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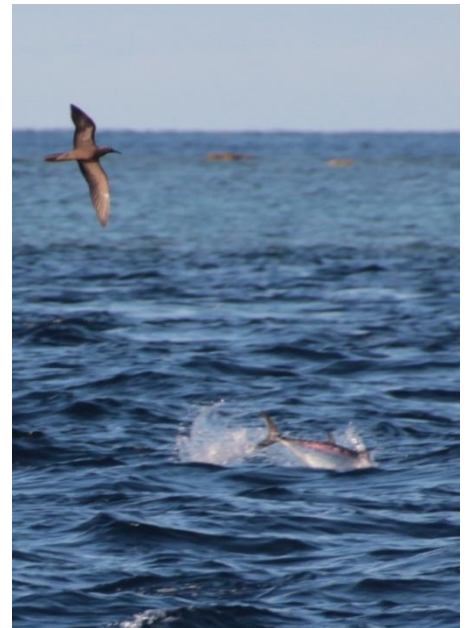
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# Foraging niche specialisation and resource use in tropical seabirds: implications for management



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for the degree of Doctor of Philosophy  
in the College of Science and Engineering  
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## ABSTRACT

Seabirds are a group of wide-ranging species with complex life histories, and an entirely marine foraging niche. Intra-species niche specialisation in seabirds appears widespread with different populations, sexes and age groups specialising in different marine resources. Seabirds in the tropics are understudied relative to those at higher latitudes. Knowledge gaps in tropical seabird foraging ecology lead to uncertainty about the prevalence of niche specialisation in tropical seabirds. Filling these gaps not only advances our understanding of how tropical seabirds use marine resources but also has important conservation management implications. This study uses regional eastern Australia to investigate three aspects of tropical seabird foraging ecology thought to drive intra-species foraging niche specialisation. The applied ecological findings of each investigation are then translated into direct management actions aimed at safeguarding the regional marine resources of the study populations and tropical seabirds in general.

Firstly, multiple years of data on foraging patterns, habitat and resource use in Wedge-tailed Shearwaters *Ardenna pacifica* breeding on a tropical and sub-tropical colony were used to investigate local adaptation of foraging strategy. Consistent dual-foraging was observed over three years in the tropical shearwater population, whereas the sub-tropical population switched from unimodal to dual-foraging and then back again. Chicks from the tropical population were consistently provisioned with local resources from southern Great Barrier Reef waters whereas adults self-provisioned on resources obtained in the central Coral Sea. The sub-tropical population used local resources in the northern Tasman Sea to sustain chicks. This local resource was shared by adults under unimodal foraging, but under dual-foraging self-provisioning adults shifted to exploit the same Coral Sea resources as tropical conspecifics. As such, chicks and adults have differently specialised foraging niches at the tropical colony but frequently shared the same foraging niche at the sub-tropical colony. Both populations showed a degree of flexibility in their foraging strategy that is related to the long-term reliability of local resources, and used persistent and reliable at-distance resources in the central Coral Sea to buffer local resource depletion.

Secondly, Wedge-tailed shearwaters from the same tropical and sub-tropical populations were used to investigate the importance facilitated foraging with tuna. Shearwater foraging behaviour was assessed relative to oceanographic covariates and predicted distributions for multiple tropical tuna species and age-classes, simulated by an existing ecosystem model (SEAPODYM). Shearwaters from both colonies undertook long-trips to deep, pelagic waters close to seamounts and foraged most often at fronts and eddies. At broad-scales, shearwaters consistently foraged in areas with higher predicted adult skipjack and micronektonic tuna densities and avoided adult Bigeye Tuna. At finer-scales, dynamic ocean features aggregated tuna of all sizes. Enhanced tuna density at these locations increased the likelihood of shearwater foraging activity. Long-trips in the tropics targeted oligotrophic waters with higher tuna densities. Long-trips in the subtropics targeted enhanced primary productivity, but in some years shifted to target the same oligotrophic, tuna-dense waters used by tropical conspecifics. As such, the foraging niche of the tropical population is consistently specialised on facilitated foraging, whereas the foraging niche of the subtropical population becomes specialised on facilitated foraging in years of low marine productivity.

Finally, GPS tracking, dietary and nutritional analysis was used to investigate sex-specific foraging in a tropical Brown Booby *Sula leucogaster* population. Sex-specific segregation was observed in: a) foraging location: females undertook longer trips, foraging at more distant locations than males; b) foraging time: male activity and foraging occurred throughout the day, while female activity and foraging increased from midday to an afternoon peak; and c) prey type: females mostly consumed flying fish, whereas males consumed equal proportions of flying fish and squid. Brown Booby diets contained five tropical prey species that significantly differed in their nutritional composition, but despite this variation no differences were found in the overall nutritional content of prey caught by each sex. The observed sex-specific niche specialisation by prey type, location and time of capture are likely driven by a combination of a division of labour, risk partitioning and competition. However, Brown Boobies may flexibly partition foraging niche by sex in response to varying competitive and environmental pressures.

Combined, these studies found intra-species niche specialisation to be prevalent in tropical seabirds from eastern Australia, and identified multiple drivers operating over several levels of resolution. Inter-population niche specialisation in Wedge-tailed Shearwaters was driven by colony-specific access to different foraging resources. Patterns of resource availability at each colony were in-turn related to differences in near-colony primary productivity and differential interactions with sub-surface predators such as tuna. Divergence in the foraging resources used by chick and adult Wedge-tailed Shearwaters was mediated by local adaptation and flexibility in adult foraging strategies, also linked to colony-specific patterns of foraging resource availability. Finally, sex-specific niche specialisation in Brown Boobies was likely driven by a combination of previously identified factors, but not convincingly by sex-specific nutritional demands.

These drivers reveal the complexity and colony-specific nature of tropical seabird foraging resources. Local resource availability varies in relation to oceanography and competition, meaning tropical seabirds have to display plasticity in foraging niche. However, this work also found that some oligotrophic, pelagic tropical waters form an important and apparently reliable resource base for tropical seabirds. This study implies that the traditional view of poor quality, unpredictable resources in tropical habitats can be offset by facilitated foraging opportunities provided by high tuna biomass.

Combining results on the persistence of foraging niche specialist groups and the location of required foraging resources, this study was able to assess current management of regional tropical seabird resources and suggest improvements. Most regional Brown Booby populations receive adequate protection of resources that are contained within the Great Barrier Reef Marine Park (GBRMP). Similarly, Wedge-tailed Shearwaters breeding within the GBRMP have resources that sustain their chicks relatively well protected by GBRMP zoning. However, the self-feeding resources used by these Wedge-tailed Shearwater populations and conspecifics in sub-tropical waters fall under the management of the Australian Marine Park Network, which is currently a 'paper park' network. The successive reduction of high protection areas in revisions of this network and the priority given to industry have led to important seabird resources being zoned within areas primarily managed by fisheries. By providing comprehensive data on spatial use, scientific rationale



for resource requirements, and ecological insight to reduce conflicts with other stakeholders, this study provides a road map for inclusion of tropical seabirds in regional zoning activities.

# TABLE OF CONTENTS

ABSTRACT.....	IV
TABLE OF CONTENTS.....	VIII
LIST OF TABLES.....	XI
LIST OF FIGURES.....	XIII
<b>CHAPTER 1: GENERAL INTRODUCTION.....</b>	<b>1</b>
1.1 Ecological niche & specialisation.....	1
1.2 Conservation and specialisation.....	1
1.3 Defining the niche and technology.....	2
1.4 Seabird niches and intra-specific specialisations.....	2
1.5 Seabird threats and intra-specific niche specialisation.....	3
1.6 Tropical seabirds and niche specialisation.....	4
1.6.1 Population niche specialisation on tuna.....	5
1.6.2 Ontogenetic niche specialisation through foraging strategy.....	6
1.6.3 Sex-specific nutritional niche specialisation.....	7
1.7 Model species.....	7
1.7.1 The Wedge-tailed Shearwater.....	8
1.7.2 The Brown Booby.....	8
1.8 Model system and conservation.....	8
1.9 Aims and objectives.....	11
<b>CHAPTER 2: FORAGING NICHE AND LOCAL ADAPTATION IN A TROPICAL PROCELLARIIFORM.....</b>	<b>14</b>
2.1 ABSTRACT.....	15
2.2 INTRODUCTION.....	15
2.3 METHODS.....	20
2.3.1 Field data collection and logger deployment.....	20
2.3.2 Foraging strategy analyses.....	22
2.3.3 Stable isotope analyses.....	23
2.3.4 Inter-annual chick condition.....	24
2.3.5 Tracking data preparation and analyses.....	25
2.4 RESULTS.....	26
2.4.1 Colony-specific foraging strategies.....	26
2.4.2 Stable Isotopes.....	30

2.4.3 Inter-annual chick condition.....	31
2.4.4 GPS analyses.....	32
2.5 DISCUSSION.....	35
2.5.1 Summary.....	35
2.5.2 Contrasting colony-specific foraging strategies and resource bases.....	36
2.5.3 Oceanography and drivers of resource availability at each colony.....	38
2.5.4 Wider tropical procellariiform foraging strategies.....	41
2.5.5 Reliable tropical pelagic resources.....	42
<b>CHAPTER 3: THE IMPORTANCE OF TROPICAL TUNA FOR SEABIRD FORAGING.....</b>	<b>44</b>
3.1 ABSTRACT.....	45
3.2 INTRODUCTION.....	45
3.3 METHODS.....	48
3.3.1 Study area and logger deployment.....	48
3.3.2 Tracking data preparation and analyses.....	49
3.3.3 Oceanographic data.....	50
3.3.4 Tropical tuna data.....	50
3.3.5 Covariate extraction.....	53
3.3.6 Multicollinearity and spatial autocorrelation.....	53
3.3.7 Statistical modelling.....	54
3.4 RESULTS.....	56
3.4.1 Tracking data.....	56
3.4.2 PCA and collinearity.....	57
3.4.3 Climatology models.....	59
3.4.4 Hi-res models.....	63
3.5 DISCUSSION.....	66
3.5.1 Wedge-tailed Shearwater distributions and oceanography.....	66
3.5.2 Tuna relationships.....	67
3.5.3 Effect of productivity gradient on long-trip destinations.....	69
<b>CHAPTER 4: SEX-SPECIFIC FORAGING IN A TROPICAL SULID.....</b>	<b>72</b>
4.1 ABSTRACT.....	73
4.2 INTRODUCTION.....	73
4.3 METHODS.....	77
4.3.1 Study area, capture and handling.....	77
4.3.2 Diet composition.....	77

4.3.3 Nutritional composition of prey and diet.....	78
4.3.4 GPS data analyses.....	78
4.3.5 Difference in movements and daily activity.....	79
4.3.6 Difference in prey species.....	79
4.3.7 Nutritional composition of prey and diets.....	79
4.3.8 Foraging performance.....	80
<b>4.4 RESULTS.....</b>	<b>80</b>
4.4.1 Adult morphometric measurements and movement.....	80
4.4.2 Daily activity budget.....	82
4.4.3 Diet composition.....	84
4.4.4 Nutritional composition of prey and diets.....	85
4.4.5 Foraging performance.....	88
<b>4.5 DISCUSSION.....</b>	<b>89</b>
4.5.1 Conclusion.....	93
<b>5 GENERAL DISCUSSION.....</b>	<b>94</b>
5.1 SUMMARY.....	94
5.2 TROPICAL SEABIRD THEORY.....	95
5.2.1 Foraging niche specialisation in tropical seabirds.....	95
5.2.2 At-distance foraging.....	95
5.2.3 Facilitated foraging.....	96
5.2.4 Sex-specific nutrition.....	97
5.3 RESOURCE BASE IDENTIFICATION.....	98
5.3.1 Far Northern GBR resource base.....	98
5.3.2 Southern GBR resource base.....	98
5.3.3 Central Coral Sea resource base.....	99
5.3.4 Northern Tasman Sea resource base.....	99
5.4 CURRENT MANAGEMENT AND SUGGESTED IMPROVEMENTS FOR RESOURCE BASES.....	100
5.4.1 Far Northern GBR resource base.....	103
5.4.2 Southern GBR resource base.....	105
5.4.3 Central Coral Sea resource base.....	107
5.4.4 Northern Tasman Sea resource base.....	109
5.5 ADDITIONAL SEABIRD BENEFITS FROM MANAGEMENT.....	110
5.6 CONCLUSION AND FURTHER STUDY.....	111
REFERENCES.....	113
APPENDICES.....	132

## LIST OF TABLES

Table 2.1 Wedge-tailed Shearwater breeding season (Feb-Mar) quality and foraging metrics collected over the course of this study. Blanks indicate data was not collected. Bimodal peaks were estimated using k-means clustering of trip durations estimated via adult attendance or GPS data respectively. GPS short trips (ST) are trips with durations $\leq 4$ days and long-trips (LT) have durations $\geq 5$ days. The manova $F$ value shows level of resource overlap (high $F$ = low overlap) between adults and chicks measured from stable isotopes ( $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ). Values given as mean $\pm$ SE.....	28
Table 2.2 Wedge-tailed shearwater stable carbon and nitrogen isotope values measured from red blood cells (mean $\pm$ SD). The $\delta^{15}\text{N}$ value of adult shearwaters from Lord Howe Island in 2015 has one outlier value ( $> 10.5$ ‰) removed.....	31
Table 3.1 Summary of oceanographic and tuna covariates used in broad and fine scale models.....	53
Table 3.2 Summary of Wedge-tailed Shearwater GPS and PTT* tracked long-trips collected during the study. The core-area is the 50% utilization distribution from kernel analysis of each tracking dataset.....	56
Table 3.3 Climatology logistical regression models of wedge-tailed shearwater presence-absence against broad scale oceanographic and tuna covariates. The following coefficients ( $\beta$ ) and std. errors (SE) are expressed in terms of a 100 unit change: tuna covariates (100 g m <sup>-2</sup> ), seamount distance (100 km) and bathymetry (100 m). All covariates have significance $p < 0.001$ . Core-area and foraging range covariate values are expressed as mean $\pm$ standard deviation.....	61
Table 3.4 Hi-res logistical regression models of wedge-tailed shearwater probability of foraging against fine scale oceanographic and tuna covariates. The strength ( $\chi^2$ ) and effect direction of each covariate is given for each of the three colony-year models. Covariates with significance $p < 0.01$ are shown in bold and the corresponding effect given, NA indicates that the covariate was not included in a model due to multicollinearity. Positive and negative effect directions are denoted by $\uparrow$ and $\downarrow$ respectively, and in the case of a polynomial relationship the value at which foraging is most or least (denoted by *) likely is given. For coefficient ( $\beta$ ) and std. error values see Appendix 1.....	64
Table 4.1 Morphological (n= 26 birds; female = 15, male = 11) and movement parameter (n= 19 birds; female = 10, male = 9) differences between males and female Brown Boobies, rearing chicks on Raine Island in December 2014. Mean $\pm$ 1 standard error for each sex is given, corresponding test statistics from anova ( $F$ -value) or Welch's t-test ( $t$ -value), and significance (Bonferroni-corrected $p$ -value). For each parameter MDC = maximum distance from the colony, MFD = mean distance of foraging from the colony, TFP = total foraging path, FTD = foraging trip duration, FT = foraging time, TT= transiting time, RT = resting time.....	81
Table 4.2 Composition of the diet of chick-rearing Brown Boobies, reflected by analysis of regurgitations collected from Raine Island in December 2014. M% = mass, N% = numerical abundance, F% = frequency of occurrence, IRI% = index of relative importance. Prey Species: S = squid <i>Sthenoteuthis</i> spp., FF = flying fish <i>Cypselurus</i> spp., BS = blue sprat <i>Spratelloides robustus</i> , SS = smooth belly sardine <i>Amblygaster leiogaster</i> , L = leatherjacket <i>Catherhines fronticinctus</i> . Regurgitations were collected from 19 birds (females = 9, males = 8, unknown sex = 2).....	85
Table 4.3 Nutritional components (% wet mass) of tropical prey species caught by Brown Boobies from Raine Island in December 2014. Values are presented as mean $\pm$ standard deviation.....	88

Table 4.4 Foraging performance and nutritional intake from single foraging trips made by six Brown Boobies, while rearing chicks on Raine Island in December 2014. MDC = Maximum distance from colony, TFP = total foraging path FTD = foraging trip duration, FT = foraging time, TT = transiting time, RT = resting time, protein = P, lipid = L, water = W, protein-to-lipid ratio = P:L, and water-to-lipid ratio = W:L.....88

Table 4.5 Differences in the foraging performance of single foraging trips made by six Brown Boobies, while rearing chicks on Raine Island in December 2014. Variation by bird sex and between the six individual birds is shown with mean  $\pm$  1 standard error, *F* (F-value), and *p* (p-value). For each parameter P=protein, L = lipid, W = water, P:L = protein-to-lipid ratio, W:L = water-to-lipid ratio, TFP = total foraging path, FTD = foraging trip duration, and FT = foraging time.....89

Table 5.1 Resource bases identified from this study, the population/sub-population groups they support and current protective measures. LHIMP = Lord Howe Island Marine Park, GBRMP = Great Barrier Reef Marine Park.....100

# LIST OF FIGURES

Fig. 1.1 Regional seascape and location of study colonies.....	9
Fig. 1.2 Schematic of thesis chapters and topics. Blue boxes indicate intra-species niche specialism investigated, red boxes indicate the element of tropical seabird theory investigated, green boxes indicate the potential demographic specialist groups, and black boxes indicate chapter contents. Chapters Two and Three use the Wedge-tailed Shearwater, whereas chapter Four uses the Brown Booby.....	13
Fig. 2.1 Tropical to subtropical gradient and population differences shown between Wedge-tailed Shearwater study colonies. Regional sea surface temperature (SST) given from 2003-2016 average for month of February (start of chick-rearing). Population estimates expressed as number of breeding pairs (BP) from Capricorn Bunker group (Dyer et al. 2005) and Lord Howe Island (Carlile & Priddel 2013).....	19
Fig. 2.2 Wedge-tailed Shearwater foraging strategies calculated for different years from adult colony attendance data at Lord Howe Island (LHI; a, b, c) and Heron Island (HER; d,e). The mean ( $\pm 2$ SE) proportion of time spent on foraging trips of different lengths by individual adults is given, with different letters identifying significant differences in means.....	27
Fig. 2.3 Time series of trip lengths made by three different pairs (a, b, c) of Wedge-tailed Shearwaters while raising chicks on Lord Howe Island in 2015. Adult parents are denoted by a red solid or blue dotted line respectively, but sexes are unknown.....	29
Fig. 2.4 Wedge-tailed shearwater stable carbon and nitrogen isotope values measured from red blood cells (mean $\pm$ SE). Filled symbols represent adult birds and hollow symbols represent chicks from: Heron Island in 2015 (circles); Lord Howe Island in 2015 (squares); and Lord Howe Island in 2016 (diamonds). The $\delta^{15}\text{N}$ value of adult shearwaters from Lord Howe Island in 2015 has one outlier value ( $> 10.5$ ‰) removed.....	30
Fig. 2.5 Wedge-tailed Shearwater chick condition (unitless) (mean $\pm$ 95% CI) in February-March of each year at: a) Lord Howe Island; and b) Heron Island. Values above the baseline condition of 0 represent good condition, whereas values below represent poor condition.....	32
Fig. 2.6 Kernel analyses of GPS tracking of short ( $\leq 4$ days) and long ( $\geq 5$ days) trips made by Wedge-tailed Shearwaters. In each case the at-sea distribution is denoted by the 99% Utilization Distribution (UD) and foraging areas denoted by the 50% UD.....	34
Fig. 2.7 GPS tracking and foraging areas (50% Utilization Distribution; UD) of short trips ( $\leq 4$ days) made by Wedge-tailed Shearwaters from: a) Heron Island in 2015; b) Lord Howe Island in 2015; and c) Lord Howe Island in 2016. Bathymetric contours give depth from 500m (white lines) to 5000m (darkest purple lines). The yellow triangle denotes the colony.....	35
Fig. 3.1 Flow chart showing input data and analyses steps taken for: A. hi-res models; and B. climatology models (separated by dotted line).....	52
Fig. 3.2 Wedge-tailed Shearwater long-trip tracking data collected from birds rearing chicks on Heron Island and Lord Howe Island between 2011 and 2016, overlaid with 50% kernel utilisation distribution (UD) core-use areas for each colony.....	57

Fig. 3.3 Ordination from principal components analysis of broad scale oceanographic and tuna covariates used in climatology models of Wedge-tailed Shearwaters breeding from (A) Heron Island, and (B) Lord Howe Island.....	58
Fig. 3.4 Ordination from principal components analysis of fine scale oceanographic and tuna covariates used in hi-res models of Wedge-tailed Shearwaters tracked with GPS from (A) Heron Island in 2015, (B) Lord Howe Island in 2015, and (C) Lord Howe Island in 2014.....	59
Fig. 3.5 GPS tracking data of breeding Wedge-tailed Shearwaters shown as (A) kernel utilisation distributions (UDs) overlaying SEAPODYM-predicted long-term mean micronektonic Bigeye Tuna biomass for march, (B) kernel UD overlaying long-term mean primary productivity for march, and (C) individual foraging trips from Heron Island overlaying SEAPODYM-predicted weekly micronektonic Skipjack Tuna biomass.....	62
Fig. 3.6 Mean (solid line) and 95% confidence interval (dotted line) predictions of Wedge-tailed Shearwater foraging probability in relation to fine scale tuna and oceanographic covariates. Density plots are overlaid showing the distributions of foraging (black line) and non-foraging (grey shade) samples for each covariate. 'Mic.' refers to micronektonic tuna age-classes.....	65
Fig. 4.1 GPS tracking of 19 (n female = 10, n male = 9) chick-rearing Brown Boobies from Raine Island in December 2014. Foraging locations (a) and kernel density based utilization distributions (UDs) of foraging locations (b) are shown for each sex.....	82
Fig. 4.2 Daily activity data for female (a) and male (b) chick-rearing Brown Boobies from Raine Island in December 2014. The histogram gives the percent of Booby foraging trips (female n=26, male n=32) at-sea in each hour, the black line is a density plot of time-stamped foraging locations from active Booby trips, scaled from 0-100. The black circles are the number of foraging trips departing and black triangles the number of foraging trips returning within each hour.....	83
Fig. 4.3 Right-angled mixture triangle (RMT) showing proportional data on three mixture components (here protein (P), lipid (L) and water (W)) in two dimensional graphs. To plot the nutritional compositions (P, L and W) in the RMT, each nutrient was expressed as a wet mass percentage of the sum of the three (Raubenheimer 2011). The circles represent prey species consumed by chick-rearing Brown Boobies from Raine Island in 2014. Grey filled circle = Blue Sprat <i>Spratelloides robustus</i> (19.1% P, 1.9% L, 79.0% W); Black filled circle = Leatherjacket <i>Catherhines fronticinctus</i> (18.4% P, 1.1% L, 80.6% W); Circle filled with lines = flying fish <i>Cypselurus</i> spp. (22.0% P, 1.3% L, 76.7% W); Black hollow circle = Smooth belly Sardine <i>Amblygaster leiogaster</i> (23.0% P, 1.9% L, 75.1% W); Black and grey filled circle = squid <i>Sthenoteuthis</i> spp. (21.9% P, 1.9% L, 76.2% W). Black triangle = male minimal realised nutritional niche (21.9% P, 1.7% L, 76.5% W) and black square = female minimal realised nutritional niche (21.7% P, 1.6% L, 76.8% W), both constrain within the minimal prey composition nutritional niche (black dot-dash line)....	87
Fig. 5.1 Foraging areas shown by kernel density 50% Utilization Distributions (UDs) that identify different resource bases from this study overlaying different Australian Marine Park zoning from 2017.....	102
Fig. 5.2 Brown Booby foraging distribution, shown by kernel density 50% Utilization Distribution (UD), and foraging ranges from the Raine Island colony situated in the far north of the Great Barrier Reef Marine Park.....	104
Fig. 5.3 Heron Island Wedge-tailed Shearwater foraging distribution, shown by kernel density 50% Utilization Distribution (UD), and foraging zones identified by McDuire (2015) in the southern Great Barrier Reef Marine Park .....	106
Fig. 5.4 Changes to the Australian Marine Park Network zoning between 2012 and 2017.....	108



# CHAPTER 1: GENERAL INTRODUCTION

## 1.1 Ecological niche & specialisation

A species ecological niche is all the abiotic and biotic resources (in multidimensional space) that it needs to maintain a viable population (Grinnell 1917, Hutchinson 1957). Niche specialisation represents a species variance in performance across a range of resources; or more simply, the breadth of resources required by the species (Devictor et al. 2010). Niche is commonly estimated at species level (Valladares et al. 2014), with intra-species niche specialisations being shown by different populations, primarily due to local adaptation (Van Valen 1965, Leimu & Fischer 2008, Banta et al. 2012). However, niche specialisation also occurs at intra-population levels. Within populations resources can be used differently between: sexes (ecological sex dimorphism; Shine 1989); ages (ontogenetic niche shift; Polis 1984); morphologies (resource polymorphism; Smith and Skulason 1996); and even individuals (Individual-level resource specialisation; Roughgarden 1974, reviewed by Bolnick et al. 2003). Accounting for intra-specific niche specialisation offers more detailed information on resources required by a species (Durell 2000), indeed some species considered generalists are actually heterogeneous collections of specialized individuals (Bolnick et al. 2003).

## 1.2 Conservation and specialisation

Two primary activities required for conserving species are: 1) predicting the effect of resource change or loss on species distribution or abundance and; 2) designing management to protect species' resource bases (Groom et al. 2006). Considering intra-species niche specialisation is important for both these activities. If intra-species groups specialise on using particular resources (e.g. habitats or diets) then they will be impacted by any change to a lesser or greater degree than the species as a whole (Durell 2000). If management is undertaken at the species level then it may target some 'average' resource for protection that unintentionally excludes specialists' resources (Bolnick et al. 2003). There is a need to consider and preserve resources for intra-species specialists because, although they may not make up the majority of a population, a reduction in specialist numbers could have a disproportionate impact on the species as a whole (Durell 2000). This is because intra-species specialists often fall into important demographic groups based on sex or age (Shoener 1986, Durell 2000). Consequently, population models and conservation management activities that treat

conspecific individuals as ecologically equivalent likely under-represent the impact of resource change and overestimate the effectiveness of resource protection, respectively (Durrell 2000, Bolnick et al. 2003).

### **1.3 Defining the niche and technology**

Niche breadth is demonstrated using proxies such as differences in morphology (Grant 1968, Clegg & Owens 2002), foraging ecology and diet (Carrascal et al. 1994; McDonald 2002), and habitat preference (Diamond 1970, Blondel et al. 1988). For species with static or small ranges and simple life-histories, such as some plants (Thuiller et al. 2005) and insects (Vogler & Desalle 1994), defining the niche, investigating specialisation and prescribing conservation measures can be relatively simple tasks. However, for species that are highly mobile and have complex life-cycles these tasks can be significantly more challenging. Until recently quantifying large-scale movement and habitat use in wild animals was limited by technological constraints. However, the advent of geolocator, satellite and Global Positioning System (GPS) miniaturised biologgers has opened the floodgates of movement ecology for almost all vertebrate groups (Kays et al. 2015, Hays et al. 2016). The simultaneous rise of satellite remote-sensing has allowed animal movements from tracking to be quantified against habitats and environmental variables, in both the terrestrial and marine realm (reviewed by Kays et al. 2015). The clear application these data have to niche theory have seen a rapid increase in ecological niche modelling or species distribution modelling studies (Franklin 2006, Elith & Leathwick 2009, Soberon & Nakamura 2009). A parallel rise has also occurred in stable isotope ecology, which cannot only infer animal movement (reviewed by Rubenstein & Hobson 2004), but also quantify diet (Fry 2006). As such the isotopic niche of a species is highly representative of its ecological niche (Bearhop et al. 2004, Newsome et al. 2007).

### **1.4 Seabird niches and intra-specific specialisations**

Seabirds are an exemplary group of mobile and complex species that, through the advance of technology, have begun to have their niche specialisations unravelled. Seabirds have a marine foraging niche, meaning all their food resources come from the sea. This reliance on the ocean has resulted in seabirds displaying many extreme life histories (Lack 1968, Ricklefs 1990), with ample opportunity for niche specialisation (Ceia & Ramos 2015). Firstly, the large ranges and strong site philopatry of seabirds means that individual

breeding populations of a single species can become locally adapted to different oceanographic conditions (Peck & Congdon 2005) or competitive pressures (Lewis et al. 2001). Seabird inter-population niche specialisation has been seen in habitat selection (Weimerskirch et al. 2009b, Paiva et al. 2010b, Mendez et al. 2017), foraging ecology (Peck & Congdon 2005, Oppel et al. 2015) and diet (Blaber et al. 1995, Jaquemet et al. 2008, Castillo-Guerrero et al. 2016). Secondly, long lives and complex social and developmental differences in seabird species lead to a number of intra-species niche specialisations (Votier et al. 2017). Niche specialisation due to age has been observed by comparing immatures and breeding adults in some species (Campioni et al. 2016, Votier et al. 2017), or shown to gradually change following ontogenetic shifts in others (Jaeger et al. 2014). Niche specialisation due to sex has also been recorded in many seabird species that show sexual-dimorphism (e.g. albatrosses, Shaffer et al. 2001; boobies, Zavalaga et al. 2007; and frigatebirds, Congdon & Preker 2004), but also in some monomorphic species (e.g. gannets, Lewis et al. 2002; and shearwaters, Peck & Congdon 2006). Additionally, individual-level niche specialisation appears prevalent in seabirds (reviewed by Ceia & Ramos 2015). Finally, the dynamism of the marine realm (Weimerskirch 2007, Wakefield et al. 2009) and sensitivity of seabirds to oceanographic changes (Peck et al. 2004), causes many species to display considerable plasticity in their niches (Hamer et al. 2007, Catry et al. 2009a, Quillfeldt et al. 2010). Niche plasticity also occurs at intra-species level, for example some seabirds only show sex-specific niche specialisation during certain breeding stages (Phillips et al. 2004), or in response to resource depletion (Paiva et al. 2017).

### **1.5 Seabird threats and intra-specific niche specialisation**

The marine foraging niche of seabirds puts them at risk from numerous anthropogenic threats, primarily commercial fisheries, pollution and climate change (Croxall et al. 2012). Commercial fisheries can impact seabird populations in two ways: 1) through direct mortality of birds as bycatch in fishing gear, for example hooking and drowning on longlines (Weimerskirch & Jouventin 1987) or tangling and drowning in drift nets (Žydelis et al. 2013); and 2) through reduced access to prey as seabirds compete with fisheries for forage fish (Cury et al. 2011, Bertrand et al. 2012). Threats such as climate change and plastic ingestion operate passively at the global-scale but are projected to have ever greater impacts on seabird populations (Grémillet & Boulinier 2009, Wilcox et al. 2015), while pollution events such as oiling have more local impacts (Wiese

& Robertson 2004). Studies that investigate the resource bases of intra-species niche specialists can be used to better understand threats to seabird populations. This is best demonstrated by the Wandering Albatross *Diomedea exulans*, which in the 1980s was identified as suffering population decline due to adult bycatch in longline fisheries (Weimerskirch & Jouventin 1987). Since then, intensive research using tracking devices, stable isotopes and demographic data has revealed the Wandering Albatross niche to be divergent and specialised between sexes and five life stages (juvenile, immature, breeding adult, sabbatical adult, and old; Weimerskirch et al. 2014). The different resource bases used by these specialist groups determines their risk of bycatch: females, juveniles and immatures which favour sub-tropical waters are more at risk from tuna longliners; while males, particularly old ones, which favour sub-Antarctic waters are more at risk from Patagonian tooth-fish longliners (Weimerskirch et al. 2006a, Weimerskirch et al. 2014). Unequal threats to different demographic cohorts of the Wandering Albatross population revealed through niche specialisation can tailor conservation management (Lascelles et al. 2016) and improve population models (Tuck et al. 2001). However, no seabird is better studied than the Wandering Albatross (> 60 years of land-based data, > 25 years of tracking data; Weimerskirch et al. 2014), and for most species the potential threats to groups of intra-species niche specialists are largely unknown.

### **1.6 Tropical seabirds and niche specialisation**

Tropical regions (waters  $\geq 23^{\circ}\text{C}$ ; Ashmole 1971) comprise almost 50% of the area of global oceans (Longhurst & Pauly 1987); however, tropical seabirds are understudied relative to those of higher latitudes (Ballance & Pitman 1999, Baduini & Hyrenbach 2003, Weimerskirch 2007). Tropical systems are considered to have lower productivity and fewer predictable physical ocean features (e.g. frontal or shelf upwelling) than temperate and polar systems (Longhurst & Pauly 1987, Weimerskirch et al. 2004, Weimerskirch 2007). Thus, the general consensus among marine ornithologists is that seabird resources in the tropics are lower in abundance and more patchily distributed than those of higher latitudes (Ashmole 1971, Ainley & Boekelheide 1983, Ballance & Pitman 1999, Weimerskirch 2007). The adaptations of tropical seabirds to their environment, such as highly efficient flight (Ballance 1995), lack of diving ability (Ashmole 1971) and flock-feeding in association with sub-surface predators (Au & Pitman 1986, Spear et al.

2007), indicates that the wealth of studies on temperate and polar seabird foraging niches have limited transferability to the tropics (Ainley & Boekelheide 1983, McDuie 2015).

Niche specialisation is thought to play an important role in tropical seabird ecology but due to lack of research there are still many knowledge gaps. Community level studies are fairly abundant and show sympatrically breeding tropical seabirds partitioning resources by each species specialising in different dietary niches (Ashmole & Ashmole 1967, Catry et al. 2009a) and/or habitat niches (Cherel et al. 2008, Young et al. 2010a, Mancini & Bugoni 2014). At intra-species level there are still many uncertainties about the prevalence of niche specialisation in tropical seabirds. This knowledge gap is confounded by data-deficiency within several aspects of tropical seabird foraging ecology that could drive niche specialisation. By investigating aspects of tropical seabird foraging ecology that are thought to drive niche specialisation we can: 1) update tropical seabird foraging ecology theory; 2) determine the prevalence certain intra-species niche specialisations in tropical seabirds; and 3) identify the resource bases used by intra-species niche specialists for conservation management.

### **1.6.1 Population niche specialisation on tuna**

Through local adaptation different populations within tropical seabird species may adopt different niche specialisations (Peck & Congdon 2005, Nunes et al. 2016, Mendez et al. 2017). Tropical seabirds are specialised into four foraging niches: 1) facilitated foraging with sub-surface predators; 2) nocturnal feeding; 3) scavenging dead cephalopods; and 4) diurnal feeding on small invertebrates (Ballance et al. 1997, Ballance & Pitman 1999, Spear et al. 2007). However, facilitated foraging with sub-surface predators, primarily tuna, is thought to be by far the most adopted foraging niche (Au & Pitman 1986, Ballance & Pitman 1999, Spear et al. 2007). Seabirds within this niche specialise on following tuna and capitalising on prey that the tuna force to the surface of the water when foraging (Ashmole & Ashmole 1967, Clua & Grosvalet 2001), through this relationship tuna act as an important resource base for tropical seabirds. However, it is not known if facilitated foraging is a species level specialisation or if inter-population plasticity means that different populations are more or less specialised on facilitated foraging due to local adaptation. A reliance on foraging with tuna puts specialised tropical seabird populations at risk from

fisheries that deplete tuna numbers, thereby decreasing facilitated foraging opportunities (Au & Pitman 1986), and cause longline mortality (Trebilco et al. 2010). In order to accurately assess the threat that tuna fisheries pose to tropical seabirds, the prevalence of intra-species specialisation in facilitated foraging shown by different populations needs to be accounted for.

### **1.6.2 Ontogenetic niche specialisation through foraging strategy**

Within tropical seabird populations different age demographics undoubtedly have specialised niches (Cherel et al. 2008, Young et al. 2010b, Mancini & Bugoni 2014); however, the foraging strategy adopted while breeding can also create age-based niche specialisation within a population. Breeding seabirds are central-place foragers (Orians & Pearson 1979), the need to regularly return to colony constrains the niche of breeding seabirds to locally available resources. When rearing chicks many seabirds use a unimodal foraging strategy, where parent birds meet their own resource needs and of those of their chicks on successive short-trips in local waters. The alternative is a dual-foraging strategy, which has been widely observed in procellariiforms (albatrosses and petrels; Weimerskirch et al. 1994, Baduini & Hyrenbach 2003, Cherel et al. 2005c). In a dual-foraging strategy parents cannot meet their own resource needs and those of chicks in local resource-poor waters. As a result, parents provision chicks with local resources obtained on short-trips, at the expense of their own condition, and then undertake periodic long-trips to more distant and presumably resource-rich waters to quickly regain their own condition (Weimerskirch 1998, Weimerskirch & Cherel 1998, Cherel et al. 2005c). Under unimodal foraging, parents and chicks are sustained by the same local resource base, and therefore share the same foraging niche. However, under dual-foraging the minimal assimilation of local resources by parents (Congdon et al. 2005) is thought to specialise their own foraging niche on a distant resource base and the niche of their chicks on a local resource base (Cherel et al. 2005c). Although dual-foraging is widely observed in temperate and polar seabirds (reviewed by Baduini & Hyrenbach 2003), to date it has only been recorded in the tropics in a shearwater (Congdon et al. 2005), petrel (Pinet et al. 2012) and tropicbird (Sommerfeld & Henny 2014). Determining the prevalence of dual-foraging in tropical seabirds and whether the expression of this phenomenon within and between populations varies in response to changing environmental conditions is important for conservation. This is because management of a dual-foraging population, in which adults and chicks have different risks associated with

their divergent niches and resources, is more complex than management of a unimodal population, in which adults and chicks share the same niche and risks.

### **1.6.3 Sex-specific nutritional niche specialisation**

Sex-specific niche specialisation has been widely observed within tropical seabird populations but with little consensus on its drivers (Lormee et al. 2005, Paiva et al. 2017). Tropical seabirds have been shown to have specialist diets (Cherel et al. 2008, Castillo-Guerrero et al. 2016), habitats (Weimerskirch et al. 2006b, Pinet et al. 2012) and foraging ecology (Congdon & Preker 2004, Lewis et al. 2005) due to sex. However, while some studies explain sex-specific niche specialisation using morphological mechanics (Zavalaga et al. 2007), others claim it is a consequence of intersexual competition (Peck & Congdon 2006), or differences in the roles of each sex (Weimerskirch et al. 2009a). In a wide range of species, foraging goals are related to a specific amount or proportion of nutrients (Raubenheimer et al. 2015). The nutritional niche is a new concept that provides a framework for finer scale examination of a species' dietary niche and resource base (Machovsky Capuska 2016). Within seabird species different ages or sexes might specialise their niche due to different nutritional needs (Lewis et al. 2002, Peck & Congdon 2006, Machovsky-Capuska et al. 2016b). For example, the increased energetic needs of the larger sex in dimorphic species or physiological costs of oviposition in females may require them to target a specific nutritional resource base (Lewis et al. 2002, Ismar et al. 2017). So far only one study of a temperate seabird has shown intra-species niche specialisation due to nutritional demands (Machovsky-Capuska et al. 2016b). The nutritional niche of a tropical seabird has never been quantified; however, divergent nutritional demands offer a parsimonious alternative to the current disparity of explanations for sex-specific niche specialisation of tropical seabirds. Conservation management that overlooks the nutritional niche may protect a perceived 'average' prey resource base that in fact does not reflect the needs of sexes with divergent nutritional niche specialisations.

### **1.7 Model species**

To investigate foraging ecology and niche specialisation in tropical seabirds, I selected two common, pelagic tropical seabird species with different but complimentary biological characteristics.

### **1.7.1 The Wedge-tailed Shearwater**

The Wedge-tailed Shearwater *Ardenna pacifica* is a widespread and numerous pan-tropical procellariiform from the Pacific and Indian oceans (Marchant & Higgins 1990). The Wedge-tailed Shearwater is a good tropical model for investigating the intra-specific niche specialisations discussed previously for the following reasons. Firstly, the species is thought to frequently associate and forage with tuna across its range (Au & Pitman 1986, Jaquemet et al. 2004, Hebshi et al. 2008); however, like all tropical species the Wedge-tailed Shearwater's purported 'reliance' on tuna has never been quantified (Catry et al. 2009b, McDuie & Congdon 2016). Secondly, while breeding Wedge-tailed Shearwater populations adopt unimodal (Baduini 2002) or dual-foraging (Congdon et al. 2005) strategies through local adaptation (Peck & Congdon 2005).

### **1.7.2 The Brown Booby**

The Brown Booby *Sula leucogaster* is similarly both widespread and abundant, and has a pan-tropical global distribution (Marchant & Higgins 1990). The Brown Booby is another good model for exploring intra-specific niche specialisations as it also displays local adaptation (Nunes et al. 2016). Additionally, Brown Boobies display clear sexual dimorphism, with females being 38% larger than males (Lewis et al. 2005) and showing different colouration on feet, face and bills (Nelson 1978). Brown Boobies also spontaneously regurgitate their prey in a relatively undigested state, which is important for nutritional analyses (Machovsky-Capuska et al. 2016a). These physiological characteristics are not displayed by the monomorphic Wedge-tailed Shearwater, which feeds chicks with highly digested prey and proventricular oil (Marchant & Higgins 1990). Therefore, the Brown Booby provides an excellent complementary model to the Wedge-tailed Shearwater for this projects' investigation.

## **1.8 Model system and conservation**

This study is situated in the Great Barrier Reef (GBR), the Coral Sea and northern Tasman Sea, Australia. Wedge-tailed Shearwaters were sampled from two populations: sub-tropical Lord Howe Island in the northern Tasman Sea; and Heron Island in the southern GBR (Fig 1.1). The Lord Howe Island Wedge-tailed Shearwater population is primarily confined to small islets off the main island (including Balls Pyramid). When considered as a whole the population has been estimated at 28,675 breeding pairs (Carlile & Priddel



2013). The Heron Island population has been estimated at 13,399 breeding pairs (Dyer et al. 2005); however, Heron Island is central within the Capricorn Bunker reef group, which collectively holds ~ 560,000 breeding pairs, the Pacific's largest Wedge-tailed Shearwater population (Dyer et al. 2005). Brown Boobies were sampled from Raine Island in the northern GBR, the largest regional population with ~ 2600 birds (Batianoff & Cornelius 2005).



**Fig. 1.1** Regional seascape and location of study colonies

There have been population declines in several tropical seabird species across the GBR, although causes remain generally unknown (Congdon et al. 2007). The Capricorn Bunker Wedge-tailed Shearwater population is thought to have declined by 40% since the 1990s (Hemson 2015). By contrast the Lord Howe Island Wedge-tailed Shearwater population appears stable (Carlile pers. comm.). The Brown Booby population on Raine Island is thought to have declined by 40% since 1993 (Batianoff & Cornelius 2005) and the population of the Swains Reefs (the second largest on the GBR) is thought to have declined by 41% since 1986 (Heatwole et al. 1996). There are no discernible terrestrial threats to the declining populations of either species (e.g. invasive predators), suggesting that inadequate at-sea resources are to blame (Batianoff & Cornelius 2005, Bunce 2015, Hemson 2015). Indeed, both species are susceptible to high sea surface temperature anomalies and suffer reduced breeding success, or even breeding failure during El Niño events (Heatwole et al. 1996, Smithers et al. 2003). In a review of GBR seabirds Congdon et al. (2007) suggest that the recent population declines could be the early impacts of climate change. Another non-mutually exclusive explanation is that population decline is linked to fisheries in the region (Hemson 2014). There is little evidence for direct mortality of tropical seabirds in fisheries gear (Trebilco et al. 2010); however, several species are known to follow vessels and their populations are influenced by discards (Blaber et al. 1998). The more supported suggestion is that tropical seabirds in the region target subsurface predator distributions for facilitated foraging opportunities, putting them in competition with fisheries (Erwin & Congdon 2007, Congdon et al. 2014, McDuie et al. 2015). The Eastern Tuna and Billfish Fishery (ETBF) is a multi-million dollar fishery in the region targeting large subsurface predators, with an annual quota of ~ 7000 tonnes (Wilson et al. 2010). The ETBF has previously overfished certain tuna stocks and has the capacity to alter the pelagic ecosystem of the region (Young et al. 2009, Griffiths et al. 2010). As such, population declines in tropical seabirds reliant on tuna for foraging could be attributed to expansion of ETBF effort since the late 1990s (Hemson 2014).

Limited knowledge of what resource bases sustain tropical seabird populations of eastern Australia means that causes of population decline and future threats are hard to pinpoint, and little information is available to advise at-sea protection (Heatwole et al. 1996, Congdon et al. 2007). Luckily, many tropical seabirds in the region breed within the Great Barrier Reef Marine Park (GBRMP), where careful zoning to protect a range

of habitats and unique features through no-take zones (Fernandes et al. 2005) likely benefits seabirds. Similarly, tropical seabirds on Lord Howe Island receive protection, albeit very locally, from the 460 km<sup>2</sup> Lord Howe Island Marine Park. However, many tropical seabird populations that breed within these well managed marine parks are thought to forage far beyond their boundaries in pelagic waters of the Coral and Tasman Seas (Peck & Congdon 2005, Erwin & Congdon 2007, Thalman et al. 2009, McDuie et al. 2015). The zoning of protected areas in these regions fall under the remit of the long-debated Australian Marine Park Network. The process of zoning this network started in 2012 and due to government changes is still underway, meaning no present protection for large expanses of the Australian Exclusive Economic Zone (EEZ). The only dedicated network of protected areas for seabirds in eastern Australia is the marine Important Bird Area and Biodiversity (IBA) network provided from a global analyses by Birdlife International (Lascelles et al. 2016). However, marine IBAs have no protection attached to them and until recently, it was unclear how they could be integrated into wider marine spatial planning (Mcgowan et al. 2017). As a result marine IBAs within Australia remain a 'paper park' network.

## **1.9 Aims and objectives**

In this thesis I examine the broad topic of intra-species niche specialisation in tropical seabirds. Using two tropical seabirds from eastern Australia I aimed to:

- 1) Investigate data-deficient aspects of tropical seabird foraging ecology: i) dual-foraging; ii) tuna reliance; iii) and nutritional niches, and determine their importance in driving niche specialisation
- 2) Identify the resource bases that sustain intra-species niche specialist groups
- 3) Apply learnings to make a best-practice model for regional seabird conservation

To achieve my aims, in chapters Two to Four I explore the resource base of an intra-species niche specialisation that forms an important demographic group within a species. Additionally, each of these chapters tests the importance of an unsubstantiated hypothesis in tropical seabird foraging ecology thought to

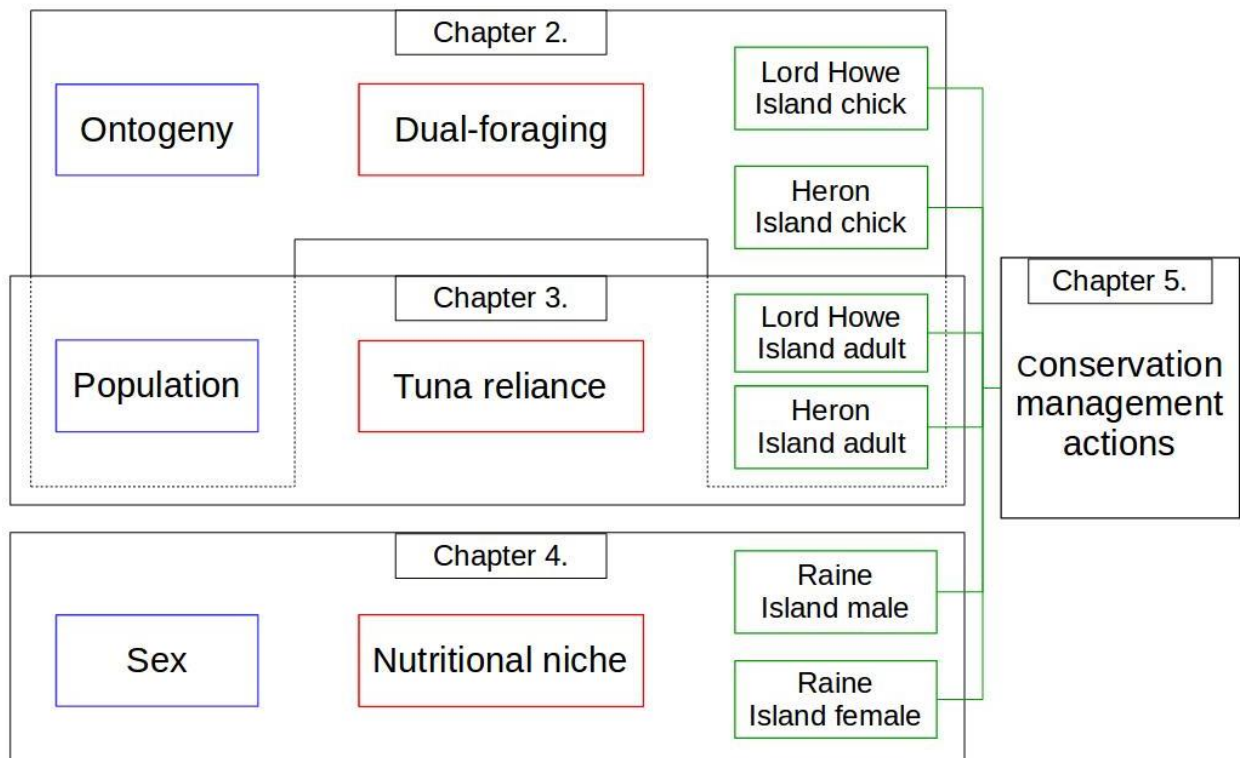
drive niche specialisation. In chapter Five I synthesize what has been learned about these niche specialists and their resource bases, and prescribe a set of direct conservation actions for each group (Fig. 1.2).

In Chapter Two I investigate how the principal foraging strategy of Wedge-tailed Shearwater populations from Heron and Lord Howe islands is shaped by local resource availability and reliability. I use multiple years of adult colony attendance data, tracking data and stable isotopes to determine if populations consistently adopt dual-foraging or unimodal foraging. Under these two foraging strategies I explore whether the niches and resource bases of adults and chicks are separated or shared as expected.

In Chapter Three I again use Wedge-tailed Shearwater populations from Heron and Lord Howe islands, this time to investigate population-level reliance on facilitated foraging with tuna. I use multiple years of adult long-trip tracking data, oceanographic data and modelled tuna distributions to determine how important tuna are for aggregating shearwater foraging relative to other ocean mechanisms. Conducting this analyses on each colony allows me to determine how specialised each population's foraging niche is upon tuna.

In Chapter Four I use the Brown Booby population of Raine Island to investigate whether sex-specific niche specialisation is driven by divergent nutritional demands between sexes. I use tracking, dietary and nutritional data to investigate whether sexes have divergent foraging niches and divergent nutritional niches.

In Chapter Five I synthesise the findings of the previous three chapters. Firstly, I discuss how my results update current theory on tropical seabird foraging ecology. Secondly, I describe the resource bases that sustain groups of population and sub-population specialists from the study. Finally, I make a set of direct management actions to safeguard the marine resources of regional tropical seabird populations.



**Fig. 1.2** Schematic of thesis chapters and topics. Blue boxes indicate intra-species niche specialism investigated, red boxes indicate the element of tropical seabird theory investigated, green boxes indicate the potential demographic specialist groups, and black boxes indicate chapter contents. Chapters Two and Three use the Wedge-tailed Shearwater, whereas chapter Four uses the Brown Booby

## **CHAPTER 2: FORAGING NICHE AND LOCAL ADAPTATION IN A TROPICAL PROCELLARIIFORM**

This chapter is in preparation for submission to *Marine Biology* as  
—Resource stability and local adaptation in a tropical procellariiform: tracking a movable feast” by  
MGR Miller and BC Congdon

## 2.1 ABSTRACT

There is limited data on foraging strategies in tropical seabirds, particularly procellariiforms. The dual-foraging strategy, which is common in higher latitude procellariiforms, requires a degree of resource reliability that is thought unlikely in tropical oceans. Here I collected and combined multiple years of data on foraging patterns, habitat and resource use in Wedge-tailed Shearwaters *Ardenna pacifica* breeding on a tropical and sub-tropical colony to investigate local adaptation of foraging strategy in each population.

I observed consistent dual-foraging over three years in the tropical shearwater population, whereas the sub-tropical population switched from unimodal to dual-foraging and then back again. Chicks from the tropical population were consistently provisioned with local resources from southern Great Barrier Reef waters whereas adults self-provisioned on resources obtained in the central Coral Sea. The sub-tropical population used local resources in the northern Tasman Sea to sustain chicks. This local resource was shared by adults under unimodal foraging but under dual-foraging self-provisioning adults shifted to exploit the same Coral Sea resources as tropical conspecifics. Both populations have a degree of flexibility in their foraging strategy that is related to the long-term reliability of local resources; the sub-tropical population showing greater variability through strategy switching. Consistently lower near-colony resource availability at the tropical colony likely puts it at higher risk from environmental perturbations, but these may be buffered, in part, by the high lipid diet of chicks. Poor near-colony foraging environments at both colonies were offset by persistent and reliable at-distance resources in the central Coral Sea. The regional scale reliance of shearwaters on this at-distance resource base cannot be overstated and its mechanics warrants further investigation.

## 2.2 INTRODUCTION

Breeding seabirds are central-place foragers (sensu Orians & Pearson 1979), needing to regularly return to land to incubate eggs or provision chicks. The early chick-rearing period is a particularly challenging time,

when parent birds have to regularly provision young chicks that have not yet accumulated sufficient lipid reserves to buffer longer breaks between feeds (Catry et al. 2006), whilst simultaneously maintaining their own body condition. Within Procellariiform (tube-nosed) seabirds, two different foraging strategies have evolved that deliver regular meals to young chicks (Baduini & Hyrenbach 2003). A unimodal foraging strategy arises when provisioning adults can obtain enough prey for both themselves and their chicks on relatively short foraging trips (1-2 days in albatrosses and shearwaters: Baduini 2002, Phillips et al. 2009); whereas a bimodal or dual-foraging strategy arises when a series of short-trips (1-3 days; Baduini & Hyrenbach 2003) in local waters are used to provision chicks at the expense of parent condition, followed by a long-trip (5-17 days) to more distant foraging sites for self-provisioning, where adults can quickly regain condition (Weimerskirch 1998, Weimerskirch & Cherel 1998). Dual-foraging parents coordinate their trips, so that while one parent provisions the chick using short-trips, the other self-feeds on a long trip. This strategy ensures frequent meal delivery to chicks via continuous short trips (Booth et al. 2000, Congdon et al. 2005, Tyson et al. 2017).

Which of these alternative foraging strategies a population adopts depends on the abundance and reliability of resources accessible from the colony. A unimodal foraging strategy maximises delivery from locally abundant resources and is thought to be more efficient for exploiting abundant but heterogeneously distributed prey in relatively productive waters (Booth et al. 2000, Baduini & Hyrenbach 2003). Conversely, a coordinated dual-foraging strategy occurs when there is reduced local resource abundance, and is thought to require reliable resources, particularly at long-trip destinations (Booth et al. 2000, Baduini & Hyrenbach 2003, Ropert-Coudert et al. 2004). Either of these strategies can be considered the principal foraging strategy of a population given the background state of resource availability, determined by general productivity surrounding the colony (Baduini & Hyrenbach 2003) and density-dependent competition for resources (Ashmole 1963, Lewis et al. 2001, Oppel et al. 2015). For example, Sooty Shearwaters *Ardenna grisea* and Short-tailed Shearwaters *A. tenuirostris* breeding in southern Australasia have local access to high productivity neritic habitat suggesting unimodal foraging; however their massive regional populations contribute to dual-foraging being the observed strategy, in order to escape near-colony competition (Weimerskirch & Cherel 1998, Shaffer et al. 2009).



However, populations can switch between foraging strategies as a facultative response to environmental heterogeneity (Peck & Congdon 2005). Populations of Cory's Shearwater *Calonectris diomedea* and Yellow-nosed Albatross *Thalassarche chlorohychnos* adopt a unimodal foraging strategy in years of high local resource availability and a dual-foraging strategy in years when local resources are depleted (Granadeiro et al. 1998, Pinaud et al. 2005). As such, through multiple years of data collection, the nature of the resources that shape a populations' foraging strategy can be inferred: consistent unimodal foraging indicates abundant and reliable local resources; consistent dual-foraging indicates a depleted but relatively predictable local resource base and highly reliable distant resources; and a switching strategy indicates an unreliable local resource base, that is sometimes abundant and sometimes depleted.

Polar and temperate regions accommodate both foraging strategies because resources tend to be abundant, due to high background productivity (Longhurst & Pauly 1987), and reliable, due to stable physical processes that enhance prey availability at upwelling, frontal and shelf zones (Ainley & Boekelheide 1983, Hunt et al. 1999, Weimerskirch 2007). For example, several albatross species from South Georgia in the southern Atlantic Ocean consistently employ a unimodal foraging strategy during chick rearing, supported by high productivity and an abundant local resource, Antarctic Krill *Euphausia superba* (Phillips et al. 2009). Conversely, temperate populations of Sooty Shearwaters and Short-tailed Shearwaters in southern Australasia consistently adopt a dual-foraging strategy during chick rearing, whereby short trips target local shelf-based prey and long trips access abundant resources aggregated by the reliably-located polar front, or Antarctic ice edge (Weimerskirch et al. 1994, Weimerskirch 1998, Klomp & Schultz 2000, Shaffer et al. 2009).

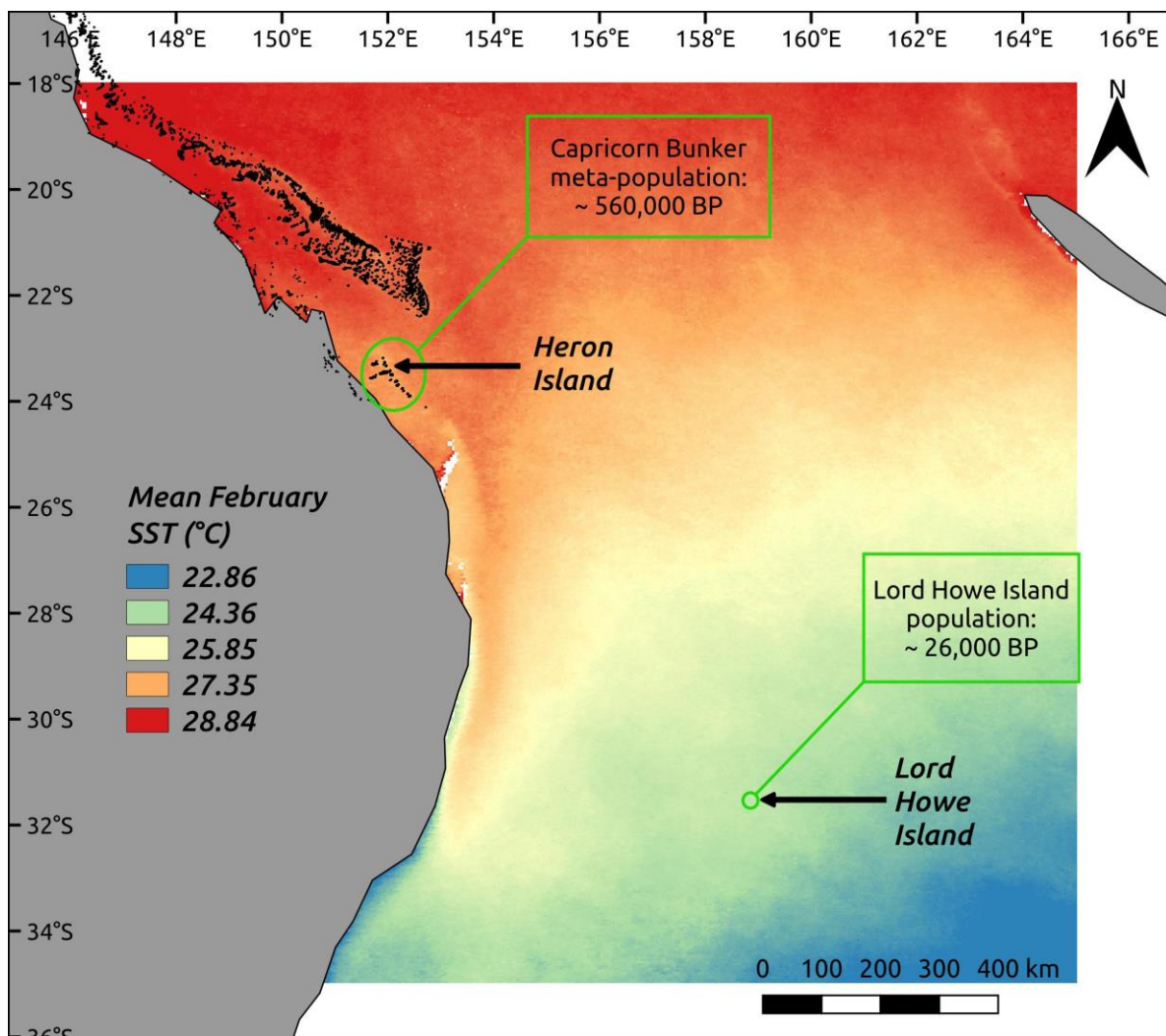
A global review of foraging strategies suggests that dual-foraging becomes more common with decreasing latitude (Baduini & Hyrenbach 2003). This is supported by research showing that sub-tropical populations of Laysan Albatross *Phoebastria immutabilis*, Black-footed Albatross *P. nigripes* and Cory's Shearwater use long-trips to reach the same abundant and reliable high latitude shelves and fronts as do temperate and sub-polar breeding birds (Fernández et al. 2001, Hyrenbach et al. 2002, Magalhães et al. 2008). Nonetheless, where productive shelves are locally accessible, subtropical populations have also been observed adopting a

unimodal foraging strategy (e.g. Baduini 2002, Navarro & González-Solís 2009). As such, it appears that the subtropics can accommodate both foraging strategies, but that dual-foraging is more prevalent due to the constraint of generally lower local resource abundance and the accessibility of higher latitude resource bases from subtropical colonies. Little is known regarding the reliability of resource bases in the sub-tropics; however, it is worth noting that the aforementioned examples of foraging strategy switching in Cory's Shearwater and Yellow-nosed Albatross both originate in the sub-tropics.

The few foraging strategy studies of pelagic seabirds in the tropics (waters  $\geq 23^{\circ}\text{C}$ ; Ashmole 1971), outside those showing unimodal foraging in boobies (Weimerskirch et al. 2006b, Oppel et al. 2015, but see Zavalaga et al 2012), have observed dual-foraging in a tropical shearwater (Congdon et al. 2005), petrel (Pinet et al. 2012) and tropicbird (Sommerfeld & Hennicke 2014). However, how tropical resources support this strategy is unclear. The assumption that dual-foraging requires a consistently accessible and reliable long-trip resource base does not fit well with current theory suggesting that tropical seabird prey resources are more unreliable and more patchily distributed than at higher latitudes (Ainley & Boekelheide 1983, Ballance & Pitman 1999, Weimerskirch 2007). As such, investigating whether dual-foraging observations from the tropics represent: a) the principal foraging strategy; or b) a mode within a switching strategy provides information on the reliability of seabird resources in the tropics.

The Wedge-tailed Shearwater *Ardenna pacifica* is a pan-tropical procellariiform from the Indian and Pacific oceans that has been observed dual-foraging (Congdon et al. 2005), unimodal foraging (Baduini 2002) and switching between the two strategies (Bond et al. 2010). Wedge-tailed Shearwater populations breeding off the east coast of Australia have been observed dual-foraging at a colony located in tropical waters (Congdon et al. 2005, Peck & Congdon 2005) with high intra-specific competition pressure (Dyer et al. 2005), but observed adopting unimodal foraging at a colony located in sub-tropical waters (Peck & Congdon 2005) with lower competitive constraints (Carlile & Priddel 2013). The tropical to subtropical and competitive gradients between these two colonies (Fig. 2.1) provides a useful framework to address research questions on how tropical seabirds adapt foraging strategies to achieve reproductive success given different local resource availability. Similar theoretical models have been constructed for procellariiforms over a sub-tropical to

temperate resource gradient (Paiva et al. 2010a, Paiva et al. 2010b) and for tropical boobies responding to competitive (Oppel et al. 2015) and environmental (Weimerskirch et al. 2009b, Castillo-Guerrero et al. 2016) pressures on resources. However, for tropical procellariiforms there is little present data upon which to construct such a model. Considering that roughly 26 species of procellariiform breed in the tropics (excluding storm petrels, which don't appear to dual-forage; Baduini & Hyrenbach 2003) this represents a significant knowledge gap.



**Fig. 2.1** Tropical to subtropical gradient and population differences shown between Wedge-tailed Shearwater study colonies. Regional sea surface temperature (SST) given from 2003-2016 average for month of February (start of chick-rearing). Population estimates expressed as number of breeding pairs (BP) from Capricorn Bunker group (Dyer et al. 2005) and Lord Howe Island (Carlile & Priddel 2013)

By collecting simultaneous information on foraging patterns, habitat and resource use and combining it with existing multi-year data sets from two long-term Wedge-tailed Shearwater study populations, I aimed to establish the principal foraging strategy used by each population (unimodal foraging, dual-foraging, or switching between the two) and determine whether differences in these strategies reflect adaptation to local and divergent resource bases. To do so I collected and combined complimentary datasets, including: 1) adult colony attendance, which can distinguish unimodal and dual-foraging strategies (Weimerskirch et al. 1994); 2) tracking data, which can distinguish the location of short and long-trip resources (Klomp & Schultz 2000); and 3) stable isotope data, which can distinguish if resources are shared between colonies, or between adults and chicks, which is assumed under unimodal but not dual-foraging (Bond et al. 2010). These data allowed me to address the following specific research questions: 1) is variation in foraging strategy driven by changes in local resource availability (magnitude or reliability) as measured by food availability to chicks (provisioning rates and chick condition)?; 2) under dual-foraging are the resources consumed by adults and chicks actually different, or the same but with differing availability in different locations?; 3) under unimodal foraging are the resources consumed by adults and chicks actually the same, or do adults partition prey obtained from the same foraging locations to provision themselves and chicks?; 4) Do two Wedge-tailed Shearwater populations that span the tropical-subtropical divide use separate resource bases, or the same communal regional resource 'pool'?; and 5) are subtropical resources really more stable and predictable than the resource bases used by a dual-foraging population in the tropics?

## **2.3 METHODS**

### **2.3.1 Field data collection and logger deployment**

This study was carried out at Heron Island (23°26' S, 151°51' E) in the Capricorn Bunker Island Group, Great Barrier Reef and Lord Howe Island (31°33' S, 159°05' E) in the northern Tasman Sea, Australia. Both islands support large breeding colonies of Wedge-tailed Shearwaters (Marchant & Higgins 1990). Data from Heron Island in 2001 were collected by Congdon et al. (2005), data from Heron Island in 2003 and Lord

Howe Island in 2004 were collected by Peck & Congdon (2005) and data from Heron Island in 2015 and Lord Howe Island in 2015 and 2016 were collected in this study. Because foraging strategies can change over the course of chick-rearing (Jakubas et al. 2014), colonies were sampled each day in the same early-chick rearing period between February and mid-March each year. Within this sampling period chicks were between ~5-45 days old and display a linear relationship between growth and age (Ramos et al. 2003).

Adult attendance data was obtained by monitoring the frequency with which parent birds return to the chick. At sampled burrows, both adults were either banded, or marked for individual recognition by placing non-toxic white correction fluid on different wings. Attendance was monitored regularly from 17:00 to 05:00 h daily. During monitoring burrow entrances were partially obstructed with natural markers (Heron Island, *Pisonia* sp. leaf; Lord Howe Island, *Araucaria* sp. fronds) that allowed adult visits to be detected but did not affect adult behaviour. If the burrow had been entered, the individual adult inside was identified. If the burrow markers were disturbed but no adult was present inside, all adults resting within a 10 m radius of the burrow were checked for identification. After each adult identification burrow markers were reset so that subsequent visits by other adults could be detected. Chicks were weighed once a day at 16:00 h using an electronic balance ( $\pm 0.1$  g) or Pesola spring balance ( $\pm 0.5$  g). Tarsus measurements were also obtained for each chick every 4 days using dial callipers ( $\pm 0.1$  mm).

Blood samples for stable isotope analyses were collected from adults ( $n=8$ ) and their chicks ( $n=8$ ) on Heron Island in 2015, Lord Howe Island in 2015 and Lord Howe Island 2016. Approximately 0.5 ml of blood was taken from either the wing or tarsal vein using a 1 ml disposable syringe and needle and transferred to a 1.5 ml microtube. With the exception of LHI chicks in 2015, all blood samples were transferred to a portable centrifuge to split whole blood into plasma and red blood cell components. All samples were frozen and stored at  $-20^{\circ}\text{C}$ . Blood is a metabolically active tissue whose isotopic ratios reflect diet during the days (plasma) or weeks-month (red blood cells) before sampling (Hobson & Clark 1992, Bearhop et al. 2002, Cherel et al. 2005b). We selected red blood cells for further analyses because they represent diet over a greater temporal span (multiple foraging trips) than plasma (the last foraging trip; Cherel et al. 2005b), and

could thus better elucidate dual-foraging from unimodal foraging behaviours (Cherel et al. 2005c, Bond et al. 2010, Alonso et al. 2012).

GPS loggers were deployed on Wedge-tailed Shearwaters at Lord Howe Island in 2015 and 2016 and concurrently at Heron Island in 2015. All loggers were deployed during the early chick-rearing period (Feb-mid March). I-gotU GT-120 GPS loggers (Mobile Action Technology) were modified to use smaller 100mAh batteries, sealed in heat-shrink tubing and programmed to obtain fixes every 10 minutes (Freeman et al. 2013). I deployed both GPS loggers to 3 central tail feathers using Tesa® 4651 Tape; total deployment weight of loggers was ~ 10.5-12 g, within the 3-5% body weight limit for the species (McDuie et al. 2015). I found no significant differences in the proportion of chicks fed each night at nests with parents carrying GPS loggers compared to control nests with unencumbered parents (Heron Island 2015,  $0.51 \pm 0.23\%$  control chicks fed night<sup>-1</sup>,  $0.48 \pm 0.3\%$  GPS chicks fed night<sup>-1</sup>, paired t-test,  $t = 0.64$ ,  $p = 0.53$ ; Lord Howe Island 2015,  $0.50 \pm 0.13\%$  control chicks fed night<sup>-1</sup>,  $0.45 \pm 0.36\%$  GPS chicks fed night<sup>-1</sup>, paired t-test,  $t = 0.66$ ,  $p = 0.51$ ; Lord Howe Island 2016,  $0.55 \pm 0.12\%$  control chicks fed night<sup>-1</sup>,  $0.52 \pm 0.53\%$  GPS chicks fed night<sup>-1</sup>, paired t-test,  $t = 0.82$ ,  $p = 0.41$ ).

### **2.3.2 Foraging strategy analyses**

All data handling and statistical analyses were performed in the statistical software environment program R, version 3.2.4 (R Core Team 2016). The foraging strategy adopted in each year was estimated from the adult attendance data. Adult foraging trip duration was defined as the time (in days) between consecutive observations of an individual at a nest. Following Congdon et al. (2005), I calculated the proportion of time spent on trips of different lengths undertaken by each individual during the sampling period to offset trip duration against frequency. I then took the mean across individuals to give the average proportion of time all birds spend on trips of different lengths per sampling season. On some occasions adults returning to the nest evaded identification (evidenced when a chick had been fed but no adult recorded), in this case one adult of the pair was randomly assigned as having returned from a foraging trip (Congdon et al. 2005, Peck & Congdon 2005). This procedure carries only a 50% chance of successful assignment of the returning adult and impacts the estimated trip length of both adults in the pair. The higher the number of unknown returns by

adult birds in a pair, the more error propagates through each foraging strategy dataset. To reduce such error I only included nests that had three or less unknown returns by adults from the pair over the sampling season (Heron Island 2001 n = 11, 2003 n=13; Lord Howe Island 2004 n=18, 2015 n = 12, 2016 n = 12). To determine whether a unimodal or dual-foraging strategy was used in each year I tested for differences between trip duration within each foraging strategy. I used Friedman tests, as each bird was repeatedly sampled, followed by post-hoc tests for multiple comparisons ( $\alpha = 0.05$ ) using the R package 'agricolae' (de Mendiburu 2016). To help distinguish unimodal from bimodal (dual-foraging) patterns in each foraging strategy I used k-means clustering to estimate the location of two peaks in each foraging strategy. To test for differences in foraging strategies between years I used Kruskal-Wallis or Mann-Whitney U-tests.

### 2.3.3 Stable isotope analyses

Red blood cell samples were prepared for stable isotope analysis by freeze-drying for 24 hours and grinding into a powder. Samples of ~ 0.2 mg were weighed and packed into tin capsules for combustion. My red blood cell samples had consistently low C:N ratios (<3.5), indicating low lipid content and that lipid extraction was not necessary (Post et al. 2007). Carbon and nitrogen stable isotope ratios were measured using a Costech Elemental Analyzer fitted with a zero-blank auto-sampler coupled via a ConFloIV to a ThermoFinnigan DeltaVPLUS using Continuous-Flow Isotope Ratio Mass Spectrometry (EA-IRMS), in the Advanced Analytical Centre at James Cook University, Cairns. To calibrate stable isotope results, three standards were analysed (protein, taipan keratin and chitin) in between every 20 blood samples. Stable isotope ratios are reported as mil unit (‰) deviations from international standards, Vienna Peedee Belemnite (VPDB) for  $\delta^{13}\text{C}$  and atmospheric  $\text{N}_2$  (AIR) for  $\delta^{15}\text{N}$ , and calculated using the equation  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N} = (\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1$ , where R = the ratio of the heavy isotope to the light isotope ( $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ) in the sample and standards.

Chick blood from Lord Howe Island in 2015 could not be centrifuged in the field due to logistical constraints. Despite whole blood and red blood cells being thought to have very similar isotope signatures (Cherel et al. 2005b), I collected both whole blood and split plasma/red blood cell samples from chicks in 2016 at Lord Howe Island to test for differences. No differences in  $\delta^{15}\text{N}$  were found between blood product



types (paired t-test,  $t = 0.83$ ,  $p = 0.44$ ) in 2016, however whole blood was found to be depleted in  $\delta^{13}\text{C}$  by 0.38 ‰ compared to red blood cells (paired t-test,  $t = 9.03$ ,  $p < 0.001$ ). As such I corrected chick whole blood from Lord Howe Island in 2015 by +0.38 ‰ to allow valid comparisons with red blood cells.

Comparing stable isotope red blood cell values between provisioning adults and their chicks can identify if adults and chicks have differently specialised foraging niches and separate resource bases (indicative of dual-foraging), or overlapping niches and resource bases (indicative of unimodal foraging) (Cherel et al. 2005c, Bond et al. 2010, Alonso et al. 2012). To compare stable isotope values between adult and chick red blood cells within each colony-year sampling combination I used multivariate analysis of variance (MANOVA), after all samples showed non-departure from normality (Mardia's test,  $p \geq 0.05$ ). To separately compare  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from adult and chick red blood cells within each colony-year sampling combination, I used independent t-tests or, in the case of departure from normality (Shapiro-Wilk test,  $p \leq 0.05$ ) or homogeneity of variance (Levene's test,  $p \leq 0.05$ ), Mann-Whitney U-tests. To separately compare  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of adult and chick red blood cells between sampling years and colonies, I used analysis of variance (Linear Model; LM) followed by post-hoc Tukey's HSD tests or, in the case of departure from normality or homogeneity of variance, Kruskal-Wallis tests followed by post-hoc tests.

#### **2.3.4 Inter-annual chick condition**

Chick condition in each year was estimated for Heron and Lord Howe Island separately due to the divergent chick growth patterns of each population (Peck & Congdon 2005, McDuie et al. 2013). At each colony a regression of chick weight against tarsus was constructed, combining chicks from all years (Heron Island 2001  $n = 26$ , 2003  $n=26$ , 2015  $n=19$ ; Lord Howe Island 2004  $n=22$ , 2015  $n = 66$ , 2016  $n = 42$ ). By averaging the residuals from this regression for chicks in any given year, I was able to obtain a measure of chick condition relative each colony baseline (Congdon et al. 2005). Values above the baseline condition of 0 represent good condition relative to body size, whereas values below represent poor condition. Chick condition was compared between years at each colony using Linear Mixed Models (LMMs) with individual chick as the random term in the package 'lme4' (Bates et al. 2015). To supplement the chick condition metric I estimated the feeding frequency at each colony, per year by calculating the proportion of chicks fed each



night (indicated by a weight maintenance or increase since the 16:00 measurement the previous day) and taking the average across the sampling period (Smithers et al. 2003). The proportion of chicks fed was compared between years at each colony using Linear Models (LMs).

### **2.3.5 Tracking data preparation and analyses**

Tracking data were pre-processed prior to analyses using a speed filter, removing points exceeding a maximum velocity of 50 km/h (McDuie et al. 2015), additionally GPS tracks were gap filled using interpolation to 10 minute interval (Freeman et al. 2013). As loggers were active for several days multiple foraging trips were observed for most individuals. I used the R 'tripsplit' function from the 'marine IBA' package (Lascelles et al. 2016) to split individual trips from multi-day GPS tracks. To identify the mean distance that each trip foraged from the colony I applied Hidden Markov Models (HMM) to the GPS data. I constructed a single HMM using the full GPS tracking dataset, including an identifier for each trip, using the package 'moveHMM' (Michelot et al. 2016). For each consecutive GPS point the step length and turning angle were calculated, producing three distributions consistent with foraging, resting and transiting behaviours observed in HMM studies of boobies (Oppel et al. 2015) and shearwaters (Dean et al. 2013). The fitted HMM was then used to classify each GPS point as either foraging, resting or transiting. As tropical seabirds can 'drift forage' (using a surface 'sit-and-wait' strategy; Connors et al. 2015), I subsequently treated foraging and resting locations as foraging. For each trip I calculated the distance of each foraging-classed GPS point from the colony and calculated the mean.

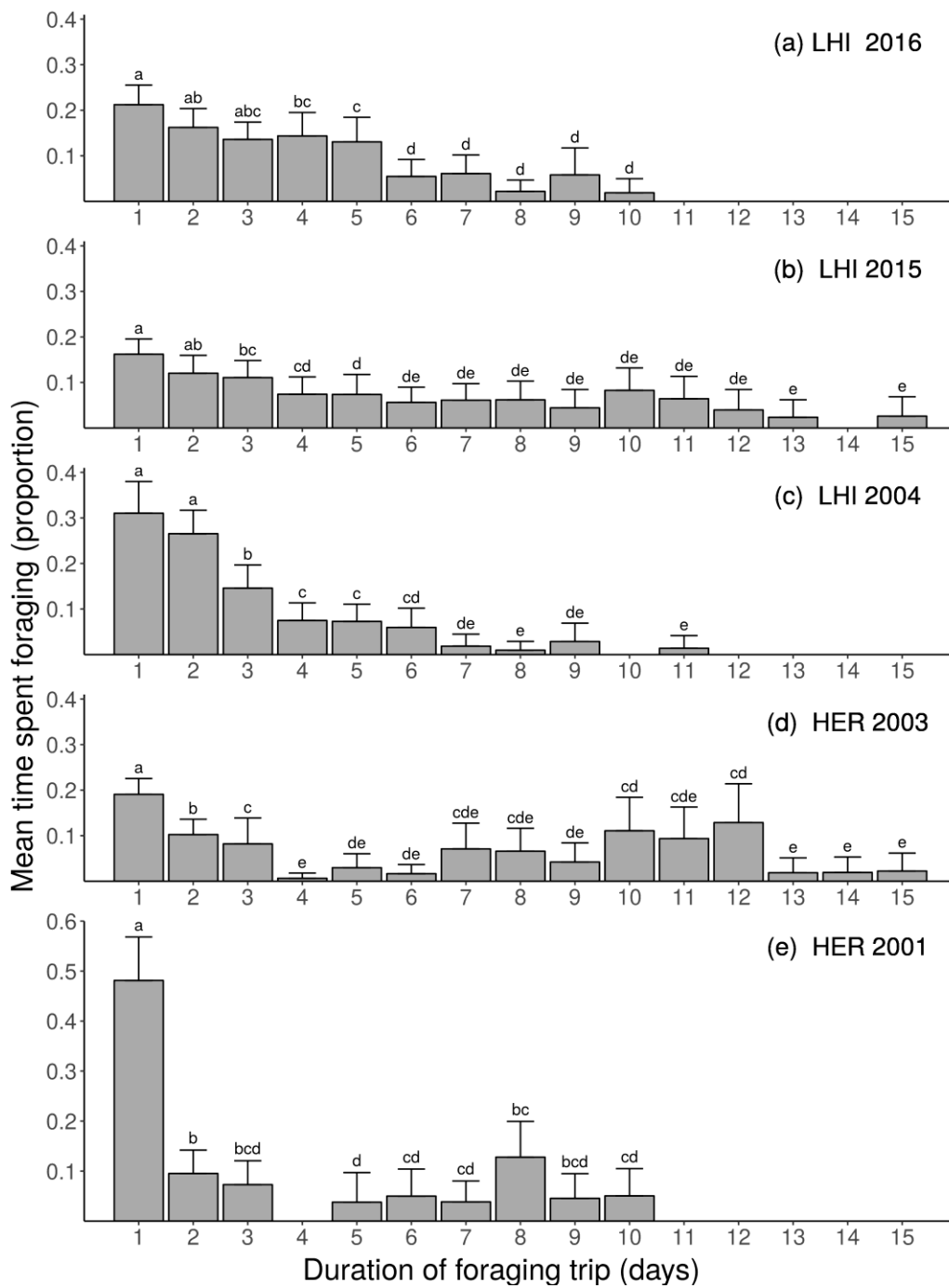
To identify differences in at-sea distribution and foraging areas related to unimodal and dual-foraging strategies I classed GPS trips as either short ( $\leq 4$  days) or long ( $\geq 5$  days) based on the dual-foraging strategy observed at Heron Island as per (Congdon et al. 2005). This classification can be used to separate chick provisioning short-trip foraging areas from long-trip adult self-feeding areas, when applied to trips arising from a unimodal foraging strategy I expected short and long trip foraging zones overlap. I employed kernel analysis on separate short and long-trip datasets, within each colony-year combination using a grid size of 0.5 km in the package 'adehabitatHR' (Calenge 2006). Kernel analysis is sensitive to the smoothing parameter ( $h$ ), which I estimated using the 'marine IBA' package (Lascelles et al. 2016) as 15 km and 31km

for short and long-trips respectively. The 99% UD was selected from resultant kernels to represent the extent of at-sea distribution, and the 50% UD was selected to represent the core-area used by shearwaters (Hamer et al. 2007). The duration and distance of foraging trips as measured by GPS were compared between the sampled colonies and years using a Generalised Linear Mixed Model (GLMM) with individual bird as the random term in the package 'lme4' (Bates et al. 2015). The differences in short and long-trip distances between and within sampled colonies and years were tested with LMs, or LMMs if there was variance within individual birds. Values are presented as mean  $\pm$  standard error (SE), unless otherwise stated.

## 2.4 RESULTS

### 2.4.1 Colony-specific foraging strategies

At Lord Howe Island in 2016 (Fig. 2.2a) and 2004 (Fig. 2.2c), the proportion of time spent on foraging trips of different length consistently decreased with increasing trip duration, indicating a unimodal foraging strategy (Friedman,  $\chi^2_8 = 157.82$ ,  $p < 0.001$ ;  $\chi^2_9 = 67.92$ ,  $p < 0.001$ , respectively). In 2015, the same unimodal pattern was observed for trips of duration  $\leq 6$  days; however, after this point the proportion of time spent on foraging trips increased with increasing trip duration, reaching a second peak at trips of around 9 days duration (Fig. 2.2b), indicating a dual-foraging strategy (Friedman,  $\chi^2_{13} = 79.91$ ,  $p < 0.001$ ). At Heron Island dual-foraging was consistently observed in both 2001 (Friedman,  $\chi^2_8 = 70.19$ ,  $p < 0.001$ ; Fig. 2.2e) and 2003 (Friedman,  $\chi^2_{14} = 119.45$ ,  $p < 0.001$ , Fig. 2.2d), identified by a clear bimodal distribution with a trough at trips of 4 days duration.



**Fig. 2.2** Wedge-tailed Shearwater foraging strategies calculated for different years from adult colony attendance data at Lord Howe Island (LHI; a, b, c) and Heron Island (HER; d,e). The mean ( $\pm 2$  SE) proportion of time spent on foraging trips of different lengths by individual adults is given, with different letters identifying significant differences in means

A switching of foraging strategy between years at Lord Howe Island resulted in a significant difference in mean foraging trip duration between years; trip length was longest during dual-foraging in 2015, followed by unimodal foraging in both 2016 and 2004 (Kruskal-Wallis,  $\chi^2_2 = 14.14$ ,  $p < 0.001$ ; Table 2.1). Although dual-foraging was consistently observed at Heron Island in all years the mean foraging trip duration was significantly longer in 2003 than in 2001 (Mann-Whitney,  $U = 12097$ ,  $p = < 0.001$ ), due to long-trips lasting on average two days longer in 2003 (Table 2.1).

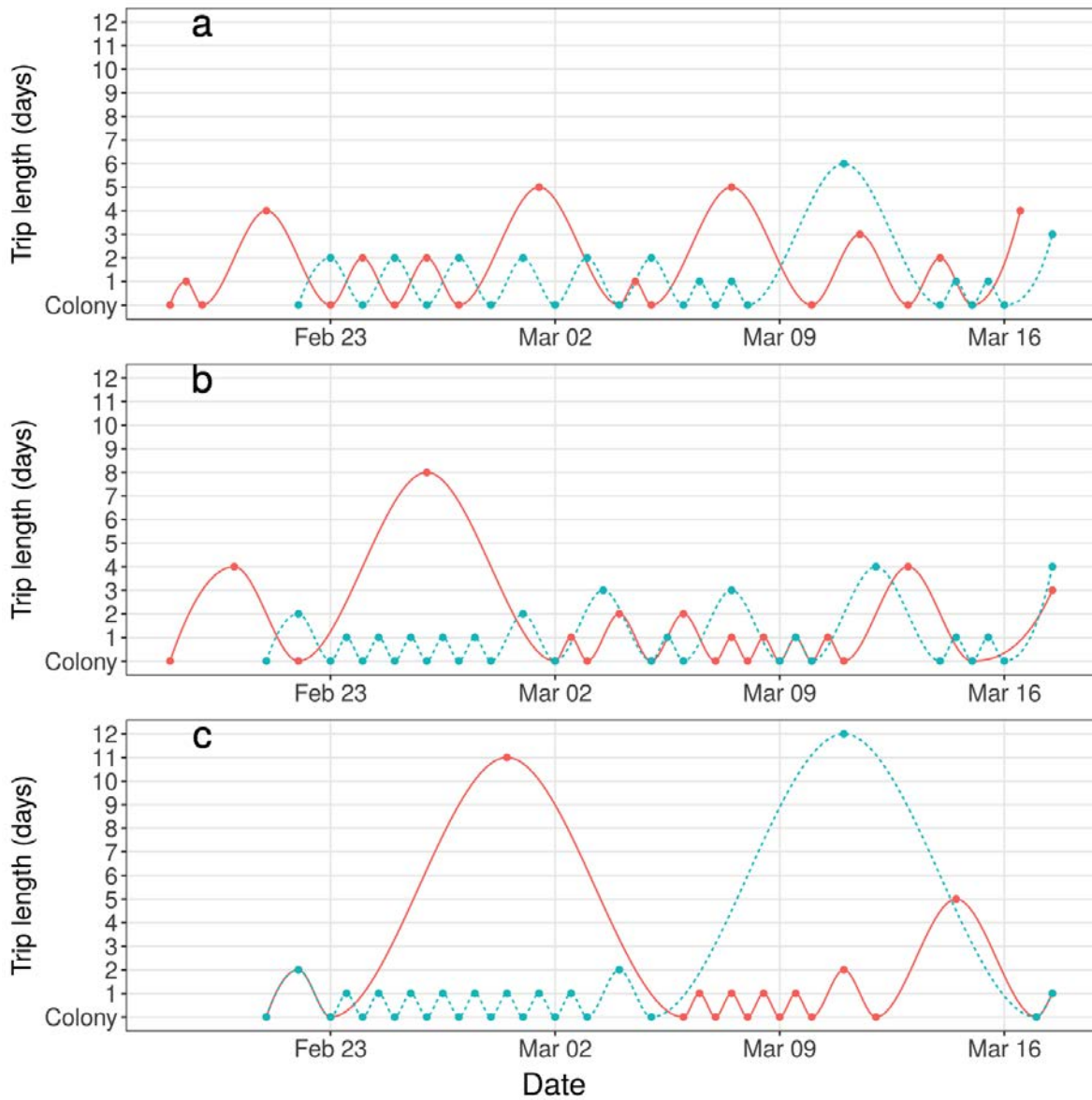
**Table 2.1** Wedge-tailed Shearwater breeding season (Feb-Mar) quality and foraging metrics collected over the course of this study. Blanks indicate data was not collected. Bimodal peaks were estimated using k-means clustering of trip durations estimated via adult attendance or GPS data respectively. GPS short trips (ST) are trips with durations  $\leq 4$  days and long-trips (LT) have durations  $\geq 5$  days. The manova  $F$  value shows level of resource overlap (high  $F$  = low overlap) between adults and chicks measured from stable isotopes ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ). Values given as mean  $\pm$  SE

Colony	Year	Chick condition	Proportion of nests fed ( $\text{day}^{-1}$ )	Attendance trip duration (days)	Attendance bimodal peaks (days)	GPS trip duration (days)	GPS bimodal peaks (days)	GPS ST distance (km)	GPS LT distance (km)	Adult-chick manova ( $F$ )
Heron	2001*	2.14 $\pm$ 4.41	0.58 $\pm$ 0.04	1.79 $\pm$ 0.16	1.19, 7.8					
Heron	2003*	-8.46 $\pm$ 4.50	0.37 $\pm$ 0.03	3.02 $\pm$ 0.25	1.47, 9.8					
Heron	2015*	19.76 $\pm$ 5.06	0.53 $\pm$ 0.05			3.86 $\pm$ 0.59	1.6, 9.5	98 $\pm$ 33	544 $\pm$ 98	40.47
Lord Howe	2004†	11.72 $\pm$ 5.54	0.53 $\pm$ 0.04	1.88 $\pm$ 0.07	1.32, 4.22					
Lord Howe	2015*	-12.54 $\pm$ 3.19	0.48 $\pm$ 0.04	2.92 $\pm$ 0.19	1.84, 8.85	3.95 $\pm$ 0.69	2.5, 12.67	99 $\pm$ 46	534 $\pm$ 169	13.62
Lord Howe	2016†	15.89 $\pm$ 3.72	0.56 $\pm$ 0.03	2.34 $\pm$ 0.12	1.27, 4.58	3.29 $\pm$ 0.36	1.64, 6.14	136 $\pm$ 17	223 $\pm$ 15	5.78

Each year is denoted either as dual-foraging (\*) or unimodal foraging (†).

The dual-foraging strategy identified at Lord Howe Island in 2015 (Fig. 2.2b) was not as clear as those identified at Heron Island (Figs. 2.2d & 2.2e). A closer examination of different individual pairs' foraging trips from Lord Howe Island in 2015 shows some pairs adopting unimodal foraging (Fig. 2.3a), some pairs

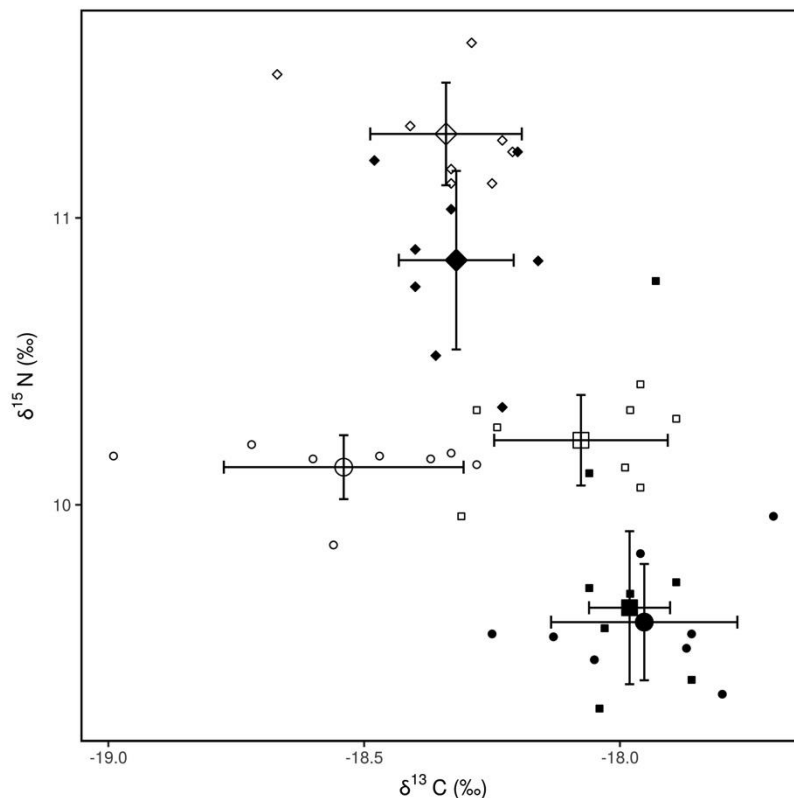
adopting coordinated dual-foraging (Fig. 2.3c) and others starting with dual-foraging and then reverting to unimodal foraging (Fig. 2.3b).



**Fig. 2.3** Time series of trip lengths made by three different pairs (a, b, c) of Wedge-tailed Shearwaters while raising chicks on Lord Howe Island in 2015. Adult parents are denoted by a red solid or blue dotted line respectively, but sexes are unknown

## 2.4.2 Stable Isotopes

There were significant differences between the stable isotope ratios of adult and chick red blood cell samples, the greatest difference was at Heron Island in 2015 (Manova,  $\lambda = 0.14$ ,  $F = 40.47$ , d.f. = 1,  $p < 0.001$ ), followed by Lord Howe Island in 2015 (Manova,  $\lambda = 0.31$ ,  $F = 13.62$ , d.f. = 1,  $p < 0.001$ ) and Lord Howe Island in 2016 (Manova,  $\lambda = 0.53$ ,  $F = 5.78$ , d.f. = 1,  $p = 0.016$ ; Fig. 2.4; Table 2.2). There were significant differences between chick and adult  $\delta^{13}\text{C}$  at Heron Island in 2015 (t-test,  $t = 5.60$ ,  $p < 0.001$ ), but no significant differences at Lord Howe Island in 2015 (Mann-Whitney,  $U = 39$ ,  $p = 0.494$ ) or 2016 (t-test,  $t = 0.30$ ,  $p = 0.766$ ). There were significant differences between chick and adult  $\delta^{15}\text{N}$  in all samples (Heron Island 2015, Mann-Whitney,  $U = 1$ ,  $p = 0.001$ ; Lord Howe Island 2015, t-test,  $t = 5.07$ ,  $p < 0.001$ ; Lord Howe Island 2016, t-test,  $t = 3.47$ ,  $p = 0.005$ ).



**Fig. 2.4** Wedge-tailed shearwater stable carbon and nitrogen isotope values measured from red blood cells (mean  $\pm$  SE). Filled symbols represent adult birds and hollow symbols represent chicks from: Heron Island in 2015 (circles); Lord Howe Island in 2015 (squares); and Lord Howe Island in 2016 (diamonds). The  $\delta^{15}\text{N}$  value of adult shearwaters from Lord Howe Island in 2015 has one outlier value ( $> 10.5$  ‰) removed

**Table 2.2** Wedge-tailed shearwater stable carbon and nitrogen isotope values measured from red blood cells (mean  $\pm$  SD). The  $\delta^{15}\text{N}$  value of adult shearwaters from Lord Howe Island in 2015 has one outlier value ( $> 10.5$  ‰) removed

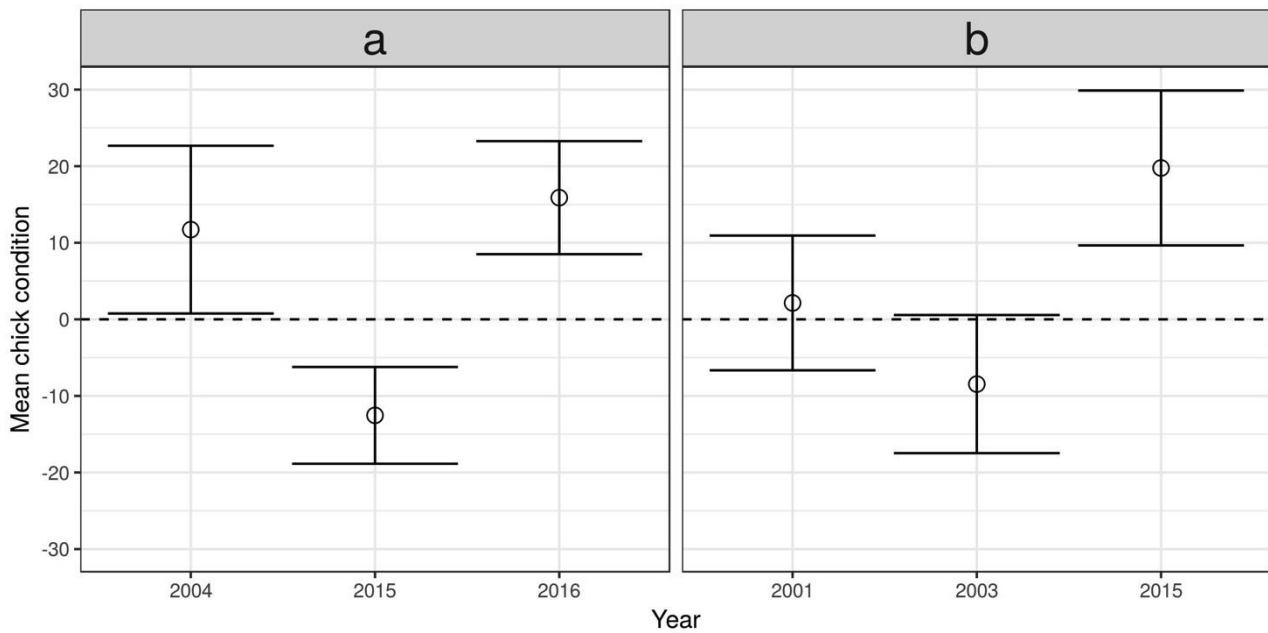
Sampling colony and year	Adult $\delta^{13}\text{C}$ (‰)	Chick $\delta^{13}\text{C}$ (‰)	Adult $\delta^{15}\text{N}$ (‰)	Chick $\delta^{15}\text{N}$ (‰)
Heron Island 2015	$-17.95 \pm 0.18$	$-18.54 \pm 0.23$	$9.59 \pm 0.20$	$10.13 \pm 0.11$
Lord Howe Island 2015	$-17.98 \pm 0.08$	$-18.08 \pm 0.17$	$9.64 \pm 0.27$	$10.23 \pm 0.16$
Lord Howe Island 2016	$-18.32 \pm 0.11$	$-18.34 \pm 0.15$	$10.85 \pm 0.31$	$11.29 \pm 0.18$

There were significant differences in the stable isotope ratios of adult red blood cells (Manova,  $\lambda = 0.17$ ,  $F = 14.61$ , d.f. = 2,  $p < 0.001$ ) and chick red blood cells (Manova,  $\lambda = 0.03$ ,  $F = 46.68$ , d.f. = 2,  $p < 0.001$ ) due to colony and sampling year (Fig. 2.4; Table 2.2). red blood cells of adults from Lord Howe Island in 2016 were significantly depleted in  $\delta^{13}\text{C}$  relative to Lord Howe Island in 2015 and Heron Island in 2015 (LM,  $F = 19.28$ , d.f. = 2,  $p < 0.001$ ). Red blood cells of chicks from Lord Howe Island in 2015 were significantly enriched in  $\delta^{13}\text{C}$  relative to Lord Howe Island in 2016 and Heron Island in 2015 (LM,  $F = 12.29$ , d.f. = 2,  $p < 0.001$ ). Differences in  $\delta^{15}\text{N}$  were consistent in adults and chicks with Lord Howe Island 2016 significantly enriched in  $\delta^{15}\text{N}$  relative to Lord Howe Island in 2015 and Heron Island in 2015 (adult red blood cells, Kruskal-Wallis,  $\chi^2_2 = 14.51$ ,  $p < 0.001$ ; chick red blood cells, Kruskal-Wallis,  $\chi^2_2 = 15.99$ ,  $p < 0.001$ ). The above statistics for Lord Howe Island 2015 were conducted with the omission of an adult  $\delta^{15}\text{N}$  outlier  $> 10.5$  ‰).

### 2.4.3 Inter-annual chick condition

The average condition of chicks varied significantly between sample years at each colony, but to a greater degree at Lord Howe Island (LMM,  $F = 18.83$ , d.f. = 2,  $p < 0.001$ ) than at Heron Island (LMM,  $F = 8.74$ , d.f. = 2,  $p < 0.001$ ). At Lord Howe Island chicks were in good condition in 2004 and 2016 and in poor condition in 2015, at Heron Island chicks were in average condition in 2001, generally poor condition in 2003 and good condition in 2015 (Fig. 2.5; Table 2.1). A lower proportion of chicks were fed per night at Heron Island in 2003 relative to 2001 and 2015 (LM,  $F = 6.98$ , d.f. = 2,  $p = 0.002$ ), whereas there was no

inter-annual difference in the proportion of chicks fed per night at Lord Howe Island (LM,  $F = 1.56$ , d.f. = 2,  $p = 0.222$ ; Table 2.1).



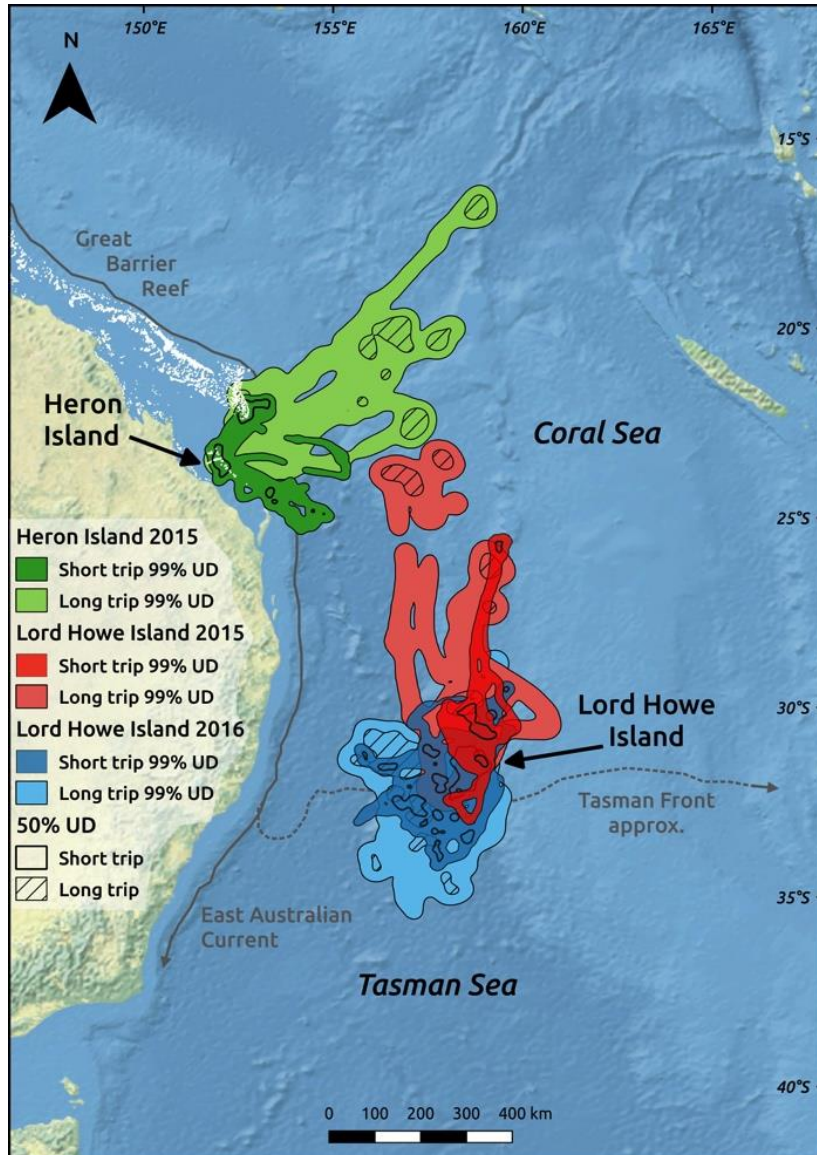
**Fig. 2.5** Wedge-tailed Shearwater chick condition (unitless) (mean  $\pm$  95% CI) in February-March of each year at: a) Lord Howe Island; and b) Heron Island. Values above the baseline condition of 0 represent good condition, whereas values below represent poor condition

#### 2.4.4 GPS analyses

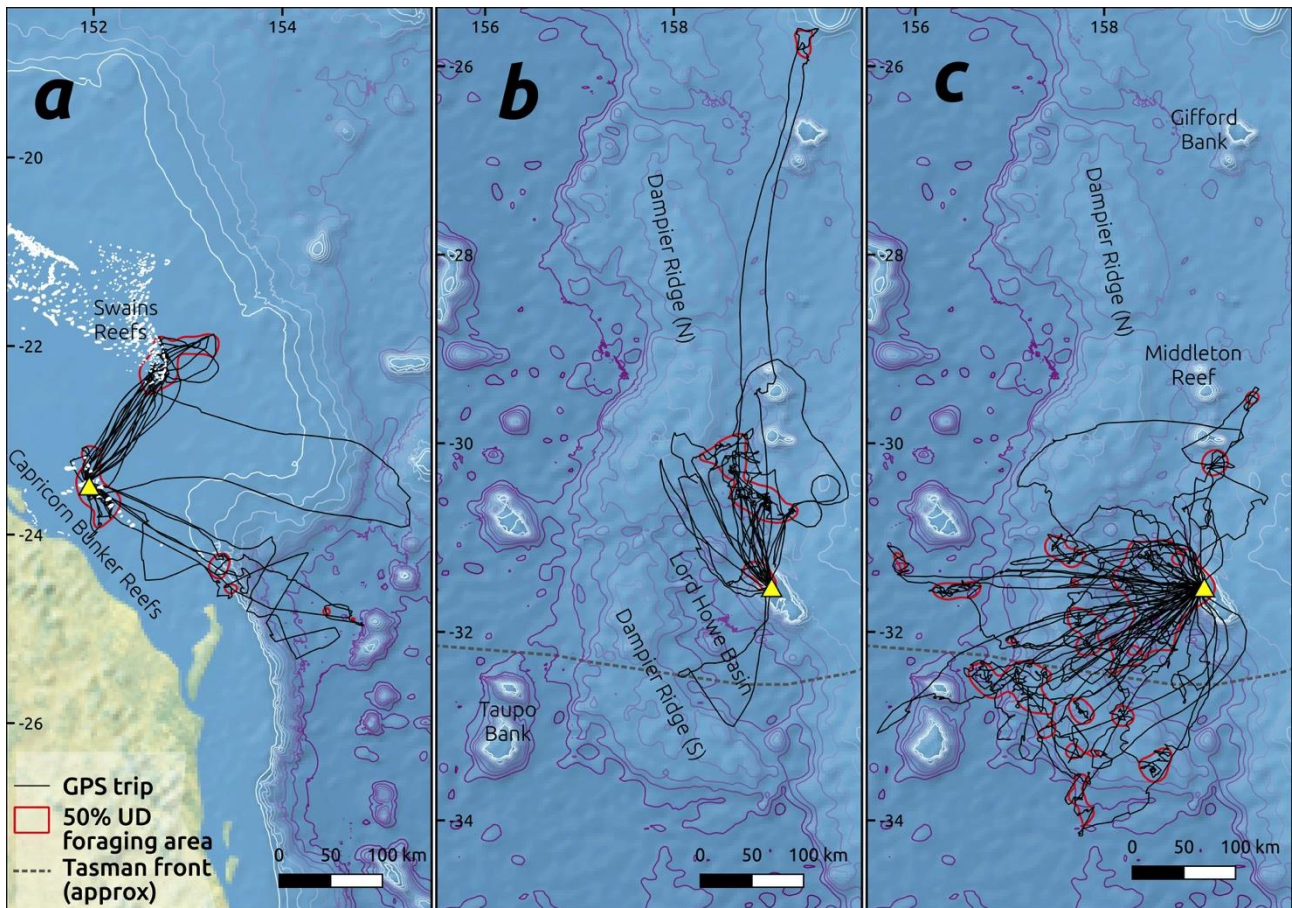
Within the early chick sampling period a total of 106 GPS trips were recorded, 28 from Heron Island 2015 and 21 from Lord Howe Island in 2015 and 57 from Lord Howe Island in 2016. The duration of foraging trips as recorded by GPS did not differ significantly between colonies or years (GLMM,  $\chi^2_2 = 1.09$ , d.f. = 2,  $p = 0.589$ ; Table 2.1). The mean foraging distance of shearwaters from Heron Island in 2015 ( $241.36 \pm 32.62$  km) and Lord Howe Island in 2015 ( $242.31 \pm 37.81$  km) was significantly greater than that of shearwaters from Lord Howe Island in 2016 ( $160.79 \pm 15.23$  km; GLMM,  $\chi^2_2 = 8.6$ , d.f. = 2,  $p = 0.013$ ). In each case, shearwaters on short-trips ( $\leq 4$  days duration) foraged significantly closer to the colony than while on long-trips ( $\geq 5$  days duration) (Heron Island 2015, LMM,  $F = 64.13$ , d.f.=1,  $< 0.001$ ; Lord Howe Island 2015, LMM,  $F = 31.69$ , d.f. = 1,  $< 0.001$ ; Lord Howe Island 2016, LMM,  $F = 24.46$ , d.f. = 1,  $< 0.001$ ; Table 2.1). There was no difference in the mean foraging distance of short-trips from either colony or year (LMM,  $F =$



0.76, d.f. = 2,  $p = 0.474$ ). However, the mean foraging distance of long-trips was significantly longer from Heron Island and Lord Howe Island in 2015, than from Lord Howe Island in 2016 (LM,  $F = 14.45$ , d.f. = 2,  $p < 0.001$ ; Table 2.1). Long-trips from Heron Island in 2015 accessed pelagic waters in the central Coral Sea (Fig. 2.6) while short-trips were distributed over the Swains and Capricorn Bunker reefs and neritic areas (Fig. 2.7a). Long-trips from Lord Howe Island in 2015 accessed the same Coral Sea waters used by Heron Island conspecifics (Fig. 2.6) while short-trips were distributed north of the island and Tasman Front, in the vicinity of Middleton Reef (Fig. 2.7b). Conversely, all trips from Lord Howe Island in 2016 were distributed south-west of the island, over the Lord Howe Basin and southern Dampier Ridge, with short and long-trips both accessing broadly the same area (Fig. 2.6; Fig. 2.7c).



**Fig. 2.6** Kernel analyses of GPS tracking of short ( $\leq 4$  days) and long ( $\geq 5$  days) trips made by Wedge-tailed Shearwaters. In each case the at-sea distribution is denoted by the 99% Utilization Distribution (UD) and foraging areas denoted by the 50% UD



**Fig. 2.7** GPS tracking and foraging areas (50% Utilization Distribution; UD) of short trips ( $\leq 4$  days) made by Wedge-tailed Shearwaters from: a) Heron Island in 2015; b) Lord Howe Island in 2015; and c) Lord Howe Island in 2016. Bathymetric contours give depth from 500m (white lines) to 5000m (darkest purple lines). The yellow triangle denotes the colony

## 2.5 DISCUSSION

### 2.5.1 Summary

By compiling multiple years of data on adult colony attendance, GPS movements and chick-adult stable isotopes signatures, the principal foraging strategies and resource base requirements for chick-rearing in two divergent populations of a tropical shearwater have been identified. The Heron Island Wedge-tailed Shearwater population consistently adopted a dual-foraging strategy in 2001 and 2003 (evidenced via adult attendance data) and 2015 (evidenced via stable isotope and GPS data). Anecdotally, the Heron Island

colony has also adopted this same dual-foraging strategy in each year it has been studied (2006, 2011 to 2014; Congdon & McDuie *unpub. data*). In contrast, the Lord Howe Island population switched foraging strategies between years: adopting a unimodal strategy in 2004 (evidenced via adult attendance data), followed by a dual-foraging strategy in 2015, and a unimodal strategy in 2016 (both evidenced via adult attendance, stable isotope and GPS data). The Heron island population exclusively used reef/neritic foraging habitat and resources during short-trips but switched to Coral Sea pelagic foraging habitat and resources during long-trips. Under unimodal foraging, the Lord Howe population accessed local near-colony resources in the northern Tasman Sea base to feed both themselves and chicks; however, when dual-foraging, adults fed chicks based on near-colony resources but exploited the same Coral Sea pelagic foraging habitat for self-provisioning as did Heron Island conspecifics.

### **2.5.2 Contrasting colony-specific foraging strategies and resource bases**

This study confirms the suggestion that Lord Howe and Heron Island use different near-colony baseline resources for chick provisioning during breeding (Peck & Congdon 2005). However, it also reveals that a dual-foraging strategy is consistently used at Heron Island, even in 'good' years, indicating the population has a perceived long-term expectation of poor local resources, whereas strategy switching is used in the Lord Howe Island population in adaptation to higher but unreliable local resource availability. These findings are consistent with previous studies demonstrating that both populations are locally adapted and show divergent morphology, physiology and foraging strategies that allow them to efficiently acquire and utilise resources from their differing baseline systems (Peck & Congdon 2005, Peck et al. 2006, Peck et al. 2008, McDuie et al. 2013). For example, when each island population is using its more frequently observed mode of foraging, both the coordinated dual-foraging strategy of Heron Island (2001 and 2015) and unimodal strategy at Lord Howe Island (2004 and 2016) have almost identical provisioning frequencies to young chicks. However, long-term differences in the magnitude and reliability of resources around each colony means that each population displays a different degree of foraging plasticity. Principally this is demonstrated by the Lord Howe population switching from unimodal to dual-foraging when chick condition was poor, while the Heron Island population did not switch to unimodal foraging in 2015 when chick condition was well above average. However, in 'poor' years some plasticity within the Heron Island population's foraging strategy was also



evident, with adults extending the duration of their long-trips by two days in 2003 compared to 2001, as has been seen in dual-foraging Little Auks *Alle alle* (Welcker et al. 2009) and Short-tailed Shearwaters (Berlincourt & Arnould 2015) during unfavourable conditions. Similarly, at Lord Howe Island, variation was seen in the frequency distribution of unimodal foraging trips between purportedly ‘good’ years, indicating that resources were more distant in 2016 (1-5 day trips) than in 2004 (1-3 day trips). Combined these results suggest that Heron Island has a consistently more impoverished near-colony resource base, and the population is likely more susceptible to reproductive failure resulting from seasonal-scale decreases in local prey availability. This is because Heron Island adults appear unable to compensate, or adjust their foraging strategy sufficiently to account for major decreases in near-colony food availability due to environmental perturbations (Smithers et al. 2003, Peck et al. 2004, Weeks et al. 2013).

The isotopic niches of adults and chicks can tell us more about foraging strategy mechanics and resource partitioning in each population. My study shows, for what I believe is the first time, that the degree of separation between adult and chick resources measured using stable isotopes is proportional to the level of dual-foraging within a population. The unimodal foraging strategy of Lord Howe Island in 2016 resulted in adults and chicks using the same resources whereas the dual-foraging strategy of Heron Island resulted in adults and chicks using different resources. The important link between the two results is that at Lord Howe Island in 2015, where dual-foraging was partially adopted by the population, the level of resource sharing by adults and chicks was between that of unimodal and dual-foraging.

Isotopic niche divergence between adults and chicks at Heron Island confirms that adults assimilate little of the near-colony resources that they feed to chicks under dual-foraging (Congdon et al. 2005). My results also support the suggestion that chicks at Heron Island receive high lipid-content prey as a means of further buffering them against the aforementioned poorer local resource availability (Peck & Congdon 2005, McDuie et al. 2013). The highly depleted  $\delta^{13}\text{C}$  values of Heron Island chicks reported here are indicative of a diet with high lipid content (Thompson et al. 2000, Cherel et al. 2005c), that is not seen in Lord Howe Island chicks. A final consideration is that the  $\delta^{15}\text{N}$  signatures of chicks were always above those of their provisioning adults, which has been seen in several other seabird species (Hodum & Hobson 2000, Cherel et

al. 2005a). This could represent resource partitioning with adults preferentially selecting higher trophic order prey to feed to chicks (Hodum & Hobson 2000), or differences in metabolism and growth rates between adults and chicks (Harding et al. 2008, Sears et al. 2009).

In 2016, during unimodal foraging, Lord Howe Island shearwaters fed on prey that were enriched in  $\delta^{15}\text{N}$  by  $\sim 1\%$  compared to the prey eaten by dual-foraging adults in 2015 from both colonies. Such enrichment could be explained by feeding on different prey types (Bearhop et al. 2002), larger sized prey (Revill et al. 2009, Mancini & Bugoni 2014), or by prey coming from two systems having different isotopic baselines (Cherel et al. 2005c, Jones et al. 2014). The difference in  $\delta^{15}\text{N}$  between prey in each year reported here is less than one trophic level ( $\sim 3.2\%$ ; Michener & Schell 1994), but too large to be explained by an increase in prey size alone (based on a regression of  $\delta^{15}\text{N}$  against fish and squid lengths in the region; Revill et al. 2009). The GPS data shows that shearwaters from Lord Howe Island foraged in different regions in the two years. It is known that there is a latitudinal gradient in baseline  $\delta^{15}\text{N}$  operating across the Coral and Tasman seas (southward enrichment; Revill et al. 2009, Hobday et al. 2011), and that the Tasman front marks a boundary between these two systems over which there is little mixing (Baird et al. 2008). This indicates that shearwaters foraging north of Lord Howe Island in 2015 likely encountered prey originating from the more  $\delta^{15}\text{N}$  depleted Coral Sea system. This is further supported by the  $\delta^{15}\text{N}$  signal not differing significantly between Lord Howe and Heron Island adults in 2015. By contrast Lord Howe adults foraging southwest of Lord Howe Island in 2016 likely encountered prey with enriched  $\delta^{15}\text{N}$  originating from the Tasman Sea system.

### **2.5.3 Oceanography and drivers of resource availability at each colony**

That the Lord Howe Island population adopted a unimodal strategy when foraging in the Tasman Sea system but dual-foraged in the Coral Sea system suggests that the former generally affords higher resource availability than the latter. The Tasman Front, separating the two systems, crosses the local foraging area used by the Lord Howe Island Wedge-tailed Shearwater population and is variable in both its position (latitudinally) and strength (Mulhearn 1987, Przeslawski et al. 2011). As such, either the Coral, or Tasman Sea systems can influence local resource abundance around Lord Howe Island at different times. Additionally, the combined activity of the East Australian Current (EAC) and Tasman Front spawn mobile

meso-scale warm-core (Griffiths & Wadley 1986, Young et al. 2001) and cold-core eddys (Baird et al. 2008), from the Coral and Tasman Sea systems respectively, that move through the populations' foraging range. This dynamism in the oceanography surrounding Lord Howe Island means that the Wedge-tailed Shearwater population cannot rely on specific oceanographic phenomena being present that generate high prey abundance within foraging distance of the colony each season. Further additional data collection across multiple seasons is necessary to determine the pattern of occurrence of these phenomena and therefore the frequently with which Lord Howe Island Wedge-tailed Shearwaters switch from unimodal to dual-foraging due to local resource depletion. However, in their absence this study suggests that the position of the Tasman Front may be a useful proxy of local resource availability and therefore breeding success at Lord Howe Island.

By contrast, the consistent dual-foraging strategy at Heron Island suggests that resource abundance is more consistently low, and that the location, reliability and oceanographic drivers of the short and long-trip resource bases need to be considered separately. The short-trip resource base is located over multiple inshore, shelf and reef habitats of the Southern GBR (McDuie 2015), which present challenges for assessing general resource availability and reliability. Firstly, local primary productivity is difficult to quantify in the areas around Heron Island because the colony is located within shallow waters of the Great Barrier Reef (GBR) lagoon, which impedes accurate satellite estimates of chlorophyll-*a* concentration (Weeks et al. 2015). The local tropical waters ( $\sim 28^{\circ}$  C during February) should engender low marine productivity (Longhurst & Pauly 1987, Peck & Congdon 2005); however, productivity at Heron Island is enhanced through shelf upwelling (Weeks et al. 2010) and terrestrial runoff (Weeks et al. 2015). Secondly, the features that control enhanced productivity (the Capricorn Eddy and river discharge, respectively) are dynamic in nature and can even sometimes inhibit shearwater foraging (e.g. Capricorn Eddy stratifying surface layers and decreasing prey availability; Weeks et al. 2013). A final important factor, mutually exclusive of productivity, that could significantly impact local resource abundance at Heron Island is competition (Ashmole 1963, Oppel et al. 2015). The Capricorn Bunker group of islands, of which Heron Island is central, holds 75% of all seabird biomass on the GBR (Stokes et al. 1997) and the largest breeding population of Wedge-tailed Shearwaters in the Pacific (Dyer et al. 2005). The resulting high intra- and inter-specific

competition pressure in the generally resource-poor waters surrounding this colony likely further contributes to unimodal foraging being a less-viable strategy for the Heron Island population.

Dual-foraging in the Heron Island population relies on a long-trip resource base in the central Coral Sea, and the reliability of resources at these sites can be assessed using a variety of data. Firstly, comparing the long-trip tracking data from 2015 with those collected by McDuie et al. (2015) in 2006, 2011 and 2012 shows Heron Island Wedge-tailed Shearwaters consistently use central Coral Sea resources in different years. This suggests that shearwaters on long-trips from Heron Island have a high *a priori* expectation of encountering resources in the central Coral Sea. Secondly, ocean modelling studies on the Coral Sea system enable characterisation of the habitat targeted by long-trips. Welch et al. (2015) found that chlorophyll regimes have lowest productivity but highest spatio-temporal reliability in the central Coral Sea (roughly between latitudes 24° S and 15° S). Within this latitudinal band, Hobday et al. (2011) identified two persistent pelagic resource bases. However, southward of 24° S these resources became increasingly unreliable as the Coral Sea system approaches the Tasman Front (Hobday et al. 2011). Heron Island Wedge-tailed Shearwaters also target seamounts in the Coral Sea region (McDuie et al. 2015) that likely provide another source of reliable resources. In general, these studies suggest that at mesoscales and above, the resource base(s) of the central Coral Sea can be reliably located by shearwaters. However, it should be noted that at finer (sub-meso) scales the eastern Coral Sea shows considerable dynamism due to eddy movement (Menkes et al. 2015), and the same processes likely influence the central Coral Sea. Thirdly, fisheries data show that the central Coral Sea is persistently targeted by the Eastern Tuna and Billfish Fishery (ETBF), indicating that the area maintains high densities of marine top predators (Trebilco et al. 2010, Wilson et al. 2010, Young et al. 2010c). As Wedge-tailed Shearwaters are known to benefit from foraging with sub-surface predators such as tuna (Au & Pitman 1986, Spear et al. 2007, Hebshi et al. 2008), large numbers of these taxa in the central Coral Sea could represent an attractive foraging resource base. A final important consideration is that the central Coral Sea is used, not only by the Heron Island population, but also by the Lord Howe Island population when local resource availability is poor. This suggests that the Lord Howe Island Wedge-tailed Shearwaters have the same high *a priori* expectation of encountering prey in the central Coral Sea as Heron Island



conspecifics, despite not utilising this resource during breeding every year. This is further testament to the reliability of this resource base.

#### **2.5.4 Wider tropical procellariiform foraging strategies**

My results show that a tropical seabird species breeding in tropical waters and under high competition pressure is constrained into a dual-foraging strategy; but when that same species breeds in sub-tropical waters under reduced competition, a unimodal foraging strategy is possible. Applying these foraging strategy results to tropical procellariiforms more generally requires disentangling how divergent biomes and competitive pressures control resource availability. In this sense Heron Island may not represent a typical tropical seabird colony being situated on a continental shelf and part of the largest reef system in the world, and by being part of a huge Wedge-tailed Shearwater meta-population. Here, terrestrial input and shelf upwelling enhance resource availability but intra-specific competition suppresses it, necessitating the observed dual-foraging strategy. For more typical tropical procellariiform colonies, such as oceanic islands with modest breeding populations (e.g. Christmas Island; Ashmole & Ashmole 1967), reduced competition might be offset by lower productivity, generating reduced resource availability and prescribing the same dual-foraging strategy. Alternatively, such locations might force breeding procellariiforms into a novel foraging strategy to obtain resources, such as an extended-unimodal (peak at two or three days, rather than one; Phillips et al. 2009) or tri-modal strategy (Shoji et al. 2015), or alternatively exclude them all together (Lack 1968). To further explore how environmental and competitive forces shape foraging strategy this study could be extended to regional Wedge-tailed Shearwater colonies at Chesterfield Reef (low competition, tropical oceanic island; Borsa et al. 2010) and Raine Island (low competition, tropical continental shelf; Batianoff & Cornelius 2005).

My results also support a growing body of literature suggesting many coordinated dual-foraging is the dominant foraging strategy in procellariiforms (Welcker et al. 2012, Tyson et al. 2017). Firstly, my consistent observations of dual-foraging from a tropical system suggest it could be prevalent in the under-studied tropical realm (but see caveats above). Secondly, I observed coordinated dual-foraging by some pairs of a population that normally adopts a unimodal foraging strategy (unrequiring of coordination). This suggests

that it may be relatively easy for procellariiform pairs, to flexibly synchronise into coordinated dual-foraging when needed. Indeed, pairs may already be primed for dual-foraging after incubation which: a) enforces pair coordination during shift changes (Davis 1988); and b) affords a greater foraging range for pairs to 'scout' a wide area for a suitable long-trip resource base, should it be needed later in breeding (Stahl & Sagar 2000).

A potential factor limiting the prevalence of flexible coordinated dual-foraging in a population is that of pair experience (Tyson et al. 2017). This could explain the partial adoption of dual-foraging I observed in the Lord Howe Island population in 2015, and represents an interesting avenue of individual-level foraging specialisation for future research.

### **2.5.5 Reliable tropical pelagic resources**

My results show that when food availability in sub-tropical waters is compromised this sub-tropical population reverts to a dual-foraging strategy so as to be able to access an alternative resource base in tropical waters, that is apparently more reliable and predictable. Together these findings are consistent with theories that seabird breeding resources are generally less abundant in tropical waters than at higher latitudes (Longhurst & Pauly 1987), but challenge ideas that tropical resources are always more spatially heterogeneous and less reliable than at higher latitudes (Ainley & Boekelheide 1983, Ballance & Pitman 1999, Weimerskirch 2007). The sub-tropical Wedge-tailed Shearwater population in this study could certainly have accessed more temperate, highly productive and reliable 'traditional' long-trip resources prescribed by the temperate dual-foraging model, such as the southeast Australian shelf-break, a popular destination for other species (Stahl & Sagar 2000, Walker & Elliot 2006, Thalman et al. 2009). But instead of heading further south during years of poor local food availability, members of this population chose to fly long distances north to access oligotrophic, pelagic tropical waters. This tells us first that the temperate model of what constitutes important seabird foraging resources (i.e. high chlorophyll-*a*) does not always apply to tropical seabirds, and second that pelagic tropical waters can simultaneously sustain breeding in multiple large seabird populations, including those from outside the tropical zone. The question that arises is how? At present we know that the central Coral Sea is typical oligotrophic 'blue-water' tropical habitat containing large numbers of sub-surface predators such as tuna (Trebilco et al. 2010, Welch et al. 2015). A quantitative assessment of the importance of these and other factors is needed to determine how this region

acts as a reliable resource base for tropical seabirds. The need to know this information is clear. My data shows that tropical pelagic seabird breeding success on the scale of the Coral and Tasman Sea basins is highly dependent on the continued stability and reliability of these long-distance foraging sites. Similar processes are also likely operating in other oligotrophic tropical oceans (e.g. Le Corre et al. 2005). If such resources become compromised then successful reproduction at dependent colonies, which can be more than a thousand kilometres distant, will eventually become non-viable.

## **CHAPTER 3: THE IMPORTANCE OF TROPICAL TUNA FOR SEABIRD FORAGING**

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### **3.1 ABSTRACT**

Foraging with tuna is a well-documented seabird strategy, referred to as facilitated foraging. However, despite this behaviour being considered almost obligatory in nutrient-poor tropical waters, little data exist on its relative importance to individual colonies. Therefore, to examine facilitated foraging under different patterns of nutrient availability I tracked Wedge-tailed Shearwaters *Ardenna pacifica* from two colonies, one tropical and one subtropical, situated in waters of contrasting productivity. Shearwater foraging behaviour was assessed relative to oceanographic covariates and predicted distributions for multiple tropical tuna species and age-classes, simulated by an existing ecosystem model (SEAPODYM). Shearwaters from both colonies undertook long-trips to deep, pelagic waters close to seamounts and foraged most often at fronts and eddies. Micronektonic and adult tuna age-classes were highly correlated in space. Predation between these tuna age-classes represents a likely source of facilitated foraging opportunities for shearwaters. At broad-scales, shearwaters consistently foraged in areas with higher predicted adult skipjack and micronektonic tuna densities and avoided adult Bigeye Tuna. At finer-scales, dynamic ocean features aggregated tuna of all sizes. Enhanced tuna density at these locations increased the likelihood of shearwater foraging activity. Long-trips in the tropics targeted oligotrophic waters with higher tuna densities. Long-trips in the subtropics targeted enhanced productivity, but in some years shifted to target the same oligotrophic, tuna-dense waters used by tropical conspecifics. I conclude that facilitated foraging with tuna is consistently important to the tropical breeding population and becomes increasingly important to the subtropical population in years of low marine productivity.

### **3.2 INTRODUCTION**

Tropical waters are generally considered less productive than their temperate counterparts (Longhurst & Pauly 1987). In temperate and polar waters, predictable physical oceanographic processes e.g. fronts, upwellings, ice and shelf edges reliably aggregate seabird prey, whereas in tropical waters seabird prey are

scarcer and more patchily distributed (Ainley & Boekelheide 1983, Ballance & Pitman 1999, Weimerskirch 2007). Despite such constraints, abundant communities of seabirds exist in tropical waters (King 1974). For tropical seabirds the single most important foraging strategy, believed to overcome poor prey predictability, is to feed in multi-species flocks in association with sub-surface predators, primarily tunas (Au & Pitman 1986, Ballance & Pitman 1999, Spear et al. 2007). Sub-surface predators are believed to be crucial for driving prey upwards and making them available to surface feeding seabirds (facilitated foraging) (Ashmole & Ashmole 1967, Clua & Grosvalet 2001). Although facilitated foraging occurs in polar (Thiebot & Weimerskirch 2013), temperate (Goyert et al. 2014) and sub-tropical waters (Clua & Grosvalet 2001, Vaughn et al. 2008), the level of seabird community reliance on sub-surface predators is unparalleled in the tropics (Ballance & Pitman 1999, Spear et al. 2007).

However, the difficulty associated with monitoring seabird and sub-surface predator activity concurrently means that facilitated foraging is often inferred. Inference comes from overlap in seabird and sub-surface predator prey items (Ashmole & Ashmole 1967, Ménard et al. 2013) and trophic niches (Kojadinovic et al. 2008, Young et al. 2010a), although often the results of such studies are inconclusive. Facilitated foraging has also been inferred, but not quantified, from overlap between seabird foraging tracks and areas of high sub-surface predator activity in commercial fisheries (Catry et al. 2009b, Weimerskirch et al. 2010, McDuie & Congdon 2016). Finally, oceanographic data has shown that the densities of tropical, diurnal, piscivorous seabirds are driven by a well-stratified, deep thermocline, which is associated with higher sub-surface predator densities (Ballance et al. 1997, Spear et al. 2001).

The bulk of our knowledge on facilitated foraging comes from at-sea observations (Au & Pitman 1986, Spear et al. 2007). At-sea observations are able to quantify instances of seabirds using facilitated foraging, but have their limitations. The cost of vessel hire has led some studies to make observations from fishing vessels. However as these vessels target sub-surface predators, results are biased towards overestimation of facilitated foraging events (Jaquemet et al. 2004, Hebshi et al. 2008). At-sea observations using transects are unbiased and have contributed significantly to our understanding of facilitated foraging, primarily in the eastern and central tropical Pacific (Au & Pitman 1986, Spear et al. 2007) and tropical Indian oceans

(Thiebot & Weimerskirch 2013). However, all at-sea survey methods are limited by the prohibitive cost of undertaking simultaneous surveys in different regions and an inability to determine the provenance of birds being observed. As such, no previously available method has been able to quantify the individual, or population-level decisions of seabirds on whether to preferentially target sub-surface predators or not. Consequently, there has been no way to determine the relative importance of facilitated foraging opportunities for specific seabird colonies. This study provides a framework to do so.

Limited availability of suitable nesting habitat can lead to seabird colonies being located where local marine resources are sub-optimal (Navarro & González-Solís 2009). Under these constraints many pelagic foraging seabirds use a bimodal foraging strategy, where 'short-trips' (1-3 days in shearwaters; Baduini & Hyrenbach 2003) in resource-poor local waters are used almost exclusively to provision chicks at the expense of adult condition. Following a series of short-trips adults undertake a 'long-trip' (5-17 days) to more distant foraging sites where they can quickly regain condition (Weimerskirch 1998, Weimerskirch & Cherel 1998). To achieve this, long-trips are said to access 'productive distant waters' (Weimerskirch 1998). As most bimodal foraging studies come from temperate and polar regions 'productive' has become synonymous for high primary productivity or chlorophyll-*a* concentration, aggregated by shelf or frontal features (Waugh et al. 1999, Catard et al. 2000, Klomp & Schultz 2000, Stahl & Sagar 2000, reviewed in Baduini & Hyrenbach 2003). Seabirds breeding in the subtropics may have the opportunity to access similar large-scale areas of high primary productivity using bimodal foraging (Paiva et al. 2010b). However, since such features are rare in tropical systems, I hypothesise that tropical-breeding seabirds target increased sub-surface predator densities as an alternative, because of the greater facilitated foraging opportunities this provides.

The Wedge-tailed Shearwater is a tropical seabird known to associate heavily with tuna when foraging in multiple regions (Au & Pitman 1986, Jaquemet et al. 2004, Hebshi et al. 2008), and has been shown to capture most of its prey through facilitated foraging (Spear et al. 2007). The Wedge-tailed Shearwater populations breeding off eastern Australia adopt a bimodal foraging strategy in tropical waters of the Coral Sea (Congdon et al. 2005) and a more unimodal strategy in sub-tropical waters of the Tasman Sea, although some long-trips are made (Peck & Congdon 2005). East Australian Wedge-tailed Shearwater populations

have access to a range of marine habitats (shelf, seamount and frontal systems; Hobday et al. 2011) and sub-surface predator populations in the region include numerous tuna species (Young et al. 2010c).

This study aims to estimate the relative importance of facilitated foraging with tropical tuna for two Wedge-tailed Shearwater populations in waters with contrasting productivity. Relative importance is quantified from spatial association between shearwater tracking data, oceanographic covariates and modelled tropical tuna distributions. Two facilitated foraging hypotheses were tested at opposing spatio-temporal scales, thus expecting that: 1) tropical tuna distributions influence the selection of Wedge-tailed Shearwater core-area locations (defined by the 50% Utilization Distribution (UD) from kernel analysis) at broad scales; and 2) tropical tuna distributions influence the likelihood of Wedge-tailed Shearwater foraging activity at fine scales. I additionally test two facilitated foraging hypotheses at opposing ends of a productivity gradient, expecting that: 3) Wedge-tailed Shearwater in tropical waters do not adhere to the temperate model of 'productive' long-trip destinations and instead target tuna; and 4) Wedge-tailed Shearwater breeding in subtropical waters adhere to the temperate model of 'productive' long-trip destinations and do not target tuna.

### **3.3 Methods**

#### **3.3.1 Study area and logger deployment**

This study was carried out at Heron Island (23°26' S, 151°51' E) in the Capricorn Bunker Island Group, Great Barrier Reef and Lord Howe Island (31°33' S, 159°05' E) in the northern Tasman Sea, Australia. Both islands support large breeding colonies of Wedge-tailed Shearwaters (Marchant & Higgins 1990). GPS loggers were deployed on Wedge-tailed Shearwaters at Lord Howe Island in 2014, 2015 and 2016 and concurrently at Heron Island in 2015, and Platform Terminal Transmitter (PTT) loggers were deployed at Heron Island in 2011 and 2013 (McDuié et al. 2015). All loggers were deployed during the chick-rearing period (Feb-April). I-gotU GT-120 GPS loggers (Mobile Action Technology) were modified to use smaller 100mAh batteries, sealed in heat-shrink tubing and programmed to obtain fixes every 10 minutes (Freeman et al. 2013). Solar-powered ARGOS PTTs (PTT-100; Microwave Telemetry, USA) relay data via satellite



and were programmed to obtain fixes continuously. GPS and PTT loggers were attached to 3 central tail feathers using Tesa® 4651 Tape, total deployment weight of both logger types was ~ 10.5-12 g, within the 3-5% body weight limit for the species (McDuie et al. 2015).

### **3.3.2 Tracking data preparation and analyses**

All data handling and statistical analyses were performed in the statistical software environment program R, version 3.2.4 (R Core Team 2016). Tracking data were pre-processed prior to analyses using a speed filter, removing points exceeding a maximum velocity of 50 km/h (McDuie et al. 2015), additionally GPS tracks were gap filled using interpolation to 10 minute interval (Weimerskirch et al. 2006b). As loggers were active for several days multiple foraging trips were observed for most individuals. To split long-trips from short-trips within multi-day GPS tracks I used the R 'tripsplit' function from the 'marine IBA' package (Lascelles et al. 2016) and isolated long-trips (>4 days duration; Congdon et al. 2005) for further analysis. I could not determine individual foraging trips within multi-day PTT tracks (due to near colony positional error) so removed all fixes from tracks within the 'short-trip zone' of 300 km around Heron Island (McDuie et al. 2015).

To identify core-areas used by each colony for each year of long-trip tracking data, I employed kernel analysis using the package 'adehabitatHR' (Calenge 2006). All locations within each colony-year combination were used with a grid size of 0.5 km and, for consistency, the same smoothing parameter ( $h$ ) of 20 km for GPS and PTT data following McDuie et al. (2015). The 50% UD was selected from resultant kernels to represent the core-area used by Wedge-tailed Shearwaters in each year (Hamer et al. 2007). To identify behavioural states and thereby identify foraging locations, I applied Hidden Markov Models (HMM) to the GPS data. I constructed a single HMM using the full GPS tracking dataset, including an identifier for each trip, using the package 'moveHMM' (Michelot et al. 2016). For each consecutive GPS point the step length and turning angle were calculated, producing three distributions consistent with foraging, resting and transiting behaviours observed in HMM studies of boobies (Oppel et al. 2015) and shearwaters (Dean et al. 2013). The fitted HMM was then used to classify each GPS point as either foraging, resting or transiting.

### 3.3.3 Oceanographic data

I created a static covariate for depth (BTY) from the 30 arc-second General Bathymetric Chart of the World (GEBCO) and calculated a static covariate for distance to seamount using the Global Seamount Database (Kim & Wessel 2011) and package 'raster' (Hijmans 2016). Gridded oceanographic data were accessed from NOAA ERDDAP servers using the 'rerddap' package (Chamberlain 2016) (Table 3.1). I accessed oceanographic climatologies in the form of long term, monthly averages: primary productivity (PRO), 1997-2016; sea surface temperature (SST), 1985-2016. The March data product was selected my covariate as it is central to the Wedge-tailed Shearwater chick-rearing period. I accessed very fine temporal scale Ekman upwelling (EKM, 1d) and sea surface height anomaly (SSHA, 1d) data as these products were cloud free. I also accessed coarser scaled data on Chlorophyll-*a* concentration (CHL, 8d), sea surface temperature (SST, 1-8d) and sea surface temperature anomaly (SSTA, 1-8d), to counter daily missing values due to cloud cover. In a further step to fill data gaps due to clouds, I blended two CHL, SST and SSTA products from different data sources to create single covariates (Table 3.1).

### 3.3.4 Tropical tuna data

Tuna covariates were generated using the Spatial Ecosystem and Population Dynamics Model (SEAPODYM). SEAPODYM is an age-structured population model describing spatial and temporal dynamics of top predator species in a direct link with prey biomass and environmental variability (Lehodey et al. 2008). SEAPODYM uses a sub-model to predict the distribution of prey, which provides a habitat-quality index for tuna that varies by age-class and species (Lehodey et al. 2010). This habitat is based on the distribution of simulated micronekton, which I here define as mobile and free-swimming macrozooplankton, fish and squid species between ~10 mm and ~250 mm in length. Micronekton are classified into functional groups by their vertical habitat and diel migration pattern, with the spatio-temporal transfer of energy between them described using allometric scaling equations and ocean currents. The top predator model describes the age-structured spatial population of tunas across four distinct life stages (termed larval, juvenile, immature young, and mature adult) and includes anthropogenic forcing in the form of effort and catch from multiple fisheries. Driving both models are ocean biophysical variables (temperature, currents, oxygen, and primary production) that characterise the marine environment of predator dynamics (Lehodey &

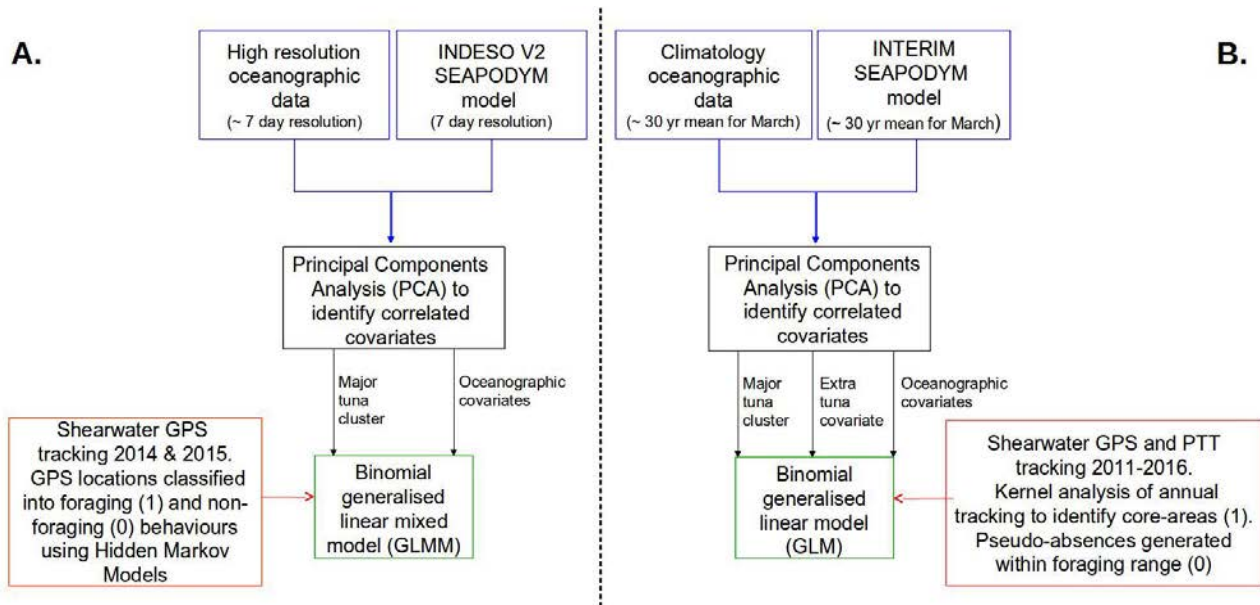
Senina 2009) and age-dependent accessibility functions describing the sub-model micronekton biomass available to top predators. SEAPODYM solves these internal models using advection-diffusion-reaction equations over a network of regularly spaced grid points and a discrete time step (e.g. 1° square x 1 month), outputting predictions on the spatial dynamics of large pelagic predators (Lehodey et al. 2008, Senina et al. 2008). SEAPODYM can be optimised and parameterised for different marine predator species and regions (Abecassis et al. 2013, Dragon et al. 2014) or different exercises, such as climate change prediction (Senina et al. 2016).

For my region SEAPODYM predictions were available on the distribution of biomass ( $\text{g m}^{-2}$ ) for three tuna species: Yellowfin Tuna *Thunnus albacares* (YFT), Bigeye Tuna *T. obesus* (BET) and, Skipjack Tuna *Katsuwonus pelamis* (SKJ). For each species I selected distributions of adult (ADU) and micronektonic (MIC) age-classes which vary spatially due to their differing access to prey, behaviour and density-dependent mortality representing cannibalism (Lehodey et al. 2008). Adult tuna are not shearwater prey. Therefore, I assume associations between Wedge-tailed Shearwaters and adult tuna represent facilitated foraging. Micronektonic tuna are between 1-3 months old with fork lengths from ~30 mm up to ~100 mm (SKJ) and ~250 mm (YFT and BET) (Davies et al. 2014, Harley et al. 2014, Langley et al. 2014), Wedge-tailed Shearwater association with micronektonic tuna could represent direct predation of smaller individuals or facilitated foraging with larger individuals. I also selected SEAPODYM predictions under fished conditions to represent real-life tuna distributions, such as heavier long-lining effort closer to the Australian east coast (Trebilco et al. 2010).

To test my hypotheses I compiled two datasets at opposing spatio-temporal scales, the first was built with broad scale, decadal-averaged data (hereafter termed the climatology dataset/model), the second built with fine scale, weekly-averaged data (defined as high resolution and hereafter abbreviated as the 'hi-res' dataset/model; Fig. 3.1). The climatology dataset included BTY, SMT, PRO, SST and tuna covariates from INTERIM parameterised SEAPODYM predictions (1° x 1 month), for the month of March (SKJ: 1979-2010 average, BET and YFT: 1986-2010 average) (Table 3.1). The hi-res dataset included BTY, SMT, CHL, SST,

SSTA, SSHA, EKM and tuna covariates from INDES0 V2 parameterised SEAPODYM predictions (0.25° x 1 week). Tuna data were not available for 2016, so hi-res models were constructed for 2014 and 2015 only.

**Fig. 3.1** Flow chart showing input data and analyses steps taken for: A. hi-res models; and B. climatology models (separated by dotted line)



**Table 3.1** Summary of oceanographic and tuna covariates used in broad and fine scale models

Covariate (units)	Abbreviation	Temporal resolution	Spatial resolution	Data source (provider)
<b>High resolution dynamic covariates</b>				
Chlorophyll- <i>a</i> concentration (mg m <sup>-3</sup> )	CHL	8 day	4 km	MODIS & VIIRS (NASA)
Sea surface temperature (°C)	SST	8 & 1 day	0.1° & 0.25°	POES & AVHRR (NOAA)
Sea surface temperature anomaly (°C)	SSTA	8 & 1 day	0.1° & 0.25°	POES AVHRR (NOAA)
Sea surface height anomaly (m)	SSHA	1 day	0.083°	HYCOM & NCODA (NRL)
Ekman upwelling (m day <sup>-1</sup> )	EKM	1 day	0.25°	Metop ASCAT
<b>Climatology and static covariates</b>				
Primary productivity (mg C m <sup>-2</sup> day <sup>-1</sup> )	PRO	Monthly (20 yr mean)	4.4 km	SeaWiFS & AVHRR (NASA & NOAA)
Sea surface temperature (°C)	SST	Monthly (30 yr mean)	4.4 km	AVHRR (NOAA)
Bathymetry (m)	BTY	Static	0.083°	GEBCO
Distance to seamount (km)	SMT	Static	0.083°	Global seamount database
<b>Tuna distribution covariates</b>				
Tuna weekly biomass distribution (g m <sup>-2</sup> )	BET_ADU, BET_MIC, YFT_ADU, YFT_MIC, SKJ_ADU, SKJ_MIC	7 day	0.25°	INDESO V2 Fished (SEAPODYM) (unavailable in 2016)
Tuna monthly biomass distribution (g m <sup>-2</sup> )	BET_ADU, BET_MIC, YFT_ADU, YFT_MIC, SKJ_ADU, SKJ_MIC	Monthly (30 yr mean)	1°	INTERIM Fished (SEAPODYM)

### 3.3.5 Covariate extraction

To standardise climatology model covariate extraction I used a 0.1 degree grid, taking all pixels within the 50% UD core-areas as presence and generating pseudo-absence pixels, defined as locations where absence is probable but uncertain, for logistical regression. Pseudo-absence pixels were randomly generated, at a rate of random 3:1 presence pixels, within a hypothetical maximum foraging range for each colony. The range was set at 1400 km from each colony (maximum distance observed in my data; Heron Island 2013), refined by

removing land and areas beyond the species range e.g. south of the sub-tropical front (del Hoyo et al. 1992). For hi-res models I reclassified behaviour-classed tracking data for logistic regression, assigning foraging and resting locations as presences, as tropical seabirds can 'drift forage' (using a surface 'sit-and-wait' strategy; Connors et al. 2015), and transiting locations as absences. I extracted values from covariates for climatology and hi-res model locations using the package 'raster' (Hijmans 2016).

### **3.3.6 Multicollinearity and spatial autocorrelation**

Collinearity between covariates is an ever present issue in regression-type analyses of ecological data (Dormann et al. 2013), and continually persistent in marine habitat modelling exercises (Goyert et al. 2014, Lavers et al. 2014, McDuie & Congdon 2016). I explored the climatology and hi-res covariate datasets for collinearity using pairwise Pearson's correlations with scatterplots of covariates (Zuur et al. 2010). I identified significant collinearity between covariates (Pearson's  $r^2 > 0.9$ ), particularly around SST and tuna covariates. To understand the sources of collinearity, identify correlated clusters and select proxy covariates to use in models, I standardised my covariates and carried out Principal Components Analyses (PCA) in the package 'vegan' (Oksanen et al. 2016). To help interpret PCA ordination plots, Pearson's  $r^2$  values were calculated between the covariates and the principal components (Quinn & Keough 2001). For each dataset I aimed to retain covariates for modelling that had a pairwise Pearson's  $r^2 < 0.5$  with others and selected a single tuna covariate that minimised correlation with non-tuna covariates, to act as a proxy for all covariates correlated within tuna clusters (Dormann et al. 2013).

Spatial autocorrelation (SAC) is another issue inherent in species distributional data, and failure to account for it can result in non-independence of model residuals causing bias in parameter estimates and increasing type I errors (Dormann et al. 2007). I checked Pearson's residuals from climatology and hi-res models for SAC using the package 'ncf' (Bjornstad 2016), calculating Moran's I values over distances: 1-2500 km (climatology models) and 1-1000 km (hi-res models). Climatology models showed high levels of SAC (Moran's  $I > 0.9$ ), to accommodate the spatial structure I calculated an autocovariate term over the 50 nearest neighbours following Bardos et al. (2015), inclusion of this term reduced model SAC to acceptable levels (Moran's  $I < 0.22$ ) (McDuie & Congdon 2016). hi-res models showed lower, but still present, levels of SAC

(Moran's  $I < 0.4$ ), I reduced SAC in this tracking dataset by subsampling locations to every third point, resulting in models with Moran's  $I < 1.5$  (Perotto-Baldivieso et al. 2012).

### 3.3.7 Statistical modelling

To test the influence of different broad scale oceanographic and tuna covariates on selection of Wedge-tailed Shearwater core-area location, I used generalized linear models (GLM). GLMs had a binary response, treating core-area locations as 1 and total foraging range pseudo-absences as 0, and were constructed separately for Lord Howe and Heron Island. To test the effect of different high-resolution oceanographic and tuna covariates on likelihood of Wedge-tailed Shearwater foraging, I used generalized linear mixed models (GLMM), fitted in package 'lme4' (Bates et al. 2015), with bird identity as the random intercept (Hamer et al. 2007, Grecian et al. 2016). GLMMs had a binary response, treating foraging or resting locations as 1 and transiting locations as 0, and were constructed separately for each year and colony (Lord Howe Island 2014, 2015 and Heron Island 2015). To effectively accommodate non-linearity, but not over-fit relationships, I permitted covariates in hi-res models to take either a linear or second-degree polynomial form. Model residuals and diagnostics were plotted and checked as per Zuur et al. (2009) and models' terms were selected using both forwards and backwards selection based on likelihood ratio tests ( $\chi^2$ ) and confidence intervals (Bolker et al. 2009). Model explanatory power was evaluated by constructing receiver operating characteristic (ROC) curves (Hanley & McNeil 1982) and calculating the associated area under the ROC curve (AUC) in package 'verification' (NCAR 2015). Goodness of fit was assessed for GLM using McFadden's pseudo  $R^2$  (Azen & Traxel 2009) in package 'pscl' (Jackman 2015) and assessed for GLMM split into marginal (var. explained by fixed effects) and conditional (var. explained by fixed + random effects) pseudo  $R^2$  components (Nakagawa & Schielzeth 2013) in package 'MuMIn' (Bartoń 2016).

## 3.4 RESULTS

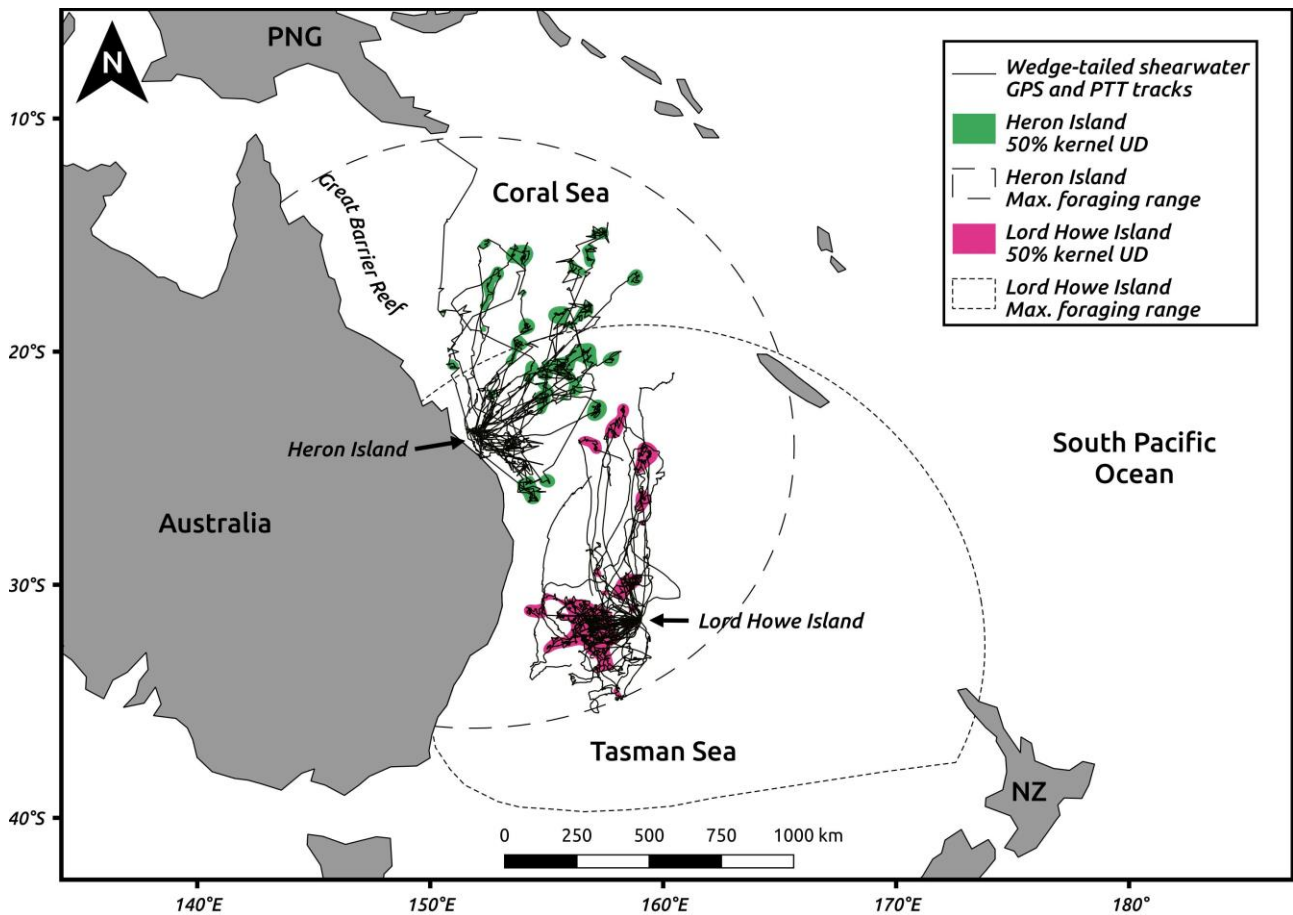
### 3.4.1 Tracking data

In total, 62 long-trips were recorded during the study. GPS battery life allowed individual shearwaters to be tracked with GPS for an average of  $5.1 \pm 1.1$  days when making long-trips lasting on average  $9 \pm 1.4$  days; representing 57% of their time at-sea (Table 3.2). Wedge-tailed shearwaters were tracked with PTTs for an average of  $8.9 \pm 0.9$  days. On average, Wedge-tailed Shearwaters on long-trips from Lord Howe Island travelled up to  $495 \pm 166$  km from their colony whereas conspecifics from Heron Island travelled up to  $672 \pm 62$  km on long-trips from their colony (Fig. 3.2). The core-areas of Wedge-tailed Shearwaters on long-trips from Heron Island were located in the same general region each year (centroid:  $19^{\circ}48'$  S,  $155^{\circ}36'$  E), whereas core-areas of conspecifics from Lord Howe Island were located in the same general region in 2014 and 2016 (centroid:  $31^{\circ}48'$  S,  $156^{\circ}42'$  E), but not in 2015 (Table 3.2).

**Table 3.2** Summary of Wedge-tailed Shearwater GPS and PTT\* tracked long-trips collected during the study. The core-area is the 50% utilization distribution from kernel analysis of each tracking dataset

Island Colony	Year	n trips	Max colony distance (km)	Trip length (km)	Tracked days	Trip length (d)	Core-area centroid (Lat, Long)
Lord Howe	2016	19	$328 \pm 114$	$1165 \pm 381$	$4.4 \pm 1.3$	$6.9 \pm 2.3$	-31.8, 157.2
Lord Howe	2015	14	$661 \pm 291$	$1986 \pm 590$	$5.9 \pm 2.3$	$9.9 \pm 3.3$	-27.7, 158.1
Lord Howe	2014	8	$498 \pm 292$	$1588 \pm 561$	$6 \pm 1.7$	$9.6 \pm 4$	-31.8, 156.2
Heron	2015	8	$625 \pm 223$	$1532 \pm 510$	$3.9 \pm 1.5$	$9.5 \pm 2$	-20.4, 156.9
Heron *	2013	9	$744 \pm 312$		$8.3 \pm 3.2$		-19.8, 154.2
Heron *	2011	3	$649 \pm 375$		$9.7 \pm 2.3$		-19.2, 155.7



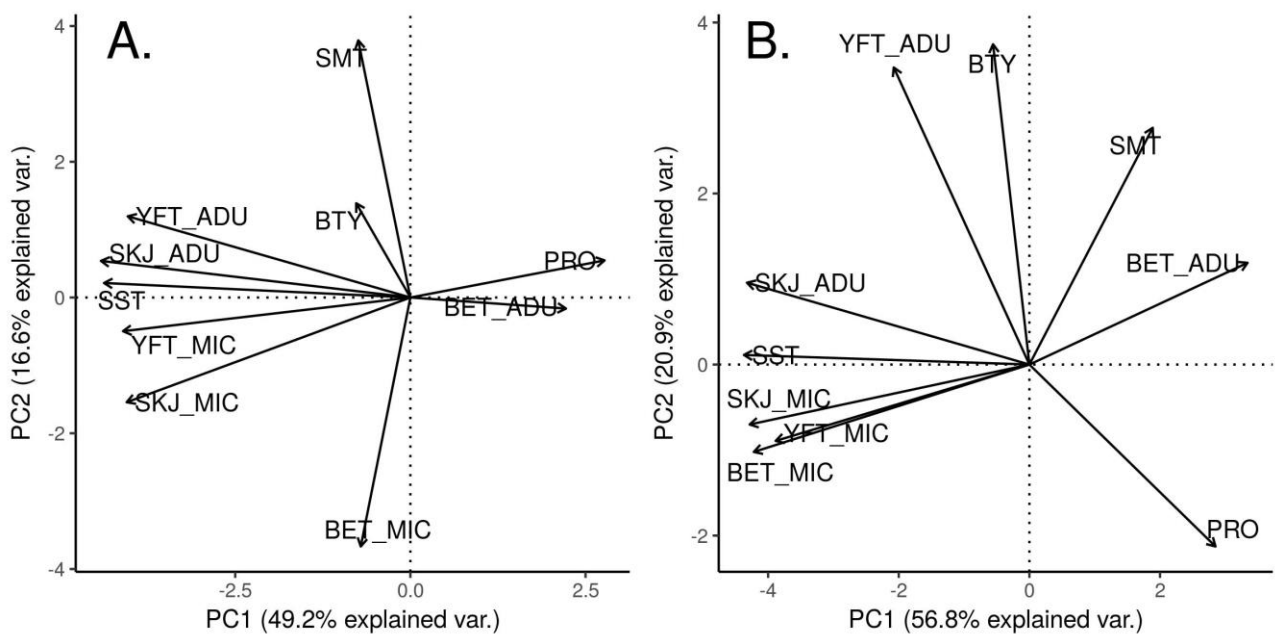


**Fig. 3.2** Wedge-tailed Shearwater long-trip tracking data collected from birds rearing chicks on Heron Island and Lord Howe Island between 2011 and 2016, overlaid with 50% kernel utilisation distribution (UD) core-use areas for each colony

### 3.4.2 PCA and collinearity

PCAs of oceanographic and tuna covariates within the climatology and hi-res datasets showed high levels of correlation between covariates and consistent clustering of the same covariates in both datasets. PCA of 10 covariates within the Heron Island climatology dataset revealed that the first 2 principal components account for 65.7% of the variance in the data (PC1 = 49.2%, PC2 = 16.5%), and for PCA of the same covariates within the Lord Howe Island climatology dataset, the first 2 principal components account for 77.7% of the variance in the data (PC1 = 56.8%, PC2 = 20.9%; Fig. 3.3). In both ordinations PC1 represents a positive

relationship with latitude: higher SST and tropical tuna biomass in the Coral Sea is associated with negative PC1 values where-as higher PRO and BET\_ADU biomass in the Tasman Sea is associated with positive PC1 values. In the Heron Island ordination PC2 represents an inverse relationship with proximity to a central seamount region and in the Lord Howe Island ordination PC2 represents a positive relationship with longitude. In both ordinations adult Skipjack Tuna (joined by adult Yellowfin Tuna in the Heron Island PCA) was clustered with micronektonic Skipjack and Yellowfin Tunas (joined by micronektonic Bigeye Tuna in the Lord Howe Island PCA), hereafter termed the 'major-tuna cluster'. In each PCA the major-tuna cluster was highly correlated with PC1 (Heron Island Pearson's  $r^2 = 0.88 - 0.96$ , Lord Howe Island Pearson's  $r^2 = 0.85 - 0.95$ ) and SST (Fig. 3.3).



**Fig. 3.3** Ordination from principal components analysis of broad scale oceanographic and tuna covariates used in climatology models of Wedge-tailed Shearwaters breeding from (A) Heron Island, and (B) Lord Howe Island

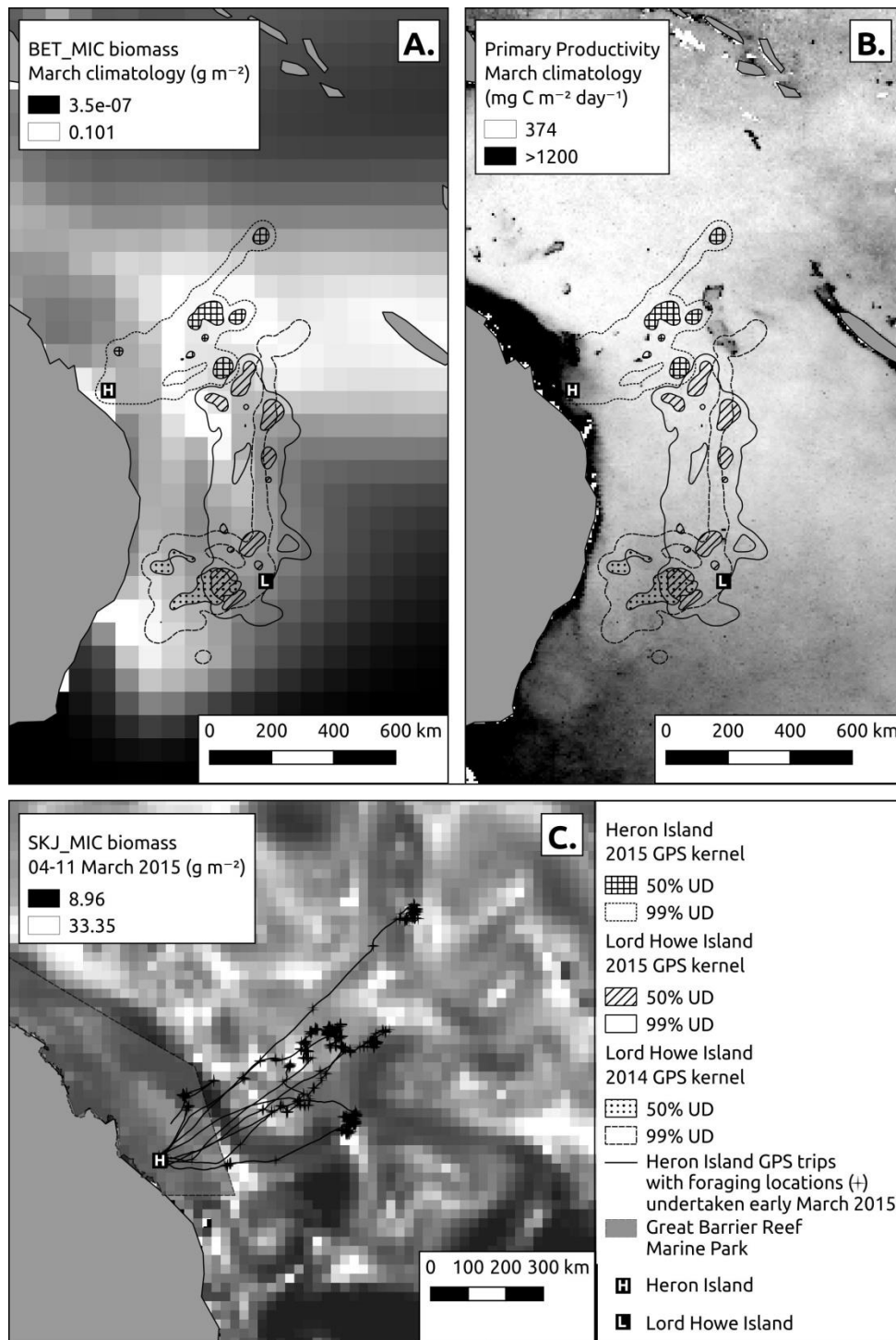
PCA of 13 covariates within the Heron Island 2015 hi-res dataset revealed that the first 2 principal components account for 56.3% of the variance in the data (PC1 = 33.9%, PC2 = 22.4%), PCA of the same



Heron Island shearwaters ( $\chi^2_1 = 263.6, p = <0.001$ ; Fig. 3.5B). Primary productivity was not significant to selection of core-area location for Wedge-tailed Shearwaters breeding on Lord Howe Island ( $\chi^2_1 = 2.46, p = 0.117$ ). Each climatology model included two tuna covariates, one as a proxy for the major-tuna cluster (selected to have minimal correlation with non-tuna covariates) and the other which was uncorrelated with the major-tuna cluster. Micronektonic yellowfin (YFT\_MIC) was the proxy and micronektonic bigeye (BET\_MIC) the uncorrelated covariate in the Heron Island model, while micronektonic bigeye was the proxy and adult yellowfin (YFT\_ADU) the uncorrelated covariate in the Lord Howe Island model (Fig. 3.3). The Heron Island climatology model predicted that for each additional 100 g m<sup>-2</sup> of tuna biomass an area contains, it is 1.04 times more likely to be selected as a core-area by Wedge-tailed Shearwaters if the tuna are micronektonic yellowfin ( $\chi^2_1 = 14.81, p = 0.001$ ), and 2.06 times more likely to be selected if the tuna are micronektonic bigeye ( $\chi^2_1 = 235.24, p = <0.001$ ). The Lord Howe Island climatology model predicted that for each additional 100 g m<sup>-2</sup> of tuna biomass an area contains, it is 1.42 times more likely to be selected as a core-area by Wedge-tailed Shearwaters if the tuna are micronektonic bigeye ( $\chi^2_1 = 70.35, p = 0.001$ ; Fig. 3.5A), but 1.71 times less likely to be selected if the tuna are adult yellowfin ( $\chi^2_1 = 15.39, p = <0.001$ ). Validation of Heron Island climatology model confirmed the final model fitted the data well (AUC = 0.97) and explained a good proportion of the variance (McFadden's  $R^2 = 0.71$ ). Validation of Lord Howe Island climatology model confirmed the final model also fitted the data well (AUC = 0.98) and explained a similar proportion of the variance (McFadden's  $R^2 = 0.75$ ).

**Table 3.3** Climatology logistical regression models of Wedge-tailed Shearwater presence-absence against broad scale oceanographic and tuna covariates. The following coefficients ( $\beta$ ) and std. errors (SE) are expressed in terms of a 100 unit change: tuna covariates ( $100 \text{ g m}^{-2}$ ), seamount distance (100 km) and bathymetry (100 m). All covariates have significance  $p < 0.001$ . Core-area and foraging range covariate values are expressed as mean  $\pm$  standard deviation

Colony	Covariate	$\beta \pm \text{SE}$	Core-area	Foraging range
Heron Island	Intercept	$1.195 \pm 1.304$		
	Primary productivity ( $\text{mg C m}^{-2} \text{ day}^{-1}$ )	$-0.025 \pm 0.002$	$425.53 \pm 42.62$	$534.80 \pm 154.28$
	Seamount distance (km)	$-0.698 \pm 0.099$	$96.38 \pm 83.85$	$167.52 \pm 125.95$
	Bathymetry (m)	$0.034 \pm 0.008$	$2756 \pm 940$	$2709 \pm 1389$
	Micronektonic Bigeye Tuna biomass ( $\text{g m}^{-2}$ )	$0.721 \pm 0.056$	$0.084 \pm 0.017$	$0.066 \pm 0.021$
	Micronektonic Yellowfin Tuna biomass ( $\text{g m}^{-2}$ )	$0.040 \pm 0.010$	$0.334 \pm 0.060$	$0.268 \pm 0.150$
	Autocovariate	$0.129 \pm 0.005$		
	Lord Howe Island	Intercept	$-4.681 \pm 0.706$	
Seamount distance (km)		$-1.169 \pm 0.176$	$84.56 \pm 45.07$	$168.10 \pm 144.98$
Bathymetry (m)		$0.048 \pm 0.010$	$3429 \pm 1069$	$2772 \pm 1359$
Micronektonic Bigeye Tuna biomass ( $\text{g m}^{-2}$ )		$0.350 \pm 0.048$	$0.067 \pm 0.010$	$0.045 \pm 0.030$
Adult Yellowfin Tuna biomass ( $\text{g m}^{-2}$ )		$-0.534 \pm 0.137$	$0.027 \pm 0.008$	$0.029 \pm 0.007$
Autocovariate		$0.112 \pm 0.004$		



**Fig. 3.5** GPS tracking data of breeding Wedge-tailed Shearwaters shown as (A) kernel utilisation distributions (UDs) overlaying SEAPODYM-predicted long-term mean micronektonic Bigeye Tuna biomass for march, (B) kernel UD overlaying long-term mean primary productivity for march, and (C) individual foraging trips from Heron Island overlaying SEAPODYM-predicted weekly micronektonic Skipjack Tuna biomass

#### 3.4.4 Hi-res models

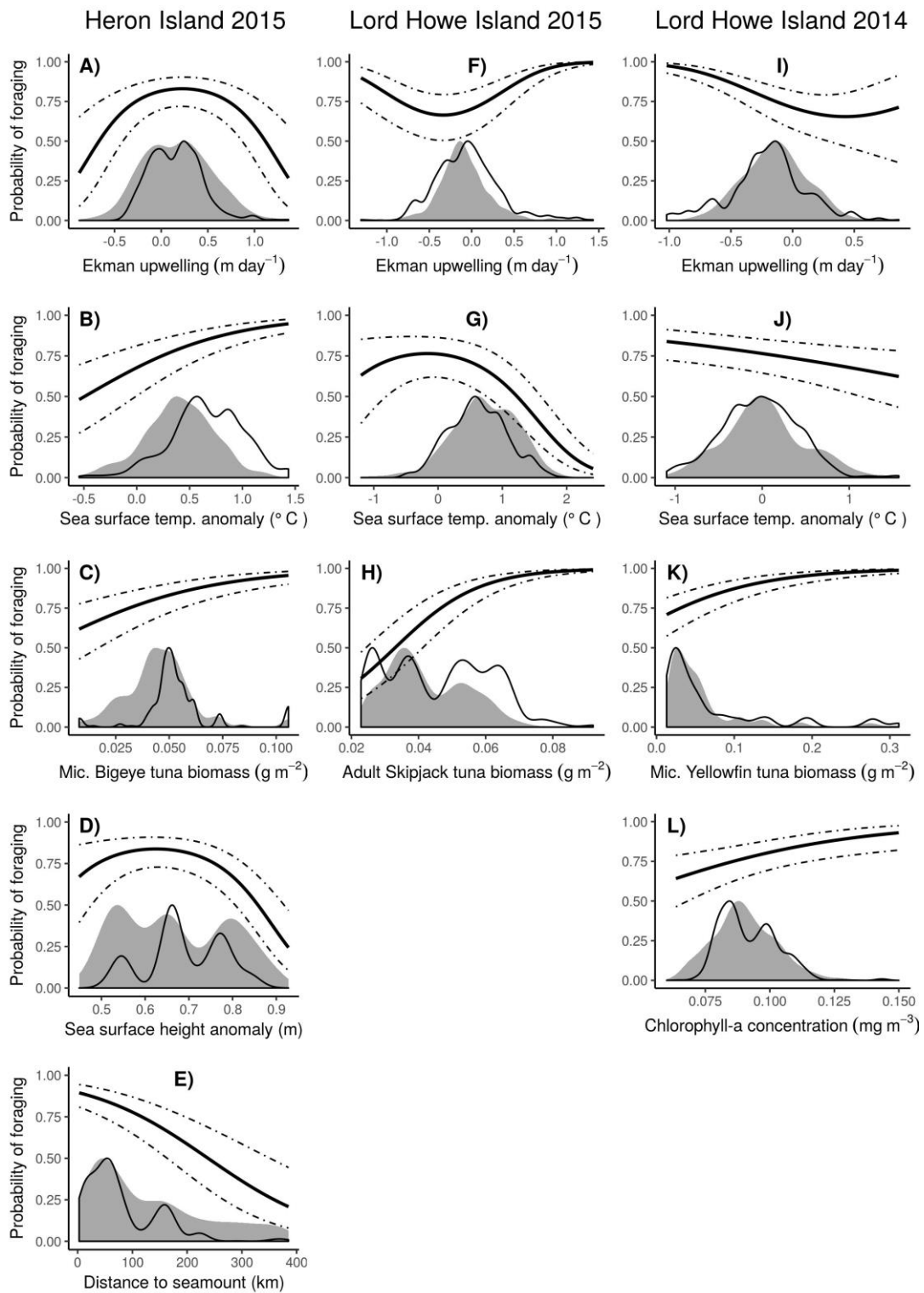
The likelihood of Wedge-tailed Shearwater foraging was not significantly influenced by bathymetry, and only shearwaters from Heron Island in 2015 were more likely to forage closer to seamounts (Table 3.4; Fig. 3.6E). Shearwaters from Lord Howe Island in 2014 were more likely to forage at higher Chlorophyll-*a* concentrations (Fig. 3.6L) while sea surface height anomalies influenced likelihood of foraging in shearwaters from Heron Island in 2015 only (Fig. 3.6D). Ekman upwelling and sea surface temperature anomalies influenced likelihood of shearwater foraging in every instance (Table 3.4; Fig. 3.6). The proxy selected to represent the major-tuna cluster was micronektonic bigeye (BET\_MIC) in the Heron Island 2015 model, adult Skipjack Tuna (SKJ\_ADU) in the Lord Howe Island 2015 model and micronektonic Yellowfin Tuna (YFT\_MIC) in the Lord Howe Island 2014 model (Fig. 3.4). Models predicted that for each additional 100 g m<sup>-2</sup> of tuna biomass an area contains, shearwaters from Heron Island in 2015 were 1.3 times more likely to forage there (Table 3.4; Fig. 3.6C), shearwaters from Lord Howe Island in 2015 were 2.23 times more likely to forage there (Fig. 3.6H) and shearwaters Lord Howe Island in 2014 were 1.13 times more likely to forage there (Fig. 3.6K). Additionally, the asymptotic nature of these predictions (Fig. 3.6C,H, K), indicates that my study models an important range of tuna biomass, including the highest density needed for maximum likelihood of foraging. Validation of the Heron Island 2015 model confirmed the final model fitted the data adequately (AUC = 0.79) and explained a good proportion of the variance (marginal R<sup>2</sup> = 0.31, conditional R<sup>2</sup> = 0.47). Validation of the Lord Howe 2015 model confirmed the final model also fitted the data adequately (AUC = 0.73) and explained a similar proportion of the variance (marginal R<sup>2</sup> = 0.29, conditional R<sup>2</sup> = 0.51). Validation of the Lord Howe 2014 model confirmed the final model fitted the data identically (AUC = 0.73) but explained a smaller proportion of the variance (marginal R<sup>2</sup> = 0.17, conditional R<sup>2</sup> = 0.30).



**Table 3.4** Hi-res logistical regression models of Wedge-tailed Shearwater probability of foraging against fine scale oceanographic and tuna covariates. The strength ( $\chi^2$ ) and effect direction of each covariate is given for each of the three colony-year models. Covariates with significance  $p < 0.01$  are shown in bold and the corresponding effect given, NA indicates that the covariate was not included in a model due to multicollinearity. Positive and negative effect directions are denoted by  $\uparrow$  and  $\downarrow$  respectively, and in the case of a polynomial relationship the value at which foraging is most or least (denoted by \*) likely is given. For coefficient ( $\beta$ ) and std. error values see Appendix 1

Covariate	Heron Island 2015		Lord Howe Island 2015		Lord Howe Island 2014	
	Effect	Strength ( $\chi^2$ )	Effect	Strength ( $\chi^2$ )	Effect	Strength ( $\chi^2$ )
Bathymetry (m)		0.40		3.80		NA
Seamount distance (km)	$\downarrow$	<b>38.77</b>		0.80		0.04
chlorophyll- <i>a</i> concentration ( $\text{mg m}^{-3}$ )		NA		NA	$\uparrow$	<b>9.67</b>
Ekman upwelling ( $\text{m day}^{-1}$ )	<b>0.22</b>	<b>16.83</b>	<b>-0.43*</b>	<b>65.61</b>	<b>0.67*</b>	<b>48.91</b>
Sea surface temperature anomaly ( $^{\circ}\text{C}$ )	$\uparrow$	<b>29.46</b>	<b>-0.17</b>	<b>101.77</b>	$\downarrow$	<b>6.57</b>
Sea surface height anomaly (m)	<b>0.62</b>	<b>33.27</b>		NA		3.27
Tuna biomass ( $\text{g m}^{-2}$ )	$\uparrow$	<b>26.07</b>	$\uparrow$	<b>230.21</b>	$\uparrow$	<b>66.14</b>





**Fig. 3.6** Mean (solid line) and 95% confidence interval (dot-dashed line) predictions of Wedge-tailed Shearwater foraging probability in relation to fine scale tuna and oceanographic covariates. Density plots are overlaid showing the distributions of foraging (black line) and non-foraging (grey shade) samples for each covariate. 'Mic.' refers to micronektonic tuna age-classes

## 3.5 DISCUSSION

### 3.5.1 Wedge-tailed Shearwater distributions and oceanography

My results show that the long-trip destinations of Wedge-tailed shearwaters breeding on Heron Island lie predominantly to the north-east of the colony in the Coral Sea, adding support for consistent use of this area over multiple years (McDuie et al. 2015). My results also show, for the first time, that during chick-rearing Wedge-tailed Shearwaters from Lord Howe Island undertake long-trips to predominantly different regions in different years. In 2014 and 2016 Wedge-tailed Shearwater long-trip destinations were distributed west of Lord Howe Island in the Tasman Sea over the Tasmantid Seamounts that run parallel to the east Australian shelf, while in 2015 long-trip destinations were predominately far to the north of Lord Howe Island in the Coral Sea, almost overlapping with conspecifics foraging from Heron Island. Whether long-trips at Lord Howe Island are undertaken as part of a coordinated dual-foraging strategy similar to that observed at Heron Island (Congdon et al. 2005), or more opportunistically is currently unknown. However, these results demonstrate that the unimodal foraging strategy observed by Peck & Congdon (2005) at Lord Howe Island during early chick rearing appears to alter in the later stages of chick-rearing (Jakubas et al. 2014), and/or between breeding seasons (Granadeiro et al. 1998).

My results show that both Wedge-tailed Shearwater populations selected core-areas in deep pelagic waters that were close to seamounts, these findings mirror those of other studies into the species' bathymetric preferences (Catry et al. 2009b, McDuie et al. 2015, McDuie & Congdon 2016). At fine scales, Wedge-tailed Shearwaters from Heron Island in 2015 were more likely to forage close to seamounts but bathymetry and seamounts did not influence conspecifics foraging from Lord Howe Island. These results indicate that marine topography may be used by Wedge-tailed Shearwaters to locate profitable foraging areas at broad but not fine scales. Fine scale foraging behaviour is likely to be triggered by sea surface temperature anomalies and Ekeman upwelling which influenced likelihood of foraging in all models. Collectively, these two dynamic covariates identify frontal areas of water mixing and associated up and down-welling. My results are

consistent with other studies that indicate that these dynamic phenomena are major mechanisms of prey aggregation for seabirds in lower latitude waters (Spear et al. 2001, Hyrenbach et al. 2006, Weimerskirch et al. 2010, McDuie & Congdon 2016).

### **3.5.2 Tuna relationships**

I found tuna distributions to influence Wedge-tailed Shearwater core-area location and likelihood of foraging in every instance, supporting both my broad scale and fine scale hypotheses. This means that Wedge-tailed Shearwaters sought out areas of increased tuna biomass, which at the regional scale are relatively stable between years, and that they home in on aggregations of tuna for foraging at fine scale. My results describe the importance of facilitated foraging opportunities in two seabird populations and are expressed in an ecologically meaningful way: using tuna density increases of  $100\text{g m}^{-2}$ , interpretable as the weight of one micronektonic tuna (165 mm long; Harley et al. 2014), or a large meal for a Wedge-tailed Shearwater. For example I predict that in 2015, for every additional micronektonic tuna encountered per  $\text{m}^2$  of ocean, it was 2.23 times more likely that Wedge-tailed Shearwaters from Lord Howe Island would forage there and 1.3 times more likely that conspecifics from Heron Island would forage there. Such predictions demonstrate the potential of my approach to quantify facilitated foraging opportunities. However, they also come with the caveat that they are only as accurate as the underlying modelled tuna distributions.

The major-tuna cluster identified in each PCA, and represented in each model by a single covariate, showed that densities of most tunas were positively associated with: each other, Wedge-tailed Shearwater selection of core-areas, and shearwater likelihood of foraging. The major-tuna cluster represents significant spatial overlap in the distribution of adult and micronektonic tunas. In locations where this cluster of tunas co-occurs a scenario is envisaged where micronektonic tuna and similar sized micronekton (30-250 mm) prey upon each other and attract adult tunas through cannibalism and inter-species predation (Allain et al. 2007, Allain 2010). Predation within the cluster takes place in epipelagic waters because micronektonic tuna have a non-developed swim bladder that confines them to surface waters (Magnuson 1973). As such, where the major-tuna cluster occurs, micronekton of appropriate size to be Wedge-tailed Shearwater prey (up to 145 mm; Harrison et al. 1983) are preyed upon by tuna in surface waters, presenting clear facilitated foraging

opportunities. To independently verify this scenario bird-borne cameras could be mounted to tropical seabirds, with the increasing miniaturisation of such technology making it a near-future possibility for smaller species like shearwaters.

Only in the Heron Island climatology model did shearwaters associate with a micronektonic tuna (bigeye) outside of the major-tuna cluster. Even small micronektonic tuna are proficient swimmers (Graham et al. 2007) and it is unlikely that Wedge-tailed Shearwaters from these colonies possess the diving ability (maximum recorded dive depth of 12m; Peck & Congdon 2006) to capture them without subsurface predator assistance during the day. This suggests that subsurface predators not considered in my models, such as cetaceans (Au & Pitman 1986), billfish (family: Istiophoridae) or Dolphinfish *Coryphaena hippurus* (Young et al. 2010c), also facilitate Wedge-tailed Shearwater foraging in this region.

At broad scales, my results suggest Wedge-tailed Shearwaters are consistent facilitated foraging commensals of adult Skipjack Tuna, intermittent facilitated foraging commensals of adult Yellowfin Tuna, and that adult Bigeye Tuna do not facilitate Wedge-tailed Shearwater foraging. Many tropical seabirds are known to associate foraging with Skipjack Tuna (Au & Pitman 1986, Jaquemet et al. 2004, Hebshi et al. 2008). Frequent seabird association with skipjack could be due to their greater biomass, relative to other tunas in tropical seas, fostering greater facilitated foraging opportunities. Additionally, the smaller size of skipjack, relative to other tunas, means that they also target suitable sized prey (mean prey length 42 mm; Roger 1994) for Wedge-tailed Shearwaters (mean prey length 57 mm; Harrison et al. 1983). However, larger yellowfin and bigeye also feed on very small prey relative to their own size (Ménard et al. 2006) and could conceivably target shearwater-sized prey. Tuna occupy different vertical niches based on their size (which limits thermal tolerance) and biology (i.e. development of the swim bladder in yellowfin and bigeye); larger tunas can spend more time foraging for prey in deep water within and below the thermocline. During the day, adult bigeye are typically found deepest, followed by yellowfin and then skipjack (Schaefer et al. 2009, Schaefer & Fuller 2013, Scutt Phillips et al. 2015). Consequently, the predominantly surface-dwelling Skipjack Tuna (and micronektonic tuna age-classes) are more often encountered by diurnal seabirds and thus more likely to serve as facilitated foraging hosts than larger adult yellowfin or bigeye.

Tuna biomass in the Coral and Tasman Seas changes throughout the year following spawning and seasonal changes in water temperature and habitat. Regional tuna spawning times are poorly known, however skipjack and yellowfin are thought to spawn year-round depending on water temperature (Schaefer 1996, Schaefer 2001) and bigeye are thought to spawn from October to December (Evans et al. 2008). Regional tuna movement broadly follows thermal boundaries (Evans et al. 2011), this is especially true for less thermally tolerant skipjack and micronektonic tunas, which SEAPODYM models to follow the southward advance of warm water in the austral summer and subsequent retreat north in the winter. This regional spawning and movement pattern causes annual densities of tunas in the major-tuna cluster to peak in the southern Coral Sea in the austral summer. In fact, adult bigeye spawning in December would produce ~250mm micronektonic offspring in March (Nicol et al. 2011). This means that skipjack and micronektonic tuna biomass peaks within the foraging range of Wedge-tailed Shearwaters at a time when they have the highest energy demands of chick-rearing. If facilitated foraging with tuna is as important for Wedge-tailed Shearwater populations as I suggest, then tuna seasonality could have an important role in shaping Wedge-tailed Shearwater breeding phenology, as proposed for productivity in Indian Ocean conspecifics (Catry et al. 2009b).

### **3.5.3 Effect of productivity gradient on long-trip destinations**

I found that the tropical Wedge-tailed Shearwater population did not adhere to the ‘temperate long-trip model’ by seeking out areas of high primary productivity, but instead targeted regions of high tuna biomass. The subtropical population at times adhered to the ‘temperate long-trip model’ but also targeted tuna. The Heron Island results are consistent with Wedge-tailed Shearwater non-breeding preferences, where birds exploit warm, oligotrophic waters in the Indian (Catry et al. 2009b) and Pacific oceans (McDuie & Congdon 2016) when freed from the need to central-place forage. My results also support the suggestion of a temporal and spatial decoupling between satellite surface-measured primary productivity and micronekton/tuna aggregation in tropical oceans (Lehodey et al. 1998, McDuie & Congdon 2016).

At broad scales the selection of core-areas by Wedge-tailed Shearwaters from sub-tropical Lord Howe Island

appeared uninfluenced by primary production. However, this was due to variation in long-trip destinations between years. In 2014 Wedge-tailed Shearwater foraging was positively associated with increased chlorophyll-*a* concentration and the population exploited sub-tropical waters west of Lord Howe Island. In 2015 shearwater foraging was negatively related to chlorophyll-*a* concentration and the population exploited tropical waters north of Lord Howe Island. In 2014 the Lord Howe Island result conforms to my prediction for a sub-tropical shearwater colony, where long-trip foraging destinations target enhanced productivity driven by oceanic fronts (Baduini & Hyrenbach 2003, Paiva et al. 2010b), but in 2015 the result does not. In 2015 Wedge-tailed Shearwater likelihood of foraging was more strongly associated with tropical tuna densities. Individuals clearly transited over waters of the Tasman Sea, which are usually high in productivity, to reach oligotrophic waters with high tuna biomass in the Coral Sea. A potential explanation is that in years like 2015, productivity in the Lord Howe region becomes reduced, through a distancing or reduction in strength of the Tasman Front (Mulhearn 1987, Przeslawski et al. 2011). Wedge-tailed shearwaters remained in sub-tropical waters to the west of Lord Howe Island in 2014 and 2016, indicating that the 2015 northward movement could mark a departure from normal conditions, however additional years of data are needed to confirm this.

Although it is unclear what triggers Wedge-tailed Shearwaters from Lord Howe Island to switch long-trip destinations, it is unequivocal that both shearwater populations preferentially target tuna in some years. At the same time of year in 2015, individuals from both populations undertook long, purpose-directed flights towards almost the exact same region of the southern Coral Sea, indicating an *a priori* expectation of high resource availability at these sites. This is not the indirect, looping flight that tropical seabirds use to exploit unpredictable resources (Weimerskirch 2007, Weimerskirch et al. 2010). Rather, it suggests that the tropical tuna biomass targeted by these flights was not patchily distributed or ephemeral at broad spatio-temporal scales. The apparent reliability of this resource suggests that in tropical systems, facilitated foraging with tuna can act as a consistently available 'productive' long-trip destination, analogous to chlorophyll-*a* concentration in temperate systems. In terms of population-level reliance on tuna I suggest that facilitated foraging with tuna is consistently important to sustain breeding in the Heron Island Wedge-tailed Shearwater population. Primary productivity *per se* appears more important to the Lord Howe Island Wedge-tailed

Shearwater population in most years, although facilitated foraging with tuna becomes an important strategy under certain conditions. As such, the relative importance of facilitated foraging for Wedge-tailed Shearwater populations appears to be dependent upon their access to reliable areas of high primary productivity.

## **CHAPTER 4: SEX-SPECIFIC FORAGING IN A TROPICAL SULID**

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## 4.1 ABSTRACT

Sexual segregation in the behaviour, morphology or physiology of breeding seabirds can be related to divergent parental roles, foraging niche partitioning or sex-specific nutritional requirements. Here I combine GPS tracking, dietary and nutritional analysis to investigate sex-specific foraging of Brown Boobies breeding on Raine Island, Great Barrier Reef, Australia. I observed sex-specific segregation in: a) foraging location: females undertook longer trips, foraging at more distant locations than males; b) foraging time: male activity and foraging occurred throughout the day, while female activity and foraging increased from midday to an afternoon peak; and c) prey type, females mostly consumed flying fish, whereas males consumed equal proportions of flying fish and squid. Brown Booby diets contained five tropical prey species that significantly differed in their nutritional composition (Protein, Lipid and Water, wet mass). Despite this variation I found no differences in the overall nutritional content of prey caught by each sex. The observed sex-specific differences in prey type, location and time of capture are likely driven by a combination of a division of labour, risk partitioning and competition. However, Brown Boobies breeding on Raine Island, and other populations, might flexibly partition foraging niche by sex in response to varying competitive and environmental pressures. In light of such potential foraging dynamism, my inconclusive exploration of nutritional segregation between sexes warrants further investigation in the species.

## 4.2 INTRODUCTION

Sexual segregation of foraging in breeding birds has been observed in many terrestrial groups, including warblers (Morse 1968; Petit et al. 1990), woodpeckers (Selander 1966) and raptors (Newton 1979). Sex-specific foraging has also been observed in many seabirds, with the proposed causal factors varying between studies. For example, niche partitioning and inter-sexual competition are suggested as drivers of sexual segregation in foraging Northern Giant Petrels *Macronectes halli* (González-Solís et al. 2000) and albatrosses *Thalassarche* spp. (Stahl and Sagar 2000; Phillips et al. 2004). Whereas a division of labour,

where partners assume different reproductive roles, is considered the principal driver of sex-specific foraging in the Alcini (*Uria*, *Alca*, and *Alle*; Elliott et al. 2010) and Masked Boobies *Sula dactylactra* (Weimerskirch et al. 2009a; Sommerfeld et al. 2013). Seabird species can also display varying levels of sexual size dimorphism, which is considered an important influence upon sexual segregation in Wandering Albatrosses *Diomedea exulans* (Shaffer et al. 2001), boobies *Sula* spp. (Zavalaga et al. 2007; Weimerskirch et al. 2009a) and frigatebirds *Fregata* spp. (Congdon and Preker 2004). However, sexual segregation also occurs in monomorphic seabirds, such as Wedge-tailed Shearwaters *Ardenna pacifica* (Peck and Congdon 2006) and gannets *Morus* spp. (Lewis et al. 2002; Ismar et al. 2017), questioning the importance of sex-specific size differences. A proposed alternative explanation for sex-specific foraging is that male and female seabirds have differing nutritional requirements (Lewis et al. 2002; Elliott et al. 2010) that can only be met by each sex foraging on different prey types, size classes and/or at locations where prey availability differs.

There is poor consensus on the drivers of sex-specific foraging in Sulids (gannets and boobies), primarily due to the varying levels of sexual size dimorphism within and between species. While gannets are considered sexually monomorphic (although females can be up to ~10% heavier than males; Cleasby et al. 2015), boobies show reverse sexual dimorphism (RSD), where females are ~14% (Red-footed *Sula sula* and Masked Boobies; Weimerskirch et al. 2006b; Weimerskirch et al. 2009a), ~31% (Blue-footed Booby *Sula nebouxii*; Guerra and Drummond 1995), or between 27% and 38% heavier than males (Brown Booby *Sula leucogaster*; Nunes et al. 2016; Lewis et al. 2005). The greater weight of female boobies has been used as a mechanistic explanation for them diving deeper (Weimerskirch et al. 2006b; Zavalaga et al. 2007), while lower flight costs attributed to the smaller body size of male Brown Boobies has been used to explain their greater foraging range (Lewis et al. 2005). The larger female has been observed to take a greater responsibility for chick provisioning (larger meals), while the smaller male specializes in nest defence in Masked Boobies (Weimerskirch et al. 2009a) and to a lesser extent in Red-footed Boobies (Lormee et al. 2005) and Blue-footed Boobies (Guerra and Drummond 1995). However, in these studies a division of labour did not appear to foster sexual segregation in foraging behaviour.

Intra-specific competition is known to drive foraging site segregation in Sulids, with competition pressure in larger populations forcing individuals to forage further from the colony (Lewis et al. 2001; Opper et al. 2015). However, little support for inter-sexual competition as a driver of foraging segregation exists in either monomorphic Northern Gannets *Morus bassanus* (Lewis et al. 2002; Cleasby et al. 2015) or sexually dimorphic boobies (Pontón-Cevallos et al. 2017; Weimerskirch et al. 2009a). This is surprising as the larger size of female boobies could enable local dominance and exclusion of males as seen in other seabirds (González-Solís et al. 2000, Stahl and Sagar 2000). A potential explanation is that different booby species often breed sympatrically and that inter-specific competition is more significant than intra-specific competition (Young et al. 2010b; Pontón-Cevallos et al. 2017, but see Weimerskirch et al. 2009b).

Nutritional segregation between sexes is an often discussed, but rarely tested, driver of seabird foraging differences (Lewis et al. 2002; Lewis et al. 2005; Peck and Congdon 2006; Sommerfeld et al. 2013). Multiple studies have compared prey items captured by male and female boobies, most finding high overlap (Weimerskirch et al. 2006b; Zavalaga et al. 2007; Weimerskirch et al. 2009a) or small differences (Castillo-Guerrero et al. 2016). However, these studies did not explore potential sexual differences in the nutritional composition of prey consumed. In a wide range of species, foraging goals are related to a specific amount or proportion of nutrients (Raubenheimer et al. 2015). Within Sulid species, nutritional requirements could vary between sexes to offset sex-specific physiological costs, such as female oviposition compensation (Lewis et al. 2002; Ismar et al. 2017). Such demands could lead to foraging segregation, so as to allow each sex to obtain prey of appropriate nutritional quality. Right-angled mixture triangle modelling (RMT) enables researchers to explore the relationships among the proportional content of nutrients in foods and diets, through visualisation in two-dimensional space (Raubenheimer 2011). To date RMTs have provided novel insights into the nutritional ecology of two Sulid species in the wild, Australasian Gannets *Morus serrator* (Tait et al. 2014; Machovsky-Capuska et al. 2016b) and Masked Boobies *Sula dactylatra tasmani* (Machovsky-Capuska et al. 2016a). These studies highlighted the nutritional complexities of marine environments and provide the only evidence of sex-specific nutritional foraging strategies in seabirds. Recently, RMT models were also used to integrate food-level approaches in a multi-nutrient framework to provide fresh insights into dietary breadth and niche theory (Machovsky-Capuska et al. 2016c). Using this

multi-nutrient framework, the dietary niche of species can be characterized across three levels: i) the “fundamental nutritional niche” known as the nutritional diet that a population needs to persist; ii) the “realised nutritional niche” defined as the observed diet of a population that can be subject to ecological constraints such as prey availability or competition, and iii) the “prey composition niche” considered as the range of ecological and physical attributes of prey that the species is able to consume.

The Brown Booby (hereafter boobies) shows consistent RSD and high local adaptation across its' global range (Morris-Pocock et al. 2011; Nunes et al. 2016), making it a good model for studying drivers of sex-specific foraging (Castillo-Guerrero et al. 2016). Locally adapted populations demonstrate different sex-specific foraging strategies: males undertake longer foraging trips than females while incubating at Johnston Atoll, Central Pacific (Lewis et al. 2005) and while chick-rearing at Dog Island, Anguilla (Soanes et al. 2015). Conversely females forage further from the colony while chick-rearing at Clipperton Island, Eastern Pacific (Gilardi 1992) and undertake longer foraging trips while chick-rearing at Isla San Ildefonso, Mexico (Weimerskirch et al. 2009b). The plasticity of sex-specific foraging behaviour shown by these Brown Booby populations is unlikely to be explained by a single underlying driver (e.g. competition, sexual size dimorphism or a division of labour). As such, sex-specific nutritional demands warrant investigation as a potential explanation for sexual segregation in this species.

Here I combined the use of global position satellite (GPS) data loggers, morphometric measurements, dietary analysis, nutritional composition of prey and nutritional modelling (RMT) to gain a better understanding of the drivers of sexual segregation in Brown Boobies from the Far Northern Great Barrier Reef (GBR), Australia. Based on a synthesis of previously available information I predict that Brown Boobies from this GBR population should: i) display RSD; ii) show sexual segregation in foraging grounds; iii) show sex-specific differences in the timing of foraging activities; iv) consume different prey based on sex; and v) have sex-specific realised nutritional niches.

## **4.3 METHODS**

### **4.3.1 Study area, capture and handling**

This study was carried out on Raine Island (144°02' E, 11°35' S), a 28-hectare, vegetated coral cay on the outer edge of the Northern GBR, Australia. The Brown Booby population on Raine Island was last estimated at 2,642 individuals between 1994-2003 (Batianoff and Cornelius 2005) and breeds year-round with a peak in November and December (Blaber et al. 1998). GPS tracking and diet sampling of Brown Boobies was undertaken during the chick-rearing phase in the first week of December 2014, when chicks were ~ one month old. I-gotU GT-120 GPS loggers (Mobile Action Technology) were programmed to obtain fixes every minute and sealed in heat-shrink tubing. Birds were captured by hand at dusk (median time = 20:22) and loggers were attached to three central tail feathers using Tesa® 4651 Tape (Weimerskirch et al. 2005). Devices weighed ~17g and remained on the birds for several days so as to gather data on consecutive foraging trips (Oppel et al. 2015). Birds were recaptured at dusk for logger retrieval. Body mass and morphometric measurements, including flattened wing chord, tarsus and culmen lengths were obtained. Additionally, for chicks associated with adults carrying loggers, I obtained chick tarsus and body mass measurements upon adult recapture. Handling of adults and chicks was limited to < 10 minutes. Boobies were sexed using facial skin, bill and foot colouration (Nelson 1978). Diet samples were opportunistically collected from adults that regurgitated upon handling at dusk (n = 9 females, n = 8 males, n = 2 sex unknown) and stored in polyethylene bags at -20 °C.

### **4.3.2 Diet composition**

Prey obtained from the regurgitations were individually weighed ( $\pm 0.1$  g), total length measured ( $\pm 0.1$  cm) and identified to the lowest possible taxonomic level using published guides (Allen 2009). For each prey species the percentage contribution of the individual to the total weight was calculated as a mass percentage (M%, Duffy and Jackson 1986). The total number of prey items contributed by an individual of a particular species was calculated as a percentage termed numerical abundance (N%), and the frequency of occurrence (F%) was calculated as the percentage of birds that had one particular species present in the regurgitation

(Schuckard et al. 2012). The above metrics were summarised using the index of relative importance (IRI), calculated for each prey species as  $IRI = F\% * (M\% + N\%)$  and expressed as a percentage (IRI%) by dividing by the sum of IRI values from all prey species (Cortés 1997).

#### **4.3.3 Nutritional composition of prey and diet**

To measure the nutritional composition of prey species and estimate the nutritional composition of boobies' diets, only undigested prey were selected for nutritional composition analyses (Tait et al. 2014). The most representative prey samples selected included flying fish (*Cypselurus* spp., n=6), Blue Sprat (*Spratelloides robustus*, n=8), Smooth belly Sardine (*Amblygaster leiogaster*, n=2), Leatherjacket (*Catherhines fronticinctus*, n=2) and squid (*Sthenoteuthis* spp., n=8). Prior to analysis, each sample was partially thawed and weighed ( $\pm 0.1$  g), dried for five days in a freeze dryer and ground in a laboratory mill. Total nitrogen (N) was measured using Kjeldahl analysis and estimated crude protein by multiplying N by a factor of 6.25 (AOAC method 981.10; AOAC 2005). The Mojonnier method was used to measure total lipid (ether extract) (AOAC 954.02; Min and Steensen 1998). Ash was measured by ignition in a furnace at 550 °C (AOAC method 920.15; AOAC 2005). Finally, moisture (hereafter water) was measured by drying the sample in a convection oven at 125 °C (AOAC method 950.46; AOAC 2002) and combining this moisture loss with initial loss from the overnight dry down.

#### **4.3.4 GPS data analyses**

All data handling and statistical analyses were performed in the statistical software environment program R version 3.2.4 (R Core Team 2017). Tracking data were speed filtered (removal of points  $> 75$  km/h), and gap filled (interpolation to 1 minute interval) prior to analyses. Individual foraging trips were extracted from multi-day tracks using BirdLife International's 'marine IBA' R package (Lascelles et al. 2016). I also calculated time spent on colony between successive foraging trips for birds that were tracked for several days. To identify behavioural states, I applied Hidden Markov Models (HMM) to the GPS data. I constructed a single HMM using the full GPS tracking dataset, including an identifier for each trip, using the 'moveHMM' R package (Michelot et al. 2016). For each consecutive GPS point the step length and turning angle were calculated, producing three distributions consistent with foraging, resting and transiting

behaviours observed in HMM studies on Sulids (Boyd et al. 2014; Oppel et al. 2015). To visualise foraging areas of sexes, I estimated 99 and 50% utilization distributions (UDs) using kernel analysis of foraging locations from the HMM, in the 'adehabitatHR' R package (Calenge 2006).

#### **4.3.5 Difference in movements and daily activity**

I estimated a range of movement parameters for each foraging trip including maximum distance away from the colony (MDC), mean foraging distance from the colony (MFD), total foraging path (TFP), foraging trip duration (FTD), foraging time (FT), transiting time (TT), resting time (RT square-root transformed) and time on colony, from the GPS data and HMM results. I constructed separate linear mixed models (LMMs) in which each movement parameter was fitted against a single predictor for sex, adult body mass, chick condition (chick mass/tarsus) and date, with individual bird as the random effect, in the 'lme4' R package (Bates et al. 2015). Bonferroni-corrected p-values for multiple comparisons were used to test for significant differences ( $\alpha = 0.05$ ). I used linear models (LMs) and quasibinomial generalized linear models (GLMs) to test for sex-specific differences in: colony departure and return times; the percentage of boobies at-sea between morning (hour <12), and afternoon (hour  $\geq 12$ ); and the number of foraging locations between morning and afternoon.

#### **4.3.6 Difference in prey species**

I tested for an association between prey species occurrence and sex of birds using chi-squared analysis. To evaluate sex-specific differences in the number of prey items and the mass of regurgitate collected from adults, I fitted each as a response against bird sex in a quasipoisson GLM. Similarly, to evaluate variation in prey species weight and length two LMs were constructed, where the log-transformed weight and length of prey were fitted against bird sex.

#### **4.3.7 Nutritional composition of prey and diets**

To assess differences in the nutritional composition of prey (comprised of different species), LMs were constructed using protein (P), lipid (L), water (W), protein-to-lipid ratio (P:L) or water-to-lipid ratio (W:L)

as responses fitted against bird sex and prey species. I present the differences in the proportional wet mass contribution of the nutritional compositions of prey items and diets using RMT modelling (Raubenheimer 2011). To estimate energy (E) supplied by nutrients in each prey, I converted macronutrient masses to energy using conversion factors of 17 kJ/g for P, and 37 kJ/g for L (NRC 1989). The data on the proportion of prey species enabled us to estimate the nutritional composition for 91.3% (wet mass) of the diet of Brown Boobies.

#### **4.3.8 Foraging performance**

To evaluate the efficiency of nutrient gains, the foraging performance parameters TFP, FTD and FT obtained for each foraging trip were divided by the quantity of each nutrient obtained, as per Machovsky-Capuska et al. (2016a). For example P (g) divided by FTD (h) to establish intake of P (g/h). Separate LMs using each combined nutrient/performance parameter were fitted against sex and individual bird, accounting for interactions. All results are presented as mean  $\pm$  standard deviation (SD).

## **4.4 RESULTS**

### **4.4.1 Adult morphometric measurements and movement**

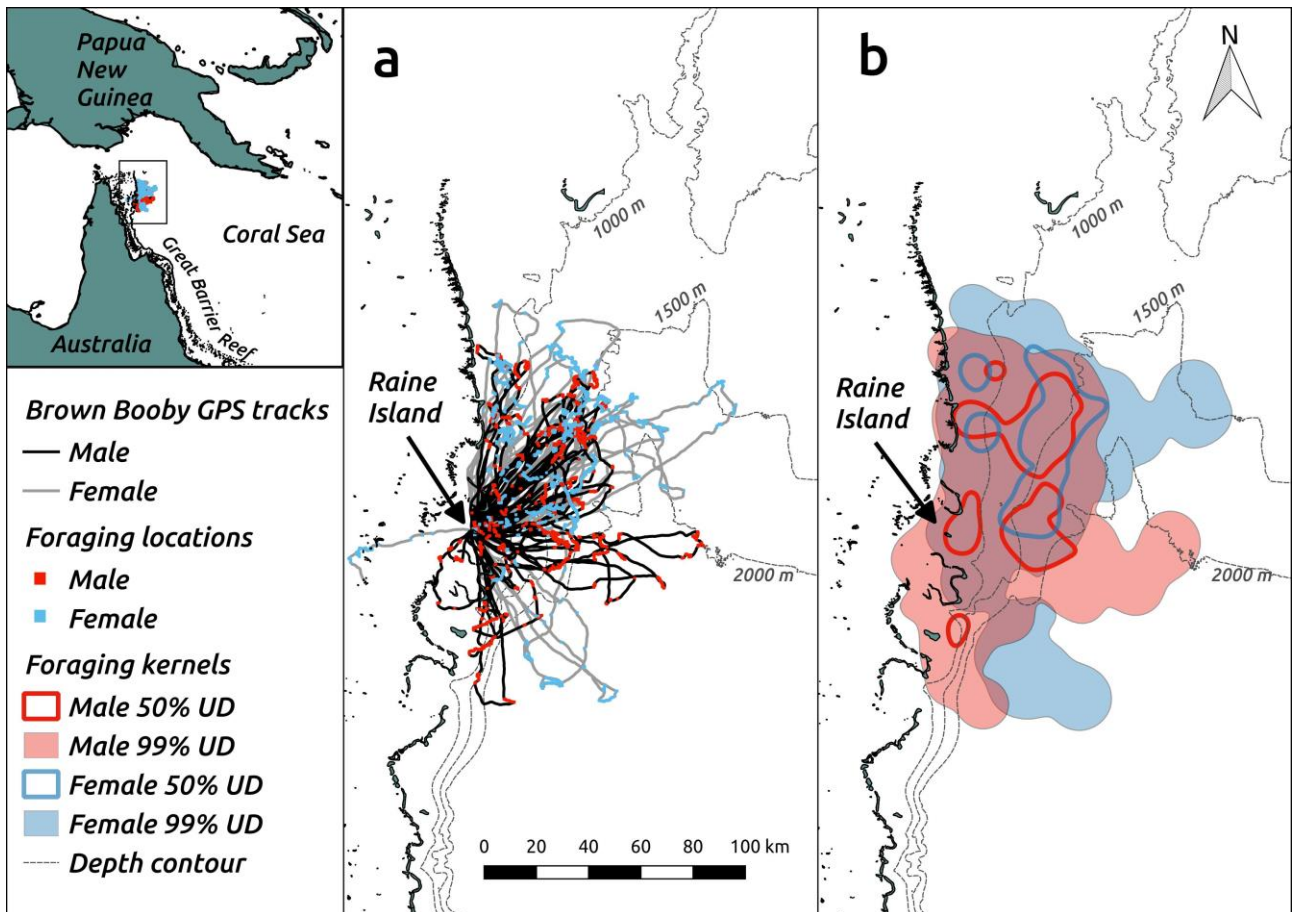
Female boobies were 16.3% heavier than males, and had longer tarsi, wings and culmens (n female = 15, n male = 11; Table 4.1). In total, 19 individuals (female = 10, male = 9) were successfully tracked, comprising 58 individual trips. Almost all trips foraged outside the reef, most over pelagic waters (depths 1000-2000m) and some at the reef edge (Fig. 4.1a). All individuals made a single foraging trip each day, except for three males that undertook a second short trip, before dusk (FTD < 2.5 h). The mean MDC that boobies travelled was  $57 \pm 22$  km (maximum of 113 km) with a mean MFD of  $47 \pm 18$  km from the colony. The mean TFP that boobies covered was  $150 \pm 59$  km, taking an average FTD of  $5.42 \pm 2.06$  hours. During trips, boobies spent a mean time of  $1.84 \pm 0.8$  hours foraging, a mean time of  $2.84 \pm 1.21$  hours transiting, and a mean time of  $0.75 \pm 0.63$  hours resting. I detected significant variation between sexes in movement parameters MDC, MFD and TFP (Table 4.1). This translated spatially into a general core-foraging area shared by sexes, but with the



female distribution more distant from the colony relative to the male distribution (Fig. 4.1b). Adult body mass, chick condition and date did not vary significantly in relation to any movement parameters. Variance was detected within the Individual bird random effect for movement parameters MFD, RT and time on colony but not MDC, TFP, FTD, FT and TT.

**Table 4.1** Morphological (n= 26 birds; female = 15, male = 11) and movement parameter (n= 19 birds; female = 10, male = 9) differences between males and female Brown Boobies, rearing chicks on Raine Island in December 2014. Mean  $\pm$  1 standard error for each sex is given, corresponding test statistics from anova (*F*-value) or Welch's *t*-test (*t* -value), and significance (Bonferroni-corrected *p*-value). For each parameter MDC = maximum distance from the colony, MFD = mean distance of foraging from the colony, TFP = total foraging path, FTD = foraging trip duration, FT = foraging time, TT= transiting time, RT = resting time

Parameter	Females	Males	Statistic	<i>p</i>
Mass (g)	1430 $\pm$ 147	1197 $\pm$ 65	<i>t</i> = 5.41	<0.001
Tarsus (mm)	50.73 $\pm$ 1.16	48.36 $\pm$ 2.46	<i>t</i> = 2.96	0.054
Culmen length (mm)	97.66 $\pm$ 2.61	93.27 $\pm$ 3.00	<i>t</i> = 3.89	0.004
Culmen height (mm)	34.60 $\pm$ 1.88	33.45 $\pm$ 1.29	<i>t</i> = 1.83	0.392
Wing chord (cm)	41.27 $\pm$ 1.13	40.36 $\pm$ 1.05	<i>t</i> = 2.09	0.238
MDC (km)	65.84 $\pm$ 4.12	50.33 $\pm$ 3.72	<i>F</i> = 7.80	0.049
MFD (km)	54.82 $\pm$ 3.22	40.51 $\pm$ 2.9	<i>F</i> = 10.92	0.012
TFP (km)	173.61 $\pm$ 11	131.71 $\pm$ 9.9	<i>F</i> = 8.05	0.044
FTD (h)	6.18 $\pm$ 0.38	4.8 $\pm$ 0.35	<i>F</i> = 7.10	0.070
FT (h)	1.95 $\pm$ 0.16	1.75 $\pm$ 0.14	<i>F</i> = 0.89	1
TT (h)	3.25 $\pm$ 0.23	2.51 $\pm$ 0.2	<i>F</i> = 5.82	0.133
RT (h)	0.92 $\pm$ 0.08	0.69 $\pm$ 0.08	<i>F</i> = 4.54	0.289
Time on colony (h)	17.6 $\pm$ 0.83	19.58 $\pm$ 0.74	<i>F</i> = 3.15	0.101

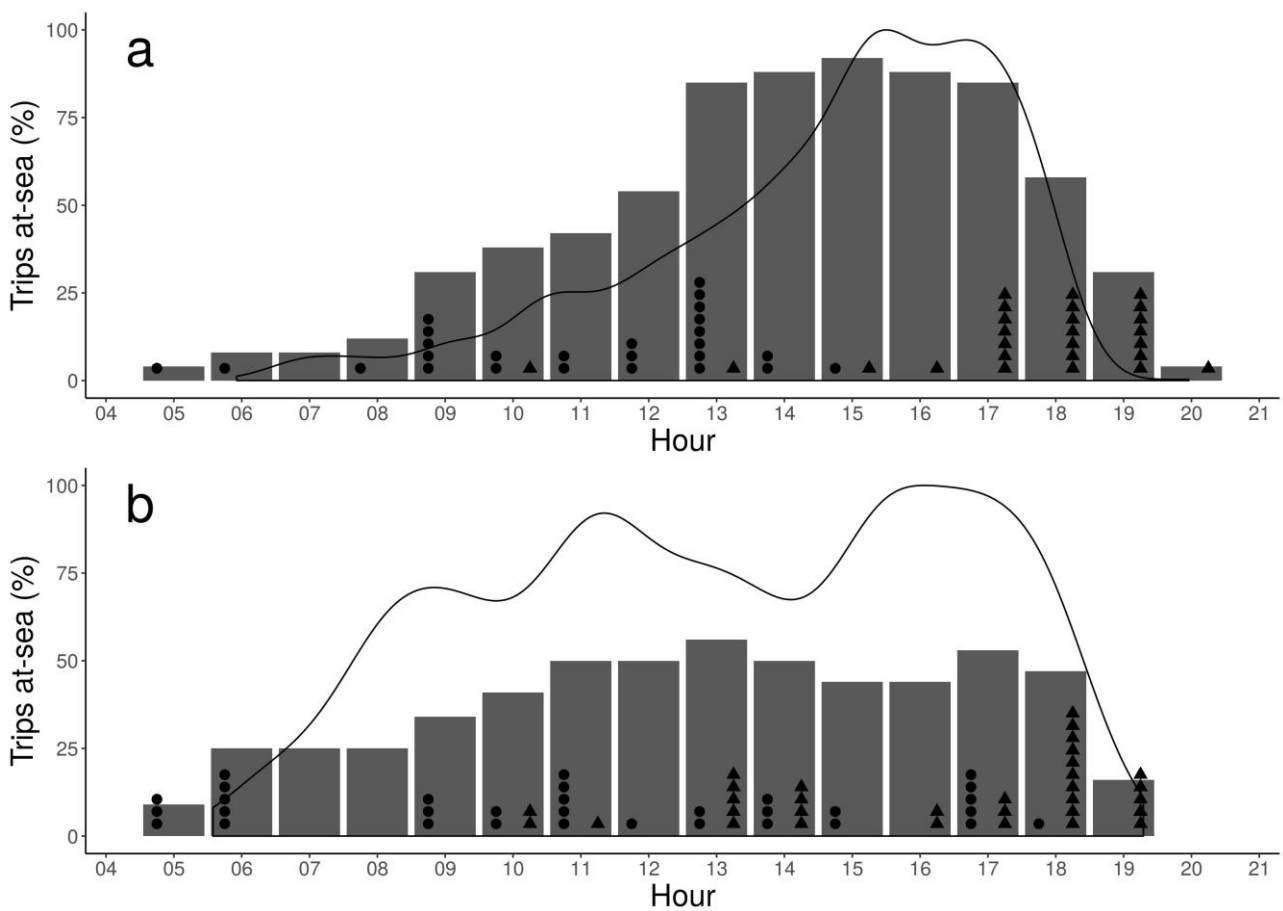


**Fig. 4.1** GPS tracking of 19 (n female = 10, n male = 9) chick-rearing Brown Boobies from Raine Island in December 2014. Foraging locations (a) and kernel density based utilization distributions (UDs) of foraging locations (b) are shown for each sex

#### 4.4.2 Daily activity budget

Boobies spent a mean time on the colony of  $18.64 \pm 2.92$  hours between successive trips, both parents returned to the colony at night and males spent longer guarding the chick during the day than females, but not significantly so (Table 4.1). Boobies were active at-sea from 05:26 to 20:57 with birds departing and returning to the colony throughout the day (Fig. 4.2). On average, sexes departed the colony at the same time (females,  $11.12 \pm 2.53$  hours, males  $11.25 \pm 4.18$  hours; LM,  $F = 0.021$ , d.f. = 1,  $p = 0.886$ ). However, female departure was concentrated in the morning (Fig. 4.2a) whereas male departure spread throughout the day (Fig. 4.2b). Females returned to the colony at a mean time of  $17.38 \pm 2.10$  hours, whereas males returned significantly earlier at a mean time of  $15.94 \pm 2.82$  hours (LM,  $F = 4.73$ , d.f. = 1,  $p = 0.034$ ). The mean percentage of female boobies at-sea during the morning ( $24.63 \pm 18.98$  %), was significantly lower than

during the afternoon ( $66.38 \pm 32.73$  %; GLM,  $F = 2.54$ , d.f. = 1,  $p = 0.135$ ; Fig. 4.2a). The mean percentage of male boobies at-sea was no different during the morning ( $32.38 \pm 14.18$  %) or afternoon ( $44.29 \pm 13.25$  %; GLM,  $F = 2.54$ , d.f. = 1,  $p = 0.135$ ; Fig. 4.2b). The average number of female booby foraging locations during the morning ( $85 \pm 74$ ) was significantly lower than during the afternoon ( $338 \pm 230$ ; LM,  $F = 8.75$ , d.f. = 1,  $p = 0.011$ ). The average number of male booby foraging locations did not differ during the morning ( $207 \pm 115$ ) or afternoon ( $244 \pm 136$ ; LM,  $F = 0.32$ , d.f. = 1,  $p = 0.578$ ).



**Fig. 4.2** Daily activity data for female (a) and male (b) chick-rearing Brown Boobies from Raine Island in December 2014. The histogram gives the percent of Booby foraging trips (female  $n=26$ , male  $n=32$ ) at-sea in each hour, the black line is a density plot of time-stamped foraging locations from active Booby trips, scaled from 0-100. The black circles are the number of foraging trips departing and black triangles the number of foraging trips returning within each hour

#### 4.4.3 Diet composition

A total of 19 regurgitations were collected ( $n = 9$  females,  $n = 8$  males,  $n = 2$  sex unknown) with a mean mass of  $96.20 \pm 13.80$  g. Of 134 individual prey items, 127 were identifiable and were comprised of four species of fish, flying fish *Cypselurus* spp., Blue Sprat *Spratelloides robustus*, Smooth belly Sardine *Amblygaster leiogaster* and Leatherjacket *Catherhines fronticinctus*, and one species of squid *Sthenoteuthis* spp. Only one prey species was present in 52.6% of regurgitates, 36.8% had two prey species present, and 10.5% had three species present. Flying fish was the most important prey species (most frequent and most abundant by mass -IRI%-) in the diet of boobies and females, in particular; whereas squid was the most important prey (IRI%) in the diet of males (Table 4.2). Overall, prey items had a mean weight of  $18.55 \pm 3.32$  g and a mean length of  $11.59 \pm 0.93$  cm. No differences were detected in number of prey items that individual foragers brought back to the colony (GLM,  $F = 0.01$ , d.f. = 1,  $p=0.917$ ). I observed a significant association between prey occurrence and sex, where flying fish was the most frequent (66.7%) for females, while squid and flying fish were equally frequent (75%) for males (Chi-square test,  $\chi^2=13.805$ , d.f. = 4,  $p < 0.05$ , Table 4.2). However, no differences were observed in the total mass of regurgitate by males or females (GLM,  $F = 0.0004$ , d.f. = 1,  $p=0.984$ ). Similarly, no differences were detected in weight (LM,  $F = 1.30$ , d.f. = 1,  $p=0.257$ ) and length (LM,  $F = 1.73$ , d.f. = 1  $p=0.192$ ) of prey items between sexes of birds.

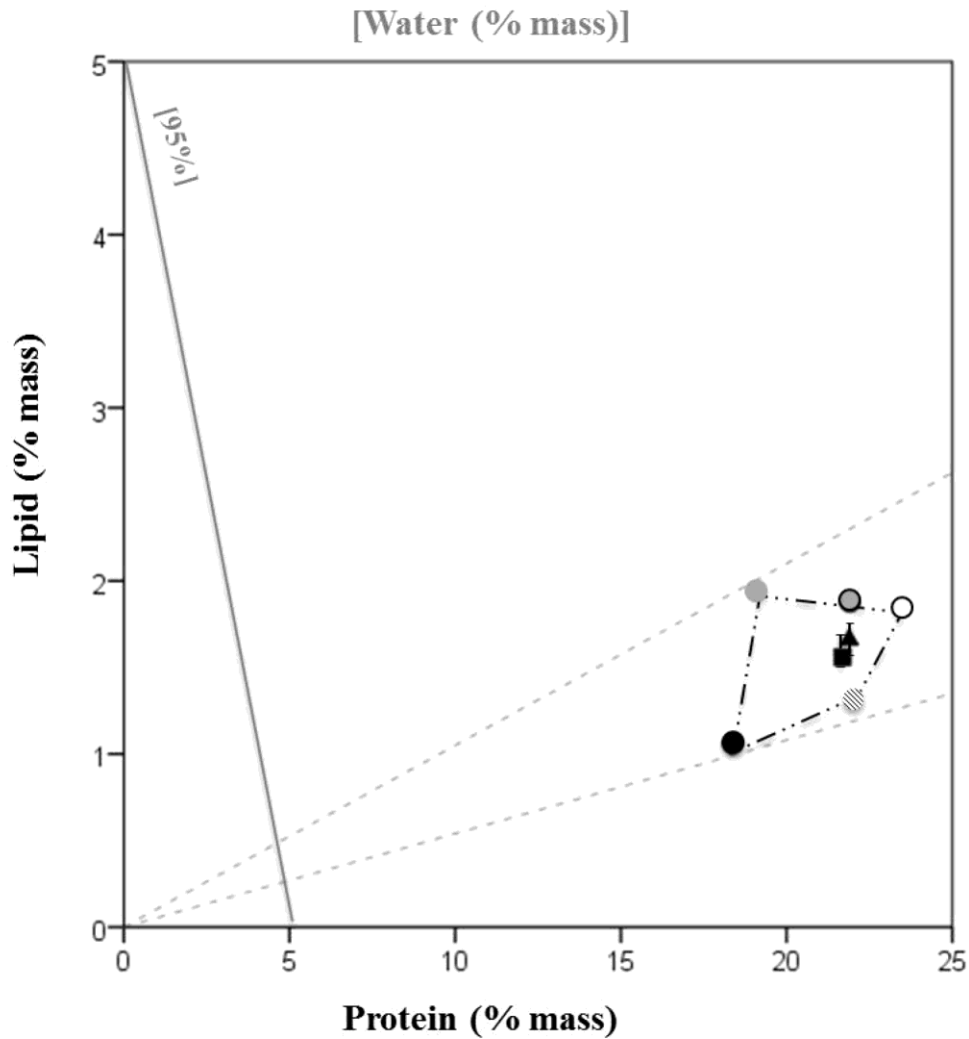
**Table 4.2** Composition of the diet of chick-rearing Brown Boobies, reflected by analysis of regurgitations collected from Raine Island in December 2014. M% = mass, N% = numerical abundance, F% = frequency of occurrence, IRI% = index of relative importance. Prey Species: S = squid *Sthenoteuthis* spp., FF = flying fish *Cypselurus* spp., BS = blue sprat *Spratelloides robustus*, SS = smooth belly sardine *Amblygaster leiogaster*, L = leatherjacket *Catherhines fronticinctus*. Regurgitations were collected from 19 birds (females = 9, males = 8, unknown sex = 2)

Prey species	Females n = 9				Males n = 8				Total birds n = 19			
	M %	N%	F%	IRI%	M %	N%	F%	IRI%	M %	N%	F%	IRI%
S	10.89	19.05	33.33	11.45	56.59	44.44	75.00	52.97	33.35	31.50	52.63	31.01
FF	47.31	50.79	66.67	75.03	41.53	46.30	75.00	46.05	47.78	49.61	73.68	65.19
BS	11.91	22.22	22.22	8.70	0.99	7.41	12.50	0.73	5.56	14.17	15.79	2.83
SS	28.82	6.35	11.11	4.48	0.00	0.00	0.00	0.00	12.46	3.15	5.26	0.75
L	1.08	1.59	11.11	0.34	0.89	1.85	12.50	0.24	0.84	1.57	10.53	0.23

#### 4.4.4 Nutritional composition of prey and diets

P, L and W wet mass proportions varied significantly between prey species (P: LM,  $F = 3.69$ , d.f. = 4,  $p < 0.05$ ; L: LM,  $F = 8.65$ , d.f. = 4,  $p < 0.05$ ; W: LM,  $F = 10.51$ , d.f. = 4,  $p < 0.001$ ). Blue Sprat had the highest mean L ( $1.9 \pm 0.43\%$ ) and highest W ( $77.35 \pm 0.91\%$ ), Smooth belly Sardine had the highest P ( $21.78 \pm 0.33\%$ ) and the lowest W ( $70.94 \pm 0.88\%$ ) and Leatherjacket had the lowest P ( $17.32 \pm 0\%$ ) and L ( $1 \pm 0\%$ ; Table 4.3). There were no significant differences in the wet mass nutritional composition of prey captured by each sex (P: LM,  $F = 0.01$ , d.f. = 1,  $p = 0.906$ ; L: LM,  $F = 0.05$ , d.f. = 1,  $p = 0.827$ ; W: LM,  $F = 0.002$ , d.f. = 1,  $p = 0.969$ ), P:L (LM,  $F = 0.20$ , d.f. = 1,  $p = 0.660$ ) and W:L (LM,  $F = 2.27$ , d.f. = 1,  $p = 0.134$ ). The RMT shows that P:L of the different prey species consumed varied from 3.7:1.0 (Blue Sprat), 8.3:1.0 (Leatherjacket), 11.6:1.0 (squid), 12.2:1.0 (Smooth belly Sardine) to 16.9:1.0 (flying fish) and provides an estimate of the Brown Booby minimal realised nutritional niche and minimal prey composition niche (Fig. 4.3). The W:L also varied considerably from 7.1:1.0 (Blue Sprat), 36.4:1.0 (Leatherjacket), 40.5:1.0 (squid), 39.7:1.0 (Smooth belly Sardine) to 58.6:1.0 (flying fish) (Fig. 4.3). No differences between sexes were

observed in the wet mass nutritional ratios (males, P:L = 13.2:1.0 and W:L = 45.4:1.0 and females, P:L= 13.2:1.0 and W:L=44.6:1.0, P:L, LM,  $F = 0.002$  d.f. = 1,  $p=0.963$  and W:L, LM,  $F = 0.011$  d.f. = 1,  $p=0.917$ , respectively) (Fig. 4.3) or in the overall dietary energy consumption (males=  $399.05 \pm 289.95$  kJ/g and females=  $362.70 \pm 257.10$  kJ/g, LM,  $F = 0.07$ , d.f. = 15,  $p=0.79$ ).



**Fig. 4.3** Right-angled mixture triangle (RMT) showing proportional data on three mixture components (here protein (P), lipid (L) and water (W)) in two dimensional graphs. To plot the nutritional compositions (P, L and W) in the RMT, each nutrient was expressed as a wet mass percentage of the sum of the three (Raubenheimer 2011). The circles represent prey species consumed by chick-rearing Brown Boobies from Raine Island in 2014. Grey filled circle = Blue Sprat *Spratelloides robustus* (19.1% P, 1.9% L, 79.0% W); Black filled circle = Leatherjacket *Catherhines fronticinctus* (18.4% P, 1.1% L, 80.6% W); Circle filled with lines = flying fish *Cypselurus* spp. (22.0% P, 1.3% L, 76.7% W); Black hollow circle = Smooth belly Sardine *Amblygaster leiogaster* (23.0% P, 1.9% L, 75.1% W); Black and grey filled circle = squid *Sthenoteuthis* spp. (21.9% P, 1.9% L, 76.2% W). Black triangle = male minimal realised nutritional niche (21.9% P, 1.7% L, 76.5% W) and black square = female minimal realised nutritional niche (21.7% P, 1.6% L, 76.8% W), both constrain within the minimal prey composition nutritional niche (black dot-dash line)

**Table 4.3** Nutritional components (% wet mass) of tropical prey species caught by Brown Boobies from Raine Island in December 2014. Values are presented as mean  $\pm$  standard deviation

Prey species	% Protein	% Lipid	% Water	% Ash
Smooth belly Sardine	21.78 $\pm$ 0.33	1.79 $\pm$ 0.11	70.94 $\pm$ 0.88	4.61 $\pm$ 0.48
<i>Amblygaster leiogaster</i> flying fish	21.01 $\pm$ 1.47	1.26 $\pm$ 0.38	73.19 $\pm$ 1.11	4.75 $\pm$ 1.07
<i>Cypselurus</i> spp. Leatherjacket	17.32 $\pm$ 0.00	1.00 $\pm$ 0.00	75.97 $\pm$ 0.00	5.00 $\pm$ 0.00
<i>Catherhines fronticinctus</i> Blue Sprat	18.7 $\pm$ 0.11	1.9 $\pm$ 0.43	77.35 $\pm$ 0.91	2.05 $\pm$ 0.37
<i>Spratelloides robustus</i> squid	21.17 $\pm$ 2.86	1.82 $\pm$ 0.62	73.65 $\pm$ 2.88	2.39 $\pm$ 0.98
<i>Sthenoteuthis</i> spp.				

#### 4.4.5 Foraging performance

Of the 19 regurgitations collected, only six were from birds carrying GPS data loggers. Therefore, these samples were used to establish foraging performance in relation to the nutritional intake (Table 4.4). No significant differences in the costs of nutrient gains (wet mass P, L, W) or in P:L or W:L, in relation to the TFP, FTD, and FT, were observed between sexes or individual birds (Table 4.5).

**Table 4.4** Foraging performance and nutritional intake from single foraging trips made by six Brown Boobies, while rearing chicks on Raine Island in December 2014. MDC = Maximum distance from colony, TFP = total foraging path FTD = foraging trip duration, FT = foraging time, TT = transiting time, RT = resting time, protein = P, lipid = L, water = W, protein-to-lipid ratio = P:L, and water-to-lipid ratio = W:L

Bird	Sex	MDC (km)	TFP (km)	FTD (h)	FT (h)	TT (h)	RT (h)	P (g)	L (g)	W (g)	P:L	W:L
23	M	13.33	39.52	1.47	0.82	0.65	0.02	27.53	1.63	95.26	16.89	58.44
17	F	69.86	182.34	6.52	2.22	3.65	0.67	13.50	1.04	46.88	12.98	45.08
26	M	77.44	213.22	6.93	2.07	4.38	0.50	6.71	0.58	23.35	11.57	40.26
11	F	66.11	188.32	8.57	2.85	3.37	2.37	8.70	0.51	30.12	16.93	58.59
1	M	38.95	93.80	2.80	1.02	1.73	0.07	4.93	0.42	17.16	11.74	40.86
35	F	33.20	79.47	4.47	2.00	1.23	1.25	26.38	6.90	54.02	3.82	7.83



**Table 4.5** Differences in the foraging performance of single foraging trips made by six Brown Boobies, while rearing chicks on Raine Island in December 2014. Variation by bird sex and between the six individual birds is shown with mean  $\pm$  1 standard error, *F* (F-value), and *p* (p-value). For each parameter P=protein, L = lipid, W = water, P:L = protein-to-lipid ratio, W:L = water-to-lipid ratio, TFP = total foraging path, FTD = foraging trip duration, and FT = foraging time

Parameter	Female	Male	<i>F</i>	<i>p</i>	Individual Birds	<i>F</i>	<i>p</i>
P/ TFP (g/km)	0.15 $\pm$ 0.03	0.26 $\pm$ 0.22	0.0004	0.979	0.21 $\pm$ 0.11	1.341	0.311
L/ TFP (g/km)	0.03 $\pm$ 0.03	0.01 $\pm$ 0.01	0.405	0.448	0.02 $\pm$ 0.01	4.928	0.091
W/ TFP (g/km)	0.37 $\pm$ 0.16	0.90 $\pm$ 0.76	0.028	0.876	0.63 $\pm$ 0.37	0.867	0.405
P:L/ TFP (g/km)	0.07 $\pm$ 0.01	0.20 $\pm$ 0.12	1.272	0.323	0.14 $\pm$ 0.06	0.325	0.599
W:L/ TFP (g/km)	0.22 $\pm$ 0.06	0.70 $\pm$ 0.39	1.794	0.252	0.46 $\pm$ 0.21	0.715	0.445
P/ FTD (g/h)	3.00 $\pm$ 1.48	7.17 $\pm$ 5.81	0.092	0.777	5.08 $\pm$ 2.84	0.877	0.402
L/ FTD (g/h)	0.59 $\pm$ 0.48	0.45 $\pm$ 0.33	0.058	0.822	0.52 $\pm$ 0.26	3.750	0.125
W/ FTD (g/h)	7.60 $\pm$ 2.48	24.82 $\pm$ 20.08	0.257	0.639	16.21 $\pm$ 9.83	0.438	0.545
P:L/ FTD (g/h)	1.61 $\pm$ 0.38	5.79 $\pm$ 2.95	2.953	0.166	3.70 $\pm$ 1.63	0.708	0.447
W:L/ FTD (g/h)	5.17 $\pm$ 1.71	20.08 $\pm$ 10.20	2.953	0.161	12.63 $\pm$ 5.70	1.159	0.342
P/ FT (g/h)	0.07 $\pm$ 0.05	0.31 $\pm$ 0.27	0.293	0.617	0.19 $\pm$ 0.13	0.653	0.464
L/ FT (g/h)	1.37 $\pm$ 1.05	0.89 $\pm$ 0.55	0.167	0.709	1.13 $\pm$ 0.54	4.239	0.109
W/ FT (g/h)	19.57 $\pm$ 4.81	48.09 $\pm$ 34.08	0.313	0.606	33.83 $\pm$ 16.66	0.414	0.555
P:L/ FT (g/h)	4.57 $\pm$ 1.33	12.57 $\pm$ 4.37	3.514	0.134	8.57 $\pm$ 2.71	1.578	0.278
W:L/ FT (g/h)	14.92 $\pm$ 5.51	43.59 $\pm$ 15.06	3.196	0.148	29.26 $\pm$ 9.62	0.378	0.572

## 4.5 DISCUSSION

As predicted, the Brown Booby population of Raine island displays RSD and, during my study period, segregated the timing and location of foraging between sexes. However, while my prediction that male and female boobies would consume different prey items was proved correct, my expectation that this would translate into sex-specific realised nutritional niches was not observed.

Firstly, the temporal differences in foraging behavior I observed between Brown Booby sexes could be due to a division of labour (Weimerskirch et al. 2009a). The ~ one month old chicks of my sampled boobies were always guarded by at least one parent (MGRM pers. obs.), suggesting this behavior may be obligatory for reproductive success. Males spent more time than females at the nest, possibly because they are better suited to territory defense (Weimerskirch et al. 2006b; Weimerskirch et al. 2009a), or to increase opportunities for extra-pair copulations (Gilardi 1992), while females made longer foraging trips. This division of labour, which provides greater foraging opportunities for females, may also allow them to recover from oviposition costs (although this is more likely during incubation than chick-rearing; Ismar et al. 2017), or to accumulate a large food payload for the chick (Weimerskirch et al. 2009a).

Alternatively, Brown Booby pairs could temporally partition foraging to minimise the risk of kleptoparasitism (Elliott et al. 2010). The observed sexual differences in Brown Booby foraging activity mirror sexual differences in the timing of chick provisioning in Lesser Frigatebirds *Fregata ariel* at the same breeding location during the December period (Congdon and Preker 2004). Raine Island supports the largest Lesser Frigatebird colony on the GBR and chick-rearing Brown Boobies are their preferred target for piracy (Batianoff and Cornelius 2005). Therefore, to minimise the impact of kleptoparasitism on chick provisioning, male boobies may risk the piracy of meals obtained on shorter, morning trips, while females return en-mass at sunset to avoid frigatebird attacks (Cruz et al. 2013).

Finally, the observation that females forage more in the afternoon could simply be a product of spatial niche partitioning (Phillips et al. 2004), where longer transit times and late arrival at the colony are a consequence of females using more distant foraging grounds not accessed by males. Females foraged for approximately the same duration while at-sea and caught the same sized prey as males. Therefore, to sustain their larger body mass and increased flight costs relative to males, females must access areas where they capture more prey items at a faster rate than males. Although I did not observe complete spatial or temporal foraging segregation between sexes, the combination of females foraging at greater distance from the colony and more often during the afternoon may allow them to feed under reduced inter-sexual and inter-specific competition, affording higher prey availability (Ashmole and Ashmole 1967; Lewis et al. 2001; Oppel et al.

2015). This may be particularly important given the potential additional foraging competition associated with the 13 other seabird species breeding on Raine Island (Batianoff and Cornelius 2005; Pontón-Cevallos et al. 2017).

My results that males consumed more squid and females more flying fish could be explained by sexes foraging in different habitats (Cleasby et al. 2015), or at different times of day (Lewis et al. 2002). Differing spatio-temporal prey encounter rates between sexes could simply be a product of constraints imposed by niche partitioning, risk avoidance or divisions of labour. Shorter male trips, whether constrained by a higher nest attendance role or competition with females, could increase encounters with juvenile squid which are evenly distributed across lagoon, passage, reef and open ocean habitats of the GBR (Moltschaniwskyj and Doherty 1995). While longer, afternoon female trips, potentially timed to protect a greater food payload from kleptoparasitism, could increase encounters with pelagic-dwelling flying fish (Randall et al. 1997). Additionally, female foraging in late afternoon could exploit a concurrent peak in subsurface predator activity (Clua and Grosvalet 2001), making particular prey more easily captured due to facilitated foraging with predatory fish and cetaceans (Ashmole and Ashmole 1967; Spear et al. 2007).

Alternatively, prey species could be distributed homogeneously across the seascape used by Raine Island Brown Boobies, and differences in prey capture relate to morphological differences between the sexes (Zavalaga et al. 2007). Male Brown Boobies have been shown to dive more frequently than females, on account of reduced energetic costs from their smaller body size (Lewis et al. 2005), while female Blue-footed Boobies dive deeper than males due to their greater body size (Zavalaga et al. 2007). In my study, higher male diving rate is hinted at by lower at-sea resting times relative to females, and, although I did not collect data on dive depths, I speculate that body size somehow influences flying fish and squid capture. My inter-sex Brown Booby prey differences mirror inter-species differences between tropical Sulids: the largest bodied, the Masked Booby, predominantly catches flying fish, whereas the smallest bodied, the Red-footed Booby, predominantly catches squid (Blaber et al. 1995; Weimerskirch et al. 2006b; Weimerskirch et al. 2009a).

My results showed that Brown Boobies from Raine Island consumed prey that differed in their nutritional composition supporting previous suggestions that marine predators forage in a nutritionally complex environment (Machovsky-Capuska et al. 2016a, b; Denuncio et al. 2017). I have also estimated, for the first time, the minimal range of prey that contributes to the food composition niche and the minimal realised nutritional niche of the Brown Booby. My findings on the realised nutritional niches between sexes revealed no significant differences in mass or energy, and they are inconsistent with previous suggestions that males and females differ in their nutritional requirements (Lewis et al. 2002; Machovsky-Capuska et al. 2016b). However, these results could be subject to potential caveats related to my relatively small sample size and difficulties in collecting regurgitations from foragers upon arrival at the colony. The latter led to the possibility that adults had already fed a portion of their foraging gains to chicks directly influencing my estimates of the prey composition and realised nutritional niches. Such caveats likely contributed to the similarities in realised nutritional niches observed between sexes, in spite of male preference for higher lipid prey (squid) relative to females. Considering that Brown Boobies at Raine Island have a dynamic diet, dominated at different times by squid, Blue Sprat and goatfish *Mulloidides* spp. (Blaber et al. 1995), I suggest that future studies aiming to describe the prey composition and nutritional niches of Sulids should collect a large number of regurgitations over as wide temporal scale as possible. The 'snap-shot' data from regurgitations could also be complemented by stable isotope mixing models, using bird blood and prey samples, to reconstruct diet over a broader time period (Inger & Bearhop 2008).

Brown Boobies display high levels of local adaptation (Morris-Pocock et al. 2011; Nunes et al. 2016) which makes them useful for understanding connections between sex-specific foraging and size dimorphism. The size of Brown Boobies has been shown to vary with primary productivity: populations of larger birds being found in productive waters and populations of smaller birds in oligotrophic waters (Nunes et al. 2016). Despite this local adaptation, RSD was consistent across the six populations sampled with females 5.2% larger and 21.0% heavier. It seems very unlikely that consistent RSD could regulate consistent sex-specific foraging strategies across the different populations in the Nunes et al. (2016) study, given the differing geographic locations (continental shelf vs. oceanic island), and productivity regimes of sampled colonies (Weimerskirch et al. 2009b; Castillo-Guerrero et al. 2016).

As such, segregation in male and female foraging may operate independently of size-dimorphism (Lewis et al. 2002), as a flexible response to resource availability (Paiva et al. 2017). My findings of foraging niche partitioning (by location, time of day and prey type) between sexes contrast with those of Pontón-Cevallos et al. (2017), that found no evidence of inter-sexual niche partitioning in breeding Brown Boobies on Raine Island. The differences could be explained by competition pressure, as Pontón-Cevallos et al. (2017) collected samples during July when breeding effort was low, whereas my study was during December and coincided with peak summer breeding activity for Brown Boobies and the majority of Raine Island seabirds (Batianoff and Cornelius 2005). By modifying their foraging behaviour (such as partitioning by sex), Brown Boobies could offset higher competition for resources at times of peak breeding (Lewis et al. 2001; Opper et al. 2015). Being able to flexibly partition foraging niche by sex in response to poor ocean conditions (Paiva et al. 2017), could also assist Brown Boobies to overcome periodic environmental variability (Castillo-Guerrero et al. 2016). This plasticity in the Brown Booby foraging strategy likely explains the disparity between various sex-specific foraging studies across the species range.

#### **4.5.1 Conclusion**

In conclusion my study found evidence for multiple drivers of sex-specific foraging in the Brown Booby population at Raine Island. My exploration of nutritional segregation between sexes, although inconclusive, provides a stepping-stone towards understanding the nutritional requirements for this species and warrants further investigation. I suggest that a combination of a division of labour, risk partitioning and competition likely drives sexual segregation in this population. More widely, RSD likely prescribes different breeding roles in the Brown Booby (larger female can deliver larger meals) but is maintained in the species as a mechanism to overcome resource variability. By being different sizes, male and female Brown Boobies have different mechanical foraging advantages and are thus able to partition more easily during reduced resource conditions. The oligotrophic waters and peak breeding season of Raine Island in December exemplify such conditions and my observed sex-specific partitioning of foraging niche (by location, time of day and prey type) demonstrated the Brown Boobies' response.

## **CHAPTER 5: GENERAL DISCUSSION**

### **5.1 SUMMARY**

In this thesis I investigated three aspects of tropical seabird foraging ecology that potentially drive intra-species foraging niche specialisation, and observed specialisation at several levels of resolution.

Firstly, I found inter-population niche specialisation in Wedge-tailed Shearwaters was driven by colony-specific access to different foraging resources. Patterns of resource availability at each colony were in-turn related to differences in near-colony primary productivity and differential interactions with sub-surface predators such as tuna. Secondly, I found that divergence in the foraging resources used by chick and adult Wedge-tailed Shearwaters was mediated by local adaptation and flexibility in adult foraging strategies, also linked to colony-specific patterns of foraging resource availability. Finally, I found sex-specific niche specialisation in Brown Boobies was likely driven by a combination of previously identified factors, but not convincingly by sex-specific nutritional demands.

Each of these findings has important implications for understanding the evolution of tropical seabird foraging ecology, and in this chapter I provide a comprehensive knowledge update. Additionally, the findings of chapters Two to Four provide information that is important for regional seabird conservation. To translate my applied ecological findings into management actions I: 1) summarise the breadth of resources required to support the specific population and sub-population groups of tropical seabirds from this study; 2) assess current regional management of these resource bases; and 3) suggest improvements to current management regimes.

## **5.2 TROPICAL SEABIRD THEORY**

### **5.2.1 Foraging niche specialisation in tropical seabirds**

Intra-species foraging niche specialisation appears prevalent in tropical seabirds. In the tropical species examined in this study I found divergent foraging niches between populations, between ontogenetic cohorts within populations and between sexes. This suggests that foraging niche specialisation in tropical seabirds operates over a range of scales from the community level (Catry et al. 2009a, Cherel et al. 2008, Young et al. 2010a) down to the individual level (Ceia & Ramos 2015). It is thought that niche partitioning is particularly strong in tropical seabirds as an adaptation to generally poor resource availability in tropical waters (Ashmole & Ashmole 1967, Cherel et al. 2008, Young et al. 2010a). My results demonstrating foraging niche overlap within demographic components of a sub-tropical shearwater population, as compared to niche separation within a tropical shearwater and a tropical booby population are consistent with these models suggesting that foraging constraints in tropical waters foster niche specialisation. Additionally, my findings that the degree of niche specialisation (by sex, age and colony) varies relative to resource availability, supports recent observations of flexible niche specialisation in low latitude seabirds (Castillo-Guerrero et al. 2011, Paiva et al. 2017). Such dynamism suggests studies into niche specialisation in tropical seabirds need to encompass multiple years if they are to reveal the complexities of tropical seabird niche specialisation (e.g. partitioning by species, sex, age, foraging strategy, and body size; Spear et al. 2007).

### **5.2.2 At-distance foraging**

In Chapter Two I investigated local adaptation in Wedge-tailed Shearwaters by determining how the principal foraging strategy of populations from Heron and Lord Howe islands is shaped by local resource availability and reliability. My results that shearwaters in tropical waters are constrained to using a dual-foraging strategy, but that conspecifics in sub-tropical waters often adopt a unimodal foraging strategy are consistent with literature suggesting that tropical seabirds display local adaptation through divergent foraging strategies (Peck et al. 2004, Mendez et al. 2013) and that resources are generally less abundant in tropical waters than at higher latitudes (Longhurst & Pauly 1987). However, I found that dual-foraging in the tropical

population, and at times the sub-tropical population, was underpinned by an apparently reliable and predictable at-distant foraging areas in oligotrophic pelagic tropical waters. This challenges current theory that tropical resources are always patchily distributed, unreliable and difficult to locate (Ainley & Boekelheide 1983, Ballance & Pitman 1999, Weimerskirch 2007). It also suggests that the temperate model of dual-foraging, where at-distance, long-trip destinations are sites of high primary productivity, may have limited transferability to the tropics. My finding that pelagic tropical waters, which make up a large proportion of global oceans (Longhurst & Pauly 1987), can be stable and predictable enough to support dual-foraging in multiple seabird populations, indicates that dual-foraging could be more widespread than previously thought among breeding seabirds (Welcker et al. 2012, Tyson et al. 2017). If this is the case, then the conservation and management of many under and un-studied tropical pelagic foraging seabird populations needs to consider a much wider potential pool of essential resources which may be in excess of 1000 km from the colony, as shown for procellariiforms in this study. The pivotal role of at-distance sites for allowing dual-foraging adult birds to regain condition means that failure to identify and protect them could have significant regional impacts for tropical seabird breeding viability.

### **5.2.3 Facilitated foraging**

In Chapter Three I investigated whether Wedge-tailed Shearwater foraging behaviour varied relative to colony-specific levels of primary productivity and access to facilitated foraging opportunities with tuna. My results that facilitated foraging was consistently important for shearwaters in tropical waters but only periodically important for conspecifics in sub-tropical waters, adds significant weight to long-standing hypotheses suggesting a higher reliance on facilitated foraging in tropical seabirds (Ainley & Boekelheide 1983, Ballance & Pitman 1999, Spear et al. 2007). However, by using modelled tuna distributions and tracking data, my study is the first to quantify population-level reliance on facilitated foraging and so truly test this hypothesis. I was able to do this at broad scales, showing that shearwaters have an *a priori* expectation of where to find tuna; and at fine scales, showing that shearwaters are more likely to forage in locations of higher tuna biomass. Again these are novel results, afforded by the study design. My results also allowed for deeper understanding of the mechanics of the facilitated foraging relationship in the Coral/Tasman Sea region, finding Skipjack Tuna the most important facilitated foraging commensal, which



is consistent with numerous other studies (Au & Pitman 1986, Jaquemet et al. 2004, Hebshi et al. 2008). In addition, I found that adult Yellowfin Tuna were only intermittently important for facilitated foraging, contrary to other studies (Au & Pitman 1986, Catry 2009), and that adult Bigeye Tuna did not facilitate shearwater foraging. Finally, by modelling oceanography, micronekton, tuna and shearwaters, my study adds another level of support for the importance of dynamic ocean features such as fronts and eddies as phenomena that aggregate predators and prey in tropical oceans (Spear et al. 2001, Hyrenbach et al. 2006, Weimerskirch et al. 2010, McDuie & Congdon 2016).

#### **5.2.4 Sex-specific nutrition**

In Chapter Four I investigated whether sex-specific foraging in the Brown Booby is driven by divergent nutritional demands between sexes. My conclusion that multiple drivers (division of labour, risk partitioning and competition) are likely responsible for sex-specific foraging in the Raine Island Brown Booby population offers insight into the disparity of previous results on the species (e.g. Gilardi 1992, Lewis et al. 2005, Weimerskirch et al. 2009b, Soanes et al. 2015). The colony-specific nature of my proposed drivers and the known high levels of local adaptation in the Brown Booby (Nunes et al. 2017) implies that different populations forage differently and partition resources between sexes differently, even when nearby (Castillo-Guerrero et al. 2016). Another layer of complexity in this story is that Brown Boobies appear to flexibly partition foraging between sexes in response to environmental variability (Castillo-Guerrero et al. 2011). As such, my inconclusive exploration of nutritional segregation between sexes could have been a product of the particular conditions at Raine Island in December 2014. Indeed, a study by Pontón-Cevallos et al. (2017) conducted just six months earlier found no evidence of sex-specific foraging at all. There are sound theoretical arguments for sex-specific nutritional demands (e.g. Lewis et al. 2002) and one supporting study of divergent sex-specific nutritional niches from a temperate Sulid (Machovsky-Capuska et al. 2016b). Therefore, several questions remain: 1) how widespread is this phenomenon in seabird species generally; 2) does it manifest more prominently in certain environments; and 3) does it only manifest at certain times e.g. pre-laying exodus? Nonetheless, nutritional data are a useful tool for understanding foraging ecology. The nutritional niche I present for the Brown Booby is the first to be estimated for a tropical seabird and allows investigation of fine-scale foraging goals e.g. if prey are targeted for their specific nutritional composition

(Raubenheimer et al. 2015). This offers an interesting new avenue to explore dietary specialisation in species, like the Brown Booby, that are considered dietary generalists (Blaber et al. 1995).

### **5.3 RESOURCE BASE IDENTIFICATION**

Identifying persistent patterns of resource utilisation within and between seabird populations as well as the environmental triggers that cause shifts in resource use is a crucial step in developing effective long-term conservation and management strategies. Seabird population-level resource use can be flexible, foraging niches becoming more specialised in times of resource scarcity and overlapping to a greater degree when resources are abundant (Castillo-Guerrero & Mellink 2011, Paiva et al. 2017). For populations that exhibit flexible patterns of resource use it is more pragmatic that management protects the most consistently used, or primary resource base. By contrast, management of populations where niche specialisation persists over time should focus on protecting the specific resources used by specialist subgroups (Durrel 2000). As such each niche specialist group in my study can be managed using a resource base that is either specific to the group in the case of persistent specialists, or within that of the wider population in the case on non-persistent specialists (Table 5.1).

#### **5.3.1 Far Northern GBR resource base**

The Far Northern GBR resource base was a consistently used resource base used by the Raine Island Brown Booby population while rearing chicks. The persistence of niche specialisation in the Raine Island Brown Booby population was difficult to assess based on my single season of data. However, other studies have shown the population does not always partitioning foraging niche between sexes (Pontón-Cevallos et al. 2017). This suggests the population has a flexible foraging niche indicating the sex-specific resource bases I observed are not generally persistent and should be managed as a combined population unit.

#### **5.3.2 Southern GBR resource base**

The Southern GBR resource base was 'specific' to Wedge-tailed Shearwater chicks from the Heron Island population. This Wedge-tailed Shearwater population consistently adopted a dual-foraging strategy resulting

in persistent foraging niche divergence between adults and chicks. As a result chicks were consistently sustained by this resource base and year-to-year variations in chick survivorship and colony productivity were directly linked to fluctuations in these near-colony resources.

### **5.3.3 Central Coral Sea resource base**

During chick-rearing the Central Coral Sea resource base was 'specific' to adult Wedge-tailed Shearwaters from the Heron Island population. The aforementioned persistent foraging niche divergence between adults and chicks from Heron Island means that adult Wedge-tailed shearwaters from Heron Island were consistently sustained by this resource base, and without it breeding on Heron Island would not be viable. Additionally, conspecific adults from Lord Howe Island also shared this resource base when adopting a dual-foraging strategy.

### **5.3.4 Northern Tasman Sea resource base**

The Northern Tasman Sea resource base was a general resource base used by the Lord Howe Island Wedge-tailed Shearwater population while rearing chicks. Foraging niche specialisation between adults and chicks in this population was flexible, dependent on foraging strategy responses to near-colony prey availability, which are driven by dynamic oceanography. In years when the population adopted unimodal foraging both adults and chicks shared this resource base, where as in years when dual-foraging was adopted only chicks were sustained by this resource base.

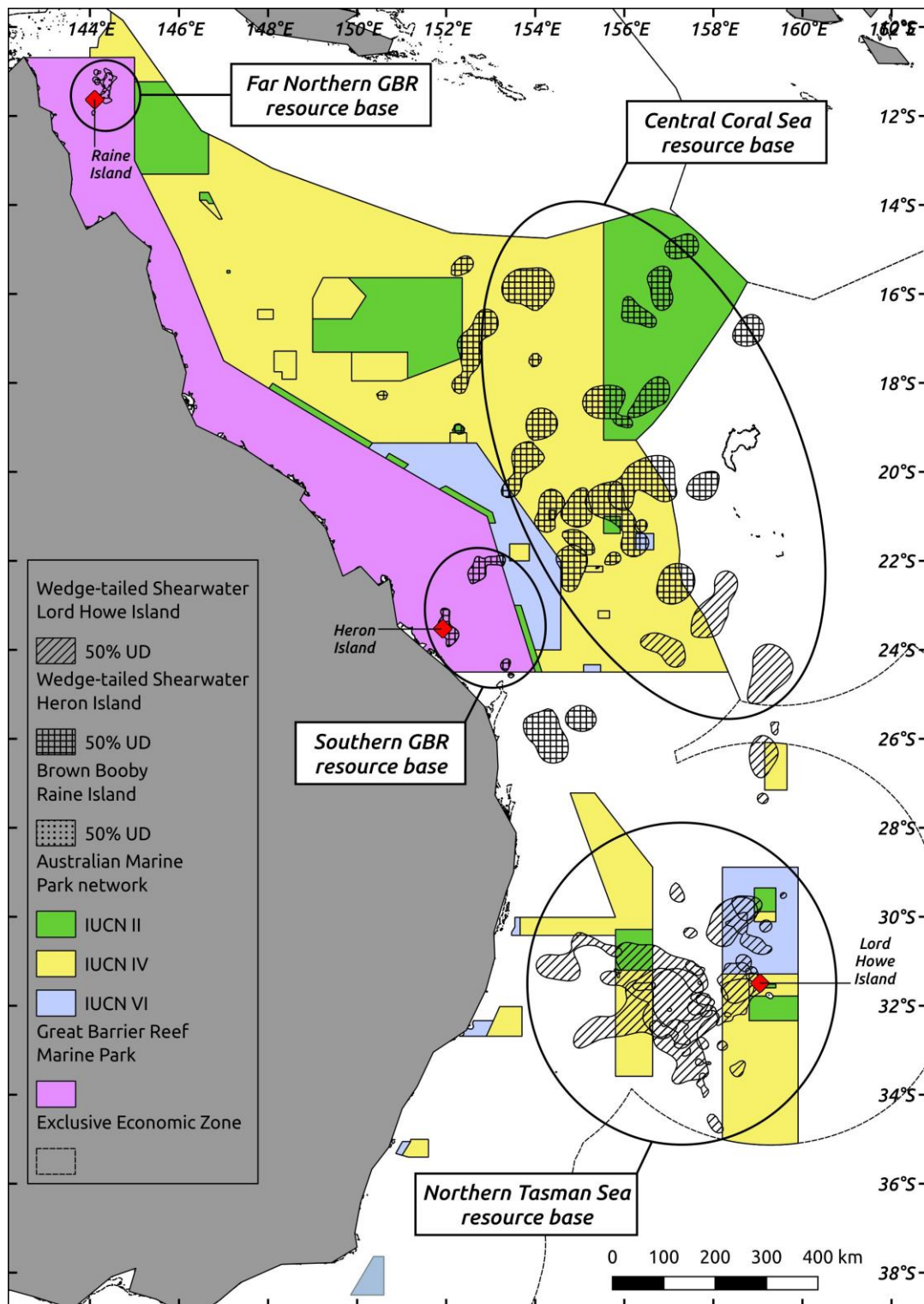
**Table 5.1** Resource bases identified from this study, the population/sub-population groups they support and current protective measures. LHIMP = Lord Howe Island Marine Park, GBRMP = Great Barrier Reef Marine Park

Resource base name	Supported species & population	Supported niche specialist group	Resource base description	Current management	Advised management
Far Northern GBR	Brown Booby, Raine Island	Whole population	Reef edge and pelagic Coral Sea areas supporting squid and flying fish	GBRMP zoning	Foraging radius extension from 45 to 113 km
Southern GBR	Wedge-tailed Shearwater, Heron Island	Shearwater chicks	Tropical reef and shelf waters of the southern Great Barrier Reef	GBRMP zoning	Reduction of General Use zones in southern GBRMP
Central Coral Sea	Wedge-tailed Shearwater, Heron Island (& periodically Lord Howe Island)	Adult shearwaters	Pelagic, oligotrophic tropical waters with high tuna biomass in the central Coral Sea	None	Upgrade Australian Marine Park designations, fill zoning gaps and regulate tuna fishery, particularly purse-seine
Northern Tasman	Wedge-tailed Shearwater, Lord Howe Island	Whole population	Productive but dynamic sub-tropical waters west of Lord Howe Island	None, LHIMP	Upgrade Australian Marine Park designations and fill zoning gaps with 223 km foraging radius

## 5.4 CURRENT MANAGEMENT AND SUGGESTED IMPROVEMENTS FOR RESOURCE BASES

Significant advances in tracking technology and techniques for understanding seabird resource use (e.g. stable isotopes) has led to an increasing number of seabird studies that identify at-sea foraging areas in need of protection (e.g. Lavers et al. 2014, Scales et al. 2015, McDuie & Congdon 2016). The global network of marine Important Bird Areas (IBAs) identified by Birdlife International demonstrates the quantity of data available for defining priority areas for at-sea protection (Lascelles et al. 2016). An important step in translating marine IBAs, or any other identified seabird area, from a 'paper park' into formalised protection is to integrate them into wider marine spatial planning. Recently, published guidelines on how to do this give seabird sites traction during spatial conservation prioritization and therefore greater influence in marine protected area networks (McGowan et al. 2017). In eastern Australia the unique large-scale marine protected

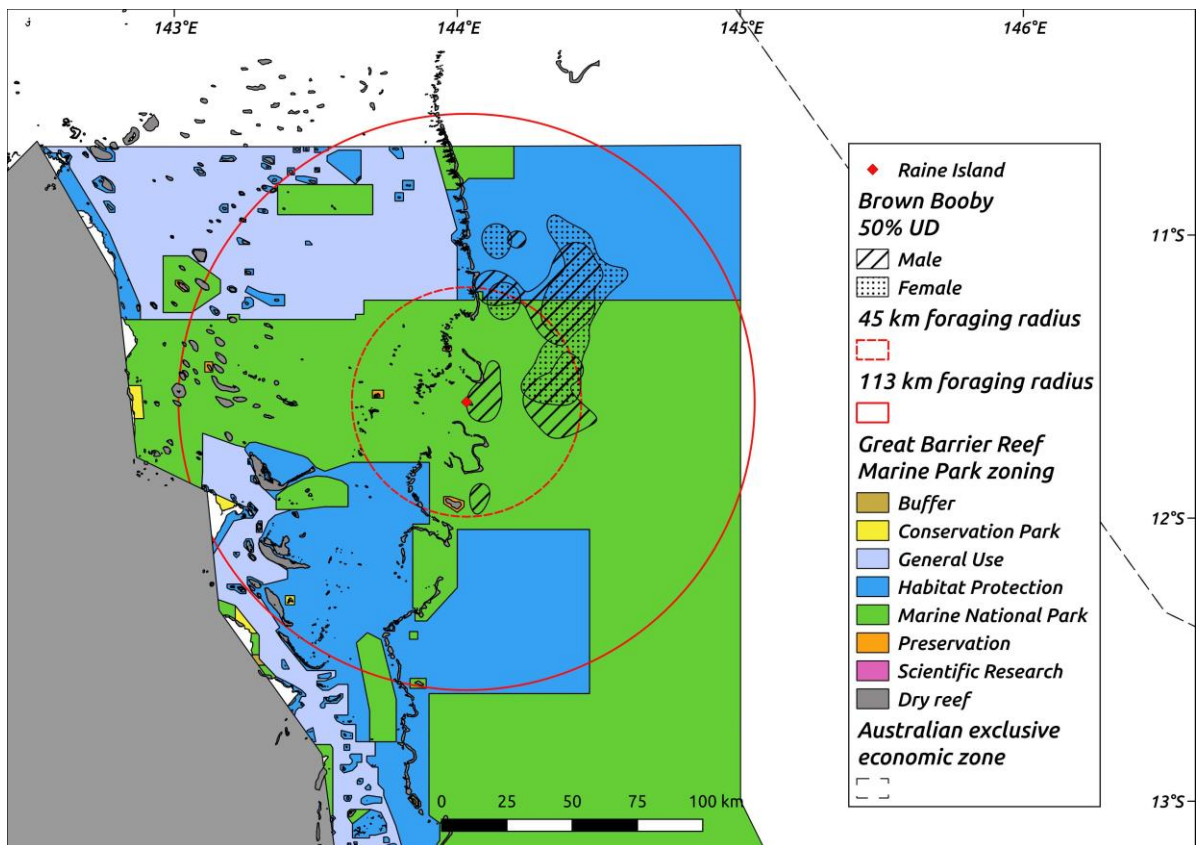
area networks of the Great Barrier Reef Marine Park (GBRMP) and Australian Marine Park Network provide a framework for allowing seabird at-sea sites to gain formal protection and management. From my study two distinct and important resource bases are located within the management boundaries of the GBRMP (the Far Northern GBR and Southern GBR resource bases), where as the Northern Tasman Sea and Central Coral Sea resource bases are currently under the management of the Australian Marine Park Network and have no official protected area status (Fig. 5.1)



**Fig. 5.1** Foraging areas shown by kernel density 50% Utilization Distributions (UDs) that identify different resource bases from this study overlaying different Australian Marine Park zoning from 2017

#### **5.4.1 Far Northern GBR resource base**

The identified Far Northern GBR resource base that sustains the Raine Island Brown Booby population while rearing chicks is almost completely within the bounds of the GBRMP (Fig. 5.2). As such it benefits from the careful zoning that has designated 33% of the park area within no-take zones (Fernandes et al. 2005). However, the resource base straddles a Marine National Park Zone in the south and Habitat Protection Zone in the north, which provide different protective measures (see Appendix 2). The former is a no-take, high protection zone, whereas the latter allows commercial and recreational line and net fishing in addition to other extractive activities (e.g. lobster and sea cucumber harvesting). As such when foraging in the northern half of this resource base Brown Boobies could suffer from competition for food with fisheries (Bertrand et al. 2012). My finding that the foraging niche of female Brown Boobies is specialised on more distant resources than males, means females are more likely to forage in the Habitat Protection Zone. Thus, a combination of niche specialisation and current zoning could put the female demographic cohort of the Raine Island Brown Booby population at greater risk than the male cohort.



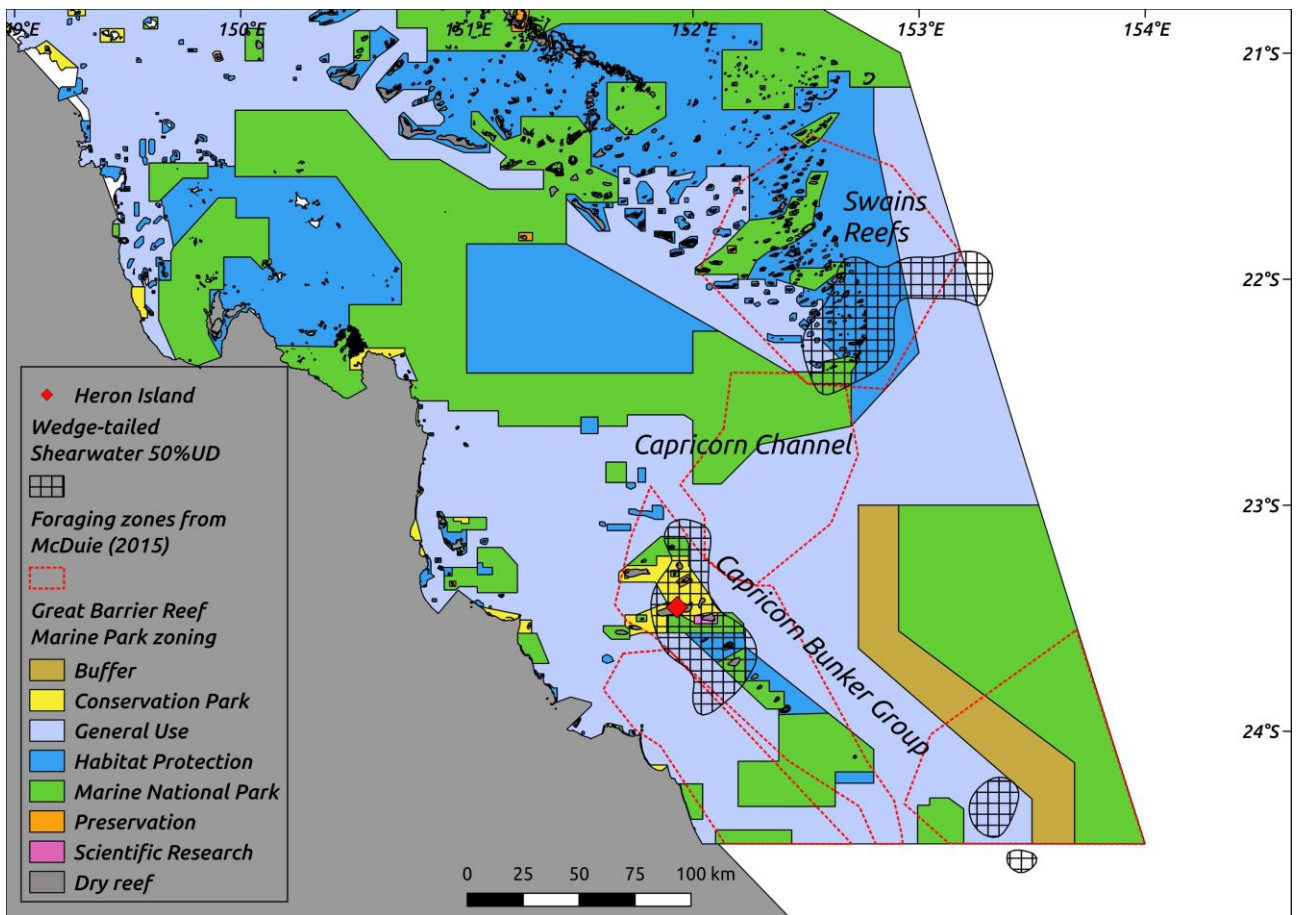
**Fig. 5.2** Brown Booby foraging distribution, shown by kernel density 50% Utilization Distribution (UD), and foraging ranges from the Raine Island colony situated in the far north of the Great Barrier Reef Marine Park

The identification of the Far Northern GBR resource base within the bounds of GBRMP and at-least half within a Marine National Park Zone means that the Raine Island Brown Booby population's food supply (based on my study) is relatively well protected. However, there is dietary evidence that Raine Island Brown Boobies are flexible in their use of resources, in some years targeting reef resources rather than pelagic resources (Blaber et al. 1995). As such pragmatic management of at-sea resources for this population should focus on all resources that the population could access, using the 'foraging radius' approach advocated for identifying marine IBAs (Birdlife International 2010, Thaxter et al. 2012, Soanes et al. 2016). The only data previously available from a GBR Brown Booby population that could inform such a radius was a maximum foraging distance of 45 km from a colony on the Swains Reefs (Bunce 2015). My finding that Raine Island Brown Boobies can forage up to 113 km from the colony means that management of Brown Boobies within the GBRMP needs to consider a much greater range of available resources than previously thought.



#### **5.4.2 Southern GBR resource base**

The Southern GBR resource base that sustains Wedge-tailed Shearwater chicks at Heron Island is primarily within the bounds of the GBRMP (Fig. 5.3). My results on where shearwaters access these resources are consistent with those identified by (McDuie 2015). These resources are located across the complete range of management zone types within the GBRMP. Near-colony resources around the Capricorn Bunker reefs are well protected with no-take, Marine National Park and restrictive Conservation Park zones. Resources from the Swains Reefs receive a lesser degree of protection falling under the Habitat Protection Zone, but still feature areas of Marine National Park zone. However, resources from inshore areas and the Capricorn channel fall under the remit of the General Use Zone, in addition to line and net fisheries this zone also allows trawling and un-permitted shipping activities. As such these resources could be associated with higher risks e.g. shipping oil pollution (Wiese & Robertson 2004). Inshore areas of the Southern GBR resource base are also impacted by terrestrial river runoff. Although the nutrients in freshwater plumes may promote primary production (Weeks et al. 2015), the sediment, herbicide loads and other potential pollutants such as plastics carried from nearby agricultural or urban areas can impact reef ecosystem functioning (Brodie et al. 2012) potentially having long-term impacts on shearwater resource availability.



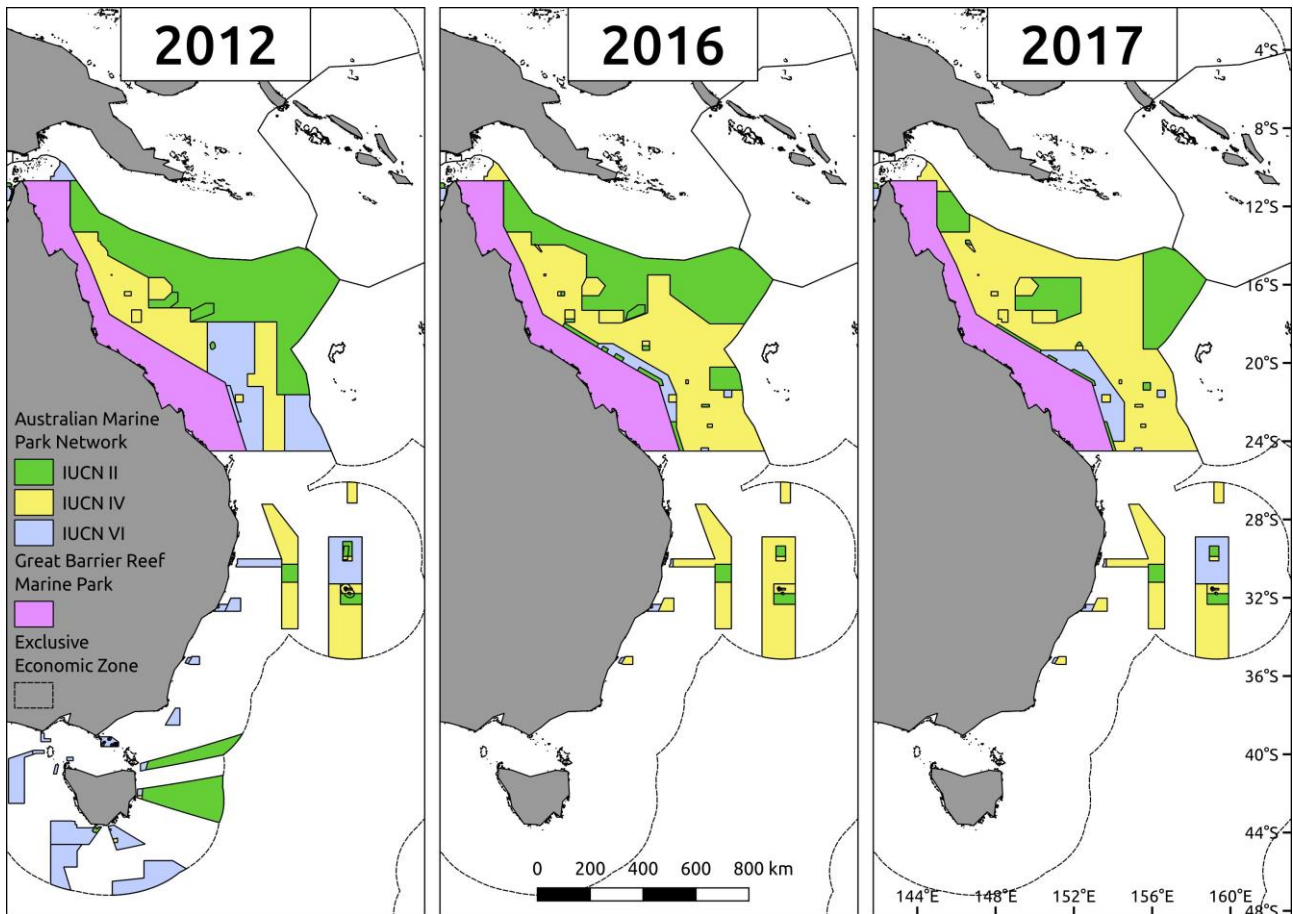
**Fig. 5.3** Heron Island Wedge-tailed Shearwater foraging distribution, shown by kernel density 50% Utilization Distribution (UD), and foraging zones identified by McDuie (2015) in the southern Great Barrier Reef Marine Park

My identification of the Southern GBR resource base primarily within the bounds of GBRMP, and managed in several areas by high-protection zoning, means that the resources which sustain chicks on Heron Island are relatively well protected. The agreement between the foraging regions used by shearwaters in this study and those used over the previous three years (McDuie et al. 2015) suggest that specific areas within the broader resource base identified are consistently targeted for chick-rearing resources. The dependence on these areas provides tangible data for input into re-zoning. This is particularly the case for the southern Swains Reefs, as this area could be upgraded from its current Habitat Protection Zone status. A final consideration is that of trawling activities, which could provide a food source for Wedge-tailed Shearwaters in the area through discards. Changes to trawling activities could impact shearwater populations and likely other seabird

populations (Capricorn Bunker Reefs hold 97% of Black Noddies *Anous minutus* on the GBR; Hulsman et al. 1997) as has been seen elsewhere in the GBR (Blaber et al. 1995).

#### **5.4.3 Central Coral Sea resource base**

The Central Coral Sea resource base that sustains adult Wedge-tailed Shearwaters from Heron Island and periodically sustains adult conspecifics from Lord Howe Island is located primarily within the Australian exclusive economic zone (EEZ) and has no current protection (Fig. 5.4). This region falls under the management jurisdiction of the Australian Marine Park Network. The process of zoning this network started in 2012 and due to government changes is still under way; meaning that currently there is no protection of seabird foraging resources across large expanses of the Australian EEZ. The zoning process has become increasingly politicised with successive drafts reducing areas of highest protection in line with requests from the industrial and business sectors, primarily fisheries. In the latest draft zoning plan (released in July 2017) the government proposed a 46% reduction in the total area of high-level no-take protection zones originally identified in 2012, prompting worry among marine scientists (Ocean Science Council of Australia 2017). This was particularly evident in the Coral Sea, which has had proposed no-take areas (Marine National Park Zone IUCN II) replaced with partial protection areas (Habitat Protection Zone IUCN IV) (Fig. 5.4) (Pressey et al. 2016). This will, in the government's own words, “increase the total area of the reserves open to fishing from 64 % to 80 %” (Frydenberg 2017). The large expanse of Habitat Protection Zone in the current draft plan allows commercial pelagic longlining, mid-water trawling and purse-seining (Australian Marine Parks 2017). These fisheries have previously overfished certain tuna stocks (Griffiths et al. 2010) and have the capacity to alter the pelagic ecosystem of the region (Young et al. 2009). As such they can threaten Wedge-tailed Shearwaters and other seabirds that are reliant on tuna for facilitated foraging through indirect suppression of forage fish availability (Au & Pitman 1986, Le Corre & Jaquemet 2005).



**Fig. 5.4** Changes to the Australian Marine Park Network zoning between 2012 and 2017

Under the most recent draft zoning plan only a small area of the Central Coral Sea resource base intersects with no-take Marine National Park zones. Although the central Coral Sea resource base covers a large area, multiple years of tracking data confirm that the area is consistently used by Wedge-tailed Shearwaters. As such, static marine boundaries offer an appropriate management avenue. My results suggest that re-zoning of the latest draft Marine National Parks network is needed to include protection for the Central Coral Sea resource base. To achieve this I suggest a new Marine National Park Zone between 18° S and 23° S that interfaces with current zoning (Fig. 5.1). This new designation would protect important seamount habitat that is known to aggregate subsurface predators in the region (Young et al. 2011). However, because of this seamounts are targeted and valued by fisheries (Young et al. 2009, Wilson et al. 2010), their influence has kept seamount habitat between 18° S and 23° S open to all fishing types throughout the Australian Marine Park process (Fig. 5.4). In order to balance economic fishery goals with seabird conservation goals, which

appear incompatible in resource competition cases such as these, seabird and fisheries management need to be coordinated and developed together using detailed ecological information. This study has shown the importance of smaller, surface-dwelling tunas such as Skipjack Tuna for the regional facilitated foraging relationship. As such management of the zone between 18° S and 23° S could be developed through seabird and fisheries collaborative management programs e.g. standard quotas for longlining for larger tunas but tighter regulation of purse-seining targeting Skipjack.

#### **5.4.4 Northern Tasman Sea resource base**

The Northern Tasman Sea resource base used by the Wedge-tailed Shearwater population at Lord Howe Island falls within the Australian exclusive economic zone (EEZ) and has no current protected status (Fig. 5.1). As with the Central Coral Sea resource base, the Northern Tasman Sea resource base falls under the management jurisdiction of the Australian Marine Park Network and has undergone the same lengthy review process. The two differences between the Tasman Sea and Coral Sea regions are: 1) that there hasn't been many major reductions in no-take areas between 2012 and 2017 in the Tasman Sea; and 2) there is a much lower coverage of zoning of any protection class in the Tasman Sea. This means that at present the Northern Tasman Sea resource base is the poorest protected resource base identified in this study, with large areas not intersecting with any zoning at all.

I have shown the importance of the Northern Tasman Sea resource base for sustaining both adult and chick cohorts of the Lord Howe Island Wedge-tailed Shearwater population. However, the dynamism of local oceanography associated with this resource base means that different areas of the Tasman Sea are used in different years. This is problematic for static protected area management (Lascelles et al. 2016). One approach for such a situation is the use of dynamic MPAs, where protection can be rotated between a subset of regions within the larger area (Game et al. 2009). Marine Protected Areas designed around shifting oceanographic features such as fronts and eddies offer an innovative new tool for the conservation of open ocean ecosystems (Hyrenbach et al. 2000) and are a potential solution to this problem into the future. However, in the short term, applying the foraging radius approach that I suggested for the similarly dynamic Raine Island Brown Booby population would result in a conservative radius of 223 km from Lord Howe

Island. This can be refined to only the westward half of the radius as my data provides almost no evidence for Wedge-tailed Shearwaters foraging east of Lord Howe Island in three years of study. A final, more pragmatic step is to use this radius to inform a new Marine National Park Zone between 30° S and 33.5° S that links the two currently parallel Habitat Protection zones together.

## **5.5 ADDITIONAL SEABIRD BENEFITS FROM MANAGEMENT**

The resource bases identified and management areas proposed have wider benefits for regional seabird populations, boosting their significance as conservation priorities. Management of the Far Northern GBR resource base for Brown Boobies would likely benefit the 14 other seabird species that breed on Raine Island. This is particularly pressing given that Raine Island is one of the most important seabird breeding sites on the GBR, but has had a reported 70% decline in the size of the seabird rookery between 1976-2003 (Batianoff & Cornelius 2005). Both the Southern GBR and Central Coral Sea resource bases were identified using Wedge-tailed Shearwater data from Heron Island, which is a central island in the Capricorn Bunker Reefs group. Collectively, the Capricorn Bunker Reefs hold the Pacific's largest Wedge-tailed Shearwater population of 560,000 breeding pairs (Dyer et al. 2005). If this meta-population of shearwaters shares the same foraging strategy and spatial distribution as the sampled population (or even partially so; Ceia et al. 2014), then the identified resources that sustain breeding at Heron Island also sustain a vast number of Wedge-tailed Shearwaters. Again, the conservation significance of these resource bases is heightened by the apparent 40% decline in the Capricorn Bunker Wedge-tailed Shearwater population since the 1990s (Hemson 2015). The apparent importance of the Central Coral Sea resource base revealed by my study also extends beyond the chick-rearing period as Wedge-tailed Shearwaters from Heron and possibly Lord Howe Island also use this area during migration, incubation and the pre-breeding exodus (Congdon *unpub. data*). Management of the Northern Tasman Sea resource base for Wedge-tailed Shearwaters would also likely benefit Lord Howe Island's wider seabird population. Similar to Raine Island, Lord Howe Island hosts 14 breeding seabird species making it an important national and global seabird rookery (Carlile & Priddel 2013). The near-endemic Providence Petrel *Pterodroma solandri* and locally declining Flesh-footed



Shearwater *Ardenna carneipes* share similar at-sea distributions to those identified for Wedge-tailed Shearwaters in this study (Carlile *unpub. data*, Thalman et al. 2009), adding further weight for conservation of the Northern Tasman Sea resource base.

## **5.6 CONCLUSION AND FURTHER STUDY**

In summary, this study demonstrates the complexities of tropical seabird foraging ecology, and how understanding this complexity in a regional context can inform conservation management. The niche specialisation approach that I have followed throughout this study revealed strong local adaptation in tropical seabird populations, with some showing periodic variation in foraging niche. This variation between and within populations presents a challenge for identifying and protecting at-sea resources for tropical seabirds because it means results cannot be easily extrapolated between colonies, or from datasets with a small temporal window. This problem is compounded by a huge regional data gap. Within the GBR, tracking data exists for just three seabird species from three colonies (most collected or summarised in this study). These data are vital for identifying colony-specific resource bases but also for informing foraging radii that can be applied to other regional colonies, the success of this extrapolation determined by the degree of local adaptation. As such, this study forms a backbone of knowledge on the spatial distribution of tropical seabird resources in eastern Australia that can be built upon by further study of different populations. As these studies gather pace, facilitated by ever cheaper tracking technology, a regional network of seabird spatial data will be able to reveal patterns in local adaptation and trends in foraging niche variation. These data can input into the intense marine spatial prioritisation and zoning activities that define protection for the marine environment of east Australia, which currently are bypassing seabirds because of this lack of at-sea knowledge. This is plainly shown in the central Coral Sea where strong industry pressure and perhaps a receptive ear, have led to important seabird resources being zoned within areas primarily managed by fisheries. The results of studies such as this one can make a case for seabirds in zoning activities by providing: comprehensive data on spatial use; scientific rationale for resource requirements; and ecological

insight to reduce conflicts with other stakeholders. In doing so management plans and zoning can be developed to include seabird needs alongside those of other ocean users.



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## APPENDICES

**Appendix 1** Logistical regression coefficients for hi-res models of wedge-tailed shearwater probability of foraging against fine scale oceanographic and tuna covariates. The following coefficients ( $\beta$ ) and std. errors (SE) are expressed in terms of a 100 unit change: tuna covariates (100 g m<sup>-2</sup>), seamount distance (SMT) (100 km)

Colony – Year	Covariate	$\beta \pm SE$
Heron Island 2015		
	Intercept	-11.829 $\pm$ 3.764
	poly(EKM)1	0.900 $\pm$ 0.392
	poly(EKM)2	-2.000 $\pm$ 0.515
	SSTA	1.499 $\pm$ 0.275
	poly(SSHA)1	3.773 $\pm$ 1.086
	poly(SSHA)2	-3.019 $\pm$ 0.775
	SMT	-0.907 $\pm$ 0.157
	BET_MIC	0.265 $\pm$ 0.052
Lord Howe Island 2015		
	Intercept	-2.583 $\pm$ 0.416
	poly(EKM)1	1.064 $\pm$ 0.163
	poly(EKM)2	1.592 $\pm$ 0.310
	poly(SSTA)1	-0.201 $\pm$ 0.230
	poly(SSTA)2	-0.604 $\pm$ 0.143
	SKJ_ADU	0.804 $\pm$ 0.055
Lord Howe Island 2014		
	Intercept	-2.182 $\pm$ 0.859
	poly(EKM)1	-1.240 $\pm$ 0.350
	poly(EKM)2	1.454 $\pm$ 0.621
	SSTA	-0.430 $\pm$ 0.167
	SSHA	0.860 $\pm$ 0.477
	YFT_MIC	0.119 $\pm$ 0.016
	Chlorophyll- <i>a</i>	0.232 $\pm$ 0.080



**Appendix 2** Guide to accepted activities within each of the Great Barrier Reef Marine Park management zones, source: Great Barrier Reef Marine Park Authority

ACTIVITIES GUIDE (see relevant Zoning Plans and Regulations for details)	General Use Zone	Habitat Protection Zone	Conservation Park Zone	Buffer Zone	Scientific Research Zone <sup>3</sup>	Marine National Park Zone	Preservation Zone	State Zoning Only	Estuarine Conservation Zone
	Aquaculture	Permit	Permit	Permit <sup>1</sup>	X	X	X	X	State Zoning Only
Bait netting	✓	✓	✓ <sup>2</sup>	X	X	X	X	✓	
Boating, diving, photography	✓	✓	✓	✓	✓ <sup>3</sup>	✓	X	✓	
Crabbing (trapping)	✓	✓	✓ <sup>4</sup>	X	X	X	X	✓	
Harvest fishing for aquarium fish, coral and beachworm	Permit	Permit	Permit <sup>1</sup>	X	X	X	X	X	
Harvest fishing for sea cucumber, trochus, tropical rock lobster	Permit	Permit	X	X	X	X	X	X	
Limited collecting	✓ <sup>5</sup>	✓ <sup>5</sup>	✓ <sup>5</sup>	X	X	X	X	✓	
Limited spearfishing (snorkel only)	✓	✓	✓ <sup>1</sup>	X	X	X	X	✓	
Line fishing	✓ <sup>6</sup>	✓ <sup>6</sup>	✓ <sup>7</sup>	X	X	X	X	✓	
Netting (other than bait netting)	✓	✓	X	X	X	X	X	✓	
Research (other than limited impact research)	Permit	Permit	Permit	Permit	Permit	Permit	Permit	Permit	
Shipping (other than in a designated shipping area)	✓	Permit	Permit	Permit	Permit	Permit	X	Permit	
Tourism programme	Permit	Permit	Permit	Permit	Permit	Permit	X	Permit	
Traditional use of marine resources	✓ <sup>8</sup>	✓ <sup>8</sup>	✓ <sup>8</sup>	✓ <sup>8</sup>	✓ <sup>8</sup>	✓ <sup>8</sup>	X	✓ <sup>8</sup>	
Trawling	✓	X	X	X	X	X	X	X	
Trolling	✓ <sup>6</sup>	✓ <sup>6</sup>	✓ <sup>6</sup>	✓ <sup>6,9</sup>	X	X	X	✓	

**PLEASE NOTE:** This guide provides an introduction to Zoning in the Great Barrier Reef Marine Parks.

- Restrictions apply to aquaculture, spearfishing and harvest fishing for aquarium fish, beachworm and coral in the Conservation Park Zone.
- No take of bream, flathead or whiting by commercial bait netters.
- Except for One Tree Island Reef (SR-23-2010) and Australian Institute of Marine Science (SR-19-2008) which are closed to public access and shown as orange, all other Scientific Research Zones are shown as green with an orange outline.
- Limited to 4 catch apparatus per person (eg. crab pots, collapsible traps or dillies).
- By hand or hand-held implement and generally no more than 5 of a species.
- Maximum of 6 hooks attached to no more than 3 hand-held rods or handlines per person.
- Limited to 1 hook attached to 1 hand-held rod or handline per person. Only 1 dory detached from a commercial fishing vessel.
- Apart from traditional use of marine resources in accordance with s.211 of the *Native Title Act 1993*, an accredited Traditional Use of Marine Resources Agreement or permit is required.
- Pelagic species only. Seasonal Closures apply to some Buffer Zones.

Detailed information is contained in the *Great Barrier Reef Marine Park Zoning Plan 2003 and Regulations* and the *Marine Parks (Great Barrier Reef Coast) Zoning Plan 2004*.

- Permits are required for most other activities not listed above.
- Commonwealth owned islands in the Great Barrier Reef Marine Park are zoned "Commonwealth Islands Zone" - shown as cream.
- All Commonwealth Islands may not be shown.
- Special Management Areas may provide additional restrictions at some locations.
- The Zoning Plan does not affect the operation of s.211 of the *Native Title Act 1993*.

**ACCESS TO ALL ZONES IS PERMITTED IN AN EMERGENCY.**