steinberg et al. 2015; Saba et al 2014; Fraser & Hofmann 2003; Quentin & Ross 2003). This variability in primary productivity is driven by variations in sea ice, wind, and water column stability and strongly influenced by the Southern Annual Mode (Saba et al. 2014; Fraser & Hofmann 2003). The relative abundance and age class structure of these krill stocks each year, in addition to being predicted by large-scale climate fluctuations, have been detected in the diets of krill

predators (Miller & Trivelpiece 2007; Fraser & Hofmann 2003; Reid et al. 1999). For example, during breeding seasons following good krill recruitment years, the diets of Adélie penguins are composed of a higher biomass of smaller-sized krill, and vice versa (Fraser & Hofmann 2003). Comparisons of penguin stomach samples and ship-based net trawls have confirmed that the diets of these predators are representative of the krill population structure in penguin foraging areas (Miller & Trivelpiece 2007; Fraser & Hofmann 2003).

Previous studies that have compared penguin foraging behavior in the context of variable krill size-class structure have focused on determining the effects of prey variability on penguin foraging effort. For example, Fraser & Hofmann (2003) found that during breeding seasons following years of strong krill recruitment at Palmer Station, Adélie penguins spent less time foraging than they did following years of poor krill recruitment. Conversely, in a study conducted in the South Shetland Islands, Miller et al. (2009) found that gentoo foraging trips were longer during years when their diets were composed of smaller-sized krill. In addition to altering their foraging behavior following years of poor krill recruitment, gentoo penguins have been found to alter their diets and feed on a higher proportion of fish when they are available (Miller et al. 2009). The results of these studies suggest that by affecting penguin foraging strategies (e.g. trip distance, dive depth), inter-annual variability in the size-class structure of krill may affect the extent of foraging niche overlap between penguin species whose breeding colonies are in close proximity. This was demonstrated by Lynnes et al. (2002) in a two-year study of foraging niche segregation between chinstrap and gentoo penguins at the South Orkney Islands. In the context of foraging niche segregation, the ability for penguins to adapt to changes in prey availability by altering their foraging behavior introduces questions such as: is the extent of interspecific foraging niche segregation observed in one year consistent across seasons? This question is difficult to answer without a long-term dataset and thus few studies (e.g. Miller et al. 2010) have investigated niche segregation among *Pygoscelis* penguins over multiple breeding seasons.

Adélie and gentoo penguins are among the focal top predators of a long-term ecological research (LTER) project based at Palmer Station, a U.S. research station on the southern coast of

Anvers Island, centrally located on the WAP. Adélie penguins have been monitored in this region since 1973 (Parmelee 1992) and were designated as the focal top predator species of the Palmer LTER project upon its inception in 1990 (Smith et al. 1995). Gentoo penguins established a founder breeding colony in this region in 1994 and have since been incorporated into the Palmer LTER top predator guild (Ducklow et al. 2007). Since monitoring began in this area, populations of Adélie penguins have declined by over 90% and the number of breeding pairs of gentoo penguins has steadily increased (Bestelmeyer et al. 2011; Ducklow et al. 2007; W. Fraser unpublished data). In addition to documenting Adélie and gentoo population trends in this area, the Palmer LTER program has conducted annual foraging studies of both species during the austral breeding season. The resulting long-term dataset provides a valuable opportunity to investigate foraging niche segregation between Adélie and gentoo penguins across multiple breeding seasons. In addition, the rapidly changing environment on the WAP and recent occurrence of sympatry between these two species provides a unique opportunity to examine the ecological consequences of climate-induced range overlap.

This study aims to determine the extent of spatial and dietary niche segregation between Adélie and gentoo penguins during the breeding season at Palmer Station over the span of a krill recruitment cycle. Data were collected during the chick-rearing phase of the penguins' reproductive cycle when the prey demand of both species is highest and thus the potential influence of competition the greatest. We used a twofold methodological approach involving biotelemetry and diet sampling to answer two questions: 1) what segregation mechanisms facilitate resource partitioning between Adélie and gentoo penguins? 2) does the degree of niche overlap between these two species remain consistent across breeding seasons with variable krill size-class structure?

Based on previous studies of the diets of Adélie and gentoo penguins in the Palmer area (Gorman 2015; Fraser & Hoffmann 2003), I expect to observe extensive overlap in the type of prey consumed by both species across breeding seasons. Because the majority of Adélie and gentoo penguins included in this study represent populations from spatially separate breeding colonies, my first prediction is that species will exhibit interspecific differences in foraging

areas. This assumption is based on the 'hinterland' model (Cairns 1989) of seabird foraging areas that predicts segregation of neighboring seabird colonies. Due to the distance of the main Adélie and gentoo breeding colonies at Palmer Station, I expect that horizontal overlap of foraging areas will be minimal. Based on previous comparisons of Adélie and gentoo penguin dive behavior (Cimino et al. 2016; Wilson 2010), I predict that a secondary mode of foraging niche segregation that I will observe between Adélie and gentoo penguins is vertical space partitioning.

To test my predictions, I used a multistep approach and first determined the extent of dietary segregation between species. Stomach samples were obtained to investigate dietary differences between species and across years and to determine krill size class structure. Following this, I used satellite and dive telemetry data to investigate the extent of horizontal and vertical partitioning of penguin foraging areas. Finally, I repeated these steps across six breeding seasons to investigate the stability of Adélie and gentoo foraging niches in the context of krill size-class structure (obtained from penguin diet samples).

Chapter 1: References

Atkinson, A., Siegel, V., Pakhomov, E., & Rothery, P. (2004). Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, 432 (7013), 100-103.

Bestelmeyer, B.T., Ellison, A.M., Fraser, W.R., Gorman, K.B., Holbrook, S.J., Laney, C.M., Ohman, M.D., Peters, D.P., Pillsbury, F.C., Rassweiler, A. and Schmitt, R.J., 2011. Analysis of abrupt transitions in ecological systems. *Ecosphere*, 2(12), pp.1-26.

Cairns, D. K. (1989). The regulation of seabird colony size: a hinterland model. *The American Naturalist,* 134(1), 141-146.

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

Clarke, A., Murphy, E. J., Meredith, M. P., King, J. C., Peck, L. S., Barnes, D. K., & Smith, R. C. (2007). Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 362(1477), 149-166.

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. *Ecology*, 42(4), 710-723.

Croxall, J.P. & Davis, L.S. (1999). Penguins: paradoxes and patterns. *Marine Ornithology* 27: 1-12.

Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M. and Fraser, W., 2007. Marine pelagic ecosystems: the west Antarctic Peninsula. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1477), pp.67-94.

Ducklow, H.W., Fraser, W.R., Meredith, M.P., Stammerjohn, S.E., Doney, S.C., Martinson, D.G., Sailley, S.F., Schofield, O.M., Steinberg, D.K., Venables, H.J. and Amsler, C.D., 2013. West Antarctic Peninsula: an ice-dependent coastal marine ecosystem in transition. *Oceanography* 26 (3).

Durant, J. M., Hjermann, D. Ø., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33(3), 271-283.

Durant, J.M., Hjermann, D.Ø., Frederiksen, M., Charrassin, J.B., Le Maho, Y., Sabarros, P.S., Crawford, R.J. and Stenseth, N.C., 2009. Pros and cons of using seabirds as ecological indicators. *Climate Research*, 39(2), 115-129.

Fraser, W. R., & Hofmann, E. E. (2003). A predator[1]s perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series*, 265, 1-15.

Fraser, W. R., Trivelpiece, W. Z., Ainley, D. G., & Trivelpiece, S. G. (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.

Fraser, W. R., & Trivelpiece, W. Z. (1996). Factors Controlling the Distribution of Seabirds: Winter-Summer Heterogeneity in the Distribution of Adélie Penguin Populations (pp. 257-272). American Geophysical Union.

Gause, G. F. (1934). Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science*, 79(2036), 16-17.

Gorman, K.B. (2015) Integrative Studies of Southern Ocean Food-Webs and Pygoscelis Penguin Demography: Mechanisms of Population Response to Environmental Change (Doctoral Dissertation). Burnaby, B.C.: Simon Fraser University.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? *Trends in ecology & evolution*, 15(2), 56-61.

Hutchinson, G.E. (1958) Concluding remarks. Cold Spring Harbour Symposium on Quantitative Biology, 22, 417–427.

Laws, R. M. (1977). Seals and whales of the Southern Ocean. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 279(963), 81-96.

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelplece, W., & Trivelplece, S. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature*, 387(6636), 897-900.

Lynch, H. J., & LaRue, M. A. (2014). First global census of the Adélie Penguin. *The Auk,* 131(4), 457-466.

Lynch, H. J., Naveen, R., Trathan, P. N., & Fagan, W. F. (2012). Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology*, 93(6), 1367-1377.

Lynnes, A., Reid, K., Croxall, J., & Trathan, P. (2002). Conflict or co-existence? Foraging distribution and competition for prey between Adélie and Chinstrap Penguins. *Marine Biology*, 141(6), 1165-1174.

Massom, R. A., & Stammerjohn, S. E. (2010). Antarctic sea ice change and variability–physical and ecological implications. *Polar Science*, 4(2), 149-186..

MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*, 39(4), 599-619.

Miller, A. K., Kappes, M. A., Trivelpiece, S. G., & Trivelpiece, W. Z. (2010). Foraging-niche separation of breeding gentoo and chinstrap penguins, South Shetland Islands, Antarctica. *The Condor*, 112(4), 683-695.

Miller, A. K., Karnovsky, N. J., & Trivelpiece, W. Z. (2009). Flexible foraging strategies of gentoo penguins Pygoscelis papua over 5 years in the South Shetland Islands, Antarctica. *Marine Biology*, 156(12), 2527-2537.

Miller, A. K., & Trivelpiece, W. Z. (2007). Cycles of Euphausia superba recruitment evident in the diet of Pygoscelid penguins and net trawls in the South Shetland Islands, Antarctica. *Polar Biology*, 30(12), 1615-1623.

Moline, M. A., Claustre, H., Frazer, T. K., Schofield, O., & Vernet, M. (2004). Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Global Change Biology*, 10(12), 1973-1980.

Mooney, H. A., & Cleland, E. E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, 98(10), 5446-5451.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 637-669.

Parmelee, D.F. 1992 Antarctic birds. Minneapolis University of Minnesota Press. 202 pp.

Piatt, J. F., Harding, A. M., Shultz, M., Speckman, S. G., van Pelt, T. I., Drew, G. S., & Kettle, A. B. (2007). Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series, 352*, 221-234.

Pianka, E. R. (1981). Competition and niche theory. *Theoretical ecology principles and applications*, 167-196

Poncet, S. (1993). The distribution and abundance of Antarctic and Subantarctic penguins. Scientific Committee on Antarctic Research (SCAR).

Quetin, L. B., & Ross, R. M. (2003). Episodic recruitment in Antarctic krill Euphausia superba in the Palmer LTER study region. *Marine Ecology Progress Series*, 259, 185-200.

Saba, G.K., Fraser, W.R., Saba, V.S., Iannuzzi, R.A., Coleman, K.E., Doney, S.C., Ducklow, H.W., Martinson, D.G., Miles, T.N., Patterson-Fraser, D.L. and Stammerjohn, S.E., 2014. Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. *Nature communications*, 5.

Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. A., & Fraser, W. R. (2010). How do polar marine ecosystems respond to rapid climate change? *Science*, 328(5985), 1520-1523.

Schoener, T. W. (1983). Field experiments on interspecific competition. *American naturalist*, 240-285.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., & Kühn, I. (2008). Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, 89(12), 3472-3479.

Sinervo, B., Mendez-De-La-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N. and Gadsden, H., 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328(5980), pp.894-899.

Steinberg, D.K., Ruck, K.E., Gleiber, M.R., Garzio, L.M., Cope, J.S., Bernard, K.S., Stammerjohn, S.E., Schofield, O.M., Quetin, L.B. and Ross, R.M., 2015. Long-term (1993–2013) changes in macrozooplankton off the Western Antarctic Peninsula. *Deep Sea Research Part I: Oceanographic Research Papers*, 101, pp.54-70.

Trivelpiece, W. Z., Trivelpiece, S. G., & Volkman, N. J. (1987). Ecological segregation of Adélie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology*, 68(2), 351-361.

Trivelpiece, W. Z., Hinke, J. T., Miller, A. K., Reiss, C. S., Trivelpiece, S. G., & Watters, G. M. (2011). Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences,* 108(18), 7625-7628.

Urban, M.C., Bocedi, G., Hendry, A.P., Mihoub, J.B., Pe'er, G., Singer, A., Bridle, J.R., Crozier, L.G., De Meester, L., Godsoe, W. and Gonzalez, A., 2016. Improving the forecast for biodiversity under climate change. *Science*, 353(6304).

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O. and Bairlein, F., 2002. Ecological responses to recent climate change. *Nature*, 416(6879), pp.389-395.

Williams, A. (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(3), 646-657.

Woehler, E. J. (1993). The Distribution and Abundance of Antarctic and Subantarctic Penguins. Scientific Committee on Antarctic Research, Cambridge, UK.

Zarnetske, P. L., Skelly, D. K., & Urban, M. C. (2012). Biotic multipliers of climate change. *Science*, 336(6088), 1516-1518.

CHAPTER 2: FORAGING NICHE SEPARATION OF ADÉLIE (PYGOSCELIS ADELIAE) AND GENTOO (P. PAPUA) PENGUINS DURING THE BREEDING SEASON AT PALMER STATION, ANTARCTICA

Abstract

Climate-induced range overlap can result in novel interactions between similar species and potentially lead to competitive exclusion. The Western Antarctic Peninsula is one of the most rapidly warming regions on Earth and is experiencing a poleward climate migration. This transition from a polar to sub-polar environment has resulted in a range expansion of the ice-intolerant gentoo penguin (*Pygoscelis papua*) and a coincident decline of ice-obligate Adélie penguins (*P. adeliae*) at Palmer Station, Anvers Island (64˚46'S, 64˚03'W). Ecologically similar species that share a limited prey resource must occupy disparate foraging niches in order to co-exist. Therefore, the aim of this study was to determine the extent of spatial and dietary niche segregation between Adélie and gentoo penguins during the breeding season at Palmer Station. This research was conducted across six austral breeding seasons, from 2010-2015, which allowed us to investigate the consistency of niche overlap in the context of resource variability. Using a twofold methodological approach involving biotelemetry and diet sampling, we found little evidence to suggest that foraging competition is a primary driver of penguin population trajectories in this region. We found substantial overlap in the diets of Adélie and gentoo penguins, who consumed primarily Antarctic krill (*Euphausia superba*), however our results showed that Adélie and gentoo penguins partitioned this shared prey resource through horizontal and vertical segregation of their core foraging areas. We did not find evidence to suggest that Antarctic krill is a limiting resource during the breeding season or that climate-induced sympatry of Adélie and gentoo penguins has resulted in competition for prey and the subsequent differing population trajectories. Rather, other physical and biological changes to the ecosystem due to the rapidly changing climate around the Antarctic Peninsula may have stronger influences on the current trends of these two species in this region.

Introduction

Species interactions play a large role in determining species distribution and community structure and have become increasingly important to understand in the context of climate change

(Urban et al. 2016; Zarnetske et al. 2012). When trophically interacting or similar species display differential responses to climate change (e.g. dispersal, extinction, and adaptation) altered biotic interactions ensue (Schweiger et al. 2008; Durant et al. 2007). Climate-induced range shifts can result in novel competitive interactions, potentially exacerbating population declines (Sinervo et al. 2010; Hughes 2000). Climate-induced range shifts toward higher elevations and higher latitudes have been observed in a wide variety of taxa including plants, butterflies, birds and mammals (Walther et al. 2002). These range shifts have been primarily due to increasing temperatures and have disproportionally affected mountaintop and polar species that already exist near the edge of their range limits (Parmesan 2006).

The ecological consequences of climate change are particularly pronounced in Polar Regions, where many species have evolved life history strategies that rely on sea ice (Moline et al. 2008). Key life history stages of these ice-obligate (or polar species) have been disrupted as a result of warming-induced habitat shifts and altered trophic interactions, mediated largely by sea ice loss (Moline et al. 2008). A notable consequence of climate warming on the WAP has been a shift in the community structure of *Pygoscelis* penguins. Ice-obligate Adélie penguins have declined significantly at nearly all breeding sites on the WAP, while ice-intolerant populations of gentoo penguins are increasing, especially at new breeding sites at their recently expanded southern range (Lynch et al. 2012).While differing tolerances for sea ice explain penguin distribution shifts, integrating species interactions in the context of these physical drivers has proven challenging (Ducklow et al. 2007; Fraser et al. 1992).

A recent hypothesis by Trivelpiece et al. (2011) postulated that penguin population declines are the result of increased competition with krill predators and a large-scale decline of krill stocks. Ecological niche theory suggests that species with similar ecological requirements cannot co-exist in a resource limited system unless they differ to some degree in how they utilize these shared resources (Gause 1934; Hutchinson 1958). Inadequate niche segregation leads to niche displacement and competitive exclusion, whereby one species outcompetes another species for a shared resource (Shoener 1983; Gause 1934). The southward expansion of gentoo penguin colonies on the WAP has introduced new potential for range overlap and competitive

interactions with Adélie penguins. Competitive exclusion has been well documented through studies of invasive species, however less is known about the outcome of species interactions following climate-induced range overlap (Mooney & Cleland 2001).

Species commonly avoid inter-specific competition by differing in their spatiotemporal distributions (Connell 1961; MacArthur 1958) and diets (Pianka 1981). These segregation mechanisms minimize niche overlap, facilitate resource partitioning, and promote stable co-existence among similar species. Few studies have investigated the foraging behavior and niche separation of sympatrically breeding Adélie and gentoo penguins (Cimino et al. 2016; Wilson 2010; Trivelpiece et al. 1987). These studies have shown that Adélie and gentoo penguins partition prey resources in space and time (Cimino et al. 2016; Trivelpiece et al. 1987, Wilson 2010). This separation of space is due largely to differences in dive depth and distance from shore, with Adélie penguins generally foraging farther from shore and at shallower depths than gentoo penguins (Cimino et al. 2016; Wilson 2010; Trivelpiece et al. 1987).

As marine predators, Adélie and gentoo penguins rely on spatially and temporally patchy prey, and have adapted flexible foraging strategies as a result. Intraspecific comparisons of Adélie and gentoo penguin foraging behavior have revealed variable dive behavior and diets across breeding sites and seasons. On the WAP, the population structure of Antarctic krill is a primary determinant of penguin dive behavior, diets and foraging effort during the breeding season (Miller et al. 2009; Miller & Trivelpiece 2008; Fraser & Hofmann 2003). In the context of foraging niche segregation, the ability for penguins to adapt to changes in prey availability by altering their foraging behavior introduces questions such as, is the extent of interspecific foraging niche segregation observed in one year consistent across seasons? This question is difficult to answer without a long-term dataset and thus few studies (e.g. Miller et al. 2010) have investigated niche segregation among *Pygoscelis* penguins over multiple breeding seasons.

This study aims to determine the extent of spatial and dietary niche segregation between Adélie and gentoo penguins during the breeding season at Palmer Station, Anvers Island across six breeding seasons. Data were collected during the chick-rearing phase of the penguins'

reproductive cycle when the prey demand of both species is highest and thus the potential influence of competition the greatest. We used a twofold methodological approach involving biotelemetry and diet sampling to answer two questions: (1) what segregation mechanisms facilitate resource partitioning between Adélie and gentoo penguins and (2) does the degree of niche overlap between these two species remain consistent across breeding seasons with variable krill size-class structure?

Based on previous studies of the diets of Adélie and gentoo penguins in the Palmer area (Gorman 2015; Fraser & Hoffmann 2003), we expect to observe extensive overlap in the type of prey consumed by both species across breeding seasons. Because the majority of Adélie and gentoo penguins included in this study represent populations from spatially separate breeding colonies, our first prediction is that species will exhibit interspecific differences in foraging areas. This assumption is based on the 'hinterland' model (Cairns 1989) of seabird foraging areas that predicts segregation of neighboring seabird colonies. Due to the distance of the main Adélie and gentoo breeding colonies at Palmer Station, we expect that horizontal overlap of foraging areas will be minimal. Based on previous comparisons of Adélie and gentoo penguin dive behavior (Cimino et al. 2016; Wilson 2010), we predict that a secondary mode of foraging niche segregation that we will observe between Adélie and gentoo penguins is vertical space partitioning.

To test our predictions, we used a multistep approach and first determined the extent of dietary segregation between species. Stomach samples were obtained to investigate dietary differences between species and across years and to determine krill size class structure. Following this, we examined satellite and dive telemetry data to investigate the extent of horizontal and vertical partitioning of penguin foraging areas. Finally, we repeated these steps across six breeding seasons to investigate the stability of Adélie and gentoo foraging niches in the context of krill size-class structure (obtained from penguin diet samples).

Materials and methods

Study site and species

Our study is part of a long-term monitoring program of Adélie and gentoo penguins breeding in the vicinity of Palmer Station (64˚46'S, 64˚03'W), Anvers Island, Antarctica (Figure 2.1). The marine environment in this area is especially productive due to the nearby Palmer Deep submarine canyon (Ducklow et al. 2007; Schofield et al. 2013) that cuts across the continental shelf from the west and allows for the passage of warm, upper circumpolar deep water from the Antarctic Circumpolar Current toward the southern coast of Anvers Island (Schofield et al. 2013). This input of nutrients promotes primary productivity during the austral summer months that support large krill stocks and a multitude of krill predators such as seabirds, seals and whales (Ducklow et al. 2007). During the summer, Adélie and gentoo penguins share similar nesting habitat on several small, rocky islands in the vicinity of Palmer Station. Our fieldwork occurred on Biscoe Point (64°48'S, 63°46'W), where Adélie and gentoo nest in mostly separate colonies, and Torgersen (64°46'S, 64°04'W) and Humble (64°45'S, 64°05'W) Islands, which are occupied solely by Adélie penguins (Figure 2.1). Fieldwork occurred during the chick rearing phase of the penguin breeding season, approximately from the end of December through mid-February between 2010 and 2015 (Figure 2.2).

Dietary analysis

In order to evaluate the extent and consistency of dietary niche partitioning between Adélie and gentoo penguins, we tested for differences in the type and size of prey consumed by both species. We collected stomach samples during roughly the same time period as tagging on an independent sample of adults. Individuals who were presumed to be returning to a nest (i.e. headed from the water's edge to the colony) were captured with a hand held net. Stomach contents were obtained using a water off-loading method (Wilson 1984) and penguins were subsequently weighed, measured and released back into the colony. We collected roughly even numbers of samples from both sexes, which we confirmed using morphometric measurements (Gorman et al. 2014). Diet samples were collected from five individuals on each sampling day and this occurred roughly every five days depending on weather conditions. Stomach samples

were drained, weighed and sorted in order to determine diet composition. We identified prey items and categorized them as either krill (*Euphausia superba* or *Thysanoessa macrura*), fish, or 'other'. We determined the percent composition of each of these prey items by weight (wet mass) as well as the frequency of occurrence of each item in the sample. We compared the composition and frequency occurrence of prey between species, sex and year using generalized linear models.

In order to compare prey availability across seasons, we determined the size-class structure of Antarctic krill found in penguin diet samples. During stomach lavage, fresher, more intact prey is typically regurgitated first, followed by more digested layers of prey. A sub-sample of 50-100 intact Antarctic krill were randomly selected from each portion of fresh sample. We measured each of these sub-sampled krill from the eye to the tip of the teslon to obtain total length and binned them into 1 of 8 size classes, in 5mm increments from 16-60 mm. We combined the two smallest size classes (16-20 and 21-25) and the two largest size classes (51-55 and 56-65) due to low frequencies. This binning resolves inter-annual changes in krill size class structure, as krill grow >5 mm per year (Siegel 1987). We calculated the proportion of krill that fell into each of eight size-classes and created size-class frequency distribution plots for each species per year. We tested for differences in size-class distributions between species each year using a Pearson's chi-squared test and calculated the mean size of krill consumed by each species to test for differences between species each year using a Welch's two sample t-test. In order to assess differences in krill recruitment strength across years, we calculated an index of recruitment (R1) which represents the proportion of the 1+ age class in the population. Following the methods of (Saba et al. 2014), we assigned krill <30mm to the 1+ age class.

Tagging

We used satellite and dive telemetry methods to determine penguin foraging locations and dive behavior. We selected adult penguins for instrumentation if they were paired and had brood-stage nests containing two chicks. Only one individual from each pair was tagged, and both sexes were represented approximately equally throughout the study period. We instrumented each penguin with a continuously transmitting ARGOS satellite tag (Sirtrack

Limited., Havelock North, New Zealand: KiwiSat202; or Wildlife Computers Redmond, WA, USA: SPOT3, SPOT-275A, SPOT-275B, or custom mold based on a SPLASH tag configuration) and a time-depth recorder (Lotek Wireless, Inc, St. John's Canada: Lotek LAT1400) that sampled at least once every 2s (resolution of 0.05 m and accuracy of $\pm$ 1m). Tags were fastened to feathers on the lower dorsal region using waterproof Tesa® tape and small plastic zip ties (Wilson & Wilson 1989). This attachment method minimized drag and allowed for easy tag removal without damaging feathers (Bannasch et al. 1994; Wilson & Wilson 1989). While we attempted to minimize potential instrumentation effects, we did not directly test for a "tag effect". Past studies have found that attaching data-logging devices to diving seabirds affects foraging efficiency, especially with regard to foraging trip duration (Croll et al. 1991; Wilson et al. 1989). Our tags were smaller and deployed for a much shorter duration (4.05 days $\pm$ 1.41) than the tags in those studies. Recent studies that have used smaller sized, streamlined tags similar to ours did not detect significant instrumentation effects (Lescroel & Bost 2005; Ballard et al. 2001). Furthermore, because the focus of this study is foraging location rather than trip duration, we do not expect our results to be influenced by tag attachment.

Analysis of penguin space-use: data and approach

To evaluate the extent of spatial niche partitioning between Adélie and gentoo penguins, we first determined the horizontal and vertical foraging range of each species. Following this, we quantified the degree of horizontal and vertical overlap between each species. These steps were repeated for each year of the study in order to determine the consistency of spatial niche partitioning between species across breeding seasons. Prior to these analyses, we filtered location data to remove inaccurate locations and characterized penguin dive types in order to remove dives that were not foraging dives (e.g. exploratory, or 'search' dives and transit dives).

ARGOS assigns error estimates based on the number of satellite passes that occur while a satellite tag is above water using either a least squares analysis or a Kalman filtering algorithm (CLS 2016). For this study, the former was used from 2010-2011 and the latter from 2012 onwards. Both algorithms classify location points as either 3,2,1, or 0, which are associated with error estimates of <250m, 250-500m, 500-1500m, >1500m, respectively, or A or B, which have

no error estimate (CLS 2016). We incorporated these estimates of error into a three-stage filtering process, following the methods of Oliver et al. (2013). We removed unreasonable locations based on penguin swimming speed (8 km/hr) (Ainley 2002), coastal geometry and erroneous terrestrial positions (class 0, A, B) located on Anvers Island. Because penguins often foraged close to shore among many small, rocky islands, locations found on these smaller islands were not removed. Location data were time matched to dive records and linear interpolation was used to estimate foraging locations for dives that occurred between known locations (within 30 minutes of a foraging bout).

We focused specifically on foraging behavior in our assessment of vertical and horizontal space-use and only included location data and dives associated with foraging (hereafter referred to as 'forage' dives). This approach allowed us to measure the true extent of each species foraging range and thus the potential for consumptive competition. We categorized penguin dive types following the methods of Cimino et al. (2016). We looked for evidence of prey encounters or pursuit, indicated by vertical undulations ('wiggles'), bottom time, or plateaus (Bost et al. 2007; Rodary et al. 2000; Kirkwood & Robertson 1997; Chappell et al. 1993). We excluded dives that indicated transit or porpoising behavior (dives <20s or <5m) (Kokubun et al. 2010; Takahashi et al. 2003; Chappell et al. 1999) and those that were exploratory in nature. These included 'search' dives that were commonly V-shaped, with minimal or no wiggles, bottom time, or plateaus. For each forage dive, we calculated an estimate of forage depth using a kernel density estimate (Scott 1992). This is the depth where the largest portion of dive time was spent, where prey encounter or pursuit was most likely to have occurred.

Determining penguin foraging areas

We created utilization distributions (UD) from known locations of penguin forage dives in order to visualize and quantify penguin foraging ranges. We pooled location data by species and by year and used kernel density estimation (KDE) techniques to determine the probability distribution of penguin foraging areas. Using the R package "ks" (Duong 2007), we calculated the areas within each of the 95% and 50% KDE contour lines in order to quantify each species overall foraging range (km^2), and core foraging area (km^2), respectively. In order to compare

pooled datasets with uneven sample sizes, we employed a data-based 'plug-in' bandwidth selector ('Hpi') which was calculated for each dataset separately (Gutowsky et al. 2015). For similar reasons, we used a fixed kernel approach that applied a consistent smoothing factor (h) across each pooled dataset. We used the default grid size (n=151 for 2D and n=51 for 3D) to compute a smoothed probability estimate for each dataset.

The number of individuals tracked and the amount of location data points used in pooled KDE significantly affect both the geographic location and size of the KDE output (Gutowsky et al. 2015; Soanes et al. 2013). Thus, caution must be taken in drawing population-wide inferences and making comparisons of pooled KDE between species and across years. Similar to previous studies, we used an iterative sub-sampling approach to determine the effect of the number of individuals included in our analyses on the overall and core foraging areas of both species for each year (Orben et al. 2015; Gutowsky et al. 2015; Soanes et al. 2013). This method allowed us to identify the presence of an asymptote where the total foraging area ceased to increase substantially because a representative number of animals from the population had been tracked. We began this procedure by selecting a single individual at random and calculating the area within each of the 50 and 95% KDE contours. We continued by selecting an additional individual (without replacement) and re-calculating these areas until all individuals were included. These steps were repeated for 100 iterations (for each year independently) in order to determine mean area and variance for each number of individuals included.

Overlap of penguin foraging areas

After defining the seasonal foraging ranges of Adélie and gentoo penguins, we quantified the extent of spatial overlap that occurred between the two species foraging areas. We used 2D KDE of foraging areas to calculate the proportion of overlap between each species' overall and core foraging range. This provided us with a simple and intuitive measure of overlap ('percent overlap') between the foraging areas of each species. We also employed the Utilization Distribution Overlap Index (UDOI), which provides a single, non-directional measure of space-use sharing that accounts for each species' underlying UD (Cooper et al. 2014; Fieberg &

Kochanny 2005). UDOI generally varies between 0 and 1, with 0 representing no overlap and 1 indicating complete overlap (Fieberg & Kochanny 2005).

Comparison of foraging dives

To determine the extent and consistency of vertical partitioning of foraging areas, we tested for differences in penguin dive depth and water column utilization. We used generalized linear mixed models (GLMM) to test for differences in dive behavior between species, by sex, and across years. We accounted for repeat sampling of individuals by including bird identity as a random effect in the models (Faraway 2006). In order to test for differences in water column utilization, we calculated a dive index (DI) for each dive (DI= dive depth/ocean depth). The response variables in these models included forage dive depth and maximum dive depth.

Three-dimensional estimates of penguin space-use

Two-dimensional KDE is a useful and common technique for quantifying the intensity of animal space-use across a 2D plane, but it is inherently limited in cases where animals utilize three-dimensions for travelling or foraging (Belant et al. 2012). For this reason, 2D KDE may inaccurately quantify the extent of space-use sharing between two species that differ in their use of a third dimension (e.g. height or depth). Because independent comparisons of the depth distribution of penguin foraging dives are limited to the vertical dimension, they also fail to completely quantify penguin space-use. 3D KDE methods have recently been implemented to solve this problem (Cooper et al. 2014; Simpfendorfer et al. 2012), and we employed this technique in order to gain a complete picture of penguin space use in the X, Y and Z dimensions. We used methods similar to our 2D KDE and quantified the extent of spatial overlap that occurred between the two species three-dimensional foraging areas. We used 3D KDE of the volume (km^3) of penguin foraging areas to calculate the proportion of overlap between each species' overall and core foraging range. Similar to our 2D methods, we determined percent overlap and calculated UDOI values in order to measure space-use sharing between Adélie and gentoo penguins across years.

Results

Dietary analysis overview

We determined whether Adélie and gentoo penguins occupy distinct dietary niches by comparing the type of prey (percent composition and frequency occurrence) and size of prey (total length of Antarctic krill) consumed by each species. We collected a total of 136 samples from Adélie penguins (77 male, 59 female) and 128 samples from gentoo penguins (64 male, 64 female). Overall, we found consistent evidence of extensive dietary overlap between species across all years of the study. We found little evidence of dietary differences between sexes for either species.

Diet composition

Antarctic krill was present in all of the Adélie and gentoo diet samples (Figure 2.3) and dominated the diets of both species by weight in all years (Figure 2.4, Table 2.1). We did not find any differences in the percent contribution of krill between penguin species ($F_{1, 262}=2.10$, p=0.148), or between sexes for either species (Adélie: $F_{1, 134}=1.15$, P=0.286; gentoo: $F_{1, 126}=1.40$, p=0.240). Adélie diets contained a lower proportion of krill in 2011 than in all other years, where there were no significant inter-annual differences ($F_{5, 130}= 15.60$, p<0.001). We did not find any differences in the percent contribution of krill in gentoo diets across years ($F_{5, 122}= 1.97$, p= 0.088). Adélie diets contained a higher percent contribution of *T. macrura* than the diets of gentoo penguins ($F_{1, 262}=9.61$, p=0.002) (Figure 2.4, Table 2.1). The diets of both Adélie and gentoo penguins contained a higher proportion of *T. macrura* in 2011 than in all other years, where there were no significant inter-annual differences (Adélie: $F_{5, 130}= 15.99$, p<0.001; gentoo: $F_{5, 122}=6.41$, p<0.001). We did not find any differences in the contribution of *T. macrura* between sexes for either species (Adélie: $F_{1, 134}=0.53$, p=0.467; gentoo: $F_{1, 126}=0.18$, p= 0.673). Gentoo diets contained a higher proportion of fish compared to Adélie diets ($F_{1, 261}=12.29$, p<0.001) (Figure 2.4, Table 2.1). The contribution of fish did not vary across years for either species (Adélie: $F_{5, 129}=1.49$, p=0.197; gentoo: $F_{5, 122}=1.64$, p=0.152), or by sex for either species (Adélie: $F_{1, 133}=3.69$, p=0.057; gentoo: $F_{1, 126}=2.43$, p=0.122). We did not find any differences in the percent contribution of 'other' prey items (e.g. isopod, amphipod and mysid species) between

species ($F_{1, 262}$=1.86, p=0.174) (Figure 2.4, Table 2.1). Adélie diets contained a higher percent contribution of these prey items in 2011 than in all other years where there were no significant differences ($F_{5, 130}$=3.55, p=0.005). We did not find any difference in the contribution of 'other' prey items in the diets of gentoo penguins across years ($F_{5, 122}$= 1.87, p=0.105). We found the percent contribution of 'other' prey items in penguin diets was marginally higher for male Adélies ($F_{1, 134}$= 4.20, p=0.042) and female gentoos ($F_{1, 126}$=4.025, p=0.047).

Frequency occurrence of prey

  T. macrura occurred less frequently in gentoo diet samples than Adélie diet samples ($X^2_{1,262}$= 5.58, p=0.018) and differed by year for both species (Adélie: $X^2_{5,130}$=43.68, p<0.001; gentoo: $X^2_{5,122}$= 25.34, p<0.001) (Table 2.1, Figure 2.3). We did not find any differences in the occurrence of *T. macrura* by sex for either species (Adélie: $X^2_{1,134}$=0.76, p= 0.383; gentoo: $X^2_{1,126}$=1.40, p=0.236). We detected evidence of fish more frequently in gentoo diets compared to Adélie diet samples ($X^2_{1,262}$= 10.16, p=0.001) (Table 2.1, Figure 2.3). The occurrence of fish in diet samples differed by year for gentoo penguins ($X^2_{5,122}$ = 23.00, p<0.001) but not for Adélie penguins ($X^2_{5,130}$ = 10.48, p=0.063). There were no differences in the occurrence of fish between sexes of either species (Adélie: $X^2_{1,134}$= 1.91, p=0.167; gentoo: $X^2_{1,126}$=0.03, p= 0.858). We did not find any difference in the frequency occurrence of 'other' prey items between species ($X^2_{1,262}$= 1.03, p=0.311) (Table 2.1, Figure 2.3). The occurrence of 'other' prey items differed by year for both species (gentoo: $X^2_{5,122}$=14.09, p= 0.015; Adélie: $F_{5, 130}$=15.16, p=0.010) and was higher in the diets of male gentoo penguins ($X^2_{1,126}$=5.42, p=0.020), but did not differ by sex for Adélie penguins ($X^2_{1,134}$= 3.12, p=0.078).

Krill size-class distribution

  Because Antarctic krill dominated the diets of both species, we compared the size-class distribution of krill found in penguin diets to test for differences in prey size preference between species. We compared the average size of krill found in diet samples and found that Adélie and gentoo penguins consumed similar-sized krill in 2010, 2011 and 2014 but not in 2012 (p=.030), 2013 (p=.050) and 2015 (p=0.04) (Figure 2.5). We compared the distribution of krill size-classes

and found that Adélie penguins consumed higher frequencies of smaller-sized krill than gentoo penguins (Figure 2.6, Table 2.2). These patterns were consistent across years despite changes in the dominant size-class of krill. The diets of both species indicated a 4-5 year cycle of krill recruitment, with the highest recruitment index (Adélie: R_1=0.26; gentoo R_1=0.21) occurring in 2013.

Overview of tagging

We tagged a total of 61 Adélie penguins (30 male, 31 female) and 48 gentoo penguins (25 male, 23 female) and recovered 100% of our tags from 2010-2015. While the earliest tag deployment occurred on 19 December and the latest tag recovery occurred on 7 February, 85% of deployment days occurred during the month of January concurrent with diet sampling (Figure 2.5). The mean number of deployment days per bird was 4.06 ± 1.41. We successfully extracted data from all but one tag, however, we excluded an average of 73% of our total dive data from our analyses, including search and transit dives, and dives without a known location. In 2014, we were left with an insufficient amount of data to make reasonable inferences of foraging areas and we removed this year from our analysis.

Penguin foraging areas

We created two-dimensional KDE in order to visualize and quantify the extent of Adélie and gentoo penguin foraging areas and we found that Adélie and gentoo penguins generally foraged southwest of and relatively close to their respective colonies (Figure 2.7). Adélie penguins consistently occupied a smaller foraging range compared to gentoo penguins (Table 2.3), especially with respect to their core foraging area, which remained roughly the same size and in the same location across all five years of the study. Foraging dives of gentoo penguins occurred 2.28 ± 0.71 kilometers farther from their breeding colony than the foraging dives of Adélie penguins (X^2 (1)=9.23, p= 0.002). However, both species concentrated their foraging effort between their respective colonies and Palmer Deep canyon (Figure 2.1, Figure 2.7).

Overlap of penguin foraging areas

We used two parameters to quantify overlap of penguin foraging areas each year. We obtained directional measures of 'percent overlap' by calculating the proportion of each species range that overlapped with the other, as well as the non-directional UDOI. We found minimal overlap near the periphery of the overall ranges (95% KDE) of each species in 3 out of 4 years (2010-12 & 2015) and no overlap in 2013 (Table 2.3). The core foraging areas of Adélie and gentoo penguins, which contained the highest density of foraging locations (50% KDE), were spatially separated in all years (Table 2.3, Figure 2.7). We obtained low UDOI values in all years of the study, indicating that the probability of space-use sharing between both species along the periphery of their ranges was low (Table 2.3).

While our main study concerned Adélie penguins tagged at Humble and Torgersen islands, we conducted a separate analysis on Adélie foraging locations of individuals who were tagged on Biscoe point (2011: n=1; 2012: n=2; 2015: n=2). The overall and core foraging ranges of these animals overlapped considerably more with the gentoo foraging area than the range of the Adélie penguins who were tagged on Humble and Torgersen islands (Figure 2.8, Table 2.4).

Comparison of foraging dives

We determined the extent of vertical separation of Adélie and gentoo foraging dives by comparing maximum dive depth and 'forage' depth between species and by year (Table 2.9). We tested for interspecific differences between gentoo penguins tagged at Biscoe point and Adélie penguins tagged at Humble and Torgersen islands and found that gentoo penguins dove significantly deeper than Adélie penguins in all years (Table 2.5). Adélie penguins generally foraged in the upper 50m of the water column (Figure 2.9), with an average forage depth of 16.03 ± 0.35 meters. The depth distribution of gentoo penguin foraging dives was wider than Adélies, and gentoo penguins generally utilized the top 100m of the water column (Figure 2.9), with an average forage depth of 36.73 ± 11.39 meters. Overall, the maximum dive depth of gentoo penguins was 40.66% deeper than Adélie penguins ($X^2(1) = 64.89$, p<0.001) and the forage depth of gentoo penguins was 41.22% deeper than Adélie penguins ($X^2(1) = 62.13$, p<0.001). We did not find any difference in dive depth between sexes for either species (Adélie:

$X^2(1)$ =0.63, p=0.428; gentoo: $X^2(1)$ =0.02, p=0.887). Both species concentrated their foraging effort during similar hours of the day (Figure 2.10). The foraging effort of both species increased through the day and peaked around 18:00 before tapering off through the night and early morning. We found the dive depth of both species increased through the day and peaked around 15:00, however this signal was stronger for gentoo penguins (Figure 2.11).

Because the foraging ranges of Adélie penguins tagged at Biscoe point in 2011, 2012 and 2015 overlapped considerably with the foraging areas of gentoo penguins also tagged at Biscoe point (Figure 2.8, Table 2.6), we conducted a separate analysis on the dive behavior of these individuals. We tested for differences in Adélie forage depth by colony location to compare the dive behavior of Adélie penguins from Biscoe point to the dive behavior of Adélie penguins from Humble and Torgersen islands. We found that Adélie penguins from Biscoe point dove deeper than Adélie penguins from Humble and Torgersen islands in 2011 ($X^2(1)$ =4.39, p=0.036) and 2012 ($X^2(1)$ =4.85, p=0.028), but not in 2015 ($X^2(1)$ =0.01 p=0.917). Furthermore, we did not find any significant differences in the dive depth of Adélie and gentoo penguins tagged at Biscoe point in 2011 ($X^2(1)$ =0.41 p=0.51) and 2012 ($X^2(1)$ =1.77 p=0.183), but in 2015, gentoo penguins dove deeper than Adélie penguins ($X^2(1)$ =16.75 p<0.001).

Because we found overlap at the periphery of Adélie and gentoo foraging ranges in 2010, 2011, 2012 and 2015, we conducted a separate analysis of penguin dive behavior within and outside of this overlap area. Adélie penguins dove deeper in overlap areas than they did in non-overlap areas in 2010 ($X^2(1)$ =12.98, p<0.001), 2011 ($X^2(1)$ =20.51, p<0.001) and 2015($X^2(1)$ =13.47, p<0.001) but not in 2012 ($X^2(1)$ =0.06, p=0.81). We did not find any differences in the dive depth of gentoo penguins between overlap and non-overlap areas, apart from the year 2011, when they dove deeper in overlap areas ($X^2(1)$ =4.69, p=0.03). In overlap areas, gentoo penguins dove significantly deeper than Adélie penguins in all years apart from 2010 ($X^2(1)$ =2.01, p=0.157).

Three-dimensional estimates of penguin space-use

We created three-dimensional utilization distributions in order to incorporate penguin foraging depth into our 2D analysis of space-use. Similar to our comparisons of penguin dive behavior, we found that gentoo penguins generally foraged across a greater range of depths compared to Adélie penguins (Figure 2.12). This behavior resulted in larger 3D estimates of foraging volume for gentoo penguins (Table 2.7). This vertical partitioning of the water column likely reduced the actual extent of range overlap observed in 2D KDE, as we observed lower estimates of percent overlap and lower UDOI values in 3D KDE compared to 2D KDE (Table 2.7).

We created separate 3D KDE of the foraging areas of Adélie penguins tagged at Biscoe point and found considerably more spatial overlap with gentoo penguins compared to what we observed when comparing the foraging areas of Adélies were tagged at Humble and Torgersen (Figure 2.13, Table 2.8). Similar to 2D KDE of these foraging ranges, these 3D KDE resulted in larger estimates of percent overlap and larger UDOI values (Table 2.8).

Discussion

Climate-induced range overlap can result in novel or increased competitive interactions between populations that ultimately influence species abundance and distribution (Walther 2002; Hughes 2000). We studied the extent and consistency of foraging niche segregation between Adélie and gentoo penguins during the breeding season for 6 consecutive years around Anvers Island on the Western Antarctic Peninsula and found little evidence to suggest that foraging competition is affecting recent population trends in this area. We found that Antarctic krill dominated the diets of both species throughout the study period, and that Adélie and gentoo penguins consumed similar size-classes of krill. Adélie and gentoo penguins partitioned this shared prey resource during the breeding season horizontally by concentrating their foraging effort in separate locations and vertically at different depths. These results provide a unique multi-year comparison of foraging niche segregation and build on previous studies that suggest that Adélie and gentoo penguins exhibit discrete foraging strategies that facilitate resource partitioning in areas of sympatry (Cimino et al. 2016; Wilson 2010; Trivelpiece et al. 1987).

Penguin diets

Inter-annual variation in the population structure of Antarctic krill affects its abundance and spatial distribution (Bernard et al. *in press*) and ultimately the foraging behavior and reproductive success of predators that rely on krill (Lynnes et al. 2004; Fraser & Hoffman 2003; Reid & Croxall 2001; Croxall et al. 1999). We observed inter-annual krill recruitment variability in the diets of both Adélie and gentoo penguins. These results agree with previous studies that have found Adélie and gentoo penguin diets reflect a 4-5 year cycle of krill recruitment (Fraser & Hoffman 2003; Miller & Trivelpiece 2007). We observed the highest frequencies of small-sized krill (16-30 mm) in penguin diets in 2013. Because penguins do not feed on larval krill (<16 mm), there is a one-year lag between when a recruitment event occurs and when it is detected in penguin diet samples (Fraser & Hofmann 2003). Therefore, our findings agree with a concurrent ship- based study in the Palmer region that detected positive abundance anomalies of krill in 2012 and 2013 (Steinberg et al. 2015). The foraging strategies of Adélie and gentoo penguins change based on krill size-class structure (Miller & Trivelpiece 2007; Lescroel & Bost 2005; Fraser & Hofmann 2003; Lynnes et al. 2002) and variation in foraging locations, depths and/or diets of penguins potentially affects the extent of foraging niche overlap between these two species. These results indicate that despite variation in krill population structure across six breeding seasons, Adélie and gentoo penguins maintained spatially separate foraging niches.

The diets of both Adélie and gentoo penguins have been found to vary temporally and by breeding locality, but those of gentoo penguins are generally more diverse than Adélie penguins (Lescroel et al. 2004; Ainley 2002; Bost & Jouventin 1990; Volkman et al. 1980). The greater flexibility of gentoo penguins to alter their diet according to prey availability has been cited as a possible reason for their stable and/or growing populations in many locations on the Antarctic Peninsula, as well as a potential mechanism of niche partitioning (Polito et al. 2015; Miller et al. 2009). We found that fish occurred more frequently in the diets of gentoo penguins than in the diets of Adélie penguins. These results are similar to what has been observed at other breeding sites along the Antarctic Peninsula (Trivelpiece et al. 1987; Volkman et al. 1980). One limitation of stomach content analysis is that it does not accurately quantify soft-bodied prey such as fish (Barrett et al. 2007). Fish is digested in penguin stomachs more quickly than krill, and thus it is

difficult to obtain a true measure of the importance of fish to penguin diets through this method alone (Polito et al. 2011). However, a recent study of the isotopic niches of Adélie and gentoo penguins in this area found that Antarctic krill was the dominant prey item of both species, and that fish was represented about evenly between both species, with the exception of one year when gentoo isotope levels indicated a slightly higher proportion of fish (Gorman 2015). The results of this study align closely with our findings that Antarctic krill is the dominant prey of both species in this region during the breeding season, and that fish is a secondary prey item that occurs more frequently in gentoo penguin diets.

Penguin foraging areas

Two possible caveats of drawing population-wide inferences of space-use from individual location data include 1) masking individual variation through pooled KDE and 2) assuming tracked individuals represent the population as a whole (Gutowsky et al. 2015). This study was conducted during a period when penguins are constrained to foraging relatively close to their breeding colonies to provision growing chicks. As a result, individual variation in foraging location is predicted to be reduced during this period compared to the post-breeding season, or compared to what would be observed in farther ranging species, such as albatrosses (e.g. Gutowsky et al. 2015; Orions & Pearson 1979). Additionally, in this study, we aimed to track a large number of individuals for a short period of time, rather than obtaining a large number of data points from fewer animals over a longer time period. While this approach allowed us to increase our sample size and minimize the chances of over- or underrepresenting any one animal, we did not directly examine the optimal number of trips (or number of data points) to include per individual (e.g. Soanes et al. 2015). Instead, we investigated the asymptotic saturation of the total area occupied in relation to the total number of animals included in our analysis. We demonstrated that overall, we tagged a sufficient number of Adélie and gentoo penguins to estimate the size and location of the core foraging areas occupied by each species during the study period (Figure 2.14). These results provide us with confidence that our estimates of horizontal overlap between foraging areas are accurate because it is unlikely that the area occupied by either species would have changed significantly had more animals been tagged. However, we found that the number of individuals required to provide reasonable estimates of

colony-wide foraging areas varied across seasons, and in a few cases (such as 2010) the total area occupied by Adélie and gentoo penguins approached, but did not reach an asymptote with the number of animals that were tagged. It is possible that those areas could have expanded further had more animals been tagged. If this expansion occurred in the direction of the other species, it might have led to a greater degree of overlap then we observed for that year. Based on the consistent size, location and separation of the Adélie and gentoo core foraging areas, it is unlikely that we would have observed an expansion of either of these ranges that would have been large enough to result in a significant increase of overlap.

Seabirds aim to minimize travel costs by foraging as close to their respective breeding colonies as possible and thus often forage in colony-specific areas (Cairns 1989). Our results indicate a difference in the location of the foraging ranges of Adélie penguins tagged on Humble and Torgersen islands and those tagged on Biscoe Point. The foraging range of Adélie penguins from Biscoe Point overlapped significantly more with the gentoo penguin range than the foraging area of Adélie penguins tagged on Humble and Torgersen islands. There were not enough Adélie penguins tagged on Biscoe to provide an accurate estimate of the absolute size and location of the foraging range of this colony, but these results provided a general idea of the foraging area. Greater overlap of the foraging ranges of Adélie and gentoo penguins from Biscoe Point colonies may indicate a higher potential for competitive interactions between these two species beyond what were able to observe in this study. However, unlike Humble and Torgersen, Biscoe is not a primary breeding colony for Adélie penguins in this region, and it is unlikely that even if there was competition between Adélie and gentoo penguins from Biscoe it would be driving region-wide population trends. Despite this, the limited data we have on the forging locations of Adélie penguins from Biscoe indicates that the potential for overlap with gentoo penguins is higher if the breeding colonies of both species are located on the same island. These findings could have greater implications in regions where Adélie and gentoo penguins are found on the same islands, or islands that are close together. The potential for horizontal overlap highlights the importance of understanding how Adélie and gentoo penguins partition resources vertically.

Comparison of foraging dives

A primary mode of niche partitioning by *Pygoscelid* penguins is foraging depth (Trivelpiece et al. 1987, Wilson 2010, Cimino et al. 2016). Interspecific differences in dive depth are thought to be driven primarily by physiological differences in body size that affect breath-holding capacity and determine the depths at which different species are most efficient (summarized in Wilson 2010). Adélie penguins are most efficient at shallow depths between 0-15 meters while gentoo penguins are most efficient at deeper depths (>60 m) (Wilson 2010). Our results indicate that Adélie and gentoo penguins concentrate their foraging effort close to, or shallower than these optimal dive depths, thereby facilitating vertical resource partitioning. Most Adélie and gentoo penguin foraging dives that occurred in our study occurred in separate locations, where this vertical partitioning of the water column may be less important for resource partitioning. However, in areas where Adélie and gentoo foraging areas overlap in the horizontal plane, vertical separation of foraging is critical for maintaining separate foraging niches. Our results indicate that in areas where the horizontal foraging ranges of Adélie and gentoo penguins overlapped, they generally maintained the vertical partitioning of dive depth observed outside of overlap areas. Gentoo penguins dove significantly deeper than Adélie penguins in peripheral overlap areas in 3 out of 4 years. We did not observe a significant difference in the dive depth of Adélie and gentoo penguins in the overlap region in 2010, but the sample size for this area was comparatively small, and this could explain why this year did not match the general trend observed elsewhere in the data (Figure 2.15). In 2011 and 2012, we did not find a significant difference in the dive depth of the Adélie and gentoo penguins that were tagged on Biscoe Point. In 2011, the lone Adélie penguin that was tagged on Biscoe dove deeper than the average for Adélie penguins in the rest of the study. In this case, we do not have a large enough sample size to discern colony-wide trends. In 2012, in addition to a limited sample size of Adélie penguins (n=2), gentoo penguins dove to shallower depths on average than they did in any other year, and we observed more vertical overlap (and no significant difference) in the depth distribution of Adélie and gentoo penguin foraging dives (Figure 2.16). Despite these exceptions, we expect that the dive behavior of Adélie penguins from Biscoe would generally match that of Adélie penguins from other colonies, and vertical separation of the water column would be maintained. A larger sample size of Adélie penguins tagged at Biscoe point would be needed to test this hypothesis.

While Cimino et al. (2016) did not investigate the dive depth of Adélie penguins from Biscoe, these authors found preliminary evidence to suggest that Adélie penguins dive deeper in overlap areas compared to non-overlap areas. Based on the deeper depth distribution of a single Adélie penguin in the overlap area, Cimino et al. (2016) postulated that prey may be less available at shallower depths in these peripheral overlap areas compared to where Adélie penguins normally concentrate their foraging effort near Humble and Torgersen islands. Building on those results, we also found that Adélie penguins generally dove deeper in areas of overlap than they did in non-overlap areas. This occurred in 3 out of the 4 years that we observed overlap at the periphery of both species ranges. Similarly, in 2 out of the 3 three years when Adélie penguins were tagged on Biscoe Point, these animals dove deeper on average than those from Humble and Torgersen. Because such a small number of Adélie penguins were tagged at Biscoe, it is difficult to say with certainty that these differences in dive depth are a true pattern and not an artifact of sample size. The same is true regarding the differences we found in Adélie dive depths in non-overlap versus overlap areas, where the sample size (number of dives that occurred) in the latter area was comparatively small. Similar to Cimino et al. (2016), we are unable to discern possible causes for these differences without further information on prey distribution in penguin foraging areas and/or a larger sample size of individuals and dives in overlap areas. Because intraspecific variation in dive behavior potentially affects the extent of vertical overlap between Adélie and gentoo penguins, understanding the mechanisms that affect dive behavior is a critical step in understanding niche segregation between these two species. For example, similar to Cimino et al. (2016), we found that gentoo penguins dove deeper in the peripheral overlap area (compared to the non-overlap area) in 2011, but in our study, this was the only year that we observed a change in gentoo dive depth. Cimino et al. (2016) hypothesized that gentoo penguins may be diving deeper as a mechanism of competitive avoidance, but we did not find additional evidence to support this theory. Future studies should continue to investigate penguin dive behavior in relation to oceanographic variables (e.g. Oliver et al. 2013) as well as incorporate fine scale prey data (e.g. Cimino et al. 2016).

Diel trends in foraging behavior

Penguins are visual predators that require light for successful prey capture, and thus foraging effort is concentrated during the daylight hours where light levels are highest (Wilson et al. 1993). In support of this, we found that Adélie and gentoo penguins concentrated their foraging effort during similar hours and that the number of foraging dives performed by both species increased throughout the day and peaked around 15:00. Because marine predators such as penguins are ineffective at hunting at night, many species of zooplankton, including Antarctic krill, display diel vertical migration (DVM), which is a strategy that allows animals to balance predator avoidance and resource acquisition (Zhou & Dorland 2004; Hays 2003; Ritz 1994). Penguins are thought to track the DVM of their prey and as a result, perform increasingly deeper dives throughout the day (Wilson et al. 1993). Our results support those of previous studies that have demonstrated that penguins track the DVM of Antarctic krill. We found that gentoo penguins exhibited a much stronger diel depth pattern than Adélie penguins, possibly as a result of differences in dive capacities and prey demands. As discussed above, the range of forage dive depths that we observed for Adélie penguins during this study indicates that Adélie penguins were able to find adequate resources at relatively shallow depths. Based on our dietary results, Adélie and gentoo penguins are consuming similar prey, so deeper dives by gentoo penguins during this study are not driven by differences in prey type. It is possible that deeper dives by gentoo penguins could explain the slight differences we observed in krill size-class frequencies, but we would need more information on the population structure of krill aggregations concurrent with penguin dive data to be certain.

An alternative explanation as to why gentoo penguins track deeper prey layers could be related to prey patch density. Antarctic krill form more compact aggregations during the daytime as a result of increased schooling behavior (Zhou & Dorland 2004). According to optimal foraging theory (Charnov 1976) penguins should maximize net energy gain while foraging. Penguins must therefore balance the higher energetic costs of deeper dives with potentially increased rates of prey capture in deeper, but denser prey patches. Because gentoo penguins have higher prey requirements than Adélie penguins during the chick-rearing period based on their body and chick size (Croll & Tershy 1998; Trivelpiece et al. 1987), they may have a higher prey

density threshold that is not met during the daytime at shallow depths. Prey density thresholds have been demonstrated in previous studies involving baleen whales (Friedlaender et al. 2006; Piatt & Methven 1992) and seabirds (Mori & Boyd 2004; Piatt 1990) that are spatially associated with prey patches only if those patches are above varying density thresholds. If krill becomes increasingly sparse in the water column throughout the day as it migrates to deeper depths, gentoo penguins may cease to focus their effort at shallow depths in order to target more profitable, deeper prey patches, something which has been shown for other krill predators in the Antarctic (Friedlaender et al. 2013, 2016). A recent study by Watanabe et al. (2014) demonstrated that patch quality affects Adélie foraging behavior. While these authors focused on the effect of prey capture rates on patch residence time, future studies may be able to build on these methods and incorporate measures of patch density and aggregation structure in order to gain a better understanding of Adélie and gentoo penguin foraging thresholds. Previous research has indicated that differing foraging thresholds facilitate resource partitioning between sympatric seabirds (Mori & Boyd 2004; Ballance et al. 1997; Piatt 1990). Thus, differing tolerances to prey density could support the coexistence of sympatric Adélie and gentoo penguins.

Inter-annual variation in dive depth by Adélie and gentoo penguins could also suggest different tolerances to prey availability. We found that the average dive depth of gentoo penguins varied across years, while the average dive depth of Adélie penguins remained relatively consistent. We did not directly test for a correlation between penguin dive depth and krill population size structure, but it is likely that the variable dive depth of gentoo penguins is the result of variation in the spatial distribution and abundance of krill. A recent study found that when krill recruitment is high, krill are more abundant at shallower depths (Bernard et al. *in press*). In this study, gentoo penguins appeared to dive to shallower depths on average, in association with strong krill recruitment years (and vice versa). The idea that gentoo penguins may vary their dive behavior between years to maximize foraging efficiency is similar to the concept of prey threshold density discussed above in the context of diel dive behavior.

While we found differences in the average dive depth between the two species throughout the entire study, it is interesting to note that inter-annual variation of gentoo penguin

dive depth resulted in varying degrees of vertical overlap with Adélie penguins. For example, in 2011 and 2015, gentoo penguins utilized a large range of depths and concentrated their foraging effort below 50 meters, deeper than most Adélie penguin foraging dives. In comparison, in 2012, gentoo penguin dives were concentrated within the top 30 meters of the water column, and more overlap between the two species was observed. It is important to keep in mind that these dives did not usually occur in the same areas, but these general patterns are likely similar in areas where species horizontal ranges do overlap. The implication of these results is that the dive behavior of gentoo penguins determines the degree of potential vertical overlap between both species. It would be interesting to address this topic in future studies in the context of Pianka's (1974) niche overlap hypothesis, which predicts greater niche overlap when resources are abundant, and increased differentiation of niches when resources are limiting. In a resource limited scenario, gentoo penguins could take advantage of their ability to exploit deeper prey, thereby maintaining vertical partitioning of resources when absolutely necessary. A similar concept was addressed in a recent study by Leon et al. (2014) that showed that Galapagos ground finches exploited the resources that they were best adapted to when prey was limited, but exhibited more extensive niche overlap when 'preferred' shared foods were abundant.

Resource limitation is a necessary condition for competition to exist (Milne 1961). While the population structure of krill varied throughout this study, it is likely that overall, prey is not limiting in this system. The recently revisited krill surplus hypothesis (Trivelpiece et al. 2011; Laws 1970; Sladen 1964) cites declines in krill stocks (Atkinson et al. 2004) as a driver of declining penguin populations on the WAP. However, a recent assessment of krill stocks in the region where this study occurred did not find evidence of a long term decline of Antarctic krill (Steinberg et al. 2015). In addition, because gentoo penguin populations have been expanding in this region, and gentoo penguins are also relying on krill as a primary prey resource, declining krill stocks would not explain increasing gentoo populations. Furthermore, both species successfully provisioned chicks throughout the study, suggesting that breeding adults were able to locate adequate prey resources within their foraging ranges. Extensive foraging ranges of Adélie penguins (e.g. 70 km) during the chick-rearing phase of the breeding season are energetically costly to breeding adults and result in reduced food loads and decreased chick mass

(Ainley 2002). We observed relatively small foraging ranges (e.g. 5-10 km for Adélie penguins) in this study, indicating that these populations were not foraging near their physiological maxima. If prey resources are not limiting in this region, this strongly suggests that competition between penguins during the breeding season is not a primary driver of local population trends.

Understanding the effects of novel or altered biotic interactions is a critical step in predicting species responses to climate change (Urban et al. 2016). It has been challenging to identify the drivers of recent penguin population shifts on the Antarctic Peninsula, where the southern range of gentoo penguins is expanding and Adélie penguin populations are in decline (Lynch et al. 2012). In this study, we compared the foraging niches of Adélie and gentoo penguins in order to determine whether range-induced overlap has caused increased foraging competition between these two species. We did not find evidence to suggest that foraging competition is driving penguin population trends in this area, or that shared prey resources are limiting. In agreement with previous studies, our results show that Adélie and gentoo penguins have disparate foraging strategies that facilitate resource partitioning through multiple dimensions. While the physical and biological factors affecting *Pygoscelid* populations along the peninsula vary by region, these results provide further evidence that climate-induced sympatry of Adélie and gentoo penguins does not necessarily result in increased competition. Rather, other physical and biological changes to the ecosystem due to the rapidly changing climate around the Antarctic Peninsula may have stronger influences on the population trajectories of these two species.

Chapter 2 References

Ainley, D. (2002). *The Adélie Penguin: Bellwether of Climate Change*. Columbia University Press.

Atkinson, A., Siegel, V., Pakhomov, E., & Rothery, P. (2004). Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, *432*(7013), 100-103.

Ballance, L. T., Pitman, R. L., & Reilly, S. B. (1997). Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology*, *78*(5), 1502-1518.

Ballard, G., Ainley, D. G., Ribic, C. A., & Barton, K. R. (2001). Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie penguins. *The Condor*, *103*(3), 481-490.

Bannasch, R.,Wilson, R. P., & Culik, B. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *Journal of Experimental biology*, *194*(1), 83-96.

Barrett, R.T., Camphuysen, K.C., Anker-Nilssen, T., Chardine, J.W., Furness, R.W., Garthe, S., Hüppop, O., Leopold, M.F., Montevecchi, W.A. and Veit, R.R., 2007. Diet studies of seabirds: a review and recommendations. *ICES Journal of Marine Science: Journal du Conseil*, *64*(9), pp.1675-1691.

Belant, J. L., Millspaugh, J. J., Martin, J. A., & Gitzen, R. A. (2012). Multi-dimensional space use: the final frontier. *Frontiers in Ecology and the Environment*, *10*(1), 11-12.

Bost, C. A., & Jouventin, P. , (1990). Evolutionary ecology of gentoo penguins (Pygoscelis papua). *Penguin biology*, 85-112.

Bost, C. A., Handrich, Y., Butler, P. J., Fahlman, A., Halsey, L. G., Woakes, A. J., & Ropert-Coudert, Y. (2007). Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. *Deep Sea Research Part II: Topical Studies in Oceanography*, *54*(3), 248-255.

Cairns, D. K. (1989). The regulation of seabird colony size: a hinterland model. *The American Naturalist*, 134(1), 141-146.

Chappell, M. A., Shoemaker, V. H., Janes, D. N., Bucher, T. L., & Maloney, S. K. (1993). Diving behavior during foraging in breeding Adélie penguins. *Ecology*, *74*(4), 1204-1215.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical population biology*, *9*(2), 129-136.

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

Cimino, M. A., Lynch, H. J., Saba, V. S., & Oliver, M. J. (2016b). Projected asymmetric response of Adélie penguins to Antarctic climate change. *Scientific Reports*, *6*.

CLS (Collecte Localisation Satellites) (2016) Argos user's manual, http://www.argos-system.org/manual/, last updated 15 June 2016.

Cooper, N. W., Sherry, T. W., & Marra, P. P. (2014). Modeling three-dimensional space use and overlap in birds. *The Auk*, *131*(4), 681-693.

Croll, D. A., Osmek, S. D., & Bengtson, J. L. (1991). An effect of instrument attachment on foraging trip duration in chinstrap penguins. *The Condor*,*93*(3), 777-779.

Croll, D. A., & Tershy, B. R. (1998). Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica. *Polar Biology*, *19*(6), 365-374.

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

Ducklow, H. W., Baker, K., Martinson, D. G., Quetin, L. B., Ross, R. M., Smith, R. C., ... & Fraser, W. (2007). Marine pelagic ecosystems: the west Antarctic Peninsula. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1477), 67-94.

Duong, T. (2007). ks: kernel density estimation and kernel discriminant analysis for multivariate data in R. Journal of Statistical Software 21 (7):1-16.

Faraway, J. J. (2016). Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models (Vol. 124). CRC press.

Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management*,*69*(4), 1346-1359.

Fraser, W. R., & Hofmann, E. E. (2003). A predator's perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series*, *265*, 1-15.

Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in the Western Antarctic Peninsula shelf waters. *Mar Ecol Progress Ser* 317:297–314

Friedlaender, A. S., Tyson, R. B., Stimpert, A. K., Read, A. J., & Nowacek, D. P. (2013). Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. *Marine Ecology Progress Series*, *494*, 281-289.

Friedlaender, A.S., Johnston, D.W., Tyson, R.B., Kaltenberg, A., Goldbogen, J.A., Stimpert, A.K., Curtice, C., Hazen, E.L., Halpin, P.N., Read, A.J. and Nowacek, D.P., 2016.

Multiple-stage decisions in a marine central-place forager. *Royal Society Open Science*, *3*(5), p.160043.

Gorman, K. B., Williams, T. D., & Fraser, W. R. (2014). Ecological sexual dimorphism and environmental variability within a community of Antarctic penguins (genus Pygoscelis). *PloS one*, *9*(3), e90081.

Gorman, K.B. (2015) Integrative Studies of Southern Ocean Food-Webs and Pygoscelis Penguin Demography: Mechanisms of Population Response to Environmental Change (Doctoral Dissertation). Burnaby, B.C.: Simon Fraser University.

Gutowsky, S. E., Leonard, M. L., Conners, M. G., Shaffer, S. A., & Jonsen, I. D. (2015). Individual-level variation and higher-level interpretations of space use in wide-ranging species: an albatross case study of sampling effects. *Frontiers in Marine Science*, *2*, 93.

Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. In *Migrations and Dispersal of Marine Organisms* (pp. 163-170). Springer Netherlands.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? *Trends in ecology & evolution*, 15(2), 56-61.

Kirkwood, R., & Robertson, G. (1997). The foraging ecology of female emperor penguins in winter. *Ecological Monographs*, *67*(2), 155-176.Lescroël, A., & Bost, C. A. (2005). Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Marine Ecology Progress Series*, *302*, 245-261.

Kokubun, N., Takahashi, A., Mori, Y., Watanabe, S., & Shin, H. C. (2010). Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Marine Biology*, *157*(4), 811-825.

De León, L. F., Podos, J., Gardezi, T., Herrel, A., & Hendry, A. P. (2014). Darwin's finches and their diet niches: The sympatric coexistence of imperfect generalists. *Journal of evolutionary biology*, *27*(6), 1093-1104.

Laws R (1977) Seals and whales of the Southern Ocean. *Philos Trans R Soc Lond* 279: 81–96.

Lescroël, A., & Bost, C. A. (2005). Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Marine Ecology Progress Series*, *302*, 245-261.

Lescroel, A., Ridoux, V., & Bost, C. A. (2004). Spatial and temporal variation in the diet of the gentoo penguin (Pygoscelis papua) at Kerguelen Islands. *Polar Biology*, *27*(4), 206-216.

Lynch, H. J., Naveen, R., Trathan, P. N., & Fagan, W. F. (2012). Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology*, *93*(6), 1367-1377.

Lynnes, A., Reid, K., Croxall, J., & Trathan, P. (2002). Conflict or co-existence? Foraging distribution and competition for prey between Adélie and Chinstrap Penguins. *Marine Biology*, 141(6), 1165-1174.

Lynnes, A. S., Reid, K., & Croxall, J. P. (2004). Diet and reproductive success of Adélie and chinstrap penguins: linking response of predators to prey population dynamics. *Polar Biology*, *27*(9), 544-554.

Miller, A. K., & Trivelpiece, W. Z. (2007). Cycles of Euphausia superba recruitment evident in the diet of Pygoscelid penguins and net trawls in the South Shetland Islands, Antarctica. *Polar Biology*, *30*(12), 1615-1623.

Miller, A. K., Karnovsky, N. J., & Trivelpiece, W. Z. (2009). Flexible foraging strategies of gentoo penguins Pygoscelis papua over 5 years in the South Shetland Islands, Antarctica. *Marine Biology*, *156*(12), 2527-2537.

Milne, A. (1961). Definition of competition among animals. In *Symposia of the Society for Experimental Biology* (Vol. 15, pp. 40-61). University Press.

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

Oliver, M. J., Irwin, A., Moline, M. A., Fraser, W., Patterson, D., Schofield, O., & Kohut, J. (2013). Adélie penguin foraging location predicted by tidal regime switching. *PloS one*, *8*(1), e55163.

Orben, R. A., Irons, D. B., Paredes, R., Roby, D. D., Phillips, R. A., & Shaffer, S. A. (2015). North or south? Niche separation of endemic red-legged kittiwakes and sympatric black-legged kittiwakes during their non-breeding migrations. *Journal of Biogeography*, *42*(2), 401-412.

Orians, G. H., and Pearson, N. E. (1979). "On the theory of central place foraging," in Analysis of Ecological Systems, eds D. J. Horn, R. D.Mitchell, and G. R. Stairs (Columbus, OH: Ohio State University Press), 155–177.

Pianka, E.R. (1974) Niche overlap and diffuse competition. *Proc Natl Acad Sci* 71:2141- 2145.

Piatt, J.F., & Methven, D.A. (1992). Threshold foraging behavior of baleen whales. *Marine Ecology Progress Series*, *84*, 205-210.

Piatt, J. F. (1990). The aggregative response of common murres and Atlantic puffins to schools of capelin. *Studies in Avian Biology*, *14*, 36-51.

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

Polito, M. J., Lynch, H. J., Naveen, R., & Emslie, S. D. (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.

Quetin, L. B., & Ross, R. M. (2003). Episodic recruitment in Antarctic krill Euphausia superba in the Palmer LTER study region. *Marine Ecology Progress Series*, *259*, 185-200.

Reid, K., Barlow, K. E., Croxall, J. P., & Taylor, R. I. (1999). Predicting changes in the Antarctic krill, Euphausia superba, population at South Georgia. *Marine biology*, *135*(4), 647-652.

Reid, K., & Croxall, J. P. (2001). Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*(1465), 377-384.

Ritz, D. A. (1994). Social aggregation in pelagic invertebrates. *Advances in marine biology*, *30*, 155-216.

Rodary, D., Wienecke, B. C., & Bost, C. A. (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*(2), 113-120.

Saba, G.K., Fraser, W.R., Saba, V.S., Iannuzzi, R.A., Coleman, K.E., Doney, S.C., Ducklow, H.W., Martinson, D.G., Miles, T.N., Patterson-Fraser, D.L. and Stammerjohn, S.E., 2014. Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. *Nature communications*, 5.

Schofield, O., H. Ducklow, K. Bernard, S. Doney, D. Patterson-Fraser, K. Gorman, D. Martinson, M. Meredith, G. Saba, S. Stammerjohn, and others. 2013. Penguin biogeography along the West Antarctic Peninsula: Testing the Canyon Hypothesis with Palmer LTER observations. *Oceanography* 26(3):204–206.

Scott, D. W. (2015). Multivariate density estimation: theory, practice, and visualization. John Wiley & Sons.

Siegel, V. (1987). Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. *Marine Biology*, *96*(4), 483-495.

Simpfendorfer, C. A., Olsen, E. M., Heupel, M. R., & Moland, E. (2012). Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. *Canadian Journal of Fisheries and Aquatic Sciences*,*69*(3), 565-572.

Sladen WJL (1964) Biologie Antarctique, eds Carrick R, Holdgate MW, Prevost J (Hermann, Paris), pp 359–365.

Soanes, L. M., Arnould, J. P., Dodd, S. G., Sumner, M. D., & Green, J. A. (2013). How many seabirds do we need to track to define home-range area? *Journal of Applied Ecology*, *50*(3), 671-679.

Steinberg, D.K., Ruck, K.E., Gleiber, M.R., Garzio, L.M., Cope, J.S., Bernard, K.S., Stammerjohn, S.E., Schofield, O.M., Quetin, L.B. and Ross, R.M., 2015. Long-term (1993–2013) changes in macrozooplankton off the Western Antarctic Peninsula. *Deep Sea Research Part I: Oceanographic Research Papers*, 101, pp.54-70.

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

Trivelpiece, W. Z., Trivelpiece, S. G., & Volkman, N. J. (1987). Ecological segregation of Adélie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology*, 68(2), 351-361.

Trivelpiece, W. Z., Hinke, J. T., Miller, A. K., Reiss, C. S., Trivelpiece, S. G., & Watters, G. M. (2011). Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences*, 108(18), 7625-7628.

Urban, M.C., Bocedi, G., Hendry, A.P., Mihoub, J.B., Pe'er, G., Singer, A., Bridle, J.R., Crozier, L.G., De Meester, L., Godsoe, W. and Gonzalez, A., 2016. Improving the forecast for biodiversity under climate change. *Science*, *353*(6304), p.aad8466.

Volkman, N. J., Presler, P., & Trivelpiece, W. (1980). Diets of pygoscelid penguins at King George Island, Antarctica. *Condor*, 373-378.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O. and Bairlein, F., 2002. Ecological responses to recent climate change. *Nature*, 416(6879), pp.389-395.

Watanabe, Y. Y., Ito, M., & Takahashi, A. (2014). Testing optimal foraging theory in a penguin–krill system. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*(1779), 20132376.

Wilson, R., (1984). An improved stomach pump for penguins and other seabirds. *Journal of Field Ornithology* 55:110–112.

Wilson RP, Puetz K, Bost CA, Culik BM, Bannasch R, Reins T, Adelung D (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Marine Ecology Progress Series*94:101–104

Wilson, R. P., & Wilson, M. P. T. (1989). Tape: a package-attachment technique for penguins. *Wildlife Society Bulletin*, 77-79.

Wilson, R. P., Coria, N. R., Spairani, H. J., Adelung, D., & Culik, B. (1989). Human-induced behaviour in Adélie penguins Pygoscelis adeliae. *Polar Biology*, *10*(1), 77-80.

Wilson, R. P. (2010). Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Functional Ecology*, 24(3), 646-657.

Zhou, M., & Dorland, R. D. (2004). Aggregation and vertical migration behavior of Euphausia superba. *Deep Sea Research Part II: Topical Studies in Oceanography*, *51*(17), 2119-2

Figures

Figure 2.1: Study area on the southern coast of Anvers Island on the Western Antarctic Peninsula (inset). Map shows Adélie and gentoo penguin colonies at Biscoe Point (green triangle) and Humble and Torgersen Islands (yellow triangle) and bathymetry of nearby area including Palmer Deep Canyon (center of map).

Figure 2.2: Timetable of penguin field studies at Palmer Station, Antarctica, from 2010-2015.

Figure 2.3: Frequency occurrence of *E. superba*, *T. macrura*, fish and 'other' prey items in Adélie and gentoo diet samples collected during the chick-rearing phase of the breeding cycle at Palmer Station, Antarctica, from 2010-2015.

Figure 2.4: Prey composition (% wet mass) of *E. superba*, *T. macrura*, fish and 'other' prey items in Adélie and gentoo diet samples collected during the chick-rearing phase of the breeding cycle at Palmer Station, Antarctica, from 2010-2015.

Figure 2.5: Mean length (mm) of Antarctic krill found in penguin diet samples from 2010-2015. P-values are derived from a Welch's t-test comparing the mean length of krill found in Adélie and gentoo diet samples each year (*p=0.05, **p=0.03, ***p=0.004).

Figure 2.6: Size-class frequency distribution of Antarctic krill in the diets of Adélie and gentoo penguins during the chick-rearing phase of the breeding season at Palmer Station, Antarctica, from 2010-2015.

Figure 2.7: Foraging areas of Adélie and gentoo penguins during the breeding season at Palmer Station, Antarctica, from 2010-2015. Red shades depict the overall foraging ranges (95% KDE) of Adélie penguins tagged at Humble and Torgersen islands (yellow triangle). Blue shades depict the overall foraging ranges of gentoo penguins tagged at Biscoe point (green triangle). Darker shades indicate overlap area and contour lines outline the core foraging ranges (50% KDE) of both species.

Figure 2.8: Foraging areas of Adélie and gentoo penguins tagged at Biscoe point (green triangle). Red shades depict the overall foraging ranges (95% KDE) of Adélie penguins and blue shades depict the overall foraging ranges of gentoo penguins. Darker shades indicate overlap area and contour lines outline the core foraging ranges (50% KDE) of both species.

Figure 2.9: Distribution of Adélie and gentoo penguin foraging dives occurring during the breeding season at Palmer Station, Antarctica, from 2010-2015. Sample size (n individuals (total dives)) displayed at bottom right of each panel. Dives only include those from Adélie penguins tagged at Humble and Torgersen islands and gentoo penguins tagged at Biscoe point.

Figure 2.10: Proportion of Adélie and gentoo penguin foraging dives occurring by hour at Palmer Station, Antarctica, from 2010-2015.

Figure 2.11: Depth (m) of Adélie and gentoo penguin foraging dives grouped by hour of the day during the breeding season at Palmer Station, Antarctica, from 2010-2015.

Figure 2.12: Three-dimensional kernel density estimates of penguin foraging areas during the breeding season at Palmer Station, Antarctica, from 2010-2015. Adélie penguins tagged at Humble and Torgersen islands are shown in red and gentoo penguins tagged at Biscoe Point are shown in blue. Lighter shades depict overall foraging areas (95% KDE) and darker shades depict core foraging areas (50% KDE).

Figure 2.12 (Continued) Three-dimensional kernel density estimates of penguin foraging areas during the breeding season at Palmer Station, Antarctica, from 2010-2015. Adélie penguins tagged at Humble and Torgersen islands are shown in red and gentoo penguins tagged at Biscoe Point are shown in blue. Lighter shades depict overall foraging areas (95% KDE) and darker shades depict core foraging areas (50% KDE).

Figure 2.12 (Continued): Three-dimensional kernel density estimates of penguin foraging areas during the breeding season at Palmer Station, Antarctica, from 2010-2015. Adélie penguins tagged at Humble and Torgersen islands are shown in red and gentoo penguins tagged at Biscoe Point are shown in blue. Lighter shades depict overall foraging areas (95% KDE) and darker shades depict core foraging areas (50% KDE).

Figure 2.13: Three-dimensional kernel density estimates of foraging areas of Adélie and gentoo penguins tagged at Biscoe Point. Adélie penguins are shown in red and gentoo penguins are shown in grey. Lighter shades depict overall foraging areas (95% KDE) and darker shades depict core foraging areas (50% KDE).

Figure 2.13 (Continued): Three-dimensional kernel density estimates of foraging areas of Adélie and gentoo penguins tagged at Biscoe Point. Adélie penguins are shown in red and gentoo penguins are shown in grey. Lighter shades depict overall foraging areas (95% KDE) and darker shades depict core foraging areas (50% KDE).

Figure 2.14: Curves display core foraging area (m²) relative to sample size (n individuals). Bands represent the 95% confidence interval of total core area (50% KDE) occupied by Adélie penguins (in red) and gentoo penguins (in blue).

Figure 2.15: Distribution of foraging dives of Adélie and gentoo penguins within areas of overlap. Sample size (n individuals (total dives)) displayed at bottom right of each panel.

Figure 2.16: Distribution of foraging dives of Adélie and gentoo penguin tagged at Biscoe Point. Sample size (n individuals (total dives)) displayed at bottom right of each panel.

Tables

Table 2.1: Comparison of Adélie and gentoo penguin diets during the chick-rearing phase of the breeding cycle at Palmer Station, Antarctica, from 2010-2015. Parameters include: percent diet composition (mean ± SD), frequency occurrence (%) and size of Antarctic krill (mean ± SD).

Year	Species	n	Percent diet composition (wet mass)				Percent frequency occurrence				
			Antarctic Krill (_Euphausia superba_)	Big-eyed krill (_Thysannoessa macrura_)	Fish	Other	Antarctic Krill (_Euphausia superba_)	Big-eyed krill (_Thysannoessa macrura_)	Fish	Other	Antarctic krill length (mm)
_2010_	Adelie	23	99.2 ± 1.8	0.4 ± 1.7	0.4 ± 0.6	0.0 ± 0.0	100	13.0	60.9	0.0	43.9 ± 3.7
	Gentoo	10	98.6 ± 2.6	0.0 ± 0.0	1.3 ± 2.6	0.1 ± 0.1	100	0.0	90.0	30.0	45.9 ± 2.8
_2011_	Adelie	25	63.6 ± 41.0	36.0 ± 41.0	0.2 ± 0.3	0.1 ± 0.3	100	56.0	40.0	24.0	43.0 ± 8.7
	Gentoo	15	93.1 ± 15.2	6.6 ± 15.3	0.3 ± 0.4	0.0 ± 0.0	100	40.0	46.7	0.0	40.0 ± 5.4
_2012_	Adelie	15	99.5 ± 0.6	0.0 ± 0.0	0.4 ± 0.5	0.1 ± 0.3	100	0.0	40.0	13.3	38.1 ± 6.2
	Gentoo	36	94.8 ± 16.0	0.0 ± 0.0	4.7 ± 14.5	0.5 ± 2.1	100	0.0	80.6	22.2	42.0 ± 2.5
_2013_	Adelie	25	99.7 ± 0.7	0.0 ± 0.0	0.2 ± 0.7	0.0 ± 0.1	100	0.0	24.0	4.0	32.8 ± 1.3
	Gentoo	20	98.5 ± 4.3	0.0 ± 0.0	1.5 ± 4.1	0.0 ± 0.2	100	0.0	40.0	5.0	34.2 ± 2.7
_2014_	Adelie	21	99.4 ± 1.1	0.0 ± 0.0	0.6 ± 1.1	0.0 ± 0.0	100	0.0	42.9	0.0	39.9 ± 4.0
	Gentoo	18	99.2 ± 1.7	0.0 ± 0.0	0.7 ± 1.4	0.1 ± 0.4	100	0.0	27.8	5.6	41.1 ± 4.4
_2015_	Adelie	27	97.0 ± 13.0	2.8 ± 13.0	0.2 ± 0.5	0.0 ± 0.0	100	11.1	22.2	3.7	44.6 ± 2.7
	Gentoo	30	98.8± 2.4	0.1 ± 0.4	1.1 ± 2.4	0.0 ± 0.0	100	0.0	53.3	6.7	46.5 ± 1.7

Table 2.2: Results of Pearson's Chi-squared test comparing the size-class distribution of Antarctic krill in Adélie and gentoo penguin diet samples from 2010-2015. Krill were binned in 5 mm increments from 16-65 mm. Because of low counts, we combined both the smallest two bins and the largest two bins for a total of 8 bins.

Year	X^2	Df	p
2010	57.00	8	<0.001
2011	376.80	8	<0.001
2012	269.78	8	<0.001
2013	47.10	8	<0.001
2014	49.14	8	<0.001
2015	151.20	8	<0.001

Table 2.3: Comparison of Adélie and gentoo foraging ranges during the chick-rearing phase of the breeding season at Palmer Station, Antarctica, from 2010-2015 (excluding 2014 and Adélie penguins tagged at Biscoe Point). Parameters include: overall (95% 2D KDE) and core (50% 2D KDE) foraging area (km^2), % overlap and the associated utilization distribution overlap index (UDOI).

Year			Adélie				Gentoo		
	Kernel density	n	Area (km^2)	% Overlap with gentoo	n	Area (km^2)	% Overlap with Adélie	UDOI
2010	95%	7	101.2	2.2	6	167.6	1.3	0.00
	50%		25.0	0.0		40.6	0.0	0.00
2011	95%	10	196.0	4.8	8	198.6	4.8	0.00
	50%		41.0	0.0		46.2	0.0	0.00
2012	95%	10	129.3	15.3	12	187.4	10.6	0.01
	50%		34.0	0.0		44.9	0.0	0.00
2013	95%	8	54.9	0.0	11	122.5	0.0	0.00
	50%		11.4	0.0		29.3	0.0	0.00
2015	95%	11	78.7	18.7	7	204.4	7.2	0.00
	50%		17.5	0.0		41.3	0.0	0.00

Table 2.4: Comparison of the foraging areas and spatial overlap of Adélie and gentoo penguins tagged at Biscoe Point during the chick-rearing phase of the breeding season at Palmer Station, Antarctica. Parameters include: overall (95% 2D KDE) and core (50% 2D KDE) foraging area (km^2), % overlap and the associated utilization distribution overlap index (UDOI).

			Adélie			Gentoo		
Year	Kernel density	n	Area (km^2)	% Overlap with gentoo	n	Area (km^2)	% Overlap with Adélie	UDOI
2011	95%	1	37.5	99.7	8	198.2	18.9	0.22
	50%		8.3	55.1		45.9	10.0	0.03
2012	95%	2	90.7	90.8	12	187.6	43.9	0.49
	50%		22.5	66.6		45.1	33.3	0.09
2015	95%		28.6	35.7	7	205.3	5.0	0.03
	50%	2	7.0	18.5		41.1	3.1	0.00

Table 2.5: Results of generalized linear mixed model comparing Adélie and gentoo dive depth by year

	Maximum depth		Forage depth	
	X^2	p	X^2	p
2010	21.23	<0.001	21.03	<0.001
2011	13.91	<0.001	12.66	<0.001
2012	14.44	<0.001	12.87	<0.001
2013	14.77	<0.001	13.11	<0.001
2015	44.07	<0.001	43.72	<0.001

Table 2.6: Comparison of Adélie penguin foraging parameters by colony location during the chick-rearing phase of the breeding season at Palmer Station, Antarctica. Parameters include: maximum depth (mean ± SD), estimated forage depth (mean ± SD), distance of foraging dives from colony (mean ± SD), dive index (mean ± SD) and proportion of benthic dives.

Year	Island	n	Maximum depth (m)	Estimated forage depth (m)	Distance from colony (km)	Dive index (DI)	Proportion of benthic dives
2011	Humble	7	26.9 ± 13.5	23.3 ± 12.1	9.5 ± 4.7	0.14 ± 0.13	0.005
	Biscoe	1	42.8 ± 16	37.2 ± 14.8	9.9 ± 3.0	0.16 ± 0.08	0
2012	Torgersen	10	13.3 ± 5.4	11.7 ± 4.8	5.8 ± 2.3	0.07 ± 0.07	0.004
	Biscoe	2	19.2 ± 10	17.0 ± 9.2	5.4 ± 3.0	.09 ± 0.31	0
2015	Torgersen	11	16.0 ± 8.1	13.9 ± 6.8	5.1 ± 1.8	0.08 ± 0.09	0.003
	Biscoe	2	14.2 ± 5.3	12.9 ± 4.8	6.6 ± 2.9	.08 ± 0.07	0

Table 2.7: Comparison of the three-dimensional foraging areas and spatial overlap of Adélie and gentoo penguins tagged at Biscoe Point during the chick-rearing phase of the breeding season at Palmer Station, Antarctica. Parameters include: overall (95% 3D KDE) and core (50% 3D KDE) foraging area (km^3), % overlap and the associated utilization distribution overlap index (UDOI).

			Adélie			Gentoo		
Year	Kernel density	n	Area (km³)	% overlap with gentoo	n	Area (km³)	% overlap with Adélie	UDOI
2010	95%	7	3.4	1.1	6	11.7	0.3	0.00
	50%		0.6	0.0		2.2	0.0	0.00
2011	95%	10	9.4	1.4	8	19.9	0.6	0.00
	50%		1.6	0.0		3.2	0.0	0.00
2012	95%	10	2.1	15.9	12	10.2	3.3	0.01
	50%		0.5	2.6		1.6	0.9	0.00
2013	95%	8	1.6	0.0	11	8.0	0.0	0.00
	50%		0.3	0.0		1.3	0.0	0.00
2015	95%	11	2.3	8.0	7	18.1	1.0	0.00
	50%		0.5	0.0		3.2	0.0	0.00

Table 2.8: Comparison of the three-dimensional foraging areas and spatial overlap of Adélie and gentoo penguins tagged at Biscoe Point during the chick-rearing phase of the breeding season at Palmer Station, Antarctica. Parameters include: overall (95% 3D KDE) and core (50% 3D KDE) foraging area (km^3), % overlap and the associated utilization distribution overlap index (UDOI).

Year	Kernel density	n	Adélie Area (km^3)	% overlap with gentoo	n	Gentoo Area (km^3)	% overlap with Adélie	UDOI
2011	95%	1	1.4	72.1	8	19.5	5.0	0.06
	50%		0.2	33.3		3.1	2.5	0.01
2012	95%	2	2.3	74.1	12	10.0	17.3	0.30
	50%		0.5	52.4		1.6	15.7	0.04
2015	95%	2	0.5	21.6	7	17.9	0.6	0.00
	50%		0.2	7.4		3.2	0.4	0.00

Table 2.9: Foraging parameters of Adélie and gentoo penguins during the chick-rearing phase of the breeding season at Palmer Station, Antarctica, from 2010-2015 (excluding 2014 and Adélie penguins tagged at Biscoe Point). Parameters include: maximum depth (mean ± SD), estimated forage depth (mean ± SD), distance of foraging dives from colony (mean ± SD), dive index (mean ± SD) and proportion of benthic dives.

Year	Species	n	Maximum depth (m)	Estimated forage depth (m)	Distance from colony (km)	Dive index (DI)	Proportion of benthic dives
2010	Adélie	7	21.5 ± 11.3	18.3 ± 10.1	7.3 ± 3.2	0.09 ± 0.07	0.001
	Gentoo	6	46.6 ± 24.1	39.8 ± 22.1	8.6 ± 3.7	0.19 ± 0.16	0.008
2011	Adélie	10	26.9 ± 13.5	23.3 ± 12.1	9.5 ± 4.7	0.14 ± 0.13	0.005
	Gentoo	8	54.4 ± 29.6	46.7 ± 27.0	9.4 ± 4.9	0.17 ± 0.14	0.006
2012	Adélie	10	13.3 ± 5.4	11.7 ± 4.8	5.8 ± 2.3	0.07 ± 0.07	0.004
	Gentoo	12	39.6 ± 27.2	34.8 ± 24.6	8.7 ± 4.8	0.16 ± 0.16	0.009
2013	Adélie	8	20.1 ± 9.1	18.1 ± 8.3	5.6 ± 2.6	0.10 ± 0.10	0.001
	Gentoo	11	35.2 ± 19.5	30.4 ± 17.2	6.8 ± 3.4	0.14 ± 0.11	0.004
2015	Adélie	11	16.0 ± 8.1	13.9 ± 6.8	5.1 ± 1.8	0.08 ± 0.09	0.003
	Gentoo	7	64.6 ± 31.5	55.1 ± 29.0	11.6 ± 5.5	0.23 ± 0.19	0.043

CHAPTER 3: GENERAL CONCLUSION

My research investigated the foraging niches of Adélie and gentoo penguins over the course of five breeding seasons at Palmer Station, Anvers Island. The primary objective of this study was to determine the extent and consistency of niche segregation between these two species through dietary comparisons and by examining their spatial distributions in three-dimensions. While I found substantial overlap in the diets of Adélie and gentoo penguins, my results showed that Adélie and gentoo penguins partition this shared prey resource through spatial segregation of their primary foraging areas and depth ranges. Furthermore, I did not find evidence that Antarctic krill is a limiting resource during the breeding season. These results do not suggest that competition for prey exists between Adélie and gentoo penguins and therefore is unlikely to be a driver of their opposing population trends at Palmer Station.

There are other possible explanations for Adélie and gentoo population trends related to biotic interactions that I did not address in this study, including reduced resources and competition with other krill predators (e.g. baleen whales) during the post-breeding season. It is possible that prey resources are limiting in the post-breeding season and/or the potential for competition between krill predators is higher during the winter. Differences in the spatial distribution of Adélie and gentoo penguins during the winter months likely play a crucial role in their opposing population trends. Differing strategies during the post- breeding season may reveal other causal mechanisms behind the opposing population trends of Adélie and gentoo penguins (Fraser et al. 1992). For example, there could be differences in the distribution and abundance of prey that is associated with gentoo habitat (nearshore) versus Adélie habitat (close to the edges of fast ice). In regions where Adélie penguin populations have declined, there is evidence that a primary driver of population declines is poor juvenile recruitment, indicating insufficient resources and/or habitat during the post-breeding season (Trivelpiece et al. 2011; Hinke et al. 2007). Future research should focus on understanding more about the ecological niches of Adélie and gentoo penguins during the post-breeding season, and the extent of resource limitation during this period.

The recent recovery of Antarctic humpback whales is a focal aspect of Trivelpiece et al's (2011) hypothesis that *Pygoscelid* population declines are the results of increased competition with krill predators. Similar to the krill surplus hypothesis (Laws 1970), this hypothesis has

proven challenging to test. Our study did not address foraging competition with whales, though there is evidence from studies conducted on the WAP, as well as in the Ross Sea that indicate significant spatiotemporal and dietary overlap between penguins and whales. A multi-year study in the Ross Sea found that the presence of minke whales affected prey availability, and the foraging trip durations of penguins during the breeding season (Ainley et al. 2006). Friedlaender et al. (2008) found evidence of overlap in prey resources utilized by Adélie penguins and humpback whales in the vicinity of Palmer Station, but no evidence to suggest that whale abundance affected the foraging behavior (foraging trip duration) of penguins. During the austral summer months, large numbers of humpback whales migrate to high latitude feeding grounds, representing a large influx of krill predators in the Palmer area during the same time prey demand by penguins is highest (Friedlaender et al. 2008). While there is potential for competition for shared prey resources in the Palmer region based on spatiotemporal overlap, the differing life history and physiological constraints of cetaceans and penguins complicate our understanding of niche segregation and competition between these two groups of animals (Friedlaender et al. 2011). It is also important to note that while many populations of baleen whales (e.g. humpback whales) have increased in recent decades, the overall abundance of baleen whales in this region is still well below what it was in the pre-whaling era. Thus, it is important to consider a long-time frame when considering the top-down effects of whales in this current ecosystem. My results build on our understanding of penguin foraging niches during the breeding season at Palmer Station, and this knowledge can be incorporated into future research that directly addresses competition between penguins and whales.

In addition to the alternative biological mechanisms discussed above, there is strong evidence suggesting that physical changes in penguin habitat are responsible for the decline of Adélie penguins on the WAP and the simultaneous expansion of gentoo penguin colonies. Gentoo penguins are an ice-intolerant species whose range on the peninsula is currently restricted to areas with less than 50% November sea ice coverage (Lynch et al. 2012). Thus, reductions in sea ice along the peninsula have resulted in more accessible habitat for gentoo penguins. The opposite is true for the ice-obligate Adélie penguin (Fraser et al. 1992). While a recent study by Lynch et al. (2012) did not find a correlation between November sea ice coverage and Adélie trends, there is ample evidence that winter sea ice conditions are important

for juvenile recruitment (Trivelpiece et al. 2011; Hinke et al. 2007; Fraser et al. 1992). An overall decline of chinstrap penguins on the WAP (a species also described as an ice-intolerant) suggests that sea ice does not explain all of the observed variability in *Pygoscelis* trends (Lynch et al. 2012; Trivelpiece et al. 2011). In addition to sea ice changes, gentoo penguins are hypothesized to be more tolerable to increases in precipitation and warmer temperatures on the WAP. Higher amounts of snow accumulation into the late spring increase the likelihood of nest flooding and chick mortality at breeding colonies (Fraser et al. 2013). Extinctions of local breeding colonies of Adélie penguins in the Palmer region have been linked to island geomorphology, due to higher snow accumulation on leeward facing slopes (Fraser et al. 2013). While both species are vulnerable to snow accumulation during nesting, gentoo penguins have the advantage of a slightly delayed breeding schedule and more flexible breeding phenology (Lynch et al. 2012; McClintock et al. 2008; Trivelpiece et al. 1987). Future research should continue to explore the effects of local and large-scale climate variability (e.g. Cimino et al. 2016b; Cimino et al. 2014).

The potential mechanisms that explain Adélie and gentoo penguin population trajectories on the WAP are complex. Here, I have demonstrated that competition between these two species during the breeding season is not a likely driver of the trends observed in the Palmer region. These results can be used to inform future studies of competition with other krill predators, such as humpback whales. The potential for competition between Adélie and gentoo penguins at other breeding sites may depend on local prey availability, colony sizes and proximity of breeding colonies. However, my results build on previous studies that have concluded that discrete foraging strategies facilitate niche segregation between Adélie and gentoo penguins in areas of sympatry. Trivelpiece et al. 1987 surmised that the differences in the foraging strategies of *Pygoscelis* penguins are not the result of competition, rather, a consequence of having evolved in different environments. Therefore, future penguin population trajectories will be determined largely by how well suited each species is to the current climate. By providing information on interspecific interactions, my results inform forecasting studies that aim to predict the effects of climate change on Adélie and gentoo penguins, and long-term monitoring programs that rely on these top predators as ecosystem sentinels.

THESIS REFERENCES

Ainley, D. (2002). *The Adélie Penguin: Bellwether of Climate Change*. Columbia University Press.

Atkinson, A., Siegel, V., Pakhomov, E., & Rothery, P. (2004). Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, *432*(7013), 100-103.

Ballance, L. T., Pitman, R. L., & Reilly, S. B. (1997). Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology*, *78*(5), 1502-1518.

Ballard, G., Ainley, D. G., Ribic, C. A., & Barton, K. R. (2001). Effect of instrument attachment and other factors on foraging trip duration and nesting success of Adélie penguins. *The Condor*, *103*(3), 481-490.

Bannasch, R.,Wilson, R. P., & Culik, B. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *Journal of Experimental biology*, *194*(1), 83-96.

Barrett, R.T., Camphuysen, K.C., Anker-Nilssen, T., Chardine, J.W., Furness, R.W., Garthe, S., Hüppop, O., Leopold, M.F., Montevecchi, W.A. and Veit, R.R., 2007. Diet studies of seabirds: a review and recommendations. *ICES Journal of Marine Science: Journal du Conseil*, *64*(9), pp.1675-1691.

Belant, J. L., Millspaugh, J. J., Martin, J. A., & Gitzen, R. A. (2012). Multi-dimensional space use: the final frontier. *Frontiers in Ecology and the Environment*, *10*(1), 11-12.

Bestelmeyer, B.T., Ellison, A.M., Fraser, W.R., Gorman, K.B., Holbrook, S.J., Laney, C.M., Ohman, M.D., Peters, D.P., Pillsbury, F.C., Rassweiler, A. and Schmitt, R.J., 2011. Analysis of abrupt transitions in ecological systems. *Ecosphere*, 2(12), pp.1-26.

Bost, C. A., & Jouventin, P. (1990). Evolutionary ecology of gentoo penguins (Pygoscelis papua). *Penguin biology*, 85-112.

Bost, C. A., Handrich, Y., Butler, P. J., Fahlman, A., Halsey, L. G., Woakes, A. J., & Ropert-Coudert, Y. (2007). Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. *Deep Sea Research Part II: Topical Studies in Oceanography*, *54*(3), 248-255.

Cairns, D. K. (1989). The regulation of seabird colony size: a hinterland model. *The American Naturalist*, 134(1), 141-146.

Chappell, M. A., Shoemaker, V. H., Janes, D. N., Bucher, T. L., & Maloney, S. K. (1993).Diving behavior during foraging in breeding Adélie penguins. *Ecology*, *74*(4), 1204-1215.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical population biology*, *9*(2), 129-136.

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

Cimino, M. A., Lynch, H. J., Saba, V. S., & Oliver, M. J. (2016b). Projected asymmetric response of Adélie penguins to Antarctic climate change. *Scientific Reports*, *6*.

CLS (Collecte Localisation Satellites) (2016) Argos user's manual, http://www.argos-system.org/manual/, last updated 15 June 2016.

Clarke, A., Murphy, E. J., Meredith, M. P., King, J. C., Peck, L. S., Barnes, D. K., & Smith, R. C. (2007). Climate change and the marine ecosystem of the western Antarctic Peninsula. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 362(1477), 149-166.

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. *Ecology*, 42(4), 710-723.

Cooper, N. W., Sherry, T. W., & Marra, P. P. (2014). Modeling three-dimensional space use and overlap in birds. *The Auk*, *131*(4), 681-693.

Croll, D. A., Osmek, S. D., & Bengtson, J. L. (1991). An effect of instrument attachment on foraging trip duration in chinstrap penguins. *The Condor*, *93*(3), 777-779.

Croll, D. A., & Tershy, B. R. (1998). Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica. *Polar Biology*, *19*(6), 365-374.

Croxall, J. P., Reid, K., & Prince, P. A. (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. & Davis, L.S. (1999). Penguins: paradoxes and patterns. *Marine Ornithology* 27: 1-12.

Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M. and Fraser, W., 2007. Marine pelagic ecosystems: the west Antarctic Peninsula. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362(1477), pp.67-94.

Ducklow, H.W., Fraser, W.R., Meredith, M.P., Stammerjohn, S.E., Doney, S.C., Martinson, D.G., Sailley, S.F., Schofield, O.M., Steinberg, D.K., Venables, H.J. and Amsler, C.D., 2013. West Antarctic Peninsula: an ice-dependent coastal marine ecosystem in transition. *Oceanography* 26 (3).

Duong, T. (2007). ks: kernel density estimation and kernel discriminant analysis for multivariate data in R. Journal of Statistical Software 21 (7):1-16.

Durant, J. M., Hjermann, D. Ø., Ottersen, G., & Stenseth, N. C. (2007). Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33(3), 271-283.

Durant, J.M., Hjermann, D.Ø., Frederiksen, M., Charrassin, J.B., Le Maho, Y., Sabarros, P.S., Crawford, R.J. and Stenseth, N.C., 2009. Pros and cons of using seabirds as ecological indicators. *Climate Research*, 39(2), 115-129.

Faraway, J. J. (2016). Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models (Vol. 124). CRC press.

Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management*, *69*(4), 1346-1359.

Fraser, W. R., & Hofmann, E. E. (2003). A predator¹s perspective on causal links between climate change, physical forcing and ecosystem response. *Marine Ecology Progress Series*, *265*, 1-15.

Fraser, W. R., Trivelpiece, W. Z., Ainley, D. G., & Trivelpiece, S. G. (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.

Fraser, W. R., & Trivelpiece, W. Z. (1996). Factors Controlling the Distribution of Seabirds: Winter-Summer Heterogeneity in the Distribution of AdéLie Penguin Populations (pp. 257-272). American Geophysical Union.

Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in the Western Antarctic Peninsula shelf waters. *Mar Ecol Progress Ser* 317:297–314

Friedlaender, A. S., Tyson, R. B., Stimpert, A. K., Read, A. J., & Nowacek, D. P. (2013). Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. *Marine Ecology Progress Series*, *494*, 281-289.

Friedlaender, A.S., Johnston, D.W., Tyson, R.B., Kaltenberg, A., Goldbogen, J.A., Stimpert, A.K., Curtice, C., Hazen, E.L., Halpin, P.N., Read, A.J. and Nowacek, D.P., 2016. Multiple-stage decisions in a marine central-place forager. *Royal Society Open Science*, *3*(5), p.160043.

Gause, G. F. (1934). Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science*, 79(2036), 16-17.

Gorman, K.B. (2015) Integrative Studies of Southern Ocean Food-Webs and Pygoscelis Penguin Demography: Mechanisms of Population Response to Environmental Change (Doctoral Dissertation). Burnaby, B.C.: Simon Fraser University.

Gorman, K. B., Williams, T. D., & Fraser, W. R. (2014). Ecological sexual dimorphism and environmental variability within a community of Antarctic penguins (genus Pygoscelis). *PloS one*, *9*(3), e90081.

Gutowsky, S. E., Leonard, M. L., Conners, M. G., Shaffer, S. A., & Jonsen, I. D. (2015). Individual-level variation and higher-level interpretations of space use in wide-ranging species: an albatross case study of sampling effects. *Frontiers in Marine Science*, *2*, 93.

Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. In *Migrations and Dispersal of Marine Organisms* (pp. 163-170). Springer Netherlands.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? *Trends in ecology & evolution*, 15(2), 56-61.

Hutchinson, G.E. (1958) Concluding remarks. Cold Spring Harbour Symposium on Quantitative Biology, 22, 417–427.

Kirkwood, R., & Robertson, G. (1997). The foraging ecology of female emperor penguins in winter. *Ecological Monographs*, *67*(2), 155-176.Lescroël, A., & Bost, C. A. (2005). Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Marine Ecology Progress Series*, *302*, 245-261.

Kokubun, N., Takahashi, A., Mori, Y., Watanabe, S., & Shin, H. C. (2010). Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Marine Biology*, *157*(4), 811-825.

Laws, R. M. (1977). Seals and whales of the Southern Ocean. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 279(963), 81-96.

De León, L. F., Podos, J., Gardezi, T., Herrel, A., & Hendry, A. P. (2014). Darwin's finches and their diet niches: The sympatric coexistence of imperfect generalists. *Journal of evolutionary biology*, *27*(6), 1093-1104.

Lescroël, A., & Bost, C. A. (2005). Foraging under contrasting oceanographic conditions: the gentoo penguin at Kerguelen Archipelago. *Marine Ecology Progress Series*, *302*, 245-261.

Lescroel, A., Ridoux, V., & Bost, C. A. (2004). Spatial and temporal variation in the diet of the gentoo penguin (Pygoscelis papua) at Kerguelen Islands. *Polar Biology*, *27*(4), 206-216.

Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelplece, W., & Trivelplece, S. (1997). Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature*, 387(6636), 897-900.

Lynch, H. J., Naveen, R., Trathan, P. N., & Fagan, W. F. (2012). Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology*, *93*(6), 1367-1377.

Lynch, H. J., & LaRue, M. A. (2014). First global census of the Adélie Penguin. *The Auk*, 131(4), 457-466.

Lynnes, A., Reid, K., Croxall, J., & Trathan, P. (2002). Conflict or co-existence? Foraging distribution and competition for prey between Adélie and Chinstrap Penguins. *Marine Biology*, 141(6), 1165-1174.

Lynnes, A. S., Reid, K., & Croxall, J. P. (2004). Diet and reproductive success of Adélie and chinstrap penguins: linking response of predators to prey population dynamics. *Polar Biology*, *27*(9), 544-554.

MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*, 39(4), 599-619.

Massom, R. A., & Stammerjohn, S. E. (2010). Antarctic sea ice change and variability–physical and ecological implications. *Polar Science*, 4(2), 149-186.

Miller, A. K., Kappes, M. A., Trivelpiece, S. G., & Trivelpiece, W. Z. (2010). Foraging-niche separation of breeding gentoo and chinstrap penguins, South Shetland Islands, Antarctica. *The Condor*, 112(4), 683-695.

Miller, A. K., Karnovsky, N. J., & Trivelpiece, W. Z. (2009). Flexible foraging strategies of gentoo penguins Pygoscelis papua over 5 years in the South Shetland Islands, Antarctica. *Marine Biology*, 156(12), 2527-2537.

Miller, A. K., & Trivelpiece, W. Z. (2007). Cycles of Euphausia superba recruitment evident in the diet of Pygoscelid penguins and net trawls in the South Shetland Islands, Antarctica. *Polar Biology*, 30(12), 1615-1623.

Milne, A. (1961). Definition of competition among animals. In *Symposia of the Society for Experimental Biology* (Vol. 15, pp. 40-61). University Press.

Moline, M. A., Claustre, H., Frazer, T. K., Schofield, O., & Vernet, M. (2004). Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Global Change Biology*, 10(12), 1973-1980.

Mooney, H. A., & Cleland, E. E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences*, 98(10), 5446-5451.

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

Oliver, M. J., Irwin, A., Moline, M. A., Fraser, W., Patterson, D., Schofield, O., & Kohut, J. (2013). Adélie penguin foraging location predicted by tidal regime switching. *PloS one*, *8*(1), e55163.

Orben, R. A., Irons, D. B., Paredes, R., Roby, D. D., Phillips, R. A., & Shaffer, S. A. (2015). North or south? Niche separation of endemic red-legged kittiwakes and sympatric black-legged kittiwakes during their non-breeding migrations. *Journal of Biogeography*, *42*(2), 401-412.

Orians, G. H., and Pearson, N. E. (1979). "On the theory of central place foraging," in Analysis of Ecological Systems, eds D. J. Horn, R. D.Mitchell, and G. R. Stairs (Columbus, OH: Ohio State University Press), 155–177.

Parmelee, D.F. 1992 Antarctic birds. Minneapolis University of Minnesota Press. 202 pp.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 637-669.

Pianka, E. R. (1981). Competition and niche theory. Theoretical ecology principles and applications, 167-196.

Pianka, E.R. (1974) Niche overlap and diffuse competition. *Proc Natl Acad Sci* 71:2141- 2145.

Piatt, J.F., & Methven, D.A. (1992). Threshold foraging behavior of baleen whales. *Marine Ecology Progress Series*, *84*, 205-210.

Piatt, J. F. (1990). The aggregative response of common murres and Atlantic puffins to schools of capelin. *Studies in Avian Biology*, *14*, 36-51.

Piatt, J. F., Harding, A. M., Shultz, M., Speckman, S. G., van Pelt, T. I., Drew, G. S., & Kettle, A. B. (2007). Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series*, 352, 221-234.

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

Polito, M. J., Lynch, H. J., Naveen, R., & Emslie, S. D. (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.

Poncet, S. (1993). The distribution and abundance of Antarctic and Subantarctic penguins. Scientific Committee on Antarctic Research (SCAR).

Quetin, L. B., & Ross, R. M. (2003). Episodic recruitment in Antarctic krill Euphausia superba in the Palmer LTER study region. *Marine Ecology Progress Series*, *259*, 185-200.

Reid, K., Barlow, K. E., Croxall, J. P., & Taylor, R. I. (1999). Predicting changes in the Antarctic krill, Euphausia superba, population at South Georgia. *Marine biology*, *135*(4), 647-652.

Reid, K., & Croxall, J. P. (2001). Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*(1465), 377-384.

Ritz, D. A. (1994). Social aggregation in pelagic invertebrates. *Advances in marine biology*, *30*, 155-216.

Rodary, D., Wienecke, B. C., & Bost, C. A. (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*(2), 113-120.

Saba, G.K., Fraser, W.R., Saba, V.S., Iannuzzi, R.A., Coleman, K.E., Doney, S.C., Ducklow, H.W., Martinson, D.G., Miles, T.N., Patterson-Fraser, D.L. and Stammerjohn, S.E., 2014. Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. *Nature communications*, 5.

Schoener, T. W. (1983). Field experiments on interspecific competition. American naturalist, 240-285.

Schofield, O., H. Ducklow, K. Bernard, S. Doney, D. Patterson-Fraser, K. Gorman, D. Martinson, M. Meredith, G. Saba, S. Stammerjohn, and others. 2013. Penguin biogeography along the West Antarctic Peninsula: Testing the Canyon Hypothesis with Palmer LTER observations. *Oceanography* 26(3):204–206.

Schofield, O., Ducklow, H. W., Martinson, D. G., Meredith, M. P., Moline, M. A., & Fraser, W. R. (2010). How do polar marine ecosystems respond to rapid climate change? *Science*, 328(5985), 1520-1523.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., & Kühn, I. (2008). Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, 89(12), 3472-3479.

Scott, D. W. (2015). Multivariate density estimation: theory, practice, and visualization. John Wiley & Sons.

Siegel, V. (1987). Age and growth of Antarctic Euphausiacea (Crustacea) under natural conditions. *Marine Biology*, *96*(4), 483-495.

Simpfendorfer, C. A., Olsen, E. M., Heupel, M. R., & Moland, E. (2012). Three-dimensional kernel utilization distributions improve estimates of space use in aquatic animals. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(3), 565-572.

Sinervo, B., Mendez-De-La-Cruz, F., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Resendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N. and Gadsden, H., 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science*, 328(5980), pp.894-899.

Sladen WJL (1964) Biologie Antarctique, eds Carrick R, Holdgate MW, Prevost J (Hermann, Paris), pp 359–365.

Soanes, L. M., Arnould, J. P., Dodd, S. G., Sumner, M. D., & Green, J. A. (2013). How many seabirds do we need to track to define home-range area? *Journal of Applied Ecology*, *50*(3), 671-679.

Steinberg, D.K., Ruck, K.E., Gleiber, M.R., Garzio, L.M., Cope, J.S., Bernard, K.S., Stammerjohn, S.E., Schofield, O.M., Quetin, L.B. and Ross, R.M., 2015. Long-term (1993–2013) changes in macrozooplankton off the Western Antarctic Peninsula. *Deep Sea Research Part I: Oceanographic Research Papers*, 101, pp.54-70.

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

Trivelpiece, W. Z., Trivelpiece, S. G., & Volkman, N. J. (1987). Ecological segregation of Adélie, gentoo, and chinstrap penguins at King George Island, Antarctica. *Ecology*, 68(2), 351-361.

Trivelpiece, W. Z., Hinke, J. T., Miller, A. K., Reiss, C. S., Trivelpiece, S. G., & Watters, G. M. (2011). Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences*, 108(18), 7625-7628.

Urban, M.C., Bocedi, G., Hendry, A.P., Mihoub, J.B., Pe'er, G., Singer, A., Bridle, J.R., Crozier, L.G., De Meester, L., Godsoe, W. and Gonzalez, A., 2016. Improving the forecast for biodiversity under climate change. *Science*, *353*(6304), p.aad8466.

Volkman, N. J., Presler, P., & Trivelpiece, W. (1980). Diets of pygoscelid penguins at King George Island, Antarctica. *Condor*, 373-378.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O. and Bairlein, F., 2002. Ecological responses to recent climate change. *Nature*, 416(6879), pp.389-395.

Watanabe, Y. Y., Ito, M., & Takahashi, A. (2014). Testing optimal foraging theory in a penguin–krill system. *Proceedings of the Royal Society of London B: Biological Sciences*, *281*(1779), 20132376.

Wilson, R., (1984). An improved stomach pump for penguins and other seabirds. *Journal of Field Ornithology* 55:110–112.

Wilson RP, Puetz K, Bost CA, Culik BM, Bannasch R, Reins T, Adelung D (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Marine Ecology Progress Series*94:101–104

Wilson, R. P., & Wilson, M. P. T. (1989). Tape: a package-attachment technique for penguins. *Wildlife Society Bulletin*, 77-79.

Wilson, R. P., Coria, N. R., Spairani, H. J., Adelung, D., & Culik, B. (1989). Human-induced behaviour in Adélie penguins Pygoscelis adeliae. *Polar Biology*, *10*(1), 77-80.

Wilson, R. P. (2010). Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Functional Ecology*, 24(3), 646-657.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromentin, J.M., Hoegh-Guldberg, O. and Bairlein, F., 2002. Ecological responses to recent climate change. *Nature*, 416(6879), pp.389-395.

Williams, A. (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(3), 646-657.

Woehler, E. J. (1993). The Distribution and Abundance of Antarctic and Subantarctic Penguins. Scientific Committee on Antarctic Research, Cambridge, UK.

Zarnetske, P. L., Skelly, D. K., & Urban, M. C. (2012). Biotic multipliers of climate change. *Science*, 336(6088), 1516-1518.

Zhou, M., & Dorland, R. D. (2004). Aggregation and vertical migration behavior of Euphausia superba. *Deep Sea Research Part II: Topical Studies in Oceanography*, *51*(17), 2119-2137.