Foraging in a dynamic environment: Movement and stable isotope ecology of marine top predators breeding at the Prince Edward Archipelago

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Foraging in a dynamic environment: Movement and stable isotope ecology of marine top predators breeding at the Prince Edward Archipelago

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Declaration

I, Tegan Carpenter-Kling (s214236447), hereby declare that this thesis submitted in the fulfilment of the requirements for the degree, Doctor of Philosophy, is my own work and that it has not previously been submitted for assessment or completion of any post graduate qualification to another university or for another qualification.

Tegan Carpenter-Kling

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Table of contents

Declaration ii

List of Tables v

List of Figures vii

Abstract xi

Acknowledgements xiii

Preface xv

Chapter 1: General Introduction 1

Coexistence of sympatric marine top predators 4

Marine top predators across a dynamic landscap 6

Studying seabird and seal foraging behaviour 7

Rationale 11

Thesis aims and structure 14

Chapter 2: Foraging in a dynamic environment: Response of four sympatric sub-Antarctic albatross species to interannual environmental variability 21

Introduction 22

Materials and Methods 26

Results 33

Discussion 43

Conclusions 50

Supplementary Material 51

Chapter 3: Dynamic resource partitioning among sub-Antarctic marine predators 56

Introduction 57

Materials and Methods 61

Results 64

Discussion 71

Conclusions 76

Supplementary Material 77

Chapter 4: A critical assessment of marine predator isoscapes within the Southern Indian Ocean 86

Introduction 87

Materials and Methods 90

Results 97

Discussion 109

Conclusion 116

Supplementary Material 117

Chapter 5: Sensitivity of δ^{13}C values of seabird tissues to combined spatial, temporal and ecological drivers: a simulation approach 119

Introduction 120

Materials and Methods 123

Results 131

Discussion 136

Conclusion 139

Chapter 6: General Discussion 140

Response of a community of marine predators to environmental variability 143

Contributions to seabird and seal stable isotope ecology 145

Towards the future 148

Final Thoughts 150

Cited literature: **152**

List of tables

Chapter 1

1.1. International Union for Conservation of Nature Red List categories and global population trends of the ten seabird and two fur seal species studied at Marion Island. Scientific names of the species and abbreviations used are given. 13

Chapter 2

2.1. Kernel utilization distribution overlap (Bhattacharyya's Affinity) at the 50% and 90% utilization distributions (UD) among three breeding seasons (Y1: 2015/16; Y2: 2016/17; Y3: 2017/18) of the four albatross species breeding on Marion Island. Significantly different UDs (at $\alpha = 0.05$, in bold) were identified by comparing the real (observed) overlap to a distribution of overlaps from 1000 permutations of the year labels. 36

2.2. Summary of generalised additive mixed effect model outcomes used to investigate the probability to switch between foraging and transiting behavioural models while at sea in relation to environmental covariates (sea surface height SSH, sea level anomaly SLA, eddy kinetic energy EKE, wind speed WIND and ocean floor slope SLOPE) of wandering, grey-headed, sooty and light-mantled albatrosses breeding on Marion Island over three breeding seasons (Y1: 2015/16; Y2: 2016/17; Y3: 2017/18). 40

Chapter 3

3.1. Results of the a) permutational multivariate analysis of variance (perMANOVA) used to compare 12 seabird and fur seal species $\delta^{13}C$ and $\delta^{15}N$ blood values among different sampling periods (three consecutive autumns and summers 2015-2017/18) as well as results of the permutational analysis of variance (perANOVA) which compared species b) $\delta^{13}C$ and c) $\delta^{15}N$ blood values separately. 66

Chapter 4

4.1. Delipidated or normalized plasma $\delta^{13}C$ and raw plasma $\delta^{15}N$ values of albatrosses, giant petrels, and penguins breeding at Marion Island, which were tracked simultaneously with GPS data loggers during 2015-2018. Number of individuals indicates number of birds with tracks and corresponding stable isotopic values. Number of tracks indicates number of tracks used to estimate mean foraging locations as multiple tracks were recorded for brooding individuals (See Materials and Methods). Values given as mean ± SD (range). 100

4.2. Pearson's correlation coefficient (R), p-value (P) and formula resulting from a Pearson's correlation between plasma $\delta^{13}C$ and $\delta^{15}N$ values of albatrosses and giant petrels versus latitude (lat) and longitude (lon) of their mean foraging locations calculated from GPS tracks. * indicates a significant correlation. 100

4.3. Plasma $\delta^{13}C$ and $\delta^{15}N$ values calculated using species-specific regression equations (Table 4.2) for the Antarctic polar (PF, 51°S) and sub-tropical (STF, 42°S) fronts following the methods of Jaeger et al. (2010). 101

4.4. Correlation coefficient (R), p-value (P) and formula resulting from a Pearson's correlation between $\delta^{13}C$ and $\delta^{15}N$ plasma values of individual penguin species as well as all species combined versus the distance between their mean foraging locations and the coastline of Marion Island (distTOcoast). * indicates a significant correlation. 101

Chapter 5

5.1. a) Simulated $\delta^{13}C$ plasma values resulting from an agent-based movement model for female northern giant petrels incubating eggs on Marion Island and accumulating daily $\delta^{13}C$ values estimated from an isotope enabled biogeochemical model (Magozzi et al. 2017); n = number of plasma $\delta^{13}C$ values resulting from 100 simulations of the model. b) – f) are modifications of the original model conditions to test for the sensitivity of $\delta^{13}C$ values of northern giant petrel plasma to different stimuli or assumptions. Modifications are: b) simulated birds assimilated $\delta^{13}C$ values from isoscapes with a temporal attenuation reflecting isotopic incorporation over trophic levels one, two and three (i.e. two, four and six months); c) the original simulation was initiated in either April or December; d) simulated birds assimilating $\delta^{13}C$ values from a single biomass-weighted yearly average rather than separate month-specific isoscapes; e) the date the simulated birds initiated breeding was changed to 15, 10, 5 days before and 5, 10, 15 days after the original start date of the movement model; f) foraging trip duration was increased by two, four and six days; g) the daily step length of simulated birds was decreased by 150 km, 100 km and 50 km and increased by 50 km, 100 km and 150 km. The effect of model conditions on the distribution of simulated $\delta^{13}C$ plasma values was investigated using Bayesian estimation for two groups and a skewed-normal model distribution. Resulting posterior estimates of the population mean, standard deviation (SD) and skewness are given with their resulting upper and lower 95% credible intervals (CI). 135

List of figures

Chapter 2

2.1. Tracks of a) wandering ($n_{2015/16}$ = 9 , $n_{2016/17}$ =16, $n_{2017/18}$ = 20), b) grey-headed ($n_{2015/16}$ =5 , $n_{2016/17}$ = 11, $n_{2017/18}$ = 10), c) sooty ($n_{2015/16}$ =5 , $n_{2016/17}$ = 10, $n_{2017/18}$ = 8) and d) light-mantled ($n_{2015/16}$ = 5 , $n_{2016/17}$ = 6, $n_{2017/18}$ = 11) albatrosses incubating on Marion Island (black triangle) over three consecutive breeding seasons. Points show locations inferred to be foraging sites in each year are denoted by different colours: purple = 2015/16, green = 2016/17 and yellow = 2017/18, in relation to the position of sub-tropical (STF), Sub-Antarctic (SAF), Antarctic Polar (PF) and Southern Circumpolar Antarctic (SACCF) fronts. 32

2.2. Monthly values of the a) Southern Annular Mode (SAM) index, b) monthly mean eddy kinetic energy of an area of the Sub-Tropical Convergence Zone (STCZ) and Andrew Bain Fracture Zone (ABFZ) eddy fields, c) mean latitude position of the Sub-Antarctic (SAF) and Antarctic Polar (PF) fronts between 35-40°E, black horizontal line shows the latitude of Marion Island, and d) monthly wind speeds averaged over the extent of the albatross tracks. Vertical solid black lines indicate the beginning of each year. Grey shaded boxes indicate months albatrosses were tracked. 34

2.3. Boxplots of trip parameters: a) path length, b) duration, and c) maximum distance calculated from foraging trips of incubating wandering, grey-headed, sooty and light-mantled albatrosses at Marion Island tracked over three consecutive breeding seasons: 1) 2015/16; 2) 2016/17 and 3) 2017/18. Boxplots show range excluding outliers, upper and lower quartiles and median with outliers indicated with dots. 37

2.4. 90% (line) and 50% (shaded area) utilization distribution contours of a) wandering, b) grey-headed, c) sooty and d) light-mantled albatrosses incubating on Marion Island (black dot) over three consecutive breeding seasons (purple: 2015/16, green: 2016/17 and yellow: 2017/18) in relation to the position of sub-tropical (STF), Sub-Antarctic (SAF), Antarctic Polar (PF) and Southern Circumpolar Antarctic (SACCF) fronts. 37

2.5. Significant smooths resulting from generalised additive mixed models showing the probability of birds being in foraging (1) and transiting (0) behavioural modes among a) wandering, b) grey-headed, c) sooty and d) light-mantled albatrosses incubating on Marion Island in relation to, from left to right: sea surface height (SSH) for major fronts in the Southern Ocean indicated by dotted lines (from left to right: South Antarctic Circumpolar (SACCF), Polar (PF), Sub-Antarctic (SAF) and sub-tropical (STF) fronts), eddy kinetic energy, sea level anomaly, wind speed and ocean floor slope over three consecutive breeding seasons (purple: 2015/16, green: 2016/17 and yellow: 2017/18). 42

2.6. Inter-individual estimated variance components for scaled environmental variables (sea surface height, eddy kinetic energy, sea level anomaly and water depth) characterizing the foraging habitat for the four albatross species incubating at Marion Island between three breeding seasons (1: 2015/16, 2: 2016/17 and 3: 2017/18). Filled circles show the estimated variance and the bars show the credible intervals around these estimates. 43

Chapter 3

3.1. Schematic diagram of the two main hypotheses detailing a) seasonal and b) interannual temporal variability in the isotopic niche space of four albatross (wandering, grey-headed, sooty and light-mantled albatrosses), two giant petrel (northern and southern giant petrels), four penguin (king (KP), gentoo (GP), macaroni (MP) and eastern rockhopper (ERP) penguins) and two fur seal species (Antarctic (GAZ) and sub-Antarctic (TRO) fur seals). 60

3.2. a) δ^{13}C and b) δ^{15}N blood values of flying (left; wandering (WA), grey-headed (GHA), sooty (SA) and light-mantled (LMSA) albatrosses, northern (NGP) and southern (SGP) giant petrels) and diving species (right; king (KP), gentoo (GP), macaroni (MP) and eastern rockhopper (ERP) penguins and Antarctic (GAZ) and sub-Antarctic (TRO) fur seals) breeding on Marion Island during three autumns (shaded, 1: 2015, 3: 2016, 5: 2017) and three summers (2: 2015/16, 4: 2016/17, 6: 2017/18). Values presented are median, 25% and 75% quartiles and range. 64

3.3. a) Proportional overlap of flying species' and b) diving species' isotopic niches (SEAc) between three consecutive autumns (lower diagonal, 1: 2015; 2: 2016; 3: 2017) and summers (upper diagonal, 1: 2015/16; 2: 2016/17; 3: 2017/18). The grey block indicates that there was no data for comparisons. Values of overlap are given in Supplementary Material S3.6. Dots indicate significant difference between sizes of niche space (SEAb). See Figure 3.2. for species abbreviations. 66

3.4. Bayesian isotopic niche area (SEAb) of 12 species of seabirds and fur seals on Marion Island during autumn (shaded, 1: 2015, 3: 2016, 5: 2017) and summer (2: 2015/16, 4: 2016/17, 6: 2017/18) over three consecutive years. See Figure 3.2. for species abbreviations. 67

3.5. Proportional overlap among each species autumn (vertical, 1: 2015, 2: 2016, 3: 2017) and summer (horizontal, 1: 2015/16, 2: 2016/17, 3: 2017/18) isotopic niches separated for a) five flying species and b) six diving species. The grey block indicates that there was no data for comparisons. Values of overlap given in Supplementary Material S3.7. Dots indicate significant difference between sizes of niche space (SEAb). See Figure 3.2. for species abbreviations. 67

3.6. a) Distance and bearing the isotopic niche centroids of three albatross, all penguin and all fur seal species breeding on Marion Island moved between summer and autumn over two breeding seasons (2015/16 and 2016/17). See Figure 3.2. for species abbreviations. 69

3.7. a) Trajectories of isotopic niche centroids of all albatross, penguin and fur seal species breeding on Marion Island over three autumns (left; 1: 2015, 2: 2016, 3: 2017) and three summers (right, 1: 2015/16, 2: 2016/17, 3: 2017/18), separated by b) flying and c) diving species. See Figure 3.2. for species abbreviations. 70

Chapter 4

4.1. Plasma δ^{13}C (left) and δ^{15}N (right) values of wandering (WA), grey-headed (GHA) and sooty (SA) albatrosses, northern (NGP) and southern (SGP) giant petrels versus their mean foraging a) latitudes and b) longitudes calculated from GPS tracks. Only significant correlations are shown (see Table 4.2). 102

4.2. Plasma δ^{13}C (left) and δ^{15}N (right) isoscapes of a) wandering, b) grey-headed and c) sooty albatrosses, and d) northern and e) southern giant petrels breeding at Marion Island, Prince Edward Archipelago (black triangle) interpolated using ordinary kriging from the isotopic values of the respective birds' plasma which were simultaneously tracked with GPS data loggers. Black points represent an individual's mean foraging location. Positions of the sub-tropical (STF), sub-Antarctic (SAF) and Antarctic polar (PF) fronts are indicated. 103

4.3. Difference between wandering (WA), grey-headed (GHA) and sooty (SA) albatross as well as northern (NGP) and southern (SGP) giant petrel plasma δ^{13}C (top right diagonal) and δ^{15}N (bottom left diagonal) isoscapes. Differences were calculated by subtracting the isoscape of the species indicated on the vertical axis from the species indicated on the horizontal axis. Due to the small overlap between isoscapes of the giant petrels their comparison is not shown. 104

4.4. a) Plasma δ^{13}C (left) and δ^{15}N (right) isoscapes calculated as the mean of 1000 bootstrapped surfaces interpolated using ordinary kriging which randomly sampled twenty-two individuals from all five flying species to account for different number of individuals per species. b) Isoscapes, using the same bootstrap technique, modelled without the species which did not exhibit a significant latitudinal gradient (i.e. sooty albatrosses were removed from the $\delta^{13}C$ isoscape and sooty and grey-headed albatrosses and northern giant petrels were removed from the $\delta^{15}N$ isoscape). Position of the sub-tropical (STF), sub-Antarctic (SAF) and Antarctic polar (PF) fronts and Marion Island (black triangle) are indicated. 105

4.5. The means and standard deviations of a) $\delta^{13}C$ and b) $\delta^{15}N$ values estimated for seven water zones and fronts: Antarctic zone (AZ), Antarctic polar front (PF), polar frontal zone (PFZ), sub-Antarctic front (SAF), sub-Antarctic zone, (SAZ), sub-tropical front (STF) and sub-tropical zone (STZ) from the species-specific isoscapes presented in Figure 4.2: wandering (WA), grey-headed (GHA) and sooty (SA) albatrosses, northern (NGP) and southern (SGP) giant petrels. 106

4.6. Plasma a) $\delta^{13}C$ and b) $\delta^{15}N$ values of gentoo (GP), macaroni (MP) and eastern rockhopper (ERP) penguins and all penguin species (ALL) combined versus the distance between their mean foraging locations calculated from GPS tracks and the coastline of Marion Island. Only significant correlations are shown. 106

4.7. Plasma $\delta^{13}C$ (left) and $\delta^{15}N$ (right) isoscapes of a) gentoo, b) eastern rockhopper and c) macaroni penguins interpolated using ordinary kriging from the isotopic composition of the respective birds' plasmas which were simultaneously tracked with GPS data loggers. Points represent mean foraging locations. Isobaths (grey) are shown at 200 m intervals with 200 m isobath in black. 107

4.8. Plasma $\delta^{13}C$ (left) and $\delta^{15}N$ (right) isoscapes of three penguin species breeding at Marion Island, Prince Edward Archipelago calculated as the mean of 1000 bootstrapped surfaces interpolated using ordinary kriging which randomly sampled 9 individuals from each penguin species to account for different number of individuals per species. Isobaths (grey) are shown at 200 m intervals with 200 m isobath in black. 108

Chapter 5

5.1. Monthly maps of the distribution of $\delta^{13}C$ of phytoplankton resulting from a processed-based carbon model produced by Magozzi et al. (2017). 123

5.2. The computational process used to simulate the movement of female incubating northern giant petrels (NGP) using an agent-based movement model. In the model, daily likelihoods, directions and extents of movement are drawn from probability distributions influenced by foraging trip duration, daily step distance, sea surface temperature (SST), water depth and phytoplankton concentration Plk[]. At the initiation of the model the simulated NGP is assigned a foraging trip duration, a decision to perform long or short trips and maximum daily step distance (Max.dist.km). During each time step, each simulated NGP may move to a new location or decide to stay where is it depending on how far it is into its foraging trip and its surroundings. The model was run for 60 days (approximate length of NGP incubation) starting on 15 August (approximate laying initiation date for giant petrels). 128

5.3. 50% and 90% kernel density based on a) GPS tracks of incubating female northern giant petrels at Marion Island 2015 and 2016; b) tracks resulting from an agent-based movement model based on movement parameters from GPS tracks in a), with c) – f) modifications of the original agent-based movement to test for the sensitivity of $\delta^{13}C$ values of NGP plasma to different stimuli. Modifications are: c) the date the simulated birds initiated breeding was changed to 15, 10, 5 days before and 5, 10, 15 days after the average laying day; d) foraging trip length was increased by two, four and six days; e) the daily step length of simulated birds was decreased by 50 km, 100 km and 150 km; f) the daily step length of simulated birds was increased by 50 km, 100 km and 150 km. 133

5.4. Box plots (range, standard deviation and mean) showing the a) measured $\delta^{13}C$ values of plasma collected from incubating female northern giant petrels at Marion Island in 2015 and 2016 (n= 15); b) Simulated $\delta^{13}C$ values of blood plasma resulting from an agent-based movement model based on incubating NGPs which accumulated daily $\delta^{13}C$ values from modified monthly isoscapes produced by Magozzi et al. (2017) which incorporated trophic attenuation over four trophic levels (i.e. eight months). c) – g) are modifications of the original agent-based movement to test for the sensitivity of $\delta^{13}C$ values of NGP plasma to different stimuli. Modifications are: c) simulated birds assimilated $\delta^{13}C$ values from modified isoscapes produced by Magozzi et al. (2017) over trophic levels one, two and three (i.e two, four, and six months), all further *in-silico* experiment assimilated $\delta^{13}C$ values from maps account for attenuation over four trophic levels; d) the original simulation was initiated in April and December; e) simulated birds assimilated $\delta^{13}C$ values from an isoscape with a temporal resolution of yearly; f) the date the simulated birds initiated breeding was changed to 15, 10, 5 days before and 5, 10, 15 days after the original start date of the movement model; g) foraging trip duration was increased by two, four and six days; h) the daily step length of simulated birds was decreased by 150 km, 100 km and 50 km and increased by 50 km 100 km and 150 km. Blue solid and the two dashed lines represent the mean and standard deviations of the $\delta^{13}C$ values which resulted from the original simulation. 134

Abstract

Marine ecosystems are experiencing rapid changes due to climate change. The associated temporal and spatial changes in resource distribution impacts on the foraging behaviour of marine top predators. If these changes negatively affect the ability of marine predators to forage efficiently, there may be dire consequences for their populations. However, evidence of foraging plasticity during adverse conditions, or generalist foraging behaviour, can allow inference about the resilience of species to environmental change and provide essential knowledge towards effective and proactive conservation measures.

I examined plasticity in the trophic ecology of 12 marine predator species breeding on Marion Island, southern Indian Ocean, over three years (2015 – 2018), a period characterized by pronounced environmental variability. Firstly, I correlated behavioural states inferred along the GPS tracks of incubating wandering, grey-headed, sooty and light-mantled albatrosses to environmental variables that are indicative of biologically productive oceanographic features. Secondly, I analysed $\delta^{13}C$ and $\delta^{15}N$ blood values in 12 marine predator species (the afore-mentioned albatrosses as well as king, gentoo, macaroni and eastern rockhopper penguins, northern and southern giant petrels and Antarctic and sub-Antarctic fur seals) over two seasons: summer and autumn. My results revealed that the foraging behaviour of all the species is, to some degree, either plastic (temporally variable isotopic niche) or general (large isotopic niche which remained similar over time), except for the king penguin (small isotopic niche which remained similar over time), a known foraging specialist. Furthermore, despite their dynamic foraging behaviour, resource partitioning among the predators was maintained over time.

Due to the ease and relatively low cost of collecting tissues for stable isotope analysis it has the potential to be a powerful tool to monitor the trophic ecology of marine predators. I thus used my simultaneously collected dataset of GPS tracks with the stable isotope blood compositions to investigate some of the assumptions underlying the inferences made from marine predator $\delta^{13}C$ and $\delta^{15}N$ blood values. I reconstructed species- and guild- specific $\delta^{13}C$ and $\delta^{15}N$ isoscapes for eight seabird species. Following this, I coupled individual-based movement models of northern giant petrels with global marine isotope models to explore the sensitivity of tissue $\delta^{13}C$ values to a range of extrinsic (environmental) and intrinsic (behavioural, physiological) drivers. My results demonstrate the strong influence of reference isoscapes on the inference of stable isotope compositions of marine predators. Furthermore, I show that caution should be used when using non-species-specific or temporally inaccurate isoscapes.

I furthermore demonstrate that biological interactions, such as competition for food resources, either past or present, as well as spatio-temporal distribution of food patches strongly influence the foraging behaviour of marine predators. These findings highlight the importance of integrating biological interactions in species distribution models which are used to predict possible distributional shifts of marine predators in the context of global changes. My thesis further developed previously available methods and presents a novel approach to investigate sources of variance in the stable isotopic composition of animals' tissues.

Key words:

Behavioural plasticity, Central place foragers, Environmental variability, Fur seals, Geolocation, Marine predators, Seabirds, Southern Ocean, Stable isotope ecology

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Preface

The project has ethics clearance from the Nelson Mandela University Animal Research Ethics Committee (A14-SCI-ZOO-012) and was approved by the Prince Edward Islands Management committee and carried out under permit from the Director-General: Department of Environmental Affairs, South Africa.

Funding for the project was obtained from the South African Department of Science and Technology (DST) and National Research Foundation (NRF), grant number: 93090, awarded to Prof. Pierre Pistorius. I was awarded a DST Centre of Excellence doctoral study bursary by the Fitzpatrick Institute of African Ornithology, University of Cape Town. The conclusions drawn and discussed are attributed to me and not the NRF.

I am the sole author of this thesis; I wrote all of the chapters and performed all data analysis. However, Chapter 2 to 5 were written as journal articles and are already published, accepted or are intended to be submitted. As the chapters are formatted as articles, the use of "we" rather than "I" is used within the text of these chapters. Co-authors on articles of chapters which are already published or submitted, including Dr Yves Cherel, Dr Azwianewi Makhado, Dr Florian Orgeret, Prof. Peter Ryan, Kim Stevens and Dr Clive Trueman, all provided valuable discussion during the respective chapter preparation and reviewed the final manuscripts.

All photographs within this thesis were taken by John Dickens.

Publications arising from my PhD:

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Carpenter-Kling T, Pistorius PA, Connan M, Reisinger RR, Magozzi S, Trueman C. 2019. Sensitivity of δ^{13}C values of seabird tissues to combined spatial, temporal and ecological drivers: a simulation approach. *Journal of Experimental Marine Biology and Ecology* 512: 12-21.

Associated publications arising from my PhD:

Reisinger RR, **Carpenter-Kling T,** Connan M, Cherel Y, Pistorius PA. ***Accepted***. Foraging behaviour and habitat-use drives niche segregation in sibling seabird species. *Royal Society Open Science*.

Carpenter-Kling T, Handley JM, Connan M, Crawford RJM, Makhado AB, Dyer BM, Froneman W, Lamont T, Wolfaardt AC, Landman M, Sigqala M and Pistorius PA. 2019. Gentoo penguins as sentinels of climate change at the sub-Antarctic Prince Edward Archipelago, Southern Ocean. *Ecological Indicators* 101: 163-172.

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Oral presentations at conferences arising from my PhD:

Carpenter-Kling T et al. 2019. Penguins' dinner: a tool for monitoring the effects of climate change. International Penguin Conference, Dunedin, New Zealand.

Carpenter-Kling T et al. 2018. Interpretation of stable isotope compositions of seabird tissues. Flock – the annual gathering of members of BirdLife South Africa, Langebaan, South Africa.

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Chapter 1:

General Introduction

The foraging behaviour of animals includes all aspects of feeding (why, what, when and how) and movement between feeding patches. An animal's fitness is directly linked to its ability to forage in such a way that energy gain is optimized (Schoener 1971; Pyke et al. 1977; Stephens and Krebs 1986). Thus, foraging behaviour evolves to maximize energy gain while minimizing energy expenditure or risks to their survival. However, as species have different movement and navigation capabilities and are faced with different environmental conditions, resource distribution and biological interactions (e.g. predation, competition and parasitism), there is an impressive diversity of foraging strategies across the animal kingdom (Nathan et al. 2008; Owen-Smith et al. 2010). It has been a long-standing goal of ecologists to explore and understand the numerous drivers of animals' movement (e.g. Ricker 1937; Hassell and Southwood 1978; Kruuk and Mills 1983) which has become increasingly important in recent times (Hays et al. 2016; Tucker et al. 2018). This is because of the rapid changes occurring in ecosystems across the globe due to climate change and/or habitat degradation and overexploitation which are changing the landscape over which animals must forage (Tucker et al. 2018). If these changes negatively affect an animals' ability to forage, it may have dire consequences on their populations (Jenouvrier et al. 2018; Cooke et al. 2019) and consequently, possibly trigger trophic cascades within their ecosystems (Kagata and Ohgushi 2006; Baum and Worm 2009; Lynam et al. 2017).

The distribution of resources across landscapes and the level of predictability largely influences animal movement (Fauchald 1999; Mueller et al. 2011; Van Moorter et al. 2013). According to the Marginal Value Theorem, within a heterogeneous landscape where resources are patchily distributed, animals are expected to employ a 'win/stay – lose/move' foraging strategy (Charnov 1976). The 'win/stay – lose/move' foraging strategy is when animals quickly transit between resource patches, remaining within a patch until their rate of energy gain is thought to be lower than the average rate of energy gain of the next. However, if the distribution of these patches is static or predictable over time (e.g. diel, tidal or seasonal), specialisation in foraging behaviour is expected to occur, as there are obvious benefits of returning to profitable foraging grounds (Futuyma and Moreno 1988; Switzer 1993;

Weimerskirch et al. 2007; Augé et al. 2014; Riotte-Lambert and Matthiopoulos 2019). In contrast, within a dynamic landscape where the distribution of resources is random (i.e. unpredictable), animals are expected to exhibit generalist foraging behaviours, maximizing net energy intake by either visiting multiple foraging habitats and/or consuming a wide diversity of prey species (Hastings 1983; Kassen 2002; Dehnhard et al. 2019).

Species, however, do not occur in isolation. When species with broadly similar functional roles occur in sympatry in ecosystems where resources are limited, competition is likely. In such cases, the principle of competitive exclusion predicts that in order to co-exist, sympatric species must segregate their resource use to minimise competitive overlap (Gause 1934; Hardin 1960). Hutchinson's (1957) formulation of the niche as an n-dimensional hypervolume states that the idealized 'fundamental' niche represents all environmental conditions which allows a particular species to survive and reproduce without biological interactions. However, interactions such as competition are important in ecological communities, forcing them to partition their niches in order to facilitate coexistence and thus occupy a portion of their 'fundamental' niche termed their 'realized' niche (Hutchinson 1957). Niche partitioning can occur along multiple ecological axes. However, understanding and gathering data to represent all the axes which define the n-dimensional niche of a species, for a given location and time, is a major challenge. The niche concept of Grinnell (1917) and Elton (1927) is easier to conceptualize. The concepts together focus on the environmental range where resource use and inter-specific interactions take place in order to quantify the probability of occurrence and abundance of species. As such, to reduce competition for food resources, animals have been shown to segregate by differentiating their foraging behaviours along three primary axes (Schoener 1971):

(1) **Space**. A classic example by MacArthur (1958), provided evidence that the coexistence of five warbler species (*Dendroica* spp.) was promoted by spatial segregation as they foraged at different heights within trees.

(2) **Diet**. For example, the coexistence of two species of moray eels (*Gymnothorax* spp.) inhabiting the Belize Barrier Reef is thought to be facilitated by differences in their diets. Both species of moray eels feed on fishes, crabs and octopus however, the spotted moray eel *G. moringa* specializes on small crabs whereas the purplemonth moray eel *G. vicinus* specializes on fish (Young and Winn 2003).

(3) **Time**. For example, Andean and Pampas cats (*Leopardus* spp.) in the high-altitude deserts of the Andes hunt for prey at different times of the diurnal cycle thus preventing direct inter-specific competition for prey and facilitating their coexistence (Lucherini et al. 2009).

Marine top predators, such as seabirds and seals, which rely on land for reproduction and/or their annual moult, are ideal model species for the study of the impact of biological interactions and environmental factors on foraging behaviour. They are extremely mobile predators navigating a highly dynamic and heterogeneous landscape (Pinaud and Weimerskirch 2007; Weimerskirch et al. 2007; De Bruyn et al. 2009; Hindell et al. 2016). The synchronized breeding in seabirds and seals and relatively high fidelity to nesting areas or breeding colonies facilitate long-term regular collection of demographic, dietary and movement data using various methods (Cairns 1988; Piatt et al. 2007; Moore 2008; Hays et al. 2019). In addition, colonial breeding and a central-place foraging strategy while breeding is often associated with significant inter- and intra-specific competition for resources, which is potentially relaxed outside the breeding season (Cherel and Hobson 2007; Cherel et al. 2008; Linnebjerg et al. 2013). They thus represent an ideal group for the study of the interlinked environmental and intra- and inter- specific interactions as drivers of foraging behaviour (e.g. Jaeger et al. 2013; Connan et al. 2014; Barger et al. 2016).

Coexistence of sympatric marine top predators

The coexistence of multiple sympatric breeding marine predators has been shown to be facilitated via segregation of foraging behaviour in the three axes previously mentioned: space, diet and time. (1) Spatially, seabirds and seals may segregate inter- and intra- specifically by foraging in disparate geographic locations (Pinaud and Weimerskirch 2007; Navarro et al. 2013a; Kuhn et al. 2014; Wege et al. 2019) or through differential use of the water column (Pickett et al. 2018). (2) Dietary, much like that of Darwin's finches (Lack 1947), seabirds for example have evolved species specific morphological characteristics which allow them to forage for different prey (Croxall and Prince 1980; Adams and Brown 1989; Ridoux 1994; Croxall et al. 1997; Cleeland et al. 2019). (3) Temporally, segregation may be facilitated by species varying the timing of their foraging activities (Phalan et al. 2007; Mackley et al. 2010) or of the peak energy demanding life stages such as breeding (Barrett et al. 1997; Clewlow et al. 2019).

Marine top predators have often been shown to respond to changes in prey distribution (e.g. Kowalczyk et al. 2015; Thorne et al. 2015; Mills et al. 2020). Potential variability in the level of resource partitioning among predators during years of spatio-temporal variability in prey distribution is however poorly understood. The optimal foraging theory suggests that during periods of prey scarcity, animals will expand their realized niche by foraging over a greater habitat range as well incorporate a greater diversity of food items into their diets (Pyke et al. 1977; Stephens and Krebs 1986). However, the classical niche theory predicts that to coexist with competitors, during times of prey scarcity, animals will contract their realized niches by specializing their foraging behaviour in an effort to avoid competing for resources (Hutchinson 1957; Schoener 1974; Pianka 1981). There are few recent studies which have investigated the interannual shifts, at a community level, in marine top predator realized foraging niches (Barger and Kitaysky 2012; Pickett et al. 2018; Tarroux et al. 2018; Hovinen et al. 2019; Fromant et al. 2020). All these studies found variation in the habitat use and diet between years as well as maintenance of dietary and/or spatial segregation. However, to my knowledge, only one of these studies – Barger & Kitaysky (2012) - presented empirical evidence of seabird species contracting their spatial and dietary axes of their realized niches in response to low prey abundance. In contrast, other studies, which focus on a single seabird or marine mammal species, have found that in response to decreased prey availability, the species expanded their spatial and/or dietary axis of their realized niches by increasing the diversity of prey eaten or habitats foraged within (Elorriaga-Verplancken et al. 2016; Choy et al. 2017; Horswill et al. 2017; Machovsky-Capuska et al. 2018; Chiu-Werner et al. 2019).

Marine top predators foraging across a dynamic landscape

Due to numerous tracking studies on marine top predators, it is now widely accepted that most species do not search randomly for prey but instead target oceanographic features which aggregate prey and facilitate their capture (Ballance et al. 2006; Weimerskirch 2007; Bost et al. 2009; Arthur et al. 2015; McIntyre et al. 2017; Saijo et al. 2017). Oceanographic features such as areas of upwelling at prominent topographical features (Cherel and Weimerskirch 2000; Hedd et al. 2001; De Bruyn et al. 2009), major oceanic fronts (Bost et al. 2009; Scales et al. 2014b) and eddies (Nel et al. 2001; Tosh et al. 2015) concentrate prey items and are thought to act as predictable foraging habitat for marine top predators (Weimerskirch 2007). Depending on the system, however, the spatial and temporal distribution of resource patches across the oceans can be subject to daily, seasonal or annual variability (Fraser and Hofmann 2003; Trathan et al. 2006; Kowalczyk et al. 2015; Thorne et al. 2015). Thus, there are strong selection pressures for marine top predators to be able to respond to variability within their environments (Bradley 1982; Komers 1997; Burke and Montevecchi 2009). Already, there is much evidence that in response to climatically induced variability in resource availability, depending on the species and location of its colony, seabirds and seals can either switch their diet to temporally available prey (e.g. Chambellant et al. 2013; Reisinger et al. 2018b; Carpenter-Kling et al. 2019a; Mills et al. 2020), utilize different foraging habitats (Kowalczyk et al. 2015; Manugian et al. 2015; Machovsky-Capuska et al. 2018; Phillips et al. 2019) or attempt to follow the distribution of their preferred prey resources (Kappes et al. 2010; Pettex et al. 2012; Bost et al. 2015; Thorne et al. 2015). However, even if this behavioural plasticity is evident within a species, suitable foraging habitats can still become inaccessible or energetically costly to reach (e.g. Péron et al. 2012; Bost et al. 2015; Thorne et al. 2015) and ultimately result in breeding failure and/or population declines (e.g. Croxall et al. 1999; Thorne et al. 2015).

Studying seabird and seal foraging behaviour

Investigating the foraging behaviour of seabirds and seals often requires data that elucidates on 'what they are eating' and/or 'where are they eating it'. As direct observations are difficult due to their extensive foraging ranges (e.g. Phillips et al. 2008) and/or underwater foraging for diving species (e.g. Saijo et al. 2017), a range of research methods are available which involves data collection from these marine predators at their terrestrial breeding and/or moulting sites. Information about what the predators are eating can be gained by using methods such as identifying prey in stomach content samples (e.g. Carpenter-Kling et al. 2019a) or faecal samples (e.g. Reisinger et al. 2018b; Xavier et al. 2018) or inferred from the stable isotope compositions of their tissues (e.g. Chambellant et al. 2013; Connan et al. 2014). Predator distributions can be inferred from ship-based surveys (Commins et al. 2014; Carroll et al. 2019). However, the development and miniaturization of animal tracking devices, allows for information to be gained about the fine-scale movement and habitat-use of marine predators which has greatly increased our ability to study their foraging ecology (Wilson and Vandenabeele 2012; McIntyre 2014; Hussey et al. 2015).

Animal telemetry, using location recording dataloggers such as global positioning system (GPS) and platform transmitter terminals (PTT) loggers, has allowed for monitoring of marine predator distribution and movement over tens to thousands of kilometres (Block et al. 2011; Delord et al. 2013; Hussey et al. 2015; Browning et al. 2018). Together with continuous improvement in computing power and accessibility, a variety of different methods have arisen to analyse animal telemetry data, providing powerful ecological insights to foraging strategies and habitat use of free-ranging predators (Block et al. 2011; Hussey et al. 2015; Reisinger et al. 2018a; Sequeira et al. 2018; Hindell et al. 2020). Statistical models, such as Hidden Markov models (Zucchini et al. 2016) and state-space models (Jonsen et al. 2005; Patterson et al. 2008), have been developed that are freely accessible and relatively user friendly, allowing behavioural information to be inferred from animal trajectories (Bennison et al. 2018). Another major leap forward in the study of marine predators is the publicly accessible, pre-processed data from satellite remote-sensing technology. These data, such as sea surface temperature and height, sea ice concentration and chlorophyll-a concentration allow for the identification and tracking of ephemeral oceanographic features which may act as marine predator foraging hotspots (Cayula and Cornillon 1992; Bakun 2006; Ansorge et al. 2009; Chapman et al. 2020). By combining pathway characteristics such as speed (e.g. Whitehead et al. 2016) or first-passage time (e.g. Pinaud and Weimerskirch 2007), and/or outputs of behavioural inference models (e.g. de Grissac et al. 2017) with satellite derived environmental data has allowed for greater understanding of the drivers of predators' foraging distributions (reviewed in Wakefield et al. 2009), identification of Areas of Ecological Significance (Reisinger et al. 2018a; Dias et al. 2019; Hindell et al. 2020) and predictions to be made on how climate change may impact their foraging distributions (Hazen et al. 2013; Cristofari et al. 2018; Krüger et al. 2018; Hückstädt et al. 2020). Knowledge of bio-physical processes that underlie links between oceanographic habitat and marine predator foraging is important for implementing holistic management that consider ecosystems in their entirety (Arkema et al. 2006; Hooker et al. 2011).

Studying the stable isotope composition of marine predator tissues has relatively recently risen as an alternative and complimentary method to conventional tracking studies (Graham et al. 2010; Hobson et al. 2010; Ramos and González-Solís 2012). The use of stable isotopes has become increasingly popular, due to the ease of collecting and storing samples, coupled with the ability to quickly generate large datasets at relatively low cost (e.g. Roscales et al. 2011). Retrospective geolocation of seabird and seal foraging areas is commonly inferred by linking the carbon ($^{13}C/^{12}C$; $\delta^{13}C$), and to a lesser extent nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$), isotope compositions of their tissues to known gradients (or isoscapes) of $\delta^{13}C$ and $\delta^{15}N$ values present at the base of their food webs (Quillfeldt et al. 2005; Cherel and Hobson 2007; Jaeger et al. 2010a). Across the global oceans, there is a strong negative latitudinal gradient in the $\delta^{13}C$ values of organisms at the base of the food web (i.e. phytoplankton), from the equator towards the poles (Magozzi et al. 2017), as well as from inshore benthic habitats to offshore pelagic habitats (Kaehler et al. 2000; Quillfeldt et al. 2005; Cherel and Hobson 2007). Whereas gradients of $\delta^{15}N$ are not as strong or predictable, the $\delta^{15}N$ values of phytoplankton tend to be lower or higher in areas of nitrogen fixation (e.g. pelagic oceans) or denitrification (e.g. upwelling regions around coastlines), respectively (Takai et al. 2000; Somes et al. 2010). However, as spatial gradient of nitrogen at the base of food webs are shallow or in some cases non-existent, the nitrogen isotopic compostions of marine predator tissues are more commonly used to inter trophic position of predator within an ecosystem. A predictable stepwise enrichment of the $\delta^{15}N$ values is observed at each trophic level (2 - 5 ‰ per trophic level) and to a lesser extent $\delta^{13}C$ (1 - 2 ‰ per trophic level; Kelly 2000; Bearhop et al. 2002; Post 2002). This is due to ^{14}N (the lighter isotope) being more important in metabolic reactions and being excreted as nitrogenous waste (Steele and Daniel 1978; Minagawa and Wada 1984; Kelly 2000). Thus, as the $\delta^{13}C$ and $\delta^{15}N$ tissue values of marine consumers provide quantitative information on both their resource (bionomic) and habitat (scenopoetic) use, they are used as proxies to investigate their trophic ecology (Newsome et al. 2007). Together, the two stable isotope ratios allow for the construction of the isotopic niche space occupied by species (e.g. Cherel et al. 2008) and individuals (e.g. Jaeger et al. 2010b). Furthermore, the isotopic composition of a marine predator's tissues reflects the prey they consumed during the time the tissue of interest was synthesized (Hobson and Clark 1993; Bearhop et al. 2002). Due to the different turnover rates of bodily tissues (e.g. liver, bone and whole blood), different samples from a single animal can therefore provide integrated information on its trophic ecology over a period of time ranging from days to years. Consequently, carbon and nitrogen stable isotopic compositions of marine predator tissues have been used to investigate differences in foraging behaviours within and between individuals (e.g. Cherel et al. 2007; Phillips et al. 2009; Jaeger et al. 2010b), between sexes (e.g. Quillfeldt et al. 2008) as well as among species (e.g. Weiss et al. 2009; Navarro et al. 2013a; Bodey et al. 2014), annual life history stages (e.g. Cherel et al. 2007; Barger et al. 2016), years (e.g. Horswill et al. 2017; Fromant et al. 2020; Ramos et al. 2020) and decades (e.g. Negrete et al. 2017).

There are, however, limitations to inferring seabirds' and seals' foraging locations and trophic levels from their tissues isotopic compositions (Shipley and Matich 2020):

(1) Isotopic spatial gradients of phytoplankton are not static. Phytoplankton are small-celled organisms with rapid growth which means their isotopic compositions reflect local and short-termed variations in oceanic conditions (McMahon et al. 2013; Hoefs 2015; Magozzi et al. 2017).

(2) Species-specific discrimination factors may offset a consumer's isotopic composition from baseline isotopic values such as diet composition, isotopic averaging and physiological fractionation through intermediate trophic level (Graham et al. 2010; Hobson et al. 2010). Therefore, several studies have attempted to reconstruct $\delta^{13}C$ and $\delta^{15}N$ predator-specific isoscapes by combining known location and distributional range (Cherel and Hobson 2007) or movement of seabirds (Phillips et al. 2009; Jaeger et al. 2010a; Roscales et al. 2011; Ceia et al. 2018; Cruz-Flores et al. 2018) to temporally matched tissue isotopic values. However, there is a need to construct and compare species-specific isoscapes in order to justify using a non-species-specific isoscape to make inferences from predator isotope tissue values.

(3) Although there is a clear latitudinal gradient of $\delta^{13}C$ and $\delta^{15}N$ values across the global oceans (Somes et al. 2010; Magozzi et al. 2017), there is no clear longitudinal gradient; therefore, predators that may be foraging in different areas but within the same water mass may have similar $\delta^{13}C$ and $\delta^{15}N$ values (Cherel and Hobson 2007; Jaeger et al. 2010a). Furthermore, benthic or inshore predators' tissues are also more enriched in ^{13}C than those of predators foraging in pelagic or offshore environments (Cherel and Hobson 2007; Brault et al. 2018). Consequently, latitudinal and inshore/ benthic vs. offshore/ pelagic foraging gradients may induce overlap in isotopic values which can lead to misinterpretations.

Rationale

A major threat that seabirds and seals are faced with is habitat or food web degradation or alteration due the direct and indirect effects of climate change (Sydeman et al. 2017; Avila et al. 2018; Grémillet et al. 2018; Dias et al. 2019; Ropert-Coudert et al. 2019). As the effects of global climate change and/or habitat degradation become more apparent (Cury et al. 2011; Constable et al. 2014; Sydeman et al. 2015; Swart et al. 2018), behavioural plasticity of species plays a key role in a populations' ability to adapt (Nussey et al. 2007; Cooke et al. 2019). Low plasticity in foraging behaviours, typical of foraging specialists, is thought to render them to be more vulnerable to habitat or food web degradation or alteration than habitat generalists (Clavel et al. 2011; Manugian et al. 2015; McIntyre et al. 2017). This is because specialist foragers are thought to be less able to explore and exploit different habitats when their preferred habitat becomes rare or is no longer able to support them. Understanding the extent to which long lived species such as seabirds and marine mammals can buffer themselves against spatially and temporally variable prey availability and possible future changes is therefore of importance in the face of our rapidly changing oceans. However, to be able to predict or anticipate how a species will respond to changes in their environment requires long-term datasets. Over the short term, this can be overcome by investigating their response to pronounced interannual environmental variability (e.g. Pettex et al. 2012).

Although tracking data allows for the fine-scale movement of marine top predators to be recorded, and many insights on their movements to be gained, the technology is still relatively expensive and limited in terms of tracking animals throughout the annual cycle. Thus, relatively few individuals can be monitored when compared to the ease and cost of collecting tissues for stable isotope analysis, which can also be used to represent different life-history stages. Monitoring the foraging ecology of marine predators is becoming increasingly useful for the identification of important foraging habitat, allowing for well-placed marine protected areas which can help mitigate some of the at-sea threats they are facing (Game et al. 2009; Ballard et al. 2012; Hindell et al. 2020). Furthermore, representing climate and ecosystem sentinels of the oceans, the monitoring of their foraging behaviour can provide important information about ecosystem health and function (Piatt et al. 2007; Moore 2008; Hazen et al. 2019). Thus, as stable isotope analysis of predator tissues allows for large datasets to be quickly generated (e.g. Roscales et al. 2011), it can be a powerful tool to complement conventional tracking studies. However, stable isotope ecology is not without its caveats and relies on set of stringent assumptions. Previously, retrospective geolocation of seabirds from isotopic ratios has been performed using static maps of isotopic gradients inferred from organisms at the base of the food web (Navarro et al. 2013b; Magozzi et al. 2017; Brault et al. 2018), particulate organic matter (Francois et al. 1993; Trull and Armand 2001; Lourey et al. 2003) or from seabird species (Cherel and Hobson 2007; Phillips et al. 2009; Jaeger et al. 2010a; Roscales et al. 2011; Ceia et al. 2018; Cruz-Flores et al. 2018) different to the seabird of interest. There is therefore a need for improved knowledge on the various drivers of marine predator tissue isotopic composition.

In this thesis, I use a combination of tracking and stable isotope data collected from 12 marine predator species (Table 1.1.) breeding on sub-Antarctic Marion Island belonging to the Prince Edward Archipelago. The data were collected over three breeding seasons, between 2015 to 2018, which were characterized by pronounced environmental variability. I used this extensive dataset to firstly perform a community assessment of flexibility in foraging behaviours of these sympatric sub-Antarctic species, and secondly, to improve knowledge about seabird stable isotope ecology with the aim of increasing the utility of stable isotope analysis for marine top predator monitoring.

The Prince Edward Archipelago is an annual breeding and moulting refuge to approximately 5 million land-breeding seabirds and seals (Ryan and Bester 2008), of which several have been well studied in terms of population and foraging ecology (see Ryan and Bester 2008; Reisinger et al. 2018a). However, the bulk of this work has been on a species-specific basis. In this thesis, I will for the first time investigate the foraging and trophic ecology of all albatross, penguin, giant petrel and fur seal species breeding on Marion Island using concurrently collected data. Six species out of the 12 studied are categorized as vulnerable, near threatened or endangered by the International Union for Conservation of Nature Red List (Table 1.1.). I analyse these data on the foraging and trophic ecology of a range of sympatric species together with data on variability in the marine environment. I thereby provide information that can be valuable for conservation and management as it can improve policy decisions and inform the designation of marine protected areas (Game et al. 2009; Grémillet and Boulinier 2009; Ballard et al. 2012; Raymond et al. 2015; Daly et al. 2018; Reisinger et al. 2018a; Hindell et al. 2020).

Table 1.1. International Union for Conservation of Nature Red List categories and global population trends of the ten seabird and two fur seal species studied at Marion Island. Scientific names of the species and abbreviations used are given.

Species	Scientific name	Abbreviation	Local population trend	Global population trend	IUCN rating
			Albatross		
Wandering	*Diomedea exulans*	WA	Stable [a]	Declining [b]	Vulnerable
Grey-headed	*Thalassarche chrysostoma*	GHA	Increasing [b]	Declining [b]	Endangered
Sooty	*Phoebetria fusca*	SA	Increasing [c]	Declining [b]	Endangered
Light-mantled	*Phoebetria palpebrata*	LMSA	Declining [c]	Declining [b]	Near Threatened
			Giant petrel		
Northern	*Macronectes halli*	NGP	Stable [a]	Increasing [b]	Least concern
Southern	*Macronectes giganteus*	SGP	Stable [a]	Increasing [b]	Least concern
			Penguin		
King	*Aptenodytes patagonicus*	KP	Stable [d]	Increasing [b]	Least concern
Gentoo	*Pygoscelis papua*	GP	Declining [e]	Stable [b]	Least concern
Macaroni	*Eudyptes chrysolophus*	MP	Declining [d]	Declining [b]	Vulnerable
Eastern rockhopper	*Eudyptes filholi*	ERP	Declining [d]	Declining [b]	Vulnerable*
			Fur seal		
sub-Antarctic	*Arctocephalus tropicalis*	TRO	Declining [f]	Stable [g]	Least concern
Antarctic	*Arctocephalus gazella*	GAZ	Increasing [f]	Declining [h]	Least concern

a: Ryan et al. 2009; b: Birdlife International 2020; c: Schoombie et al. 2016; d: Crawford et al. 2009; e: Crawford et al. 2014; f: Wege et al. 2016; g: Hofmeyr 2015; h: Hofmeyr 2016

* IUCN rating given for southern rockhopper *Eudyptes chrysocome*, as IUCN and Birdlife International have not yet updated their records to include the reclassification of the rockhopper penguin breeding on Marion Island as the eastern rockhopper penguin (Pan et al. 2019).

Thesis aims and structure

The focus of this chapter was to introduce the theoretical concepts central to the questions in this thesis. The data chapters (chapters 2 to 5) are written in the style of stand-alone scientific journal articles. I make cross-references among these chapters, but some repetition may occur. Chapter 6 summarises and integrates key findings and provides suggestions for future research.

There are two leading themes within this thesis: firstly, how a community of sympatric marine top predators respond to environmental variability and secondly the robustness of stable isotope analysis to study seabird foraging ecology. Over three years, four albatross, two giant petrel, four penguin and two fur seal species breeding on Marion Island were tracked with GPS loggers during their respective breeding seasons and concurrently blood was sampled for stable isotope analysis. Blood was then again collected for stable isotope analysis during April, a period where all species were present on the island and were either not breeding or reaching the end of their breeding season. These data allow for novel investigations into the flexibility and consistency in the foraging behaviour of species within a community using concurrently collected data.

Chapter 2: Foraging in a dynamic environment: Response of four sympatric sub-Antarctic albatross species to interannual environmental variability

The spatio-temporal distribution of resources across marine environments is determined by multiple scale-dependent physical and biological processes (Scales et al. 2014a; Lévy et al. 2015). At the macro- (100 – 1000 kms) and meso- scales (10 kms), oceanographic features, such as upwelling at prominent topographical features (e.g. De Bruyn et al. 2009), major oceanic fronts (e.g. Bost et al. 2015) and eddies (e.g. Nel et al. 2001) aggregate prey and act as predictable foraging grounds for marine predators (Weimerskirch 2007; Bost et al. 2009; Wakefield et al. 2009; Scales et al. 2014b). However, environmental variability can alter these complex bio-physical processes resulting in varying degrees of predictability in resource location across different time scales (Fraser and Hofmann 2003; Trathan et al. 2006; Brown et al. 2010). As the survival and reproduction of animals is dependent on their ability to forage efficiently (Schoener 1971; Pyke et al. 1977; Stephens and Krebs 1986), their ability to respond to spatio-temporal changes in prey patches has important implications for their population trajectories (Jenouvrier et al. 2018; Cooke et al. 2019). In this chapter, I use GPS loggers in combination with remotely sensed environmental data to investigate interannual habitat use of four incubating albatross species during a period which was characterized by particularly pronounced climatic variability (2015–2017), indicated by anomalous Southern Annular Mode index (https://legacy.bas.ac.uk/met/gjma/sam.html).

Specifically, I:

- Model probable foraging locations along GPS tracks of individuals to determine habitat preferences of the different species during each year;
- Quantify intra-species spatial overlap in foraging areas between years;
- Compare the interannual habitat use of each species.

I hypothesize:

- The wandering albatrosses incubating at Marion Island are generalized in their foraging habitat-use and have an extensive foraging distribution which will remain consistent among years. The wandering albatrosses, breeding elsewhere, have been shown to be generalist in term of their foraging habitat use (Weimerskirch 2007). Their foraging strategy is characterized by searching large areas and foraging in multiple foraging habitats during a single foraging trip.
- With regards to the grey-headed, sooty and light-mantled albatrosses I propose two hypotheses:
    1. The species remain faithful to a particular foraging habitat and is thus inflexible in terms of its foraging behaviour.

(2) The species switches between two or more discernibly different foraging habitats in response to environmental variability and is thus flexible in terms of its foraging behaviour (e.g. Xavier et al. 2003).

The grey-headed and light-mantled albatrosses, breeding elsewhere, have been shown to switch between foraging habitats between years, depending on the interannual foraging habitat quality (Xavier et al. 2003b; Phillips et al. 2005). To my knowledge, the interannual foraging behaviour of the sooty albatross elsewhere and none of the three species breeding at Marion Island has been studied.

- The response of a given albatross species is dependent on the predictability of its preferred foraging habitat (Riotte-Lambert and Matthiopoulos 2019). A species which forages within a predictable prey-concentrating oceanographic feature, such as a major frontal zone, will remain faithful to this feature with interannual variability in foraging effort. However, a species which prefers to forage within more ephemeral features, such as mesoscale eddies, will use a foraging strategy that involves searching for temporally available foraging patches and thus will show interannual differences in foraging habitat use. Alternatively, as typical of predators foraging for prey with unpredictable distributions, a species will employ a generalist foraging strategy, searching multiple foraging habitats for prey.

Chapter 3: Dynamic resource partitioning among sub-Antarctic marine predators

Marine predators have been shown to respond to spatio-temporal variability in their environments by switching their diets to prey that are more abundant at a given time (e.g. Mills et al. 2020) or adjusting their foraging behaviour to follow the movement of preferred features (e.g. Bost et al. 2015) or utilize different foraging habitats (e.g. Phillips et al. 2019). Coexistence of sympatric marine predators has largely been attributed to partitioning of food resources through space, diet and time. However, interannual consistency of resource partitioning among predators has rarely been investigated. In this chapter I investigate the consistency of resource partitioning among ten seabird species and two fur seal species breeding on Marion Island during two seasons over three consecutive years using $\delta^{13}C$ and $\delta^{15}N$ values of their blood as proxies for their trophic ecology.

Specifically I:

- Define isotopic niches for each species during each season and year;
- Investigate the contraction or expansion of each species isotopic niche between seasons and among years;
- Investigate the consistency in resource partitioning among species during each season by calculating the overlap among species isotopic niches;
- Investigate seasonal and interannual shift in species isotopic niches.

I hypothesize:

- Species' isotopic niche space and resource partitioning will vary between summer and autumn as a result of different foraging constraints. The summer isotope compositions represent a time when all species are under strong central place foraging constraints, while in autumn many can forage further afield whereas some are even more constrained. Thus, I expect that changes in foraging constraints between summer and autumn will be linked to the size of the niche occupied by the species.
- Resource partitioning within a community is persistent over years despite variability in the isotopic niche of each species. The foraging strategies of the seabirds and fur seals breeding on Marion Island are likely to have been moulded by two strong evolutionary pressures, firstly to be able to efficiently forage for prey across a dynamic environment, and secondly to minimize possible competition for resources among the ecologically similar species within their communities. Therefore, I expect that the interannual niche space of these 12 marine predators will be dynamic, however, despite this, interspecific resource partitioning will be maintained.

Chapter 4: A critical assessment of marine predator isoscapes within the Southern Indian Ocean

The $\delta^{13}C$ and $\delta^{15}N$ compositions of marine predators' tissues have been widely used to investigate intra- and inter-specific interactions and competition for resources (e.g. Cherel et al. 2014; Ramos et al. 2020). The stable isotopic composition of a predator's tissue depends on a number of intrinsic (behavioural and physiological) and extrinsic (environmental) variables (Graham et al. 2010; Hobson et al. 2010; Shipley and Matich 2020) including:

(1) Spatial patterns in the isotopic composition of organisms at the base of their food webs (i.e. phytoplankton);

(2) Discrimination factors which may offset a consumer's isotopic composition from baseline isotopic values such as diet composition, isotopic averaging and physiological fractionation through intermediate trophic levels;

(3) Isotopic turnover rates and physiological transformation in the consumer.

In this chapter I investigate whether these three major factors determining a marine predator's isotopic compositions lead to differences within species-specific isoscapes. I use GPS-based foraging trips and blood plasma isotopic values of five Procellariiformes and three Sphenisciformes to build and compare species-specific $\delta^{13}C$ and $\delta^{15}N$ isoscapes in the Southern Indian Ocean.

Specifically I:

- Assign individuals' $\delta^{13}C$ and $\delta^{15}N$ blood plasma values to an estimated mean foraging location;
- Interpolate species-specific isoscapes using ordinary kriging;
- Compare gradients of species-specific isoscapes among species as well as with previously modelled marine predator-level and baseline isoscapes.

I hypothesize:

- Spatial patterns in the seabirds' $\delta^{13}C$ and $\delta^{15}N$ isoscapes are a reflection of known spatial patterns within the baseline isotopic values present at the scale of a species distribution range (i.e. latitudinal vs inshore/offshore gradients).

- Trophic level (i.e. diet composition) accounts for differences between species-specific isoscapes.

Chapter 5: Sensitivity of $\delta^{13}C$ values of seabird tissues to combined spatial, temporal and ecological drivers: a simulation approach

Spatial patterns of isotopic values of organisms (i.e. phytoplankton) at the base of marine food webs are not static. The rapid growth of phytoplankton means their isotopic compositions could reflect local and short-term variations in oceanic conditions (Graham et al. 2010; McMahon et al. 2013; Magozzi et al. 2017). Therefore, static maps of $\delta^{13}C$ values of phytoplankton across the global oceans capture large scale latitudinal patterns of isotopic variability but may be relatively poor predictors of isotopic compositions at any particular place and time. In this chapter I combine an individual-based movement model of northern giant petrels with global marine isotope models to explore the sensitivity of seabird tissue $\delta^{13}C$ values to a range of extrinsic (environmental) and intrinsic (behavioural, physiological) drivers.

Specifically I:

- Develop an agent-based movement model of the northern giant petrels based on movement characteristics of their GPS tracks and habitat preferences (i.e. sea surface temperature, bathymetry and chlorophyll-a);
- Simulate blood plasma $\delta^{13}C$ values of simulated northern giant petrels returning from a foraging trip by integrating the temporally specific isoscapes produced by Magozzi et al. (2017) and correcting for, where possible, discrimination rates and isotopic averaging within the consumer;
- Perform in-silico experiments to investigate 1) the effect of the choice of reference isoscape used on inference of predator $\delta^{13}C$ values, and 2) the effect of predator behavioural changes on their $\delta^{13}C$ compositions.

I hypothesize:

- Due to temporal integration of phytoplankton δ^{13}C values into the tissue of a high-level predator and the relatively large distribution range of the northern giant petrels, the simulated northern giant petrel's tissues' isotopic compositions do not reflect short-term changes in the spatial pattern of phytoplankton.
- Behavioural changes which alter the foraging duration or range of the simulated northern giant petrels have the greatest impact on their simulated blood plasma δ^{13}C.

Chapter 6: General Discussion

Chapter 6 concludes the thesis. I discuss and integrate the main findings of each of my chapters and how my findings contribute towards the foraging and stable isotope ecology of the studied seabirds and seals. In addition, I make general recommendations towards future studies focusing on top predator foraging and stable isotope ecology.

Chapter 2:

Foraging in a dynamic environment: Response of four sympatric sub-Antarctic albatross species to interannual environmental variability

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Introduction

The spatial distribution of resources and its predictability across time is a major driver of animal movement (Fauchald 1999; Weimerskirch 2007; Mueller et al. 2011; Riotte-Lambert and Weimerskirch 2013; Van Moorter et al. 2013). If the distribution of resource patches is static or temporally predictable (e.g. daily, seasonally), specialisation in foraging behaviour is expected to occur (Pyke et al. 1977; Futuyma and Moreno 1988; Switzer 1993). For example, when animals forage within predictable resource patches they should exhibit site fidelity, frequenting habitats or areas that are known to be productive (Augé et al. 2014; Arthur et al. 2015). In contrast, animals foraging in dynamic landscapes, where the distribution of resources is unpredictable, are expected to exhibit some flexibility in aspects of their foraging behaviour (Hastings 1983; Kassen 2002). By so doing, they thus optimize the probability of prey encounter by utilizing a variety of foraging habitats (Gilmour et al. 2018; Dehnhard et al. 2019) and/or searching extensively for food resources (Weimerskirch 2007; Mueller et al. 2011).

The spatio-temporal distribution of resources across marine environments is determined by multiple scale-dependent physical and biological processes (Scales et al. 2014a; Lévy et al. 2015). At macro- (100-1000 kms) to meso-scales (10 kms), areas of upwelling at prominent topographical features, major oceanic fronts and eddies concentrate prey resources and act as predictable foraging grounds for marine predators (Weimerskirch 2007; Bost et al. 2009; Wakefield et al. 2009; Scales et al. 2014b). However, environmental variability can alter these complex bio-physical processes resulting in varying degrees of predictability in resource location across different time scales (Fraser and Hofmann 2003; Trathan et al. 2006; Brown et al. 2010).

The way marine predators respond to variability in their environments and associated predictability of prey patches varies between life-history stages, species and populations (Sydeman et al. 2015). For example, the foraging duration of breeding seabirds is constrained by their need to regularly return and perform nest duties at a central location (Phillips et al. 2008). Thus, it is expected that due to limited time to search for prey, they would have suitable foraging strategies to cope with potential variability in prey distribution (Riotte-Lambert and Matthiopoulos 2019). Indeed, many seabird species respond to climatic variability and associated changes in resource availability by either switching their diet to temporally available prey (Machovsky-Capuska et al. 2018; Carpenter-Kling et al. 2019a), utilizing different foraging habitats (Cleeland et al. 2019; Phillips et al. 2019; Geary et al. 2020), or following the distribution of preferred prey (Kappes et al. 2010; Pettex et al. 2012). However, even if they demonstrate such behavioural plasticity, suitable foraging habitats may become inaccessible or energetically costly to reach during climatically anomalous years (e.g. Bost et al. 2015), potentially resulting in breeding failure and/or population declines (e.g. Croxall et al. 1999; Thorne et al. 2015). Thus, in light of the rapid habitat degradation and increased environmental variability imposed by climate change, the ability of a species to respond has important implications for their foraging efficiency and population trajectories (Jenouvrier et al. 2018; Cooke et al. 2019).

The Prince Edward Archipelago, situated in the southwest Indian Ocean sector of the Southern Ocean, consists of two islands (Marion and Prince Edward islands) and hosts more than five million breeding seabirds and seals (Ryan and Bester 2008). Important foraging habitats of these predators include eddies (~100 km in diameter with a longevity of months; Lutjeharms and Valentine 1988; Durgadoo et al. 2010)and oceanic fronts (~1000 km in diameter and consistently present but varying in latitudinal position at a monthly scale; Lutjeharms 1985). To the north of the islands, warm-core eddies are spawned as the Agulhas Return Current interacts with the sub-Antarctic (SAF) and sub-tropical (STF) fronts within the sub-tropical convergence zone (STCZ; Lutjeharms and Valentine 1988; Naik et al. 2015). To the south of the islands, the fast-flowing Antarctic polar front (PF) interacts with the South-west Indian Ridge at the Andrew Bain Fracture Zone (ABFZ) resulting in upwelling of nutrient rich waters and cold core eddy formation (Ansorge and Lutjeharms 2003; Durgadoo et al. 2010). These major frontal zones (i.e. SAF and PF) and eddies are known to be rich in zooplankton, forage fish and cephalopods (Koubbi 1993; Pakhomov and Perissinotto 1997; Pakhomov and Froneman 1999) which are common prey items of seabirds (Cherel and Klages 1998) and seals (Klages and Bester 1998; de

Bruyn et al. 2009). Thus, it is not surprising that grey-headed albatrosses (GHA) *Thalassarche chrysostoma* (eddies at STCZ and ABFZ; Nel et al. 2001), southern elephant seals *Mirounga leonina* (SAF, PF and eddies at ABFZ; Tosh et al. 2015; Massie et al. 2016) and king penguins *Aptenodytes patagonicus* (PF; Pistorius et al. 2017), breeding at the Prince Edward Archipelago, all forage at these mesoscale features.

These important foraging habitats of seabirds and seals breeding at the Prince Edward Archipelago are subject to interannual climatic variability. Eddy production in the Southern Ocean correlates to wind stress, indicated by the Southern Annular Mode index (SAM; Thompson and Wallace 2000; Morrow et al. 2010). A positive SAM index indicates the strengthening and contraction of the Southern Hemisphere westerly winds towards Antarctica (Marshall 2003). During periods of an anomalously positive SAM index, there is a general increase in the occurrence of eddies in the Antarctic and sub-tropical zones with a lag response of two to three years, although effects differ regionally (Meredith and Hogg 2006; Morrow et al. 2010). The SAM index has been predicted to become increasingly positive over the next century (e.g. Gillett and Fyfe 2013). Seabirds respond both positively (e.g. Weimerskirch et al. 2012) and negatively (e.g. Fay et al. 2017; Sauser et al. 2018) to strengthening of the westerly winds within the Southern Ocean and the associated changes in their foraging habitats. In addition, the latitudinal position of the two major ocean fronts (SAF and PF) straddling the archipelago is highly variable and is predicted to migrate southward in response to future changes in climate (Kim and Orsi 2014; Wilson et al. 2016; but see Meijers et al. 2012; Chapman et al. 2020). The response of marine predators to environmental variability can be quantified using a variety of approaches including stable isotope analysis (e.g. Fort et al. 2010), monitoring of demographic parameters (e.g. Inchausti et al. 2003; Weimerskirch 2018) and assessing foraging behaviour through deployment of tracking instrumentation (e.g. Kappes et al. 2010; Phillips et al. 2019). Here, we investigate variability in foraging behaviour of the four albatross species (wandering *Diomedea exulans* (WA), GHA, sooty *Phoebetria fusca* (SA) and light-mantled *P. palpebrata* (LMSA) albatrosses) breeding on Marion Island over three consecutive years (2015/16 to 2017/18), a period which was characterized by particularly pronounced climatic variability, indicated by a positive SAM index anomaly during 2015 which became increasingly negative towards the end of 2016 (https://legacy.bas.ac.uk/met/gjma/sam.html).

Specifically, we investigate the response of birds to environmental variability by quantifying interannual changes in their foraging behaviour along two axes: spatial distribution and habitat use. We propose three possible hypotheses as to how albatross species may respond to variability within their environment:

1) **Faithful hypothesis**: A species has a consistent spatial distribution or uses a particular foraging habitat (such as fronts, eddies or shelf edge) or a combination of the two, despite environmental variability.
2) **Flexible hypothesis:** Among years, a species switches between two or more discernibly different foraging habitats in response to environmental variability.
3) **Nomad hypothesis:** A species does not have any foraging habitat preference but consistently searches large areas for resources (i.e. spatial distribution will be similar between years, ranging across a wide range of oceanic habitats).

We predicted that the response of a given albatross species to be dependent on the predictability of its preferred foraging habitat (Riotte-Lambert and Matthiopoulos 2019). If a species forages within a predictable prey concentrating oceanographic feature, such a major frontal zone, we expected that the species will remain faithful to this feature with interannual variability in foraging effort. However, if a species prefers to forage within more ephemeral features, such as mesoscale eddies, we expected that it will either exhibit flexible foraging strategies, foraging within areas of highest eddy presence, or be nomadic and search vast areas for suitable foraging areas.

At other colonies, WA have been shown to be generalist in term of their foraging habitat use (Weimerskirch 2007). Their foraging strategy is characterized by searching large areas and foraging in multiple foraging habitats during a single foraging trip (Nel et al. 2002; Weimerskirch 2007). Therefore, we predict that the WA incubating at Marion Island are generalized in their foraging habitat use and have an extensive foraging distribution which will remain consistent among years (Nomad hypothesis). The GHA and LMSA, breeding elsewhere, have been shown to switch between foraging habitats between years, depending on the interannual foraging habitat quality (Xavier et al. 2003c; Phillips et al. 2005). To our knowledge, interannual variability in foraging behaviour of the SA has not yet been investigated but we expect similar behaviour to that of LMSA. Therefore, in terms of the GHA, SA and LMSA, we predict that these species will adjust their foraging habitats in response to environmental variability and demonstrate flexibility in foraging behaviour (Flexible hypothesis). Alternatively, they may be faithful to a particular foraging habitat and are thus inflexible in terms of their foraging behaviour (Faithful hypothesis).

Materials and Methods

All data analyses were performed in the R statistical environment (R version 3.6.3.; R Core Team 2020).

Location data

Over three consecutive breeding seasons (2015/16, 2016/17 and 2017/18), GPS data loggers (CatLog-S GPS loggers, Perthold Engineering LLC USA, 50×22×8 mm, 34 g) were deployed on four albatross species on Marion Island during the incubation period (46°55′ S; 37°40′ E): wandering (WA), grey-headed (GHA), sooty (SA) and light-mantled (LMSA) albatrosses (Supplementary Material S2.1). Loggers recorded locations at one-hour interval and were retrieved after one foraging trip. All deployments were within colonies on the south-east coast of Marion Island as well as within GHA colonies along an inland ridge on the south side of the island.

Following the removal of erroneous locations using a McConnel speed filter (*trip* package; Sumner 2016) based on a conservative movement speed threshold of 135 $km \cdot h^{-1}$ (Phillips et al. 2008), trip parameters were calculated for each individual foraging trip. Path length (sum of great circular distances between consecutive locations), maximum distance reached (great circular distance to the furthest point reached from the colony) and trip duration (time between departure and return of the bird to its colony) were calculated (*geosphere* and *trip* packages; Sumner 2016; Hijmans 2019).

Track segmentation

Foraging activity along a seabird's track is characterised by high sinuosity (i.e. frequent turning) and low flight speeds and can be distinguished from direct and fast transit to and from the colony (Benhamou 1992; Pinaud and Weimerskirch 2007). Here, a Bayesian state-space model was used to segment tracks into two behaviours: foraging and transit (*bsam* package; Jonsen et al. 2005; Jonsen 2016). Specifically, a first-difference correlated random walk with behaviour switching (DCRWS) was implemented separately for each species. The DCRWS model estimates a behavioural state (b; range 1 - 2) for each location based on the speed, turning angle, and move persistence (auto-correlation) within the track, with lower b values indicating transiting behaviour and higher values indicating foraging behaviour (Jonsen et al. 2005). To segment tracks into either foraging or transiting, GPS locations with $b < 1.25$ were identified as transiting and GPS location with $b > 1.75$ were identified as foraging (Jonsen et al. 2007). Prior to further analysis, locations with b values between 1.25 and 1.75 were removed. This resulted in the removal of 24.0 % of all locations. Furthermore, all locations recorded at night were removed as they could not readily be distinguished as resting or "sit and wait" foraging (Phalan et al. 2007; Pinaud and Weimerskirch 2007). Locations within 15 km of the coast of Marion Island were removed to avoid overrepresentation of this area, as albatrosses often preen on the water close to their colonies before departing on a foraging trip (Granadeiro et al. 2017).

Environmental data

To investigate the association between the foraging behaviour of albatrosses and oceanographic features, five environmental variables were considered: four satellite-derived measures of altimetry: sea surface height (SSH), sea-level anomaly (SLA), eddy kinetic energy (EKE) and wind speed, and one static variable: ocean floor slope (Supplementary Material S2.2). Sea surface temperature was not used as it is highly correlated to SSH. Environmental variables were extracted for each location identified as foraging or transiting by the DCRWS. A Spearman's correlation matrix revealed that there was no collinearity (coefficient < 0.7) between any of the extracted environmental variables (Dormann et al. 2013).

Within the Southern Ocean, fronts are identifiable by the SSH values (Supplementary Material S2.3; Swart et al. 2010). SSH values of mesoscale eddies can be identical to values associated with fronts (Lamont et al. 2019). Thus, to confirm birds' association with eddies, EKE was also used (Supplementary Material S2). The SLA was used to investigate association with either cyclonic (< -0.25 m) or anticyclonic (> 0.25 m) eddies (see Dragon et al. 2010). Wind speed, zonal winds and meridional winds have previously been shown to impact the foraging behaviour of albatrosses (Weimerskirch et al. 2012), and thus they were included within the analysis. However, as the three components are heavily correlated only wind speed was included as a proxy for all three wind components. Ocean floor slope, calculated as the gradient of bathymetry (*raster* package; Hijmans 2020), was used to identify bathymetric features such as continental shelves, fracture zones or sea mounts. EKE and slope values were log transformed to improve homoscedastic and normality of residuals.

Detection of variability within the marine environment

To assess environment variability during our study period the following was plotted over a five-year period (2014 – 2018). Firstly, monthly SAM indices (https://legacy.bas.ac.uk/met/gjma/sam.html) were plotted. Secondly, monthly eddy activity was calculated for the eddy field in the lee (to the east) of the ABFZ and an area of the STCZ (Ansorge and Lutjeharms 2003; Naik et al. 2015) by averaging the EKE within two bounding boxes which encompassed these areas (Supplementary Material S2.4). The bounding box to characterize the ABFZ eddy field was chosen following the methods of Asdar (2018), who characterized this eddy field and studied its EKE. The bounding box of the STCZ eddy field was chosen based on this area previously being shown to be of importance to foraging seabirds (Nel et al.

2001) and seals (Tosh et al. 2015; Massie et al. 2016). Thirdly, the mean latitudinal position of the SAF and PF between 35-45°E was calculated monthly, following Asdar (2018). Lastly, monthly wind speed averaged over the extent of albatrosses' tracks were plotted.

Spatial distribution

Interannual differences in trip parameters (i.e. path length, duration and maximum distance) were investigated using permutational analysis of variance (PERANOVA; *coin* package; Hothorn et al. 2008). Within separate models, trip parameters were set as the response variable and species and year and their interaction set as the predictor variable. Where necessary, this was followed by pairwise permutation tests (*rcompanion* package; Mangiafico 2019) with false discovery rate corrections (Benjamini and Hochberg 1995).

Intraspecific overlap in spatial foraging distribution between years was investigated using a kernel density analysis (Worton 1989) based on locations inferred to be where albatrosses were foraging. The geographic locations were transformed to Cartesian coordinates using a Lambert Cylindrical Equal Area projection before utilization distributions (UD) were calculated on a 50-km grid (*adehabitatHR* package; Calenge 2006). A species-specific smoothing parameter (h) was calculated by calculating UDs for each individual using the automated h selection ('href') and a species-specific h value taken as the average of these values. The 95% and 50% UD contours were calculated to represent the foraging range and core foraging areas of each species, respectively. Overlap among breeding seasons was calculated using Bhattacharyya's affinity (Bhattacharyya 1943). The null hypothesis of year UDs not overlapping was tested by permuting track labels between years 1000 times and calculating the overlap for each permutation. P-values were estimated as the proportion of times the observed overlap was greater than the permuted overlap.

Foraging habitat preference

Generalized additive mixed models (GAMMs) were used to quantify the correlation between albatross foraging behaviour and environmental variables (Wood 2006). Because outliers can have a strong influence on model fit, an Outlier Test based on an Analysis of Regression in R -student was used to identify outliers ((following methods of Tew Kai and Marsac 2010). Specifically, binomial GAMMs with a logit link function were used with individual identity as a random factor, to allow for individual variation (*mgcv* package; Wood 2006). Behaviour, i.e. foraging (1) or transiting (0), was set as the response variable and the interactions between all environmental variables and year as predictor variables. Treating the putative behavioural mode of the birds at a given location as the binomial response variable in the GAMMS enabled the comparison of environmental conditions at locations where birds were likely foraging with conditions at locations where they were likely transiting. This allowed for the probability of each species to be in either behavioural state to be assessed as a function of the given environmental variables. Smoothers were fitted to each environmental variable using cubic regression splines with shrinkage to avoid over fitting (Wood 2006). As a GAMM inference relies upon independence between observations, spatial correlation between observations was accounted for by incorporating a smooth longitude by latitude interaction term in models (Dormann 2007; Cleeland et al. 2019). Smoothing splines were estimated via restricted maximum likelihood (REML). Year was included as a categorical variable in the fixed effects part of each model using the ‘by’ argument to the gam function in the *mgcv* package, allowing smooths to be generated for each environmental variable for each year. To test whether including year produced a more parsimonious model, the Akaike Information Criterion (AIC) resulting from models including and excluding year were compared and the model with the lowest AIC value was selected (Pedersen et al. 2019). In terms of the environmental variables, model selection was performed using best subset selection (James et al., 2013), which involves building models with all possible combinations of predictor terms and selecting the best model as the one with the lowest AIC value. Separate models were built for each species. For all species, models which included year and all environmental variables resulted in the lowest AIC values and thus only models including year are reported in the results. In addition, concurvity among environmental variables was tested for and was found to be below 0.5 for all variables. To allow for comparison between species, fitted values were back transformed to probability using the *plogis* function.

Variability in foraging habitat

Interannual variance in foraging habitat use by individuals of different species was investigated using multivariate Bayesian mixed models (*MCMCglmm* package; Hadfield 2010). Only values of the environmental variables at foraging locations were included as a multivariate response variable within models and were scaled with a z-transformation. Year and species were included as a fixed effect to allow for between-year and -species variation and individual ID nested within species as a random intercept to account for repeat measures within individuals. To estimate a per species and year variance value for each environmental variable, a heterogenous residual variance structure was fitted with species variance nested within year. Models with and without a heterogenous residual variance structure and fixed effect were compared, with the best model being selected based on the lowest deviance information criterion (DIC) score. All models including a heterogenous residual variance structure and fixed effects were found to have lower DIC scores than their counterparts. Visual checks for posterior distributions and autocorrelation were used to ensure convergence.

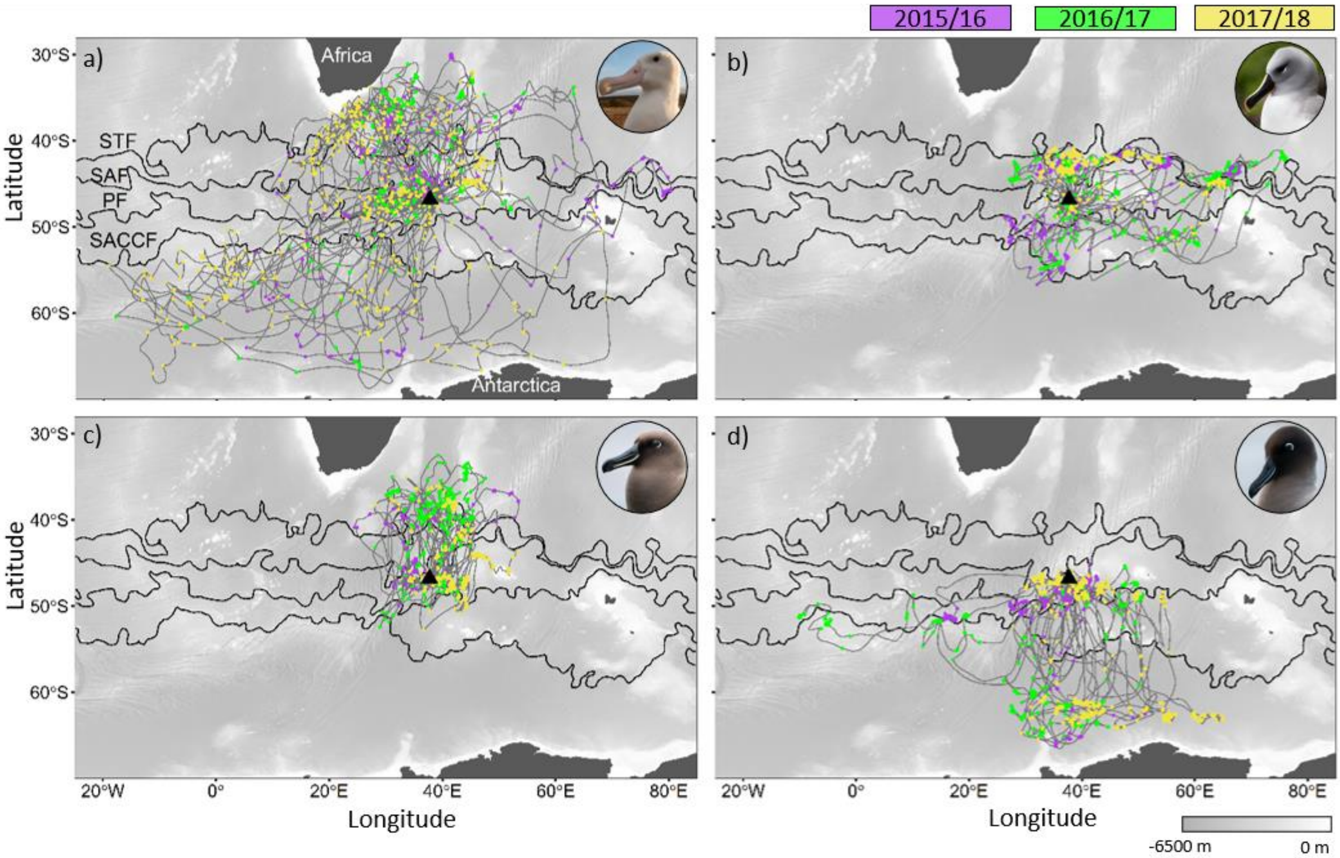


Figure 2.1. Tracks of a) wandering ($n_{2015/16} = 9$, $n_{2016/17} = 16$, $n_{2017/18} = 20$), b) grey-headed ($n_{2015/16} = 5$, $n_{2016/17} = 11$, $n_{2017/18} = 10$), c) sooty ($n_{2015/16} = 5$, $n_{2016/17} = 10$, $n_{2017/18} = 8$) and d) light-mantled ($n_{2015/16} = 5$, $n_{2016/17} = 6$, $n_{2017/18} = 11$) albatrosses incubating on Marion Island (black triangle) over three consecutive breeding seasons. Points show locations inferred to be foraging sites in each year are denoted by different colours: purple = 2015/16, green = 2016/17 and yellow = 2017/18, in relation to the position of sub-tropical (STF), Sub-Antarctic (SAF), Antarctic Polar (PF) and Southern Circumpolar Antarctic (SACCF) fronts.

Results

Over the three years, 116 complete foraging trips of incubating albatrosses were recorded, 45 trips for WA, 26 trips for GHA, 23 trips for SA and 22 trips for LMSA (Figure 2.1; Supplementary material S2.1). These trips covered an extensive area, ranging from Africa to Antarctica (Figure 2.1). The distribution of the WA covered this area, with evidence of foraging across all frontal zones (Figure 2.1a). In contrast, the three smaller albatrosses had more restricted foraging ranges and exhibited directed travel towards areas where they switched to a foraging behavioural mode (Figure 2.1b-d, Supplementary Material S2.5).

Environmental variability

During 2015, there was a positive SAM index anomaly, which became increasingly negative toward the end of 2016 (Figure 2.2a). During the five years considered (2014-2018), maximum monthly EKE values of the STCZ and ABFZ eddy fields were observed during October and November 2015, respectively (Figure 2.2b). The monthly EKE values at both eddy fields then followed a decreasing trend toward the end of 2016 and 2017, respectively, before gradually increasing (Figure 2.2b). Compared to the latitudinal position of the SAF during 2014, the front was relatively close to the island throughout the duration of the study (Figure 2.2c). The PF gradually moved closer to the island over the duration of the study, from an average of 49.8°S in October 2015 to 48.3°S in January 2018, representing approximately 160 km (Figure 2.2c). Over the three breeding seasons, wind speed within the foraging distribution of the albatrosses was highest in 2015/16 and lowest during 2016/17 (Figure 2.2d).

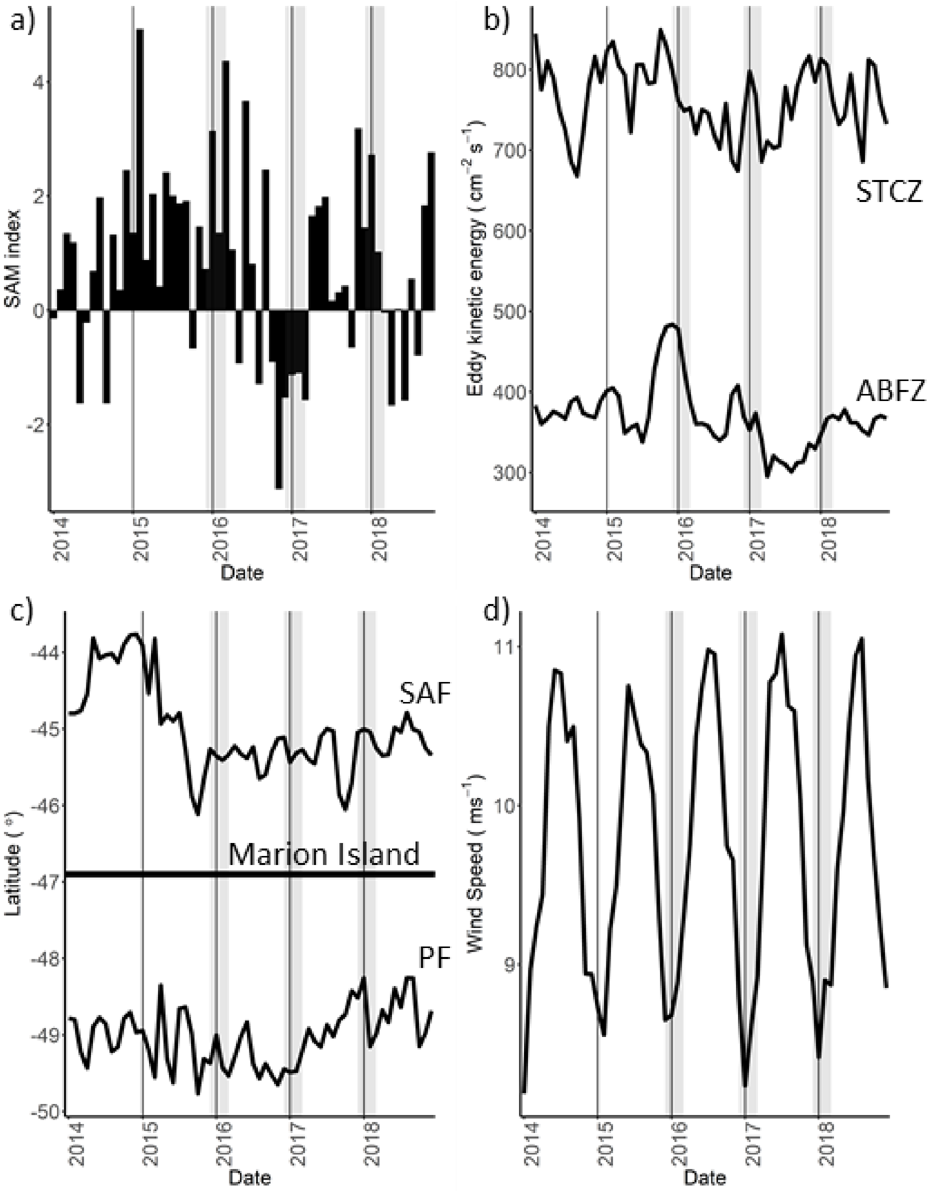


Figure 2.2. Monthly values of the a) Southern Annular Mode (SAM) index, b) monthly mean eddy kinetic energy of an area of the Sub-Tropical Convergence Zone (STCZ) and Andrew Bain Fracture Zone (ABFZ) eddy fields, c) mean latitude position of the Sub-Antarctic (SAF) and Antarctic Polar (PF) fronts between 35-40°E, black horizontal line shows the latitude of Marion Island, and d) monthly wind speeds averaged over the extent of the albatross tracks. Vertical solid black lines indicate the beginning of each year. Grey shaded boxes indicate months albatrosses were tracked.

Spatial distribution

A significant interaction between year and species was found for all trip parameters (Figure 2.3; $p < 0.01$). Post-hoc pairwise comparisons revealed that, within species, foraging trips were similar in duration, path length and maximum distance reached across years for all species ($p > 0.05$ for all comparisons; Figure 2.3). However, WA and LMSA foraging trips were significantly longer and they travelled farther from the island than GHA and SA (Figure 2.3, Supplementary Material S2.1).

Over all three years, the foraging ranges (90% UD) of the study species were generally consistent among years, with > 50% overlap for almost all between-year comparisons within species (Figure 2.4; Table 2.1). Overlap of the core foraging areas (50% UD) was more consistent among years for WA (20.8–28.5%) and GHA (30.5–35.6%) compared to that of the SA (5.1–9.1%) and LMSA (0–25.6%). During 2015/16, compared to other years, WA exhibited an additional core foraging area east of the Kerguelen Plateau (Figure 2.4a).

GHA exhibited the highest interannual overlap in their core foraging areas and foraging ranges (Table 2.1), resulting from consistent foraging along the STCZ (Figures 2.1b and 2.4b). However, only during 2015/16 and 2016/17 was foraging evident south-west of the island within the ABFZ eddy field (Figure 2.4b). The absence of GHA foraging around the ABFZ eddy field in 2017/18 coincided with the lowest monthly EKE recorded during December when the albatrosses were tracked (Figure 2.2b; 2015: 483.5 $cm^{-1} \cdot s^{-2}$; 2016: 369.6 $cm^{-1} \cdot s^{-2}$; 2017: 329.3 $cm^{-1} \cdot s^{-2}$).

Interestingly, even though SA exhibited the most restricted foraging range in terms of longitude (longitudinal range covered: 24.5 – 53.45 °) among all species (WA: -19.5 – 53.5 °; GHA: 22.0 – 76.2 ° and LMSA: -10.2 – 65.0 °; Figure 2.4), they had the lowest degree of overlap between core foraging areas among years (Table 2.1). In all three years, SA 50% UDs were north of the island, however, during 2015/16 and 2017/18, they extended southward into the Polar Frontal Zone (PFZ), the region between the SAF and PF (Figure 2.4c).

LMSA consistently foraged south of the island, with 90% UD contours reaching the Antarctic continent in all three years (Figure 2.4d). Similar to GHA, a core foraging area in 2015/16 was found within the ABFZ eddy field (Figure 2.4b, d). Like SA, LMSA had a core foraging area within the PFZ in 2017/18 when the PF was farther north than usual (Figures 2.2c and 2.4d).

Table 2.1. Kernel utilization distribution overlap (Bhattacharyya's Affinity) at the 50% and 90% utilization distributions (UD) among three breeding seasons (Y1:2015/16; Y2: 2016/17; Y3:2017/18) of the four albatross species breeding on Marion Island. Significantly different UDs (at α = 0.05, in bold) was identified by comparing the real (observed) overlap to a distribution of overlaps from 1000 permutations of the year labels.

		At the 50% UD				At the 90% UD			
Species	Year Comparison	Observed overlap	Permuted overlap (mean ± SD)	p-value	p-value 95% CI	Observed overlap	Permuted overlap (mean ± SD)	p-value	p-value 95% CI
Wandering	Y1 vs Y2	25.97	23.12 ± 5.00	0.65	0.62 - 0.68	60.04	54.86 ± 5.48	0.83	0.81 - 0.86
	Y1 vs Y3	20.77	19.78 ± 5.69	0.53	0.50 - 0.56	53.42	55.53 ± 6.03	0.35	0.32 - 0.38
	Y2 vs Y3	28.50	28.26 ± 5.14	0.50	0.47 - 0.53	56.37	68.25 ± 4.61	0.25	0.22 - 0.27
Grey-headed	Y1 vs Y2	30.35	19.89 ± 8.23	0.96	0.94 - 0.97	66.48	51.46 ± 9.58	0.96	0.95 - 0.97
	Y1 vs Y3	32.31	28.02 ± 7.71	0.66	0.63 - 0.69	39.49	61.24 ± 8.37	0.84	0.82 - 0.87
	Y2 vs Y3	35.60	33.41 ± 4.75	0.65	0.62 - 0.68	61.92	63.45 ± 6.36	0.38	0.35 - 0.41
Sooty	**Y1 vs Y2**	**5.10**	**24.24 ± 8.09**	**0.03**	**0.02 - 0.04**	**60.9**	**74.51 ± 5.91**	**0.03**	**0.02 - 0.05**
	Y1 vs Y3	9.05	21.38 ± 8.11	0.07	0.06 - 0.09	52.53	69.57 ± 8.78	0.06	0.05 - 0.08
	Y2 vs Y3	**7.31**	**25.67 ± 8.98**	**0.04**	**0.03 - 0.05**	**63.89**	**76.78 ± 5.43**	**0.03**	**0.02 - 0.04**
Light-mantled	Y1 vs Y2	0.00	13.63 ± 7.41	0.08	0.07 - 0.10	37.19	56.74 ± 10.39	0.06	0.04 - 0.07
	Y1 vs Y3	25.58	21.67 ± 7.91	0.66	0.63 - 0.69	55.58	62.75 ± 8.35	0.20	0.17 - 0.22
	Y2 vs Y3	15.74	21.15 ± 7.86	0.20	0.18 - 0.23	50.83	64.84 ± 8.02	0.06	0.04 - 0.07

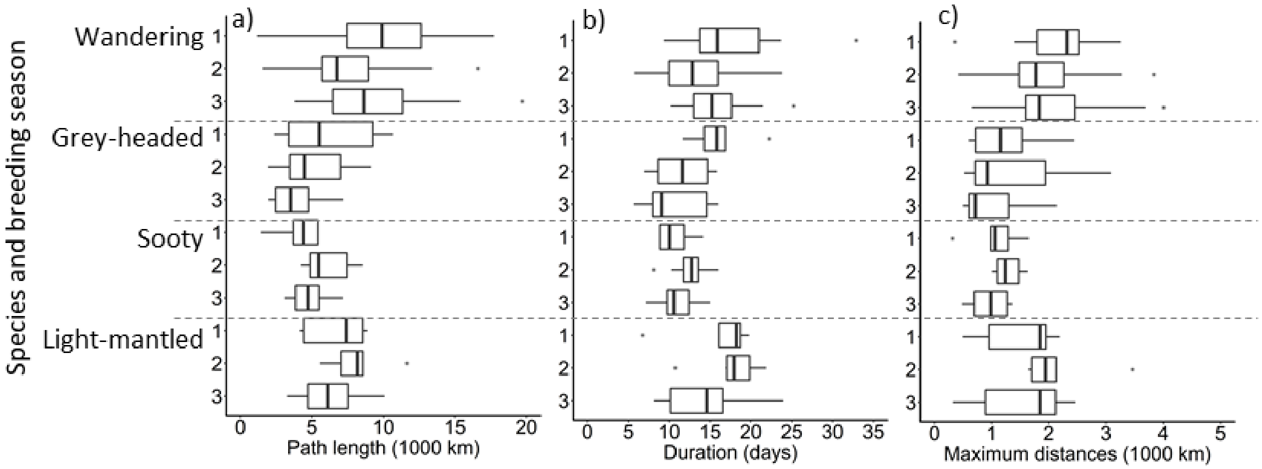


Figure 2.3. Boxplots of trip parameters: a) path length; b) duration and c) maximum distance calculated from foraging trips of incubating wandering, grey-headed, sooty and light-mantled albatrosses at Marion Island tracked over three consecutive breeding seasons: 1) 2015/16; 2) 2016/17 and 3) 2017/18. Boxplots show range excluding outliers, upper and lower quartiles and median with outliers indicated with dots.

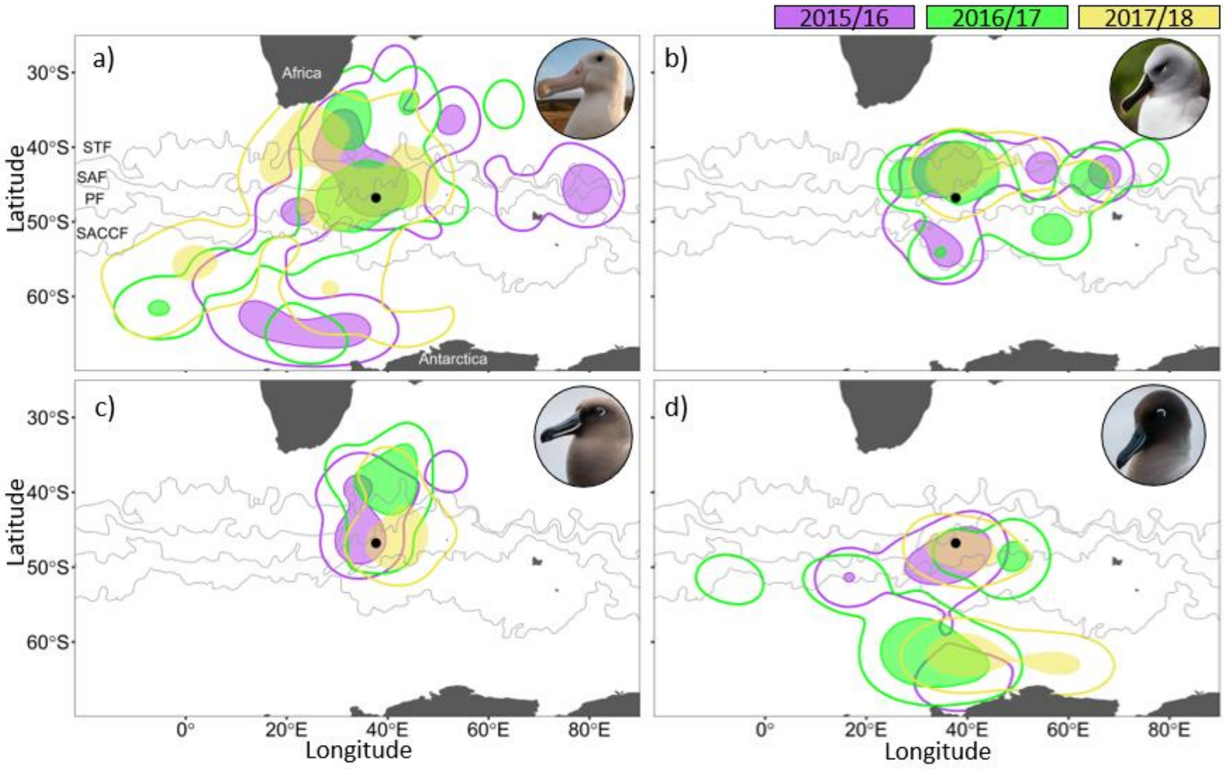


Figure 2.4. 90% (line) and 50% (shaded area) utilization distribution contours of a) wandering, b) grey-headed, c) sooty and d) light-mantled albatrosses incubating on Marion Island (black dot) over three consecutive breeding seasons (purple: 2015/16, green: 2016/17 and yellow:2017/18) in relation to the position of sub-tropical (STF), Sub-Antarctic (SAF), Antarctic Polar (PF) and Southern Circumpolar Antarctic (SACCF) fronts.

Foraging habitat preference

The probability to switch from transiting to foraging behaviours, in response to a particular suite of environmental variables during a foraging trip, varied across species and years (Figure 2.5; Table 2.2). Foraging of WA were significantly correlated to SSH values between the PF and SAF (i.e. PFZ) and above the STF during 2015/16 and below the PF in 2016/17 (Table 2.2; Figure 2.5). During both these years, WA were more likely to forage within anticyclonic eddies, evident by foraging behaviour being significantly correlated to relatively high EKE and SLA values (Table 2.2; Figure 2.5; Supplementary Material S2.4). The first two years (2015/16 and 2016/17) were characterized by a high probability of foraging in areas of steep gradient of the ocean floor slope (Table 2.2; Figure 2.5). However, during all three years, foraging of WA was significantly correlated to low wind speeds, whereas transiting was significantly correlated to high wind speeds (Figure 2.5).

The significant correlations between GHA foraging locations and high SLA and EKE values suggest that this species foraged within cyclonic eddies in all three years (Table 2.2; Figure 2.5). However, during 2016/17, although the GHA foraging behaviour was significantly explained by SLA it was not by EKE (Table 2.2). In addition, during the last two years of the study, foraging behaviour of GHA was significantly correlated to SSH values that correspond to the north of the PF and SAF, respectively as well as high wind speeds (Table 2.2; Figure 2.5).

Surprisingly, the foraging areas of SA were poorly correlated with any of the environmental variables (Table 2.2; Figure 2.5). In 2015/16, foraging was only significantly correlated to SSH values along the SAF and STF, whereas in 2016/17, foraging locations were correlated with high EKE values (Table 2.2). During 2017/18, foraging was only correlated with steep gradients of the ocean floor (> 4000 m; Table 2.2; Figure 2.5). However, foraging of SA was significantly correlated to low wind speeds in 2015/16 and high wind speeds in 2016/17 and 2017/18 (Figure 2.5).

LMSA foraging locations were significantly correlated to low SSH values and positive SLA values over all three years (Table 2.2; Figure 2.5). In addition, during 2015/16, LMSA were significantly more likely to forage in areas with high EKE values whereas during 2017/18 they were significantly more likely to forage in areas with low EKE values (Table 2.2). However, in 2017/18, LMSA tended to forage in areas of relatively low EKE (Table 2.2; Figure 2.5). Over all three years the LMSA were significantly more likely to forage in low wind speeds as well as within high wind speeds during 2015/16 (Table 2.2; Figure 2.5).

Variability in foraging habitats

The multivariate Bayesian mixed model revealed that the variance in environmental variable values (i.e. SSH, EKE, SLA, wind speed and ocean floor slope) experienced by birds when foraging differed between years and species (Figure 2.6). Unexpectedly, during the first two years, SA exhibited a much greater variance in foraging habitat used compared to all other species. Foraging of individual SA occurred at a large range of environmental variable values, especially compared to GHA and LMSA (Supplementary Material S6). Similarly, the consistently high variance in habitat use exhibited by WA could be attributed to individuals foraging across a large range of environmental variable values (Supplementary Materials S2.6 and S2.7). Both GHA and LMSA showed decreasing variance in environmental variable values at foraging locations over the three years (Figure 2.6). This corresponded to both species having a higher density at specific values of SSH and SLA, during 2017/18 compared to other years (Supplementary Material S2.7) and individuals foraging over relative narrow ranges of environmental variable values (Supplementary Material S2.6).

Table 2.2. Summary of generalised additive mixed effect model outcomes used to investigate the probability to switch between foraging and transiting behavioural models while at sea in relation to environmental covariates (sea surface height SSH, sea level anomaly SLA, eddy kinetic energy EKE, wind speed WIND and ocean floor slope SLOPE) of wandering, grey-headed, sooty and light-mantled albatrosses breeding on Marion Island over three breeding seasons (Year 1: 2015/16; Year 2: 2016/17; Year 3: 2017/18).

Species	Term	edf		Chi. Sq	p-value	Dev. Expl. (%)
Wandering	**s(SSH): Year 1**	**3.48**	**3.82**	**18.92**	**<0.01**	26
	s(SSH): Year 2	2.80	3.3	8.06	0.06	
	s(SSH): Year 3	1.00	1.00	1.42	0.23	
	s(EKE): Year 1	**3.01**	**3.53**	**15.15**	**<0.01**	
	s(EKE): Year 2	**3.08**	**3.58**	**9.07**	**0.03**	
	s(EKE): Year 3	1.15	1.28	0.56	0.63	
	s(SLA): Year 1	**3.31**	**3.75**	**20.01**	**<0.01**	
	s(SLA): Year 2	**3.74**	**3.96**	**28.67**	**<0.01**	
	s(SLA): Year 3	1.53	1.89	1.74	0.32	
	s(WIND): Year 1	**1.19**	**1.36**	**10.76**	**<0.01**	
	s(WIND): Year 2	**1.00**	**1.00**	**23.79**	**<0.01**	
	s(WIND): Year 3	**1.00**	**1.00**	**4.54**	**0.03**	
	s(SLOPE): Year 1	**1.00**	**1.00**	**6.99**	**<0.01**	
	s(SLOPE): Year 2	**3.55**	**3.89**	**19.14**	**<0.01**	
	s(SLOPE): Year 3	1.51	1.86	3.58	0.22	
Grey-headed	s(SSH): Year 1	2.51	2.93	4.30	0.17	41.3
	s(SSH): Year 2	**3.38**	**3.77**	**15.27**	**<0.01**	
	s(SSH): Year 3	**2.96**	**3.37**	**35.08**	**<0.01**	
	s(EKE): Year 1	**2.41**	**2.95**	**13.04**	**<0.01**	
	s(EKE): Year 2	1.00	1.00	1.26	0.26	
	s(EKE): Year 3	**3.59**	**3.90**	**13.49**	**<0.01**	
	s(SLA): Year 1	**2.63**	**3.19**	**9.82**	**0.02**	
	s(SLA): Year 2	**2.61**	**3.14**	**20.72**	**<0.01**	
	s(SLA): Year 3	**1.59**	**1.97**	**11.49**	**<0.01**	
	s(WIND): Year 1	1.31	1.54	0.85	0.41	
	s(WIND): Year 2	**2.79**	**3.28**	**11.33**	**0.02**	
	s(WIND): Year 3	**1.39**	**1.68**	**5.49**	**0.03**	
	s(SLOPE): Year 1	1.00	1.00	0.02	0.89	
	s(SLOPE): Year 2	2.21	2.76	2.45	0.32	
	s(SLOPE): Year 3	**1.00**	**1.00**	**5.26**	**0.02**	
Sooty	**s(SSH): Year 1**	**2.81**	**3.24**	**9.86**	**0.02**	35.9
	s(SSH): Year 2	1.00	1.00	0.30	0.58	
	s(SSH): Year 3	2.15	2.60	2.82	0.39	
	s(EKE): Year 1	1.00	1.00	0.44	0.51	
	s(EKE): Year 2	**3.66**	**3.93**	**38.70**	**<0.01**	
	s(EKE): Year 3	1.00	1.00	0.86	0.35	
	s(SLA): Year 1	1.00	1.00	1.60	0.21	
	s(SLA): Year 2	1.96	2.43	2.57	0.44	
	s(SLA): Year 3	1.30	1.53	0.80	0.44	
	s(WIND): Year 1	**3.39**	**3.77**	**22.28**	**<0.01**	
	s(WIND): Year 2	**3.36**	**3.78**	**30.79**	**<0.01**	
	s(WIND): Year 3	**2.99**	**3.48**	**14.16**	**<0.01**	
	s(SLOPE): Year 1	**1.00**	**1.00**	**4.26**	**0.04**	
	s(SLOPE): Year 2	1.00	1.00	3.72	0.05	
	s(SLOPE): Year 3	1.00	1.00	0.37	0.54	
Light-mantled	**s(SSH): Year 1**	**2.51**	**3.05**	**14.61**	**<0.01**	44.5
	s(SSH): Year 2	**1.00**	**1.00**	**7.18**	**<0.01**	
	s(SSH): Year 3	**3.42**	**3.80**	**34.44**	**<0.01**	
	s(EKE): Year 1	**2.34**	**2.86**	**17.83**	**<0.01**	
	s(EKE): Year 2	2.49	3.04	5.08	0.17	
	s(EKE): Year 3	**1.00**	**1.00**	**34.36**	**<0.01**	
	s(SLA): Year 1	**3.06**	**3.57**	**23.21**	**<0.01**	
	s(SLA): Year 2	**3.80**	**3.97**	**78.14**	**<0.01**	
	s(SLA): Year 3	**3.69**	**3.93**	**44.41**	**<0.01**	
	s(WIND): Year 1	**2.76**	**3.20**	**17.43**	**<0.01**	
	s(WIND): Year 2	**3.25**	**3.67**	**13.27**	**<0.01**	
	s(WIND): Year 3	**3.32**	**3.75**	**27.89**	**<0.01**	
	s(SLOPE): Year 1	2.00	2.50	2.61	0.46	
	s(SLOPE): Year 2	1.00	1.00	0.002	0.96	
	s(SLOPE): Year 3	2.19	2.63	1.75	0.42	

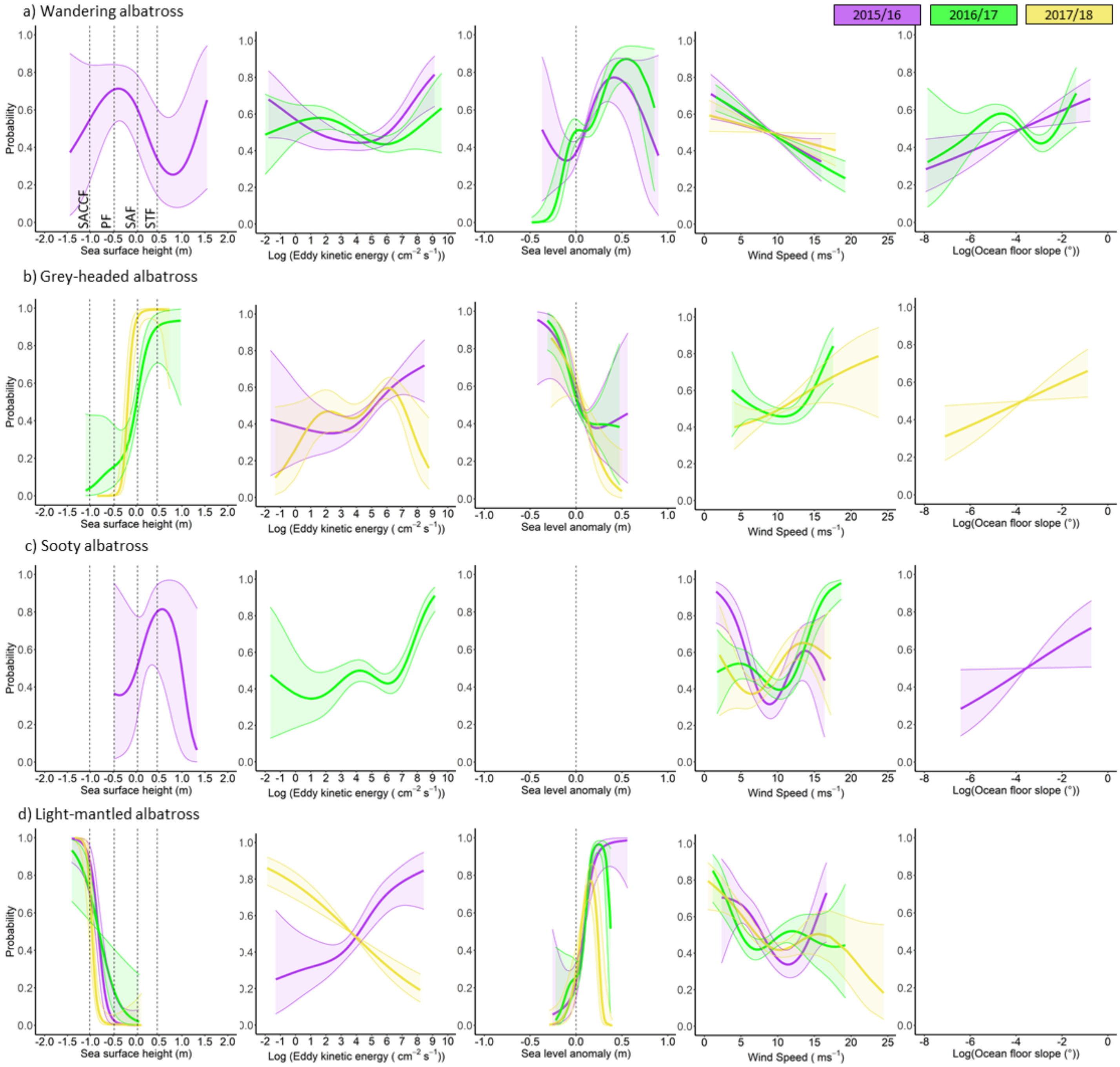


Figure 2.5. Significant smooths resulting from generalised additive mixed models showing the probability of birds being in foraging (1) and transiting (0) behavioural modes among a) wandering, b) grey-headed, c) sooty and d) light-mantled albatrosses incubating on Marion Island in relation to, from left to right: sea surface height (SSH) for major fronts in the Southern Ocean indicated by dotted lines (from left to right: South Antarctic Circumpolar (SACCF), Polar (PF), Sub-Antarctic (SAF) and sub-tropical (STF) fronts), eddy kinetic energy, sea level anomaly, wind speed and ocean floor slope over three consecutive breeding seasons (purple: 2015/16, green: 2016/17 and yellow: 2017/18).

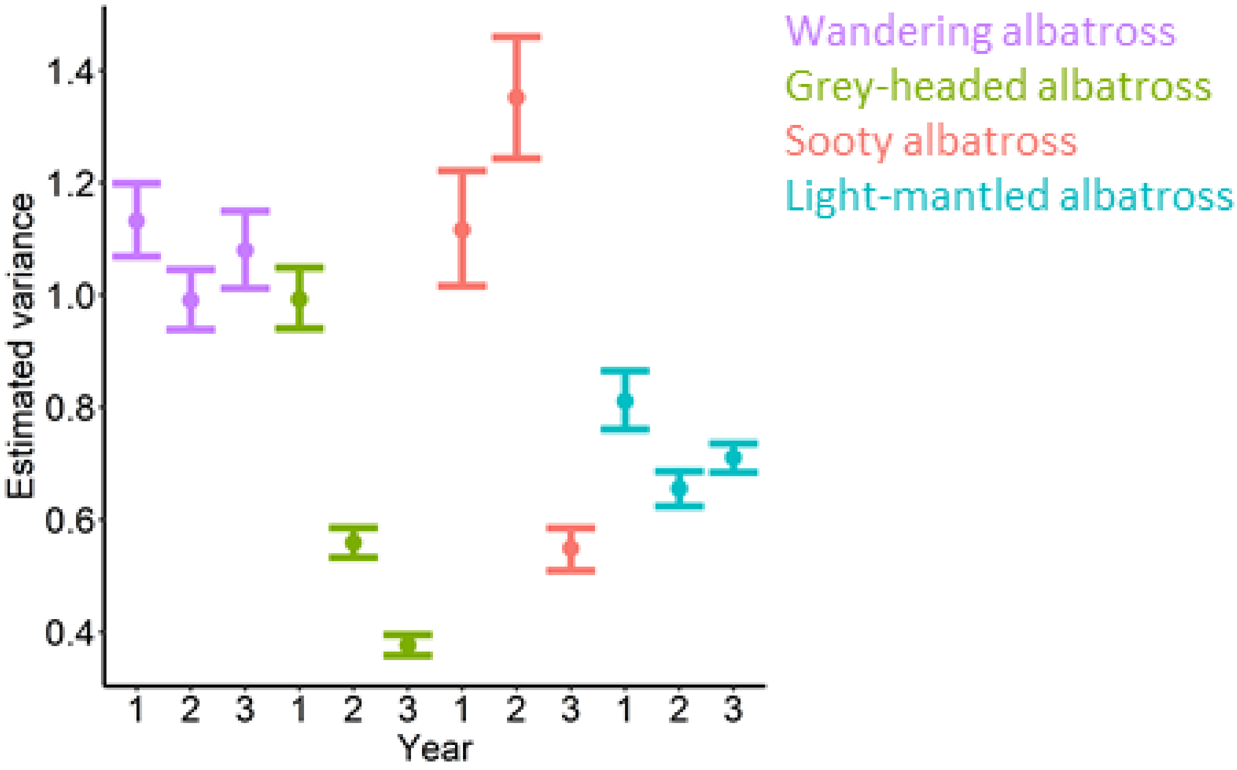


Figure 2.6. Inter-individual estimated variance components for scaled environmental variables (sea surface height, eddy kinetic energy, sea level anomaly and water depth) characterizing the foraging habitat for the four albatross species incubating at Marion Island between three breeding seasons (1: 2015/16, 2: 2016/17 and 3: 2017/18). Filled circles show the estimated variance and the bars show the credible intervals around these estimates.

Discussion

We have investigated the response in foraging behaviour of breeding sympatric albatross species to environmental variability using concurrently collected tracking data over three consecutive years. Results from WA provided strong support for our "nomad hypothesis" as individuals exploited an extensive area and demonstrated large variance in inter-individual foraging habitat use. By comparison, the smaller albatrosses provided partial evidence towards two of our hypotheses. All three smaller albatrosses showed consistency in spatial distribution, supporting the "faithful hypothesis". However, the interannual differential use of foraging habitat by GHA and LMSA also provided partial support for our "flexible hypothesis". Furthermore, the high variance in habitat use by SA indicated that this species was not faithful to a particular foraging habitat thus providing partial evidence toward our "nomad hypothesis". Overall, our results provide clear evidence of flexibility in albatross foraging behaviour in response to environmental variability.

The wandering albatross: A true nomad?

Throughout the three years, WA were consistently distributed across an extensive area and their foraging behaviour was associated with low wind speeds whereas they were more likely to transit in high wind speeds. There was evidence of WA foraging at several oceanographic features known to have elevated productivity, including, but not restricted to, the edge of the Agulhas Bank and retroflection, eddies in the proximity of the STCZ and ABFZ and within major fronts (Figure 2.1, Supplementary Material S2.5). This wide-ranging spatial distribution and foraging habitat use has previously been described as typical for WA breeding at Marion Island (Nel et al. 2002) and elsewhere (Weimerskirch 2007; Phillips et al. 2008; Cleeland et al. 2019). These birds cover large areas by employing a looping foraging strategy (Weimerskirch 2007), frequently transiting between bouts of foraging. This differs from a commuting foraging strategy, where birds move directly towards a foraging area then return directly to their colonies (Weimerskirch 2007).

Previously, WA have been observed to segregate foraging ranges among sexes and age classes (Nel et al. 2002; Weimerskirch et al. 2005, 2012; Lecomte et al. 2010; de Grissac et al. 2017). Incubating female WA typically forage in warmer, more northern waters than males (Nel et al. 2002; Weimerskirch et al. 2012). Furthermore, younger incubating males usually forage north of the PF, farther north than older incubating males, which regularly forage south of 60°S (Lecomte et al. 2010). This suggests that WA are not true nomads but that their foraging behaviour is structured to limit intra-specific competition for prey. However, the consistent use of multiple habitats across individuals can be considered nomadic feeding behaviour, especially compared to those species that commute to favoured foraging areas (Weimerskirch 2007).

Weimerskirch et al. (2012) showed that as a response to an increasingly more positive SAM index and associated increases and southward migration of the Southern Ocean's westerly wind belt, the foraging ranges of both male and female WA breeding on the Crozet Archipelago is shifting southward. This study presents the first record of WA incubating on Marion Island traveling south of 60°S, with 25% of tracked individuals (n = 44) travelling south of 60°S and 34% south of 55°S. Nel et al. (2002) found that only one of 11 (9%) incubating WA on Marion Island tracked during the late 1990s briefly ventured below 55°S. However, Weimerskirch et al. (1993) observed incubating WA from Possession Island (Crozet Archipelago) foraging south of 60°S, so it is hard to know whether the Marion Island population has shifted their foraging range farther south since 1990s, or whether this result is simply an artefact of the greater number of individuals tracked compared to Nel et al. (2002).

Grey-headed and light-mantled albatrosses: Flexible faithfulness

Both GHA and LMSA exploited two different foraging habitats, with their use differing among years. Over the three years, GHA consistently foraged in and around eddies in the proximity of the STCZ, however, only during 2015/16 and 2016/17 was there evidence of GHA foraging south-west of the island, within the ABFZ eddy field. The complete absence of the GHA in this area during 2017/18 corresponded to the lowest monthly EKE recorded for the ABFZ during December, when all small albatrosses were tracked (Figure 2). Previously, GHA incubating on Marion Island have been inferred to forage within both the STCZ and the ABFZ eddy fields (Nel et al. 2001). The monthly EKE for the ABFZ eddy field was 444.9 $cm^{-1} \cdot s^{2}$ during December 1997, when GHA were tracked by Nel et al. (2001), which is similar to the monthly EKE during years when we found GHA foraging with the ABFZ eddy field. Together with the findings of Nel et al. (2001), we show that incubating GHA only forage within the ABFZ eddy field when there is high EKE, indicative of eddy presence.

Major frontal systems are known to be important foraging habitats of breeding GHA from other colonies (Xavier et al. 2003a; Scales et al. 2016; Cleeland et al. 2019). As at Marion Island, differential use of two habitats in response to environmental variability has been found for GHA rearing chicks on Bird Island, South Georgia (Xavier et al. 2003a). In years with ‘good’ environmental conditions, Bird Island GHA were more likely to forage at the PF and feed on cephalopods, resulting in higher breeding success (Xavier et al. 2003c, a, 2013). By comparison, in years when GHA mainly foraged on krill in Antarctic waters they experienced poorer breeding success. However, although the proportion of cephalopod, fish and krill within the diet of the GHA rearing chicks at Marion Island remains relatively consistent between years, there is high interannual variance in the species composition of these taxa (Hunter and Klages 1989; Nel et al. 2001; Richoux et al. 2010; Connan et al. 2014). The findings of these studies highlight the flexibility in GHA foraging behaviour across its range. However, contrasting population trends at Marion (increasing; BirdLife International 2020) and Bird (steadily decreasing; Pardo et al. 2017; Poncet et al. 2017) islands suggest that resilience of this species to climate change will be population specific, despite their foraging flexibility.

Most LMSA from Marion Island foraged in two areas: within the PFZ or well south of the Southern Circumpolar Antarctic (SACCF), close to the Antarctic continent. However, two of 22 tracked birds travelled west and five remained relatively close to the island north of 55°S. Interestingly, LMSA only foraged within the ABFZ eddy field in 2015/16, when monthly EKE for this area was at its highest (Figure 2.2; Supplementary Material S2.4). Unlike GHA, individual LMSA that travelled south often foraged within both key foraging habitats during a single trip. The use of a habitat close to their colonies as well as far south, along the coast of Antarctica, seems to be typical behaviour of LMSA across their distribution (Phillips et al. 2005; Delord et al. 2013; Cleeland et al. 2019). However, LMSA breeding on the Crozet and Kerguelen archipelagos increase their use of their distant Antarctic foraging grounds during the more energy demanding chick-rearing stage, relative to during incubation (Delord et al. 2013). In addition, even though Phillips et al. (2005) found evidence of LMSA foraging in two different habitats, they inferred that LMSA take little or no prey in the PFZ due to the low incidence of sub-Antarctic cephalopod species in their diet. This does not seem to be the case for LMSA breeding on Marion Island. Previous investigations into the diet composition of LMSA breeding at Marion Island found similar proportions of sub-Antarctic and Antarctic cephalopod species (Cooper and Klages 1995; Connan et al. 2014). This suggests that both of these habitats are important foraging grounds for this population of LMSA.

Sooty albatross: Faithful nomads

The interannual variability in foraging behaviour of SA was perhaps the most unexpected. Most individuals transited between foraging bouts all along their tracks, without evidence of direct movement towards a terminal point. This was evident in the very high variance in the values of environmental variables used while foraging (Figure 2.6) and large spread of values experienced by individuals, although only during the initial two years of the study (Supplementary Material S2.5). The low variance during the last year corresponded to a greater number of individuals remaining within the PFZ and SAF and not travelling north of the STF. These results suggest that SA are foraging habitat generalists that are particularly flexible in their foraging behaviour. Across populations of SA, whether colonies are north (Tristan and Amsterdam islands) or south of the STF (Gough, Crozet and Marion islands), core foraging areas of SA are situated just north of the STF (this study; Pinaud and Weimerskirch 2007; Delord et al. 2013; Schoombie et al. 2017). Whether SA breeding elsewhere are ‘faithful nomads’ is difficult to say, as previous studies involving this species have not focussed on consistency in habitat use (Pinaud and Weimerskirch 2007; Delord et al. 2013; Schoombie et al. 2017).

The importance of the sub-tropical convergence to incubating albatrosses on Marion Island

Over all three years of the study, three albatross species (WA, GHA and SA) foraged within and around eddies originating at the STCZ (Supplementary Material S2.4). Although this oceanographic feature does exhibit some inter- and intra-annual variability, it consistently represents the area of highest EKE within the Southern Ocean (Meredith and Hogg 2006). Thus, the STCZ appears to represent a predictable foraging area for predators breeding at Marion Island. In agreement, GHA (Nel et al. 2001) and SA (Schoombie et al. 2017) breeding at Marion Island and other seabirds breeding on the neighbouring Crozet Archipelago (Weimerskirch et al. 2005; Pinaud and Weimerskirch 2007) have been found to forage within and around eddies produced at the STCZ. Interestingly, the only species not utilizing this feature or not foraging north of the island (LMSA) is the only albatross species that has been declining at both Marion Island (Ryan et al. 2009; Schoombie et al. 2017) and the Crozet Archipelago over the past decade (Weimerskirch 2018; Weimerskirch et al. 2018). Inchausti et al. (2003) found that contrasting trends in breeding success of seabirds breeding on Crozet and Kerguelen Archipelagos correlated to the different species’ foraging distribution. Seabird species which foraged south of the PF experienced lower breeding success during climatically anomalous years, whereas the breeding success of seabirds which foraged in sub-tropical water was higher.

Resilience to environmental change

Behavioural plasticity plays a key role in the ability of organisms to adjust to environmental variability and change (Beever et al. 2017). Here we showed that incubating WA, GHA, SA and LMSA are flexible in their spatial distribution and foraging habitat use either by exhibiting behaviours which are typical of foraging habitat generalists or the ability to switch between habitats or a combination of the two. Although it is difficult to quantify behavioural plasticity directly, this flexibility in foraging habitat use and distribution indicates that species in this study exhibited a degree of foraging behavioural plasticity even though there was a low per year sample size. WA are likely to be at least partially buffered against changing environmental conditions due to their broad use of habitats, especially since WA breeding success is either positively correlated to environmental variability or change (Inchausti et al. 2003; Weimerskirch et al. 2012) or is not correlated at all (Rolland et al. 2010; Lewis et al. 2012). These are encouraging findings, as it potentially indicates some resilience of albatrosses to environmental variability and change (Kappes et al. 2010; Beever et al. 2017).

In many instances, fluctuations in albatross breeding success have been related to environmental conditions, with years of anomalous climatic conditions often resulting in decreased breeding success (Veit et al. 1993; Croxall et al. 1999; Inchausti et al. 2003; Pinaud et al. 2005; Kappes et al. 2010; Nevoux et al. 2010; Weimerskirch et al. 2012; Thorne et al. 2015). In all instances where breeding success was negatively correlated to environmental variability, albatrosses had to increase their energy expenditure to either track preferred habitats (Kappes et al. 2010; Thorne et al. 2015) or switch to exploit other habitats (Pinaud et al. 2005). Similarly, an increase in breeding success of the WA breeding at the Crozet Archipelago was correlated with a decrease in energy expenditure linked to increased wind speeds that resulted in faster flight speeds and shorter foraging trips (Weimerskirch et al. 2012). The lack of a difference in trip parameters between years for all species in this study suggests that interannual changes in foraging habitat and distribution did not require increased foraging effort or energy. However, Thorne et al. (2015) found that during a strong La Nina event, foraging trip parameters of incubating Laysan albatrosses *Pheobastria immutabilis* did not change compared to pre-La Nina conditions. Nonetheless, once chicks hatched parents travelled further than previously recorded during the brooding stage, resulting in lowered breeding success during the La Nina event.

It is therefore important to note that this study only tracked incubating individuals. During this breeding stage, foraging trip duration and foraging range is limited by the fasting capabilities of their partners, which is much greater than that of a newly hatched and growing chick. Nel et al. (2001) showed that once a GHA egg hatches, adult GHA breeding at Marion Island no longer travel to the STCZ and all foraging activity is restricted around prey aggregating mesoscale eddies in the lee of the ABFZ. As a result of climate change, southward shifts of the major frontal zones within the Southern Ocean has been predicted (Kim and Orsi 2014; Wilson et al. 2016; but see Meijers et al. 2012; Chapman et al. 2020). Asdar (2018) recently showed that if there is a 1° latitudinal shift, either north or south, in the position of the PF, the PF will no longer interact with the ABFZ, producing fewer eddies. This could result in the loss of an important and predictable foraging habitat for GHA brooding chicks at Marion Island. Interannual variability in foraging habitat during the brooding stage has not been studied for any of the other albatrosses on Marion Island. It is thus important to expand on the findings of this study and investigate the foraging behaviour of albatrosses during brooding, especially how they respond to environmental variability during this time.

Future climate scenarios suggest an increase in SAM index values over the next century in response to climate change (Gillett and Fyfe 2013). As this is associated with an increase in wind speed in the Southern Ocean it is likely that this will have a positive influence on the number of prey aggregating mesoscale eddies (Meredith and Hogg 2006; Morrow et al. 2010). However, further investigations are needed to understand the regional effects of increasingly positive SAM indices on existing eddy fields which act as important foraging habitat to the seabirds and seals breeding on Marion Island, such as the STCZ and ABFZ eddy fields. Furthermore, as shown by Weimerskirch et al. (2012), increased wind speeds could increase the foraging efficiency of albatrosses by increasing their flying speeds while transiting and thus decreasing their overall trip durations. However, due to highly positive SAM indices predicted by 2080, the wind speed south of Marion Island is expected to increase, whereas wind speed to the north of the island is expected to decrease (Weimerskirch et al. 2012). This may have a negative impact on those flying seabird species which forage to the north of Marion Island.

Study limitations and future priorities

A limitation to our study is that variation in habitat use between sexes was not taken into consideration. Previously, segregation of foraging areas between the sexes of WA incubating on Possession Island (Lecomte et al. 2010; Weimerskirch et al. 2012) and GHA incubating on Bird Island (Phillips et al. 2004) has been shown. Due to our relatively small sample size of birds sampled each year (Supplementary Material S2.1) it is possible that yearly differences we have observed were influenced by an unbalanced number of males and females sampled each year. Future research on these study species at Marion Island would benefit from considering intrinsic (e.g. sex, age) and extrinsic (e.g. con- and inter- specific interactions) influences on foraging habitat preference and spatial distribution.

Conclusions

Our findings highlight foraging plasticity in four albatross species in response to environmental variability. Future investigations should include other breeding stages during the annual cycles of the albatrosses, coupled with demographic studies to further our understanding of behavioural plasticity and population responses. Furthermore, as this study has investigated the response in foraging behaviour of albatrosses at the population level, a future logical progression would be to investigate individual variability in foraging behaviour as well as a comparison between populations with different external stressors (e.g. fisheries; Barbraud et al. 2012; Grémillet et al. 2018). This study, however, demonstrates the importance of elucidating links between oceanography and behaviour to understand the response of seabirds to climate variability and change.

Supplementary Material

Supplementary Material S2.1. Summary of tracks recorded via GPS data loggers deployed on incubating wandering, grey-headed, sooty and light-mantled albatrosses on Marion Island over three breeding seasons (2015/16-2017/18) and corresponding trip parameters. Values reported are mean ± SD.

Common name	Year	Tracks (n)	Locations (n)	Start date	End date	Path length (km)	Duration (day)	Maximum distance (km)
Wandering albatross	2015/16	9	2943	2016/01/22	2016/03/02	9619.7 ± 4821.4	18.4 ± 7.0	2220.7 ± 915.7
	2016/17	16	2916	2017/02/21	2017/04/01	7529.6 ± 3935.2	13.3 ± 5.2	1854.5 ± 895.8
	2017/18	20	7453	2018/02/02	2018/03/12	9238.2 ± 3877.8	15.7 ± 4.0	2055.8 ± 919.9
Grey-headed albatross	2015/16	5	1832	2015/11/29	2015/12/27	4084.4 ± 1659.1	16.2 ± 3.9	1288.5 ± 743.4
	2016/17	11	3038	2016/11/27	2016/12/24	6061.0 ± 1592.6	11.7 ± 3.3	1356.4 ± 901.8
	2017/18	10	2533	2017/11/25	2017/12/14	4788.7 ± 1328.5	10.6 ± 4.0	970.9 ± 524.9
Sooty albatross	2015/16	5	1022	2015/11/26	2015/12/16	2741.5 ± 1274.6	10.7 ± 2.3	1057.4 ± 490.6
	2016/17	10	2950	2016/11/23	2016/12/18	1994.3 ± 480.6	12.4 ± 2.1	1278.7 ± 236.7
	2017/18	8	2085	2017/11/22	2017/12/13	2179.0 ± 800.1	11.0 ± 2.5	954.7 ± 349.6
Light-mantled albatross	2015/16	5	1250	2015/11/28	2016/01/02	6675.1 ± 2269.4	15.9 ± 5.3	1484.3 ± 724.9
	2016/17	6	1517	2016/11/26	2016/12/29	8146.7 ± 2056.4	17.6 ± 3.8	2132.1 ± 687.2
	2017/18	11	3646	2017/11/24	2018/01/05	6304.2 ± 2160.3	14.1 ± 4.7	1546.3 ± 762.1

Supplementary Material S2.2. Environmental variables: spatial and temporal resolutions and source.

Variable	Abbreviation	Spatial resolution	Temporal resolution	Source
Sea surface height (m)	SSH	0.25°	Daily	CMEMS[a]
Sea level anomaly (m)	SLA	0.25°	Daily	CMEMS[a]
Eddy kinetic energy	EKE	0.25°	Daily	CMEMS [a, b]
Wind speed		0.25°	Daily	CERSAT [c]
Bathymetry (m)		0.02°	-	GEBCO [d]

[a] Ssalto/Duacs produced and distributed by the Copernicus Marine Environment Monitoring Service (CMEMS, http://marine.copernicus.eu)

[b] Downloaded as geostrophic velocities (U and V components) and computed as $EKE = 0.5 \times (U^2 + V^2)$

[c] Downloaded from CERSAT web portal (http://www.ifremer.fr/cersat)

[d] General Bathymetric Chart of the Oceans hosted by the British Oceanographic Data Centre (http://www.gebco.net/data_and_products/gridded_bathymetry_data/)

Supplementary Material S2.3. Sea surface heights (SSH) used to identify major fronts within the Southern Ocean, following the methods of Rintoul (2009a, b) and Swart et al. (2010)

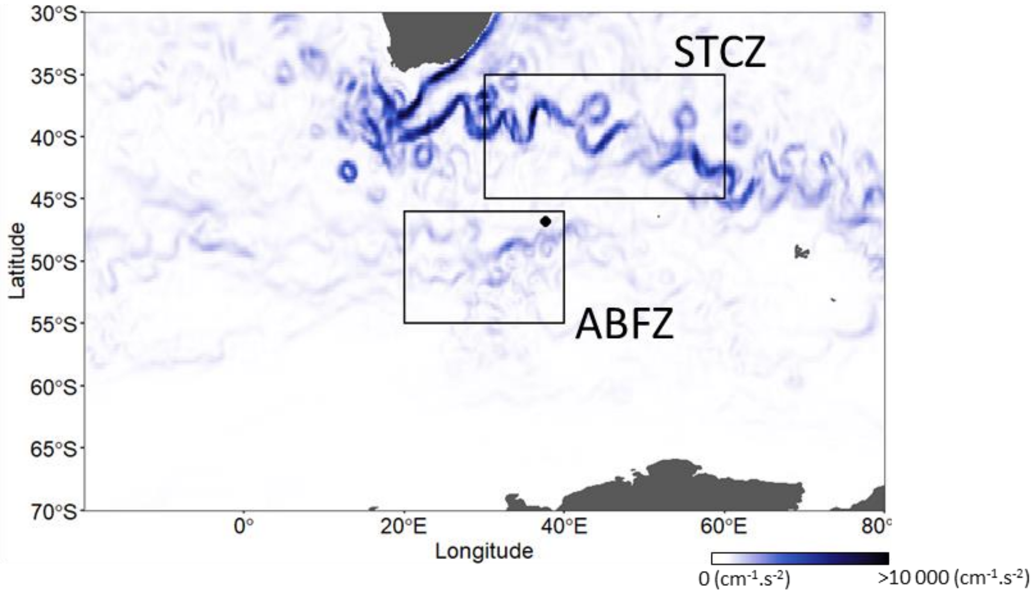
Front	Sea surface height (m)		
	Northern boundary	Middle	Southern boundary
sub-Tropical	0.5700	0.4600	0.3500
sub-Antarctic	0.2400	0.0300	-0.1700
Antarctic Polar	-0.3000	-0.4800	-0.6300
South Antarctic Circumpolar	-0.9430	-1.0157	-1.0884

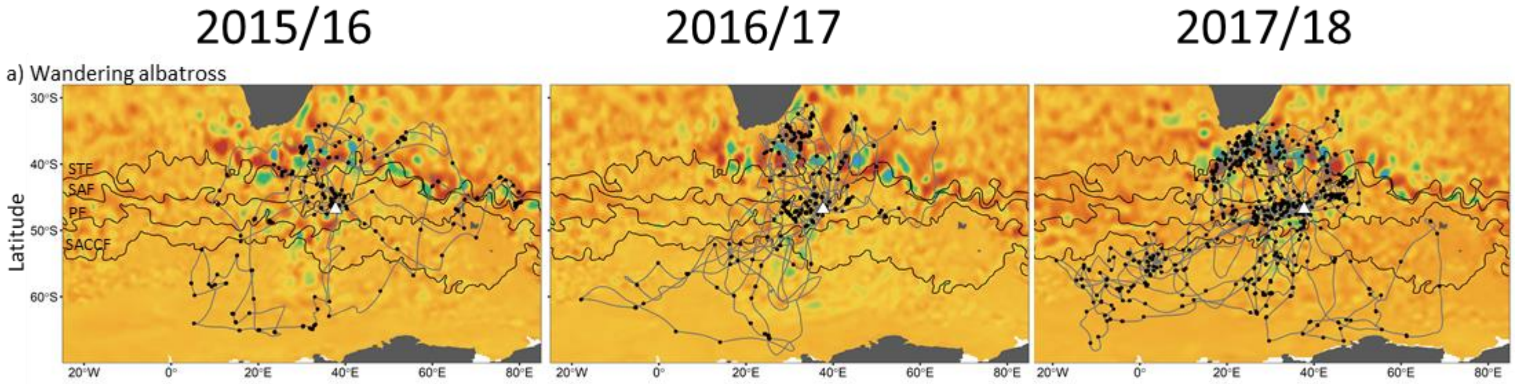
Supplementary Material S2.4. a) Bounding boxes of areas used to investigate monthly variability in eddy kinetic energy of two major eddy fields within the Southern Ocean: sub-Tropical Convergence Zone (STCZ) and the Andrew Bain Fracture Zone (ABFZ) and b) graphical representation of bounding boxes overlaying a map of eddy kinetic energy, black dot represents the Prince Edward Archipelago.

a)

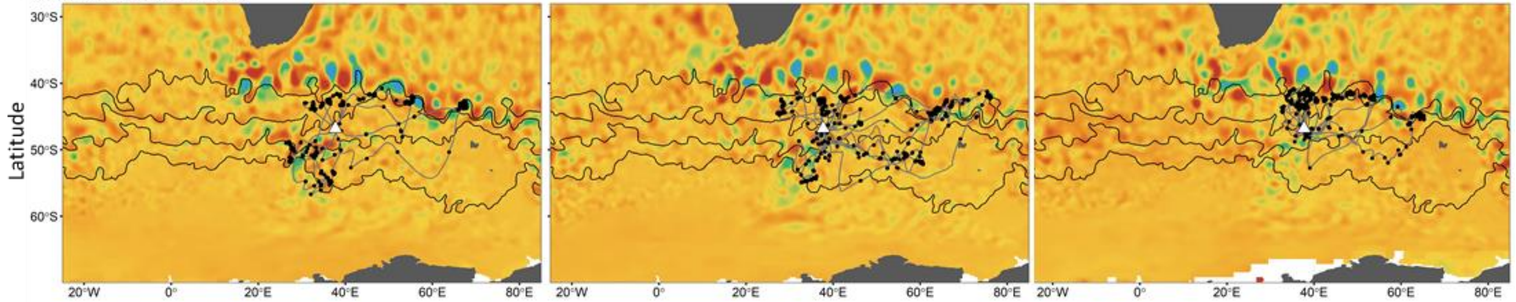
Eddy field	Longitude	Latitude
STCZ	30; 60	-46; -35
ABFZ	20; 40	-55; -46

b)

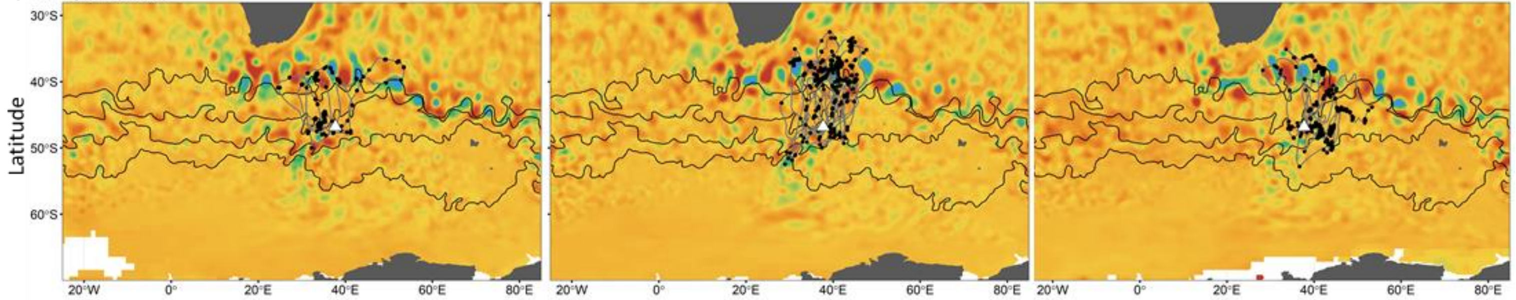




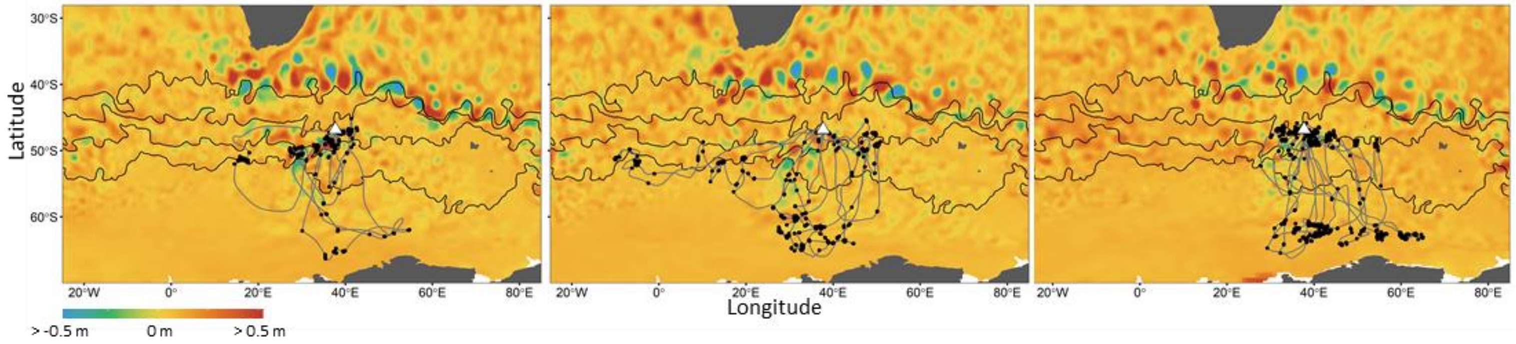
a) Wandering albatross



b) Grey-headed albatross



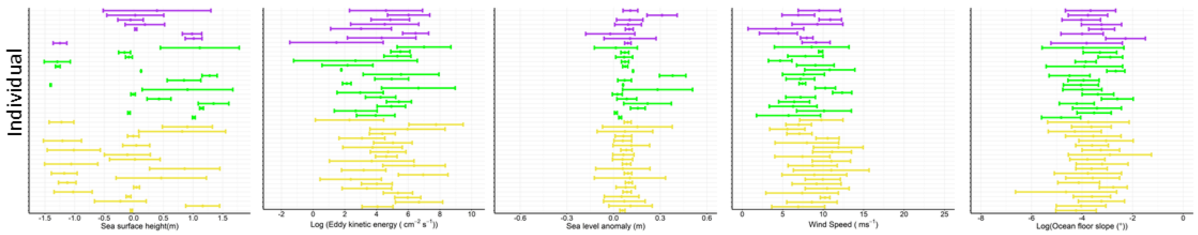
c) Sooty albatross



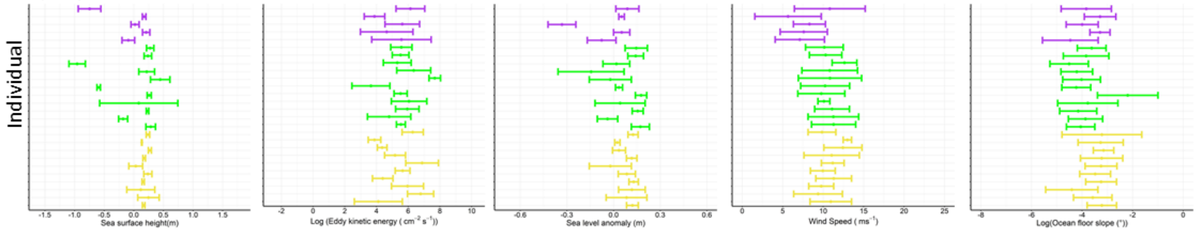
d) Light-mantled albatross

Supplementary Material S2.5. GPS tracks and locations identified as foraging by a Bayesian space state model of a) wandering, b) grey-headed, c) sooty and d) light-mantled albatrosses incubating on Marion Island over three breeding seasons (left to right: 2015/16; 2016/17 and 2017/18) overlain on maps of sea level anomaly which was averaged over the time period of the tracks shown on the respective map. Breeding season specific December positions of sub-Tropical (STF), sub-Antarctic (SAF), Antarctic Polar (PF) and Southern Antarctic Circumpolar (SACCF) fronts are shown as black lines and Marion Island (white triangle).

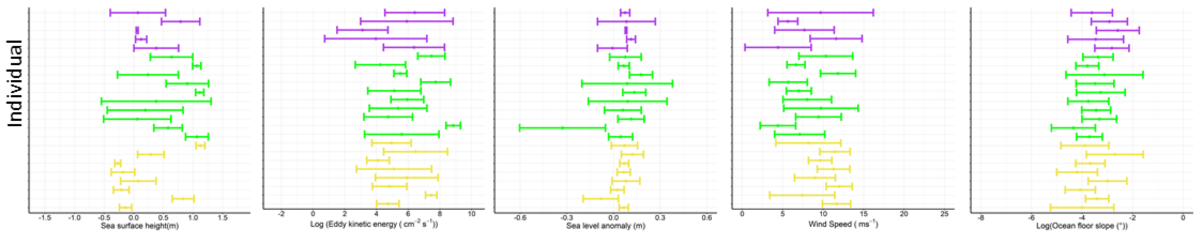
a) Wandering albatross



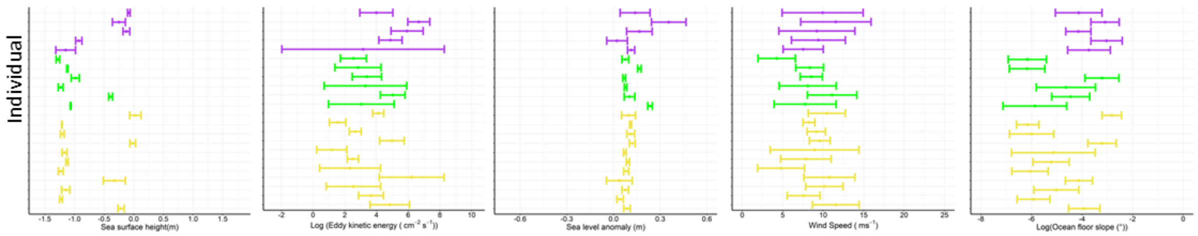
b) Grey-headed albatross



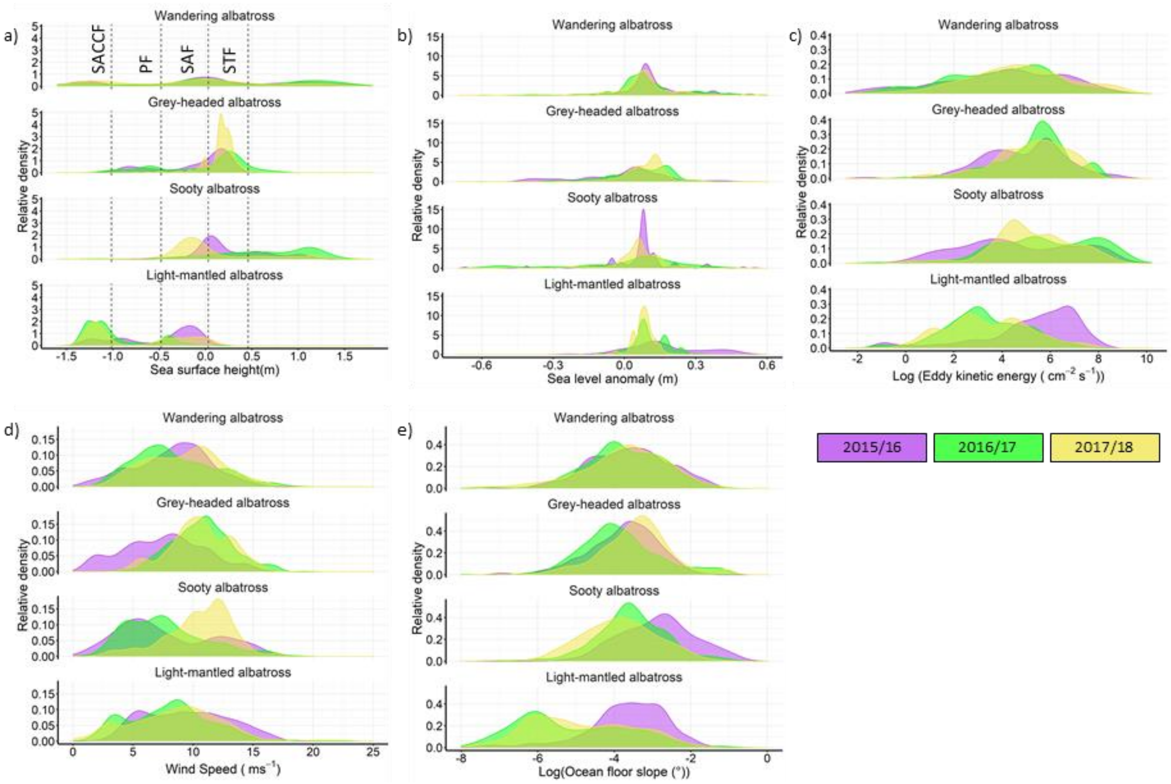
c) Sooty albatross



d) Light-mantled albatross



Supplementary Material S2.6. Median and median absolute deviance of environmental variables under GPS locations along the trajectories of incubating a) wandering, b) grey-headed, c) sooty and d) light-mantled albatross which were identified as the birds being in a foraging behavioural mode. Data are shown for breeding seasons: 2015/16 (purple), 2016/17 (green) and 2017/18 (yellow).



Supplementary Material S2.7. Density plots of a) sea surface height, b) sea level anomaly, c) eddy kinetic energy, d) wind speed and e) ocean floor slope at GPS locations along the trajectories of albatrosses breeding at Marion Island which were identified as the bird most likely being in a foraging behavioural mode. Densities are shown separately for each year: 2015/16 (purple), 2016/17 (green) and 2017/18 (yellow).

Chapter 3:

Dynamic resource partitioning in a sub-Antarctic marine predator community

Carpenter-Kling T, Connan M, Reisinger RR, Ryan PG, Makhado A and Pistorius PA. **To be submitted**. Dynamic resource partitioning in a sub-Antarctic marine predator community. *Functional Ecology*.

Introduction

Resource segregation among species is typically viewed in light of the competitive exclusion principle, according to which competitors for identical resources cannot co-exist (Gause 1934; Hardin 1960). Theoretically, species should limit overlap along various resource-use axes. In dynamic environments, however, species have to also respond to fluctuations in resource availability to maintain fitness (Van Moorter et al. 2013; Riotte-Lambert and Matthiopoulos 2019). According to the optimal foraging theory, when food resources are abundant, animals will specialize their foraging behaviour and target preferred food items and habitats, while during food scarcity they will generalize their foraging behaviour by consuming a greater diversity of food items (Stephens and Krebs 1986; Perry and Pianka 1997). At the same time, when resources are limited, competition among ecologically similar species is thought to increase, promoting a decrease in interspecific niche overlap (Pianka 1974). Thus, classical niche theory (Hutchinson 1957; Pianka 1974; Schoener 1974) predicts that during periods of relative food scarcity, animals will adjust their foraging behaviour to decrease interspecific competition for resources by becoming more specialised. Understanding these dynamic patterns of resource-use among species is important for elucidating the mechanisms whereby communities of species respond to dynamic environments.

Land-breeding marine predators, such as seabirds and seals on sub-Antarctic islands, are ideal species to study dynamic resource use at a community level. During summer, multispecies assemblages, often numbering in the millions, aggregate on sub-Antarctic islands to breed (e.g. Ryan and Bester 2008). The coexistence of these species has largely been attributed to partitioning of their trophic niches (González-Solís et al. 2000; Phillips et al. 2004; Cherel et al. 2007; Jaeger et al. 2010, 2013; Connan et al. 2014; Pickett et al. 2018), with a greater degree of partitioning evident within taxonomic groups (Connan et al. 2019). However, these predators face intra- and inter- annual variability in habitat and prey availability through environmental fluctuations and due to their life-history (Sydeman et al. 2015; Phillips et al. 2017). The ability of marine predators to reach distant foraging habitats fluctuates during the breeding season, since time available for foraging at sea is primarily determined by the fasting capabilities of their partners or offspring (Bester and Bartlett 1990; Wege et al. 2014; Phillips et al. 2017). Furthermore, due to the aggregation of land-breeding predators foraging from a central location, prey availability is thought to decline outward from these central locations as the breeding season progresses, likely leading to increased competition for available prey (Ashmole 1963; Furness and Birkhead 1984). As the breeding season progresses (and compared to the non-breeding period), seabird species contract and further segregate their trophic niches in response to potential increased resource competition and lower prey availability (Barger et al., 2016; Cherel et al., 2008, 2014; Cherel & Hobson, 2007). This is consistent with the prediction of the classical niche theory. However, the distribution of prey also varies inter-annually due to the dynamic nature of the marine environment (Scales et al. 2014; Lévy et al. 2015). Marine predators can buffer themselves against prey limitation by being generalist foragers (Chapter 2; Dehnhard et al. 2019) or by having flexible foraging behaviours whereby they switch prey species (Carpenter-Kling et al. 2019a; Mills et al. 2020) and/or foraging habitats (Chapter 2; Phillips et al. 2019). However, some species do not seem to alter their foraging behaviour, and even manage to track dynamic habitats over time (e.g. major frontal zones; Bost et al. 2015).

Here, we investigate the trophic niche dynamics and maintenance of inter-specific resource partitioning over time among 12 marine predator species breeding in sympatry on a sub-Antarctic island. During autumn and summer over three consecutive years, we use the carbon ($^{13}C/^{12}C$; $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$; $\delta^{15}N$) isotopic composition of the predators' whole blood to estimate their isotopic niche (hereafter referred to as 'niche') as a proxy for their trophic niche, with $\delta^{13}C$ indicating spatial distribution and $\delta^{15}N$ indicating trophic position within an ecosystem (Newsome et al. 2007). As the six flying species and six diving species are already segregated due to their foraging mode (Croxall and Prince 1980), we independently investigate maintenance of resource partitioning within these two groups. The flying species were the wandering *Diomedea exulans* (WA), grey-headed *Thalassarche chrysostoma* (GHA), sooty *Phoebetria fusca* (SA) and light-mantled *P. palpebrata* (LMSA) albatrosses and northern *Macronectes halli* (NGP) and southern *M. giganteus* (SGP) giant petrels, and diving species were the king *Aptenodytes patagonicus* (KP), gentoo *Pygoscelis papua* (GP), macaroni *Eudyptes chrysolophus* (MP) and eastern rockhopper *E. filholi* (ERP) penguins and sub-Antarctic *Arctocephalus tropicalis* (TRO) and Antarctic *A. gazella* (GAZ) fur seals. We test the following hypotheses:

1. Species' isotopic niche space and resource partitioning varies between summer and autumn as a result of different foraging constraints

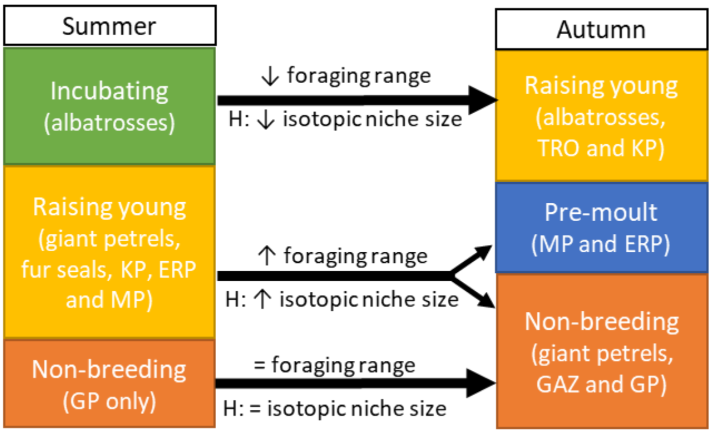
The summer isotope compositions represent a time when all species are under strong central place foraging constraints, while in autumn many can forage further whereas some are even more limited (Figure 3.1a). Thus, we expect that change in foraging constraints between summer and autumn will be directly linked to size of the niche occupied by the species (Figure 3.1a).

2. Resource partitioning within a community is persistent over years despite variability in the isotopic niche of each species

As a response to environmental variability, marine predators may forage for different prey species (e.g. Reisinger et al. 2018; Carpenter-Kling et al. 2019a) or within different habitats (Chapter 2; Cleeland et al. 2019) between years. Over our study period there was pronounced environmental variability as indicated by an anomalously positive Southern Annual Mode index in 2015 (https://legacy.bas.ac.uk/met/gjma/sam.html) and large latitudinal movement (~1 – 2°) of major fronts (Chapter 2). This affected the spatio-temporal distribution of regional prey aggregating oceanographic features such as mesoscale eddies (Chapter 2; Thompson and Wallace 2000; Morrow et al. 2010). We therefore expect inter-annual movement in the niches of most species (Figure 3.1b). Species that are known to be diet (GP; Carpenter-Kling et al. 2019a) or foraging habitat (WA and SA, Chapter 2) generalists may either remain consistent between years (i.e. consistently generalist) or completely change between years (i.e. plasticity in foraging behaviour). On the contrary, species that are known to be diet and foraging habitat specialists with low foraging behaviour plasticity (KP; Bost et al. 2015) are expected to have relatively static isotopic niches. The foraging behaviour of sympatric species, however, has evolved to both cope with the dynamic nature of the environment (Chapter 2;

Bost et al. 2009; Wakefield et al. 2009) as well as to facilitate their coexistence, particularly via partitioning of food resources (e.g. Connan et al. 2014; Pickett et al. 2018). Therefore, we predict that even though the niches of species may be dynamic between years, the 12 marine predators will partition their trophic niches and this partitioning will be maintained over time, evident as minimal overlap between niches.

a) **Hypothesis 1: Seasonally dynamic isotopic niche space as a result of different foraging constraints**



b) **Hypothesis 2: Interannual variability in the isotopic niche of each species with maintenance of resource partitioning among species:**

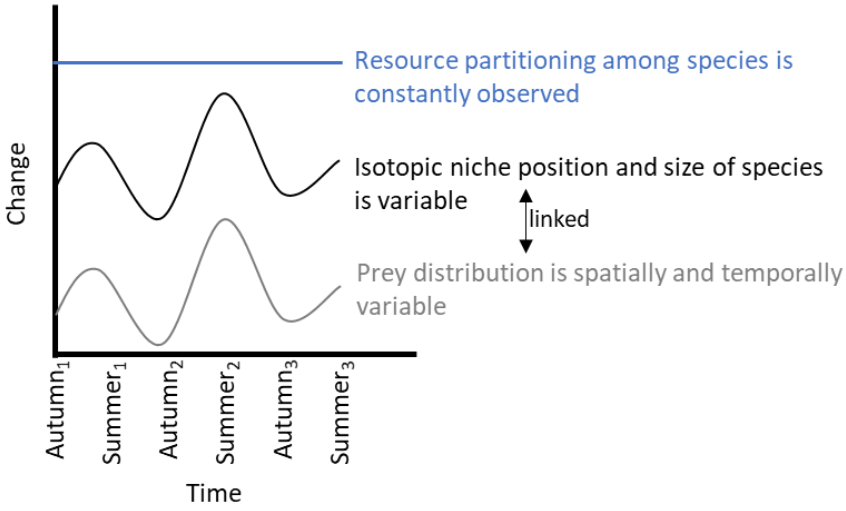


Figure 3.1. Schematic diagram of the two main hypotheses detailing a) seasonal and b) interannual temporal variability in the isotopic niche space of four albatross (wandering, grey-headed, sooty and light-mantled albatrosses), two giant petrel (northern and southern giant petrels), four penguin (king (KP), gentoo (GP), macaroni (MP) and eastern rockhopper (ERP) penguins) and two fur seal species (Antarctic (GAZ) and sub-Antarctic (TRO) fur seals).

Materials and Methods

Study species and sample collection

All four albatross (WA, GHA, SA and LMSA) and penguin (KP, GP, MP and ERP) species, and both giant petrel (NGP and SGP) and fur seal (TRO and GAZ; females) species breeding along the south and south-east coast of Marion Island (46.9° S, 37.7° E) were studied. Over three consecutive years, up to 20 individuals of each species were sampled during two seasons: autumn (April 2015, 2016 and 2017) and the following summer (December – February 2015/16, 2016/17 and 2017/18) with a few exceptions due to differing annual breeding chronology of WA and giant petrels as well as low numbers of LMSA adults present during autumn (Supplementary Material S3.1).

Approximately 0.5 ml of blood was collected per individual using a heparinized needle and immediately stored in 70% ethanol and frozen until preparation for stable isotope analysis (Hobson et al. 1997). The whole blood was then dried at 50°C for 48 hrs before being powdered using a mortar and pestle. The isotopic composition of carbon and nitrogen in aliquots (~0.4 mg) of samples were determined by combusting samples in a Flash 2000 organic elemental spectrometer via a Conflo IV gas control unit (Thermo Scientific, Germany). All samples were processed at the Stable Light Isotope Unit at the University of Cape Town, South Africa. Replicate measurements of internal laboratory standards indicated minimal standard deviations within and among runs (Merck gel: $SD_{\delta 13C} = 0.2$ ‰, $SD_{\delta 15N} < 0.1$ ‰; valine: $SD_{\delta 13C} < 0.2$ ‰, $SD_{\delta 15N} = 0.1$ ‰; seal bone:$SD_{\delta 13C} < 0.2$ ‰, $SD_{\delta 15N} < 0.1$ ‰). All in-house standards were calibrated against International Atomic Energy Agency standards. Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Whole blood has a rapid turnover rate and represents an animal’s diet integrated over a period of two to four weeks prior to sampling (Hobson and Clark 1992; Dalerum and Angerbjörn 2005). Thus, the samples collected during summer gives dietary information for incubating albatrosses, giant petrels and ERP, brooding MP, lactating fur seals and non-breeding GP (Supplementary Material S3.1). The samples collected during autumn give dietary information of early chick rearing WA, mid-late chick rearing GHA and SA, KP with a chick within a crèche, non-breeding giant petrels, GAZ and GP, pre-moult foraging trip of the ERP and MP, lactating TRO (Supplementary material S3.1).

High lipid contents within tissue samples, detected by a C:N mass ratio > 3.5 in tissues for aquatic animals (Post et al. 2007), can lead to artificially low δ^{13}C values which may lead to misinterpretation of δ^{13}C tissue values (DeNiro and Epstein 1977; Cherel et al. 2005b). Most whole blood samples collected had a C:N mass ratio within normal ranges (Supplementary Material S3.2) except blood samples collected from MP and ERP during autumn (C:N > 3.5). Samples from MP and ERP were collected from moulting birds during autumn (Supplementary Material S3.2). During this time, the MP and RHP are fasting, using their endogenous nutrient stores for nutrition (Cherel et al. 2005a). Although the effects of this metabolic process is minimal on δ^{15}N, the process leads to an increase in circulating lipids within the blood (Cherel et al. 2005a). An effect of lipids on δ^{13}C was evident for both species due to the significant increase of their C:N mass ratios of their blood between summer and autumn (paired t-test : MP: $t = -10.58$, $df = 72.75$, $p < 0.01$; ERP: $t = -8.72$, $df = 72.46$, $p < 0.01$). This was corrected by mathematically normalizing blood δ^{13}C values following Post et al. (2007).

Statistical analyses

Differences within and among predators' δ^{13}C and δ^{15}N blood values over time were first investigated using a permutational multivariate analysis of variance (perMANOVA, R package *vegan*; Oksanen et al. 2019) with sampling period, species and the interaction between them as predictor variables within the model. There were six sampling periods within our study i.e. autumn 2015, summer 2015/16, autumn 2016, summer 2016/17, autumn 2017, summer 2017/18. We did not test for the interaction between season and year as early (summer) and late (autumn) breeding were only covered for two breeding seasons. This was followed by a permutational analysis of variance (perANOVA, R package *lmPerm*; Wheeler and Torchiano 2016), performed separately for the predators δ^{13}C and δ^{15}N values with sampling period, species and the interaction between them set as predictor variables within the model.

When necessary, perANOVAs were followed by pairwise permutational tests (R package *rcompanion*; Mangiafico 2019) with false discovery rate corrections (Benjamini and Hochberg 1995).

To visualize species isotopic niches (i.e. niches), standard ellipse areas corrected for small sample size (SEAc; R package *SIBER*; Jackson et al. 2011) were calculated for each season and year. To investigate the expansion or contraction of the species niches, the size of the niche occupied by each species during each sampling period was calculated and compared within and between species. To accomplish this, Bayesian standard ellipse areas (SEAb) were calculated, which allows for robust statistical comparisons (Jackson et al. 2011). The probability of Bayesian ellipses being larger or smaller relative to the compared group was computed as the proportion of ellipse one that was smaller than ellipse two. Two SEAb were considered to be significantly different when more that 95% of the posterior estimates of one group were smaller than those of another group (Jackson et al. 2011). Following this, the proportion of overlap among these ellipses within and between species was calculated. Niche overlap can vary between 0 (no overlap) and 1 (ellipse one is completely within ellipse two).

To track the movement of niches in time, the Euclidean distance (‰) and bearing (0 – 360°) between the centroids of the two-dimensional isotopic space of each year and season (i.e. autumn: 2015, 2016 and 2017 and summer: 2015/16, 2016/17 and 2017/18) were calculated for each species (Layman et al. 2007; Turner et al. 2010). The distance (path length) and direction of temporal isotopic shifts between autumns and between summers were independently compared between species by testing whether the differences in path length and direction between two species were statistically different against the null hypothesis that they do not differ from zero, through residual permutation procedure using 9999 permutations following Turner et al. (2010).

Results

On average, 18 ± 4 and 17 ± 4 samples were collected per species during autumn and summer of each of three years, respectively, representing 115 WA, 97 GHA, 94 SA, 20 LMSA, 117 NGP, 118 SGP, 111 KP, 53 GP, 112 MP, 111 ERP, 78 TRO and 91 GAZ samples (Supplementary Materials S3.1 and S3.2). Significant isotopic segregation was observed between species as well as movement of most species' niches across seasons and years (Figure 3.2, Supplementary Material S3.3). This was indicated by a significant interaction term between species and sampling period as shown by the perMANOVA and perANOVAs for both δ^{13}C and δ^{15}N values (Table 3.1; Figure 3.2; Supplementary Material S3.4).

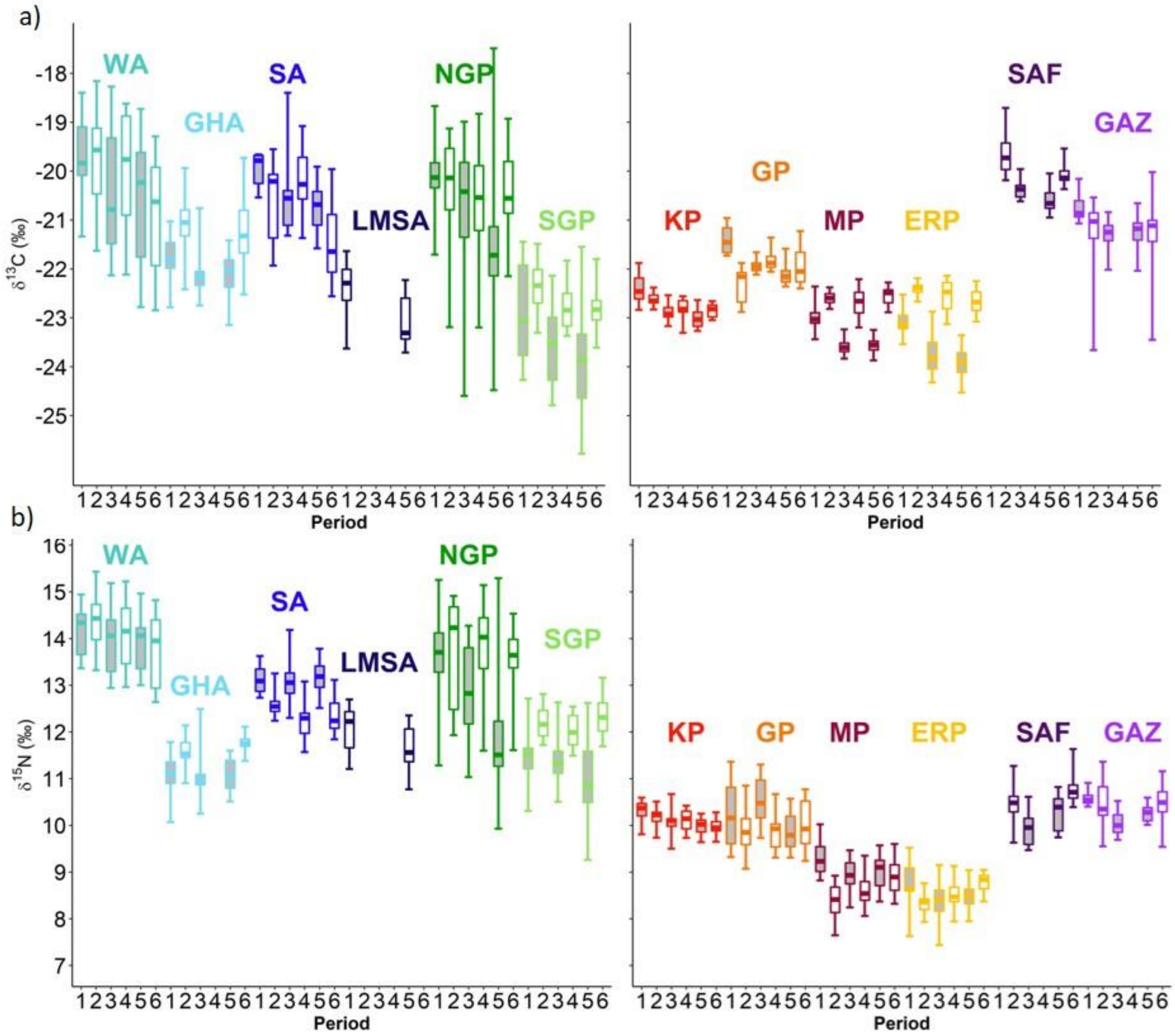


Figure 3.2. a) δ^{13}C and b) δ^{15}N blood values of flying (left; wandering (WA), grey-headed (GHA), sooty (SA) and light-mantled (LMSA) albatrosses, northern (NGP) and southern (SGP) giant petrels) and diving species (right; king (KP), gentoo (GP), macaroni (MP) and eastern rockhopper (ERP) penguins and Antarctic (GAZ) and sub-Antarctic (TRO) fur seals) breeding on Marion Island during three autumns (shaded, 1: 2015, 3: 2016, 5: 2017) and three summers (2: 2015/16, 4: 2016/17, 6: 2017/18). Values presented are median, 25% and 75% quartiles and range.

Seasonal dynamics of resource partitioning among marine predators

Overall, despite the niches occupied by individual species being variable between seasons (Figure 3.2; Supplementary Material S3.3), resource partitioning among species was maintained in both summer and autumn (Figure 3.3). This was evident by very low overlap between niches (proportional overlap < 0.01; Figure 3.3; Supplementary Material S3.3). The exceptions were the summer and autumn niches of the MP and ERP and the summer niches of the WA and NGP which consistently overlapped (Figure 3.3; Supplementary Material S3.4).

At the species level, the WA niches were most consistent between seasons, indicated by similar δ^{13}C and δ^{15}N blood values (Figure 3.2, Supplementary Material S3.5), Bayesian niche sizes (Figure 3.4) and consistently high overlap across seasons (Figures 3.3. and 3.5; Supplementary Material S3.6). The remaining species occupied almost completely different niches between autumn and summer as evidenced by a low overlap between the individual species' autumn and summer niches (Figure 3.5, proportional overlap: GHA, SA, SGP, ERP, MP and TRO < 0.1 and GP, KP, GAZ and NGP < 0.25; Supplementary Material S3.7) and different seasonal δ^{13}C and δ^{15}N values (Figure 3.2; Supplementary Material S3.4). The respective niche sizes of the GHA, SA, NGP and MP were consistently similar between autumn and summer whereas the SGP consistently occupied significantly smaller isotopic niches during summer compared to during autumn and vice versa for the isotopic niches of ERP and GAZ (Figures 3.4 and 3.5). The size of the KP, GP and TRO seasonal isotopic niches was variable however there was no clear size differences between the seasons (Figures 3.4 and 3.5).

For the majority of species (WA, GHA, NGP, SGP, KP and TRO), the movement of their niche centroids from summer to autumn correlated with a decrease in both δ^{13}C and δ^{15}N values (Figure 3.6), with few exceptions (MP, ERP, SA, GP and GAZ). The direction and distance movement by the MP and ERP niche centroids between seasons was consistent whereas the movement of the SA, GP and GAZ niche centroids was more variable (Figure 3.6). The results of the residual permutations, however, showed that species centroids moved in a consistent direction between seasons (Supplementary Material S3.8).

Table 3.1. Results of the a) permutational multivariate analysis of variance (perMANOVA) used to compare 12 seabird and fur seal species $\delta^{13}C$ and $\delta^{15}N$ blood values among different sampling periods (three consecutive autumns and summers 2015-2017/18) as well as results of the permutational analysis of variance (perANOVA) which compared species b) $\delta^{13}C$ and c) $\delta^{15}N$ blood values separately.

perMANOVA

a) ($\delta^{13}C$; $\delta^{15}N$) ~ species * sampling period + species + sampling period

Term	F-value	df	R^2	P-value
Species	639.84	11	0.82	<0.01
Sampling period	32.23	5	0.02	<0.01
Species*sampling period	6.17	47	0.03	<0.01

perANOVA

b) $\delta^{13}C$ ~ species * sampling period + species + sampling period

Term	P-value
Species	<0.01
Sampling period	<0.01
Species*sampling period	<0.01

perANOVA

c) $\delta^{15}N$ ~ species * sampling period + species + sampling period

Term	P-value
Species	<0.01
Sampling period	<0.01
Species*sampling period	<0.01

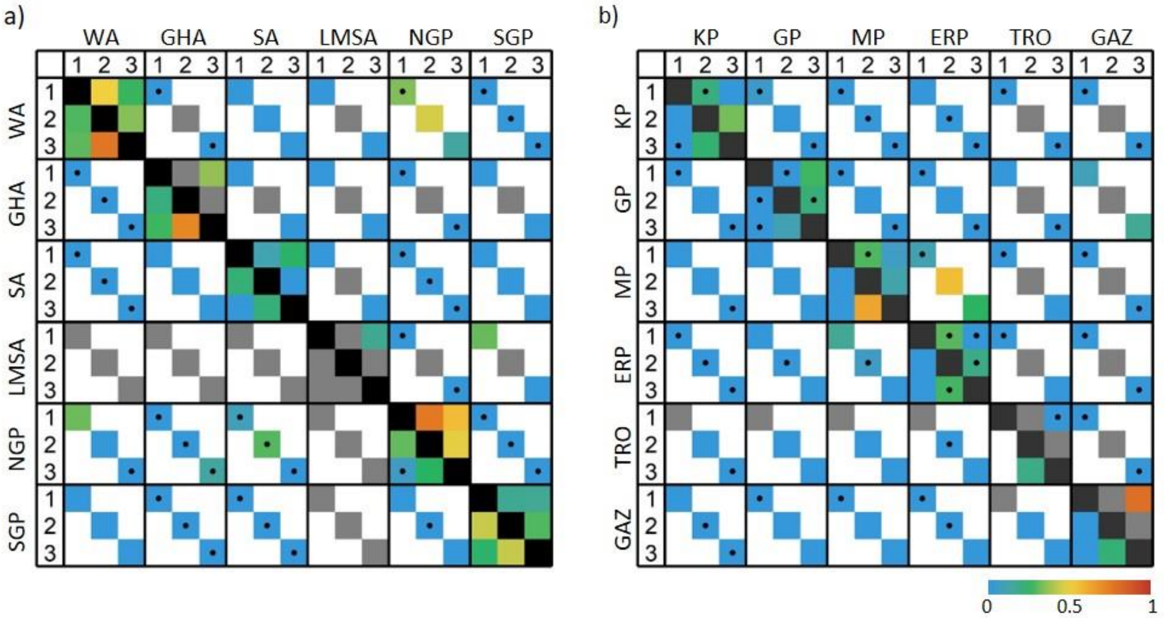


Figure 3.3. a) Proportional overlap of flying species' and b) diving species' isotopic niches (SEAc) between three consecutive autumns (lower diagonal, 1: 2015; 2: 2016; 3: 2017) and summers (upper diagonal, 1: 2015/16; 2: 2016/17; 3: 2017/18). The grey block indicates that there was no data for comparisons. Values of overlap are given in Supplementary Material S3.6. Dots indicate significant difference between sizes of niche space (SEAb). See Figure 3.2. for species abbreviations.

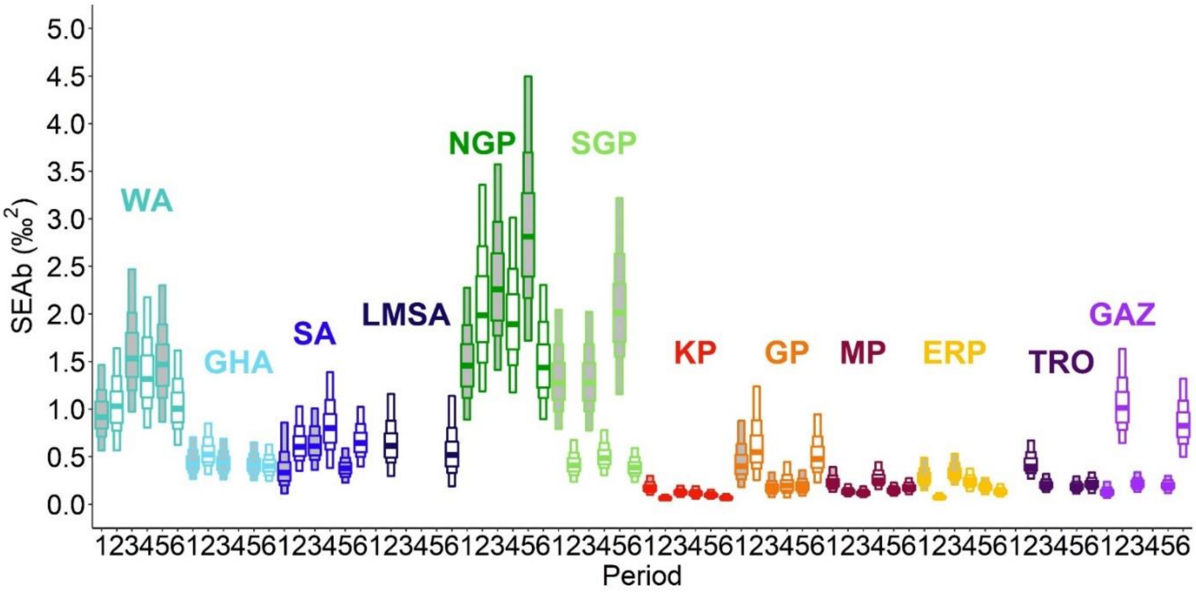


Figure 3.4. Bayesian isotopic niche area (SEAb) of 12 species of seabirds and fur seals on Marion Island during autumn (shaded, 1: 2015, 3: 2016, 5: 2017) and summer (2: 2015/16, 4: 2016/17, 6: 2017/18) over three consecutive years. See Figure 3.2. for species abbreviations.

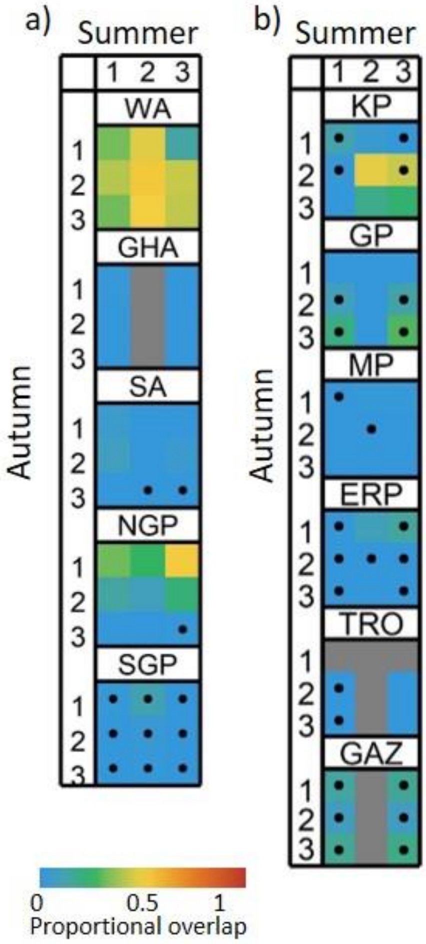


Figure 3.5. Proportional overlap among each species autumn (vertical, 1: 2015, 2: 2016, 3: 2017) and summer (horizontal, 1: 2015/16, 2: 2016/17, 3: 2017/18) isotopic niches separated for a) five flying species and b) six diving species. The grey block indicates that there was no data for comparisons. Values of overlap given in Supplementary Material S3.7. Dots indicate significant difference between sizes of niche space (SEAb). See Figure 3.2. for species abbreviations.

Interannual dynamics of resource partitioning among marine predators

The observed overlap or complete segregation of species' niches during either autumn or summer was mostly maintained across years (Figure 3.3), even though individual species seasonal niches varied significantly between years (Figure 3.2; Supplementary Material 3.3). This was evident by the significant change in species $\delta^{13}C$ and/or $\delta^{15}N$ values (Figure 3.2., Supplementary Material S3.4) and low between year overlap of most species seasonal niches (i.e. proportional overlap < 0.5) except for summer niches of the WA, NGP and GAZ (Figure 3.3). However, the sizes of the flying species' and fur seals' autumn and summer niches were consistent between years whereas the sizes of the penguin's niches varied significantly between years (Figures 3.3 and 3.4). Furthermore, larger distances were moved by the species' niche centroids between autumns (flying species range: 0.03 – 2.27 ‰; diving species: 0.06 – 0.82 ‰) compared to between summers (flying: 0.07 – 1.33 ‰; diving: 0.07 – 0.53 ‰; Figure 3.7).

Between summers, the isotopic niche centroid of all the species moved the furthest distance between 2015/16 and 2017/18, except for the centroids of the GHA, GAZ and MRP summer niches which moved the furthest distance between 2015/16 and 2016/17 (Figure 3.7). The $\delta^{13}C$ values of the WA, LMSA, SGP, KP, ERP and TRO summer isotopic niche centroids became progressively lower over the three years (Figure 3.6). The $\delta^{15}N$ values of the WA, LMSA and KP centroids also became progressively lower, while those of the ERP and TRO centroids became progressively higher (Figure 3.7). The $\delta^{15}N$ values of the GP and MP centroids increased as the summers progressed, with both species' centroids having lower $\delta^{13}C$ in summer 2017/18 than summer 2015/16 (Figure 3.7). There was no clear trend in the direction the remaining species (SA, GHA, NGP and GAZ) summer isotopic niche centroids moved between years (Figure 3.7). However, the distance and direction which all species' isotopic niche centroids moved between summers were statistically similar (Supplementary Material S3.9) with few exceptions.

A clear pattern emerged over the three years with declining autumn δ^{13}C and δ^{15}N values observed for most species (Figure 3.7). Exceptions to this trend were for the δ^{13}C and δ^{15}N values of the GHA, MP and GAZ which increased between 2016 and 2017 and the δ^{13}C and δ^{15}N values of the SA centroids between 2015 and 2017, the SA, ERP and TRO centroids between 2016 and 2017 and the GP centroid between 2015 and 2016 which decreased and increased, respectively. However, the results of the residual permutation procedures (Supplementary Material S3.10) showed that the direction and distance moved by the centroids of all species between autumn 2015 and 2016 were similar (Figure 3.7b and 3.7c).

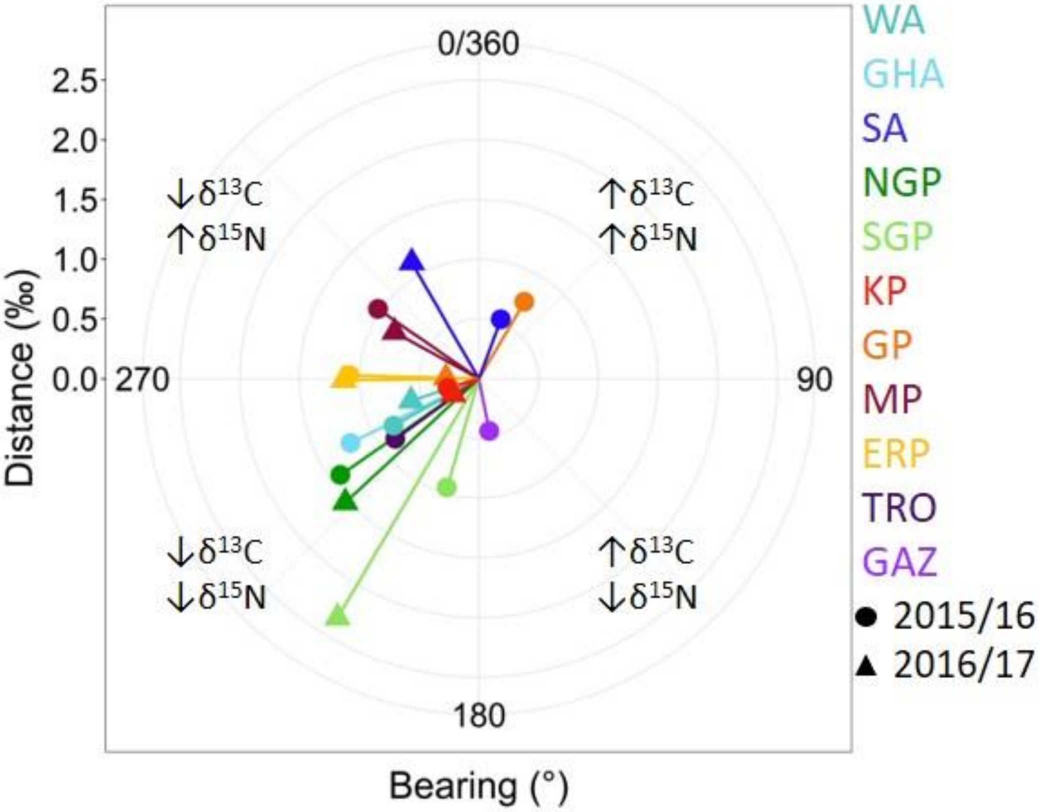


Figure 3.6. a) Distance and bearing the isotopic niche centroids of three albatross, all penguin and all fur seal species breeding on Marion Island moved between summer and autumn over two breeding seasons (2015/16 and 2016/17). See Figure 3.2. for species abbreviations.

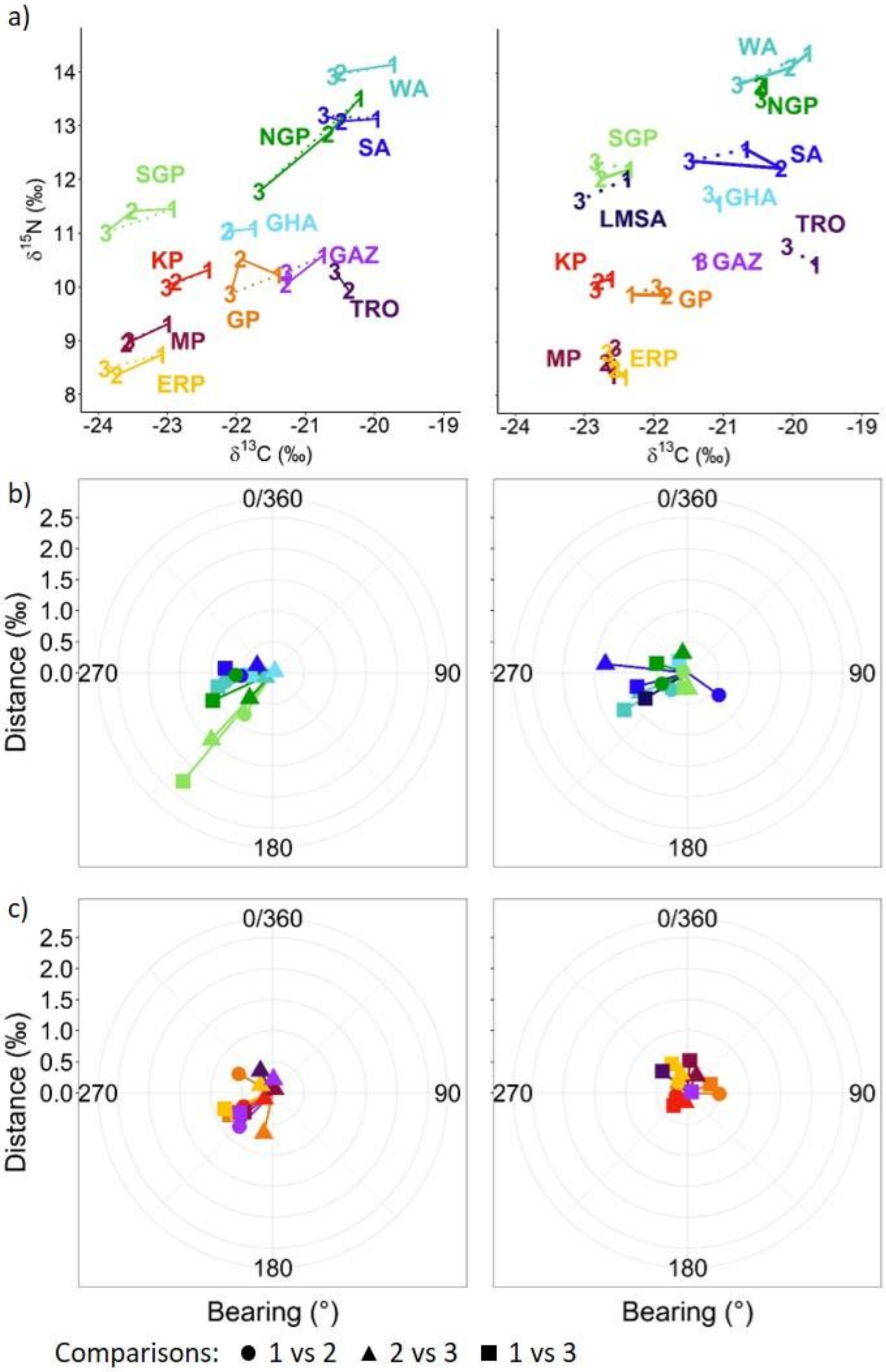


Figure 3.7. a) Trajectories of isotopic niche centroids of all albatross, penguin and fur seal species breeding on Marion Island over three autumns (left; 1: 2015, 2: 2016, 3:2017) and three summers (right, 1: 2015/16, 2: 2016/17, 3: 2017/18), separated by b) flying and c) diving species. See Figure 3.2. for species abbreviations.

Discussion

Using $\delta^{13}C$ and $\delta^{15}N$ whole blood values, we showed that there was significant variation in the seasonal and interannual isotopic niches of marine predators within different taxonomic group, however, resource partitioning within these taxonomic groups was maintained over time. Our results thus highlight two major factors driving the foraging behaviour of these animals. Firstly, most of these species have foraging behaviours that are either sufficiently flexible or general to cope with resources that are variable in space and time (Dehnhard et al. 2019; Riotte-Lambert and Matthiopoulos 2019). Secondly, whether due to historic or present competition for resources (Connell 1980), these predators have foraging strategies which minimize inter-specific overlap in food or foraging habitat preferences.

Temporal dynamics of marine predators' isotopic niches

The low overlap between predators' autumn and summer niches over the years shows that their foraging behaviour varies substantially between seasons, most likely due to differential foraging constraints associated with different life history phases. This is underscored by the fact that there was greater movement of niches between autumns compared to between summers. This is likely due to lower constraints on foraging range during autumn; that is niches were more variable year-to-year in autumn than in summer because species were better able to track dynamic oceanographic features. For example, the $\delta^{13}C$ values of the GHA and SA correlate to what is known about their seasonal foraging behaviour. While incubating (summer), the two albatross species forage primarily north of the island, reaching further distances than during chick rearing (autumn; Chapter 2; Phalan et al. 2007; Froy et al. 2015). However, while rearing a chick, GHA primarily forages south of the island (Nel et al. 2001), consuming Antarctic prey (Richoux et al. 2010; Connan et al. 2014). In constrast, SA keep foraging north of the island, consuming sub-tropical prey (Connan et al. 2014; Schoombie et al. 2017). The lower $\delta^{15}N$ blood values of GHA during autumn may be due to a switch in diet composition or feeding of a chick: GHA parents have been shown to provide higher trophic level and more nutritious prey to their offspring while digesting lower trophic level and less nutritious prey themselves (Richoux et al. 2010).

The seasonal niches of the study species were variable between years. This is likely a response to inter-annual environmental variation since prey switching based on temporal availability (Reisinger et al. 2018; Carpenter-Kling et al. 2019a) or foraging in more profitable habitats (Chapter 2; Kappes et al. 2010; Arthur et al. 2015) are common strategies in marine top predators. However, a relatively small inter-annual variability in isotopic niche space was found for the WA and KP. These are the only two species for which plasticity in foraging distribution (Bost et al. 2015; Pistorius et al. 2017) or diet composition (Adams and Klages 1987; Xavier et al. 2003) has not been observed. However, the relatively small niche space and low variation in $\delta^{13}C$ and $\delta^{15}N$ values of the KP, and contrastingly large niche space and variation in isotopic values of the WA, is typical of their foraging strategies. That is, the WA is a foraging habitat generalist, with an extensive foraging distribution (Pinaud and Weimerskirch 2007; Weimerskirch 2007) whereas the KP is a foraging habitat specialist, consistently targeting the Antarctic Polar front (Bost et al. 2015).

Maintenance of resource partitioning among predators over time

The maintenance of resource partitioning among the 12 predators indicates firstly that these predators may presently or historically be foraging in a resource limited environment and in order to maintain coexistence, they partition food resources (Jaeger et al. 2013; Pickett et al. 2018). Secondly, although prey distribution within this area of the ocean is characteristically variable in space and time (Trathan et al. 2007; Lévy et al. 2015), resource distribution is likely predictable as predators were able to successfully maintain seasonal resource partitioning over years. For example, Dehnhard et al. (2020), found evidence of little to no resource partitioning among three sympatric fulmarine species breeding in Antarctica across the annual cycle. The authors explained that this lack of partitioning among the three closely related species was linked to the highly productive but highly spatio-temporally variable (i.e. unpredictable) nature of their environment. They hypothesised that the observed generalist foraging behaviour of these birds evolved to maximize prey encounter in this ‘unpredictable’ environment, even though it most likely increased the potential for competition within and among sympatric species. Furthermore, some studies suggest that due to the super abundance of Antarctic krill *Euphausia superba* in Antarctic waters, their predators may not have to partition their diet and foraging habitats in order to avoid competitive exclusion (Croxall et al. 1997; Jaeger et al. 2013). The clear segregation among predators' niches in this study indicates that resources are presently or have been historically not in abundance and limited, as found for other sub-Antarctic islands (Cherel et al. 2007; Jaeger et al. 2010; Navarro et al. 2013; Bodey et al. 2014).

The foraging habitat used by the mollymawks (i.e. GHA, SA and LMSA) breeding on Marion Island was shown to become decreasingly variable from summer 2015/16 to 2017/18, potentially due to deteriorating foraging conditions (Chapter 2). However, here we showed that the size of the mollymawks' isotopic niches remained similar, which corresponds to a similar variance in foraging habitat use and prey eaten during the study period. This may be explained by the 2 – 4 weeks integration time of dietary information into whole blood of seabirds (Cherel and Hobson 1992; Bearhop et al. 2002). Chapter 2 examined a single foraging trip (approximately 2 weeks long) towards the end of incubation of each animal. Individual GHA (Xavier et al. 2003, 2013) and LMSA (Phillips et al. 2005) have been shown to vary their diet and use of foraging habitat during the same breeding stage, switching to temporally more productive foraging areas. Therefore, the blood isotopic values of the GHA, LMSA and SA may have captured the initial 'exploratory' foraging trip where the mollymawks may have foraged in sub-optimal foraging habitats before switching to a more productive one (Riotte-Lambert and Matthiopoulos 2019).

Presumably linked to the prey's temporal availability, the dominant prey species in diet of the GP, MP and ERP breeding at Marion island switches between allochthonous pelagic crustaceans, such as *Euphausia vallentini* and *Thysanoessa vicina*, to the autochthonous benthic crustacean*, Nauticaris marionis* or to consuming more fish (Brown and Klages 1987; Adams and Brown 1989; Carpenter-Kling et al. 2019a). Due to the relatively large populations of MP and ERP breeding on Marion Island (Crawford et al. 2003, 2006), and similarities in their diet composition it was expected that these three penguin species would compete for resources during summer. However, the GP is a diet generalist (Lescroël et al. 2004; Carpenter-Kling et al. 2019a) and during summer, unlike the MP and ERP, they do not have the additional energy demands of a chick. Thus, we expected the GP to be more flexible in terms of diet compared to that of the MP and ERP. Horswill et al. (2016) showed that in response to low prey availability, MP breeding on Bird Island, South Georgia increased the variability in their resource use and thus the size of their realized niches. If the same holds for MP breeding on Marion Island, the congruent increase in the size of the MP and ERP isotopic niches during summers 2015/16 and 2017/18 may have been in response to decreased prey availability. In addition, as these three penguins forage for similar prey, the increase in size of the GP isotopic niches (i.e. increased variation in resource use) during summers 2015/16 and 2017/18 may have also been to minimize interspecific resource competition with the two crested penguins during a period of relatively low prey abundance.

Previously, high overlap and congruent composition shifts in the diet of the two fur seals between years and seasons has been shown (Reisinger et al. 2018), despite GAZ having weaned that season's offspring by autumn while TRO is still caring for dependent young (Bester and Bartlett 1990). Wege et al. (2019), however, showed that, while breeding, the two fur seal species did not use all foraging habitat available to them and suggested that this was possible to reduce at sea interactions between the two ecologically similar species. Our findings agree with that of Reisinger et al. (2018) and Wege et al. (2019) as we found complete and maintained segregation of the fur seals' isotopic niches which was mainly driven by large differences in their δ^{13}C values (i.e. difference foraging habitat use) and not δ^{15}N values (i.e. trophic level), even though there was significant movement of their isotopic niches between years and seasons. We did, however, expect some overlap between the isotopic niches of the KP and fur seals as their diets are dominated by myctophid fishes (Adams and Klages 1987; Reisinger et al. 2018). This lack of overlap may be due to differences in species-specific discrimination factors which may offset a consumer's isotopic values from baseline values (Shipley and Matich 2020), thus allowing for limited comparison of δ^{13}C and δ^{15}N tissue values between taxonomic groups.

Is there evidence for a shift in baseline isotopic gradients?

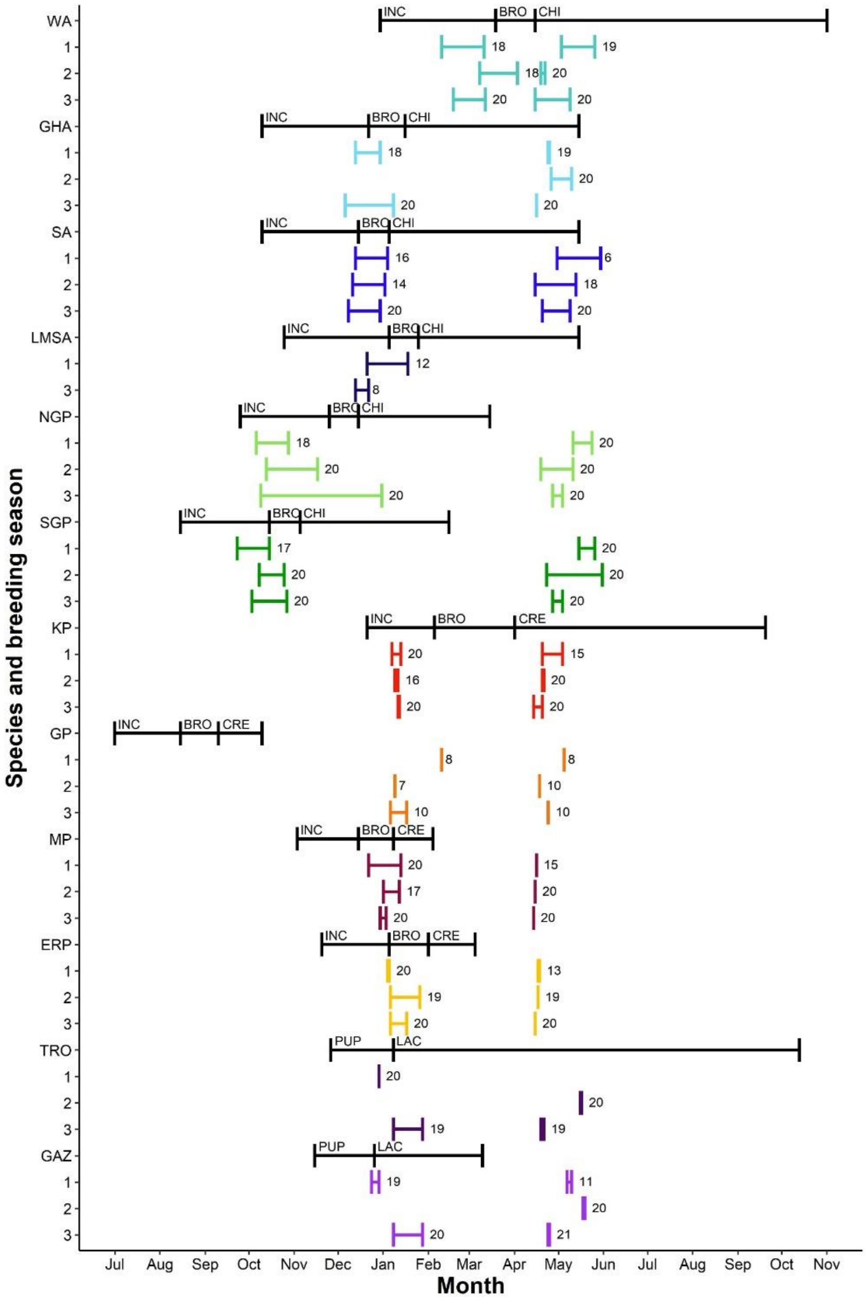
The congruent declines in the δ^{13}C and δ^{15}N blood values of multiple species suggest a possible shift in the isotopic gradients at the base of the food web, as found by Ramos et al. (2020) and Tarroux et al. (2018). However, only the species which are known to forage within (KP; Bost et al. 2015; Pistorius et al. 2017) or below (MP and ERP autumn only; SGP, LMSA, WA and GHA; Nel et al. 2001, 2002; Whitehead et al. 2016; Reisinger et al. In press; Chapter 2) the Antarctic Polar Front exhibited progressively lower δ^{13}C values. This coincided with the Antarctic Polar Front flowing closer to the Prince Edward Archipelago as the years progressed (March (autumn) 2015: 49.6 °S, 2016: 49.5 °S, 2017: 49.2 °S (10.6 km) and November (summer): 2015: 49.4 °S, 2016: 49.6 °S, 2017/18: 48.4 °S (77.9 km); Chapter 2). Since travelling time to waters south of the Antarctic Polar Front should be inversely correlated with the time spent foraging south of that front, the movement of the Antarctic Polar Front is likely a driver behind the progressively more negative δ^{13}C values of SGP, LMSA, WA and GHA as well as autumn δ^{13}C values of the MP and ERP. Further evidence to support this was that the NGP and SA, which are known to forage almost exclusively north of Marion Island during summer (Schoombie et al. 2017; Reisinger et al. In press), did not share this declining pattern in their summer δ^{13}C blood values. Instead, the SA summer δ^{13}C blood values followed the movement of core foraging areas found in Chapter 2, i.e. the key foraging area of the SA was found closer to Marion Island in 2015/16 and 2017/18, and further north in 2016/17.

Although we argue that there was no shift in the baseline isotopic gradients, this confounding factor in the stable isotopic composition of marine predator tissue values is rarely considered. Spatial gradient of δ^{13}C and δ^{15}N values of organisms at the base of the food web are dynamic and respond quickly to fluctuating environmental variability (e.g. Kurle and McWhorter 2017; Magozzi et al. 2017). Interestingly, the monthly isoscapes produced by Magozzi et al. (2017) showed a stronger latitudinal gradient of phytoplankton δ^{13}C values during summer, with higher and lower values evident between South Africa and Antarctica, respectively, compared to autumn. However, the δ^{13}C blood values of most predators decreased between summer and autumn, even though the regional baseline isoscape was more positive. Therefore, although temporal variability in baseline isotopic gradients most likely introduces some variance into predators' tissues isotopic compositions (Chapters 4 and 5), it seems unlikely to be driving the patterns we observed. Future investigation should combine fine-scale logging devices (such as GPS loggers) and stable isotope analysis to further elucidate possible influences of temporal changes in the baseline isotopic gradients on marine predator tissue composition (e.g. Chapters 4 and 5; Trueman et al. 2019).

Conclusions

Here, we have provided evidence towards both of our hypotheses. We showed that the 12 species' trophic niches were dynamic seasonally due to seasonal foraging constraints as well as dynamic at the interannual scale most likely due to environmental variability which is assumedly correlated to spatio-temporal variability in the distribution of their prey. Importantly, we provided clear evidence that resource partitioning within taxonomic groups was maintained despite the evident dynamic foraging behaviour of the predators. This is consistent with the prediction of the classical niche theory (Hutchinson 1957; Pianka 1974; Schoener 1974) which predicts that during periods of relative food scarcity, animals will adjust their foraging behaviour to decrease interspecific competition. However, the consistent partitioning of resources among the predators over all three years indicates that the resources of these predators are either historically or presently limited and their coexistence is promoted by partitioning along their trophic axes of their ecological niche. This has important consequences for those studies which aim to predict distributional changes of species considering predicted changes in climate (e.g. Hindell et al. 2020; Somveille et al. 2020). Indeed, the majority of these investigations only investigate the environmental factors/ axes which influences a species distribution and rarely incorporate the influence of interspecific interactions.

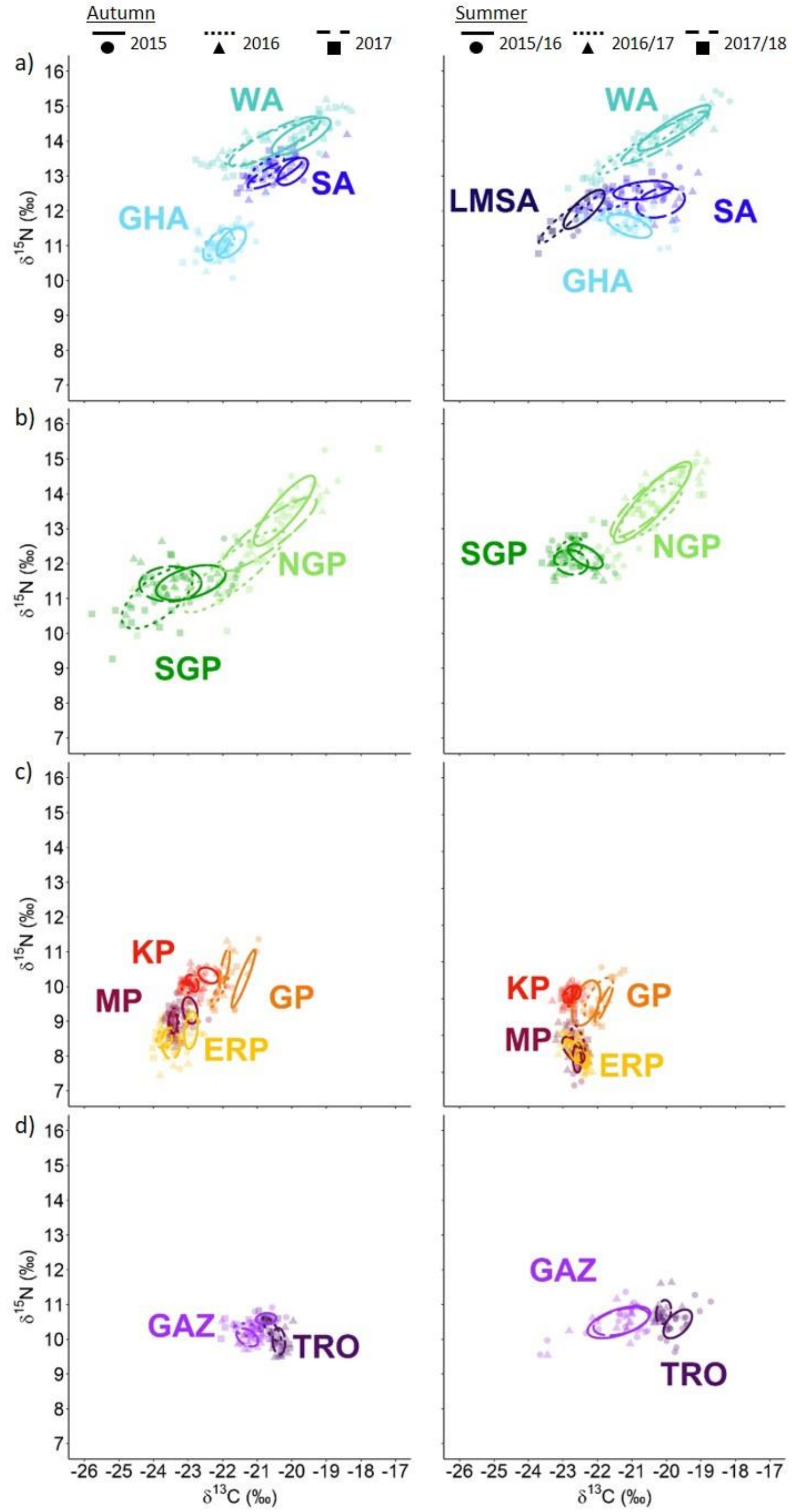
Supplementary Material



Supplementary Material S3.1. Approximate incubation (INC), brooding (BRO), chick rearing (CHI), chick créching (CRE), pupping (PUP) and lactation (LAC) periods and two periods when individuals (number sampled next to period) of wandering (WA; Jones et al. 2016), grey-headed (GHA; FitzPatrick unpubl. data; Tickell and Pinder 1975), sooty and light-mantled (SA and LMSA; Berruti 1979; Schoombie et al. 2016) albatrosses, northern and southern giant petrels (NGP and SGP; Cooper et al. 2001), king (KP; du Plessis et al 1994; Charrassin and Bost 2001), gentoo (GP; Crawford et al. 2003), macaroni and eastern rockhopper (MP and ERP; Crawford et al. 2006) penguins and sub-Antarctic and Antarctic (TRO and GAZ; Kerley 1983; Hofmeyr et al. 2007) fur seals breeding on Marion Island over three consecutive years (1: 2015/16, 2: 2016/17 and 3: 2017/18).

Supplementary Material S3.2. δ^{13}C and δ^{15}N whole blood values and corresponding C:N ratios of 12 marine predators breeding on Marion Island over three years (2015 – 2017) during autumn and summer. "-" indicates no data. Mean ± SD (range) values are given.

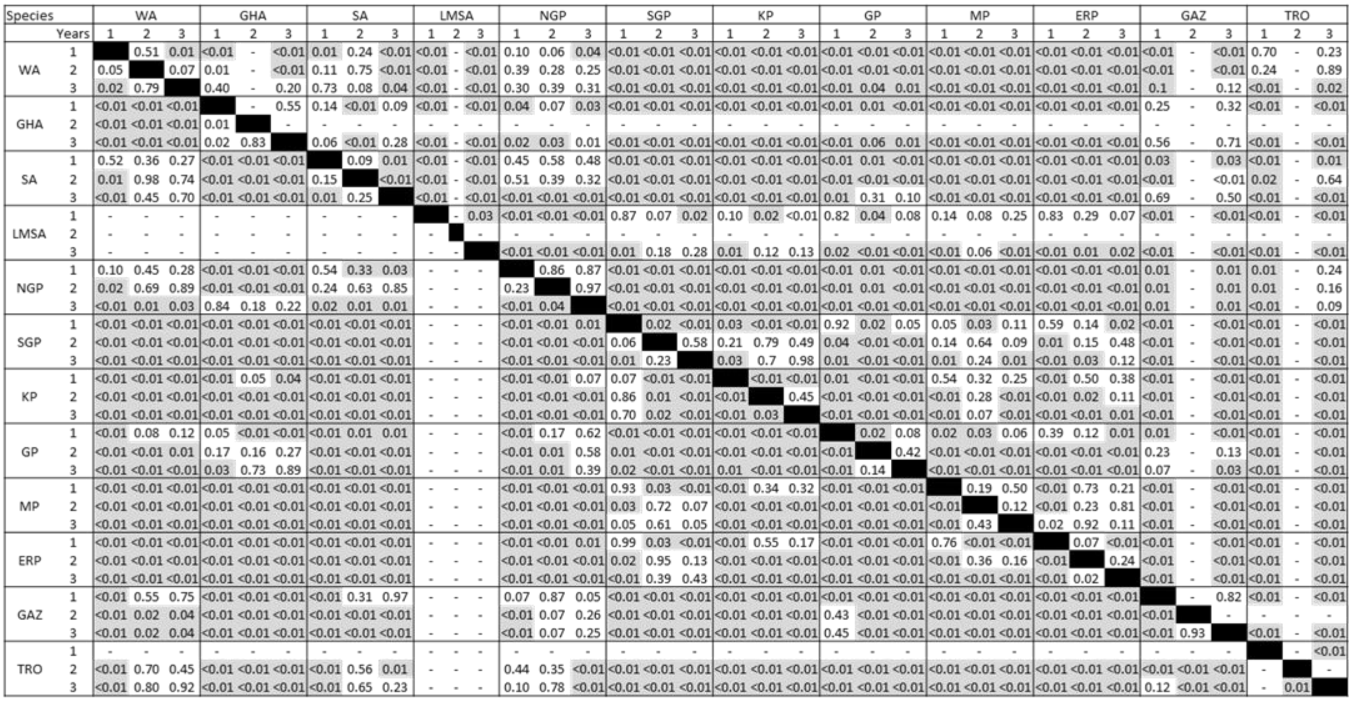
	Autumn					Summer				
Species	Year	n	δ^{13}C	δ^{15}N	C:N ratio	Year	n	δ^{13}C	δ^{15}N	C:N ratio
Albatrosses										
Wandering	2015	19	-19.7 ± 0.8 (-21.3; -18.4)	14.1 ± 0.5 (13.4; 14.9)	3.4 ± 0.0 (3.3; 3.4)	2015/16	18	-19.8 ± 1.0 (-21.6; -18.2)	14.4 ± 0.6 (13.3; 15.4)	3.4 ± 0.0 (3.3; 3.5)
	2016	20	-20.5 ± 1.3 (-22.1; -18.3)	14.0 ± 0.7 (12.9; 15.2)	3.4 ± 0.0 (3.3; 3.4)	2016/17	18	-20.0 ± 1.2 (-22.1; -18.6)	14.1 ± 0.7 (13.0; 15.2)	3.3 ± 0.0 (3.2; 3.4)
	2017	20	-20.6 ± 1.3 (-22.8; -18.7)	13.9 ± 0.6 (13.0; 15.0)	3.3 ± 0.0 (3.2; 3.4)	2017/18	20	-20.8 ± 1.1 (-22.9; -19.3)	13.8 ± 0.7 (12.6; 14.8)	3.6 ± 0.6 (3.1; 4.5)
Sooty	2015	6	-20.0 ± 0.4 (-20.5; -19.7)	13.1 ± 0.3 (12.7; 13.6)	3.4 ± 0.1 (3.3; 3.5)	2015/16	16	-20.7 ± 0.8 (-21.9; -19.6)	12.6 ± 0.3 (12.2; 13.2)	3.3 ± 0.0 (3.2; 3.4)
	2016	18	-20.5 ± 0.8 (-21.3; -18.4)	13.1 ± 0.4 (12.3; 14.2)	3.4 ± 0.1 (3.3; 3.5)	2016/17	14	-20.2 ± 0.7 (-21.4; -19.1)	12.2 ± 0.4 (11.6; 13.1)	3.4 ± 0.1 (3.3; 3.5)
	2017	20	-20.7 ± 0.5 (-21.6; -19.9)	13.2 ± 0.4 (12.5; 13.8)	3.4 ± 0.1 (3.2; 3.5)	2017/18	20	-21.5 ± 0.8 (-22.6; -20.0)	12.4 ± 0.4 (11.8; 13.1)	3.3 ± 0.0 (3.2; 3.3)
Grey-headed	2015	19	-21.7 ± 0.4 (-22.8; -21.0)	11.1 ± 0.4 (10.1; 11.8)	3.2 ± 0.0 (3.1; 3.3)	2015/16	18	-21.1 ± 0.6 (-22.4; -19.9)	11.6 ± 0.3 (10.9; 12.1)	3.4 ± 0.0 (3.4; 3.6)
	2016	20	-22.1 ± 0.4 (-22.8; -20.8)	11.0 ± 0.4 (10.2; 12.5)	3.3 ± 0.1 (3.2; 3.4)	2016/17		-	-	-
	2017	20	-22.1 ± 0.4 (-23.1; -21.4)	11.1 ± 0.3 (10.5; 11.6)	3.2 ± 0.0 (3.2; 3.3)	2017/18	20	-21.2 ± 0.7 (-22.5; -19.7)	11.8 ± 0.2 (11.4; 12.1)	4.0 ± 0.7 (3.2; 4.7)
Light-mantled	2015		-	-	-	2015/16	12	-22.4 ± 0.6 (-23.6; -21.6)	12.0 ± 0.5 (11.2; 12.7)	3.3 ± 0.1 (3.2; 3.4)
	2016		-	-	-	2016/17		-	-	-
	2017		-	-	-	2017/18	8	-23.1 ± 0.6 (-23.7; -22.2)	11.6 ± 0.5 (10.8; 12.3)	3.2 ± 0.0 (3.2; 3.3)
Giant petrels										
Northern	2015	20	-20.2 ± 0.9 (-21.7; -18.7)	13.5 ± 1.0 (11.3; 15.2)	3.4 ± 0.0 (3.4; 3.6)	2015/16	17	-20.4 ± 1.1 (-23.2; -19.1)	13.8 ± 1.1 (11.9; 14.9)	3.4 ± 0.0 (3.4; 3.5)
	2016	20	-20.7 ± 1.3 (-24.6; -19.0)	12.8 ± 1.0 (11.0; 14.3)	3.4 ± 0.0 (3.3; 3.5)	2016/17	20	-20.5 ± 1.1 (-23.2; -18.8)	13.8 ± 1.0 (11.6; 15.1)	3.4 ± 0.0 (3.3; 3.5)
	2017	20	-21.7 ± 1.4 (-24.5; -17.5)	11.8 ± 1.2 (9.9; 15.3)	3.4 ± 0.0 (3.3; 3.4)	2017/18	20	-20.5 ± 0.9 (-22.1; -18.9)	13.5 ± 0.8 (11.6; 14.5)	3.5 ± 0.1 (3.4; 3.7)
Southern	2015	20	-22.9 ± 1.0 (-24.3; -21.4)	11.5 ± 0.5 (10.3; 12.7)	3.4 ± 0.0 (3.3; 3.4)	2015/16	18	-22.4 ± 0.5 (-23.3; -21.5)	12.2 ± 0.3 (11.7; 12.8)	3.4 ± 0.0 (3.3; 3.4)
	2016	20	-23.5 ± 0.9 (-24.8; -22.1)	11.4 ± 0.5 (10.5; 12.6)	3.4 ± 0.0 (3.4; 3.5)	2016/17	20	-22.8 ± 0.5 (-23.4; -21.8)	12.0 ± 0.3 (11.5; 12.5)	3.4 ± 0.0 (3.3; 3.4)
	2017	20	-23.9 ± 1.0 (-25.8; -21.6)	11.0 ± 0.8 (9.3; 12.6)	3.4 ± 0.1 (3.4; 3.6)	2017/18	20	-22.8 ± 0.4 (-23.6; -21.8)	12.4 ± 0.4 (11.7; 13.2)	3.4 ± 0.0 (3.3; 3.4)
Penguins										
King	2015	15	-22.4 ± 0.3 (-22.8; -21.9)	10.3 ± 0.2 (9.8; 10.6)	3.3 ± 0.1 (3.2; 3.4)	2015/16	20	-22.6 ± 0.1 (-22.8; -22.4)	10.2 ± 0.2 (9.7; 10.5)	3.3 ± 0.0 (3.3; 3.4)
	2016	20	-22.9 ± 0.2 (-23.2; -22.5)	10.1 ± 0.2 (9.5; 10.7)	3.3 ± 0.0 (3.3; 3.4)	2016/17	16	-22.8 ± 0.2 (-23.3; -22.6)	10.1 ± 0.2 (9.7; 10.4)	3.4 ± 0.0 (3.3; 3.4)
	2017	20	-23.0 ± 0.2 (-23.3; -22.6)	10.0 ± 0.2 (9.6; 10.2)	3.3 ± 0.0 (3.3; 3.4)	2017/18	20	-22.8 ± 0.1 (-23.1; -22.7)	10.0 ± 0.2 (9.7; 10.3)	3.3 ± 0.0 (3.3; 3.4)
Gentoo	2015	8	-21.4 ± 0.3 (-21.7; -21.0)	10.2 ± 0.8 (9.3; 11.4)	3.2 ± 0.0 (3.2; 3.3)	2015/16	8	-22.3 ± 0.4 (-22.9; -21.9)	9.9 ± 0.6 (9.1; 10.8)	3.6 ± 0.4 (3.3; 4.6)
	2016	10	-21.9 ± 0.1 (-22.1; -21.7)	10.5 ± 0.5 (9.7; 11.3)	3.4 ± 0.0 (3.3; 3.4)	2016/17	7	-21.8 ± 0.2 (-22.1; -21.4)	9.9 ± 0.5 (9.3; 10.7)	3.3 ± 0.0 (3.2; 3.3)
	2017	10	-22.1 ± 0.2 (-22.4; -21.6)	9.9 ± 0.4 (9.3; 10.6)	3.2 ± 0.0 (3.1; 3.2)	2017/18	10	-22.0 ± 0.4 (-22.4; -21.2)	10.0 ± 0.5 (9.2; 10.8)	3.3 ± 0.0 (3.3; 3.3)
Macaroni	2015	15	-22.9 ± 0.2 (-23.3; -22.4)	9.3 ± 0.4 (8.8; 10.0)	3.4 ± 0.1 (3.2; 3.6)	2015/16	20	-22.6 ± 0.1 (-22.8; -22.4)	8.4 ± 0.4 (7.6; 8.9)	3.3 ± 0.0 (3.2; 3.4)
	2016	20	-23.4 ± 0.1 (-23.7; -23.2)	9.0 ± 0.3 (8.2; 9.5)	3.5 ± 0.1 (3.4; 3.7)	2016/17	17	-22.7 ± 0.3 (-23.2; -22.2)	8.6 ± 0.3 (8.1; 9.3)	3.3 ± 0.0 (3.3; 3.4)
	2017	20	-23.4 ± 0.1 (-23.7; -23.2)	9.0 ± 0.4 (8.4; 9.6)	3.5 ± 0.1 (3.4; 3.7)	2017/18	20	-22.6 ± 0.2 (-22.9; -22.3)	8.9 ± 0.4 (8.3; 9.6)	3.4 ± 0.1 (3.2; 3.5)
Rockhopper	2015	13	-22.9 ± 0.2 (-23.2; -22.5)	8.7 ± 0.5 (7.6; 9.5)	3.5 ± 0.1 (3.3; 3.7)	2015/16	20	-22.4 ± 0.1 (-22.7; -22.2)	8.3 ± 0.2 (7.9; 8.8)	3.4 ± 0.0 (3.3; 3.4)
	2016	19	-23.5 ± 0.3 (-23.8; -23.0)	8.4 ± 0.4 (7.4; 9.1)	3.6 ± 0.2 (3.2; 3.9)	2016/17	19	-22.6 ± 0.3 (-23.1; -22.1)	8.5 ± 0.3 (7.9; 9.1)	3.4 ± 0.1 (3.2; 3.5)
	2017	20	-23.7 ± 0.2 (-24.0; -23.2)	8.5 ± 0.3 (8.0; 9.0)	3.6 ± 0.1 (3.3; 3.9)	2017/18	20	-22.7 ± 0.2 (-23.1; -22.2)	8.8 ± 0.2 (8.4; 9.1)	3.7 ± 0.6 (3.3; 4.8)
Fur seals										
Sub-Antarctic	2015		-	-	-	2015/16	20	-19.7 ± 0.4 (-20.2; -18.7)	10.4 ± 0.4 (9.6; 11.3)	3.5 ± 0.0 (3.4; 3.5)
	2016	20	-20.4 ± 0.2 (-20.6; -20.0)	9.9 ± 0.4 (9.5; 10.6)	3.4 ± 0.0 (3.3; 3.5)	2016/17		-	-	-
	2017	19	-20.6 ± 0.3 (-20.9; -20.1)	10.3 ± 0.4 (9.7; 10.8)	3.4 ± 0.0 (3.3; 3.5)	2017/18	19	-20.1 ± 0.2 (-20.4; -19.5)	10.8 ± 0.3 (10.4; 11.6)	3.3 ± 0.0 (3.3; 3.4)
Antarctic	2015	11	-20.7 ± 0.3 (-21.1; -20.2)	10.6 ± 0.2 (10.4; 10.9)	3.4 ± 0.0 (3.3; 3.4)	2015/16	19	-21.4 ± 0.9 (-23.7; -20.5)	10.5 ± 0.4 (9.6; 11.4)	3.5 ± 0.0 (3.4; 3.5)
	2016	20	-21.3 ± 0.3 (-22.0; -20.8)	10.0 ± 0.3 (9.7; 10.5)	3.4 ± 0.0 (3.3; 3.4)	2016/17		-	-	-
	2017	21	-21.3 ± 0.4 (-22.0; -20.7)	10.3 ± 0.2 (10.0; 10.6)	3.5 ± 0.0 (3.4; 3.5)	2017/18	20	-21.3 ± 0.8 (-23.4; -20.0)	10.5 ± 0.4 (9.5; 11.2)	3.5 ± 0.5 (3.2; 4.7)



Supplementary Material S3.3. Standard ellipse areas corrected for small sample size (SEAc) calculated from the $\delta^{13}C$ and $\delta^{15}N$ blood values of a) wandering (WA), grey-headed (GHA), sooty (SA) and light-mantled (LMSA) albatrosses, b) northern (NGP) and southern (SGP) giant petrels, c) king (KP), gentoo (GP), macaroni (MP) and eastern rockhopper (ERP) penguins and d) Antarctic (GAZ) and sub-Antarctic (TRO) fur seals breeding on Marion Island over three years (2015 – 2018) during autumn (left) and summer (right).

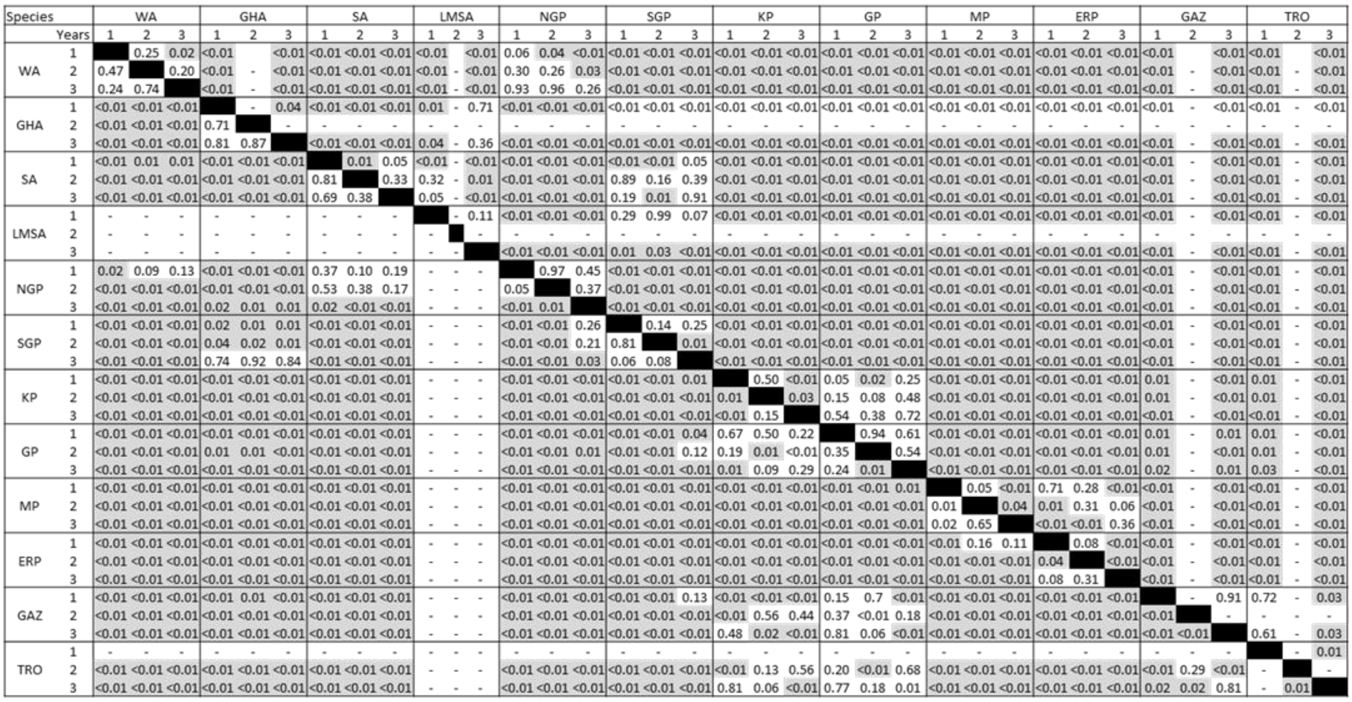
Supplementary Material S3.4. Comparison of 12 seabirds and fur seals a) δ^{13}C and b) δ^{15}N blood values between three consecutive autumns (1: 2015, 2: 2016, 3: 2017, lower diagonal) and between summers (1: 2015/16, 2: 2016/17; 3: 2017/18, upper diagonal), separately. Values reported are the resulting p-values of post-hoc pairwise permutational tests with false discovery rate corrections for multiple comparisons. See Supplementary Material S3.1. for species abbreviations.

a)



Species		WA			GHA			SA			LMSA			NGP			SGP			KP			GP			MP			ERP			GAZ			TRO		
	Years	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
WA	1		0.51	0.01	<0.01	-	<0.01	0.01	0.24	<0.01	<0.01	-	<0.01	0.10	0.06	0.04	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	0.70	-	0.23
	2	0.05		0.07	0.01	-	<0.01	0.11	0.75	<0.01	<0.01	-	<0.01	0.39	0.28	0.25	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	0.24	-	0.89
	3	0.02	0.79		0.40	-	0.20	0.73	0.08	0.04	<0.01	-	<0.01	0.30	0.39	0.31	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.04	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.1	-	0.12	<0.01	-	0.02
GHA	1	<0.01	<0.01	<0.01		-	0.55	0.14	<0.01	0.09	<0.01	-	<0.01	0.04	0.07	0.03	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.25	-	0.32	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	0.01		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	<0.01	<0.01	<0.01	0.02	0.83		0.06	<0.01	0.28	<0.01	-	<0.01	0.02	0.03	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.06	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.56	-	0.71	<0.01	-	<0.01
SA	1	0.52	0.36	0.27	<0.01	<0.01	<0.01		0.09	0.01	<0.01	-	<0.01	0.45	0.58	0.48	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.03	-	0.03	<0.01	-	0.01
	2	0.01	0.98	0.74	<0.01	<0.01	<0.01	0.15		<0.01	<0.01	-	<0.01	0.51	0.39	0.32	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	0.02	-	0.64
	3	<0.01	0.45	0.70	<0.01	<0.01	<0.01	0.01	0.25		<0.01	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	0.31	0.10	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.69	-	0.50	<0.01	-	<0.01
LMSA	1	-	-	-	-	-	-	-	-	-		-	0.03	<0.01	<0.01	<0.01	0.87	0.07	0.02	0.10	0.02	<0.01	0.82	0.04	0.08	0.14	0.08	0.25	0.83	0.29	0.07	<0.01	-	<0.01	<0.01	-	<0.01
	2	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-		<0.01	<0.01	<0.01	0.01	0.18	0.28	0.01	0.12	0.13	0.02	<0.01	<0.01	<0.01	0.06	<0.01	<0.01	0.01	0.02	<0.01	-	<0.01	<0.01	-	<0.01
NGP	1	0.10	0.45	0.28	<0.01	<0.01	<0.01	0.54	0.33	0.03	-	-	-		0.86	0.87	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	-	0.01	0.01	-	0.24
	2	0.02	0.69	0.89	<0.01	<0.01	<0.01	0.24	0.63	0.85	-	-	-	0.23		0.97	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	-	0.01	0.01	-	0.16
	3	<0.01	0.01	0.03	0.84	0.18	0.22	0.02	0.01	0.01	-	-	-	<0.01	0.04		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	-	0.01	<0.01	-	0.09
SGP	1	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	0.01		0.02	<0.01	0.03	<0.01	<0.01	0.92	0.02	0.05	0.05	0.03	0.11	0.59	0.14	0.02	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	0.06		0.58	0.21	0.79	0.49	0.04	<0.01	<0.01	0.14	0.64	0.09	0.01	0.15	0.48	<0.01	-	<0.01	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	0.01	0.23		0.03	0.7	0.98	0.01	<0.01	<0.01	0.01	0.24	0.01	<0.01	0.03	0.12	<0.01	-	<0.01	<0.01	-	<0.01
KP	1	<0.01	<0.01	<0.01	<0.01	0.05	0.04	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	0.07	0.07	<0.01	<0.01		<0.01	<0.01	0.01	<0.01	<0.01	0.54	0.32	0.25	<0.01	0.50	0.38	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	0.86	0.01	<0.01	<0.01		0.45	<0.01	<0.01	<0.01	<0.01	0.28	<0.01	<0.01	0.02	0.11	<0.01	-	<0.01	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	0.70	0.02	<0.01	<0.01	0.03		<0.01	<0.01	<0.01	<0.01	0.07	<0.01	<0.01	<0.01	0.01	<0.01	-	<0.01	<0.01	-	<0.01
GP	1	<0.01	0.08	0.12	0.05	<0.01	<0.01	<0.01	0.01	0.01	-	-	-	<0.01	0.17	0.62	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		0.02	0.08	0.02	0.03	0.06	0.39	0.12	0.01	0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	0.01	0.17	0.16	0.27	<0.01	<0.01	<0.01	-	-	-	<0.01	0.01	0.58	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		0.42	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.23	-	0.13	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	0.03	0.73	0.89	<0.01	<0.01	<0.01	-	-	-	<0.01	0.01	0.39	0.02	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	0.14		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.07	-	0.03	<0.01	-	<0.01
MP	1	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	0.93	0.03	<0.01	<0.01	0.34	0.32	<0.01	<0.01	<0.01		0.19	0.50	<0.01	0.73	0.21	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	0.03	0.72	0.07	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		0.12	<0.01	0.23	0.81	<0.01	-	<0.01	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	0.05	0.61	0.05	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.43		0.02	0.92	0.11	<0.01	-	<0.01	<0.01	-	<0.01
ERP	1	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	0.01	0.99	0.03	<0.01	<0.01	0.55	0.17	<0.01	<0.01	<0.01	0.76	<0.01	<0.01		0.07	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	0.02	0.95	0.13	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.36	0.16	<0.01		0.24	<0.01	-	<0.01	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	0.39	0.43	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.02		<0.01	-	<0.01	<0.01	-	<0.01
GAZ	1	<0.01	0.55	0.75	<0.01	<0.01	<0.01	<0.01	0.31	0.97	-	-	-	0.07	0.87	0.05	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		-	0.82	<0.01	-	<0.01
	2	<0.01	0.02	0.04	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	0.07	0.26	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.43	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		-	-	-	-
	3	<0.01	0.02	0.04	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	0.07	0.25	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.45	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.93		<0.01	-	<0.01
TRO	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	<0.01
	2	<0.01	0.70	0.45	<0.01	<0.01	<0.01	<0.01	0.56	0.01	-	-	-	0.44	0.35	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-		-
	3	<0.01	0.80	0.92	<0.01	<0.01	<0.01	<0.01	0.65	0.23	-	-	-	0.10	0.78	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.12	<0.01	<0.01	-	0.01	

b)



Species		WA			GHA			SA			LMSA			NGP			SGP			KP			GP			MP			ERP			GAZ			TRO		
	Years	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
WA	1		0.25	0.02	<0.01		<0.01	<0.01	<0.01	<0.01	<0.01		<0.01	0.06	0.04	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		<0.01	<0.01		<0.01
	2	0.47		0.20	<0.01	-	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	0.30	0.26	0.03	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	3	0.24	0.74		<0.01	-	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	0.93	0.96	0.26	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
GHA	1	<0.01	<0.01	<0.01		-	0.04	<0.01	<0.01	<0.01	0.01	-	0.71	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	0.71		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	<0.01	<0.01	<0.01	0.81	0.87		<0.01	<0.01	<0.01	0.04	-	0.36	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
SA	1	<0.01	0.01	0.01	<0.01	<0.01	<0.01		0.01	0.05	<0.01	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.05	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.81		0.33	0.32	-	0.01	<0.01	<0.01	<0.01	0.89	0.16	0.39	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.69	0.38		0.05	-	<0.01	<0.01	<0.01	<0.01	0.19	0.01	0.91	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
LMSA	1	-	-	-	-	-	-	-	-	-		-	0.11	<0.01	<0.01	<0.01	0.29	0.99	0.07	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	2	-	-	-	-	-	-	-	-	-	-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	-	-	-		<0.01	<0.01	<0.01	0.01	0.03	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
NGP	1	0.02	0.09	0.13	<0.01	<0.01	<0.01	0.37	0.10	0.19	-	-	-		0.97	0.45	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.53	0.38	0.17	-	-	-	0.05		0.37	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	0.02	0.01	0.01	0.02	<0.01	<0.01	-	-	-	<0.01	0.01		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
SGP	1	<0.01	<0.01	<0.01	0.02	0.01	0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	0.26		0.14	0.25	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	0.04	0.02	0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	0.21	0.81		0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	0.74	0.92	0.84	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	0.03	0.06	0.08		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
KP	1	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	0.01		0.50	<0.01	0.05	0.02	0.25	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	-	<0.01	0.01	-	<0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01		0.03	0.15	0.08	0.48	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	-	<0.01	0.01	-	<0.01
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.15		0.54	0.38	0.72	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
GP	1	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	0.04	0.67	0.50	0.22		0.94	0.61	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	-	0.01	0.01	-	<0.01
	2	<0.01	<0.01	<0.01	0.01	0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	0.01	<0.01	<0.01	0.12	0.19	0.01	<0.01	0.35		0.54	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	-	<0.01	0.01	-	<0.01
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	0.09	0.29	0.24	0.01		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.02	-	0.01	0.03	-	<0.01
MP	1	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01		0.05	<0.01	0.71	0.28	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.01		0.04	0.01	0.31	0.06	<0.01	-	<0.01	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.02	0.65		<0.01	<0.01	0.36	<0.01	-	<0.01	<0.01	-	<0.01
ERP	1	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.16	0.11		0.08	<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.04		<0.01	<0.01	-	<0.01	<0.01	-	<0.01
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.08	0.31		<0.01	-	<0.01	<0.01	-	<0.01
GAZ	1	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	0.13	<0.01	<0.01	<0.01	0.15	0.7	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		-	0.91	0.72	-	0.03
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.56	0.44	0.37	<0.01	0.18	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		-	-	-	-
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.48	0.02	<0.01	0.81	0.06	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01		0.61	-	0.03
TRO	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-	0.01
	2	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.13	0.56	0.20	<0.01	0.68	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.29	<0.01	-		-
	3	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	-	-	-	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.81	0.06	<0.01	0.77	0.18	0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	0.02	0.02	0.81	-	0.01	

Supplementary Material S3.5. Comparison of 12 seabirds and fur seals a) δ^{13}C and b) δ^{15}N blood values between summer (horizontal, 1: 2015/16, 2: 2016/17, 3: 2017/18) and autumn (vertical, 1: 2015, 2: 2016, 3: 2017) over three years. Values reported are the resulting p-values of post-hoc pairwise permutational tests with false discovery rate corrections for multiple comparisons. See Supplementary Material S3.1. for species abbreviations. Significant results are shaded. "–" indicates no data available for comparison.

a)

Species	Year	1	2	3
WA	1	0.89	0.40	<0.01
	2	0.08	0.30	0.45
	3	0.05	0.20	0.65
GHA	1	<0.01	-	0.01
	2	<0.01	-	<0.01
	3	<0.01	-	<0.01
SA	1	0.08	0.54	<0.01
	2	0.52	0.25	<0.01
	3	0.79	0.01	<0.01
LMSA	1	-	-	-
	2	-	-	-
	3	-	-	-
NGP	1	0.58	0.44	0.40
	2	0.53	0.64	0.58
	3	0.01	0.01	0.01
SGP	1	0.04	0.55	0.77
	2	<0.01	<0.01	0.01
	3	<0.01	<0.01	<0.01
KP	1	0.01	<0.01	<0.01
	2	<0.01	0.25	0.55
	3	<0.01	<0.01	<0.01
GP	1	<0.01	0.03	0.01
	2	0.02	0.21	0.89
	3	0.14	0.05	0.41
MP	1	<0.01	<0.01	<0.01
	2	<0.01	<0.01	<0.01
	3	<0.01	<0.01	<0.01
ERP	1	<0.01	<0.01	<0.01
	2	<0.01	<0.01	<0.01
	3	<0.01	<0.01	<0.01
GAZ	1	0.04	-	0.04
	2	0.69	-	0.90
	3	0.66	-	0.86
TRO	1	-	-	-
	2	<0.01	-	<0.01
	3	<0.01	-	<0.01

b)

Species	Year	1	2	3
WA	1	0.23	0.87	0.1
	2	0.09	0.64	0.38
	3	0.03	0.41	0.54
GHA	1	<0.01	-	<0.01
	2	<0.01	-	<0.01
	3	<0.01	-	<0.01
SA	1	<0.01	<0.01	<0.01
	2	<0.01	<0.01	<0.01
	3	<0.01	<0.01	<0.01
LMSA	1	-	-	-
	2	-	-	-
	3	-	-	-
NGP	1	0.49	0.42	1
	2	0.02	0.01	0.03
	3	<0.01	<0.01	<0.01
SGP	1	<0.01	<0.01	<0.01
	2	<0.01	<0.01	<0.01
	3	<0.01	<0.01	<0.01
KP	1	0.04	0.03	<0.01
	2	0.26	0.69	0.08
	3	<0.01	0.05	0.70
GP	1	0.33	0.30	0.51
	2	0.03	0.03	0.05
	3	0.96	0.97	0.51
MP	1	<0.01	<0.01	0.01
	2	<0.01	0.01	0.61
	3	<0.01	<0.01	0.38
ERP	1	0.01	0.12	0.65
	2	0.82	0.29	<0.01
	3	0.07	0.88	<0.01
GAZ	1	0.49	-	0.5
	2	<0.01	-	<0.01
	3	0.05	-	0.02
TRO	1	-	-	-
	2	<0.01	-	<0.01
	3	0.24	-	<0.01

Supplementary Material S3.6. a) Proportional overlap among isotopic niches (SEAc) of a) flying and b) diving species breeding on Marion island among three consecutive autumns (lower left diagonal, 1: 2015, 2: 2016, 3:2017) and summers (upper right diagonal, 1: 2015/16, 2: 2016/17, 3: 2017/18). "-" indicates no data available for comparisons. See Supplementary Material S3.1. for species abbreviations.

a)

Species		WA			GHA			SA			LMSA			NGP			SGP		
	Year	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
WA	1	■	0.50	0.26	< 0.01			< 0.01			0.00			0.33			0.00		
	2	0.28	■	0.34		-			< 0.01			-			0.45			0.00	
	3	0.29	0.78	■			< 0.01			< 0.01			0.00			0.12			0.00
GHA	1	0.00			■	-	0.35	< 0.01			0.00			< 0.01			0.00		
	2		< 0.01		0.20	■	-		-			-			-			-	
	3			< 0.01	0.26	0.72	■			< 0.01			0.00			< 0.01			0.00
SA	1	< 0.01			0.00	0.00	0.00	■	0.09	0.24	0.00			0.01			0.00		
	2		< 0.01			0.00	0.00	0.21	■	< 0.01		-			< 0.01			0.00	
	3			< 0.01		0.00	0.00	< 0.01	0.21	■			0.00			< 0.01			0.00
LMSA	1	-			-			-			■	-	0.16	0.00			0.30		
	2		-			-			-		-	■	-		-			-	
	3			-			-			-	-	-	■			0.00			< 0.01
NGP	1	0.31			0.00			0.07			-			■	0.77	0.56	0.00		
	2		< 0.01			< 0.01			0.28			-		0.25	■	0.48		0.00	
	3			< 0.01			0.12			< 0.01			-	0.05	0.25	■			0.00
SGP	1	0.00			< 0.01			0.00			-			0.00			■	0.15	0.15
	2		0.00			0.00			0.00			-			0.00		0.43	■	0.28
	3			0.00			0.00			0.00			-			< 0.01	0.24	0.43	■

b)

Species		KP			GP			MP			ERP			TRO			GAZ		
	Year	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
KP	1	■	0.19	< 0.01	0.03			< 0.01			< 0.01			0.00			0.00		
	2	< 0.01	■	0.32		0.00			< 0.01			< 0.01			-			-	
	3	0.00	0.22	■			0.00			< 0.01			< 0.01			0.00			0.00
GP	1	0.00			■	< 0.01	0.26	< 0.01			< 0.01			0.00			0.07		
	2		0.00		0.00	■	0.2		0.00			0.00			-			-	
	3			0.00	0.00	0.09	■			< 0.01			0.00			0.00			0.15
MP	1	0.00			0.00			■	0.28	0.05	0.09			0.00			0.00		
	2		0.00			0.00		0.00	■	0.1		0.56			-			-	
	3			0.00			0.00	0.00	0.63	■			0.25			0.00			0.00
ERP	1	0.00			0.00			0.15			■	0.28	< 0.01	0.00			< 0.01		
	2		0.00			0.00			0.05		0.00	■	0.18		-			-	
	3			0.00			0.00			< 0.01	0.00	0.27	■			0.00			0.00
TRO	1	-			-			-			-			■		< 0.01	0.00		
	2		0.00			0.00			0.00			0.00		-	■			-	
	3			0.00			0.00			0.00			0.00	-	0.18	■			0.00
GAZ	1	0.00			0.00			0.00			0.00			-			■		0.81
	2		0.00			0.00			0.00			0.00			0.00		< 0.01	■	
	3			0.00			0.00			0.00			0.00			0.00	< 0.01	0.21	■

Supplementary Material S3.7. Proportional overlap among each species autumn (vertical, 1: 2015, 2: 2016, 3: 2017) and summer (horizontal, 1: 2015/16, 2: 2016/17, 3: 2017/18) isotopic niches separated as a) flying species and b) diving species. “–” indicates no data available for comparison.

a)

Year	1	2	3
Wandering albatross			
1	0.32	0.47	0.12
2	0.40	0.52	0.43
3	0.31	0.50	0.42
Grey-headed albatross			
1	0.01	-	< 0.01
2	0.00	-	< 0.01
3	< 0.01	-	< 0.01
Sooty albatross			
1	0.03	< 0.01	0.00
2	0.06	< 0.01	0.02
3	< 0.01	< 0.01	< 0.01
Northern giant petrel			
1	0.31	0.25	0.51
2	0.12	0.07	0.21
3	< 0.01	< 0.01	0.01
Southern giant petrel			
1	0.01	0.09	< 0.01
2	< 0.01	0.01	< 0.01
3	0.00	0.01	< 0.01

b)

Year	1	2	3
King penguin			
1	0.09	0.02	0.00
2	0.01	0.47	0.43
3	0.00	0.17	0.22
Gentoo penguin			
1	0.00	< 0.01	< 0.01
2	0.07	< 0.01	0.11
3	0.19	< 0.01	0.27
Macaroni penguin			
1	0.00	0.01	0.01
2	0.00	0.00	0.00
3	0.00	0.00	0.00
Rockhopper penguin			
1	0.00	0.07	0.12
2	0.00	0.00	0.00
3	0.00	0.00	0.00
sub-Antarctic fur seal			
1	-	-	-
2	0.00	-	< 0.01
3	0.00	-	0.00
Antarctic fur seal			
1	0.12	-	0.15
2	0.06	-	0.06
3	0.15	-	0.17

Supplementary Material S3.8. Comparison of the path length and direction of isotopic shifts between summer and autumn for two breeding seasons (2015/16 and 2016/17) of eight marine predator species. Values presented are the resulting empirical p-values estimated from permutations procedures (Turner et al. 2010). Significant differences are shaded. See Supplementary Material S3.1. for species abbreviations.

Species	Path length P value	Direction P value
WA	0.57	0.62
SA	0.14	0.08
NGP	<0.01	0.51
SGP	0.76	0.71
KP	0.96	0.47
GP	0.36	0.13
MP	0.57	0.79
ERP	0.90	0.92

Supplementary Material S3.9. Difference in the path length (upper right diagonal) and direction (lower left diagonal) of isotopic shifts between three consecutive summers: a) 2015/16 vs 2016/17, b) 2016/17 vs 2017/18 and c) 2015/16 vs 2017/18 of 12 marine predator species and empirical p-values estimated from permutations procedures (Turner et al. 2010). Significant differences are shaded. “-” indicates no data for comparisons See Supplementary Material S3.1. for species abbreviations.

a) **Summer 2015/16 versus summer 2016/17**

Species	WA	GHA	SA	LMSA	NGP	SGP	KP	GP	MP	ERP	TRO	GAZ
WA		-	0.24 (0.28)	-	0.31 (0.16)	0.07 (0.74)	0.19 (0.36)	0.13 (0.62)	0.12 (0.56)	0.16 (0.42)	-	-
GHA	-		-	-	-	-	-	-	-	-	-	-
SA	80.92 (0.08)	-		-	0.55 (0.02)	0.17 (0.43)	0.43 (0.07)	0.11 (0.69)	0.36 (0.12)	0.40 (0.09)	-	-
LMSA	-	-			-	-	-	-	-	-	-	-
NGP	56.71 (0.29)	-	24.21 (0.66)	-		0.38 (0.09)	0.12 (0.55)	0.44 (0.15)	0.19 (0.35)	0.15 (0.47)	-	-
SGP	22.99 (0.68)	-	57.94 (0.28)	-	33.73 (0.54)		0.26 (0.22)	0.06 (0.81)	0.19 (0.36)	0.23 (0.27)	-	-
KP	32.28 (0.56)	-	48.64 (0.37)	-	24.43 (0.65)	9.30 (0.86)		0.32 (0.26)	0.07 (0.71)	0.03 (0.87)	-	-
GP	48.11 (0.38)	-	32.81 (0.56)	-	8.60 (0.88)	25.12 (0.66)	15.83 (0.78)		0.25 (0.37)	0.29 (0.30)	-	-
MP	67.57 (0.19)	-	31.51 (0.57)	-	55.72 (0.30)	89.45 (<0.01)	80.15 (0.08)	64.32 (0.23)		0.04 (0.83)	-	-
ERP	86.58 (0.03)	-	12.50 (0.82)	-	36.71 (0.50)	70.44 (0.17)	61.14 (0.26)	45.32 (0.41)	19.01 (0.72)		-	-
TRO	-	-	-	-	-	-	-	-	-	-		-
GAZ	-	-	-	-	-	-	-	-	-	-	-	

b) **Summer 2016/17 versus summer 2017/18**

Species	WA	GHA	SA	LMSA	NGP	SGP	KP	GP	MP	ERP	TRO	GAZ
WA		-	0.51 (0.05)	-	0.57 (0.02)	0.5 (0.04)	0.66 (0.01)	0.61 (0.06)	0.51 (0.04)	0.5 (0.04)	-	-
GHA	-		-	-	-	-	-	-	-	-	-	-
SA	28.28 (0.59)	-		-	1.07 (<0.01)	1.01 (<0.01)	1.17 (<0.01)	1.12 (<0.01)	1.02 (<0.01)	1.01 (<0.01)	-	-
LMSA	-	-	-		-	-	-	-	-	-	-	-
NGP	70.77 (0.15)	-	80.96 (0.07)	-		0.07 (0.77)	0.10 (0.68)	0.05 (0.87)	0.05 (0.82)	0.06 (0.79)	-	-
SGP	82.29 (0.06)	-	69.43 (0.17)	-	11.52 (0.82)		0.17 (0.47)	0.11 (0.68)	0.02 (0.94)	0.01 (0.98)	-	-
KP	51.53 (0.33)	-	79.81 (0.09)	-	19.24 (0.70)	30.76 (0.55)		0.05 (0.85)	0.15 (0.53)	0.16 (0.50)	-	-
GP	69.34 (0.19)	-	41.06 (0.47)	-	39.90 (0.48)	28.38 (0.63)	59.13 (0.29)		0.10 (0.73)	0.11 (0.71)	-	-
MP	40.41 (0.44)	-	68.68 (0.18)	-	30.36 (0.55)	41.88 (0.43)	11.12 (0.82)	70.26 (0.18)		0.01 (0.97)	-	-
ERP	87.55 (0.02)	-	64.17 (0.21)	-	16.79 (0.74)	5.26 (0.91)	36.02 (0.49)	23.11 (0.68)	47.15 (0.37)		-	-
TRO	-	-	-	-	-	-	-	-	-	-		-
GAZ	-	-	-	-	-	-	-	-	-	-	-	

c) **Summer 2015/16 versus summer 2017/18**

Species	WA	GHA	SA	LMSA	NGP	SGP	KP	GP	MP	ERP	TRO	GAZ
WA		0.94 (<0.01)	0.34 (0.16)	0.39 (0.16)	0.93 (<0.01)	0.67 (0.01)	0.88 (<0.01)	0.79 (0.01)	0.66 (0.01)	0.65 (0.01)	0.65 (0.01)	1.12 (<0.01)
GHA	82.76 (0.05)		0.61 (0.02)	0.56 (0.06)	0.01 (0.95)	0.28 (0.25)	0.06 (0.78)	0.15 (0.59)	0.28 (0.23)	0.29 (0.22)	0.30 (0.21)	0.17 (0.46)
SA	14.71 (0.74)	68.05 (0.15)		0.05 (0.86)	0.59 (0.02)	0.33 (0.18)	0.54 (0.02)	0.45 (0.12)	0.33 (0.18)	0.32 (0.19)	0.31 (0.20)	0.78 (<0.01)
LMSA	1.11 (0.98)	83.87 (0.04)	15.82 (0.75)		0.55 (0.06)	0.28 (0.30)	0.49 (0.09)	0.41 (0.20)	0.28 (0.30)	0.27 (0.32)	0.26 (0.34)	0.73 (0.02)
NGP	46.95 (0.32)	50.28 (0.30)	61.66 (0.20)	45.84 (0.38)		0.26 (0.27)	0.05 (0.83)	0.14 (0.62)	0.27 (0.26)	0.28 (0.24)	0.28 (0.24)	0.18 (0.43)
SGP	45.62 (0.32)	37.14 (0.42)	30.91 (0.50)	46.73 (0.36)	87.42 (0.02)		0.21 (0.36)	0.12 (0.65)	<0.01 (0.99)	0.01 (0.95)	0.02 (0.94)	0.45 (0.06)
KP	11.22 (0.79)	86.02 (0.03)	25.93 (0.56)	10.11 (0.84)	35.73 (0.44)	56.84 (0.22)		0.09 (0.74)	0.22 (0.36)	0.23 (0.33)	0.23 (0.32)	0.24 (0.30)
GP	9.65 (0.85)	73.12 (0.14)	5.06 (0.92)	10.76 (0.84)	56.60 (0.28)	35.98 (0.48)	20.86 (0.68)		0.13 (0.65)	0.14 (0.62)	0.14 (0.61)	0.33 (0.25)
MP	56.14 (0.23)	41.10 (0.37)	70.85 (0.12)	55.03 (0.29)	9.19 (0.82)	78.24 (0.08)	44.92 (0.33)	65.79 (0.19)		0.01 (0.96)	0.02 (0.95)	0.45 (0.05)
ERP	89.31 (<0.01)	7.92 (0.86)	75.98 (0.09)	88.20 (0.01)	42.36 (0.36)	45.06 (0.33)	78.09 (0.08)	81.04 (0.07)	33.17 (0.46)		0.01 (0.98)	0.46 (0.05)
TRO	69.61 (0.14)	13.15 (0.76)	54.90 (0.25)	70.72 (0.15)	63.44 (0.18)	23.99 (0.59)	80.83 (0.06)	59.97 (0.24)	54.25 (0.25)	21.07 (0.62)		0.47 (0.05)
GAZ	16.58 (0.70)	66.19 (0.16)	1.87 (0.96)	17.69 (0.72)	63.53 (0.18)	29.05 (0.51)	27.80 (0.53)	6.93 (0.89)	72.72 (0.11)	74.11 (0.10)	53.04 (0.26)	

Supplementary Material S3.10. Difference in the path length (upper right diagonal) and direction (lower left diagonal) of isotopic shifts between three consecutive autumns: a) 2015 vs 2016, b) 2016 vs 2017 and c) 2015 vs 2017 of 12 marine predator species and empirical p-values estimated from permutation procedures in brackets (Turner et al. 2010). Significant differences are shaded. "-" indicates no data for comparisons See Supplementary Material S3.1. for species abbreviations.

a) **Autumn 2015 versus autumn 2016**

	WA	GHA	SA	LMSA	NGP	SGP	KP	GP	MP	ERP	TRO	GAZ
WA		0.38 (0.26)	0.26 (0.50)	-	0.03 (0.92)	0.18 (0.58)	0.26 (0.45)	0.15 (0.7)	0.16 (0.63)	0.08 (0.81)	-	0.01 (0.97)
GHA	3.40 (0.86)		0.11 (0.76)	-	0.41 (0.22)	0.19 (0.57)	0.12 (0.74)	0.22 (0.58)	0.21 (0.54)	0.29 (0.41)	-	0.36 (0.31)
SA	5.65 (0.82)	2.25 (0.93)		-	0.30 (0.45)	0.08 (0.84)	<0.01 (0.97)	0.11 (0.81)	0.10 (0.81)	0.18 (0.67)	-	0.25 (0.55)
LMSA	-	-	-		-	-	-	-	-	-	-	-
NGP	44.36 (0.07)	47.76 (0.06)	50.01 (0.11)	-		0.22 (0.51)	0.29 (0.40)	0.19 (0.64)	0.20 (0.56)	0.12 (0.73)	-	0.05 (0.89)
SGP	7.26 (0.70)	3.86 (0.84)	1.61 (0.95)	-	51.62 (0.05)		0.08 (0.82)	0.03 (0.94)	0.02 (0.96)	0.10 (0.78)	-	0.17 (0.64)
KP	14.51 (0.48)	17.91 (0.39)	20.16 (0.44)	-	29.85 (0.19)	21.77 (0.30)		0.11 (0.79)	0.10 (0.79)	0.17 (0.62)	-	0.25 (0.50)
GP	39.49 (0.18)	36.09 (0.20)	33.84 (0.29)	-	83.85 (0.01)	32.23 (0.24)	54.00 (0.10)		0.01 (0.98)	0.07 (0.87)	-	0.14 (0.73)
MP	25.34 (0.25)	28.74 (0.20)	30.99 (0.27)	-	19.02 (0.36)	32.60 (0.16)	10.83 (0.61)	64.83 (0.06)		0.08 (0.83)	-	0.15 (0.68)
ERP	22.06 (0.32)	25.47 (0.26)	27.72 (0.31)	-	22.29 (0.32)	29.32 (0.21)	7.55 (0.72)	61.56 (0.08)	3.27 (0.88)		-	0.07 (0.85)
TRO	-	-	-	-	-	-	-	-	-	-		-
GAZ	34.03 (0.17)	37.43 (0.14)	39.68 (0.20)	-	10.33 (0.62)	41.29 (0.12)	19.52 (0.40)	73.52 (0.05)	8.69 (0.69)	11.96 (0.60)	-	

b) **Autumn 2016 versus autumn 2017**

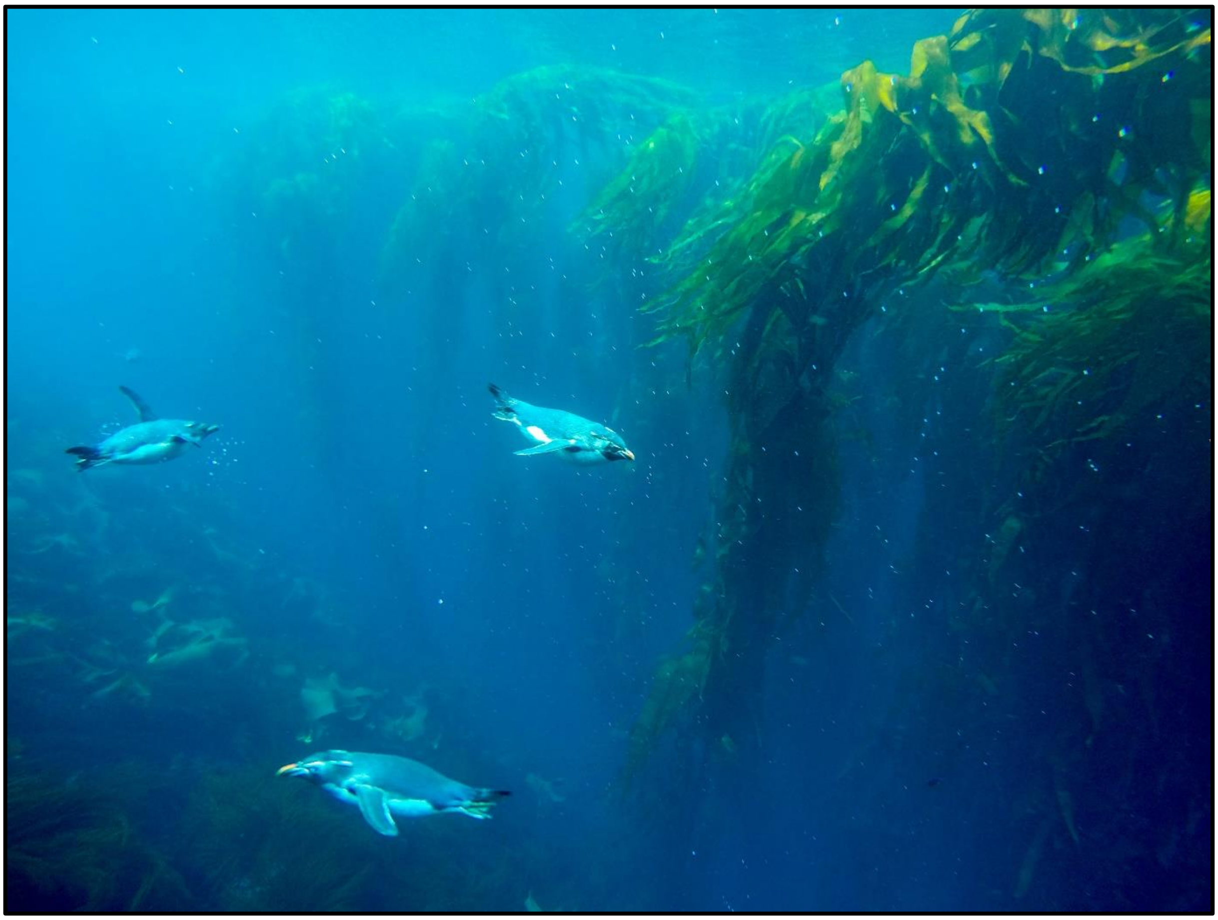
	WA	GHA	SA	LMSA	NGP	SGP	KP	GP	MP	ERP	TRO	GAZ
WA		0.10 (0.70)	0.14 (0.58)	-	1.33 (<0.01)	0.42 (0.13)	0.03 (0.89)	0.53 (0.10)	0.08 (0.77)	0.09 (0.71)	0.27 (0.30)	0.08 (0.74)
GHA	4.51 (0.92)		0.24 (0.36)	-	1.42 (<0.01)	0.51 (0.06)	0.13 (0.61)	0.63 (0.06)	0.02 (0.92)	0.19 (0.45)	0.37 (0.18)	0.18 (0.48)
SA	55.20 (0.24)	59.70 (0.20)		-	1.18 (<0.01)	0.27 (0.30)	0.11 (0.67)	0.39 (0.22)	0.22 (0.40)	0.05 (0.85)	0.13 (0.62)	0.06 (0.81)
LMSA	-	-	-		-	-	-	-	-	-	-	-
NGP	16.03 (0.70)	11.52 (0.78)	71.23 (0.12)	-		0.91 (<0.01)	1.29 (<0.01)	0.80 (0.02)	1.40 (<0.01)	1.23 (<0.01)	1.06 (<0.01)	1.24 (<0.01)
SGP	16.20 (0.70)	11.69 (0.78)	71.40 (0.12)	-	0.17 (0.98)		0.38 (0.15)	0.11 (0.69)	0.49 (0.07)	0.32 (0.23)	0.15 (0.56)	0.33 (0.21)
KP	5.32 (0.90)	0.82 (0.99)	60.52 (0.20)	-	10.70 (0.80)	10.87 (0.79)		0.50 (0.12)	0.11 (0.66)	0.06 (0.81)	0.24 (0.37)	0.05 (0.83)
GP	46.32 (0.33)	41.81 (0.39)	78.49 (0.08)	-	30.29 (0.51)	30.12 (0.51)	40.99 (0.39)		0.61 (0.07)	0.44 (0.17)	0.26 (0.39)	0.45 (0.16)
MP	25.16 (0.56)	20.65 (0.63)	80.36 (0.06)	-	9.13 (0.82)	8.96 (0.83)	19.84 (0.64)	21.16 (0.64)		0.17 (0.51)	0.35 (0.19)	0.16 (0.52)
ERP	62.44 (0.18)	66.94 (0.15)	7.24 (0.86)	-	78.46 (0.07)	78.64 (0.07)	67.76 (0.14)	71.25 (0.13)	87.60 (0.02)		0.18 (0.49)	0.01 (0.96)
TRO	89.12 (0.01)	84.61 (0.03)	35.68 (0.42)	-	73.09 (0.11)	72.92 (0.11)	83.80 (0.04)	42.80 (0.37)	63.96 (0.17)	28.44 (0.51)		0.19 (0.46)
GAZ	56.60 (0.23)	52.10 (0.26)	68.20 (0.15)	-	40.58 (0.37)	40.40 (0.36)	51.28 (0.26)	10.29 (0.82)	31.44 (0.46)	60.96 (0.18)	32.52 (0.46)	

c) **Autumn 2015 versus autumn 2017**

	WA	GHA	SA	LMSA	NGP	SGP	KP	GP	MP	ERP	TRO	GAZ
WA		0.54 (0.14)	0.13 (0.75)	-	1.36 (<0.01)	0.16 (0.67)	0.22 (0.56)	0.13 (0.78)	0.35 (0.36)	0.09 (0.83)	-	0.29 (0.46)
GHA	9.10 (0.46)		0.40 (0.37)	-	1.90 (<0.01)	0.70 (0.06)	0.32 (0.40)	0.41 (0.37)	0.19 (0.63)	0.45 (0.25)	-	0.25 (0.52)
SA	18.9 (0.24)	9.80 (0.52)		-	1.50 (<0.01)	0.29 (0.52)	0.09 (0.85)	0.01 (0.99)	0.22 (0.63)	0.05 (0.92)	-	0.15 (0.75)
LMSA	-	-	-		-	-	-	-	-	-	-	-
NGP	36.01 (0.02)	45.11 (0.01)	54.91 (0.02)	-		1.20 (<0.01)	1.58 (<0.01)	1.49 (<0.01)	1.71 (<0.01)	1.45 (<0.01)	-	1.65 (<0.01)
SGP	10.68 (0.38)	19.78 (0.12)	29.58 (0.10)	-	25.33 (0.06)		0.38 (0.32)	0.29 (0.53)	0.51 (0.18)	0.25 (0.53)	-	0.45 (0.26)
KP	14.23 (0.27)	23.32 (0.10)	33.13 (0.09)	-	21.79 (0.11)	3.55 (0.77)		0.09 (0.84)	0.13 (0.74)	0.13 (0.74)	-	0.07 (0.87)
GP	12.94 (0.42)	22.04 (0.19)	31.84 (0.15)	-	23.07 (0.18)	2.26 (0.88)	1.29 (0.93)		0.22 (0.62)	0.04 (0.93)	-	0.16 (0.74)
MP	20.29 (0.14)	29.39 (0.05)	39.19 (0.06)	-	15.72 (0.24)	9.61 (0.45)	6.06 (0.64)	7.35 (0.64)		0.26 (0.52)	-	0.06 (0.87)
ERP	4.35 (0.73)	13.45 (0.31)	23.25 (0.19)	-	31.66 (0.04)	6.33 (0.61)	9.88 (0.47)	8.59 (0.60)	15.94 (0.25)		-	0.20 (0.64)
TRO	-	-	-	-	-	-	-	-	-	-		-
GAZ	17.17 (0.22)	26.27 (0.08)	36.07 (0.08)	-	18.84 (0.18)	6.49 (0.62)	2.94 (0.82)	4.23 (0.80)	3.12 (0.82)	12.82 (0.38)	-	

Chapter 4:

A critical assessment of marine predator isoscapes within the southern Indian Ocean



Carpenter-Kling T, Pistorius PA, Reisinger RR, Cherel Y, Connan M. 2020. A critical assessment of marine predator isoscapes within the Southern Indian Ocean. Movement Ecology 8: 29.

Introduction

Some of the greatest threats faced by land-breeding marine predators are experienced at sea. These include bycatch-risk and changes in food availability as a result of competition with fisheries and climate change (Avila et al. 2018; Dias et al. 2019; Ropert-Coudert et al. 2019). Therefore, to implement effective conservation-based marine spatial planning there is a growing need to better understand the at-sea distribution of marine predators (Grémillet and Boulinier 2009; Ballard et al. 2012; Daly et al. 2018). This has led to an impressive growth in the number of tracking studies in recent years (reviewed in Harcourt et al. 2019), often with the general aim of providing policy-relevant information on important habitat for the respective study species (Hays et al. 2019). However, dataloggers are still cumbersome for small species (e.g. some burrowing seabird species) and deployment of loggers on study animals requires significant amounts of time in the field, especially when instruments need to be retrieved. Stable isotope ecology as a tool for retrospective geolocation of predator foraging grounds has relatively recently emerged as an alternative and complimentary method to conventional tracking studies (Hobson et al. 2010; Ramos and González-Solís 2012). Stable isotope analysis of body tissues is relatively cheap, less demanding in terms of field time and as a result allows for easy sampling of a greater number of individuals than would often be incorporated in tracking studies (e.g. Roscales et al. 2011)

The precision and accuracy of retrospective geolocation of marine predators based on their isotopic composition is primarily reliant on two important factors. Firstly, the reliance on the availability of reference maps of the relevant isotopic gradients, known as "isoscapes" (Graham et al. 2010). In marine systems, marine predator movement is commonly inferred by linking the ratios of the stable isotopes of carbon ($^{13}C/^{12}C$; $\delta^{13}C$), and to a lesser extent nitrogen ($^{14}N/^{15}N$; $\delta^{15}N$), of their tissues to known gradients of $\delta^{13}C$ and $\delta^{15}N$ values present at the base of their food webs (e.g. Jaeger et al. 2010a; Connan et al. 2014; Whitehead et al. 2017). Across the global oceans, there is a strong negative latitudinal gradient in the $\delta^{13}C$ values of phytoplankton, from the equator towards the poles (Magozzi et al. 2017), as well as from inshore benthic habitats to offshore pelagic habitats (Kaehler et al. 2000;

Quillfeldt et al. 2005; Cherel and Hobson 2007). Whereas gradients of δ^{15}N are not as strong or predictable, the δ^{15}N values of phytoplankton tend to be lower or higher in areas of nitrogen fixation (e.g. pelagic oceans) or denitrification (e.g. upwelling regions around coastlines), respectively (Takai et al. 2000; Somes et al. 2010). Secondly, a good working knowledge of potential discrimination factors which may offset a consumer's isotopic composition from baseline isotopic values is required. These discrimination factors may vary with diet composition, isotopic averaging as well as physiological fractionation through intermediate trophic levels, isotopic turnover rates and physiological transformation in the consumer (Graham et al. 2010; Hobson et al. 2010). This includes tissue-specific retention times, as isotopic turnover of different tissues varies greatly (Hobson and Clark 1993).

Previously, studies which estimated oceanic δ^{13}C and δ^{15}N isoscapes have largely used organisms close to the base of the food web (e.g. Navarro et al. 2013b; Magozzi et al. 2017; Brault et al. 2018) or particulate organic matter (Francois et al. 1993; Trull and Armand 2001; Lourey et al. 2003). The isotope ratios of organisms near the base of the food web (e.g. phytoplankton) or particulate organic matter are influenced by broad scale and localized chemical element circulation and physical oceanographic features (McMahon et al. 2013). Furthermore, due to the high turnover rate of these organisms, their isotope ratios may change daily (Hoefs 2015). However, due to temporal integration of isotopic ratios from the base of the web through to higher predators (O'Reilly et al. 2003), the stable isotopic compositions of marine predator tissues are not expected to reflect these short-term changes in the baseline but rather reflect more consistent isotope gradients.

The estimation of δ^{13}C and δ^{15}N predator-specific isoscapes requires information on the movement of the predator during the time which the body tissue of interest incorporated its isotope composition (e.g. Jaeger et al. 2010a; Ceia et al. 2018). While breeding, marine predators such as seabirds are central place foragers, regularly returning to their nest to provide care to their offspring (Phillips et al. 2008). Therefore, due to the ease of recapture of individuals after single foraging trips and collection of tissues for stable isotope analysis, seabirds represent ideal study species to investigate inter-specific differences in marine predator-level $\delta^{13}C$ and $\delta^{15}N$ isoscapes. In addition, the dichotomy in foraging mode presented in seabirds, and their associated foraging constraints, provides an opportunity to compare flying (e.g. albatrosses and giant petrels), and diving (penguins) seabirds. The vast inter-specific differences in the at-sea foraging distribution of seabirds furthermore allow for both the investigation of isoscapes over geographically extensive areas as well as inter-specific differences in isoscapes within locations utilised by multiple species.

Several studies have attempted to reconstruct $\delta^{13}C$ and $\delta^{15}N$ predator-specific isoscapes by combining known location and distributional range (Cherel and Hobson 2007) or movement of seabirds (Phillips et al. 2009; Jaeger et al. 2010a; Roscales et al. 2011; Ceia et al. 2018; Cruz-Flores et al. 2018) to temporally matched tissue isotopic values. The blood plasma of wild birds has a half-life of a few days and it is generally assumed that $\delta^{13}C$ and $\delta^{15}N$ values of seabird blood plasma reflects approximately seven days bioaccumulation of isotope values of prey prior to sampling (Hobson and Clark 1993; Bearhop et al. 2002). This makes it an ideal tissue to link to fine-scale tracking data as the movements of the birds can be known with high accuracy several days prior to sampling. However, integrating concurrently collected $\delta^{13}C$ and $\delta^{15}N$ blood plasma values with fine-scale tracking data has rarely been done and only in a single-species context (Jaeger et al. 2010a; Ceia et al. 2018). Here, we combine fine-scale GPS tracking data and concurrent blood plasma isotopic values of five Procellariiformes (albatrosses and petrels) and three Sphenisciformes (penguins) species to produce species and guild specific $\delta^{13}C$ and $\delta^{15}N$ isoscapes within the Southern Indian Ocean. We assigned an individual's isotopic values to a time integrated mean foraging location and use these data to investigate spatial patterns of a species $\delta^{13}C$ and $\delta^{15}N$ plasma values. The study aims to investigate the influence of species on the determination of $\delta^{13}C$ and $\delta^{15}N$ isoscapes as well as differences between predators with different movement modes (flying vs. diving). We hypothesized that the $\delta^{13}C$ and $\delta^{15}N$ tissue values of most species exhibit a spatial gradient and the extent and strength of this gradient is dependent on the species foraging range with the following predictions:

1. *Influence of seabird species on the detection of large-scale spatial variability in δ^{13}C and δ^{15}N isoscapes.* We predict that due to the vast distances travelled by flying species during a single foraging trip, their δ^{13}C and δ^{15}N tissue values will reflect known baseline latitudinal δ^{13}C and δ^{15}N gradients (e.g. Somes et al. 2010; Magozzi et al. 2017). However, due to sharp changes in baseline δ^{13}C values at frontal zones (Francois et al. 1993), we predict that if individuals of a species do not cross different major fronts within the Indian sector of the Southern Ocean, the δ^{13}C values of that species' tissues will not reflect a spatial gradient.

2. *δ^{13}C and δ^{15}N isotopic values of major fronts and water zones within seabird species isoscapes.* We predict that within the isoscapes of species which crossed one or more major fronts, there will be consistent stepwise increases at major fronts from south to north.

3. *Influence of seabird species on the detection of fine scale spatial variability in δ^{13}C and δ^{15}N isoscapes.* Previously, it has been shown that an inshore/offshore and benthic/pelagic effect can be detected in the isotopic values of seabirds (Hobson et al. 1994; Cherel and Hobson 2007; Harris et al. 2016). Thus, due to the more limited foraging range of penguins compared to that of the flying species in this study, we predict that the δ^{13}C and δ^{15}N plasma values of penguins will not reflect a latitudinal gradient, but will rather reflect the inshore/offshore and benthic/pelagic foraging habitat of the species.

Materials and Methods

Study Site and Species

The Prince Edward Archipelago is located in the Indian sector of the Southern Ocean between the sub-Antarctic and Antarctic polar fronts (Ansorge and Lutjeharms 2002). Ascending from a depth of approximately 3000m, the archipelago consists of two islands, Marion Island (~240 km^2) and Prince Edward Island (~45 km^2), which are located 19 km apart and separated by a shallow inter-island shelf that ranges from 40 to 400m in depth (Pakhomov and Froneman 1999). These two islands provide breeding grounds for more than five million seabirds and seals (Ryan and Bester 2008).

This study includes three of the four albatross species (wandering *Diomedea exulans*, grey-headed *Thalassarche chrysostoma* and sooty *Phoebetria fusca* albatrosses), both giant petrel species (northern *Macronectes halli* and southern *M. giganteus* giant petrels) and three of the four penguin species (gentoo *Pygoscelis papua*, macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chyrsocome filholi* penguins) breeding at Marion Island.

Data Collection

Field work was conducted between August to March 2015/16 – 2017/18, along the south-east coast of Marion Island (46°54'S; 37°45'E) during the breeding seasons of the respective study species (Supplementary Material S4.1). GPS data loggers (CatLog-S GPS loggers, Perthold Engineering LLC USA, 50 x 22 x 8 mm, ~24.5 g) were deployed on individuals that were either incubating or brooding small chicks. In total, loggers were deployed on 176 individuals, which included 32 wandering, 28 grey-headed and 22 sooty albatrosses, 27 northern and 23 southern giant petrels and 17 gentoo, 18 macaroni and 9 eastern rockhopper penguins. Loggers were set to record geographic locations at hourly intervals for flying birds (i.e. albatrosses and giant petrels) and two-minute intervals for penguins.

Loggers were retrieved after 1.2 ± 0.5 foraging trips for flying birds and 1.7 ± 0.9 foraging trips for penguins (Table 4.1). Upon retrieval of GPS loggers, ~ 1 ml of blood was collected from the tarsal vein of flying birds or the brachial vein of penguins using a sterile heparinised 25 gauge needle. Approximately 0.5 ml of the blood was centrifuged within 3-4 hrs after collection, separated into red blood cells and plasma, stored in 70% ethanol and frozen until preparation for stable isotope analysis (Hobson et al. 1997).

GPS Analysis

A foraging trip was defined as the last location on land until the first location back on land. Land-based locations were removed for further analysis. Unrealistic GPS locations were identified and removed using a speed filter algorithm (R package *trip*; Sumner 2016). Unrealistic locations were identified as those requiring movement speeds greater than 135 km h^{-1} (Phillips et al. 2008) for flying birds and greater than 10 km h^{-1} for penguins (Baylis et al. 2019). Post-filtering, positions were linearly interpolated at one-hour intervals for the flying birds' trips (R package *adehabitatLT*; Calenge 2006). The filtered data for penguins were processed using a continuous-time correlated random walk (CRAWL) model to estimate the approximate movement track at regular intervals (R package *crawl*; Johnson et al. 2008). The intervals set in the CRAWL models were the same as the intervals at which the loggers were set to record geographic locations (i.e. two min). When penguins are underwater, GPS signal is lost, resulting in irregular time intervals between locations; the CRAWL method fits a movement model to estimate locations at regular time intervals rather than assuming linear movement between irregular location estimates (Tremblay et al. 2006). Prior to further analysis, all GPS locations within a 2 km (penguins) or 15 km (flying birds) buffer around the island were removed to avoid an upward bias created by birds leaving and returning from foraging trips. This resulted in removal of all giant petrels that foraged exclusively within penguin and seal rookeries at the island.

Identification of foraging behaviour along GPS tracks

Foraging activity along a seabird's track is characterised by high sinuosity (i.e. frequent turning) and low flight speeds and can be distinguished from direct and fast transit to and from the colony (Benhamou 1992; Pinaud and Weimerskirch 2007).

To determine foraging locations along individual tracks of flying seabirds, Expectation Maximization binary Clustering (EMbC) was used (R package *EMbC*; Garriga et al. 2019). This method uses an unsupervised clustering algorithm based on maximum-likelihood Gaussian mixture models that produces biologically interpretable behavioural classifications from flying seabird tracking data (de Grissac et al. 2017; Jones et al. 2018). Derived from the turning angle and speed between successive GPS locations, the EMbC determines four behavioural classification categories, obtained from the four combinations of high and low values of turning angle and speed. Locations categorized to have low speeds and high turning angles are considered as the birds 'actively sitting' and can be considered as the birds being in a behavioural foraging phase (de Grissac et al. 2017).

The EMbC did not perform well on the penguin data. However, for diving predators, speed is a useful proxy of foraging behaviour (Trathan et al. 2008; Whitehead et al. 2016), with slower speeds (reduced horizontal displacement) typically associated with increased foraging activity (Sato et al. 2004). Speeds between successive GPS locations were calculated and speeds which were lower than a species average speed were identified as foraging locations.

Stable Isotope Analysis

The high lipid contents within blood plasma, detected by a C:N mass ratio > 3.5 in tissues for aquatic animals (Post et al. 2007), leads to artificially low δ^{13}C values (DeNiro and Epstein 1977; Cherel et al. 2005b). This may lead to misinterpretation when inferring foraging locations of consumers from their δ^{13}C tissue values. Mathematical normalization equations developed for a particular species or tissue may not be appropriate for another (Post et al. 2007; Logan et al. 2008), while chemical extraction methods may artificially increase δ^{15}N values (Sotiropoulos et al. 2004). Therefore, δ^{13}C and δ^{15}N values were obtained from lipid extracted and raw plasma, respectively.

Blood plasma was dried at 50°C for 48 hrs before being powdered using a mortar and pestle. Where possible, each plasma sample was divided into two aliquots: lipids were extracted from one half of the sample while the other half was analysed without lipid extraction. Lipids were removed by immersing powdered plasma in a 2:1 chloroform: methanol solution with a solvent volume three to five times greater than sample volume. Samples were then vortexed for 10 seconds every 10 minutes for one hour before being centrifuged for five minutes. The supernatant containing lipids was discarded, and samples dried at 50°C overnight.

For small plasma samples where lipid extraction was not possible (two wandering, six grey-headed and one sooty albatross samples and two gentoo and five macaroni penguin samples), raw material was analysed so that true δ^{15}N values could be obtained. To calculate lipid corrected δ^{13}C values, species-specific mathematical normalization equations were developed using delipidated and raw plasma samples used in this study as well as others collected during the same breeding seasons but not presented here (Pistorius unpub. data), so that sample size could be increased. A species-specific normalized δ^{13}C value was calculated using the difference of δ^{13}C values ($\Delta\delta^{13}$C) and C:N ratios (ΔC:N) between non-delipidated plasma (δ^{13}C and C:N) and delipidated plasma ($\delta^{13}C_{del}$ and C:N_{del}) for each individual (eqn 1 and eqn 2, respectively). A linear regression between $\Delta\delta^{13}$C and the ΔC:N ratio was then calculated thus giving an intercept (c) and slope (m) for each species-specific equation (eq. 3). Equation 3 was used to calculate $\Delta\delta^{13}$C for the samples that did not have a lipid free counterpart with ΔC:N for the raw samples calculated as the difference between their C:N and the average C:N of the delipidated samples.. Finally, a corrected δ^{13}C ($\delta^{13}C_{cor}$) was calculated for samples without a lipid free counterpart using eq. 4. Species-specific equations (eq. 3) and sample sizes are given in Supplementary Material S4.2.

$$\Delta\delta^{13}\mathrm{C} \ = \ \delta^{13}\mathrm{C}_{\mathrm{del}} - \delta^{13}\mathrm{C} \qquad \text{eqn 1}$$

$$\Delta\mathrm{C{:}\,N} \ = \ \ \mathrm{C{:}\,N}_{\mathrm{del}} - \mathrm{C{:}\,N} \qquad \text{eqn 2}$$

$$\Delta\delta^{13}\mathrm{C} = \frac{\Delta\mathrm{C{:}N}_{\mathrm{ave}} + \mathrm{c}}{\mathrm{m}} \qquad \text{eqn 3}$$

$$\delta^{13}C_{\mathrm{cor}} = \delta^{13}\mathrm{C} + \Delta\delta^{13}\mathrm{C} \qquad \text{eqn 4}$$

The isotopic values of carbon and nitrogen in aliquots (~0.4 mg) of homogenized delipidated and raw plasma samples were determined by combusting samples in a Flash 2000 organic elemental spectrometer via a Conflo IV gas control unit (Thermo Scientific, Germany). All samples were processed at the Stable Light Isotope Unit at the University of Cape Town, South Africa. Replicate measurements of internal laboratory standards indicated minimal standard deviations within and among runs (Merck gel: $SD_{\delta 13C}$ = 0.2 ‰, $SD_{\delta 15N}$ < 0.1 ‰; valine: $SD_{\delta 13C}$ < 0.2 ‰, $SD_{\delta 15N}$ = 0.1 ‰; seal bone:$SD_{\delta 13C}$ < 0.2 ‰, $SD_{\delta 15N}$ < 0.1 ‰). All in-house standards were calibrated against International Atomic Energy Agency standards. Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for δ^{13}C and δ^{15}N values, respectively.

Estimation of Isoscapes

Blood plasma has a half-life of a few days (Hobson and Clark 1993). It was therefore assumed that the δ^{13}C and δ^{15}N values of the seabirds' blood plasma reflected approximately seven days bioaccumulation of isotope value of prey prior to sampling. The isotope value of a seabird's tissue is a moving temporal window of what it has ingested (Hobson and Clark 1993; Bearhop et al. 2002). Thus, a geographic location that would represent an individual's single δ^{13}C and δ^{15}N plasma values was estimated by identifying cells where the individual was likely foraging (see Identification of foraging behaviour along GPS tracks) and weighting each of these cells by the proportion of time spent foraging within a given cell. Calculating the mean of these weighted positions resulted in a time-integrated weighted mean foraging location for each individual. In the case of brooding albatrosses (grey-headed and sooty albatrosses only) and penguins, where more than one foraging trip was recorded, multiple trips were included in further analyses if they did not exceed seven days prior to blood collection.

The proportion of time spent per cell was calculated for each individual (R package *trip*; Sumner 2016). Since the path length and duration of albatrosses and giant petrels was much greater than that of the penguins, two different grid sizes were used for flying and diving seabirds when calculating time spent per cell. The grid cell size was estimated by taking the average distance that the flying or diving species travelled in 2 hours (as location interval for flying birds was one hour) and rounding up to the nearest 0.05°. This resulted in grid cell sizes of 0.5° for flying birds and 0.05° for diving birds.

Possible geographic gradients were investigated using Pearson's correlation to identify relationships between δ^{13}C and δ^{15}N values of plasma and mean foraging latitude and longitude (in flying species) or distance to coastline (in diving species). As all penguin species only moved within ~0.5° of latitude, their blood plasma isotope values are unlikely to be affected by latitude and distance to coastline was thus used to investigate a possible inshore to offshore gradient. To visualize δ^{13}C and δ^{15}N isoscapes, species-specific geostatistical models were used to interpolate δ^{13}C and δ^{15}N values among the mean foraging locations. Ordinary kriging is a spatial interpolation method which relies on the notion of autocorrelation as a function of distance (Wackernagel 1995) and has been shown to perform well when estimating isoscapes from point locations (Magozzi et al. 2017; St. John Glew et al. 2019). Thus, ordinary kriging was used (R package *gstat*; Pebesma 2004), with best fit variograms identified using the R package *automap* (Hiemstra et al. 2009). Interpolations were made onto the same grid used to calculate time-spent per cell per individual, with extent of the grid being a convex hull around a species mean foraging locations with a 0.5° or 0.05° buffer for flying species and penguins, respectively. Isoscapes estimated for each species were then subtracted from one another to allow for comparison among the isocapes produced for each species, following the methods used by St John Glew et al. (2019).

The mean foraging location and plasma isotope values from all species within a guild (i.e. flying birds and penguins) were then combined to produce guild-specific $\delta^{13}C$ and $\delta^{15}N$ isoscapes. To account for the different number of individuals per species, a bootstrap approach was used. This approach involved randomly sampling 22 and 9 individuals (the lowest number of individuals per flying and penguin species, Table 4.1) sampled 1000 times from each of the flying and penguin species, respectively, and used to produce new $\delta^{13}C$ and $\delta^{15}N$ isoscapes. The mean of these isoscapes was then calculated to present guild-specific isoscapes which consider different number of individuals per species.

To investigate possible $\delta^{13}C$ and $\delta^{15}N$ values characteristic of main fronts and water masses within the Southern Ocean, isotopic values were extracted within one degree along the sub-tropical, sub-Antarctic and Antarctic polar fronts as well as for sub-tropical, sub-Antarctic, polar frontal and Antarctic water zones. Front positions were estimated from satellite derived sea surface height (Ssalto/Duacs produced and distributed by the Copernicus Marine Environment Monitoring Service http://marine.copernicus.eu) averaged over December of the three years of the study (2015-2017). Following Swart et al. (2010), the fronts were identified from the following sea surface heights: sub-tropical: 0.92 m, sub-Antarctic: 0.03 m and Antarctic polar: -0.48 m. The four water zones identified were considered as the following: the subtropical (north of the sub-tropical front), the sub-Antarctic (between the sub-tropical and sub-Antarctic fronts), the polar frontal zone (between the sub-Antarctic and Antarctic polar fronts) and the Antarctic (south of the Antarctic polar front). In addition, the $\delta^{13}C$ and $\delta^{15}N$ values of the Antarctic polar (51°S) and sub-tropical fronts (42°S) were back calculated using estimated regression equations following Jaeger et al. (2010a).

All data analyses were performed using R version 3.6.3. (R Core Team 2020). All values are reported as mean ± standard deviation and significance is specified as $p \leq 0.05$.

Results

Over the duration of the study, 176 birds were tracked, and their blood plasma analysed for $\delta^{13}C$ and $\delta^{15}N$ values (Table 4.1).

Influence of seabird species on the detection of large-scale spatial variability in $\delta^{13}C$ and $\delta^{15}N$ isoscapes

The $\delta^{13}C$ blood plasma values of all flying seabird species were positively correlated to their mean foraging latitude and significantly so with the exception of the sooty albatross (Table 4.2, Figure 4.1). The correlation between the mean foraging latitude and $\delta^{13}C$ plasma values of the grey-headed albatross was the strongest ($R = 0.83$) followed closely by the wandering albatross ($R = 0.78$) and southern ($R = 0.37$) and northern ($R = 0.37$) giant petrels. On the other hand, none of the species $\delta^{13}C$ plasma values and mean foraging longitudes were significantly correlated (Table 4.2; Figure 4.2). These findings were apparent in $\delta^{13}C$ isoscapes interpolated for the wandering and grey-headed albatrosses where a clear north to south gradient of $\delta^{13}C$ values can be seen (Figure 4.2a and 4.2b). The comparison between the wandering and grey-headed albatross isoscapes showed that the grey-headed albatross $\delta^{13}C$ isoscape was ~1‰ greater than that of wandering albatross within the area of overlap, that is north of the sub-tropical front (Figure 4.3). This was reflected with the species regression equations (Figure 4.1) with greater $\delta^{13}C$ values being predicted for the grey-headed albatross than the wandering albatross at similar latitudes. Although the correlation between mean foraging latitude and $\delta^{13}C$ values of northern and southern giant petrels were significant, the correlation was not as apparent in the interpolated surface (Figure 4.2d and 4.2e). No pattern could be discerned from the interpolated surface resulting from the sooty albatross's mean foraging locations and $\delta^{13}C$ values (Figure 4.2c).

The $\delta^{15}N$ plasma values of two of the five flying species were significantly and positively correlated to mean foraging latitude, namely the wandering albatross and southern giant petrel (Table 4.2, Figure 4.2). Contrastingly, the $\delta^{15}N$ plasma values of sooty albatrosses, which were not significantly correlated to mean foraging latitude (Table 4.2), were significantly correlated to mean foraging longitudes (Table 4.2, Figure 4.2c). The resulting interpolated surface of mean foraging location and $\delta^{15}N$ plasma values of the wandering albatross and southern giant petrel showed clear gradients of $\delta^{15}N$ values from north to south (Figure 4.2a and 4.2e). However, the resulting wandering albatross $\delta^{15}N$ isoscape was ~1‰ greater than that of the southern giant petrel across the interpolated surface (Figure 4.3). On the contrary, the interpolated surfaces resulting from the mean foraging locations and $\delta^{15}N$ plasma values of sooty albatrosses showed a gradient from west to east (Figure 4.2c).

The $\delta^{13}C$ and $\delta^{15}N$ plasma values of all flying seabirds combined were significantly correlated with mean foraging latitude ($R = 0.73$, $p < 0.01$ and $R = 0.44$, $p < 0.01$, respectively; Table 4.2, Figure 4.1a, b) but not to mean foraging longitude ($R = 0.12$, $p = 0.17$ and $R = 0.24$, $p = 0.19$, respectively). The resulting isoscapes, interpolated from mean foraging locations and plasma $\delta^{13}C$ values of all flying seabirds showed a clear south to north gradient in $\delta^{13}C$ values (Figure 4.4a). As $\delta^{15}N$ plasma values of the flying seabirds were not as strongly correlated to latitude ($R = 0.44$), the resulting $\delta^{15}N$ isoscape did not result in a clear south – north gradient, relative to the $\delta^{13}C$ isoscape (Figure 4.4a). However, there was also an increase in $\delta^{15}N$ values from south – north with the higher $\delta^{15}N$ values in the north-west area of the isoscape compared to those of the north-east (Figure 4.4a).

As a post-hoc analysis, all species for which $\delta^{13}C$ (sooty albatrosses) and $\delta^{15}N$ (grey-headed and sooty albatrosses and northern giant petrel) plasma values were not significantly related to their mean foraging latitude were removed and the remaining isoscapes were re-interpolated (Figure 4.4b). This resulted in a similar δ^{13}C isoscape to the previously estimated δ^{13}C isoscape (Figure 4.4a). However, the resulting δ^{15}N isoscape now showed a clear north to south gradient (Figure 4.4b).

δ^{13}C and δ^{15}N isotopic values of major fronts and water zones within seabird species isoscapes

From each species-specific isoscape derived from flying seabirds (Figure 4.2), mean isotopic values of the sub-tropical, sub-Antarctic and Antarctic polar fronts as well as four geographical water zones (sub-tropical, sub-Antarctic, polar frontal and Antarctic water zones) were estimated (Figure 4.5, Supplementary Material S4.3). There were noticeable increases in δ^{13}C values at the Antarctic polar and sub-Antarctic fronts within isoscapes interpolated for wandering and grey-headed albatrosses as well as for at the sub-tropical and sub-Antarctic fronts compared to surrounding water zones (Figure 4.5, Supplementary Material S4.3). With regards to δ^{15}N values, there were noticeable decreases for water zones from north to south within the interpolated areas for the wandering albatross and southern giant petrel, whereas the remaining species (sooty and grey-headed albatrosses and northern giant petrel) showed no clear trend (Figure 4.5, Supplementary Material S4.3). Following Jaeger et al. (2010), regression equations calculated here (Table 4.2) were also used to back calculate the δ^{13}C and δ^{15}N values in plasma of the Antarctic polar and sub-tropical fronts at 51°S and 42°S (Table 4.3). The resulting δ^{13}C values varied much less at both the Antarctic polar (-21.6 ± 0.6 ‰) and sub-tropical fronts (-20.3 ± 0.9 ‰) than the resulting δ^{15}N values (12.5 ± 1.4 ‰ and 13.1 ± 1.8 ‰; respectively).

Fine scale spatial variability in δ^{13}C and δ^{15}N isoscapes estimated from seabird tissues

No significant correlations were found between the distance to the coast and mean foraging location of the penguin species and their corresponding δ^{13}C and δ^{15}N plasma values (Table 4.4, Figures 4.6 and 4.7). However, the δ^{15}N plasma values of all penguins combined was significantly correlated with the distance between their mean foraging locations and the coastline of Marion Island (Table 4.4; Figure 4.8). Furthermore, both δ^{13}C and δ^{15}N penguin-specific isoscapes showed a clear gradient of higher values closer to the island, in waters shallower than 200 m, to lower values further away, in deeper waters (Figure 4.8).

Table 4.1. Delipidated or normalized plasma δ^{13}C and raw plasma δ^{15}N values of albatrosses, giant petrels, and penguins breeding at Marion Island, which were tracked simultaneously with GPS data loggers during 2015-2018. Number of individuals indicates number of birds with tracks and corresponding stable isotopic values. Number of tracks indicates number of tracks used to estimate mean foraging locations as multiple tracks were recorded for brooding individuals (See Materials and Methods). Values given as mean ± SD (range).

Common name	Number of individuals	Number of tracks per species	Number of tracks per individual	δ^{13}C (‰)	δ^{15}N (‰)
Albatrosses					
Wandering	32	32	1.0 ± 0.0 (1; 1)	-20.7 ± 1.5 (-23.6; -18.4)	14.0 ± 1.0 (12.1; 15.5)
Grey-headed	28	36	1.3 ± 0.5 (1; 2)	-20.2 ± 1.0 (-22.0; -18.5)	11.4 ± 0.4 (10.4; 12.4)
Sooty	22	36	1.6 ± 0.7 (1; 3)	-20.8 ± 0.7 (-22.2; -19.8)	12.0 ± 0.4 (11.4; 13.1)
Giant petrels					
Northern	27	29	1.1 ±0.3 (1; 2)	-19.8 ± 1.2 (-22.7; -17.1)	14.4 ± 0.8 (12.7; 15.9)
Southern	23	25	1.1 ± 0.3 (1; 2)	-22.7 ± 0.5 (-23.6; -21.8)	12.8 ± 0.4 (12.3; 13.4)
Penguins					
Gentoo	17	26	1.5 ± 0.9 (1; 4)	-21.7 ± 0.6 (-23.2; -20.9)	10.2 ± 0.5 (9.5; 11.4)
Macaroni	18	29	1.6 ± 0.8 (1; 3)	-22.3 ± 0.2 (-22.7; -22.0)	8.8 ± 0.3 (8.0; 9.2)
Rockhopper	9	19	2.1 ± 1.1 (1; 4)	-22.6 ± 0.2 (-22.9; -22.1)	8.6 ± 0.4 (7.7; 9.1)

Table 4.2. Pearson's correlation coefficient (R), p-value (P) and formula resulting from a Pearson's correlation between plasma δ^{13}C and δ^{15}N values of albatrosses and giant petrels versus latitude (lat) and longitude (lon) of their mean foraging locations calculated from GPS tracks. * indicates a significant correlation.

	δ^{13}C vs Latitude			δ^{13}C vs Longitude			δ^{15}N vs Latitude			δ^{15}N vs Longitude		
Species	R	P	Formula	R	P	Formula	R	P	Formula	R	P	Formula
All species combined												
	0.73	<0.01*	δ^{13}C = 0.21 (lat) - 11.25	0.12	0.17	δ^{13}C = 0.02 (lon) - 21.48	0.44	<0.01*	δ^{15}N = 0.12 (lat) + 18.29	0.24	0.19	δ^{15}N = 0.02 (lon) + 13.33
Albatrosses												
Wandering	0.78	<0.01*	δ^{13}C = 0.17 (lat) - 12.76	0.21	0.25	δ^{13}C = 0.03 (lon) - 21.55	0.76	<0.01*	δ^{15}N = 0.11 (lat) + 19.19	0.24	0.19	δ^{15}N = 0.02 (lon) + 13.33
Grey-headed	0.83	<0.01*	δ^{13}C = 0.24 (lat) - 8.81	0.27	0.17	δ^{13}C = 0.03 (lon) - 21.40	-0.11	0.57	δ^{15}N = 0.01 (lat) + 10.74	-0.36	0.06	δ^{15}N = 0.02 (lon) + 12.09
Sooty	0.25	0.27	δ^{13}C = 0.06 (lat) - 18.00	-0.02	0.93	δ^{13}C = 0.004 (lon) - 20.63	0.09	0.69	δ^{15}N = 0.01 (lat) + 12.67	-0.45	0.03*	δ^{15}N = 0.06 (lon) + 14.35
Giant Petrels												
Northern	0.37	0.05*	δ^{13}C = 0.17 (lat) - 12.71	-0.31	0.11	δ^{13}C = 0.09 (lon) - 16.79	0.29	0.14	δ^{15}N = 0.08 (lat) + 17.81	-0.16	0.43	δ^{15}N = 0.03 (lon) + 15.33
Southern	0.47	0.02*	δ^{13}C = 0.10 (lat) - 17.73	-0.07	0.77	δ^{13}C = 0.01 (lon) - 22.52	0.58	<0.01*	δ^{15}N = 0.09 (lat) + 17.43	-0.12	0.58	δ^{15}N = 0.01 (lon) + 12.99

Table 4.3. Plasma $\delta^{13}C$ and $\delta^{15}N$ values calculated using species-specific regression equations (Table 4.2) for the Antarctic polar (PF, 51°S) and sub-tropical (STF, 42°S) fronts following the methods of Jaeger et al. (2010)

	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
Species	PF	STF	PF	STF
Albatrosses				
Wandering	-21.4	-19.9	13.6	14.6
Grey-headed	-21.6	-19.4	10.3	10.4
Sooty	-21.1	-20.5	12.2	12.3
Giant petrels				
Northern	-21.4	-19.9	13.7	14.5
Southern	-22.6	-21.8	12.7	13.5

Table 4.4. Correlation coefficient (R), p-value (P) and formula resulting from a Pearson's correlation between $\delta^{13}C$ and $\delta^{15}N$ plasma values of individual penguin species as well as all species combined versus the distance between their mean foraging locations and the coastline of Marion Island (distTOcoast). * indicates a significant correlation.

	$\delta^{13}C$ vs distTOcoast			$\delta^{15}N$ vs distTOcoast		
	R	P	Formula	R	P	Formula
All species combined						
	-0.26	0.08	$\delta^{13}C$ = 0.01 (distTOcoast) - 21.99	-0.49	<0.01*	$\delta^{15}N$ = 0.03 (distTOcoast) + 9.69
Penguins						
Gentoo	0.03	0.92	$\delta^{13}C$ = 0.01 (distTOcoast) - 21.74	-0.10	0.71	$\delta^{15}N$ = 0.03 (distTOcoast) + 10.32
Macaroni	0.08	0.77	$\delta^{13}C$ = 0.001 (distTOcoast) - 22.33	-0.10	0.70	$\delta^{15}N$ = 0.002 (distTOcoast) + 8.80
Rockhopper	0.66	0.05*	$\delta^{13}C$ = 0.02 (distTOcoast) - 22.82	-0.13	0.74	$\delta^{15}N$ = 0.01 (distTOcoast) + 8.67

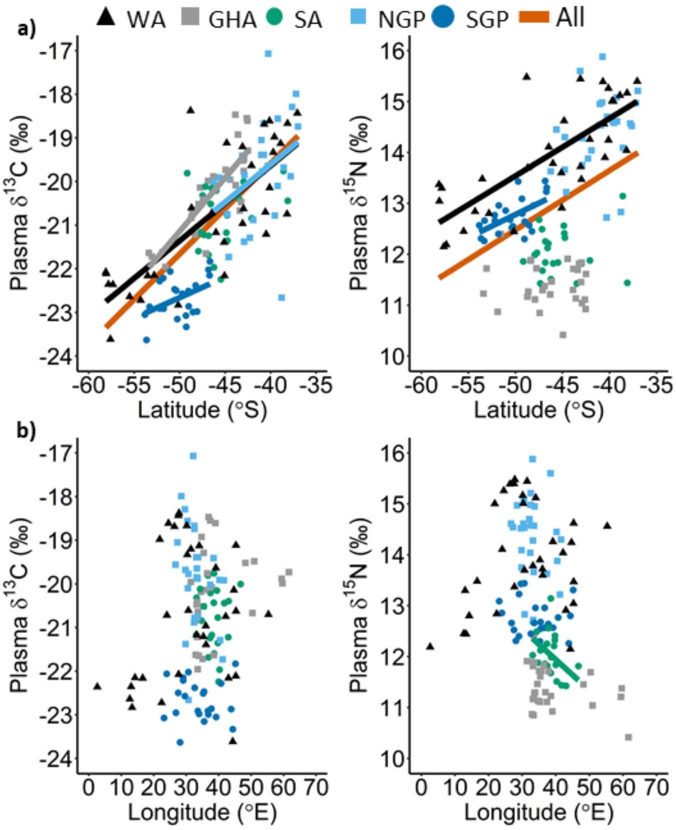


Figure 4.1. Plasma $\delta^{13}C$ (left) and $\delta^{15}N$ (right) values of wandering (WA), grey-headed (GHA) and sooty (SA) albatrosses, northern (NGP) and southern (SGP) giant petrels versus their mean foraging a) latitudes and b) longitudes calculated from GPS tracks. Only significant correlations are shown (see Table 4.2)

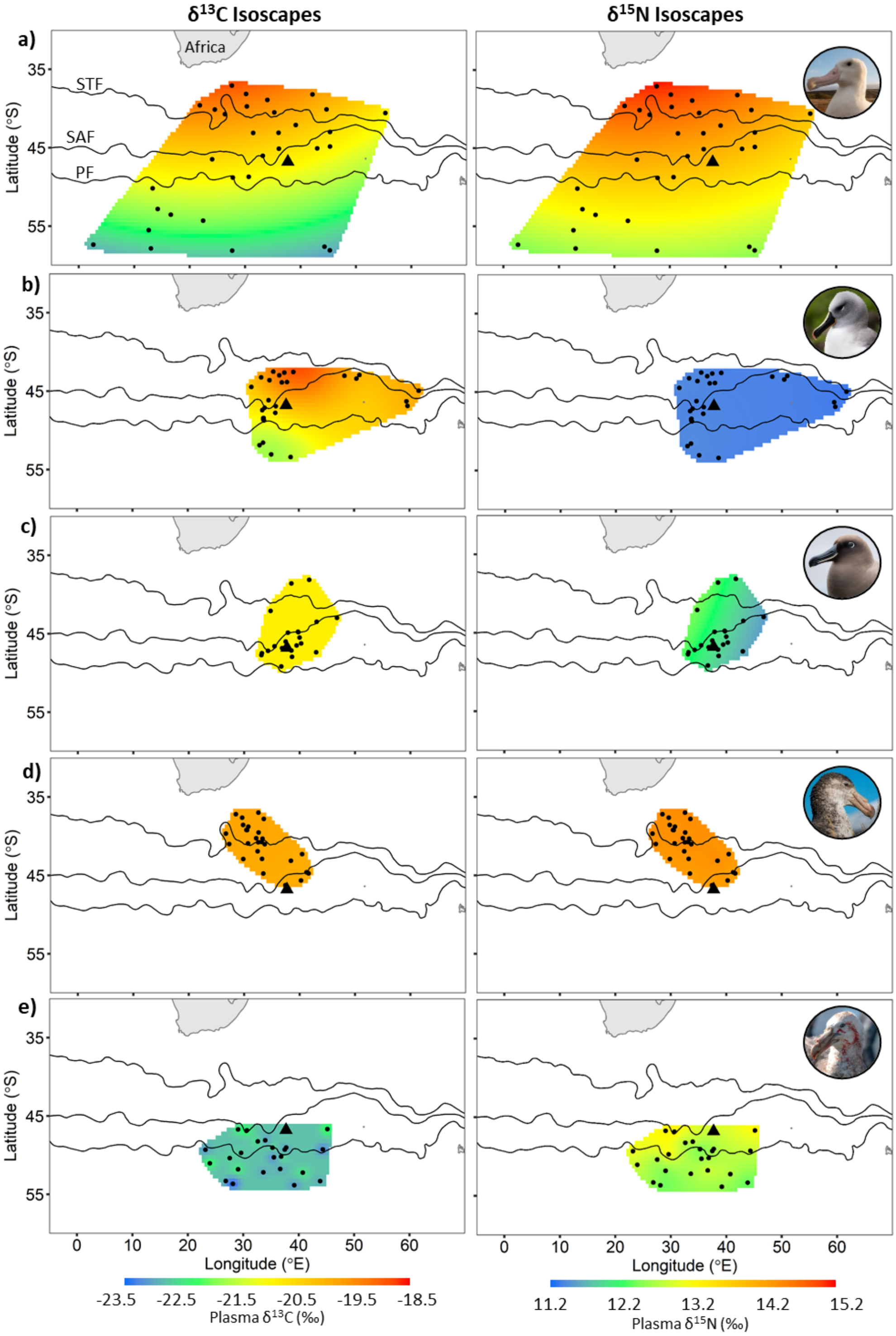


Figure 4.2. Plasma $\delta^{13}C$ (left) and $\delta^{15}N$ (right) isoscapes of a) wandering, b) grey-headed and c) sooty albatrosses, and d) northern and e) southern giant petrels breeding at Marion Island, Prince Edward Archipelago (black triangle) interpolated using ordinary kriging from the isotopic values of the respective birds' plasma which were simultaneously tracked with GPS data loggers. Black points represent an individual's mean foraging location. Positions of the sub-tropical (STF), sub-Antarctic (SAF) and Antarctic polar (PF) fronts are indicated.

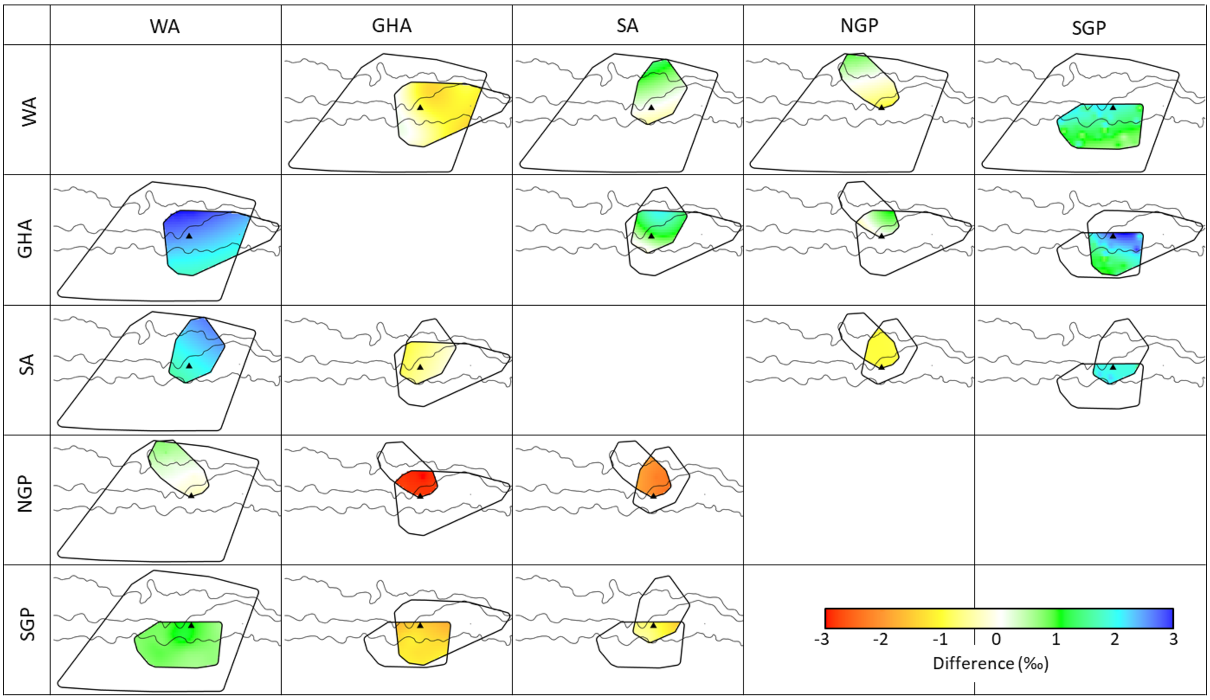


Figure 4.3. Difference between wandering (WA), grey-headed (GHA) and sooty (SA) albatross as well as northern (NGP) and southern (SGP) giant petrel plasma δ^{13}C (top right diagonal) and δ^{15}N (bottom left diagonal) isoscapes. Differences were calculated by subtracting the isoscape of the species indicated on the vertical axis from the species indicated on the horizontal axis. Due to the small overlap between isoscapes of the giant petrels their comparison is not shown.

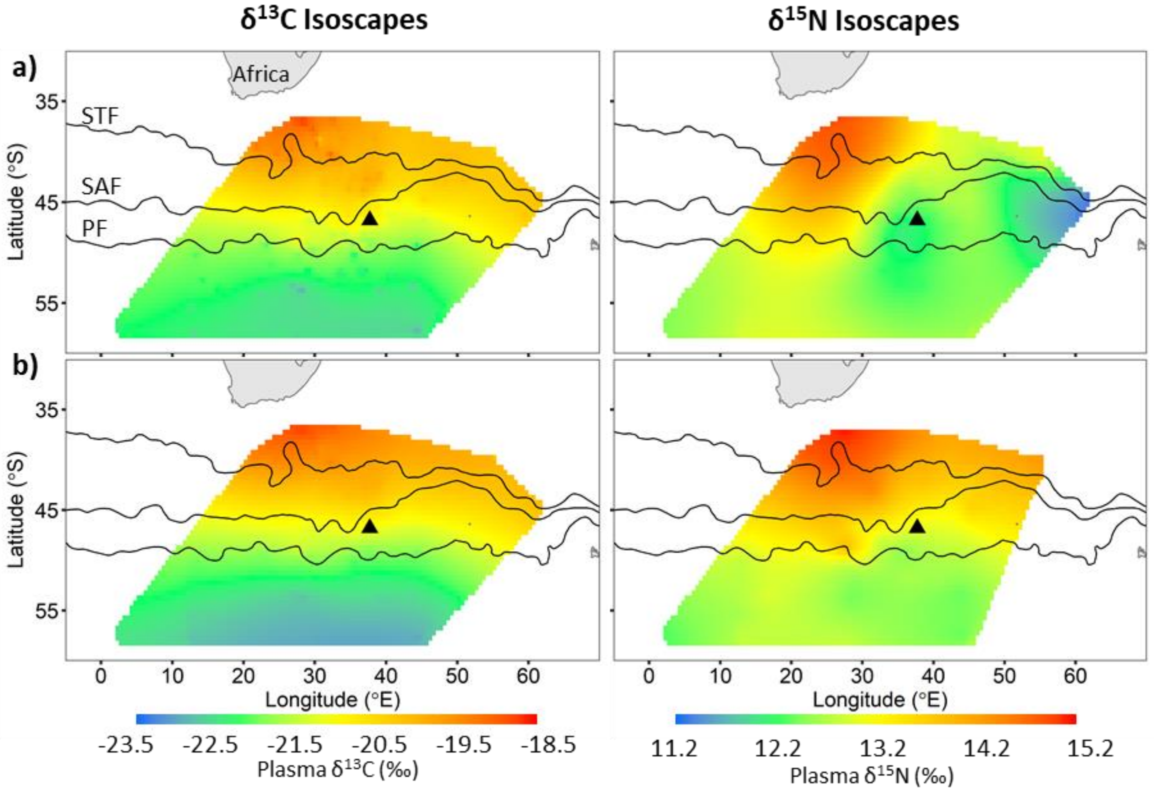


Figure 4.4. a) Plasma $\delta^{13}C$ (left) and $\delta^{15}N$ (right) isoscapes calculated as the mean of 1000 bootstrapped surfaces interpolated using ordinary kriging which randomly sampled twenty-two individuals from all five flying species to account for different number of individuals per species. b) Isoscapes, using the same bootstrap technique, modelled without the species which did not exhibit a significant latitudinal gradient (i.e. sooty albatrosses were removed from the $\delta^{13}C$ isoscape and sooty and grey-headed albatrosses and northern giant petrels were removed from the $\delta^{15}N$ isoscape). Position of the sub-tropical (STF), sub-Antarctic (SAF) and Antarctic polar (PF) fronts and Marion Island (black triangle) are indicated.

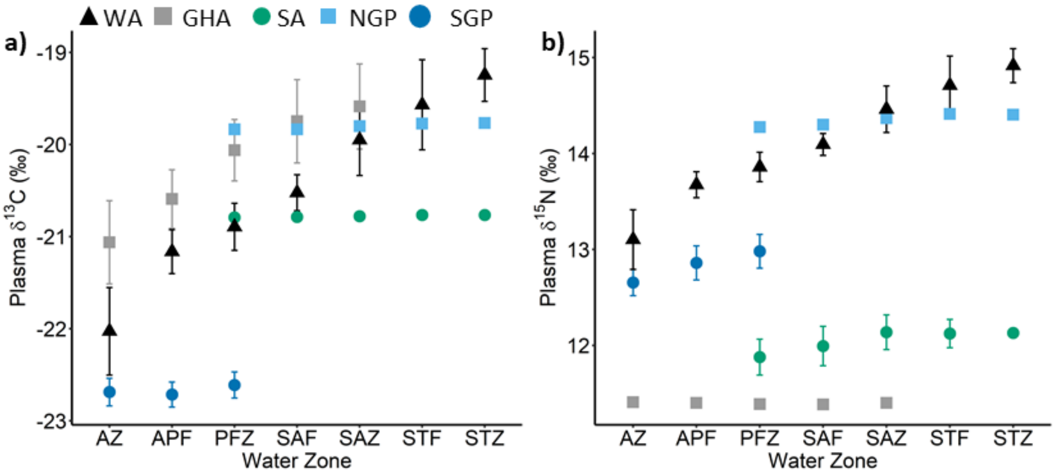


Figure 4.5. The means and standard deviations of a) δ^{13}C and b) δ^{15}N values estimated for seven water zones and fronts: Antarctic zone (AZ), Antarctic polar front (PF), polar frontal zone (PFZ), sub-Antarctic front (SAF), sub-Antarctic zone, (SAZ), sub-tropical front (STF) and sub-tropical zone (STZ) from the species-specific isoscapes presented in Figure 4.2: wandering (WA), grey-headed (GHA) and sooty (SA) albatrosses, northern (NGP) and southern (SGP) giant petrels.

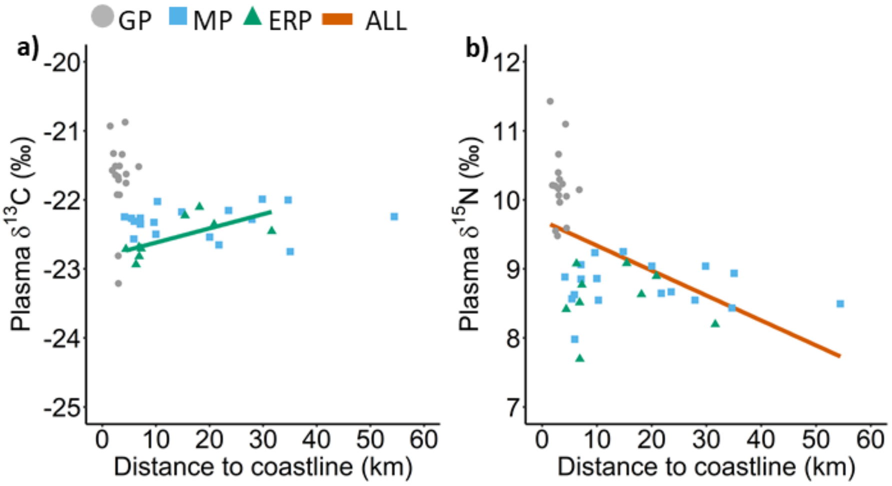


Figure 4.6. Plasma a) δ^{13}C and b) δ^{15}N values of gentoo (GP), macaroni (MP) and eastern rockhopper (ERP) penguins and all penguin species (ALL) combined versus the distance between their mean foraging locations calculated from GPS tracks and the coastline of Marion Island. Only significant correlations are shown.

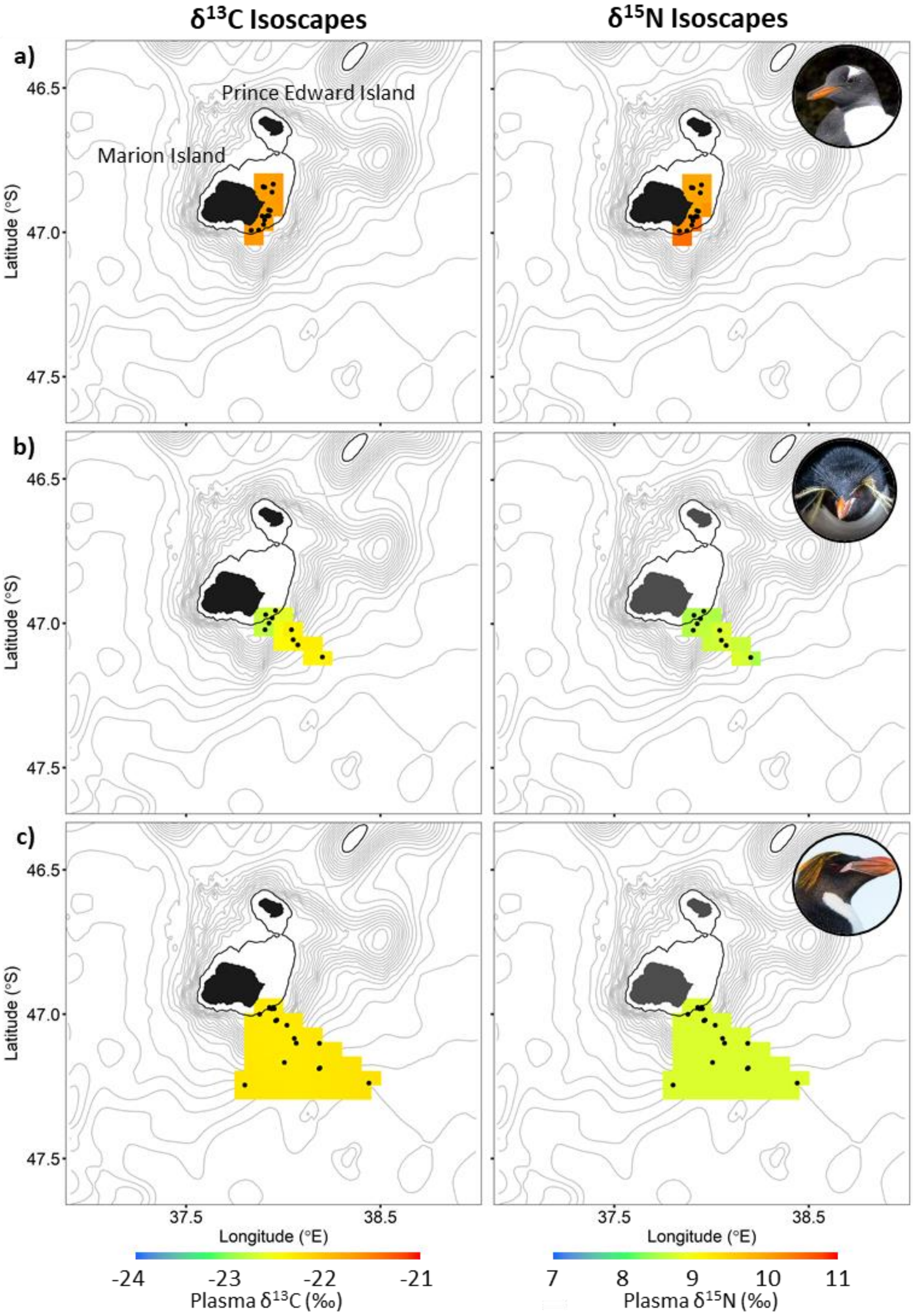


Figure 4.7. Plasma δ13C (left) and δ15N (right) isoscapes of a) gentoo, b) eastern rockhopper and c) macaroni penguins interpolated using ordinary kriging from the isotopic composition of the respective birds' plasmas which were simultaneously tracked with GPS data loggers. Points represent mean foraging locations. Isobaths (grey) are shown at 200 m intervals with 200 m isobath in black.

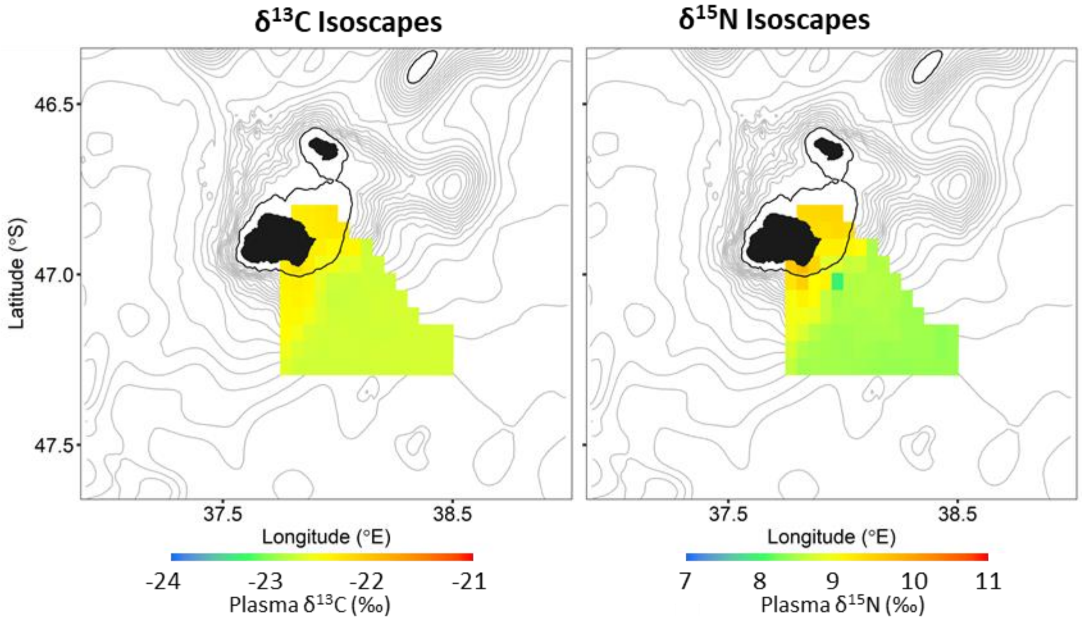


Figure 4.8. Plasma $\delta^{13}C$ (left) and $\delta^{15}N$ (right) isoscapes of three penguin species breeding at Marion Island, Prince Edward Archipelago calculated as the mean of 1000 bootstrapped surfaces interpolated using ordinary kriging which randomly sampled 9 individuals from each penguin species to account for different number of individuals per species. Isobaths (grey) are shown at 200 m intervals with 200 m isobath in black.

Discussion

By combining fine-scale tracking data and stable isotope analysis, we present a critical assessment of concurrent $\delta^{13}C$ and $\delta^{15}N$ gradients across a marine predator assemblage. This study revealed latitudinal spatial gradients in both $\delta^{13}C$ and $\delta^{15}N$ plasma values for far-ranging seabirds (i.e. albatrosses and giant petrels) as well as inshore/offshore gradients for near-ranging seabirds (penguins). Despite demonstrating clear potential for using seabird tissue samples for retrospective geolocation, the inter-specific differences in $\delta^{13}C$ and $\delta^{15}N$ isoscapes cautions against using non-species-specific isoscapes for studying marine predator foraging distributions.

Influence of seabird species on the detection of large-scale spatial variability in $\delta^{13}C$ isoscapes

Strong positive correlations were found between the mean foraging latitudes and $\delta^{13}C$ plasma values of two out of the five flying seabird species, namely the wandering and grey-headed albatrosses. Differences between these two species isoscapes (Figures 4.2, 4.3 and 4.4) as well as the lack of gradients found within the $\delta^{13}C$ isoscape of the remaining species is likely due to differences in diet (Cherel and Klages 1998) and the use of different oceanographic features as foraging grounds (Nel et al. 2001, 2002; Reisinger et al. 2018a).

Influence of diet on a species-specific $\delta^{13}C$ isoscape

It was difficult to discern any spatial gradient within the $\delta^{13}C$ isoscapes of the northern and southern giant petrels and the sooty albatross. This lack of a strong latitudinal gradient in the $\delta^{13}C$ plasma values of these species may be attributed to their more unpredictable diet. For example, at Marion Island the diet of all three species may contain large proportions of seabird and marine mammal carrion (Hunter and Brooke 1992; Cooper and Klages 1995). The relatively narrow range of both the southern giant petrel and sooty albatross $\delta^{13}C$ plasma values (Table 4.1) may suggest that either they preyed on the same seabird carrion or different carrion that had been foraging in similar areas. Without concurrent stomach content sample analysis this is largely speculation, however the lack of spatial gradient found for the $\delta^{13}C$ and $\delta^{15}N$ plasma values of the southern giant petrel and sooty albatross does indicate that caution is needed when using non-species specific isoscapes to infer foraging locations of seabirds from their δ^{13}C tissue values.

Influence of foraging habitat on a species-specific δ^{13}C isoscape

Grey-headed albatrosses from Marion Island remain largely south of the sub-tropical front (this study; Nel et al. 2001), whereas wandering albatross (this study; Nel et al. 2002) frequently move north of the sub-tropical front. However, both species are likely foraging within and around biologically productive eddies that result from interactions between the Agulhas Return Current, sub-tropical and sub-Antarctic fronts (Naik et al. 2015), or within the fronts themselves (Nel et al. 2001; Weimerskirch 2007; Bost et al. 2009). As δ^{13}C values at the base of marine food webs have been shown to significantly correlate with primary productivity and nutrient availability (Francois et al. 1993; Trull and Armand 2001), birds foraging around or within mesoscale eddies originating from the same oceanographic feature are likely to have elevated δ^{13}C tissue values compared to species that forage outside of fronts and eddies. Thus, the higher δ^{13}C plasma values at lower latitudes for the grey-headed albatross compared to other species (Figures 4.3 and 4.4) may result from the grey-headed albatross preferentially foraging in highly productive eddies (Nel et al. 2001). This is further supported by the similar δ^{13}C values found for the wandering and grey-headed albatrosses and northern giant petrel within the sub-tropical front as well as within the sub-Antarctic and sub-tropical water zones (Figure 4.5; Supplementary Material S4.3).

Influence of baseline δ^{13}C gradient on a species-specific isoscape

The δ^{13}C combined species isoscape as well as that of the wandering albatross closely aligns with previously published isoscapes for this region, which used similar methods but only with a single species (wandering albatross; Jaeger et al. 2010a), used whole blood of close-ranging seabirds (e.g. Cherel and Hobson 2007) or baseline values (e.g. Magozzi et al. 2017). Previous studies, which have used a coupled physics-biochemistry model (Magozzi et al. 2017) or satellite tracking coupled with predator tissue values (Jaeger et al. 2010a) to produce δ^{13}C isoscapes for the Indian sector of the Southern Ocean, have shown uniform south-north latitudinal gradient in $\delta^{13}C$ values. In agreement, presented here is a large-scale south-north $\delta^{13}C$ isoscape, albeit with slightly non-uniform latitudinal gradient in $\delta^{13}C$ values. The isoscape presented by Magozzi et al. (2017) had a greater range of $\delta^{13}C$ values between southern Africa and Antarctic (-32 to -16 ‰) compared to our isoscapes (-23 to -18 ‰). Our predator-based isoscape may differ to that of Magozzi et al.'s (2017) for two reasons. Firstly, they modelled the distribution of $\delta^{13}C$ values of phytoplankton and not seabirds. Secondly, Magozzi et al. (2017) showed that in the Indian sector of the Southern Ocean, $\delta^{13}C$ values of phytoplankton become increasingly more negative with the transition of summer to winter months. Therefore, the narrower range of $\delta^{13}C$ values obtained in our $\delta^{13}C$ isoscape can be related to the enrichment of $\delta^{13}C$ values due to fractionation through multiple trophic levels from phytoplankton to seabirds (Michener and Schell 1994; Post 2002), as well as the temporal integration of spatially and temporally variable $\delta^{13}C$ phytoplankton values (Chapter 5).

Other influences on seabirds $\delta^{13}C$ isoscapes

The isoscape map and regression equation of Jaeger et al. (2010) for the wandering albatross tracked from Crozet Archipelago (using similar methods used here), revealed higher $\delta^{13}C$ values with a steeper $\delta^{13}C$ gradient (range: -25.0 to -19.1 ‰) than we found for Marion Island wandering albatrosses (range: -23.6 to -18.4 ‰) over similar latitudes (~38 - 58°S). This could be an artefact of differences in diet between the two populations of wandering albatrosses (Cherel and Klages 1998). However, the mean $\delta^{15}N$ plasma value of the wandering albatross in our study (mean: 14.0 ‰; range: 12.1 to 15.5‰) and Jaeger et al.'s (2010) study (14.0 ‰; 11.2 to 15.8 ‰) was the same, indicating that individuals from the two populations were foraging at similar trophic levels. Rather, a difference in the methods used to remove lipids from plasma between the two studies (cyclohexane (Jaeger et al. 2010) versus a 2:1 chloroform to methanol mix (our study)) may explain the slightly more negative $\delta^{13}C$ values reported by Jaeger et al. (2010). This is supported by the fact that Jaeger et al. (2010) reported a higher C:N ratio (4.1) than we found for the wandering albatross plasma (3.5), which indicates that Jaeger et al. (2010)'s samples had a higher percentage of lipids than ours. Because lipids can lead to artificially low $\delta^{13}C$ values (DeNiro and Epstein 1977; Cherel et al. 2005a), this may explain their lower $\delta^{13}C$ plasma values.

These findings once again highlight the importance of removing or accounting for lipids when inferring the retrospective foraging location of seabirds from their δ^{13}C tissue values (Post 2002; Cherel et al. 2005b). During different life-history stages, seabirds undergo differential levels of nutritional stress, such as periods of fasting, which may result in an increase of lipids circulating in the bloodstream (Cherel et al. 2005a). As previously mentioned, this can lead to artificially low δ^{13}C values (DeNiro and Epstein 1977; Cherel et al. 2005b). However, as δ^{13}C blood values are not (or little) otherwise affected when seabirds undergo nutritional stress (Cherel et al. 2005b), we believe the δ^{13}C isoscapes produced here are transferable across life-history stages of seabirds.

Influence of seabird species on the detection of large-scale spatial variability in δ^{15}N isoscapes

This study revealed a south to north gradient of the wandering albatross and southern giant petrel δ^{15}N plasma values whereas δ^{15}N plasma values of the grey-headed and sooty albatrosses and northern giant petrel lacked a south to north gradient. However, the δ^{15}N plasma values of the sooty albatross did present a relatively weak west to east gradient. The δ^{15}N value of predators' tissues is a combination of their trophic position and δ^{15}N values of organisms at the base of the food chain (Michener and Schell 1994; Post 2002). Therefore, as presented by Jaeger et al. (2010), there are two possible and non-exclusive hypotheses to explain systematic spatial variability in seabird δ^{15}N tissue values: firstly, a dietary shift of the predators or its prey throughout the predator's distributional range and secondly a change in the baseline nitrogen values.

Influence of diet on a species-specific δ^{15}N isoscape

Jaeger et al. (2010) provided evidence for the first hypothesis by using previous studies of the wandering albatross diet to show that, although the wandering albatross breeding at Crozet Archipelago feed on squid across their range, Antarctic squid species feed at lower trophic levels than sub-Antarctic and tropical squid species (Navarro et al. 2013b), which may result in the latitudinal gradient of δ^{15}N plasma values. The same data is not available for the wandering albatross breeding at

Marion Island, but it is reasonable to assume that this is also a factor driving the spatial gradient of the wandering albatross $\delta^{15}N$ plasma values within this study.

Influence of baseline $\delta^{15}N$ gradient on a species-specific $\delta^{15}N$ isoscape

Although diet is undoubtedly an important contributing factor to the $\delta^{15}N$ plasma values of the birds within this study, this study provides evidence towards Jaeger et al. (2010)'s second hypothesis: baseline $\delta^{15}N$ values influence the latitudinal gradient in $\delta^{15}N$ plasma values of seabirds. Evidence supporting this argument is that the wandering albatross and southern giant petrel had similar regression slopes between mean foraging latitudes and $\delta^{15}N$ plasma values. The difference between these two species $\delta^{15}N$ isoscapes was homogenously 1 ‰ across overlapping areas (Figure 4.3), which may reflect difference in their diets (Cherel and Klages 1998). Furthermore, the wandering albatross and southern giant petrel $\delta^{15}N$ isoscapes as well as the $\delta^{15}N$ isoscape resulting from the combination of their data (Figure 4.4b) resembled the latitudinal gradients previously found for $\delta^{15}N$ values across the Indian sector of the Southern Ocean for seabirds (wandering albatross: Jaeger et al. 2010) and baseline values (Somes et al. 2010). The values within these $\delta^{15}N$ isoscapes ranged between ~12 ‰ in the south and ~15 ‰ in the north, closely matching the ~2 ‰ modelled gradient in baseline $\delta^{15}N$ values between Antarctica and the coastline of southern Africa (Somes et al. 2010). This indicates that these spatially variable baseline values propagate up the food chain and can be observed in the $\delta^{15}N$ tissue values of the seabirds. These are important findings for the use of stable isotope analysis for the retrospective geolocation of marine consumers. Previously, $\delta^{13}C$ values of predator tissues have been used for retrospective geolocation, however, agreement among trends found within $\delta^{15}N$ isoscapes in this study and two others (Jaeger et al. 2010; Somes et al. 2010) provide evidence toward the use of $\delta^{15}N$ tissue values as an additional tool for retrospective geolocation. It further emphasizes the importance of taking the spatial gradients of $\delta^{15}N$ values into account when inferring trophic level from $\delta^{15}N$ tissue values. Of course, it is also important to consider the diet composition and corresponding trophic level of predators and how this may vary within the population (e.g. among age-classes or between sexes) since there is an enrichment of 0.5 – 1 ‰ for $\delta^{13}C$ values and 3 – 5 ‰ for $\delta^{15}N$ values per trophic level (Michener and Schell 1994; Post 2002).

Influence of foraging habitat on a species-specific $\delta^{15}N$ isoscape

Even though the $\delta^{15}N$ plasma values of the sooty albatross did not show any correlation with latitude, the correlation between their $\delta^{15}N$ plasma values and longitude may still provide evidence towards the second hypothesis (i.e. baseline $\delta^{15}N$ gradient influence on marine predator $\delta^{15}N$ tissue values). Foraging of sooty albatross breeding at Marion Island within 20 - 25° longitude is largely concentrated along the South West Indian Ridge (Schoombie et al. 2017). The interaction between the fast-flowing Antarctic Circumpolar Current and this ridge results in zones of upwelling as well as meandering of fronts and eddy formation (Ansorge and Lutjeharms 2005). Consequently, pockets of high productivity all along the ridge may cause periodically higher $\delta^{15}N$ values at the base of the food web (DiFiore et al. 2006). This may explain the longitudinal gradient in the $\delta^{15}N$ values between individual sooty albatross feeding closer to the ridge (between 20 – 25°E) and further downstream of it. Without concurrent stomach content samples of the tracked birds or samples of phytoplankton in the birds' foraging areas, no definite conclusion can be drawn. Compound specific stable isotope analysis could be used in future investigations to overcome these uncertainties (Whiteman et al. 2019).

Fine scale spatial variability in δ13C and δ15N isoscapes estimated from seabird tissues

This is the first study to combine the use of GPS dataloggers and the carbon and nitrogen stable isotope values of penguins to investigate fine-scale isotopic variability across space. It was found that even though all three penguin species stayed much closer to the island (0.5° latitudinal range) than the albatrosses and giant petrels (30° latitudinal range), they had lower $\delta^{13}C$ plasma values than most of the flying seabirds (Table 4.1). This indicates that, while their isotopic values may be affected by latitudinal gradients in $\delta^{13}C$ and $\delta^{15}N$ stable isotopes (this study; Jaeger et al. 2010; Somes et al. 2010; Magozzi et al. 2017), there are other factors impacting their isotopic values. These factors are most likely related to the major differences in foraging ecology between penguins and flying seabirds as well as regional physical features which contribute to fine scale spatial variability in baseline isotopic values at the Prince Edward Archipelago compared to elsewhere (Kaehler et al. 2000; Pakhomov et al. 2004; Allan et al. 2013).

The inshore consumers at the Prince Edward Archipelago, like the gentoo penguin (Carpenter-Kling et al. 2017), derive their energy from external and internal sources. The external source is a result of allochthonous prey species being advected and concentrated around the archipelago by the Antarctic Circumpolar Current (Perissinotto and McQuaid 1992; Ansorge et al. 1999). Internally, due to the island mass effect, there is localized enhancement of biological productivity (Perissinotto and Duncombe Rae 1990; Ansorge et al. 1999). Due to these two different energy sources, autochthonous species (e.g. microphytoplankton, benthic krill *Nauticaris marionis*, and fish), particularly benthic species, have higher values of both δ^{13}C and δ^{15}N compared to allochthonous species (e.g. sub-Antarctic krill *Euphausia vallentini*) found in the vicinity of the archipelago or in the surrounding pelagic waters (Kaehler et al. 2000; Pakhomov et al. 2004; Allan et al. 2013).

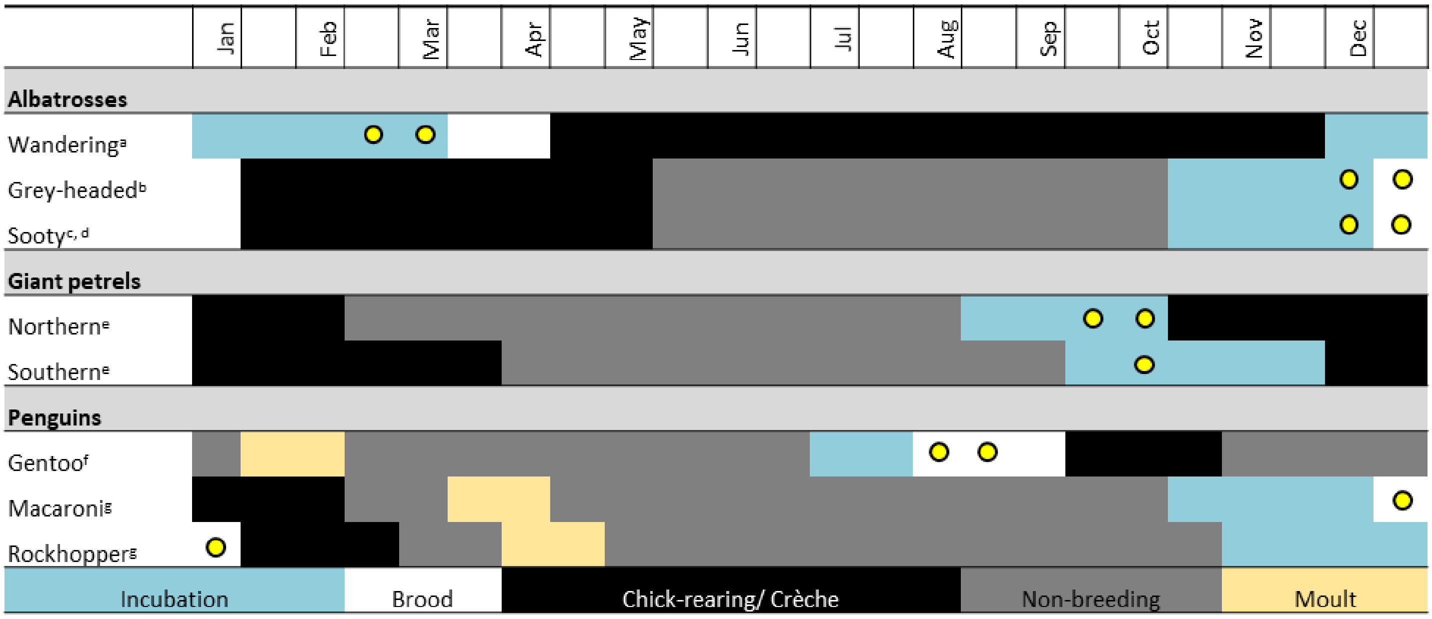
The δ^{13}C and δ^{15}N isoscapes of penguins are therefore a combination of their diet and foraging habitat. The gentoo penguin breeding on Marion Island are strictly inshore foragers and are typically benthic foragers but they can also forage pelagically (Carpenter-Kling et al. 2017). Their diet at Marion Island is highly variable, composed of mainly benthic fish and an autochthonous benthic crustacean (i.e. *Nauticaris marionis*) but can contain large proportions of pelagic crustaceans and juvenile fish if they are available (Adams and Klages 1989; Carpenter-Kling et al. 2019a). In contrast, the crested penguins (macaroni and eastern rockhopper penguins) are typically pelagic foragers with the eastern rockhopper penguin also exhibiting the ability to forage benthically (Tremblay and Cherel 2000; Whitehead 2017). Although the brooding macaroni penguin reach further distances away from the island than the brooding eastern rockhopper penguin (this study; Whitehead 2017), the diet of both species is almost completely dominated by allochthonous pelagic krill species (i.e. *Euphausia vallentini* and *Thysanoessa vicina*), with small amounts of fish being eaten by both species (Brown and Klages 1987; Pistorius unpub. data; Department of Environment, Forestry and Fisheries unpub. data). Thus, the inshore/offshore gradient in both $\delta^{13}C$ and $\delta^{15}N$ plasma values of penguins in this study is largely related to the benthic and autochthonous foraging ecology of the gentoo penguin and the pelagic, allochthonous foraging ecology of the crested penguins. Cherel and Hobson (2007) similarly attributed the higher $\delta^{13}C$ tissue values of shelf-feeding gentoo penguin at the Kerguelen Islands to local enhanced productivity and benthic feeding. In addition, although it has not been investigated for seabirds, there is the possibility of foraging depth having an impact on the isotopic values of penguins' tissues, as seen in tunas (Houssard et al. 2017).

Conclusion

Using a multi-species approach this study shows that large and regional scale systematic spatial variability of $\delta^{13}C$ and $\delta^{15}N$ values at the base of the marine food web propagates through trophic levels and is reflected in the isotopic values of top predators' tissues. This study provides evidence for the effect of baseline $\delta^{15}N$ values on predator $\delta^{15}N$ tissues values. This result emphasizes the importance of considering $\delta^{15}N$ oceanic isoscapes in studies that incorporate stable isotopic values of marine predators to investigate their trophic ecology. Although these baseline values propagate through the food chain and are reflected across multiple marine predator species, they are not reflected in all species. This may be as a result of the movement of prey species or foraging of individuals across major water zones and fronts. It is therefore important when possible to estimate and apply species-specific isoscapes or have a good understanding of any factors and pathways affecting marine predators' isotopic values when studying marine predator stable isotope ecology. It is further important to note that this study was performed using the stable isotope values of seabirds' plasma, which may not reflect stable isotope values of other tissues such as whole blood or feathers (Jaeger et al. 2010). With seasonal variation in the gradient of baseline $\delta^{13}C$ highlighted in Magozzi et al. (2017), future investigation should include intra- and interannual variability in stable isotope compositions detected at the top predator level.

Supplementary Material

Supplementary Material S4.1. Approximate dates of different breeding stages throughout the year for wandering, grey-headed and sooty albatrosses, northern and southern giant petrels and gentoo, macaroni and eastern rockhopper penguins breeding at Marion Island, sub-Antarctic. Yellow dots represent approximate times when GPS data loggers were deployed on birds and blood plasma was collected for stable isotope analysis.



Jones et al. (2009)[a]; FitztPatrick Institute unpub. data[b]; Berruti (1979)[c]; Schoombie et al. (2016)[d]; Cooper et al. (2001)[e]; Crawford et al. (2003)[f]; Crawford et al. (2006)[g]

Supplementary Material S4.2. Species-specific normalizing equations calculated from plasma samples (N) with both delipidated and raw plasma for wandering, grey-headed and sooty albatrosses and gentoo and macaroni penguins breeding at Marion Island, sub-Antarctic.

Species	N	Normalizing equation	mean ΔC:N mass ratio used	C:N mass ratio of raw plasma	C:N mass ratio of delipidated plasma
Albatrosses					
Wandering	66	$\Delta\delta^{13}C = (\Delta C:N + 0.4497) / 0.1936$	3.45	4.27 ± 0.18	3.45 ± 0.15
Grey-headed	41	$\Delta\delta^{13}C = (\Delta C:N + 0.2298) / 0.5647$	3.49	4.39 ± 0.35	3.49 ± 0.11
Sooty	34	$\Delta\delta^{13}C = (\Delta C:N + 0.5582) / 0.1782$	3.45	4.26 ± 0.18	3.45 ± 0.11
Penguins					
Gentoo	29	$\Delta\delta^{13}C = (\Delta C:N + 0.3075) / 0.2996$	3.59	4.26 ± 0.15	3.59 ± 0.10
Macaroni	51	$\Delta\delta^{13}C = (\Delta C:N - 0.07724) / 0.5526$	3.57	4.44 ± 0.20	3.57 ± 0.08

Supplementary Material S4.3. Corresponding plasma a) δ13C (‰) and b) δ15N (‰) values given as mean ± SD (range) for different water zones and fronts (AZ: Antarctic zone, PF: polar front, PFZ: polar frontal zone, SAF: sub-Antarctic front, SAZ: sub-Antarctic zone, STF: sub-tropical front and STZ: sub-tropical zone) estimated from isoscapes interpolated from mean foraging locations and plasma isotopic values of wandering, grey-headed and sooty albatrosses, northern and southern giant petrels breeding at Marion Island.

	Species	Water zone						
		AZ	PF	PZF	SAF	SAZ	STF	STZ
a)	**$\delta^{13}C$**							
	Albatrosses							
	Wandering	-22.0 ± 0.5 (-23.0; -20.9)	-21.2 ± 0.2 (-21.7; -20.7)	-20.9 ± 0.3 (-21.6; -20.4)	-20.5 ± 0.2 (-21.0; -20.2)	-20.0 ± 0.4 (-20.9; -19.0)	-19.6 ± 0.5 (-20.7; -18.8)	-19.2 ± 0.3 (-20.0; -18.9)
	Grey-headed	-21.1 ± 0.5 (-21.7; -20.3)	-20.6 ± 0.3 (-21.3; -20.1)	-20.1 ± 0.3 (-21.1; -19.3)	-19.7 ± 0.5 (-20.6; -19.1)	-19.6 ± 0.5 (-20.4; -18.8)		
	Sooty			-20.8 ± 0.0 (-20.8; -20.8)	-20.8 ± 0.0 (-20.8; -20.8)	-20.8 ± 0.0 (-20.8; -20.8)	-20.8 ± 0.0 (-20.8; -20.8)	
	Giant petrels							
	Northern			-19.8 ± 0.0 (-19.9; -19.8)	-19.8 ± 0.0 (-19.9; -19.8)	-19.8 ± 0.0 (-19.8; -19.7)	-19.8 ± 0.0 (-19.8; -19.8)	-19.8 ± 0.0 (-19.8; -19.7)
	Southern	-22.7 ± 0.1 (-23.5; -22.2)	-22.7 ± 0.1 (-23.3; -22.5)	-22.6 ± 0.1 (-23; -21.9)				
b)	**$\delta^{15}N$**							
	Albatrosses							
	Wandering	13.1 ± 0.3 (12.5; 13.8)	13.7 ± 0.1 (13.4; 13.9)	13.9 ± 0.2 (13.5; 14.2)	14.1 ± 0.1 (13.8; 14.3)	14.5 ± 0.2 (13.8; 15.1)	14.7 ± 0.3 (14.0; 15.2)	14.9 ± 0.2 (14.5; 15.2)
	Grey-headed	11.4 ± 0.0 (11.4; 11.5)	11.4 ± 0.0 (11.4; 11.5)	11.4 ± 0.0 (11.3; 11.4)	11.4 ± 0.0 (11.3; 11.4)	11.4 ± 0.0 (11.3; 11.5)		
	Sooty			11.9 ± 0.2 (11.6; 12.3)	12.0 ± 0.2 (11.6; 12.4)	12.1 ± 0.2 (11.7; 12.4)	12.1 ± 0.1 (11.8; 12.3)	
	Giant petrels							
	Northern			14.3 ± 0.0 (14.2; 14.3)	14.3 ± 0.0 (14.2; 14.3)	14.4 ± 0.0 (14.2; 14.5)	14.4 ± 0.0 (14.4; 14.5)	14.4 ± 0.0 (14.2; 14.5)
	Southern	12.7 ± 0.1 (12.4; 13.1)	12.9 ± 0.2 (12.5; 13.2)	13 ± 0.2 (12.5; 13.3)				

Chapter 5:

Sensitivity of $\delta^{13}C$ values of seabird tissues to combined spatial, temporal and ecological drivers: a simulation approach

Carpenter-Kling T, Pistorius PA, Connan M, Reisinger RR, Magozzi S, Trueman C. 2019. Sensitivity of $\delta^{13}C$ values of seabird tissues to combined spatial, temporal and ecological drivers: a simulation approach. *Journal of Experimental Marine Biology and Ecology* 512: 12-21

Introduction

Stable isotope ecology has become a common and powerful tool for retrospective geolocation of animals in both marine (e.g. Graham et al. 2010) and terrestrial systems (e.g. West et al. 2014). Approximate foraging locations of consumers can be reconstructed by linking the stable isotope compositions of their tissues to spatial models of the isotopic composition of organisms at the base of food webs. In marine systems, animal movement is commonly inferred by linking the ratios of the stable isotopes of carbon ($^{13}C/^{12}C$; $\delta^{13}C$) of predator tissues to latitudinal gradients in $\delta^{13}C$ values of phytoplankton ($\delta^{13}C_{plk}$; Jaeger et al. 2010a; MacKenzie et al. 2011; Trueman et al. 2012; Bird et al. 2018; Trueman and St John Glew 2018).

The accuracy and precision associated with isotope-based reconstruction of animal movements depends on the quality of the reference spatial models of the underlying isotopic gradients, commonly termed isoscapes. Isoscape models of $\delta^{13}C_{plk}$ are typically constructed by spatial interpolation between empirical reference data sampled from known locations (Francois et al. 1993; Quillfeldt et al. 2005; Mackenzie et al. 2014; Trueman et al. 2017). Interpolation models may also include predictive statistical relationships between widely measured environmental variables and reference isotope data (Wunder 2010; Mackenzie et al. 2014; West et al. 2014) or isotopic values of predator tissue for which movements were known (Cherel and Hobson 2007; Jaeger et al. 2010a). The uncertainty associated with isoscape models clearly increases with decreasing spatial coverage of reference samples. In marine systems, phytoplankton are at the base of food webs. They are small-celled organisms with rapid growth which means their isotopic compositions reflect local and short-term variations in oceanic conditions (Graham et al. 2010; Magozzi et al. 2017).Therefore, static maps of $\delta^{13}C_{plk}$ across the global oceans capture large scale latitudinal patterns of isotopic variability but may be relatively poor predictors of isotopic compositions at any particular place and time. This reduces the confidence that can be placed in isotope-based inferences about animal movements. In the open ocean, gathering reference samples from regularly spaced spatially extensive locations is particularly challenging; consequently, relatively few ocean basin-scale isoscape models have been created, and no temporally-explicit sample-based isoscapes have been created for oceanic ecosystems (Trueman and St John Glew 2018).

As isotope-based geolocation is primarily concerned with carbon and nitrogen in marine systems, interpretation of the spatial signal is inherently intertwined with variation in diet and physiological isotopic transformations through the food web between primary production and consumer tissues. Consequently, the isotopic composition of a mobile consumer's tissue depends on a number of intrinsic (behavioural and physiological) and extrinsic (environmental) variables:

(4) spatio-temporal variations of stable isotope compositions of phytoplankton at the base of the food web,
(5) location(s) of consumers over the timescale of isotopic incorporation,
(6) isotopic averaging and physiological fractionation through intermediate trophic levels, and
(7) isotopic turnover rates and physiological transformations in the consumer.

The isotopic expression associated with the variables expressed above is usually incompletely known and interpreting stable isotope compositions of mobile marine consumers is challenging. Simulation modelling provides a framework to identify those variables likely to impact the isotopic compositions of consumer tissues, given a context-specific interaction between the scale and nature of baseline isotopic variability, foraging range, phsyiology, and food web interactions.

Magozzi et al. (2017) developed a process-based carbon isotope model to predict the spatio-temporal distribution of $\delta^{13}C$ values in phytoplanton ($\delta^{13}C_{plk}$) across the global ocean at one degree spatial and monthly temporal resolution (Figure 5.1). The model uses an ocean general circulation model of intermediate complexity, averaged over 10 years (2001-2010) to minimize the effect of interannual variability, combined with general assumptions related to carbon isotope fractionation to produce monthly isoscapes. It provides a spatio-temporal framework for *in-silico* modelling and experimentation to better understand the movement of marine predators using intrinsic stable isotope markers (Bird et al. 2018; St John Glew et al. 2018; Trueman & St John Glew 2018).

Here, we explore the likely sensitivity of δ^{13}C values of marine predator tissues to a suite of environmental and ecological variables using *in-silico* experiments. We simulate the at-sea movement and distribution of a land-breeding marine predator, by building a simple agent-based movement model. The agent based model outputs time and location which are then integrated with the temporally-specific isoscapes produced by Magozzi et al. (2017) to simulate expected δ^{13}C values in the predator's tissues. We then explore the sensitivity of simulated tissue δ^{13}C values to intrinsic and extrinsic drivers by systematically varing terms in the agent based model or in the isoscape model.

Simulation results are compared to isotopic data measured from individual consumers equipped with global positioning system (GPS) devices. We investigate 1) the effect of the choice of reference isoscape used on inference of predator δ^{13}C values, and 2) the effect of predator behavioural changes on their δ^{13}C compositions. We use female northern giant petrels *Macronectes halli* (NGP) incubating eggs at sub-Antarctic Marion Island as a model species, but note that the approach outlined here could be adapted to explore the potential drivers behind isotopic variability for any mobile marine consumer principally by modifying the agent based model rules to approximate foraging behaviour and isotopic integration rates for the study species and tissue type.

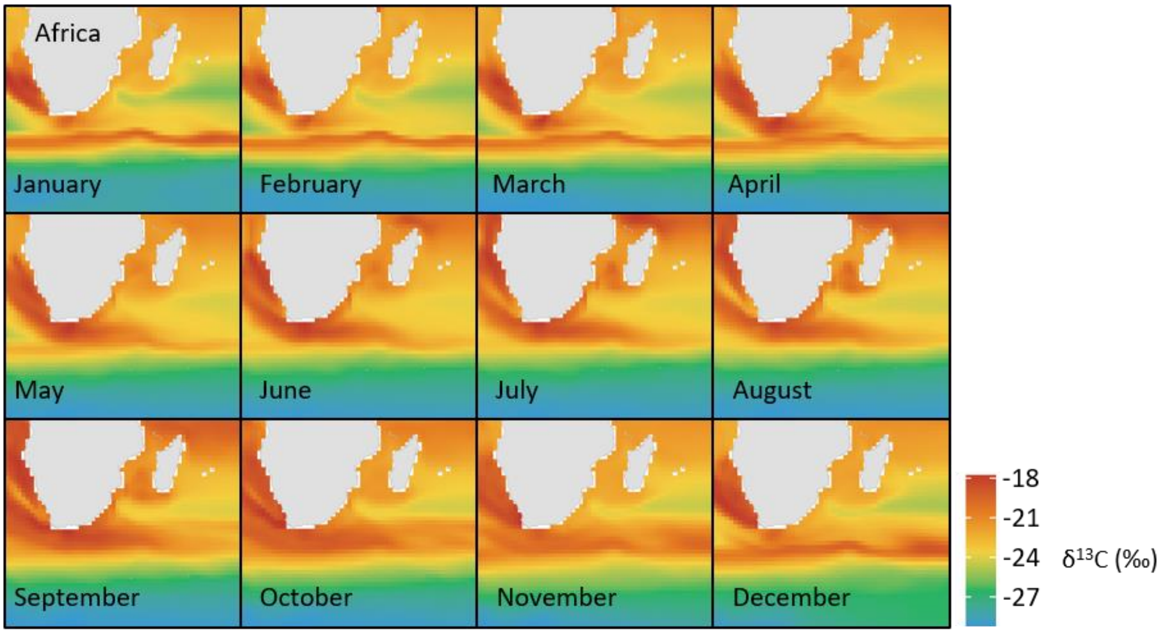


Figure 5.1. Monthly maps of the distribution of δ^{13}C of phytoplankton resulting from a processed-based carbon model produced by Magozzi et al. (2017).

Materials and Methods

Study site and species

The Prince Edward Archipelago is made up of the larger Marion Island (240 km^2) and Prince Edward Island (45 km^2) and provides critical breeding and moulting habitat for approximately 5 million seabirds and seals (Ryan & Bester 2008). It is located in the Indian sector of the Southern Ocean within the Polar Frontal Zone, between the sub-Antarctic front (SAF) in the north and Antarctic polar front (APF) in the south (Ansorge and Lutjeharms 2002).

On Marion Island there are approximately 400 northern giant petrel (NGP) breeding pairs (Ryan et al. 2009). Eggs are laid in mid-August and are incubated for approximately 60 days (Cooper et al. 2001). Parental duties are evenly distributed between parents (Cooper et al. 2001). Male NGPs are primarily scavengers, feeding on penguin and seal carrion, whereas females tend to rely on marine prey resources – fish, crustaceans and cephalopods (Hunter and Brooke 1992; Forero et al. 2005).

Data collection

Field work

Field work was conducted along the south-east coast of Marion Island (46°54’S; 37°45’E) during September and October 2015 and 2016. Global positioning system loggers (CatLog-S GPS loggers, Perthold Engineering LLC USA, 50 × 22 x 8 mm, 8 g) covered in heat shrink tubing for water-proofing were deployed on 20 female NGPs (2015: n = 6 and 2016: n = 14). Loggers were programmed to record locations hourly. To facilitate retrieval of devices, loggers were deployed during late incubation.

At retrieval of GPS data loggers after one foraging trip, ~1 ml of blood was collected from the tarsal vein using a heparinised 25 gauge needle. Approximately half of the blood sample was stored directly in 70 % ethanol and frozen until preparation for further analysis. The remainder of the blood was centrifuged within 3-4 hours after collection, separated into red blood cells and plasma, stored in 70% ethanol and frozen until preparation for stable isotope analysis. Seventy percent ethanol has been shown to be an effective method of preserving blood without affecting its isotopic composition (Hobson et al. 1997).

GPS analyses

GPS locations indicating unrealistic movement speeds were identified by plotting the speed between consecutive GPS locations and removing those which were identified as outliers (2 of the total 966 locations). From the filtered data, new positions were linearly interpolated at one hour intervals (R package: *adehabitatLT*; Calenge 2006) and the average duration, distance travelled and maximum distance from breeding ground were calculated for each trip.

Stable isotope analyses

Plasma was dried at 50°C for 24-48 h before being powdered. Lipids are depleted in ^{13}C (DeNiro and Epstein 1977); therefore, lipids were removed from plasma samples by immersing powdered plasma in a 2:1 chloroform:methanol solution with a solvent volume three to five times greater than sample volume. Samples were then vortexed for 10 seconds every 10 minutes for one hour before being centrifuged for five minutes. The supernatant containing lipids was discarded, and samples dried at 50°C overnight.

The isotopic compositions of carbon and nitrogen in aliquots (~0.4 mg) of homogenized delipidated plasma samples were determined by combusting samples in a Flash 2000 organic elemental analyser and passing gasses through a Delta V Plus isotope ratio mass spectrometer via a Conflo IV gas control unit (Thermo Scientific, Germany). All samples were processed at the Stable Light Isotope Unit at the University of Cape Town, South Africa. Replicate measurements of internal laboratory standards indicated minimal standard deviations within and among runs (Merck gel: $\delta^{13}C = 0.2$ ‰, $\delta^{15}N < 0.1$ ‰; valine: $\delta^{13}C < 0.2$ ‰, $\delta^{15}N = 0.1$ ‰; seal bone: $\delta^{13}C < 0.2$ ‰, $\delta^{15}N < 0.1$ ‰). All in-house standards were calibrated against International Atomic Energy Agency standards. Carbon is expressed in terms of its value relative to Vienna PeeDee Belemnite.

Model framework

Stable isotope baseline model

We used the monthly isotopic prediction surfaces for $\delta^{13}C_{plk}$ produced by Magozzi et al. (2017) as primary inputs for simulation modelling. To account for trophic attenuation of $\delta^{13}C$ values through trophic levels, we produced a new suite of monthly prediction surfaces estimating isotopic compositions of four successive trophic levels by calculating a moving average of each cell of the $\delta^{13}C$ isotopic maps. The initial model predicts $\delta^{13}C$ values in phytoplankton (trophic level 1) at monthly resolution. We developed surfaces for additional time-integration steps by creating a moving average over 2 months (trophic level 2), 4 months (trophic level 3) and 6 months (trophic level 4) successively.

Environmental baseline

Sea-surface temperature (°C, 1° resolution) and phytoplankton abundance (mmol $N.m^{-3}$, for combined diatom and non-diatom communities) were extracted at monthly intervals from the same NEMO--MEDUSA simulations used to estimate $\delta^{13}C_{plk}$ values (Yool et al. 2013; Magozzi et al. 2017). Water depth (m, 1° resolution) was extracted from the General Bathymetric Chart of the Oceans (GEBCO) global bathymetry dataset (http://www.gebco.net/data_and_products/gridded_bathymetry_data/).

Agent-based northern giant petrel movement model

We draw on an agent-based model (ABM) to provide time-specific location data for integration with isoscape models. It is important to note that the ABM is not developed as a tool to infer movement behaviour. In principle an ABM could be developed with relatively few movement rules and large numbers of repeat simulations. Alternatively, a highly constrained ABM could be developed ideally yielding few unrealistic movement or position estimates. For this example, we develop a relatively basic ABM informed from data logging GPS data to reduce computational time associated with running very large combinations of unlikely parameter fields.

The movements of incubating female NGPs were simulated using a simple agent-based model (Figure 5.2). In the model, daily direction and extent of movement are drawn from probability distributions influenced by foraging trip duration, daily step distance, sea surface temperature, water depth and phytoplankton concentration (as a proxy for zooplankton food availability). Although the model is limited to using these variables to simulate the movement of NGPs, we feel they are adequate as Reisinger et al. (unpubl. data) showed that sea surface temperature, chlorophyll-a concentration and depth are important drivers of these birds' movement. It is important to note that the aim of the model is simply to provide movement tracks that broadly replicate known movements and not as an exploration of potential ecological drivers of movement. Movement rules were established based on known movement parameters:

(i) Daily step distance. The GPS tracks (n=20) of incubating female NGPs revealed the birds performed two types of trips: (1) a smaller maximum daily step distance (n=4; 331.01 ± 115.02 km per day) remaining close to the island or (2) a greater daily step distance (n=16; 965.01 ± 112.17 km per day) travelling further afield from the island. Therefore, within the movement model, the modelled NGPs could choose to perform either type of trip, with the probability of choosing to remain close to the island set as 15%.

(ii) Foraging trip length. Mean foraging trip duration, based on GPS tracks, was 8± 2 days and this was then used as foraging trip duration of the modelled NGPs. Furthermore, when either leaving for or returning from a foraging trip, NGPs displayed more directed movement either towards favoured environmental conditions or toward the island, respectively, compared to during the middle of the foraging trip.

(iii) Food availability. Phytoplankton concentration was included as a proxy for food availability. If phytoplankton concentrations were above 38 mmol $N.m^{-3}$, the mean probability of remaining in that cell was increased by 30%.

(iv) Sea surface temperature. Simulated NGPs were more likely to move towards warmer temperatures up to a maximum of 22.0°C. If sea surface temperatures were < 19.5 or > 22.0°C (temperatures which are typically associated with the Agulhas Current, Valentine & Lutjeharms 1984), the mean probability of moving away from the current cell was increased to 80%.

(iv) Water depth. Female NGPs preferred open water to shelf regions and were coded to prefer foraging in water depths between 4000-4500 m and were less likely to move towards waters outside this range.

Modelled birds left for their first foraging trip on 15 August, the mean egg laying date (Cooper et al. 2001), and simulations lasted for approximately 60 days, the approximate incubation time of an NGP (Cooper et al. 2001). Birds alternated between incubation shifts (i.e. remaining on the nest to incubate their egg while their partner departed on a foraging trip) and foraging trips.

R code of agent-based movement model presented here is deposited at Carpenter-Kling et al. (2019): https://doi.org/10.6084/m9.figshare.7531445.v1

Values within this section are given as mean ± standard deviation.

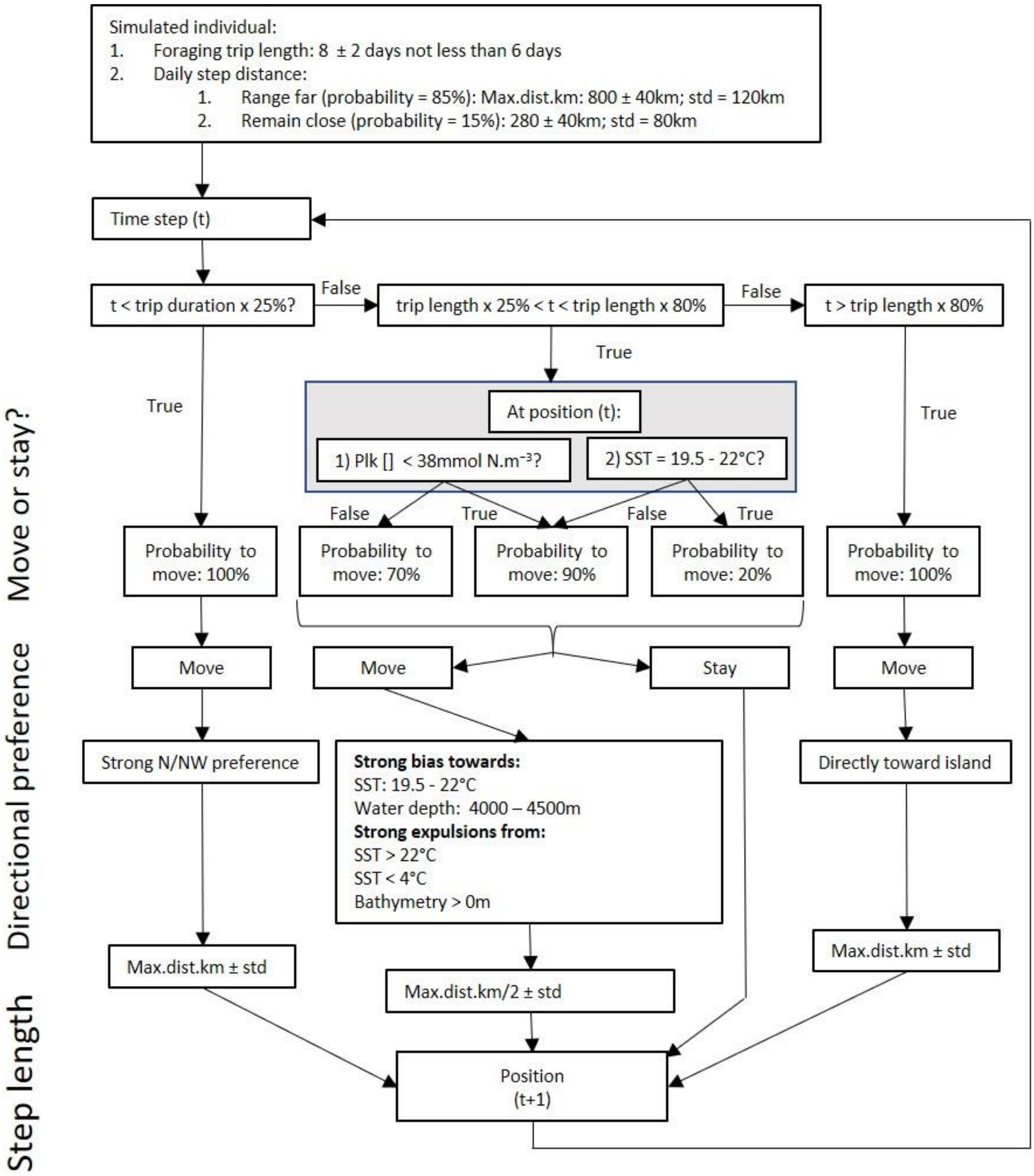


Figure 5.2. The computational process used to simulate the movement of female incubating northern giant petrels (NGP) using an agent-based movement model. In the model, daily likelihoods, directions and extents of movement are drawn from probability distributions influenced by foraging trip duration, daily step distance, sea surface temperature (SST), water depth and phytoplankton concentration Plk[]. At the initiation of the model the simulated NGP is assigned a foraging trip duration, a decision to perform long or short trips and maximum daily step distance (Max.dist.km). During each time step, each simulated NGP may move to a new location or decide to stay where is it depending on how far it is into its foraging trip and its surroundings. The model was run for 60 days (approximate length of NGP incubation) starting on 15 August (approximate laying initiation date for giant petrels).

Simulating blood δ^{13}C tissue values

For each location produced during a movement simulation model, the δ^{13}C value reflecting δ^{13}C$_{plk}$ values integrated as a moving average across the previous 6 months was sampled, simulating potential temporal averaging across four trophic levels. The blood plasma δ^{13}C values of modelled birds returning from a foraging trip were calculated by firstly weighting δ^{13}C values by the relative abundance of food at that location (inferred from model phytoplankton concentrations). While fasting, the δ^{13}C values of animal tissue may decrease as the animal may incorporate ^{13}C depleted lipids into proteins to meet energy demands (Cherel et al. 2005a). To simulate the impact of fasting during incubation on blood δ^{13}C values, δ^{13}C values assimilated during days associated with fasting were down-weighted by multiplying by 0.1. Attenuation of prey δ^{13}C values into bird tissues was simulated using a moving average of 7 days, the approximate turnover rate of plasma (Hobson and Clark 1992). The δ^{13}C blood value on the day the bird returned to the island was taken to represent that foraging trip.

Testing sensitivity of blood δ^{13}C values with in-silico experiments

The effect of temporal variation in the reference isoscape on predator δ^{13}C tissue values

Previously, retrospective geolocations of marine predators have been made from temporally-static isoscapes which represent single trophic levels (e.g. Francois et al. 1993; Cherel et al. 2007). Here, we investigated the potential influence of three components of temporal variability in baseline isotopes on consumer tissue carbon isotope values. We tested:

i) Temporal attenuation in stable isotope compositions with increasing trophic level: For each position of a simulated NGP resulting from the original movement model δ^{13}C values were extracted from the suite of maps using moving averages of 1 month, 2 months and 4 months (approximating trophic attenuation over 1, 2 and 3 trophic levels *See Stable isotope baseline model*).

ii) Temporal resolution in baseline isoscapes: To identify the difference expected when estimating isotopic compositions based on a single static isoscape compared to temporally varying reference isoscapes, a single biomass-weighted annual average isoscape was calculated by averaging all the monthly isoscapes and weighting relative monthly values by the total biomass in each month.

iii) Seasonal mis-matching: To investigate whether using a single temporal isoscape, but from a different season, would have an influence on the δ^{13}C plasma values of NGPs, the original movement model was initiated four months before and after the original starting date (i.e. 15 April and 15 December).

The effect of predator behavioural changes on their isotope composition

During years of variable prey availability, some species of seabirds have shown plasticity in the date they initiate breeding (e.g. Dobson et al. 2017) and foraging effort (e.g. Green et al. 2015; Whitehead et al. 2017). By making the following modifications to the agent-based movement model, we investigated whether behavioural changes such as these would influence the δ^{13}C composition of NGPs' plasma:

i) Laying initiation date: The date the female NGPs initiated breeding was changed by 15 days before and after mean date of laying (15 August; Cooper et al. 2001)at increments of 5 days.

ii) Foraging trip duration: The mean foraging trip duration of NGPs (8 ± 2 days) was increased to 14 days at 2 day increments.

iii) Daily step length: The daily step length was increased and decreased by 150 km at increments of 50 km.

Statistical analysis

Kernel density distributions (Worton 1989) were used to visualize the distribution of time spent at sea of real and modelled NGPs (R package *adehabitatHR*; Calenge 2006). The most appropriate smoothing factor was chosen using the ad hoc method (Worton 1989) and grid size was set at 1°, matching the resolution of the underlying environmental maps. The 50% and 95% kernel contours were calculated and plotted as they are thought to represent the home range and core areas of use by an animal (Fieberg and Kochanny 2005).

Distributions of most of the δ^{13}C plasma values of simulated birds returned by the agent-based movement models, and their modifications were negatively skewed, reflecting the variable use of sub-polar and polar regions with relatively low model-predicted δ^{13}C values. To compare the distributions of δ^{13}C plasma values between model runs we used Bayesian estimation for two groups with a skewed-normal distribution family (R package *brms*; Bürkner 2017) to estimate the mean, standard deviation and skewness of δ^{13}C plasma values.

Results

The agent-based movement model successfully reproduced broad foraging distribution and movement path characteristics of female NGP's (Figure 5.3 a, b). Simulations correctly identified the two core areas where the NGPs spent time while at sea, one closer to Marion Island and the other along the coast of southern Africa. The movement model based on 100 simulated individuals resulted in 356 simulated blood plasma δ^{13}C values.

Measured δ^{13}C values of NGP plasma (-20.0 ± 1.1‰ (mean±SD), n=15, Figure 5.4a) were higher than simulated δ^{13}C plasma values (-22.4 ± 1.4‰ (mean±SD); Figure 5.4b) resulting from the original movement model. As simulated NGPs accumulated plankton δ^{13}C values, our model did not incorporate the process of δ^{13}C discrimination through the food web (bioaccumulation of carbon's heavier isotope (^{13}C) opposed to its lighter isotope (^{12}C); Newsome et al. 2010). Our model outputs therefore simulate the senstitivy of NGP plasma proteins to expected temporal and spatial variations in the isotopic baseline in the absence of additional isotopic variation related to diet composition.

The effect of temporal variation in the reference isoscape on predator δ^{13}C tissue values

The degree of temporal averaging between plankton and predator tissues influenced simulated blood plasma δ^{13}C compositions. Compared to our control simulation using temporal averaging of 6 months (simulated for trophic level 4), δ^{13}C plasma values in NGPs assimilating δ^{13}C values from isoscapes with one, two and four month moving averages were lower (Table 5.1, Figure 5.4). The resulting plasma δ^{13}C plasma values using temporal averaging windows of two, four and six all were more negatively skewed and had a greater range (Table 5.1, Figure 5.4). However, a moving average of 2 months (theoretical trophic level of 2) resulted in δ^{13}C plasma values with a similar mean value.

The original model simulated isoscape conditions for August, changing the reference isoscape for a simluated isoscape reflecting conditions either four months before (April) or after (December) had a large effect on the estimated δ^{13}C plasma values (Table 5.1; Figure 5.4). Birds initiating their trips in April had higher mean δ^{13}C plasma values and birds initiating their simulations in December had lower δ^{13}C plasma values. Changing the resolution of the reference isoscape from monthly to yearly did not lead to a significant change in δ^{13}C plasma values (Table 5.1, Figure 5.4).

The effect of predator behavioural changes on their isotope composition

Some of the modifications in behaviour of the birds within the agent-based movement model led to noticeable changes in resulting δ^{13}C plasma values (Figure 5.4). When modelled birds initiated laying 15 days before and after the average laying date of NGPs, resulting δ^{13}C plasma values were higher and lower, respectively (5.1, Figure 5.4), even though all simulations led to almost identical at-sea distributions (Figure 5.3c). Increasing the length of a foraging trip by four and six days led to lower and more negatively skewed plasma δ^{13}C values (Table 5.1, Figure 5.4) which correlated to expansions in the simulated birds at-sea distribution (Figure 5.3). Decreasing and increasing the step length of the simulated birds did not result in greatly different δ^{13}C plasma values (Table 5.1; Figure 5.4) even though there was minor contraction and expansion respectively of at-sea distribution (Figure 5.3e; f).

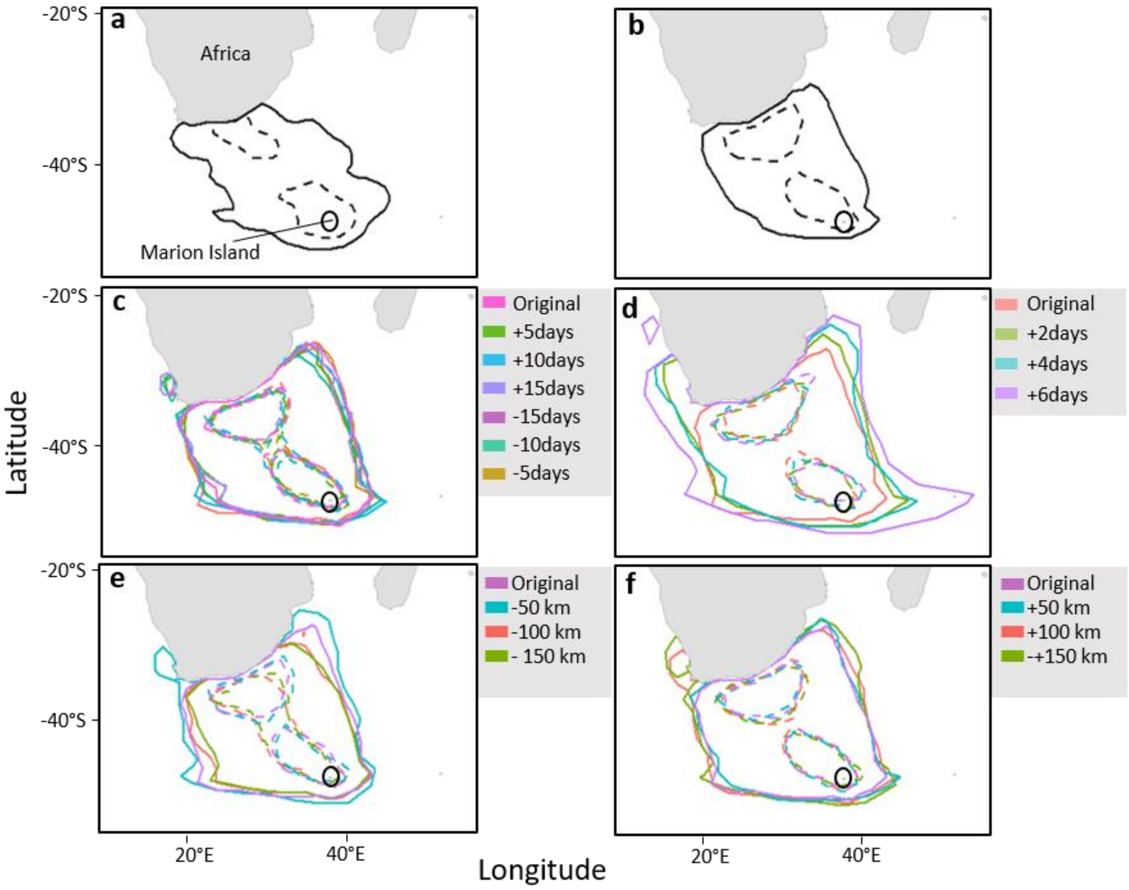


Figure 5.3. 50% and 90% kernel density based on a) GPS tracks of incubating female northern giant petrels at Marion Island 2015 and 2016; b) tracks resulting from an agent-based movement model based on movement parameters from GPS tracks in a); c) – f) modifications of the original agent-based movement to test for the sensitivity of δ^{13}C values of NGP plasma to different stimuli. Modifications are: c) the date the simulated birds initiated breeding was changed to 15, 10, 5 days before and 5, 10, 15 days after the average laying day d) foraging trip length was increased by two, four and six days e) the daily step length of simulated birds was decreased by 50 km, 100 km and 150 km and f) the daily step length of simulated birds was increased by 50 km, 100 km and 150 km.

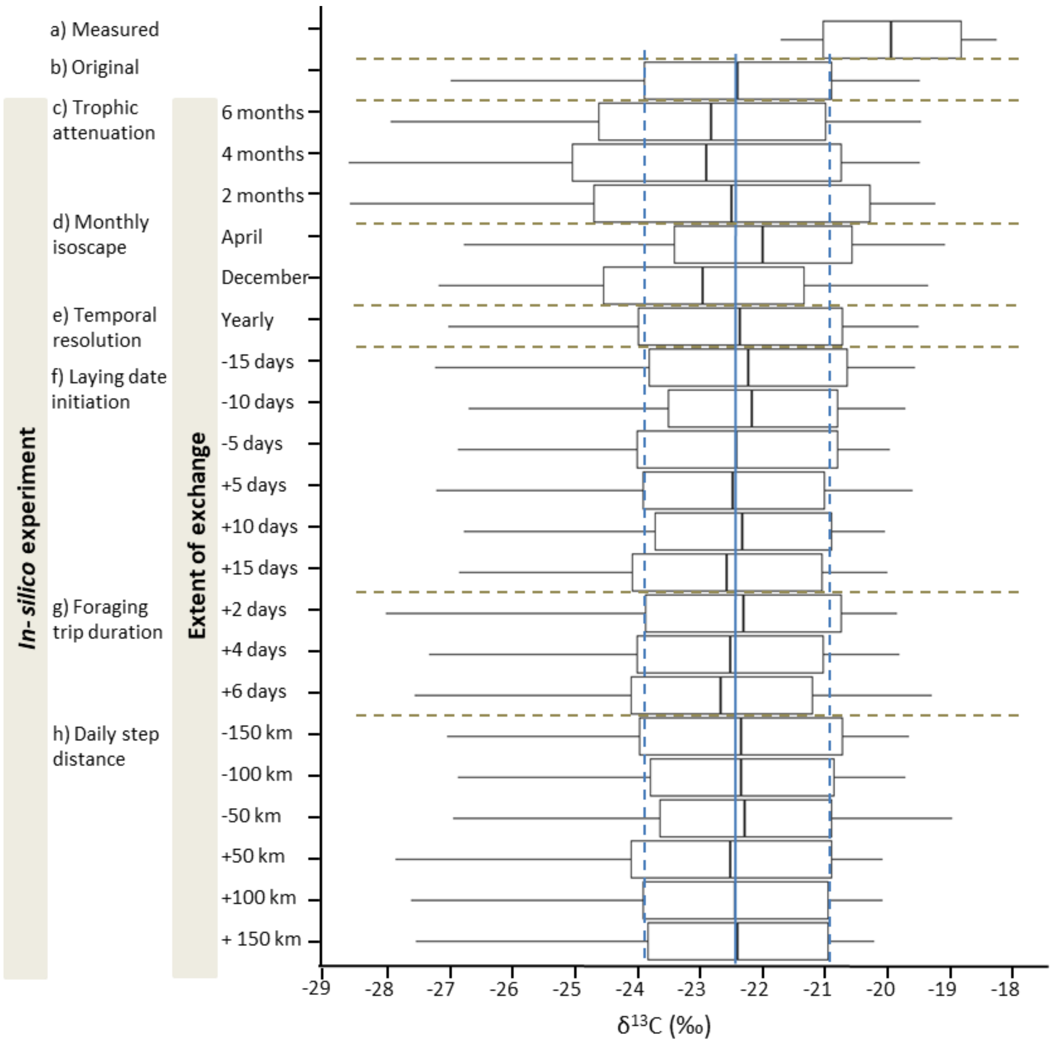


Figure 5.4. Box plots (range, standard deviation and mean) showing the a) measured $\delta^{13}C$ values of plasma collected from incubating female northern giant petrels at Marion Island in 2015 and 2016 (n= 15); b) Simulated $\delta^{13}C$ values of blood plasma resulting from an agent-based movement model based on incubating NGPs which accumulated daily $\delta^{13}C$ values from modified monthly isoscapes produced by Magozzi et al. (2017) which incorporated trophic attenuation over four trophic levels (i.e. eight months). c) – g) are modifications of the original agent-based movement to test for the sensitivity of $\delta^{13}C$ values of NGP plasma to different stimuli. Modifications are: c) simulated birds assimilated $\delta^{13}C$ values from modified isoscapes produced by Magozzi et al. (2017) over trophic levels one, two and three (i.e two, four, and six months), all further *in-silico* experiment assimilated $\delta^{13}C$ values from maps account for attenuation over four trophic levels d) the original simulation was initiated in April and December; e) simulated birds assimilated $\delta^{13}C$ values from an isoscape with a temporal resolution of yearly; f) the date the simulated birds initiated breeding was changed to 15, 10, 5 days before and 5, 10, 15 days after the original start date of the movement model; g) foraging trip duration was increased by two, four and six days; h) the daily step length of simulated birds was decreased by 150 km, 100 km and 50 km and increased by 50 km 100 km and 150 km. Blue solid and the two dashed lines represent the mean and standard deviations of the $\delta^{13}C$ values which resulted from the original simulation.

Table 5.1. a) Simulated δ^{13}C plasma values resulting from an agent-based movement model basfor female northern giant petrels incubating eggs on Marion Island and accumulating daily δ^{13}C values estimated from an isotope enabled biogeocheimcal model Magozzi et al. (2017) n = number of plasma δ^{13}C values resulting from 100 simulations of the model. b) – f) are modifications of the original model conditions to test for the sensitivity of δ^{13}C values of NGP plasma to different stimuli or assumptions. Modifications are: b) simulated birds assimilated δ^{13}C values from isoscapes with a temporal attenuation reflecting isotopic incorporation over trophic levels one, two and three (i.e. two, four and six months) c) the original simulation was initiated in either April or December d) simulated birds assimilating δ^{13}C values from a single biomass-weighted yearly average rather than separate month-specific isoscapes e) the date the simulated birds initiated breeding was changed to 15, 10, 5 days before and 5, 10, 15 days after the original start date of the movement model; f) foraging trip duration was increased by two, four and six days; g) the daily step length of simulated birds was decreased by 150 km, 100 km and 50 km and increased by 50 km, 100 km and 150 km. The effect of model conditions on the distribution of simulated δ^{13}C plasma values was investigated using Bayesian estimation for two groups and a skewed-normal model distribution. Resulting posterior estimates of the population mean, standard deviation (SD) and skewness are given with their resulting upper and lower 95% credible intervals (CI).

In-silico experiment	Extent of Change	Temporal resolution of isoscape:	Isoscape representing attenuation over:	n	Mean (CI)	SD (CI)	Skewness (CI)
a) Original model		Monthly	4 trophic levels	356	-22.5 (-22.6: -22.3)	0.3 (0.3: 0.4)	-4.9 (-6.6: -3.6)
b) Trophic attenuation							
	6 months	Monthly	3 trophic levels	356	-22.9 (-23.3: -22.5)	0.5 (0.3: 1.0)	-5.5 (-9.5: -5.2)
	4 months	Monthly	2 trophic levels	356	-23.0 (-23.4: -22.6)	0.7 (0.5: 1.1)	-6.9 (-11.1: -3.4)
	2 months	Monthly	1 trophic level	356	-22.6 (-23.0: -22.3)	0.7 (0.5: 1.1)	-5.7 (-9.3: -2.4)
c) Monthly isoscape							
	April	Monthly	4 trophic levels	325	-22.1 (-22.4: -21.8)	0.3 (0.1: 0.7)	-4.6 (-8.2: -1.4)
	December	Monthly	4 trophic levels	348	-23.0 (-23.4: -22.6)	0.4 (0.2: 0.8)	-3.7 (-7.0: -0.7)
d) Temporal resolution							
		Yearly	4 trophic levels	357	-22.5 (-22.8: -22.1)	0.4 (0.2: 0.8)	-4.9 (-8.5: -1.8)
e) Laying initiation date							
	-15 days	Monthly	4 trophic levels	354	-22.4 (-22.7: -22.0)	0.4 (0.2: 0.8)	-6.6 (-11.0: -3.0)
	-10 days	Monthly	4 trophic levels	349	-22.2 (-22.6: -21.9)	0.2 (0.1: 0.7)	-5.1 (-9.3: -1.6)
	-5 days	Monthly	4 trophic levels	366	-22.5 (-22.8: -22.1)	0.4 (0.2: 0.8)	-6.7 (-11.5: -3.0)
	+5 days	Monthly	4 trophic levels	357	-22.5 (-22.9: -22.2)	0.3 (0.1: 0.7)	-4.4 (-7.9: -1.2)
	+10 days	Monthly	4 trophic levels	354	-22.4 (-22.8: -22.1)	0.3 (0.1: 0.7)	-4.9 (-9.4: -2.2)
	+15 days	Monthly	4 trophic levels	368	-22.6 (-23,0: -22.3)	0.4 (0.2: 0.8)	-4.5 (-8.2: -1.4)
f) Foraging trip duration							
	+2 days	Monthly	4 trophic levels	299	-22.4 (-22.8: -22.0)	0.4 (0.2: 0.8)	-5.5 (-10.1: -1.8)
	+4 days	Monthly	4 trophic levels	244	-22.6 (-23.0: -22.2)	0.4 (0.2: 0.8)	-3.7 (-7.4: -0.6)
	+6 days	Monthly	4 trophic levels	198	-22.7 (-23.1: -22.3)	0.4 (0.1: 0.8)	-2.7 (-6.1: 0.4)
g) Daily step length							
	-150 km	Monthly	4 trophic levels	343	-22.4 (-22.8: -22.1)	0.4 (0.2: 0.8)	-5.7 (-10.0: -2.2)
	-100 km	Monthly	4 trophic levels	364	-22.4 (-22.8: -22.1)	0.3 (0.1: 0.8)	-4.6 (-8.1: -1.4)
	-50 km	Monthly	4 trophic levels	335	-22.4 (-22.7: -22.0)	0.2 (0.1: 0.7)	-3.4 (-7.1: -0.8)
	+50 km	Monthly	4 trophic levels	344	-22.6 (-22.9: -22.2)	0.4 (0.2: 0.8)	-7.6 (-13.4: -3.4)
	+100 km	Monthly	4 trophic levels	350	-22.5 (-22.9: -22.2)	0.3 (0.1: 0.7)	-5.6 (-9.8: -2.0)
	+150 km	Monthly	4 trophic levels	342	-22.5 (-22.8: -22.2)	0.3 (0.1: 0.7)	-6.4 (-11.3: -2.6)

Discussion

This study introduces a method to perform controlled experiments on the sensitivity of δ^{13}C tissue values of free ranging marine predators by using *in-silico* models. Our intention was to generate a platform allowing us to explore the sensitivity of tissue isotope values to separate drivers of isotopic variance which in nature act simultaneously and potentially interactively. We build agent based movement models to generate experimental datapoints reflecting the time and space occupied by our consumer, and isoscape models to simulate the isotopic composition of diet expected at that time and place. The nature of the coupled model system chosen reflects a balance of transparency (i.e. relatively simple models) with realism and computational demands. We argue that for sensitivity testing as described here, generating simple models conditioned on general movement rules is preferable as the trade-off is weighted towards ease of comprehension of results. More complex, but realistic model systems may be more appropriate for drawing inference from measured data.

Daily plasma δ^{13}C values of female NGPs incubating at Marion Island were simulated by mimicking the daily at-sea movement and distribution of these birds using a relatively simple agent-based movement model. Mutations of this movement model allowed us to investigate how the δ^{13}C value of a marine predator's tissue might respond to variations in foraging behaviour and temporal dynamics of the isotopic baseline and food web. Mutations to the movement model led to significant variability in the simulated NGP δ^{13}C plasma values providing evidence to the importance of using temporally accurate isoscapes for retrospective geolocation of marine predators.

The effect of temporal variation in the reference isoscape on predator δ^{13}C tissue values

While the diet of specific seabird species are generally confined to a relatively narrow range of trophic levels, the proportion of dietary constituents can show substantial temporal and spatial as well as inter-specific variability (Quillfeldt and Masello 2013). Partitioning sources of variance within stable isotope measurements is difficult, simulation modelling allows us to exclude or explicitly define sources of variance and quantify their likely contribution to variance in consumer tissue isotopic compositions.

The *in-silico* experiments we performed within this study showed that in the absence of any isotopic variance associated with diet composition, changes in temporal averaging of δ^{13}C values across trophic levels (i.e. trophic attenuation) can strongly influence the distribution of δ^{13}C plasma values of seabirds. This is a noteworthy finding, as the temporal relationship between the creation of an isoscape, and temporal attenuation of short term variation through the food web are important considerations for (or limitations to) finer scale retrospective geolocation of marine predators.

By allowing the simulated NGPs in this study to incorporate δ^{13}C values from isoscapes within a different period of the year (i.e. April and December) and from a different temporal resolution (i.e. yearly), we tested the effect of environmentally realistic levels of temporal variability in baseline isoscapes on the plasma δ^{13}C value of marine predators. As simulations initiated at different times of the year resulted in differences in both skewness and mean simulated plasma δ^{13}C values of the birds, we have provided evidence supporting the use of temporally resolved isoscapes for refined retrospective geolocation of marine predators. However, biomass-weighted annual average δ^{13}C isoscape models provided a reasonable representation of more temporally explicit simulations. This is in agreement with previous studies which successfully used temporally static isoscapes to limit retrospective geolocation of seabirds' foraging areas from δ^{13}C tissue values within the Southern Ocean to water masses or fronts (e.g. Cherel et al. 2014; Whitehead et al. 2017; Connan et al. 2018).

Many of the alterations made to either the agent-based model or the reference isoscape resulted in changes to the distribution of simulated δ^{13}C plasma values, but not necessarily to the average value. We suggest that distributions of isotopic compositions of measured animals may similarly provide more ecological information than estimates of population average isotopic compositions.

The effect of predator behavioural changes on their isotope composition

Changes in breeding phenology (e.g. Dobson et al. 2017) or foraging effort (e.g. Green et al. 2015; Whitehead et al. 2017) of seabirds are often interpreted in terms of interannual variability in prey availability. Here, we used our female NGP agent-based movement model to investigate whether these behavioural changes would also lead to changes in predator $\delta^{13}C$ tissue values. We found that only the extreme changes in laying initiation date lead to significantly different plasma $\delta^{13}C$ values (i.e. 15 days before and after average laying date).

Increased foraging trip duration of simulated NGPs led to an extension of at-sea distribution and significantly different $\delta^{13}C$ values. This supports the common interpretation that foraging location is the most important driver of marine predator $\delta^{13}C$ tissue values (Graham et al. 2010; Newsome et al. 2010), and is unsurprising in a region with large, directional (latitudinal) gradients in the isotopic compositions of primary producers. However, increasing the daily step length of the simulate NGPs did not result in significant changes in their $\delta^{13}C$ values, even though there were some range contraction or expansion. This is likely an artefact of the birds' preference for sea surface temperatures between 19.5 – 22.0°C, which lead to similar core foraging areas despite changing step lengths.

Caveats

The simulation results presented here are context-dependent. The Southern Ocean is characterised by large, persistent latitudinal gradients in $\delta^{13}C$ values which likely dominate the response of predicted tissue $\delta^{13}C$ values to changes in temporal or spatial variables. We recommend taking a simulation sensitivity approach specific to a study region as a desk-based initial step within the design of field sampling protocols, and prior to interpretation of stable isotope data from consumer tissues.

It is important to note that the monthly isoscapes used within this study are simulations and are not expected to accurately represent $\delta^{13}C$ values at local and short timescales. Simulations were produced from a 10 year average of climatic variables, reducing potential interannual variation (Magozzi et al. 2017). We stress that the current study uses models to explore potential isotopic sensitivity to environmental and ecological variables, rather than attempting to infer location or behaviour based on measured data. In addition, we did not simulate intrinsic physiological factors that may influence the carbon isotopic value of marine predators' tissues, such as reproduction (Hobson and Clark 1992;

Connan et al. 2017), nutritional stress (Hobson et al. 1993) or differential routing of carbon –containing metabolic compounds (Newsome et al. 2010).

Conclusion

In summary, we show that *in silico* simulations provide a method of testing the sensitivity of consumer tissue isotope compositions to multiple simultaneous sources of variance. In our case study we show that caution should be used when comparing $\delta^{13}C$ values of marine predators' tissues between seasons and years as temporal variation in baseline compositions has potential to confound isotopic variances that are commonly inferred to represent differences in either foraging location and/or diet composition.

The method presented here is applicable to any consumer which moves around its environment to forage. It is not restricted to the use of Magozzi et al. (2017)'s monthly isoscapes or the rules of our agent-based movement model: future investigations can use other isoscapes, including terrestrial isoscapes (e.g. West et al. 2014), more complex or different movement models, and or isotopically variable diets.

Chapter 6:
General Discussion

Due to environmental changes, including rising temperatures, retreating sea ice and ocean acidification, marine ecosystems across the globe are expected to undergo considerably alterations over the next few decades (Poloczanska et al. 2013, 2016; Sydeman et al. 2015; Swart et al. 2018). These changes will directly impact organisms at the base of marine food webs with important knock-on effects for higher trophic level organisms, such as marine predators (Walther 2010; Avila et al. 2018; Dias et al. 2019; Ropert-Coudert et al. 2019). The resilience of marine predators to such changes is difficult to predict, but understanding how species respond to variability in their environments may allow for strong inferences and forecasts to be made (e.g. Cristofari et al. 2018). These inferences and forecasts are powerful tools in developing efficient conservation measures (Lewison et al. 2012; Guisan et al. 2013; Hays et al. 2019).

Environmental change or variability, however, is unlikely to influence a single species within an ecosystem. Instead biological interactions among species, at the same or at different trophic levels, are expected to be influenced and possibly altered in the face of climate change (Tylianakis et al. 2008; Walther 2010). It is therefore important to investigate the response of multiple species to food web or habitat alterations to allow for a more comprehensive understanding of the effects of environmental change or variability. Sub-Antarctic islands represent ideal ‘natural laboratories’ to investigate the impacts of climate on an ecological community of marine animals. These islands are breeding and moulting refuges to multispecies assemblages of land dependent marine top predators such as seabirds and seals. The central-place foraging while breeding and relatively high philopatry exhibited by these animals allows for long-term monitoring of their demography and foraging behaviour parameters (e.g. diet and foraging distribution).

Over the past two decades, the foraging ecology of different seabird and seal species breeding on the Prince Edward Archipelago has been reasonably well investigated (e.g. Nel et al. 2002, 2001; Makhado et al. 2008, 2013, 2018; De Bruyn et al. 2009; Richoux et al. 2010; Arthur et al. 2015, 2017; Tosh et al. 2015; Pistorius et al. 2017; Schoombie et al. 2017; Carpenter-Kling et al. 2017, 2019; McIntyre et al.

2017). However, there are relatively few studies which include multiple species (Connan et al. 2014; Whitehead et al. 2016, 2017; Reisinger et al. 2018b; Wege et al. 2019) and only two which include species from different family groups (Reisinger et al. 2018a; Connan et al. 2019). This motivated the first major aim of my thesis, which was to investigate the concurrent trophic response of ten seabird and two fur seal species breeding on Marion Island to interannual environmental variability, using tracking and stable isotope data (Chapters 2 (Carpenter-Kling et al. In press) and 3 (Carpenter-Kling et al. 2020)). This aim resulted in a large dataset of stable isotope information that was temporally matched to the GPS tracks of multiple seabird species. This allowed for the novel investigation of some of the assumptions upon which the stable isotopic ecology of marine predator is based (Chapter 4 (Carpenter-Kling et al. 2020) and 5 (Carpenter-Kling et al. 2019b)).

This is the first time that concurrently collected tracking and stable isotope data from seabirds and seals breeding on Marion Island have been collated to investigate consistency within their trophic ecology over multiple years. I further used this data to critically assess seabird-level isoscapes as well as developed a novel and relatively simple agent-based movement model that can be used to investigate various extrinsic influences on the stable isotopic composition of consumers. The research highlights of my thesis are as follows:

- The first description of the at-sea distribution of the light-mantled albatross from Marion Island during their incubation period.
- The identification of the sub-tropical convergence as a particularly important and consistent foraging habitat for Marion Island albatrosses during their incubation period.
- The Andrew Bain Fracture Zone eddy field provides an important foraging habitat for all albatrosses incubating on Marion Island, however, its interannual strength and production of prey aggregating mesoscale eddies is influenced by the position of the Antarctic Polar Front.
- The trophic ecology and foraging behaviour of the nine seabird (except for the king penguin) and two fur seal species is highly plastic is likely influenced by environmental variability.

- Resource partitioning among marine predators breeding on Marion Island is maintained over time despite variability in their trophic ecology. This indicates that biological interactions, such as competition for food historically or presently, are important factors shaping the foraging behaviour of these marine predators.
- Seabird-level $\delta^{13}C$ and $\delta^{15}N$ isoscapes are variable between species, I highlight the influence of different foraging modes (flying vs diving), diet compositions and foraging distributions among the species in the determination of their isosocapes.
- Temporal variability in baseline $\delta^{13}C$ isoscapes is likely to influence the isotopic composition of marine predator tissues.

Response of a community of marine predators to environmental variability

A major driver of animal movement is the predictability of their resource distribution (Weimerskirch 2007; Riotte-Lambert and Matthiopoulos 2020). The more predictable an animal's food resource distribution becomes, the more they rely on those resources and develop specializations in foraging behaviour such as foraging habitat fidelity or site fidelity (Pyke et al. 1977; Switzer 1993; Rodríguez-malagón et al. 2020). In contrast, animals foraging in a dynamic environment where resource distribution is less predictable are expected to develop generalist or flexible foraging behaviours to maximize probability of prey encounter (Weimerskirch 2007; Mueller et al. 2011; Gilmour et al. 2018; Dehnhard et al. 2019). Flexible or generalist foraging behaviours may play a key role in the ability of a species to adapt to changes in its environment (Nussey et al. 2007; Cooke et al. 2019). Species with low levels of behavioural plasticity are thought to be more vulnerable to changes in their environments (Clavel et al. 2011; Manugian et al. 2015; McIntyre et al. 2017), as they are less able to explore and exploit different habitats when their preferred prey becomes limiting.

The Southern Ocean is an interesting environment in that it has both large scale and highly productive foraging habitats which marine predators seem to be able to locate reliably despite environmental variability (e.g. king penguins and the Antarctic Polar Front; Bost et al. 2015), as well as foraging habitats which are ephemeral in space and time such as mesoscale eddies, and are targeted by a suite of foraging marine predators (Nel et al. 2001; Bon et al. 2015; Tosh et al. 2015; Whitehead et al. 2016). Using GPS tracking and stable isotope data collected over three consecutive years (2015 to 2017), I provide evidence that foraging plasticity or habitat generalism (e.g. wandering albatross) is inherent to animals foraging for resources that are spatially and temporally dynamic. The only species that showed little variability in its seasonal and annual trophic ecology was the king penguin, which is characterized by being an extreme foraging habitat specialist (Bost et al. 2015; Pistorius et al. 2017; Cristofari et al. 2018). The specialist foraging behaviour of the king penguin most likely evolved due to the highly predictable location of the productive Antarctic Polar Front (Bost et al. 2009, 2015).

As behavioural plasticity plays a key role in the ability of organisms to adjust to environmental variability and change (Beever et al. 2017), it is likely that the species investigated in my thesis will, at least to some extent, be resilient to climate change. The exception is the king penguin. This agrees with the findings of Cristofari et al. (2018), who predicts that the king penguin population breeding on Marion Island is likely to become regionally extinct by 2100 due to the negative impact on their foraging efficiency as their preferred foraging habitat shifts southward as a result of climate change. Previously, interannual variability in the foraging habitat preference of albatrosses incubating on Marion Island was not known and their distribution was assumed to be that which was found by single year studies (Nel et al. 2001, 2002; Schoombie et al. 2017). The finding of my thesis thus highlights the importance of researching and further understanding the movement and diet of marine predators, especially in response to environmental variability. As well placed Marine Protected Areas can alleviate some of the threats marine predator face at sea (Game et al. 2009; Ballard et al. 2012), a greater understanding of the dynamic trophic ecology of animals can inform decisions made by policy makers and conservation managers (Hays et al. 2019).

Contributions to seabird and fur seal stable isotope ecology

Seabirds and marine mammals are climate and ecosystem sentinels (Piatt et al. 2007; Moore 2008; Hazen et al. 2019). They are upper trophic level species and as such changes in their diet composition (e.g. Carpenter-Kling et al. 2019a; Mills et al. 2020), habitat use (e.g. Kappes et al. 2010; Thorne et al. 2015), body condition (Choy et al. 2017) and demographic parameters (Laake et al. 2018) reflect changes in their ecosystems. However, to identify anomalous behaviours that may indicate changes in ecosystem state requires long-term monitoring of relevant parameters (Hazen et al. 2019). Since seabirds and seals annually aggregate on land to breed it is relatively easy to monitor changes in their demographic parameters such as breeding success or breeding population size (e.g. Crawford et al. 2014). Conventional methods used to measure changes in habitat use and diet, such as location tracking devices (e.g. GPS devices) or collection of stomach content samples, are often limited in sample size and require specialized skills to analyse. A complementary approach to these techniques is the collection of tissues for stable isotope analysis, tissue samples can be analysed relatively quickly, and provide values that are more standardised across studies than the results of tracking analyses or stomach content analyses (e.g. Chapter 3; Roscales et al. 2011; Ramos et al. 2020).

The interpretation of stable isotope compositions of marine predators' tissues, however, is not without its caveats. Although, consumers' δ^{13}C and δ^{15}N tissue values are primarily determined by their foraging location and trophic level, respectively (Newsome et al. 2007), there are other factors which cause variation in isotopic values. Such factors include baseline isotopic gradients, physiological state of the animal, physiological fractionation through intermediate trophic levels and transformation in the consumer, diet composition and behaviour of the consumer and isotopic turnover rates (reveiwed in: Graham et al. 2010; Hobson et al. 2010; Shipley and Matich 2020). Therefore, in this thesis, I aimed to improve interpretations of marine predator isotopic compositions. Specifically, I addressed three main factors which introduce variance into consumer isotopic tissue values:

(1) temporal changes in baseline isotopic gradients;

(2) Species-specific variance (e.g. diet composition and different fractionation pathways);

(3) influence of the behaviour of marine predators on their isotopic composition.

By combining fine-scale GPS tracking data and concurrent blood plasma isotopic values of five Procellariiformes (wandering, grey-headed and sooty albatrosses and northern and southern giant petrels) and three Sphenisciformes (gentoo, eastern rockhopper and macaroni penguins) I produced species- and guild-specific $\delta^{13}C$ and $\delta^{15}N$ isoscapes for part of the Southern Indian Ocean (Chapter 4). Of the far-ranging flying species (i.e. the Procellariiformes), I found that the $\delta^{13}C$ isoscapes of only the grey-headed and wandering albatrosses and the $\delta^{15}N$ isoscapes of only the wandering albatross and southern giant petrel resembled previously published baseline (Somes et al. 2010; Magozzi et al. 2017) and seabird-level isoscapes (Cherel and Hobson 2007; Jaeger et al. 2010; Walters et al. 2010). These gradients, as well as the lack of any spatial gradient in the $\delta^{13}C$ and $\delta^{15}N$ isoscapes in the remaining species, were contributed to species-specific differences in diet and foraging habitat. With regards to the close-ranging penguin species, their $\delta^{13}C$ and $\delta^{15}N$ isoscapes exhibited an inshore to offshore spatial gradient, agreeing with findings for gentoo penguins at the Kerguelen Archipelago (Cherel and Hobson 2007). I attribute this fine-scale spatial gradient, firstly to increased productivity within local waters around Marion Island due to the ‘island mass effect’ (Perissinotto and Duncombe Rae 1990; Ansorge et al. 1999) and secondly to the diet and foraging behaviour of the penguins. In summary, my results show that large scale and regional scale systematic spatial variability of $\delta^{13}C$ and $\delta^{15}N$ values at the base of the marine food web propagates through trophic levels and is reflected in the isotopic values of top predators’ tissues but, most importantly, they do not seem to be reflected in all species.

The investigation of other extrinsic factors that may influence the stable isotopic composition of a marine predator, such as seasonal variation in baseline isoscapes or changes in the predators’ behaviour, requires extensive and repeated sampling. To overcome this hurdle, I used *in-silico* experiments to investigate 1) the effect of the reference isoscape used on inference of predator $\delta^{13}C$ values, and 2) the effect of predator behavioural changes on their $\delta^{13}C$ compositions (Chapter 5). To do this I simulated the at-sea movement and distribution of the northern giant petrel by building an agent-based movement model. I then coupled the agent-based movement model with the monthly isoscapes produced by Magozzi et al. (2017) to simulate expected $\delta^{13}C$ values in the predator's tissues. By systematically varying terms in the agent-based model or in the isoscape model, I explored the sensitivity of simulated tissue $\delta^{13}C$ values to the influence of the monthly accurate isoscapes as well as changes in the behaviour of the simulated northern giant petrels. The changes to the foraging behaviour of the simulated northern giant petrels (i.e. increased foraging trip duration and path length) had a minimal effect on the simulated $\delta^{13}C$ tissue values. However the change in laying date had a significant effect. The greatest effect on the $\delta^{13}C$ tissue values of the simulated northern giant petrel was the reference isosocape used, indicating the importance of temporally accurate isoscapes for refined retrospective geolocation of marine predators from their $\delta^{13}C$ tissue values.

By combining stable isotope compositions of marine predator tissues, fine-scale tracking data, and *in-silico* experiments, I show that reference isoscapes can change the inferences made from stable isotope values of marine predator tissues. The findings of Chapters 4 and 5 indicate that caution must be used when comparing isotope values of marine predators' tissues between seasons and years, since temporal variation in baseline compositions can confound isotopic variances that are commonly inferred to represent differences in either foraging location and/or diet composition. Furthermore, caution must be used when using non-specific isoscapes to infer a marine predator's trophic ecology. When studying marine predator stable isotope ecology, it is therefore important when possible to estimate and apply species-specific isoscapes or have a good understanding of any factors and pathways affecting marine predators' isotopic values.

The two methods used and developed in Chapters 4 and 5, are powerful tools that can be used, firstly, to identify possible isoscapes within other geographic areas (methods in Chapter 4, similar to methods by Jaeger et al. 2010 and Walters et al. 2020) and, secondly, to investigate the influence of various extrisic factors on the interpretation of consumers isotopic composition (Chapters 4 and 5). Neither method is restricted to marine consumers - they are applicable to any consumer that moves around its environment to forage (see Trueman et al. 2019 which used where the agent-based movement model presented in Chapter 5 was used to recontruct the movements of a blue whale *Balaenoptera musculus* based on isotopic composition of its baleen plate). However, the strong latitudinal $\delta^{13}C$ and $\delta^{15}N$ baseline isoscapes across the majority of the Southern Ocean are largely due to the lack of obstacles in the westerly flowing Antarctic Circumpolar Current and thus may be unique to this area. Other areas that may experience higher rates of environmental variability, such as areas of upwelling, may exhibit greater temporal turnover or instability of baseline isoscapes (e.g. Kurle and McWhorter 2017). The application of the agent-based movement model method from Chapter 5 requires isoscapes of the region of interest, which capture any spatial and temporal variability in baseline stable isotope values. However, previous knowledge of the isoscapes present is not needed for the methods used in Chapter 4 to reconstruct isoscapes either using marine top predators (e.g. Cherel and Hobson 2007; Jaeger et al. 2010; Walters et al. 2020) or other marine organisms (e.g. Brault et al. 2018; Pethybridge et al. 2018; Ohshimo et al. 2019).

Towards the future

Species distribution models refer to statistical models, or an ensemble of these models, that relate the occurrence of a species to environmental variables (Elith and Leathwick 2009; Franklin 2010; Guisan et al. 2013). They have been used to identify important areas for seabirds and seals and subsequently areas that should receive high conservation priority (Ballard et al. 2012; Raymond et al. 2015; Dias et al. 2018; Reisinger et al. 2018a; Baylis et al. 2019; Handley et al. 2020; Hindell et al. 2020). Importantly, these models have also been used to predict (Hazen et al. 2013; Krüger et al. 2018; Birkmanis et al. 2020; Hindell et al. 2020; Hückstädt et al. 2020) how these important areas may shift in response to the anticipated changes in climate (Cavanagh et al. 2017). The findings of Chapter 2 and Chapter 3 highlighted two important factors that many of these models do not consider when making their predictions, which may lead to over or under estimations of species distribution. Firstly, that the habitat and resource use of marine predators is variable between years and life history stages (e.g. Thorne et al. 2015). Secondly, that inter-specific interactions, either presently or historically, are important extrinsic factors driving the trophic ecology of marine predators. For example, Wege et al. (2019) showed that the two fur seal species on Marion Island did not use all of the suitable foraging habitat available to them while breeding and this was most likely to reduce inter-specific competition for resources. Previously, studies have incorporated inter-colony (Catry et al. 2013; Wakefield et al. 2014; Bolton et al. 2019) and inter-specific competition (Wakefield et al. 2017) for resources into their species distribution models. However, successfully incorporating and accounting for competitive interactions within and among species into species distribution models requires relatively large amount of tracked individuals breeding in different colonies (Wakefield et al. 2017). Future research should build on findings in this thesis to try and incorporate intra- and inter-specific interactions and foraging plasticity as well as other external stressors (e.g. fisheries) and internal drivers of movement (such as life history stages) into the species distribution models. However, this does not undermine the importance of single and multiple species studies which investigate a subset of movement drivers. Any improvement on previous knowledge increases the understanding of natural systems and can lead to improved management and conservation strategies.

In chapters 4 and 5, I highlight the need for temporally accurate and species-specific isoscapes to enhance inferences made from the isotopic values of marine predator tissues. The ideal next step would be to investigate possible changes in species-specific isoscapes over time. However, this is likely unfeasible as it requires a large amount of concurrently collected tracking and stable isotope data. An alternative way forward would be to further investigate species-specific intrinsic factors (e.g. species-specific discrimination factors) which leads to variance in isotope values (reviewed in Shipley and Matich 2020). By using this information, future research should build process-based carbon and nitrogen isotope models that predict spatio-temporal distributions of the isotope composition of different marine predators, similar to the approach used by Magozzi et al. (2017) to model the monthly distribution of phytoplankton δ^{13}C composition across global oceans. However, the investigation of species-specific discrimination factors requires controlled experiments of animals in captivity, which is unlikely for far-ranging and protected marine predator species. I presented two methods in my thesis: combining stable isotope values of blood plasma and fine-scale tracking data to build species-specific isoscapes (Chapter 4) and building agent-based movement models coupled with temporally accurate isoscapes to perform *in-silico* experiments on the sensitivity of marine predator δ^{13}C tissue values (Chapter 5). These methods may present a more easily accessible and less invasive route to investigate drivers of the isotopic composition of marine predators.

Final thoughts

Far-ranging marine predators are inherently difficult to study. The relatively large extent of their distributions makes it exceedingly difficult to try and account for all factors that may influence where, when, and how they forage and the decisions they make leading up to a feeding event. Furthermore, the temporal and spatial distribution of the prey aggregating oceanographic features on which they focus their foraging efforts are determined by multiple dimensions of coupled biophysical factors (Scales et al. 2014a; Lévy et al. 2015), factors which are changing with global warming (e.g. Swart et al 2018; Chapman et al. 2020). In this thesis, I tried to untangle and understand the various factors which influence the foraging behaviour of marine predators. I provided evidence that seascape dynamics (the degree of resource patch predictability) and biological interactions (past or present) largely influence the trophic ecology of marine predators. I achieved this by using and comparing tracking and stable isotope data from multiple species collected over multiple years. The full extent of a species foraging behaviour is difficult to quantify, thus highlighting the importance of multi-year and long-term monitoring of marine predators' movement and dietary parameter.

I tested key assumptions on which the use of stable isotope analysis in marine predator trophic ecology is based by investigating various factors which may induce variance in the stable isotope composition of marine predator tissues. I showed that inferences made about the stable isotope composition of marine predator tissues rely heavily on the reference isoscapes used. I also provided new species and guild specific isoscapes for seabirds with in the southern Indian Ocean. However, there are still many variance inducing factors that I could not account for, such as temporal variability in baseline isoscapes or influence of predator specific fractionation pathways. Thus, stable isotope composition of animal tissue remains a complementary tool to more conventional methods that provide more empirical information about the trophic ecology of animals such as tracking and collection of stomach content samples. My investigations did, however, highlight the important precautions that should be taken when using stable isotope composition of tissues and I suggested avenues for further research.

As predicted changes in climate become our planet’s new reality, its is important to know how animals will respond so that calculated and precautionary conservation and management strategies can be put in place. It is, however, impossible to accurately and precisely predict how species will respond with regards to any aspect of their physiology or ecology. Long-term and/or mutli-year studies on multiple species within an ecological community adds to the growing body of knowledge on how animals may respond to environmental variability and change. Their continuation is thus of critical importance as it increases the confidence surrounding any prediction made and consequently, allows for strategic conservation and management plans.

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