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CRITICAL FORAGING LOCATIONS AND OCEANOGRAPHIC RELATIONSHIPS FOR GREAT BARRIER REEF BREEDING SEABIRDS

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ABSTRACT

Pelagic seabirds are completely reliant upon the marine environment for all resources, but conservation strategies largely ignore critical at-sea food resources. Little is known of trophic mechanisms influencing prey availability for tropical seabirds. Until now, most studies of tropical regions focused on specific oceanographic characteristics in the marine environment, and often single species, with widely varying results. Consequently, is has been difficult to unequivocally determine the relative importance of mechanisms. Therefore, this study aimed to track a tropical Procellariiform through all life phases, to analyse multiple components simultaneously and to develop a comprehensive understanding of the linkages in tropical systems and model of tropical seabird foraging ecology.

Key foraging areas for wedge-tailed shearwaters breeding in the Australian Great Barrier Reef (GBR), and related oceanographic characteristics, were identified and mapped at three spatial scales. GBR breeding shearwaters are the first tropical Procellariiform to have been found to conduct a lengthy trans-equatorial migration, moving to a single core-use non-breeding foraging ground near Micronesia, ~6000km from the breeding colony. This area was characterised by low primary productivity ([Chl *a*]), low wind speeds and positive sea level anomalies (SLAs). A combination of characteristics suggest that foraging occurs at the peripheries of large to mesoscale eddies where fronts likely aggregate prey. The overlap of shearwater foraging activity with the Western Central Pacific Tuna Fishery (WCPTF), and documented links between tuna and frontal systems in this region suggest that sub-surface predator activity further enhances prey availability to these non-breeding seabirds.

During breeding, shearwaters undertook long, self-provisioning trips, to reach distant foraging sites between 300km and ~1000km from the colony. Foraging areas were characterised by deep water near areas of steep bathymetric change and commonly had strong associations with positive SLAs and medium current speeds. Again, these results are consistent with shearwaters foraging in convergence zones at the periphery of eddies. Contrary to expectations, foraging sites were not associated with elevated levels of primary productivity. Furthermore, identified foraging locations were not within currently managed areas of the GBR Marine Park. An overlap with tuna fishery suggests a similarly important association with sub-surface predators in this region.

Finally, short, chick-provisioning trips, were undertaken within 300km of the colony. This conclusively demonstrated the use of foraging grounds at two separate spatial scales during chick-rearing. Five separate topographically unique foraging zones were used during these short trips. All were in areas of steep bathymetric change where the activity of the 'Capricorn Eddy' generated frontal activity. A range of oceanographic parameters was shown to influence foraging activity, their relative importance differing among zones and seasons. More intense foraging was associated with rapidly changing sea-surface temperature (SST) gradients, as well as negative SST and [Chl *a*] anomalies. Combined, these results demonstrate strong links to the presence, movement and intensity of the Capricorn Eddy. An additional strong association with frontal formations where freshwater river plumes merge with the Eddy in a coastal, inshore foraging zone also highlights the previously unrealised importance of terrestrial inputs on shearwater reproductive success. This is, to my knowledge, a phenomenon not previously been seen to influence foraging pelagic seabirds in tropical regions. Therefore, resources used for chick provisioning are reliant upon two unique phenomena, the Capricorn Eddy and freshwater input.

The results in this study highlight a number of significant facts relevant to shearwater foraging ecology. First, wedge-tailed shearwaters forage at three spatial scales, implying that management and conservation priorities must be considered separately for each location. Second, mesoscale oceanographic phenomena, primarily eddies, their peripheries and convergence zones, are broadly important to shearwaters, influencing foraging activity at all spatial scales. Third, elevated [Chl *a*] is not an important influence in general, which directly contrasts with most previous seabird studies. Fourth, SSTs are generally important, as expected, and specific, narrow temperature ranges demonstrate links with foraging areas. Fifth, that sub-surface predator interactions may be very important to adult shearwaters when self-provisioning during both breeding and non-breeding. Finally, much of the environment shown to be important to shearwaters currently has little, if any, management and/or conservation strategies in place that consider the needs of pelagic seabirds.

These data form a general model of tropical seabird foraging ecology which demonstrates the importance of mesoscale oceanic phenomena, especially eddies, convergences, and freshwater input, to foraging pelagic seabirds.

Inter-annual variations suggest that climate-driven processes can heavily affect the oceanography and dynamics of foraging grounds, supporting previous links between climate-driven variation and variations in prey availability to wedge-tailed shearwaters. Therefore, these factors should be considered in future modelling and mapping of ideal or remaining habitat. Combined, these results reveal the complexity of oceanography and ocean dynamics that drive prey availability in tropical seabird foraging areas, and highlight the fact that some previously supposed factors of importance are not necessarily so. Therefore, determining optimal foraging habitat for tropical pelagic foraging seabirds is a complicated process and multiple oceanographic parameters must be assessed to best define the trophic mechanisms and processes that drive foraging activity and prey accessibility.

This comprehensive data set can be used to determine best practise strategies for the protection and conservation of wedge-tailed shearwaters. Identified foraging locations are priority target areas in which threats to seabirds can now be assessed. Threat assessment will help ensure optimal management and conservation efforts are implemented and carried out in critical foraging locations which will help to mitigate any impacts that may arise from climate-driven variation on foraging habitat. The results can also be applied in a global context to identify internationally recognised, candidate protected areas, such as Marine Important Bird Areas (MIBAs) in tropical systems. Additionally, my findings highlight potential new selection criteria, such as some quantification of sub-surface predator interactions that should perhaps be considered for use in identifying MIBAs in tropical regions.

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1. BACKGROUND AND GENERAL INTRODUCTION

1.1 Importance of global oceans

Marine ecosystems are central to biological processes on earth (Hoegh-Guldberg and Bruno, 2010). Covering 71% of the planet, they produce oxygen, absorb heat and carbon, provide essential food and play a major role in regulating the earth's climate. Habitability of locations for marine organisms is often dependent on weather conditions which are regulated by ocean '*conveyor belts'* such as that of the Atlantic Ocean which drives the Gulf Stream (Rahmstorf, 1999). Oceanic currents are propelled by winds and these currents in turn generate upwellings that mix cool, nutrient rich deep waters with the surface layer, promoting primary productivity. This drives the short marine food chain and explains aggregations of predators and prey in these locations which are '*hotspots*' of biodiversity in the open oceans (Worm et al., 2003, Worm et al., 2006). The loss of species and populations impairs the ocean's ability to recover from perturbations and can drive the loss of ecosystem services and regime shifts (Upton, 1992, Steele, 1998). Therefore, the health of these systems is fundamental to life on this planet and it is critical to protect them and the species that rely on them to maintain essential ecosystem function.

1.2 Threats to the marine environment

There are numerous stressors which threaten the marine environment including habitat destruction, overfishing, extraction such as mining, pollution, debris and invasive species introduction (Rogers and Laffoley, 2011). Threats are primarily driven by human activities and the most severe of these is climate change (Syvitski et al., 2005, Walling, 2006, Hoegh-Guldberg and Bruno, 2010). Climate change can have serious, negative effects on the marine environment affecting sea levels, ocean temperatures and chemistry, wind and current systems, nutrient supplies and the food chain (Hoegh-Guldberg and Bruno, 2010, Doney et al., 2012). Climate-change is also reported to drive unnaturally rapid changes and extremes in global and regional weather like storms and El Niño Southern Oscillation (ENSO) cycles (Hennicke and Flachsbarth, 2009, Wingfield et al., 2011, Coumou and Rahmstorf, 2012). Such variations can cause substantial changes in marine systems, altering trophic food webs (Walther et al., 2002, Winder and Schindler, 2004) and, if they increase in frequency and severity as predicted, negative impacts at all trophic levels will be exacerbated (IPCC, 2013).

1.3 Seabirds and the marine environment

Seabirds are completely reliant upon the marine environment for food. They are also highly sensitive to changes in that environment which makes them useful monitors and good indicators of changes in marine food supplies (Cairns, 1987, Heithaus et al., 2008, Parsons et al., 2008). Their reliance also makes them susceptible to certain threatening processes. The most prominent threats to seabirds have been suggested to be fisheries activities, pollution and negative impacts from climate-change processes in the medium to long-term (Croxall et al., 2012). Overfishing can negatively affect seabirds via the direct mortality of individuals in fishing equipment (Brothers et al., 1999). Fisheries can also reduce the amount of food available to foraging birds via the direct removal of forage-fish (Becker and Beissinger, 2006, Cury et al., 2011, Bertrand et al., 2012) or through the removal of sub-surface predators with which they interact when foraging (Au and Pitman, 1986, Worm et al., 2006).

Upper level predators such as seabirds, have a fundamental role in food webs and directly influence the structure and function of marine communities (Heithaus et al., 2008). Reductions in their numbers or changes in community structure can have considerable ecological consequences through top-down trophic cascades (Bruno and O'Connor, 2005, Worm et al., 2006, Heithaus et al., 2008). As marine consumers in a highly heterogeneous environment where locating sufficient food can be challenging, seabirds cover hundreds, even thousands of kilometres when searching for food

(Croxall, 1987, Ballance et al., 2001). The ephemeral nature of the marine environment means food items tend to be scarce and patchily distributed (Ashmole1971; Weimerskirch 2007). As a result, seabirds' foraging activity is concentrated in areas where prey availability is increased (Ballance et al., 2001). Therefore, their foraging behaviour reveals the locations of scattered food resource hotspots.

1.4 Dual-foraging strategies and post-breeding behaviour

Seabirds spend much of their lives searching for food and often repeatedly use specific locations where prey encounters are predictable (Croxall, 1987). However, when breeding, seabirds are '*central-place foragers'* and constrained to foraging within a certain distance of the colony by the need to return for incubation or to feed their chick (Orians and Pearson, 1979). Prey near seabird colonies is thought be depleted in zones around seabird colonies – a phenomenon called 'Ashmole's halo' (Ashmole, 1963, Ashmole, 1971, Birt et al., 1987). Some seabird taxa deal with local prey reductions by employing a '*dual-foraging*' strategy which utilises two discrete foraging areas (Weimerskirch, 1998, Magalhaes et al., 2008). This strategy is commonly observed in the most pelagic of seabirds, the Procellariiformes (tube-nosed seabirds), which include the albatrosses, petrels and shearwaters (Croxall, 1987, Ballance et al., 2001). For example, blue petrels (*Halobaena caerulea*) (Chaurand and Weimerskirch, 1994), sooty shearwaters (*Puffinus griseus*) (Weimerskirch, 1998) and wandering albatrosses (*Diomedea exulans*) (Weimerskirch et al., 1997), alternate multiple short trips to provision chicks, with a single long trip during which they self-provision. Short trips occur near the colony in areas that have generally low prey availability, while on longer trips, adults travel to distant, more productive locations to obtain food for self-maintenance (Chaurand and Weimerskirch, 1994, Weimerskirch et al., 1994, Weimerskirch, 1998). Once breeding has concluded, seabirds are no longer constrained to the colony. Therefore, many of these species, such as Cory's (*Calonectris diomedea*) and sooty shearwaters (Shaffer et al., 2006, González-Solís et al., 2007, Hedd et al., 2012) conduct a lengthy, post-breeding migration to productive hotspots far from their breeding colony.

1.5 Enhanced prey availability in non-tropical systems

With many studies of seabirds from non-tropical regions focused on the Procellariiformes, there is a great deal of detailed information available on their prey environments, foraging relationships and mechanisms that enhance prey availability. Temperate or polar foraging hotspots, often in pelagic regions, are almost always characterised by enhanced primary productivity (measured by satellite derived [Chl *a*]), which is considerably higher in cooler oceans than in tropical waters (Raymont, 1980). Enhanced [Chl *a*] leads to increased zooplankton which is then consumed by the fish that are prey for numerous top predators (Valiela, 1995). [Chl *a*] enhancement is generally driven by large-scale oceanic phenomena (Palacios et al., 2006). For example, many species strongly associate with upwellings characteristic of the California Current System or the Benguela upwelling (Becker and Beissinger, 2003, Ainley et al., 2005, Grémillet et al., 2008). For terns and shearwaters of the Indian Ocean, eddies and convergence zones produce the increased productivity and enhanced prey availability they search for (Hyrenbach et al., 2006), while for other species, their optimal foraging grounds are located where currents converge near the continental shelf break (Ainley and Jacobs, 1981). In fact, this kind of interaction of water movement with bathymetric or topographic features (e.g. seamounts or shelf edges) often generates increases in [Chl *a*] and prey enhancement (Owen, 1981, Wolanski and Hamner, 1988, Hunt Jr. et al., 1990, Bost et al., 2009). Such phenomena also create frontal systems, where a horizontal thermal gradient creates a vertical thermal boundary (Owen, 1981, Lutjeharms et al., 1985). They are also definable through other quantifiable oceanographic parameters including anomalies in sea-surface temperatures (SST), [Chl *a*] or the height of the sea (sea-level anomalies: SLAs), bathymetry or topographic, features such as seamounts, and currents (Haney et al., 1995, Palacios et al., 2006, Fauchald, 2009). These factors reveal the presence of identifiable oceanographic features such as eddies, fronts, convergences or upwellings (Garvine, 1974, Oschlies and Garçon, 1998, Palacios et al., 2006) and signal oceanic mechanisms that contribute to the aggregation of prey (Strub and James, 2000, Reese and Brodeur, 2006). Consequently, prey availability and advantageous foraging for seabirds can be directly linked to specific physio-chemical parameters and marine features (Ballance et al., 2001).

1.6 Oceanographic mechanisms in non-tropical waters

Large-scale highly productive phenomena such as fronts, in temperate and polar systems are generally stable features**,** and so, are relatively predictable to predators. In fact, frontal systems are recognisable by, and attract, large numbers of seabirds (Schneider, 1990, Waugh et al., 1999, O'Hara et al., 2006). However, when these habitats change, the abundance and distribution of prey can vary. This is most frequently caused by predictable seasonal variation or current climate-related conditions (Ballance et al., 2001). There is one model proposed to explain relationships between food availability and oceanography, and it relates to climate variation. The '*upwelling suppression model*' is only known from temperate environments (Cox et al., 2000), and describes seasonal-scale impacts to the physio-chemical factors of the ocean, productivity and the food chain, and is generally related to climate-change processes such as ENSO. Under specific climatic circumstances thermal stratification due to warmed sea surface (Barber and Chavez, 1983, Cane, 1983) causes the suppression of the upwellings which drive enhanced productivity (Hunt Jr, 1995, Cox et al., 2000, Vargas et al., 2007). When this occurs, it can heavily impact prey availability and hence, longevity and breeding success of seabird populations (Schreiber and Schreiber, 1984, Boersma, 1998, Croxall et al., 2012). However, trends that explain systematic processes in one environment may not necessarily apply in others, due to considerable differences in climate, oceanography and prey availability, such as the marked differences between tropical and non-tropical regions (Longhurst and Pauly, 2012)

1.7 Enhanced prey availability in tropical systems

In contrast to the wealth of information available on foraging sites and relationships with oceanographic mechanisms influencing prey availability to seabirds at higher latitudes, there is relatively poor information about these relationships in tropical systems. Tropical oceans are considered to be comparatively low in resources and not known to have the same types of highly productive areas that provide a reliable food supply in non-tropical zones (Ballance et al., 2001). Despite the differences between tropical and non-tropical systems, some factors that influence prey aggregation have been found in both. For instance, great frigatebirds (*Fregata minor*) of the Indian Ocean forage in association with mesoscale (10-100's km) eddies (Weimerskirch et al., 2004). Other species, including red-footed boobies (*Sula sula*) and wedge-tailed shearwaters (*Ardenna pacifica*), concentrate their foraging on areas of enhanced productivity (Weimerskirch et al., 2005, Cecere et al., 2013). However, it remains unclear what causes these productivity enhancements. By contrast, some foraging grounds have been linked to factors not commonly related to foraging behaviour. For example, Pinet et al. (2011) postulate that non-breeding Barau's petrels (*Pterodroma baraui*) *'overwinter'* in regions where strong, consistent winds drive oceanic frontal systems, but direct evidence for the existence of fronts was lacking.

The causes of variations or reductions in prey availability to seabirds in tropical systems are less predictable than the drivers known from temperate or polar regions. Most commonly, they are related to increased SSTs that are correlated with varying ENSO conditions (Schreiber and Schreiber, 1984, Anderson, 1989, Vargas et al., 2006). In Australia's Great Barrier Reef (GBR) for example, a strong sensitivity to even small elevations in SST drove reduced seabird breeding participation and impacts to reproductive success (Smithers et al., 2003, Peck et al., 2004, Devney et al., 2009).

1.8 **Oceanographic mechanisms in the tropics - sub-surface predator associations**

Oceanographic phenomena that drive prey availability such as fronts, eddies and upwellings, are generally less stable and predictable in tropical regions (Weimerskirch et al., 2005, Weimerskirch, 2007). In fact, some seabirds such as Pacific albatrosses which breed slightly north of the Tropic of Cancer, preferentially forage at predictable, productive oceanic features well-outside tropical regions and far from the colony (Hyrenbach et al., 2002), rather than conducting shorter trips to nearer tropical zones. This suggests that tropical breeding seabirds may have to accommodate a variety of potential limitations that could affect long-term survivorship and breeding success (Croxall et al., 2012). This also means that mechanisms driving prey availability may differ from those in non-tropical systems. The mechanism most frequently cited to improve access to prey for foraging tropical seabirds is interactions with sub-surface predators such as dolphins and tuna (Au and Pitman, 1986, Au and Pitman, 1988). The predatory activity of these taxa beneath the ocean's surface, make prey accessible to foraging seabirds by driving it to the surface from depth (Au and Pitman, 1988). This relationship is said to be particularly beneficial for tropical seabirds because they primarily capture prey near the ocean's surface and, with the higher clarity of tropical waters, prey are often deeper and less accessible than in the higher latitudes (e.g. Jaquemet et al., 2004, Le Corre and Jaquemet, 2005, Ballance et al., 2006) .

1.9 Tropical Procellariiform foraging strategies

The few studies of foraging strategies available for tropical Procellariiformes indicate they commonly employ short duration trips to areas of elevated productivity when provisioning chicks (Ballance et al., 2001, Baduini, 2002, Cecere et al., 2013). However, only one tropical Procellariiform population has been confirmed to employ a dual-foraging strategy during breeding, as seen in their temperate counterparts (Congdon et al., 2005). Evidence from isotopic analysis suggests that Barau's petrels of the Indian Ocean also utilise this strategy (Kojadinovic et al., 2008), but this has yet to be confirmed by tracking analysis. Wedge-tailed shearwaters of the GBR employ long and short duration trips, but the exact locations and habitat characteristics of foraging sites are unknown (Congdon et al., 2005). Only two non-breeding tropical Procellariiformes have been tracked but strategies and oceanographic drivers were disparate. Wedge-tailed shearwaters of the Indian Ocean dispersed regionally to various locations characterised by elevated productivity and overlap with known tuna fisheries (Catry et al., 2009b). Barau's petrels, by contrast, conducted a lengthy longitudinal migration to a core foraging ground characterised by high, consistent winds (Pinet et al., 2011). Neither conducted the lengthy, trans-equatorial migrations to productive '*hotspots*' commonly seen in temperate or polar Procellariiformes.

1.10 Developing a model for the tropics

To date, the majority of tropical studies have focused on specific components of the environment (e.g. [Chl *a*], SST, bathymetry or SLAs, representing eddies, upwellings or convergence zones) and how they affect seabird foraging (e.g. Weimerskirch et al., 2004, Catry et al., 2009b, Cecere et al., 2013; but see Le Corre 2001). Studies examined different characteristics or species, and results contrasted.

Therefore, to unequivocally determine the relative importance of mechanisms such as fronts, eddies or upwelling to prey accessibility in the tropics, is problematic. Consequently, with the data currently available, it is difficult to develop a comprehensive overall picture of how these components interact with one another to influence prey availability or foraging. Therefore, a detailed, cohesive study which examines all the various components simultaneously, similar to comprehensive studies conducted in temperate systems (Ainley and Boekelheide, 1984, Ainley et al., 2005), is necessary to obtain an understanding of the linkages in tropical systems. Exploring the relationships between a tropical seabird and its oceanographic environment, across both breeding and non-breeding phases, will allow me to produce a hypothetical model of the oceanographic factors that influence foraging activity of a pelagic seabird in the Great Barrier Reef and Coral Sea. With this information I can develop a paradigm of the trophic mechanisms that drive prey availability in tropical systems. The two primary pieces of information necessary to develop this model are:

1) The specific locations of foraging grounds used by a species throughout multiple years
2) A clear and meticulous analysis **o**f a detailed set of oceanographic parameters that characterise foraging locations to determine the trophic mechanism/s that produce favourable feeding conditions.

1.11 Model species: Wedge-tailed shearwaters

Wedge-tailed shearwaters are a widespread, numerous Procellariiform of approximately 5 million individuals globally, and are said to be in decline due to unsustainable levels of exploitation, persecution, predation by invasive species and the over-exploitation of tuna fisheries (Brooke, 2004). They breed in the tropical Pacific and Indian Ocean as well as some sub-tropical and temperate areas, particularly in Australia (Dyer and Hill, 1991, del Hoyo et al., 1992, Dunlop et al., 2002, Bancroft et al., 2004, Hutton et al., 2008). Current knowledge of the tropical breeding populations is limited to the GBR and Indian Ocean populations and a few sub-tropical populations (Baduini, 2002, Peck and Congdon, 2005, Cecere et al., 2013). This species displays typical K-selected life history traits characteristic of pelagic foraging seabirds - slow growth, delayed fecundity, low reproductive output and they are long-lived (Ashmole 1971). They breed in the summer months subsequent to a lengthy winter migration (Jaquemet et al., 2004, Congdon et al., 2005, Catry et al., 2009b), nest in burrows where they incubate eggs for ~50 days and spend approximately 3-4 months rearing chicks (Roberts et al., 1975, Ackerman et al., 1980, Byrd et al., 1983). Wedge-tailed shearwaters of the GBR dual-forage, alternating long and short trips, but the locations of these foraging excursions have not been identified nor has it been ascertained if these are in different foraging environments. They forage at sea during daylight hours and their diet is little known but expected to consist primarily of small forage-fish and squid (Imber and Berruti, 1979, Baduini, 2002, Catry et al., 2009a). Their nocturnal returns to the colony for chick provisioning makes making them relatively easy to study. Wedge-tailed shearwaters are excellent models for the purposes of this study for a number of reasons:

1) Studying a tropical Procellariiform provides a practical basis to make comparisons with the volume of literature on Procellariiformes in both temperate and tropical regions.
2) Of the tropical seabird species studied on the Great Barrier Reef (GBR), wedge-tailed shearwaters have been shown to be the most sensitive to changes in background resource availability related to climate variation (Congdon, et al. 2007).
    a) SST variations of approximately 1.5 - 3°C that occur on both a daily and seasonal scale negatively affect prey availability to this species (Smithers et al., 2003, Peck et al., 2004, Weeks et al., 2013). For example, Peck et al (2004) observed negative correlations between fluctuating foraging success (affecting meal size, feeding frequency and chick growth) with daily variations in SST both within and among seasons. By contrast, Black noddies, another species that breeds in very large numbers on the same islands as GBR Wedge-tailed shearwaters, are susceptible to SST related food impacts when temperatures increased by ~4°C. Therefore, smaller SST variations affect shearwaters making them more sensitive to these impacts.
    b) Seasonal scale ENSO – driven SST increases have produced dramatically reduced reproductive success (Smithers et al., 2003).

    c) Food reductions have been linked to variations in the position and intensity of the Capricorn Eddy, a mesoscale oceanographic phenomenon in the region of their breeding colony which (Weeks et al., 2013). However, it has not been known until now if Wedge-tailed shearwaters actually foraged in association with this phenomenon.

3) This sensitivity to a range of impacts related to daily and longer-term climate and ocean driven variation means Wedge-tailed shearwaters are good indicators of climate-driven changes in this tropical marine environment.
4) The temporal scales of breeding and non-breeding foraging behavior are comparable to Procellariiformes of temperate environments - dual-foraging during chick-rearing and a lengthy, post-breeding absence from the colony (6-7 months). However, whether these locations are spatially disconnected is currently unknown.
5) Wedge-tailed shearwaters forage in multispecies flocks (Sealy, 1973, Mills, 1998), often with other seabird taxa that have different demography and life history characteristics (Ballance et al., 2001). Wedge-tailed shearwaters of the GBR/Coral Sea region are known to forage in association with other pelagic foraging species such as the sooty tern and common noddy (*Anous stolidus*) (Congdon et al., 2007). Their Indian Ocean counterparts are said to obtain prey when foraging in multi-species flocks over 500-1000m areas (Jaquemet et al., 2004). In fact, the seabird community of the GBR/Coral Sea is extensive with 24 breeding species on the GBR and 13 on Coral Sea islands, from three foraging guilds (inshore, offshore and pelagic) and many more non-breeding visitors to the region (Congdon et al., 2007, GBRMPA, 2008). Across the Coral Sea, New Caledonia is another significant seabird breeding location hosting 26 breeding species (Benoit and Bretagnolle, 2002, Spaggiari et al., 2007). Therefore, Wedge-tailed shearwaters may interact with some of these species when foraging.

These characteristics make Wedge-tailed shearwaters ideal general models for examining the potential effects of variation in resource availability on a number of pelagic foraging seabird taxa. Therefore, conclusions derived from studying GBR Wedge-tailed shearwaters, potentially apply to multiple species.

Current conservation efforts primarily focus on seabird breeding colonies, while at-sea food resources are largely ignored. Most information used to generate general conservation and management strategies for seabirds is based upon conclusions derived from research in temperate systems. However, the emergence of results from the tropics, which contrast with findings from temperate systems, raises the question of whether this is appropriate or applicable. The clear, unified model describing mechanistic processes driving prey availability in temperate environments is not available for the tropics. Moreover, research suggests there may be substantial differences. For example, large aggregations of sub-surface predators appear to play a vital role in enhancing prey availability to tropical seabirds. If so, overfishing of tuna may pose an increased threat in tropical systems. Clearly, identifying the mechanisms that cause food to be available (or unavailable) to tropical seabirds, will aid in minimising threats, and mitigate cumulative impacts.

1.12 Study aims and objectives

This study aims to improve the understanding of tropical seabird foraging ecology and relationships with food resource environments and prey availability. It will have a particular emphasis on locations of critical foraging resources, oceanographic characteristics of those places, and the trophic mechanisms that influence the availability and accessibility of prey. The study will focus on a population that breeds on Heron Island in the GBR, which is part of one of the largest populations globally (~2 million birds across the Coral Sea) (Congdon et al., 2007). To accomplish my aims the objectives are four-fold:

1. To determine whether wedge-tailed shearwaters forage at multiple spatial scales and accurately identify the precise locations of those foraging grounds, by conducting an extensive tracking study throughout both breeding and non-breeding phases.
2. To characterise the oceanographic factors and features that distinguish critical food resource habitats for tropical pelagic foraging seabirds
3. To demonstrate their function in contributing to foraging activity at any given temporal or spatial scale of foraging, and unambiguously highlight

the presence of important or influential oceanic mechanisms such as fronts, eddies or upwellings

4. To evaluate the applicability of my findings in a conservation and management context and contribute towards designing appropriate and relevant management strategies for the protection of tropical species.

1.13 Thesis structure and hypotheses

The four objectives listed above are addressed in Chapters 2 to 5. In Chapter 2 I document the long-distance, trans-equatorial migration conducted by non-breeding wedge-tailed shearwaters and characterize the oceanography and dynamics that influence that distant foraging ground. In the following three chapters I address the foraging resources used during the chick rearing phase of the breeding period for this species. Chapter 3 identifies the distant locations of foraging grounds which are used by wedge-tailed shearwaters when self-provisioning and briefly addresses location-specific oceanographic characteristics. Chapter 4 expands that study with additional years of tracking providing corroborative evidence of preferred foraging locations observed in Chapter 3; increases the resolution of oceanography studied to accurately characterize factors of influence; and describe in detail the oceanographic relationships between these distant foraging grounds and regional ocean dynamics. In Chapter 5 I complete the same process for critical foraging resources used by wedge-tailed shearwaters for provisioning chicks. This details the exact locations and oceanographic characteristics of repeatedly used foraging grounds and discusses the primary mechanisms that influence foraging patterns and activity in the near-colony environment. Lastly, in Chapter 6, I discuss the findings obtained in the former chapters in an ecological context and synthesize the discoveries from this body of work into a conceptual model of tropical seabird foraging associations in tropical marine systems. This incorporates a focus on assessing and improving the management and conservation strategies for tropical seabird populations.

2. NON-BREEDING MIGRATION OF TROPICAL SHEARWATERS

This chapter has been published in Marine Ecology Progress Series as a manuscript entitled:

"Trans-equatorial migration and non-breeding habitat of tropical shearwaters: implications for modelling pelagic Important Bird Areas" by Fiona McDuie and Bradley C. Congdon.

The entire chapter was written by Fiona McDuie, with co-authors providing intellectual input to the design and implementation of the research and editorial contributions to the paper. Data collection, data analyses and production of tables and figures were conducted by Fiona McDuie.

2.1 ABSTRACT

Variability of prey availability in the marine environment can drive many seabirds to migrate following breeding. While targeted long-distance, latitudinal migrations are common in temperate-breeding species including Procellariiformes, regional dispersal or longitudinal migration is more common in tropical species. Wedge-tailed shearwaters (*Ardenna pacifica*) that breed on the Great Barrier Reef, Australia, depart their colony for an extended period after breeding. I used miniature geolocators to track adults through a ~6000 km migration to core non-breeding foraging grounds in Micronesia. This lengthy, trans-equatorial migration to a single foraging area contrasts with patterns observed in other Wedge-tailed shearwater populations and tropical Procellariiformes. Their migratory pattern was similar to that observed for temperate Procellariiformes but the oceanographic characteristics of non-breeding habitats were significantly different. Core-use habitat, defined by 50% UD kernels, had high sea-surface temperatures averaging 28°C, very low wind speeds (4-6m^{-s}) and low primary productivity ([Chl *a* 0.026 mg m^3]); features normally associated with poor foraging habitat. However, foraging activity was strongly linked to positive sea-level anomalies, indicating the presence of anti-cyclonic eddies at foraging sites. These eddies can be associated with oceanic frontal systems. Such frontal activity is known to aggregate micronekton and facilitate increased sub-surface predator feeding in this region of the Western-Central Pacific Tuna Fishery.

Consequently, my results suggest that eddies, frontal activity and feeding associations with sub-surface predators enhance prey availability to non-breeding shearwaters beyond levels expected based on standard indices of primary production. This study characterises winter foraging habitat for GBR Wedge-tailed shearwaters in a region which may be a hotspot for other seabirds and apex predators including the endangered leatherback turtle. It is the first study of a tropical system to simultaneously assess the full set of oceanographic features considered important for modelling pelagic Important Bird Areas (IBA). My findings clearly identify the need for IBA modelling in the tropics to go beyond standard indices of productivity by including measures of frontal activity and assessments of biological interactions. Consequently, this study provides a model for improved prediction for candidate Marine IBAs throughout tropical regions.

2.2 INTRODUCTION

In the pelagic marine environment, where the distribution and abundance of prey is strongly influenced by oceanographic or other environmental factors, food availability can vary significantly between seasons (Weimerskirch et al., 2002). Such variation drives many seabirds to either disperse or migrate following breeding; behaviour that is particularly common in temperate-breeding species including Procellariiformes (tube-nosed seabirds) (e.g. González-Solís et al., 2007, Guilford et al., 2009). Consequently, the conservation of wide-ranging pelagic/migratory seabirds such as Procellariiformes requires the identification and effective management of both breeding and non-breeding foraging environments, along with a detailed understanding of the functional relationships between oceanography and prey availability at these locations.

Temperate Procellariiformes that migrate, travel long distances to non-breeding foraging grounds at high latitudes. In some cases, all individuals of a population converge on a single high-productivity location. For example, Manx (*Puffinus puffinus*) (Guilford et al., 2009) and Flesh-footed shearwaters (*Ardenna carneipes*) consistently use the same non-breeding locations over multiple years (Reid et al., 2013). Populations of other species, such as Cory's (*Calonectris diomedea*) and Sooty shearwaters (*A. grisea*), disperse more widely and exploit several non-breeding areas (Shaffer et al., 2006, González-Solís et al., 2007, Hedd et al., 2012). However, regardless of whether one or multiple non-breeding areas are used, migration end-points are considered oceanic 'hotspots' where elevated ocean productivity driven by upwelling and large-scale frontal systems enhances prey availability (Phillips et al., 2005, Phillips et al., 2006, Shaffer et al., 2006, Hedd et al., 2012). At the same time of year, productivity in breeding areas is low by comparison. Consequently, the marked seasonal difference in food availability between breeding and non-breeding grounds is considered to be the principal mechanism driving this migratory behaviour (Phillips et al., 2005, Shaffer et al., 2006, Guilford et al., 2009, Hedd et al., 2012).

Tropical systems are distinctly more aseasonal with few oceanic phenomena producing productivity at the scale observed in temperate systems. For this reason the mechanisms driving migratory behaviour and the choice of non-breeding foraging habitat in tropical Procellariiformes are largely unknown. Banding studies suggest that, like temperate species, many tropical species disperse or migrate away from breeding colonies in the non-breeding season. Some perform large-scale directed migrations such as Gould's petrels (*Pterodroma leucoptera*; Priddel et al., 2014) or Christmas shearwaters (*P. nativitatis*) (Everett and Pitman, 1993) which migrate longitudinally across the Pacific. However, unlike temperate species, others do not travel great distances from the colony but disperse more locally. For example, Newell's shearwaters (*Puffinus newelli*) disperse to areas relatively close to their Hawaiian breeding colonies (Pitman, 1986). Anecdotally, this is thought to be because frontal systems bring nutrient-rich, highly productive waters within reach of non-breeding birds (Polovina et al., 2001)

I know of only two previous tracking studies of tropical Procellariiformes that considered the physical oceanography of non-breeding foraging grounds. Both are in the Indian Ocean and each has revealed species-specific non-breeding dispersal/migratory behaviour. They suggest that for tropical species, the mechanisms driving choice of non-breeding foraging habitat differ to those used by temperate species. Barau's Petrels (*Pterodroma baraui*) of Reunion Island migrate longitudinally to multiple foraging areas in a restricted region of the central and eastern Indian Ocean approximately 5000 km from their breeding colony (Pinet et al., 2011). By contrast, Wedge-tailed shearwaters (*A. pacifica*) that breed in the Seychelles dispersed to various locations throughout the Central Indian Ocean basin between 1000 km and 3700 km from breeding colonies (Catry et al., 2009b, Pinet et al., 2011)

Importantly, regardless of the pattern of dispersal, or the distance travelled, in all non-breeding areas identified in these two studies the ocean was notably warm and relatively low in primary productivity, with no evidence of the level of upwelling observed in temperate systems (Catry et al., 2009b, Pinet et al., 2011). Instead, consistent strong winds, associated oceanic fronts and/or the correlated activity of sub-surface predators were posited as the principal drivers of increased prey availability. For example, the non-breeding at-sea distributions of Wedge-tailed shearwaters corresponded with locations having high commercial catch of Yellowfin (*Thunnus albacares*) and Skipjack (*Katsuwonus pelamis*) tuna (Catry et al., 2009b). Both tuna are predatory species that drive forage fish towards the surface when feeding, thereby increasing prey accessibility to surface-foraging seabirds. Consequently, it is wind-driven frontal activity and/or sub-surface predator numbers at non-breeding locations, as opposed to direct primary productivity per se, that is thought to define them as critical foraging areas for tropical species.

Foraging associations between breeding seabirds and subsurface predators have been observed for many species in tropical environments. This has led to them being considered more important in tropical than temperate systems (Au and Pitman, 1986, Jaquemet et al., 2004, Jaquemet et al., 2005, Weimerskirch et al., 2006). The tracking studies outlined above also propose that frontal systems and interactions with sub-surface predators play a greater role in creating and maintaining viable non-breeding foraging habitat for tropical species. However, current evidence for the general applicability of these findings across oceans, species and populations from other low latitude breeding sites is lacking.

Wedge-tailed shearwaters breeding in the tropical waters of the southern Great Barrier Reef (GBR), Australia, leave breeding colonies in May and return in October/November. However, until now, where they over-winter and the characteristics of their non-breeding habitat have remained unknown. Therefore, this study aimed to establish where Wedge-tailed shearwaters of the southern GBR spend the 5-6 month non-breeding period, to determine the physical oceanographic characteristics of these non-breeding foraging grounds, and ascertain the likely oceanographic phenomena at these locations that support and/or enhance prey availability. In particular, data were used to determine if these sites are consistently and predictably characterised by warm, low productivity waters having high, wind-driven frontal and/or sub-surface predator activity, as predicted by tropical non-breeding foraging site characteristics elsewhere.

2.3 MATERIALS AND METHODS

2.3.1 Geolocator tracking

This study was conducted at Heron Island (23° 26’ S, 151° 51’ E), in the Capricorn Bunker Group of islands of the southern Great Barrier Reef (GBR) Marine Park, Australia. To ascertain migratory routes and overwinter foraging locations I deployed 30 BAS (British Antarctic Survey) MK19 (2.5g) global location sensing [GLS] loggers (Biotrack, UK) on adult shearwaters which were identified with individually numbered metal bands on the left tarsus. The devices were deployed in April 2012, late in the breeding season. In all 23 devices were retrieved, either after individuals returned to the breeding colony in late November 2012, or at the start of the chick-rearing period in February/March 2013. The remaining 7 were not found, possibly due to ‘sabbatical’ periods of no reproduction (Mougin et al., 1997), or overwinter mortality. Tracking data were obtained from 15 of these devices. The remainder either malfunctioned after deployment or failed to download and data were not recoverable by the manufacturer.

GLS devices should ideally be calibrated at the breeding colony prior to deployment to identify the optimal parameters to be used in obtaining accurate locations upon data download. However, for logistical reasons GLS devices were deployed in early April close to the March equinox (21 March) when loggers are known to have poor resolution due to equivalent day/night lengths (Phillips et al., 2004). Consequently, I completed a post-retrieval calibration (>5 days) at Heron Island in addition to the pre-deployment calibration, to ensure accurate calibration.

Adult shearwaters, which were individually identified with numbered leg bands, were caught by hand on their return to the burrow at night or when they exited the nest. I optimized GLS deployment and retrieval by selecting individuals known to have nested in the same burrow/area for >2 concurrent seasons. The GLS was cable-tied and glued with marine epoxy to a strip of Velcro Onewrap©, which was then wrapped around the bird’s lower right tarsus. The total deployment weight was 4.6g, representing approximately 1.3% of the birds’ weight. This is well below the recommended maximum weight of deployments (~3-5%; Kenward, 2001). At four nests I was able to deploy on both adults of a known long-term breeding pair. At the remaining 22 nests only one adult of a pair was fitted with a GLS.

The primary function of geolocators is to calculate position from reading ambient light levels relative to time (Wilson et al., 2002). Geolocators measure and log ambient light levels every minute with the maximum level every 5 minutes being recorded. This provides estimates of latitude and longitude of each bird twice a day from day length, and the time of local midday relative to Greenwich Mean Time (GMT) (Phillips et al., 2004). Activity (wet/dry) status of the logger is sampled every 3 seconds. This allows recording of the internal temperature (representing sea temperatures) if the logger is wet continuously for 25 minutes. If a logger remains dry at night this indicates the bird may be on land/breeding colony, so I could derive departure and return to the colony from immersion data. This information coincided with clear and lengthy migratory north and southbound movements from and returning to the colony in position data retrieved from loggers.

GLS logger deployments did not deter birds from returning to feed their chick on subsequent days, indicating no desertion as a result of handling or deployment. Furthermore, on retrieval of loggers after 7-10 months, I observed no injury to birds' legs, with the exception of one individual which had very mild callusing on the inside of the tarsus, nor any apparent attempts by birds to remove the loggers (damage to Velcro or casings).

2.3.2 Data analysis

2.3.2.1 *GLS*

Data were downloaded using BAStrak software Communicate© and Decompressor©. Light data curves were edited in BASTrak's Transedit2© program, using a threshold setting of 16 and sun elevation correction set at -3.5 based on the analysis of calibration data. This process calculates a latitude/longitude position of the logger at noon and midnight GMT. During editing, all data points were individually assessed and exclusions made as follows: any locations derived from curves with interruptions around sunrise and sunset, or that required unrealistic flight speeds (>35 km h–1 sustained over a 48 h period), were identified and exclud (according to Catry et al., 2009b). Points over land were not removed as this can potentially bias the overall centres of distribution (Guilford et al., 2009). Nevertheless, known natural history of Procellariiform seabirds indicates that such points are unlikely to represent authentic locations of birds.

Inferential gaps in GLS data can result from both the lack of accuracy of position around the equinoxes and during periods of heavy 'shading'. Therefore, data were excluded for a minimum of 10-15 days before and after the equinoxes (21 March and 21 September) and when significant shading events occurred. Shading is often the result of bad weather and GLS data are notoriously unreliable in these instances (Phillips et al., 2004, Shaffer et al., 2005). In temperate regions the accuracy of positions obtained with GLS has been estimated at 186 ± 114 km (mean error ± SD; SDs of 1.66° and 1.82° of latitude and longitude, respectively) (Phillips et al., 2004) and of 202 ± 171 km (Shaffer et al., 2005).

The return to the colony was identified from the first instance of a logger remaining dry at night combined with position data that indicated lengthy migratory flight patterns either away from or returning to the colony. Finally, sea-surface temperatures (SSTs) can be used in combination with light-based longitudes to improve or obtain estimates of latitudes (which are notoriously less accurate) on days when light-based geolocation is unreliable (Shaffer et al., 2005). However, our batch of GLS proved to have malfunctioning temperature switches which made temperatures derived from logger readings unreliable.

2.3.2.2 *Kernel Analysis*

Locations obtained from the GLS were mapped and visually examined in ArcGIS 10.2 for Desktop (ESRI). Key overwinter areas for GBR Wedge-tailed shearwaters were identified via kernel density estimation (KDE). This method is a widely-used tool to transform point distributions into density estimates (Bowman, 1985, Worton, 1989, Wood et al., 2000). Utilization distribution (UD) contours represent areas of use at different densities (25, 50, 75, 95%). I focus on the 95% and 50% kernel density contours as they are generally considered to represent the home range, or extent of maximum-use, and core-use habitat respectively (Powell, 2000, Wood et al., 2000, Iverson and Esler, 2006), and these guidelines are commonly used for foraging seabirds (Wood et al., 2000, Phillips et al., 2005, Hamer et al., 2007, Burger and Shaffer, 2008).

KDEs and UDs were produced for two periods: 1) the entire non-breeding period (May – November), and 2) and the Southern Hemisphere winter months only (June, July and August) to analyse data of the core-use area without including migration (May and October-November) and the periods of low logger accuracy (September). As Wedge-tailed shearwaters of the Indian Ocean disperse to multiple core foraging locations in their non-breeding period, I also produced 50 and 95% UDs for all birds individually. This allowed me to visualise overlap among individuals and confirm whether there was one or multiple primary winter core-use areas. Migratory routes were generally uniform and core winter foraging areas predominantly overlapped (see results), so I used the pooled data for analysis.

All kernel analyses were performed in R version 3.0.3 (R Core Team 2013) using the Adehabitat LT (long term) and HR (home range) packages (Calenge, 2006, Calenge, 2014) to identify the maximum extent of foraging area and core-use foraging areas. Smoothing factor (h) was used with a cell size of 186 based on GLS error. Shape files were exported to ArcGIS 10.2 for Desktop with the rgdal (Bivand et al., 2013) and shapefiles (Stabler, 2006) packages and the kernel density map was projected in the World Geodetic System (WGS) 1984 geoid.

2.3.3 Bird foraging and non-foraging areas

For our selected analyses (details below), it was necessary to compare predictor variables between places where birds were most likely to be foraging and those they were not. This differentiation provides the binomial response variable for analysis. The foraging area is the core-use 50% kernel, the area most strongly preferred by birds and where they were most likely to be foraging (Hamer et al., 2007). This area constitutes 50% most densely concentrated points (approximately one point per ~2640km^2). To derive the comparative non-foraging area, I extracted the 50% kernel from the 95% maximum range extent kernel, classifying this remaining area as the maximum-use /

non-foraging area. Within this non-foraging area I generated a random set of 'pseudo-absence' or non-foraging points to match the number of points in the corresponding set of foraging data for the winter months (Jun/Jul & Aug). These locations are pseudo-absence since Wedge-tailed shearwaters did in fact occur within the 95% kernel, but in the low densities (approximately one point per ~15000km^2.) that suggest foraging activity is unlikely (Hamer et al., 2007). Equal proportions of foraging and non-foraging points are said to produce the most reliable results and highest predictive accuracy for boosted regression trees, the selected analysis for this study (Barbet-Massin et al., 2012). Non-foraging points were generated in ArcGIS 10.2 for Desktop, producing the binomial response variable which was used to compare the oceanographic characteristics of the core-use and maximum-use winter areas.

2.3.4 Oceanographic parameters

To determine any influence of oceanography on the winter core foraging area (50% kernel) where Wedge-tailed shearwaters spent the majority of the months of June, July and August, I explored a set of seven environmental/oceanographic factors in this study (Table 2.1). Those of principal interest were the parameters suggested by Birdlife International for assessment in pelagic area habitat modelling for Marine Important Bird Areas (MIBAs); i.e. bathymetry (m), sea-surface salinity (SSS, psu), upwellings/eddies (derived from mean sea level anomalies (SLA, mm)), wind speed (Wind, ms^{-1}), sea surface temperatures (SST in °C), presence of seamounts and chlorophyll *a* ([Chl *a*], mg m3). Data on these variables are readily available for the region.

Table 2.1: Oceanographic variable names, resolution and sources used in the environmental analyses of winter migratory foraging areas of Wedge-tailed shearwaters of the GBR.

Variable name (abbrev.) (unit)	Description	Data source
Sea Level Anomaly (SLA) (mm)	Mapped monthly mean Sea Level Anomaly; 0.25 x 0.25°resolution	Ssalto/*Duacs - DT MSLA*, AVISO Satellite Altimetry Data http://www.aviso.oceanobs.com/en/
Summary wind speed (Wind) (ms^{-1})	Monthly means of Wind speeds 1 x 1° resolution	NOAA Aquarius Scatterometer L2_EVSCI_V1.3.5; NOAA Oceancolor Web http://oceancolor.gsfc.nasa.gov)
Bathymetry (m)	Ocean bathymetry	NODC http://www.ngdc.noaa.gov

Sea surface salinity (SSS) (psu)	Monthly mean sea-surface salinity; 1 x 1° resolution	Aquarius Sea Surface Salinity (SSS) SCI V.2 NOAA Oceancolor Web (http://oceancolor.gsfc.nasa.gov).
Sea-surface temperature (SST) (°C)	Monthly mean sea-surface temperatures; 4 km resolution	Aquarius Sea Surface Temperatures (SST) 4 µ night time
Distance to Seamount (Distseam) (°)	Distance to the nearest seamount	(http://www.gebco.net/data_and_products/undersea_feature_names); Deep Reef Explorer high resolution depth model GBR/Coral Sea (Beaman, 2010) (http://www.deepreef.org/projects); list of Pacific Seamounts (http://www.ldeo.columbia.edu/~small/PacificSmts/); Seamount Biogeosciences Network Catalog (http://earthref.org/SC/).
[Chlorophyll *a*] [Chl *a*] (mg m^3)	Monthly mean [Chl *a*]; 4 km resolution	Aqua MODIS Chlorophyll *a* concentrations ([Chl *a*])

Oceanographic data from high-resolution satellite imagery analysis were downloaded at the highest spatial resolution, extracted and converted to raster format in ArcGIS 10.2 Desktop from CSV, HDF or NetCDF formats. I used monthly composite images for all parameters to minimise data loss resulting from cloud cover. The data were then combined into a single file of the three boreal summer months (winter months for shearwaters – June, July and August).

All oceanographic rasters were overlaid with bird foraging and non-foraging points for extraction of predictor variable data from the corresponding pixels (latitude/longitude locations) by month for June, July and August (to match the resolution of oceanographic data). Monthly data were then exported as shapefiles and collated to the year of tracking for analysis and modelling in R (R Core Team, 2013). Oceanographic parameters can be affected by light refraction, shallow water or presence of land in any given pixel of the satellite images so erroneous data points were identified, assessed and removed.

2.3.5 Statistical analysis and modelling

To evaluate the combined influence of environmental variables on the foraging activity of shearwaters I used predictive modelling techniques. Recent developments in ecological systems modelling and statistical methods have highlighted the fact that ensemble methods like regression trees are very effective in evaluating and exhibiting complicated relationships among numerous variables to provide powerful ecological insights (Elith et al., 2008, Buston and Elith, 2011).

Boosted regression trees (BRT) are one of these machine-learning techniques that are currently considered to have superior predictive performance when compared with traditional regression models (Desalegn and Beierkuhnlein, 2010, Oppel et al., 2012). Ensemble methods like BRTs are very effective in evaluating and exhibiting complicated relationships among numerous variables (Elith et al., 2008, Buston and Elith, 2011). They can also cope with numerous variables of different classes, random and missing data, the potential for numerous interactions and binomial response variables such as presence/absence (in the case of this study foraging/non-foraging). Further, in investigating relationships with environmental variables in marine ecosystems, there is a strong possibility that relationships between predictor and response variables will not be strictly linear. BRT is one of the most effective methods of analysing non-linear relationships such as those expected between predictor and response variables in marine ecosystems (De'Ath, 2007, Oppel et al., 2012). Finally, BRT improves performance by combining many models for prediction and includes stochasticity to reduce variance in the model and improve accuracy. Overall, this makes BRT the most appropriate choice in analysing data such as that generated in the current study. Modelling was conducted in R version 3.0.3 (Hijmans and Elith, 2013, R Core Team, 2013) using gbm.step and the library packages gbm, dismo and pROC (Ridgeway, 2007, Elith et al., 2008, Robin et al., 2011, Hijmans et al., 2013).

Boosted regressions establish a rule set derived from model parameters that minimizes the predictive deviance (the minimum error for predictions to independent samples) (Elith et al., 2008)In this case, it is the combination of environmental predictors that best predict the response variable (forage activity).This can be optimized by identifying the optimal learning rate, tree complexity (the number of nodes in the trees, the variable that controls which interactions are fitted), and number of trees (iterations) (Elith et al., 2008, Elith and Leathwick, 2013). Once an optimal model is selected, the variable interactions can be queried and investigations can be made on the most important factors (by way of variable ranks)

The modelling process used the Bernoulli (binomial) error distribution began with a fast learning rate of 0.01 and tree complexity of one less than the number of predictor variables being considered (in this case 7 and 5). A flexible, stepwise approach was used nominating the model to begin with 50 trees and increase at intervals of 50 trees per run until the optimal number of trees for the input parameters or the maximum number of trees (10000) was reached. If the minimum number of trees (1000, as recommended by Elith et al., 2008) was not reached, or the maximum (10000, as determined by Ridgeway, 2007) exceeded, the learning rate and tree complexity were adjusted until the model performance improved and the model was optimised. Optimal model predictive performance is indicated by minimum CV (predictive) deviance and high Area Under the Receiver Operating Characteristic (ROC) Curve (AUC) values, combined with an appropriate number of trees (Fielding and Bell, 1997, Elith et al., 2008). Randomness was introduced where necessary to improve model performance using bag fraction values between 0.5-0.75, as these are found to give best results for binomial responses. Upon first model run each individual oceanographic parameter was assessed through the partial variance plots and plots of fitted vs. predicted values. Outliers such as SST values that represent erroneous pixels (45.007°C), or positive bathymetry values, were identified, assessed and removed.

Boosted regression results are interpreted through the relative influence of predictor variables. The contribution of each variable is scaled to percentages and the fitted functions are visualised with partial dependence plots which display the influence of a variable after accounting for the average effects of all others in the model. Fitted values for each of the predictors used in the model are also plotted and these graphs provide the weighted means of the fitted values relative to each predictor (Elith et al., 2008). Plots were produced in R (R Core Team, 2013) with the gbm.plot and gbm.plot.fits functions.

2.3.6 Model Simplification

Non-informative predictor variables can degrade BRT model performance by increasing variance, and these variables can be dropped through model simplification. This is analogous to backward selection in regression (Elith et al., 2008). The simplification process begins by removing the variable with the least influence on model prediction, refits the model and sequentially repeats this process until the resulting standard error of the CV deviance exceeds that of the original model. This results in a more parsimonious model. Models were simplified in R using ‘GBM.Simplify’ (Ridgeway, 2007, Elith et al., 2008, R Core Team, 2013).

2.3.7 Multicollinearity or correlation of predictor variables

In conducting environmental analyses, there is the potential for environmental factors to be non-independent. When this occurs, excessive correlation among predictors can confound the ability of a model to identify the optimal set of explanatory variables (Ridgeway, 2007, Elith et al., 2008, Elith and Leathwick, 2013). In the case of regression trees, which are quite resilient to highly correlated predictors, multicollinearity is most likely to negatively affect the ability to interpret the model (Kuhn, 2008). However, strong correlation among predictor variables suggests that, from a statistical predictive perspective, they are indistinguishable from one another. Therefore, it is important to conduct visual and statistical assessments of the data for correlation among predictors to determine which, if any variables should be dropped from the model to improve accuracy of interpretation. Spatial autocorrelation (SAC) is a pattern in which observations are related to one another by their geographic distance and can effect model predictive performance (Crase et al., 2012). SAC of variables was assessed with spline correlograms, using the ‘ncf’ package (BjØrnstad, 2013) in R (R Core Team 2013). Correlation coefficients with values +1 are completely correlated and those of -1 completely dispersed. Values between approximately -0.3 to +0.3 are considered moderate and generally acceptable (Cohen, 1988)

Correlations among predictor variables, multicollinearity scatterplot matrices, correlation coefficients and Variance Inflation Factors (VIFs) were visualised and investigated in R using the ‘car’, ‘usdm’, ‘MASS’ and ‘clusterGeneration’ packages (Venables and Ripley, 2002, Fox and Weisberg, 2011, Naimi, 2013, Qiu and Joe, 2013). The most commonly used threshold value for correlations is 0.7 (Dormann et al., 2013); I also used this value. There are many maximum VIF threshold values cited as optimal in the literature (mostly >10) (Marquaridt, 1970, Neter et al., 1989, Kennedy, 1992, Mason et al., 2003, Hair et al., 2006), I selected the more conservative value of four recommended by a number of studies (Rogerson, 2001, O’Brien, 2007, Dormann et al., 2013). When predictors exhibited high levels of collinearity (indicated by above-threshold VIF values) or strong correlation (also above-threshold values), the variable with the highest value was removed as the first step in model simplification. Consistent correlations between [Chl *a*] and [Chl *a*] anomalies generally did not affect results as one or both were almost always removed from the final, simplified models. Distance to land was consistently and strongly correlated with most or all bathymetric variables resulting in its exclusion from all analyses.

2.3.8 Cross-validation of model

Data in BRT must be cross-validated to optimise the model predictive ability and estimate the optimal number of iterations. Using the 'gbm.step' package in R (Ridgeway, 2007, Elith et al., 2008, R Core Team, 2013), subsets of data are systematically removed for testing against those remaining. Geographic subsets have been determined to yield the most reliable results in BRT (Barbet-Massin et al., 2012), so my data were delineated latitudinally into three equal subsets for cross-validation. BRT results presented are the CV (predictive) deviance and its standard error (± 1), AUC values; the factors of strongest influence and notable interactions.

2.4 RESULTS

2.4.1 Analyses and errors

Many of our GLS tracks showed considerable shading and data errors in late July and August 2013. The month of August is the main monsoon season in the northern hemisphere (Martinez et al., 1998, Qu and Lukas, 2003). Consequently, these shading events may have been associated with an extreme storm event - typhoon Hakui - which tracked through the area used by Wedge-tailed shearwaters between 1 and 7 August 2012 (RSMC, 2012), causing heavy cloud cover that potentially affected data acquisition and accuracy. There were no excessively strong correlations (>0.70) or variance inflation factor values >4 in the analysis.

2.4.2 Broad movement patterns

Individual KDE/UD produced for each bird showed consistency of migratory pathways and core-use areas among individuals allowing pooling to a single kernel for oceanographic analysis (Fig. 2.1). KDE/UD of the entire migration (May – November) was used to visualise broad movement patterns of the birds throughout the non-breeding period (1392 locations). To assess greater detail of flight and activity patterns, further KDE/UD were produced for the migration pathway and the winter months (June, July and August) which are shown on Fig. 2.1.

Wedge-tailed shearwaters remained within the tropics during the non-breeding period, conducting a northwards migration from Heron Island in the southern GBR, to non-breeding foraging grounds in the area of the Caroline Islands and seamounts in the Federated States of Micronesia, the Magellan Seamounts and the Mariana Trench (Fig. 2.1). The migration crossed the Equator and exceeded a distance of 6000 km. The non-foraging area of maximum-use (the 95% kernel) and the core-use foraging area (50% kernel bound by ~140°E - 160°E and 7°N - 20°N) are centred on and to the southeast of the Mariana Trench over latitude 12°N and longitude 148°E. The average duration of the entire non-breeding period away from Heron Island was 161.9 (152-178) days.

Wedge-tailed shearwaters showed striking temporal consistency of departure from the breeding colony (Table 2.2) with most individuals departing the colony within a 7 day period beginning on the 16th of May. Only two individuals departed after the 22nd of May. There was an average outbound migration length of 21.5 days (range 14-53 d) to reach the core-use non-breeding area. Initially birds moved in a north-easterly direction towards the central Pacific Ocean (Fig. 1). After passing Vanuatu or the Solomon Islands and Nauru they then tracked along the Gilbert Ridge and circled north and west over the Marshall Seamounts and Micronesia to reach non-breeding grounds. All but 4 individuals took 14-19 days to arrive in core non-breeding areas (50% kernel; Table 2.2).

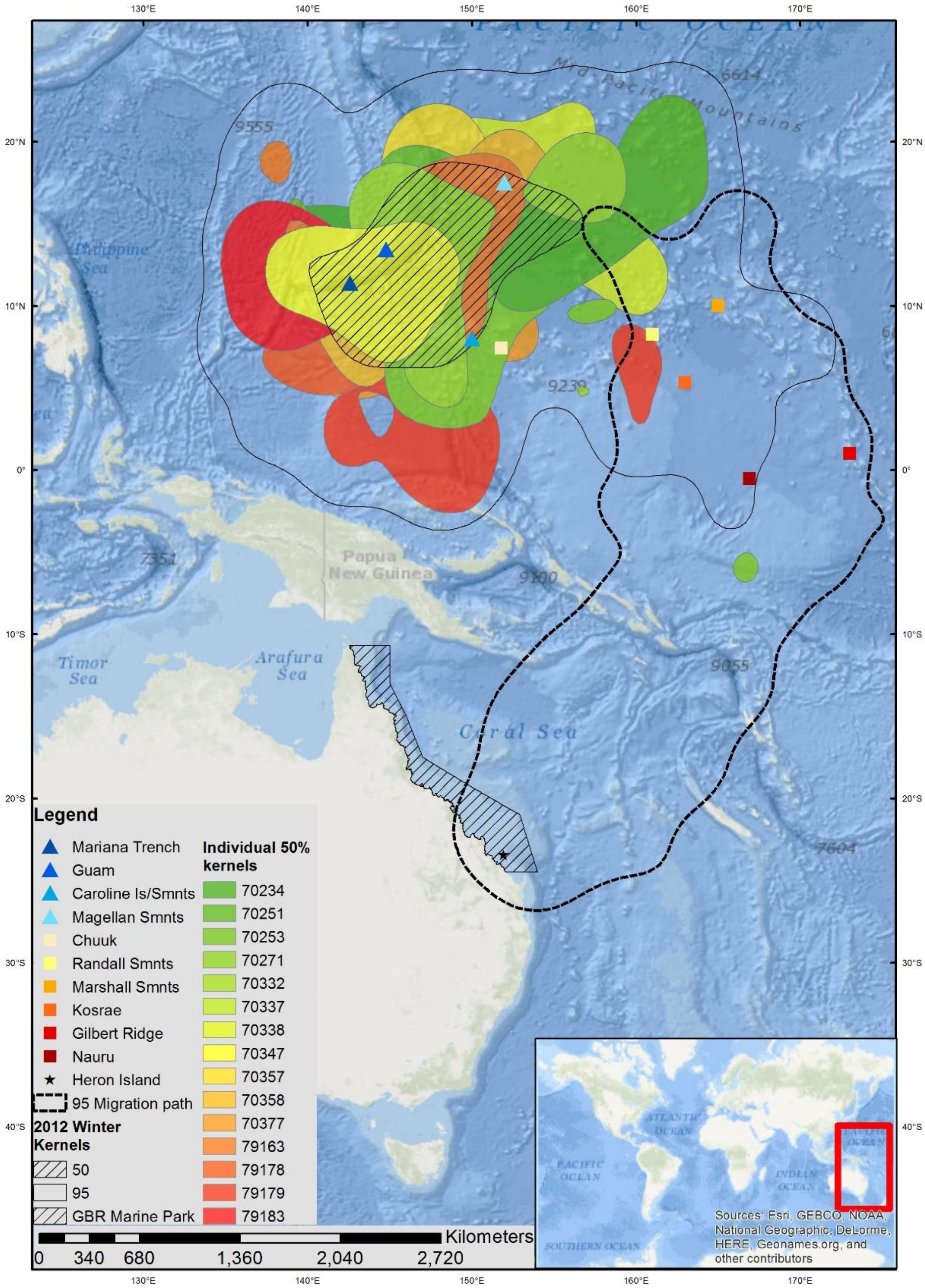

Figure 2.1: Non-breeding season migration data for 15 adult Wedge-tailed shearwaters from Heron Island on the Great Barrier Reef (GBR) tracked from May to October/November 2012. Core-use (50 percent UD - the lined area in the centre) and maximum use (95 percent UD - thin black outermost line) foraging area kernels for the winter months (June, July, August and September) for all birds are indicated. Core-use kernels (50 percent UD) for each of the 15 individual birds are represented by the smaller kernels in orange and green shades. The black dashed outline represents the migration pathway (95 percent UD) kernel used during May, Jun, September, October and November. Geographic stopover (□) and core-area locations (Δ) are indicated on the map with coloured points.

Wedge-tailed shearwaters showed striking consistency of departure from the breeding colony. Most individuals departing the colony within a 6-day period beginning on the 16th May. Only two individuals departed after the 22^{nd} of May. Initially birds moved in a north-easterly direction towards the central Pacific Ocean. After passing Vanuatu or the Solomon Islands and Nauru they then circled north and west and passed through Micronesia to reach non-breeding grounds, Individuals took approximately 2-3 weeks to arrive in core non-breeding areas (50% kernel).

Table 2.2: Summary of 2012 Heron Island Wedge-tailed shearwater winter non-breeding migration data. Timing and duration of overwinter migration, outbound migration and time spent in the core (50%) and maximum-use (95%) area. * Values uncertain or unknown due to equinox data loss.

BIRD ID	DEPARTURE FROM HERON IS.	RETURN TO HERON IS.	MIGRATION DURATION (DAYS)	ARRIVAL IN 50% CORE-USE AREA	COLONY TO CORE-USE AREA (DAYS)	TIME SPENT IN CORE-USE AREA (DAYS)
70234	22-May	16-Nov	178	5-Jun	14	144
70251	16-May	16-Oct	153	8-Jul	53	87
70253	23-May	3-Nov	164	6-Jun	14	125
70271	3-Jun	8-Nov	158	11-Jul	38	102
70332	22-May	25-Oct	156	8-Jun	17	123
70337	16-May	26-Oct	163	2-Jun	17	129
70338	22-May	29-Oct	160	24-Jun	33	111
70347	22-May	14-Nov	176	6-Jun	15	146
70357	19-May	3-Nov	168	3-Jun	15	142
70358	16-May	23-Oct	160	31-May	15	138
70377	22-May	24-Oct	155	8-Jun	17	*
79163	20-May	7-Nov	171	3-Jun	14	138
79178	18-May	24-Oct	159	6-Jun	19	*
79179	22-May	24-Oct	155	17-Jun	26*	26*
79183	21-May	16-Oct	148	1-Jun	15	144
MEAN			161.9		21.5	117.6
± S.E.			2.1		2.9	10.8
RANGE			152-178		14-53	26-146

Return to the Heron Island colony was not as synchronous as the outward migration, with return dates ranging over a month beginning mid-October (Table 2). In general, return migration was more direct. Once in the southern hemisphere birds appeared to follow a similar flight path to that of the outbound migration (Fig. 1). Unfortunately, the timing of the southbound migration fell close to the September equinox which caused significant data losses from late August into early October. As a result, data resolution from the return migration is consistently lower with portions of each return track needing to be inferred.

2.4.3 Stopovers

Most birds migrated relatively continuously and reached core-use non-breeding grounds in less than 20 days (Table 2). The Marshall and Randall Seamount groups west of the Marshall Islands, the Magellan Seamount chain to the east of the Mariana Trench and the states of Chuuk, Pohnpei and Kosrae were important foraging/'stopover' destinations, with all but 2 individuals spending time in these locations prior to reaching the 50% core area. This highlights some temporal inconsistency among individual migratory patterns. The three longest trips tracked along, or visited a more easterly seamount ridge that extends from Tuvalu to the Marshall Islands and then northwest to the Mariana Trench.

2.4.4 Non-breeding foraging activity

Most birds spent the greater portion of their time during the non-breeding period in the 50% core-use kernel, mostly during the months of June, July and August. The core-use kernel is located over a region which encompasses the East Mariana Basin, western Caroline Islands, Mariana trough, Mariana Islands, Magellan Seamount chain and the Mariana Trench – the deepest point in the World's oceans (Fig. 2.1). Lengthy gaps in the data for some individuals during the month of August, together with heavy data losses through September, preclude our ability to precisely determine the time spent within the core foraging kernel area. Nevertheless, most birds were active within the 50% kernel when I began to lose tracking accuracy in early to mid-August, and were still there when it was regained in early October.

2.4.5 Oceanography of winter core-use area

I analysed the influence of a set of explanatory oceanographic variables spanning the non-breeding region (Table 2.3), on bird foraging (568 foraging locations) and non-foraging (568 non-foraging locations) with BRT. The CV deviance of the BRT model was 0.395, SE. 0.014, and resulted in a high AUC value of 0.975 using 1550 trees (Fig. 2.2). Model simplification retained all variables in the model.

Table 2.3: Environmental predictor variables, their measured range, means (± SE) of core-use and maximum use areas and the relative influence in the boosted regression model of shearwater presence in the overwinter foraging (core-use) and non-foraging (maximum-use) areas.

Variable	Mean core-use area	Range core-use area	Mean max-use area	Range max-use area	Rel. infl (%)
SLA (mm)	1551±314	749 – 2079	877±771	-1759 – 2642	46.6
WIND (ms^{-1})	5±0.5	4.02 - 6.38	5.3±0.9	3.46 - 7.31	15.2
BATH (m)	-4558 ±1643	-214 – -9174	-4319±1118	-278 – -6625	10.5
SSS (psu)	34.4±0.2	33.93 – 34.92	34.5±0.4	33.65 – 35.35	9.1
SST (°C)	29.02±0.2	28.04 – 29.48	28.8±0.3	27.67 – 29.54	8.5
Distseam (°)	0.35±0.3	0 – 1.78	0.67±0.7	0 – 3.36	6.1
[Chl *a*] (mg m^3)	0.026±0.01	0.005 – 0.09	0.04±0.03	0.008 – 0.16	4.0

The strongest determinant of occurrence of shearwaters in the core-use foraging area was sea-level anomalies (SLA). The mean SLA in the core area was considerably higher than that in the 95-50% maximum-use area (Table 2.3, Fig.2. 2). Further, the birds used only areas with positive SLAs between 1000 mm and 2000 mm, which was a narrow subset of those available to them during the months spent in the core-use foraging area (Fig. 2.3).

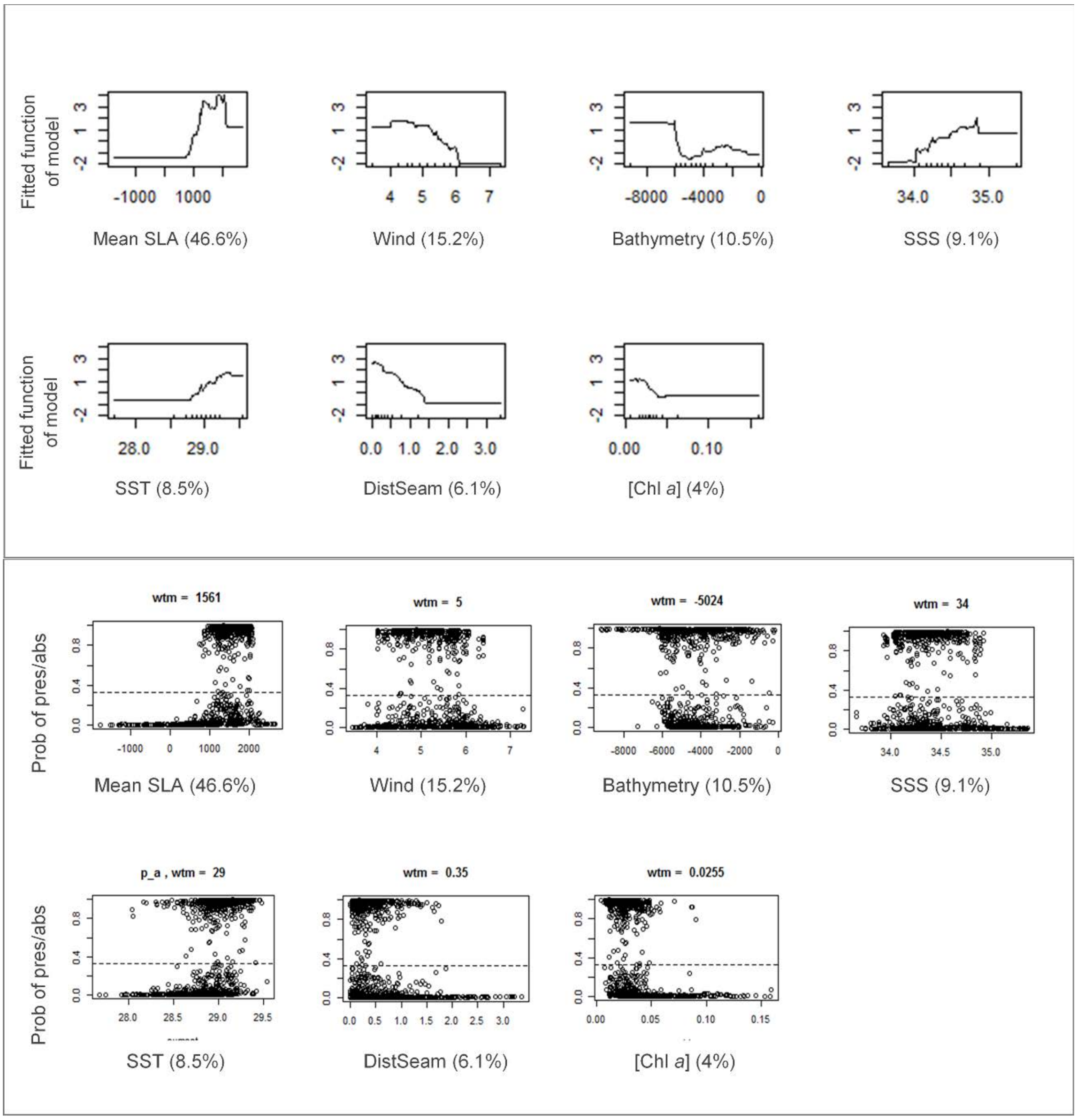

Figure 2.2: BRT model results of influential oceanographic parameters of Wedge-tailed shearwater non-breeding foraging areas. Partial dependence plots (top) show the relative influence of each factor on the activity of birds (core-use area in which birds are more likely to be foraging/present vs maximum-use area where birds are most likely transiting/‘pseudo-absent’) after accounting for the influence of all other factors (fitted functions of the model range from -2 which is lowest likelihood of occurrence to 3, the maximum likelihood of occurrence). Rug plots across the inside bottom axis show the distribution of bird presences across each variable in deciles. For an explanation of the variables and their units refer Table 1. Fitted Value plots (bottom) show the probability of birds occurring at any given value of each factor (these are the values of the data predicted by the model), relative to each explanatory variable. The weighted means (wtm) of each are indicated at the top of the plots.

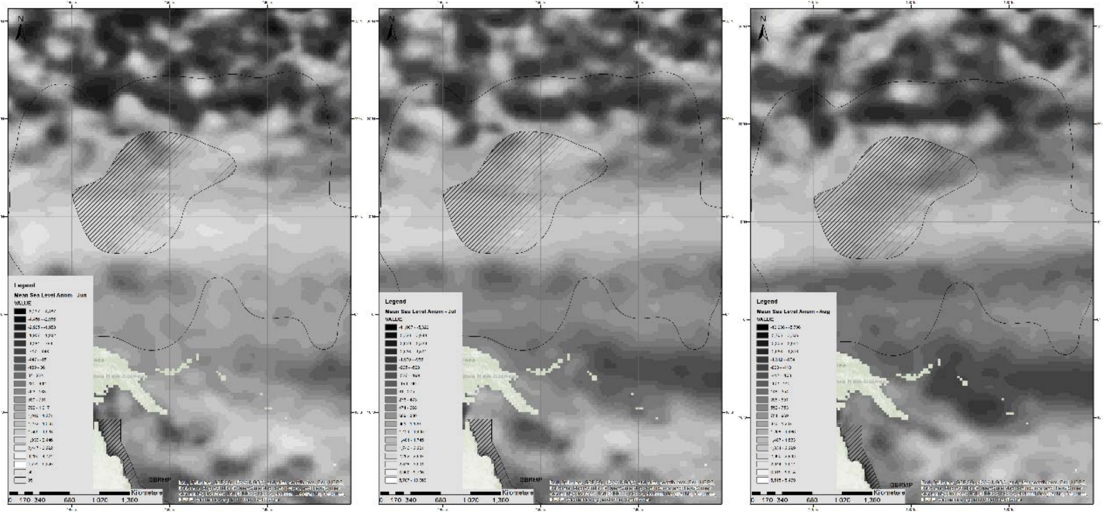

Figure 2.3: Sea level anomaly (SLA) maps of the Wedge-tailed shearwater non-breeding region through the winter months - June (left), July (centre) and August (right) - with the 50 percent (striped area) and 95 percent (black outline) winter foraging kernels overlaid. Lightest areas on the map indicate strongest positive SLAs and the blackest areas strongly negative anomalies. The lighter grey shades within the core use area are indicative of the moderately positive anomalies (~1000-2000 mm) that occur in the region where shearwaters are more likely to be foraging.

Wind speed exerted a strong influence of 15% in the model. Absolute wind speeds in core foraging areas were relatively low, ranging from 3-8 ms^1 across the region. Birds only occurred in a narrow range of wind speeds available to them, between ~ 4 - 6 ms^1, (~7.7 to 11 knots, Table 3).

The ocean depth of the region was an important predictor in the model of bird occurrence in the core-use area. This was anticipated given that a large section of the core-use area was located over the Mariana trench. Average depth in the core-use area was greater than that of the maximum-use area (Table 2.3). Furthermore, birds were always most likely to occur over the greatest depths (>6000 m; Fig.2 .2), and were often found in association with intermediate depths (4000-6000 m; Fig. 2.2). The regional topography, notably proximity to seamounts, had a negligible influence on the model but birds were nevertheless always predicted to be considerably nearer to seamounts in the core-use than maximum-use area (Table 2.3).

The sea surface salinity (SSS) of the oceans is about 35 psu (Lewis 1980). The SSS available to migratory shearwaters in their non-breeding region was generally lower (Table 3) with birds using a narrow range of values (34-35 psu). Wedge-tailed shearwaters were not predicted to occur in places where SSS was >35 psu (Fig. 2.2).

Absolute sea-surface temperatures (SSTs) were relatively unimportant in the model but were generally high across the total region, with minimal variation (27.7-29.5 °C; Table 2.3). However, in water below ~28.25°C shearwaters were never predicted to occur at high densities (Fig. 2.2).

While primary productivity ([Chl *a*] had the weakest influence on the model overall, the core-use area of GBR Wedge-tailed shearwaters was characterised by very low primary productivity ([Chl *a*] compared with the maximum-use area (Table 2.3, Fig. 2.2). Across the range of values, the lowest (below 0.05 mg m^3) were the most likely to explain the occurrence of foraging shearwaters (Fig. 2.2). In addition, Wedge-tailed shearwaters were not predicted to occur in regionally high [Chl *a*] areas (greater than 0.1 mg m^3). Nevertheless, the low level of influence in the model means this factor does not contribute to explaining the occurrence or not of shearwaters in the core or maximum-use areas.

The entire non-breeding region is prolific in the occurrence of seamounts and birds were always predicted to be nearer seamounts while foraging (Table 2.3). Most foraging birds were < 1° from seamounts and were never predicted to forage > 2° away (Fig. 2.2). Nevertheless, because the average distance to seamounts in the maximum-use region was also relatively close (Table 2.3), this resulted in a fairly small influence of this relationship over the ability of the model to predict occurrence.

In interpreting these BRT models it is also important to consider pairwise interactions (Elith et al. 2008). Only two such interactions were observed in the model. The first one was a strong interaction between SLA and bathymetry (491.8) that showed increasing bird foraging activity predicted over very deep bathymetry (> 6000 m) at SLA of 1000-2000 mm. SLA also strongly interacted with wind speeds in this model (720.4), where the occurrence of birds at 1500-2000 mm mostly occurred at wind speeds of 3-5 ms^1.

2.5 DISCUSSION

2.5.1 Migration patterns

The non-breeding migration patterns and behaviour of Wedge-tailed shearwaters breeding in the southern Great Barrier Reef (GBR), Australia, do not conform with the behavioural patterns observed for other migratory Procellariiformes tracked to date. GBR breeding shearwaters conduct a trans-equatorial migration converging on a single, core-use foraging area centred on the Federated States of Micronesia and the Mariana Trench, bathymetrically notable for being the deepest point in the world's oceans (Ritchie, 1958).

This pattern is strikingly similar to the lengthy between hemisphere migrations conducted by temperate Procellariiformes, rather than to the longitudinal non-breeding dispersal previously observed in Wedge-tailed shearwaters and other tropical Procellariiformes of the Indian Ocean (Catry et al., 2009b, Pinet et al., 2011). There is only one other tropical breeding Procellariiform that displays any kind of trans-equatorial movement during the non-breeding period - the New Caledonian subspecies of Gould's petrel (*Pterdroma leucoptera caledonia*). However, rather than migrating northward this population moves to the Eastern Tropical Pacific, dispersing to multiple core foraging areas which are in fact, primarily south of the Equator (Priddel et al., 2014).

2.5.2 Characteristics of the wintering area

Oceanographic characteristics of Wedge-tailed shearwater non-breeding foraging areas differ from those seen in previous studies of Procellariiformes. Unlike the winter foraging areas of temperate species, which are most frequently associated with elevated [Chl *a*] levels, Wedge-tailed shearwater wintering areas were typically characterised by very low primary productivity. Nevertheless, temperature and surface Chl were relatively unimportant, even when the former is high and the latter is low.

Similarly, other factors known to influence tropical species such as consistent strong prevailing winds (Pinet et al., 2011) were not observed in our study. Instead, wind speeds in non-breeding areas of Wedge-tailed shearwaters were very low (4-6 ms-^{1}; 7.7-11 knots), with these areas encompassing the Inter-tropical Convergence Zone (ITCZ or 'the doldrums') (Soloviev and Lukas, 1997), which causes a weakening of regional prevailing winds (Wyrtki and Meyers, 1976, Philander et al., 1987). Therefore, unlike Barau's petrel (Pinet et al., 2011), it is unlikely that strong winds within the core area contribute as significantly to frontal formation or prey availability.

The parameter which exerted the strongest influence over the distribution of foraging Wedge-tailed shearwaters in the present study was the very strong effect of moderately positive sea level anomalies (SLAs). This is the first time feeding relationships with SLAs have been reported for a tropical Procellariiform (Fig. 3). Positive SLAs indicate the presence of anticyclonic mesoscale eddies and indicate the approximate position and diameter of the eddy (Atwood et al., 2010, Jose et al., 2014) and these moved across the core-use foraging region through the boreal summer months. Mesoscale eddies are known to help aggregate prey that are targeted by seabirds (Lima et al., 2002, Sabarros et al., 2009).

Moderate SLAs, rather than strong positive or negative anomalies (<5 or >30 respectively), have been directly associated with increased recruitment of sardines (*Sardinops sagax*) (Hardman-Mountford et al., 2003), and likely other micronekton species that are prey for Procellariiform seabirds. Micronekton maxima are generally found in mesoscale eddies at the edges of the warmest waters (Young et al., 2001, Drazen et al., 2011). Overall, these associations, particularly the strong links with positive SLAs, suggest that mesoscale anti-cyclonic eddies are the primary oceanographic factor driving the foraging of shearwaters in core-use areas.

Currently, it is unclear precisely what oceanic processes concentrate prey at the edges of eddies (Sabarros et al., 2009). In temperate regions foraging associations with mesoscale oceanographic phenomena have been linked to enhanced primary productivity in surface waters (e.g. Polovina et al., 2001, Bograd et al., 2004, Saraceno et al., 2005). However, there was no evidence of elevated productivity associated with SLAs in the core non-breeding foraging area of GBR shearwaters. However, satellites only perceive [Chl *a*] at the surface and currently, we do not clearly understand the role of sub-surface productivity in stratified environments. For example, in situ sampling has shown that significant primary productivity at the thermocline can be associated with nutrient depleted surface layers. This phenomenon is called the Typical Tropical Structure (TTS) (Herbland et al., 1983) and has been related to high tuna and forage-fish biomass in the tropical Atlantic (Lebourges-Dhaussy et al., 2000). Such relationships clearly demonstrate a direct link between low surface productivity and elevated prey availability to top predators.

In the Western Pacific, temporal and spatial decorrelation between measures of primary production ([Chl *a*]) and the biomass of species at higher trophic levels, such as micronekton, may be caused by strong equatorial currents that advect productive water westward (Lehodey et al., 1998). In westward moving waters [Chl *a*] decreases as micronekton abundance increases, such that [Chl *a*] is depleted by the time large aggregations of micronekton reach the Western Pacific Warm Pool. If seabirds preferentially target micronekton, they would be expected to aggregate in areas with higher prey biomass. Hence, this phenomenon may explain how very low productivity ([Chl *a*]) in shearwater foraging areas can be associated with increased prey availability. This kind of decoupling is also thought to explain low productivity in the migratory destinations of Sooty shearwaters of the Atlantic Ocean (Hedd et al., 2012).

2.5.3 Associations with sub-surface predators

Despite performing a trans-equatorial migration, in general, the oceanographic characteristics of core non-breeding foraging areas for GBR breeding Wedge-tailed shearwaters are consistent with those observed for other tropical Procellariiformes (Catry et al., 2009a, Pinet et al., 2011). Correlations with frontal activity and/or commercial tuna catches has led previous authors to suggest that prey aggregation and sub-surface predator feeding at frontal margins are the most important characteristics driving tropical seabird foraging distributions (Catry et al., 2009a, Pinet et al., 2011), independent of (or even despite) low levels of observed primary productivity.

Therefore, a potential associated, or possible alternative mechanism driving the assemblage of GBR shearwaters in their non-breeding area is that they migrate in order to forage in direct association with increased sub-surface predator activity (particularly of tuna species). This is the model proposed to explain non-breeding distributions of Wedge-tailed shearwaters in both the Pacific (Ballance et al., 1997) and Indian (Catry et al., 2009a). Oceans, where considerable overlap with commercial tuna catch has been seen. Similarly, the region surrounding the core non-breeding foraging area of GBR shearwaters supports a commercially important fishery; the Western and Central Pacific Ocean Tuna Fishery (WCPTF), which produces the world's highest catch rates of tuna (Lehodey et al., 1997).

Our data provide the first indication that GBR Wedge-tailed shearwaters potentially interact with tuna while on their wintering grounds. Thus implying that facilitate foraging with subsurface predators may be important to the over-winter survival of these birds. Unfortunately, it is not possible to directly quantify the level of interaction using currently available data. However, the confirmation of such interactions are important and ongoing, as over-fishing is already cited as one of the primary causes contributing to global declines of both tuna and Wedge-tailed shearwaters (IUCN, 2013).

2.5.4 Conclusion

This study identifies the non–breeding foraging area that is important to migratory Wedge-tailed shearwaters of the GBR. The sample size in this study was relatively small and from a single year and migratory patterns may vary from year to year so, further years of tracking would be required to assess consistency of use and the relative importance of this region to this population. Interestingly, the same area is utilised by Streaked shearwaters (*Calonectris leucomelas*) that breed in Japan and migrate to the region during their non-breeding period (Takahashi et al., 2008, Yamamoto et al., 2014). Regional seamounts are known to support enhanced biodiversity and are effective aggregation points for pelagic predators (Morato et al., 2008), and the area is also used by endangered leatherback turtles (Roe et al., 2014). Therefore, this region may be a biodiversity hotspot for a number of apex predators. In addition, I demonstrate that, while the trans-equatorial migratory behaviour of this breeding population to a single foraging ground is so far unique to any tropical Procellariiform, the characteristics of their non-breeding foraging habitat are consistent with that of populations in other tropical regions. I see clear and strong associations with moderate positive SLAs that may indicate eddies and/or oceanic frontal activity, highlighting key factors driving beneficial foraging associations in tropical oceans. This sets tropical systems apart from those at higher latitudes, where elevated primary productivity is considered the principal driver of seabird foraging distributions. Our findings also highlight the need for ongoing research to quantify foraging associations with sub-surface predators in non-breeding areas as these foraging associations likely have important conservation implications, particularly given the significance of these interactions in other tropical regions. If true, the success of future seabird conservation may be intimately linked to the development and maintenance of sustainable pelagic fisheries in these same regions.

3. DISTANT FORAGING SITES FOR SELF-PROVISIONING

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The entire chapter was written by Fiona McDuie, with co-authors providing intellectual input to the design and implementation of the research and editorial contributions to the paper. Data collection, data analyses and production of tables and figures were conducted by Fiona McDuie.

3.1 ABSTRACT

To determine whether breeding tropical shearwaters use '*at-distance'* foraging locations during the long-trip phase of their bimodal foraging cycle, I deployed PTT satellite tracking devices on adult Wedge-tailed Shearwaters *Ardenna pacifica* of the Great Barrier Reef (GBR), Australia, during the chick-rearing period of three breeding seasons.

During the long-trip phase (8–14 d), a component of a bimodal pattern of foraging not seen previously in a tropical shearwater, birds travelled to distant sites in the Coral Sea between 300 and 1 100 km from the breeding colony, primarily to the north and east. At-distance foraging sites were in deeper water and closer to seamounts than were near-colony foraging sites used for chick provisioning, a combination of features indicating enhanced prey availability at these at-distance locations.

These findings imply that long-term reproductive success at this and likely other GBR colonies is strongly dependent on the continued stability of these at-distance locations, yet at present all are outside the current Great Barrier Reef Marine Park management zone. To adequately conserve GBR seabirds and other marine species using these resources, a conservation strategy integrated with current management practices is needed for the open waters of the Coral Sea.

3.2 INTRODUCTION

Procellariiform seabirds that breed in areas of low productivity are unable to simultaneously provide for chicks and maintain their own physical condition using only locally available food resources. Parents of temperate species overcome this limitation by using a bimodal foraging cycle composed of (1) multiple short trips to nearby, often resource-poor local waters to provision the chick, and (2) a single long trip to foraging grounds of higher productivity “at-distance” from the colony to replenish adult body reserves depleted during the short-trip phase (Weimerskirch et al., 1993, Weimerskirch, 1998, Magalhaes et al., 2008).

For this strategy to be viable, the food supply at distant foraging grounds must be reliable and provide sufficient return to offset the energetic costs of both the chick provisioning cycle and additional travel. As a consequence, at-distance foraging locations for temperate species consistently occur in regions of high productivity (Catard et al., 2000, Becker and Beissinger, 2003, Weimerskirch, 2007), where specific bathymetric or oceanographic features drive large forage-fish aggregations and increased prey encounter rates (Gende and Sigler, 2006). In years when local productivity is sufficient, some species are known to facultatively switch to a unimodal provisioning pattern using only near-colony resources (Granadeiro et al., 1998, Waugh et al., 2000, Welcker et al., 2009). This strategic variation further suggests that bimodal foraging is directly linked to poor levels of local prey availability.

In contrast, a model by Ropert-Coudert *et al.* (2004) highlights the disadvantages of extended travel to more distant foraging grounds during breeding in Adelie penguins (*Pygoscelis adeliae*) of the southern Ross Sea. This species is known to use a bimodal foraging strategy composed of long and short duration trips (Clarke et al., 1998, Clarke, 2001, Angelier et al., 2008). However, foraging individuals consistently undertake both trip types to the same foraging locations (Ballard et al., 2010). Similarly, in little auks (*Alle alle*), Wojczulanis-Jakubas *et al.* (2010) hypothesize that increased surface resting time in nearby foraging grounds, rather than extended travel time to distant locations, is their strategy. These models imply that when resources are patchy or unreliable, it is more advantageous for adults to replenish body reserves at near-colony foraging grounds while also minimizing the energetic costs of short-trip travel by not returning to the colony each night.

Little is known about how tropical Procellariiformes deal with the energetic constraints of breeding, especially as they are unlikely to be able to access highly productive temperate waters to compensate for poor local resource availability (Congdon et al., 2005). Wedge-tailed Shearwaters, (*Ardenna pacifica)*, that breed in the subtropics, in Hawaii and on Lord Howe Island, access 'near-colony' foraging sites that enable them to maintain condition, while simultaneously provisioning chicks. These populations use a uni-modal foraging strategy (Baduini, 2002, Peck and Congdon, 2005). By contrast, a breeding colony of these shearwaters in the tropical waters of the Australian Great Barrier Reef (GBR) is known to employ a bimodal foraging cycle during the chick-rearing portion of breeding season, interspersing multiple, short, 1-2 d trips with a long-trip averaging 8 -10 d. During short-trips, changes in adult body mass suggest the majority of food obtained is provisioned to the chick and that adult reserves are depleted. The demonstrated increase in adult mass over the subsequent long-trip implies this trip serves to replenish lost condition (Congdon et al., 2005, Peck and Congdon, 2005).

While the adults at this GBR colony do use a bi-modal foraging strategy, it is not known whether trips are conducted in two discrete foraging habitats with adults traveling to distant foraging grounds on the longer trips, or in one habitat, with adults remaining in the relatively oligotrophic near-colony waters of the GBR (Congdon et al., 2005). If the former is true, then the viability of Wedge-tailed Shearwater colonies on a regional scale is likely dependent on a small number of at-distance sites where there is enhanced prey accessibility. Since the Wedge-tailed Shearwater populations of the southern GBR are amongst the largest in the Pacific (Dyer et al., 2005), such key foraging sites may have considerable conservation importance.

My objective in this study was to examine the long-trip foraging behaviour of Wedge-tailed Shearwaters breeding on Heron Island, in the southern GBR, to determine whether they travel to distant locations on these trips, or merely spend more time in foraging. I also aimed to (1) identify the potential number and location of these sites, (2) determine if they are associated with specific bathymetric phenomena known to enhance prey availability to top predators, and (3) determine their relationship to current conservation and management zones.

3.3 METHODS

3.3.1 Study site and methods

This study was conducted at Heron Island (23° 26’ S, 151° 51’ E), in the Capricorn Bunker Group of reefs in the Great Barrier Reef (GBR) Marine Park, Australia (Fig. 3.1), in February and March 2006, 2011 and 2012. The timing coincided with the chick-rearing portion of the Wedge-tailed Shearwater breeding season (Table 3.1), which runs from October to May with chicks hatching in early February. The bimodal foraging cycle occurs throughout the chick-rearing period. To ascertain the timing of adult foraging trip cycles, I monitored the arrival and departure of each adult at 20–30 nests daily. Burrow entrances were partially obstructed with markers that allowed adult visits to be detected, with nests being checked every 10 min. Nests were then obstructed with clear plastic so that adults could be captured on departure from the nest. At this time, individuals were identified and weighed; chick weights were also taken to determine meal masses. Knowing adult visitation schedules and timing enabled us to predict when adults would likely depart on long trips. In some instances, both adults were found to visit the nest on the same night. This was a clear indication that the adult that had been attending the nest the previous week was about to depart on a long trip (Congdon et al., 2005), so a logging device was deployed. Otherwise, I deployed the logging device on the short-tripping adult on the eighth day of its short-trip cycle, in anticipation of long-trip departure. Long trips were defined as longer than five days (Congdon et al., 2005), during which time the bird did not return to the colony to provision the chick.

Solar-powered ARGOS Platform Terminal Transmitters (PTT-100) (Microwave Telemetry, USA) provide precise location information (accuracy ~150-250m) in “real-time” via ARGOS satellites (http://www.argos-system.org). PTTs weighing 9-11.2g; measuring ~ h: 17 mm, l: 36 – 40 mm, d: 16 mm, were mounted at the base of an adult’s tail feathers with TESA© tape for the duration of one long-trip per adult (3 in 2006; 4 in 2011 and 6 in 2012). I deployed devices on adults weighing > 380g in order to maintain the weight of the transmitter within the accepted 3-5% body weight limits for seabirds (Kenward, 2001, Phillips and Croxall, 2003) and devices only ever remained attached for one single long trip**.** Adult weight range of Heron Island Wedge-tailed Shearwaters during breeding is ~ 350-500g (McDuie & Congdon *unpub. data*). No evidence of birds attempting to remove the tape, the device, or any damage to tail feathers was observed. Devices were deployed on adults upon their exit from the nest following chick feeding. Duty cycles for transmitters in 2006 and 2012 were set to 12h on/48h off (default factory setting by manufacturer) while in 2011 setting was on “continuous”, which means production of location fixes is fairly consistent, depending upon device battery power, and at least once daily (Table 3.1). Batteries recharge via solar power, resulting in obligatory downtime for recharge that causes occasional interruptions in data. I would recommend use of the continuous setting in tropical environments where there appears to be sufficient sunlight for frequent recharge, thereby considerably increasing the amount and resolution of data obtained. Moreover, this better allows assumptions on types of activity and when birds are more likely to be actively searching or foraging for prey.

Based on average flight speeds of ~30-33 km h^{-1} observed in this, as well as other studies, I removed any data points that required flight speeds > 50 km h^{-1} or > 35 km h^{-1} sustained over 48 hrs (following Catry et al., 2011). Unfortunately, due to the temporal irregularity of fixes and obligatory recharge down-times, it is not possible to distinguish between foraging and transit activity. Therefore, I employed kernel density estimation (KDE) to estimate the home range of the birds with utilization distribution (UD) contours (25, 50, 75, 99%) The 99% and 50 % UD contours (kernels) represented the observed overall and core-use foraging areas for long-tripping shearwaters, respectively. Foraging, (i.e. when birds are moving at low speeds with many changes in direction), is more likely to accrue larger numbers of satellite fixes over an area than when birds are transiting more rapidly over the same area. Therefore, core-use areas (50 % kernels) indicate the most important locations and are more likely to highlight foraging activity (Hamer et al., 2007, Catry et al., 2009b).

Greater than 90% of short-trips used for chick provisioning are 1-2 d (Congdon et al., 2005) and foraging occurs primarily during daylight hours. Therefore, to determine if birds on long-trips consistently foraged outside the area used during short-trip cycles, a maximum short-trip foraging distance was defined as the area that could be accessed by an adult on a two day foraging trip with average flight speeds of ~30 km h^{-1}. This delineated an area of ~300km radius from the colony. Results from the 50% kernel analysis were then overlaid on this region to determine if the majority of long-trips fell outside this zone.

3.3.2 Analyses

Kernel analyses were performed in R version 2.15.2 (R Core Team, 2013) using the adehabitat package (Calenge, 2006, Calenge, 2014, see chapter 2, pages 19-21), KDEs were created with a smoothing factor (h) of 20 km based on shearwater foraging ecology and transmitter accuracy. Inter-annual differences in duty cycles resulted in widely divergent numbers of fixes obtained from loggers among years (Table 3.1). For this reason I produced separate kernel densities for each year on one map to highlight overlap and differentiation of core-use areas between and among years.

To determine if at-distance foraging locations were more closely associated with specific bathymetric features known to enhance prey availability, data-logger points within each 50% long-trip kernel were designated as the most likely to be foraging locations (Powell, 2000, Wood et al., 2000, Iverson and Esler, 2006), (n = 309; Table 3.1). The characteristics of bathymetry and topography in these areas were compared with those in the maximum-use or non-foraging area (n = 309) produced randomly from within the defined maximum short-trip foraging zone. To undertake this analysis, Etopo1 Ice surface bathymetry data (1 km resolution) were downloaded from the US National Geographic Data Center (http://www.ngdc.noaa.gov/mgg/global/relief/ETOPO1/image/).

3.3.3 Oceanography

Seamounts, in particular, are a distinctive bathymetric feature known to increase prey availability to marine apex predators such as seabirds (Morato et al., 2008, Morato et al., 2010a). Therefore, I also tested whether data-logger points within each 50% long-trip foraging kernel were closer to seamounts than locations within the short-trip foraging zone. This analysis was done with ArcGIS 10.2 for desktop. The seamount location map was produced from: the Global database of undersea features (http://www.gebco.net/data_and_products/undersea_feature_names), Deep Reef Explorer high resolution depth model for the Great Barrier Reef and Coral Sea (http://www.deepreef.org/bathymetry/65-3dgbr-bathy.html) (Heap, 2008, Beaman, 2010), and the Seamounts Catalog of the Seamount Biogeosciences Network (SBN)(http://earthref.org/SC/). I assessed distance to the nearest seamount and difference in the average depth of points in foraging and non-foraging locations with Welch's two-sample *t*-tests in R, which assume unequal variances and applies the Welch’s df modification (R Core Team, 2013).

Table 3.1: Tracking data from Wedge-tailed shearwaters 2006, 2011 and 2013a.

Logger ID	Bird ID	Deployment dates	Duration of trip, d (d with fixes)	Total number of fixes	Average fixes d-1 (only days with fixes)	Maximum distance from Heron Island
			2012			
56054[b]	20	27 Feb-7 Mar	8 (4)	9	2.25	800
56055	28	28 Feb-11 Mar	13 (8)	15	1.88	540
62359	30	17-30 Mar	14 (7)	19	2.71	535
62361	36	2-12 Mar	11 (6)	20	3.33	675
62359	48	8-16 Mar	9 (6)	18	3.00	385
62361[b]	50	16-23 Mar	8 (3)	10	3.33	-
			2011			
56054	1	12 Feb-4 Mar	21 (9)	157	7.48	720
56054	10	5-14 Mar	9 (9)	107	11.89	385
56055	3	16 Feb-1Mar	13 (13)	158	12.16	1150
56055	17	3-10 Mar	7 (7)	54	7.71	340
			2006			
62359	5	18 Feb-2 Mar	14 (8)	32	4.00	750
62360	2	13-27 Feb	14 (7)	31	4.43	580
62361	4	9-24 Feb	15 (7)	15	2.14	550

[a] Deployment data from PTT-100 satellite transmitters for all Wedge-tailed shearwaters long foraging trips.

[b] Logger failures in 2012 resulted in two incomplete tracks. Bird #62361 was unlikely to have reached its maximum distance and was not included in further analyses.

3.4 RESULTS

In total, I obtained 645 fixes from 13 transmitter deployments during the study, 309 of which were within the 50% kernels (n=41, 2006; n=205, 2011and n=59, 2012; Table 3.1; Fig. 3.1). The average length of a long trip was 12d SD 1.97 and average lengths by year were: 2006:14.3d SD 0.76; 2011: 12.5d SD 2.17; 2012: 10.5d SD 1.61. The average maximum distances travelled from the colony each year were: 2006: 626.67 km, 2011: 648.75 km and 2012: 587 km.

Eleven of 13 tracks provided position fixes for the full length of a long trip, although not always for each day of tracking. The remaining two loggers, on Birds #62361 and #56055, lost their antenna and only tracked for 2.5 and 4 d of an 8 d trip, respectively. In general, birds reached the maximum extent of their long-trips around the halfway point. Therefore, it is unlikely Bird #62361 was tracked to, or near, its maximum distance from the colony and so this track was excluded from further analyses. Otherwise, all birds on long-trips travelled to locations that were > 300 km from the breeding colony and all but one adult travelled > 450 km. The maximum distance travelled by an adult in a single day of constant flight was 450-500 km, giving an average sustained speed flight of ~30-35 km/h during daylight hours.

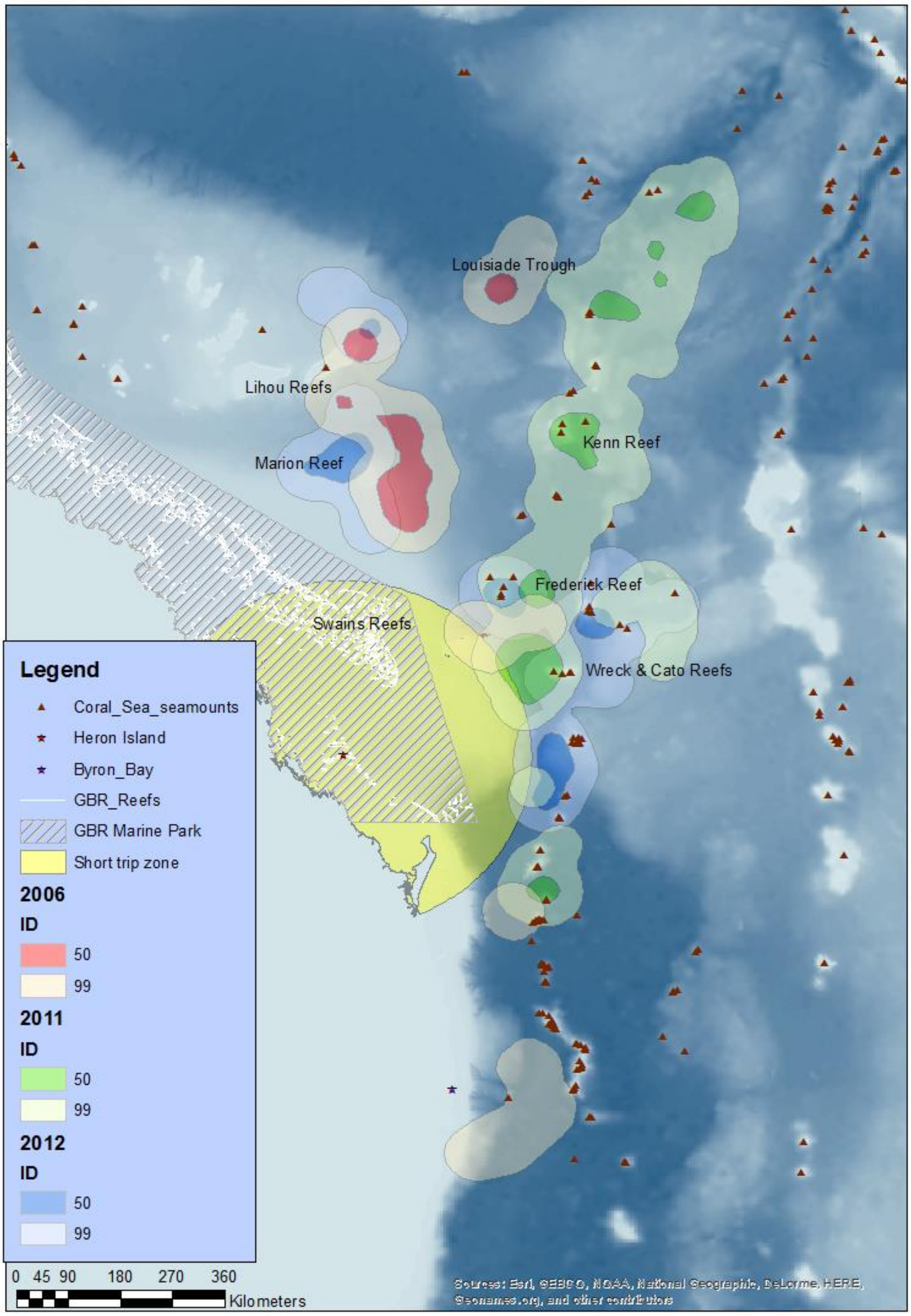


Figure 3.1: Regional map of Coral Sea with 50% and 99% kernels – all years of tracking. PTT electronic satellite transmitter tracks of 13 long-tripping Wedge-tailed shearwaters of Heron Island, Great Barrier Reef (GBR) in 2006 (red shades), 2011 (green shades) & 2012 (blue shades). Kernels are mapped with the darker coloured areas representing the 50% (core-use) kernels and lighter areas the 99% (maximum use) kernels. Non-use region is designated by the yellow area extending to a maximum radius of 300km from the Heron Island colony, which is indicated by red star. The GBR Marine Park is indicated by the dark grey striped zone. Seamounts are indicated by brown triangles.

In 2006, two individuals travelled northward: one stopping within the Swains Reefs National Park and at Marion Reefs (Fig. 3.1), a maximum distance of ~ 500 km from Heron Island. The second travelled further northward visiting Lihou Reef Nature Reserve and the Louisiade Trough in the central Coral Sea, a round trip of almost 2,000 km. The third individual spent a number of days off the northern coast of New South Wales (NSW), approximately 750 km south of Heron Island. It followed a deep ocean seamount ridge on its return and spent almost a week foraging off the edge of the continental shelf ~400 km east of Heron Island.

In 2011, three adults travelled to locations in the central eastern Coral Sea at distances of 400 (Wreck reefs), 700 (seamounts) and 1,100 (Louisiade Trough) km from Heron Island (Fig. 3.2). All locations were well outside the Great Barrier Reef Marine Park (GBRMP). The fourth adult tracked in 2011 spent approximately a week foraging at a location ~ 200 – 250 km southeast of Heron Island, reaching a maximum distance of approximately 340 km.

In 2012, birds were tracked to the same region north of Heron Island as in 2006 and 2011**,** as far as the Lihou Reefs (Fig. 3.1). They also travelled to the east around Cato, Wreck, Kenn and Frederick Reefs (Fig. 3.1), to other locations visited by birds in 2011. Birds from all years routinely conducted long trips in excess of 2,000 km. There was some congruence among core-use areas (50% kernels) across years but in each year birds were also tracked to one or more additional locations not used previously (Fig. 3.1).

In both 2011 and 2012, multiple tracks followed a deep ocean seamount ridge extending through the Coral Sea northeast of Heron Island (Fig. 3.2). During these trips, foraging occurred in the vicinity of Wreck, Kenn and Frederick Reefs (Fig. 3.1) or the nearby continental shelf edge, as well as adjacent to the Louisiade Trough 1,200 km northeast of Heron Island. Shearwater long-trip foraging locations (50% kernels) were significantly closer to seamounts and in deeper water (bathymetry) than non-foraging locations (99% kernels; Table 3.2).

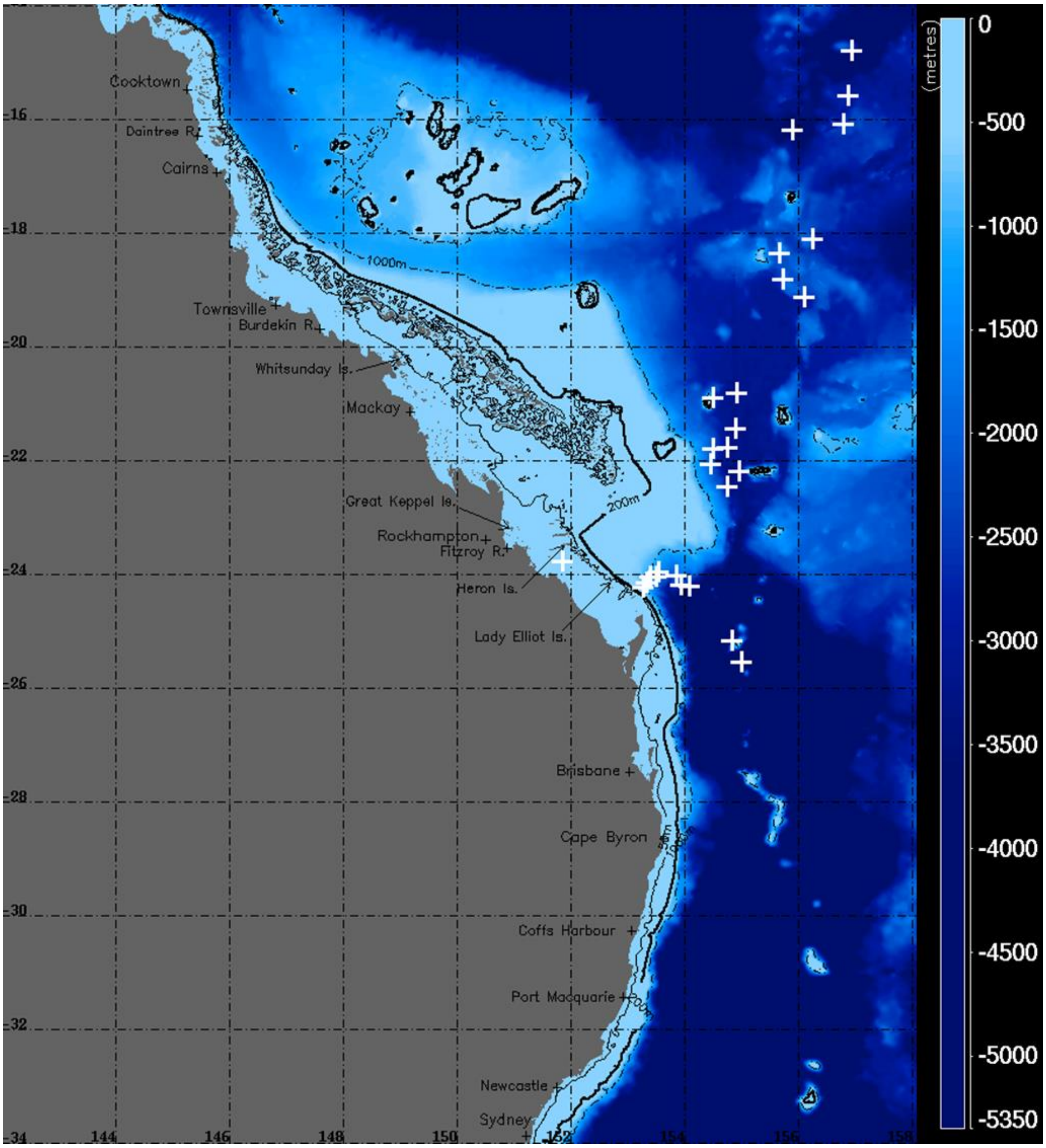


Figure 3.2: "At-distance" foraging tracks with regional bathymetry in 2011. Long-trip foraging tracks from Heron Island, GBR (n = 4), determined from electronic satellite transmitters deployed on Wedge-tailed Shearwaters during the breeding season are overlaid on bathymetric gradient map of the GBR and Coral Sea region. Crosses show fixes from shearwater tracks highlighting occasions when shearwaters were positioned over seamounts or steep bathymetric gradients/drop-offs.

3.5 DISCUSSION

On long-trips, adult Wedge-tailed Shearwaters at Heron Island foraged a long way from the breeding colony. Long-trip foraging areas were consistently outside the zone adults could access on short, chick-provisioning trips of 1-2 d at average flight speeds. Therefore, in general, tropical Wedge-tailed Shearwaters of the southern GBR access foraging locations for self-provisioning that are both outside and independent of sites used to obtain food for chicks. This result implies that adults do not self-provision by remaining at-sea locally and longer to offset the energetic cost of returning to the colony each day (as suggested in the model of Ropert-Coudert et al., 2004, and Wojczulanis-Jakubas et al., 2010).

Instead, my results suggest that Heron Island shearwaters travel to distant locations in order to access sites that provide greater prey availability than near-colony sites, as seen in temperate Procellariiform species (Weimerskirch et al., 1994, Weimerskirch and Cherel, 1998). In support of this I find clear links between bathymetry and long-trip foraging locations. Long-trip foraging sites are characterized by deep water in close proximity to rapidly changing bathymetric gradients near seamounts. Such areas are known to be associated with increased biodiversity (Clark et al., 2010) and also to facilitate prey aggregation and use by top predators such as seabirds and tuna (Blaber, 1986, Haney et al., 1995, Morato et al., 2008).

Tropical seabirds have well-known foraging associations with sub-surface predators that enhance prey availability by driving forage fish toward the surface when they feed (Au and Pitman, 1988, Le Corre and Jaquemet, 2005, Spear et al., 2007). Importantly, my results also imply that prey availability near the colony is unlikely to be able to support both chick and adult requirements simultaneously and that access to at-distance foraging locations is necessary to maintain viable shearwater colonies in this region. These findings are consistent with previous findings that the tropical waters surrounding Heron Island are relatively low in productivity (Peck et al., 2004).

There are a number of possible explanations for the variation in at-distance foraging locations used by Wedge-tailed Shearwaters from one year to another. Firstly, location choice may simply differ among individuals with some adults having preferred locations, a trait that has been observed in both Shy Albatross *Thalassarche cauta* (Hedd et al., 2001) and Cory's Shearwaters *Calonectris diomedea* (Paiva et al., 2010). Similarly, variations in parental sex, age, experience or even starting physical condition may influence at-distance foraging location choice (e.g. Norris, 1967, Weimerskirch et al., 1997). Conversely, birds may, on any given day, depart on a foraging trip with the choice of foraging location being influenced by day-to-day, or season-to-season, spatial and temporal variation in environmental parameters such as wind speed and direction (Navarro and González-Solís, 2009), ocean productivity (Navarro and González-Solís, 2009), sea surface temperature (SST) (O'Hara et al., 2006), salinity (de León and Mínguez, 2003), or patterns of oceanic circulation (Reese and Brodeur, 2006). The importance of these various parameters in determining at-distance foraging location choice remains to be tested.

There is a trade-off between potential energy gains and expenditure on long distance flight for central-place foraging seabirds (Weimerskirch, 1998), such as Wedge-tailed Shearwaters. The fact that these pelagic foraging seabirds travel such great distances in order to replenish their body reserves implies that the use of distant foraging grounds must be advantageous and profitable. Accordingly, these sites are likely known locations that provide some guaranteed rate of prey encounter upon which fitness and long-term reproductive rates and success depend.

Importantly, the majority of at-distance foraging locations detected in the present study, and the locations most heavily used, occur outside the current GBR Marine Park management zone. It is not known whether Wedge-tailed Shearwater populations breeding elsewhere in the Coral Sea region, particularly New Caledonia, are also dependent on the same or similar locations. If so, the breeding success of this species both in the GBR and throughout the region may be strongly dependent on the continued stability of food availability at these locations. Moreover, Wedge-tailed Shearwaters are known to forage in mixed-species flocks (Ballance et al., 1997, Jaquemet et al., 2004), so numerous other seabird species representing different foraging guilds may be similarly dependent upon these same food resource environments.

Wedge-tailed Shearwaters are particularly sensitive to climate-driven changes in the marine environment (Smithers et al., 2003, Peck et al., 2004, McDuie et al., 2013, Weeks et al., 2013). They are also sensitive to oceanographic variations known to impact breeding participation and food availability to other less trackable seabird species of the GBR (Smithers et al., 2003, Devney et al., 2010). This, as well as the fact that Wedge-tailed Shearwaters are wide-spread and abundant (IUCN, 2013), means they represent a suitable "umbrella species" (Lambeck, 1997) useful for identifying a wide range of human-induced impacts on upper trophic level marine predators (Roberge and Angelstam, 2004) and for developing strategies to effectively manage critical seabird foraging habitats of the GBR and Coral Sea region.

4. THE IMPORTANCE OF EDDIES AND FRONTS FOR BREEDING TROPICAL PROCELLARIIFORMES WHEN SELF-PROVISIONING

This chapter is in preparation for submission to Marine Ecology Progress Series as: “The importance of eddies and fronts for self-provisioning, breeding tropical Procellariiformes” by F McDuie, S. J. Weeks, M.G.R. Miller and B. C. Congdon.

The entire chapter was written by Fiona McDuie, with co-authors providing intellectual input to the design and implementation of the research and editorial contributions to the paper. Data collection, data analyses and production of tables and figures were conducted by Fiona McDuie.

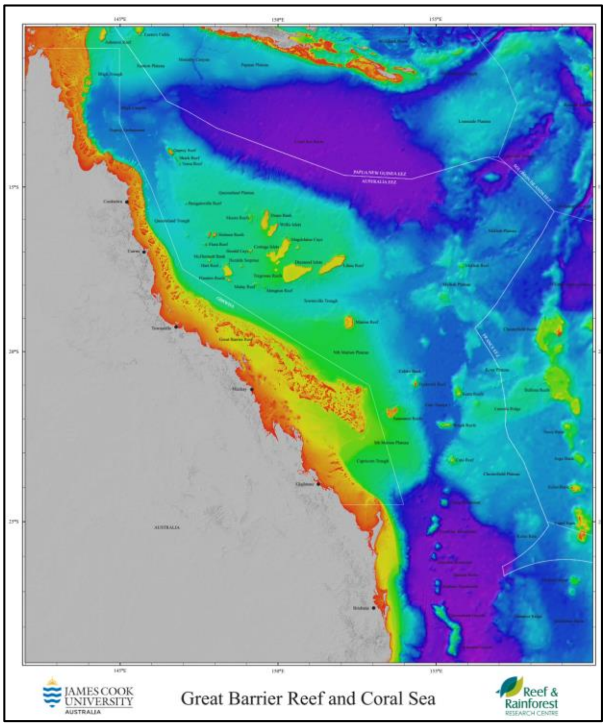


Figure from Beaman, R.J. (2010) Showing the Great Barrier Reef and Coral Sea region where wedge-tailed shearwaters forage during long trips from the Heron Island colony.

4.1 ABSTRACT

There is relatively substantive knowledge of the mechanisms driving prey distribution and availability to upper level predators in temperate marine environments but less so for the tropics. Breeding wedge-tailed shearwaters (*Ardenna pacifica*) of the Great Barrier Reef (GBR) use locations 'at-distance' from the colony when self-provisioning during long-trips of their bimodal foraging cycle. I deployed PTT satellite transmitters on adult shearwaters over four breeding seasons to identify preferred foraging locations. This was overlaid with high resolution, satellite derived oceanographic data to characterise important foraging grounds and understand the mechanistic drivers in these places.

Long foraging trips culminated at foraging locations that were always greater than 300km and up to 1400km from the Heron Island colony, in the Coral Sea. Site use varied among years but specific locations were reused within and among seasons. Foraging sites are generally characterized by deep water in close proximity to rapidly changing bathymetric gradients, near seamounts. In most years sites were strongly influenced by low to moderately positive sea level anomalies and moderate current speeds. Combined, these characteristics unambiguously describe use of local to mesoscale upwellings, eddies and frontal systems adjacent to seamounts or other topography and highlight their importance for enhancing prey availability to shearwaters at convergences and eddy peripheries. These phenomena result from large-scale ocean currents interacting with rapid bathymetric change. They are known to be associated with increased biodiversity and also to facilitate prey aggregation and use by sub-surface predators such as billfish and tuna.

In general, seabird foraging activity at these sites is not correlated with elevated primary productivity. Importantly, most frequently used at-distance foraging sites are outside the management zone of the GBR Marine Park (GBRMP) and this information will help identify potentially critical at-sea foraging areas for chick-rearing seabirds that are chronically under-represented in conservation strategies for pelagic species.

4.2 **INTRODUCTION**

4.2.1 Conservation and climate change

Seabird conservation efforts conventionally focus on breeding colonies and tend to disregard at-sea food resources. However, for conservation to be effective it is essential to protect not only colony environments but also important oceanic feeding grounds. This could be particularly important for seabirds like the Procellariiformes (tube-nosed seabirds) that feed entirely in the pelagic environment which are the most remote and homogeneous areas of the ocean (Wommack et al., 2011). Adequate protection of foraging grounds can only be afforded with accurate knowledge of the precise locations of these critical areas and the mechanisms that enhance prey availability. Such information may be even more important to the conservation of tropical seabird foraging environments, which are considered relatively resource-poor. Limitations to the extent and availability of viable foraging resources increases the threat posed by climate-driven changes, such as those which occur under the influence of the El Niño Southern Oscillation (ENSO). These impacts, particularly those associated with increases in sea-surface temperatures (SSTs) have affected seabirds globally (Schreiber and Schreiber, 1984, Anderson, 1989, Smithers et al., 2003, Devney et al., 2009). It seems clear that, should detrimental climate-driven changes increase in severity or number, the negative impacts to seabirds and their resource environments, would also increase concurrently.

4.2.2 Dual foraging and productivity

Beneficial foraging areas and ‘hotspots’ of prey availability or productivity are often remotely situated, at-distance from seabird breeding colonies. Central-place foraging seabirds are constrained in the distance they can travel when foraging by the need to provision their chick. Procellariiform species often counteract the low profitability of near-colony foraging grounds by employing a dual-foraging strategy to reach distant locations far from the colony, which, in the case of temperate/sub-polar Procellariiformes, are generally more productive areas (Chaurand and Weimerskirch, 1994, Weimerskirch et al., 1994, Weimerskirch, 1998, Baduini and Hyrenbach, 2003, Weimerskirch, 2007). By contrast, the distant foraging grounds of a dual-foraging tropical Procellariiform, the wedge-tailed shearwater (*Ardenna pacifica*), appear to be more related to bottom topography rather than direct measures of productivity *per se*, but these relationships have not been quantified in detail (McDuie et al., 2015).

Productivity, in the examples above, refers to chlorophyll *a* concentrations which are used as a proxy to represent prey availability and abundance (Paiva et al., 2010). It is with measurements such as these that the location of large-scale, system-regulating oceanographic phenomena can be identified, through gradients or abrupt changes in observable levels of these parameters (Saraceno et al., 2005).Variations, gradients and the presence of oceanic phenomena such as frontal systems, eddies and upwellings, can then be tested to determine their influence on distribution of seabirds. For example, seabirds of the California Current System, including various Procellariiformes, gathered along upwellings and frontal features identified by elevated chlorophyll *a* concentrations (Ainley et al., 2005). Similarly, Shy albatrosses (*Thalassarche cauta*) breeding around Tasmania forage in shelf areas at which productivity is enhanced by the interaction of currents (Brothers et al., 1998). Seabird foraging activity is frequently correlated with productivity and prey aggregations driven by fronts, eddies and other ocean dynamics across large-scale oceanic environments, as illustrated by these examples.

4.2.3 Thermal ocean boundaries

In the pelagic environment, vertical mixing of cooler, nutrient and oxygen-rich sub-surface water can create measureable thermal gradients which enhance productivity (Owen, 1981, Lutjeharms et al., 1985, Spear et al., 2001, Hunt Jr and Schneider, 2009). Thermal boundaries can regulate prey movement and availability (Weimerskirch et al., 1995, Waugh et al., 1999) and many marine predators target such gradients due to the potential for increased interaction with prey (Morato et al., 2008, Drazen et al., 2011). Bost *et al.* (2009) in their review, demonstrate this link with a correlation between maximum seabird density and prey aggregations at Southern Ocean frontal convergence zones defined by SST gradients. Foraging seabirds in the Pacific and Indian Oceans have also been associated with horizontal frontal convergences characterised by anomalous SSTs (Spear et al., 2001, Hyrenbach et al., 2006, Jaquemet et al., 2014).

4.2.4 Ocean dynamics

However, it is not only thermal or productivity gradients which highlight the presence of mesoscale oceanographic features. Anomalies in the height of the sea surface revealed undefined mesoscale features in the southern Indian Ocean, and highlighted the fact that grey-headed albatross (*Thalassarche chrysostoma*) foraged at the interface between the extremes of positive and negative anomalies (Nel et al., 2001). Other species, including sooty (*Sterna fuscata*) and bridled terns (*S. anaethetus*) and wedge-tailed shearwaters have also been found to be significantly more common in sub-tropical convergence zones of the Indian Ocean (Hyrenbach et al., 2006). So, in general, mesoscale oceanic phenomena including eddies, convergence zones and up and downwellings affect biological processes, biodiversity and the aggregation of prey (Boehlert and Genin, 1987, Haney et al., 1995, Morato et al., 2010a) and these links can be revealed by various physio-chemical oceanographic parameters of the water.

4.2.5 Sub-surface predator interactions

However, seabirds are not the only predators that converge on micronekton, the small free-swimming organisms including forage-fish, at marine hotspots (Blackburn, 1968, Brodeur and Yamamura, 2005). Distributions of sub-surface predatory marine species like tuna have also been related to these aggregations in the periphery of anticyclonic eddies (Bertrand et al., 2002, Sabarros et al., 2009, Tew Kai and Marsac, 2010, McDuie et al., 2015). Interactions between seabirds and tuna are widely known from tropical regions (Au and Pitman, 1986, Jaquemet et al., 2004, Weimerskirch et al., 2005). In fact, in the tropical Indian Ocean, almost all seabirds are said to forage in association with tuna and cetaceans (Jaquemet et al., 2004, Le Corre and Jaquemet, 2005, Catry et al., 2009b), perhaps because the clarity of tropical oceans deters prey species from the surface waters, making them less accessible to surface foraging seabirds. As a result these species rely on sub-surface predators to drive their prey close to the surface (Le Corre and Jaquemet, 2005). However, if all three taxa (seabirds, tuna and prey) aggregate at eddy peripheries, eddies may be the mechanism driving the association. Accumulations of top predators often attract and are targeted by commercial fisheries (Sund et al., 1981, Mugo et al., 2010). Tuna fisheries are one of the most important examples of large-scale commercial operations and are known to greatly overlap with seabird foraging distributions, which could put seabirds at risk through depleting prey availability and irreparable damage to key resources (Le Corre and Jaquemet, 2005, Polacheck, 2006, McDuie et al., 2016).

4.2.6 Tropical environments

Oligotrophic tropical waters do not exhibit the strongly enhanced primary productivity or large-scale upwellings and frontal systems that attract seabirds in temperate marine environments (Weimerskirch et al., 1994, Ainley et al., 2005, Weimerskirch, 2007). However, seabird foraging has been linked with localised productivity in tropical regions. For example, great frigatebirds in the Mozambique Channel foraged in areas of enhanced productivity which were at the peripheries of anticyclonic eddies (Weimerskirch et al., 2004) where prey aggregations are also enhanced (Sabarros et al., 2009). Similarly, chick-rearing wedge-tailed shearwaters from Aride Island, Seychelles, converged on areas characterised by elevated primary productivity when foraging (Cecere et al., 2013). Nevertheless there is little information on the trophic or oceanographic mechanisms that drive prey availability to seabirds in tropical environments. Consequently, our understanding of how prey are aggregated and how beneficial foraging associations are increased, is limited.

4.2.7 Great Barrier Reef

Wedge-tailed shearwaters breeding in the southern GBR are one of only two tropical species known to dual-forage (Congdon et al., 2005, Pinet et al., 2012). Wedge-tailed shearwaters of the GBR access distant locations during longer (~8 d) foraging trips (McDuie et al., 2015, chapter three).Yet, oceanographic characteristics of these foraging grounds and mechanistic drivers have not been extensively quantified. Shearwaters also known to be more sensitive than other sympatric species to climate-driven oceanic changes in food availability (Smithers et al., 2003, Weeks et al., 2013). Finally, they forage in mixed species flocks ((Ballance et al., 2001) and have slow-growing chicks (~14 wk to fledge) (Pettit et al., 1984). Combined, these factors make wedge-tailed shearwaters ideal indicator species for impending impacts of climate driven changes to oceanography or to food resources in tropical regions. An adult's ability to rear and fledge a chick is dependent upon its ability to locate sufficient food. Sites used for this purpose may be geographically isolated, causing reliance upon limited foraging areas. If these areas are depleted, birds may be forced to travel further afield, increasing energy costs (Weimerskirch, 1998, Weimerskirch et al., 2003). This would impair their ability to maintain their own condition, causing negative impacts to chick feeding and reduced reproductive success and increasing vulnerability to a number of environmental, climatic and/or anthropogenic processes (Piatt et al., 1999, Harding et al., 2007, Shultz et al., 2009). Therefore, it is critical to identify and quantify locations that reliably supply sufficient food resources to self-provisioning birds during breeding. Furthermore, characterising these places allows predictions to be made on the larger-scale oceanographic conditions and features that are crucial to breeding season success and population persistence.

The only features that are currently known to have any link with distant, breeding season foraging locations of wedge-tailed shearwaters in the Coral Sea, are deep ocean seamounts, near which shearwaters regularly forage (chapter three). Seamounts disrupt currents, affect circulation and produce an intricate system of relatively small-scale currents (Church, 1987, Gourdeau et al., 2008, Choukroun et al., 2010). These interactions generate oceanic features such as fronts, convergences, upwellings and eddies (Roden, 1987, Boehlert, 1988, Bograd et al., 1997, Beaman, 2010), of the kind which influence prey availability and foraging of seabirds (Ballance et al., 2001). Therefore, with currents entering the Coral Sea and interacting with the seamounts within (Church, 1987, Ridgway and Dunn, 2003, Gourdeau et al., 2008), it is likely that these phenomena exist in the areas where shearwaters forage to self-provision. However, no evidence of any association between foraging shearwaters and these kinds of features, or any other oceanographic variables, has yet been produced. To be able to determine the mechanisms that drive prey availability in critical, distant foraging locations, it is necessary to examine a diverse set of oceanographic parameters to characterise foraging habitat and highlight the presence of important oceanic features that drive advantageous foraging. This would enable characterisation of ‘good’ foraging habitat for this tropical seabird, and aid in the management of critical, at-sea food resources which are currently, entirely unmanaged.

4.2.8 Aims

The aim of this study was to determine the mechanistic processes that drive prey availability and beneficial foraging association at distant foraging environments for a tropical pelagic seabird. I tracked adult breeding wedge-tailed shearwaters to determine the location of likely foraging grounds used by adults on long-foraging trips. High resolution oceanographic and environmental data were used to describe the oceanographic characteristics of adult's self-provisioning foraging locations, to quantify the birds' interaction with the marine environment and determine the trophic mechanisms which may drive tropical wedge-tailed shearwaters foraging activity.

4.3 METHODS

4.3.1 Study site and population monitoring:

This study was conducted at Heron Island (23° 26' S, 151° 51' E), in the southern Great Barrier Reef (GBR) Marine Park, Australia in February 2006, February/March 2011 and 2012 and February-April, 2013. Electronic tracking devices (Microwave Telemetry, USA; PTT-100) were deployed on chick rearing, wedge-tailed shearwaters to track them to foraging sites used during the long-trips of their bi-modal foraging cycle (Congdon et al., 2005). Higher resolution GPS logging devices could not be used for these trips of greater than 5-6 days because of battery size and weight constraints. A total of 30 nests were monitored daily throughout each study period in 2006, 2011, 2012, and 86 in 2013, to ascertain the timing of adult foraging trip cycles, determine changeovers between parent birds from short to long trip cycles, growth of chicks, meal masses and condition of adults. When both adults visited the nest on the same night, (indicating a short/long trip changeover), a transmitter was deployed in the adult which had been attending the nest the previous week (Congdon et al., 2005). If both adults were never observed together, the transmitter would be deployed on the short-tripping adult on the eighth day of its chick-provisioning cycle, in anticipation of long-trip departure. Devices were deployed on adults upon their exit from the nest following chick feeding.

Solar-powered ARGOS Platform Terminal Transmitters (PTT) provide variable location information (accuracy ~150m-15km) in 'real-time' via ARGOS satellites (http://www.argos-system.org). Only the three most accurate fix estimation levels were retained (3, 2 and1; 150-550m) with minimum 4 messages and a fourth estimation level (0; ~1500m) when it visually fit track progression. The lowest three (A, B and Z) were excluded. Data were further assessed for speed. As the fastest commute ever observed by an individual bird was 450 km in approximately 10hrs, fixes that suggested flight speeds >50 km h^{-1} or >35 km h^{-1} sustained over 48 hrs were removed (following Catry et al., 2011).

Devices measure ~17 x 36 - 40 x 16 mm, weigh 9-11.2g and were mounted at the base of an adult's tail feathers with TESA© tape for the duration of one long-trip per adult (n = 3 in 2006; n = 4 in 2011 and n = 6 in 2012). Devices were only deployed on adults weighing greater than 380g (max. weight = ~540g) to maintain the deployment weight within the accepted 3-5% body weight limits for seabirds (Kenward, 2001, Phillips and Croxall, 2003)**.** No evidence of birds attempting to remove the tape, the device, or any damage to tail feathers was observed. Accuracy of PTTs and numbers of location fixes varies depending on time of day, sun availability and numbers of satellites available. The numbers of fixes obtained depended on duty cycles pre-programmed by the manufacturer. In 2006 and 2012 PTTs had been set to 12 hours on/48hours off (default factory setting) while in 2011 and 2013 a '*continuous*' setting was used, which produces more consistent location fixes daily (Table 4.1). Solar panels recharge batteries causing obligatory downtime which results in data interruptions. These factors cause variation in the number of data points obtained from any given track which limits the ability to analyse and interpret variations in individual bird activity. Also, an additional 18 partial long-trip tracks were obtained from inadvertent tracking with GPS (which were being used to obtain data on short-trip cycles). Chapter five (page 104-6) details the process used identifying foraging and non-foraging locations and erroneous data for the GPS devices.

Table 4.1: Summary of long-trip foraging data for wedge-tailed shearwaters. Fix locations from the PTT tracks are total foraging points from core-use foraging areas (50%UD), including points from the buffer zone (300km from the colony). *GPS fixes include all tracked fixes as foraging points. Non-foraging points are the remainder of points classed as non-foraging by Area Restricted Search. Foraging locations are cases in the 50%UD excluding the points from the buffer zone and non-foraging locations are the pseudo-absence points produced from within the remainder of the non-foraging area (95% UD).

	No. tracks	Fix locations	Exclusions (buffer zone)	Foraging locations	Non-foraging locations
2006	3	65	25	40	40
2011	4	290	84	206	206
2012	6	131	72	59	59
2013	10	676	272	404	404
2013GPS	18	6561*	3014	2061	1486

4.3.2 Data analysis

4.3.2.1 *Identifying core and maximum use areas*

The low resolution data retrieved from PTT transmitters, the inter-annual differences in numbers of individuals tracked and in numbers of fixes among years (Table 4.1), made it difficult to accurately determine where birds were actually foraging. Therefore, it was necessary to identify areas of higher usage and consider these most likely to represent foraging grounds, as opposed to the widest area used by tracked birds, where fixes are more likely to represent birds moving or in transit (Hamer et al., 2007, Catry et al., 2009b).

4.3.2.2 *Kernel Density Estimation - foraging/non-foraging areas*

Kernel Density Estimation (KDE) analysis was used to identify areas of core-use and the maximum range of individual birds. These estimations are particularly useful with lower resolution data such as that from PTTs. Where higher numbers of fixes occur 50% utilization distribution (UD) contours, or kernels, are created. The 50% kernels indicate the most highly used areas and are more likely to represent foraging activity (Hamer et al., 2007). All actual PTT location fixes in the 50% kernels were defined as foraging points. The second kernels created were 95% UD kernels. These represent the overall observed distribution of fixes for an individual (the maximum range extent). By excluding the 50% kernels from this maximum-use area, a transit or non-foraging zone is created. Within this external area a random set of '*pseudo-non-foraging*' points, were generated in ArcGIS 10.2 for Desktop with latitude/longitude identifiers. The total sample size of '*pseudo-non-foraging*' points generated per individual was equal to the number of data points within the 50% kernel for that same individual. This process produced a binomial foraging/non-foraging response variable for further analysis and allowed the comparison of oceanographic characteristics in foraging vs. non-foraging areas at the smallest scale possible. Equally proportioned binomial response data sets are said to produce the most reliable results and highest predictive accuracy for boosted regression trees (BRT) (Barbet-Massin et al., 2012), the analysis type selected for the current study.

Kernels were created using a smoothing factor (h) of 20 km which was based on the scale of foraging ascertained from the much higher resolution and more accurate GPS tracks (see below, and chapter 5). Therefore, the same scale was used for PTT tracks. KDE analyses were performed and kernels created for each month (Feb 2006; Feb & Mar 2011; Mar 2012; and Feb, Mar & Apr 2013) of tracking, matching resolution of oceanographic data. Kernel analyses were performed in R version 3.0.3 (R Core Team, 2013) using the adehabitat LT and HR packages (Calenge, 2006). Shape files were exported to ArcGIS 10.2 for Desktop with the OGR Shapefiles package and the kernel density map was projected in the World Geodetic System (WGS) 1984 geoid. Data assessment and manipulation were completed in ArcGIS 10.2 for Desktop.

To identify foraging and non-foraging areas in the high resolution 2013 GPS tracks, these data were run through First-Passage Time (FPT) analysis to identify Area Restricted Search locations (ARS) (Fauchald and Tveraa, 2003, Pinaud and Weimerskirch, 2007). These ARS points are classed as actual foraging locations while the non-ARS points from the same tracks are considered non-foraging locations (as per chapter five). FPT and ARS and were completed using the 'adehabitatLT' package (Calenge, 2006) in R version 3.0.3 (R Core Team, 2013). This is a considerably higher resolution analysis and provides more accurate estimation of foraging vs. non-foraging areas.

4.3.2.3 *Identifying buffer/exclusion zones*

Wedge-tailed shearwaters are central-place foragers and long trips always necessitate transiting to and from the colony. The culmination points of shearwater long foraging trips were always greater than 300km from the colony. Therefore, any long trip foraging locations observed within this extent were either locations of birds 'in-transit' to their furthest long trip foraging grounds, or birds foraging opportunistically while en route to and from more distant areas. As this study aimed to characterise the bird's final choice of foraging location, all PTT observations within 300km of Heron Island were removed, creating a 'buffer zone' based on geographic and bathymetric designations outlined in McDuie et al. (2015, chapter three). This also avoided overlap of locations with short trip destinations (which were always within 300km of Heron Island, chapter 5).

4.3.3 Oceanographic parameters

In total, 14 oceanographic and environmental variables that were seen as proxies for ecological processes including prey availability (Torres et al., 2008) were selected (Table 4.2) to characterise the marine environment of foraging grounds. Raw data, with the exception of distance parameters, were obtained as monthly climatologies from high resolution satellite imagery at 1.5km resolution (www.gpem.uq.edu.au/oceanography). The Etopo 1 Ice surface bathymetry data set was used and change of depth in metres per kilometre calculated to represent the bathymetric gradient or slope. Subsequently, contours were created at 100m intervals to identify the areas of steepest slope (top 20%) Regional seamount location data (latitude/longitude), obtained from numerous sources (chapter two, page 22), were compiled into a comprehensive list and mapped in ArcGIS 10.2 for Desktop. MODIS sea-surface temperature (SST) and Chlorophyll *a* ([Chl *a*]) data (absolute and anomalous values) were used. Anomalies indicate the difference between monthly and long-term (2002 – 2012) climatologies. Degrees of change in SST per km horizontal distance contours, at intervals of 0.02, were created for the highest 25% of SST gradients to identify the strongest gradients and indicate the presence of frontal systems.

Mapped sea level anomalies (SLAs) from merged AVISO altimetry satellites, represent mean difference between the sea surface height and mean sea level, and are used to identify up or downwellings (positive/negative anomalies) (Hyrenbach et al., 2006). Current speed (CDSP), which provide a measure of the currents at a given location based on the SLA, were calculated using the U and V components of current velocity (UVel/VVel; CDSP = ((U^2) + (V^2)) ^0.5). Foraging may be related to proximity to certain features; so, distance between foraging/non-foraging points and the nearest seamounts, SST front, steep slope, land and the colony was calculated using the Euclidian distance tool in ArcGIS 10.2 for Desktop.

All oceanographic data were imported to ArcGIS 10.2 for Desktop as GeoTIFF files and mapped as layers in which every single pixel has a value. These layers were overlaid on the kernel maps and values for each oceanographic variable were matched to the corresponding bird foraging and non-foraging points (latitude/longitude locations) by month; extracted for each track; and exported as shape files. They were then collated to the year of tracking and converted to CSV files for analysis and modelling in R (R Core Team, 2013). Oceanographic parameters can be affected by light refraction, cloud cover, shallow water (<200m depth) or presence of land in any given pixel from the satellite images and produce excessive values. These erroneous data were identified and removed.

Table.4.2: Definition of oceanographic variables, their measurements and data sources.

Term	Measurement	Description	Downloaded from/Calculated by
Chla (month)	mg m^{-3}	[Chlorophyll *a*]	NASA OceanColor Web: MODIS (oceancolor.gsfc.nasa.gov)
ChlaA (month)	mg m^{-3}	[Chl *a*] anomalies	NASA OceanColor Web: MODIS (oceancolor.gsfc.nasa.gov)
SST (month)	Degrees (°C)	Sea surface temperature (SST)	NASA OceanColor Web: MODIS (oceancolor.gsfc.nasa.gov)
SSTa (month)	(°C)	SST anomalies	NASA OceanColor Web: MODIS (oceancolor.gsfc.nasa.gov)
SSTGrad (month)	(°C) metre	SST gradient (front)	NASA OceanColor Web: MODIS (oceancolor.gsfc.nasa.gov)
DistSSTgradient	Degrees dist.	Distance to nearest steep (25%) SST gradient(front)	ArcGIS 10.2 for Desktop F McDuie
Bathymetry	Metres depth	Depth of ocean floor	http://www.ngdc.noaa.gov/mgg/global/relief/ETOPO1/image/
Bath.grad	m km^{-1}	Steepness of slope. Depth change over distance	Biophysical Oceanography Group, University of Queensland (www.gpem.uq.edu.au/oceanography)
DistSlope	Degrees dist.	Distance to nearest steep (25%) bathymetric gradient/slope	ArcGIS 10.2 for Desktop F McDuie
Coldist	Degrees dist.	Distance to the colony	ArcGIS 10.2 for Desktop F McDuie
Photic Depth	Metres depth	Water transparency measured by Secchi disk	Biophysical Oceanography Group, University of Queensland (www.gpem.uq.edu.au/oceanography)
DistSeam	Degrees	Distance to nearest seamount	ArcGIS 10.2 for Desktop F McDuie from: the Global database of undersea features http://www.gebco.net/data_and_products/undersea_feature_names/); the Deep Reef Explorer high resolution depth model for GBR and Coral Sea (http://www.deepreef.org/projects/48-depth-model-gbr.html); the gbr.features.shp and gbr.dryreef.shp under the Group Layer 'GBRMPA features', copyright to the Commonwealth of Australia (2007) - data courtesy of the Great Barrier Reef Marine Park Authority (Heap, 2008, IHO, 2008); the list of Pacific Seamounts (http://www.ldeo.columbia.edu/~small/PacificSmts/); Seamounts Catalog of the Seamount Biogeosciences Network (SBN) (http://earthref.org/SC/).
SLA	mm	Mapped sea level anomaly	AVISO (http://www.aviso.altimetry.fr/en).
Current Speed	cm s^{-1}	Current speed cm/ second	AVISO (http://www.aviso.altimetry.fr/en).

4.3.4 Statistical analysis and modelling

Boosted Regression Trees (BRTs) were identified as the most appropriate method to analyse the data obtained. For details of analytical methods, refer to chapter two, pages 25-28. In the current analysis, default values and model runs followed recommendations by Elith et al. (2008) and used a Bernoulli (binomial) error distribution. Model parameters in this study used a tree complexity of one less than the number of predictor variables being considered in any analysis; began with a fast learning rate of 0.01; and a stepwise increase of trees beginning with 50 and increasing to a maximum of 10000. Randomness was introduced when necessary to improve model performance using bag fraction values between 0.5-0.75, the learning rate and tree complexity were adjusted until the model performance improved and the model was optimised.

4.4 RESULTS

4.4.1 Foraging ground locations

Most birds on long trips (>4 days duration) foraged to the north and east of Heron Island, but some trips occurred to the south, reaching a southernmost point near Byron Bay (Fig. 4.1). No long-trip final destinations occurred within 300km of the colony. The greatest distance any bird tracked was 1400km from the colony (Fig. 4.1). Numbers of tracked locations differed among years according to the number of individual birds tracked, logger type and the duty cycle setting of the PTT (continuous – 2011, 48hr off/12hr on – remaining years, Table 4.1). The strongest models of relationships between foraging site use and oceanographic parameters were those with the most data: the GPS tracks from 2013 and PTT in 2011 (Table 4.3).

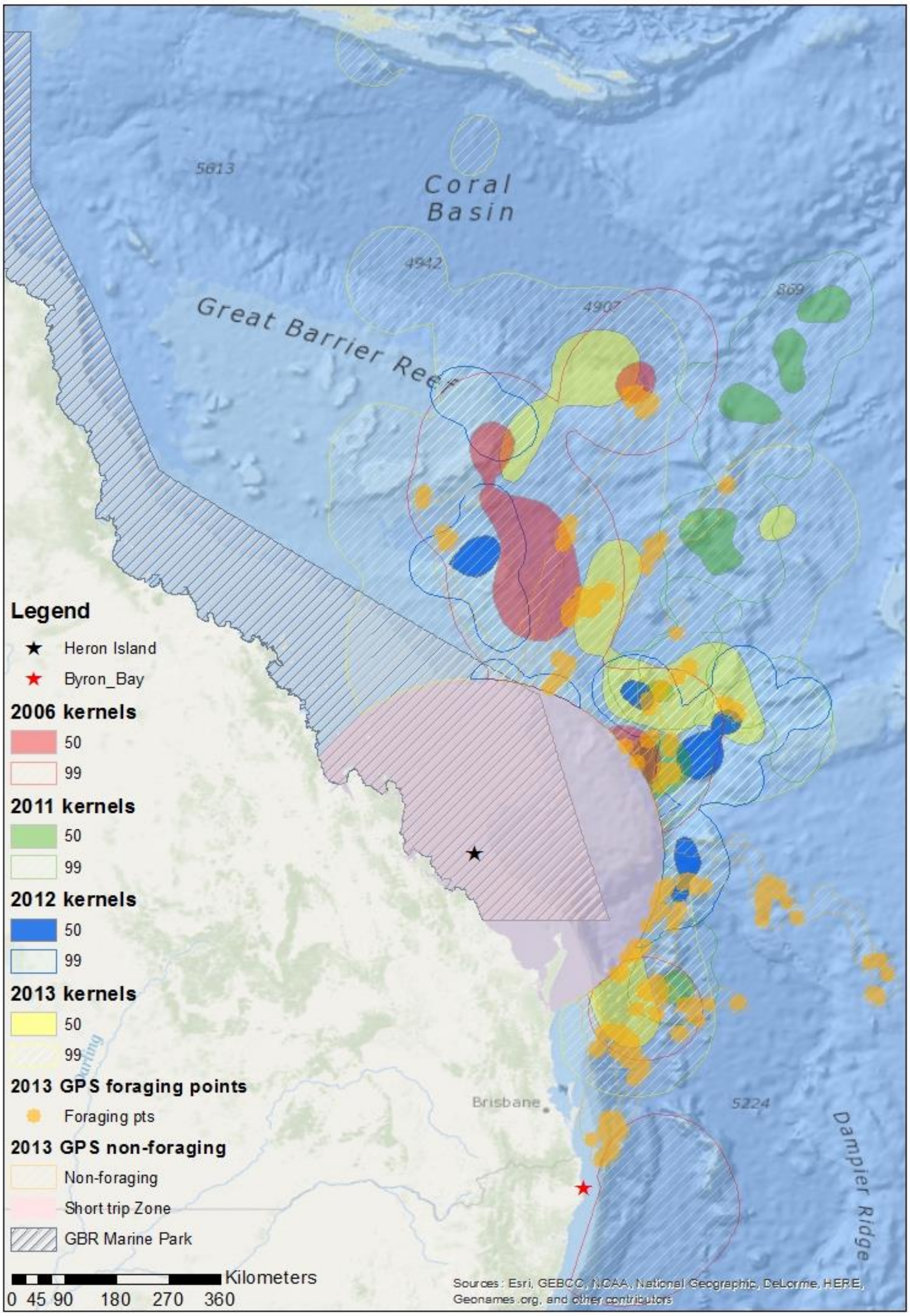


Figure 4.1: Map of wedge-tailed shearwater foraging, PTT 2006-2013, 50% and 99% UD kernels and GPS 2013 true foraging and non-foraging points. Grey striped area is GBR Marine Park showing all foraging occurs outside that area. Pink area is the short-trip zone within a radius of 300km of Heron Island. Black star is Heron Island and red star is Byron Bay.

Table 4.3: Results from BRT analyses for each year of long trip tracking of wedge-tailed shearwaters. Predictive deviance, s.e and AUC are reported from the simplified models as well as primary peak values from frequency distributions of oceanographic variables, followed by those variables' positions in order of influence (in parentheses). For descriptions of variables see Table 4.2.

YEAR	**2006**	**2011**	**2012**	**2013**	**2013GPS**
CV dev ±SE	0.828±0.81	0.601±0.089	0.777±0.042	0.694±0.028	0.461±0.035
AUC	0.8931	0.9476	0.8989	0.9273	0.9659
Relative influence of factors of simplified models					
1	**Chlamonth**	**MSLA**	**Slope**	**CDSP**	**MSLA**
	< 0.06	**6.5**	**606**	**8 & 21**	**9.5**
2	Bathymetry	SST	MSLA	Bathymetry	DistSeam
	-1550	28.5-29	9	-2850	0.84
3	Slope	SSTA	Bathymetry	MSLA	CHL*a*A
	230	0.12	-2400	14.4	-0.001
4	SSTA	Current Speed	Dist to slope	Dist seamount	Bathymetry
	-0.4	13	0.06	0.96	-2777
5	SST		CDSP	SST	CDSP
	28.25		22	27.5	21
6	DistSlope		DistSSTgrad	DistSlope	DistSSTgrad
	0.04		0.06	0.24	0.24
7	CHL*a*A				SST
	-0.004				26.9

4.4.2

2013 had the greatest number of birds tracked by PTT and was the only year with any GPS tracking of long trips. Therefore, this year produces the highest resolution analyses of the links between foraging sites and oceanography. The BRT model fits well when optimised to six oceanographic factors, with a predictive deviance of 0.694 ± S.E. 0.028 and an AUC of 0.9273. There was a strong relationship between foraging site locations and both current speed and SLA. ~43% of the model's ability to predict where birds are foraging is based on the values of these two factors (Fig. 4.2a & c). Shearwaters were more likely to be found foraging in positive SLAs of 6 - 8cm; with some at >18cm and -3cm. Current speeds of ~25-28 ms^{-1} interacted strongly with the deepest bathymetry (> 4000 m) and SLAs of 6-8 cm. Bathymetry was the second most important predictor of bird distribution with birds generally foraging in depths > 4000m from the wide range available to them of 0-5000m (Fig. 4.2b – 20.9%). Likewise, the seamount ridge was important with birds always foraging within 1° of the nearest seamount (Fig. 4.2d – 17.7%). While some relatively cool temperatures occurred in the places birds transited (as low as 25.5°), the SSTs in foraging locations were primarily between 27 – 28.5°C peaking at 27.25°C (Fig 4.2e – 10.1%).

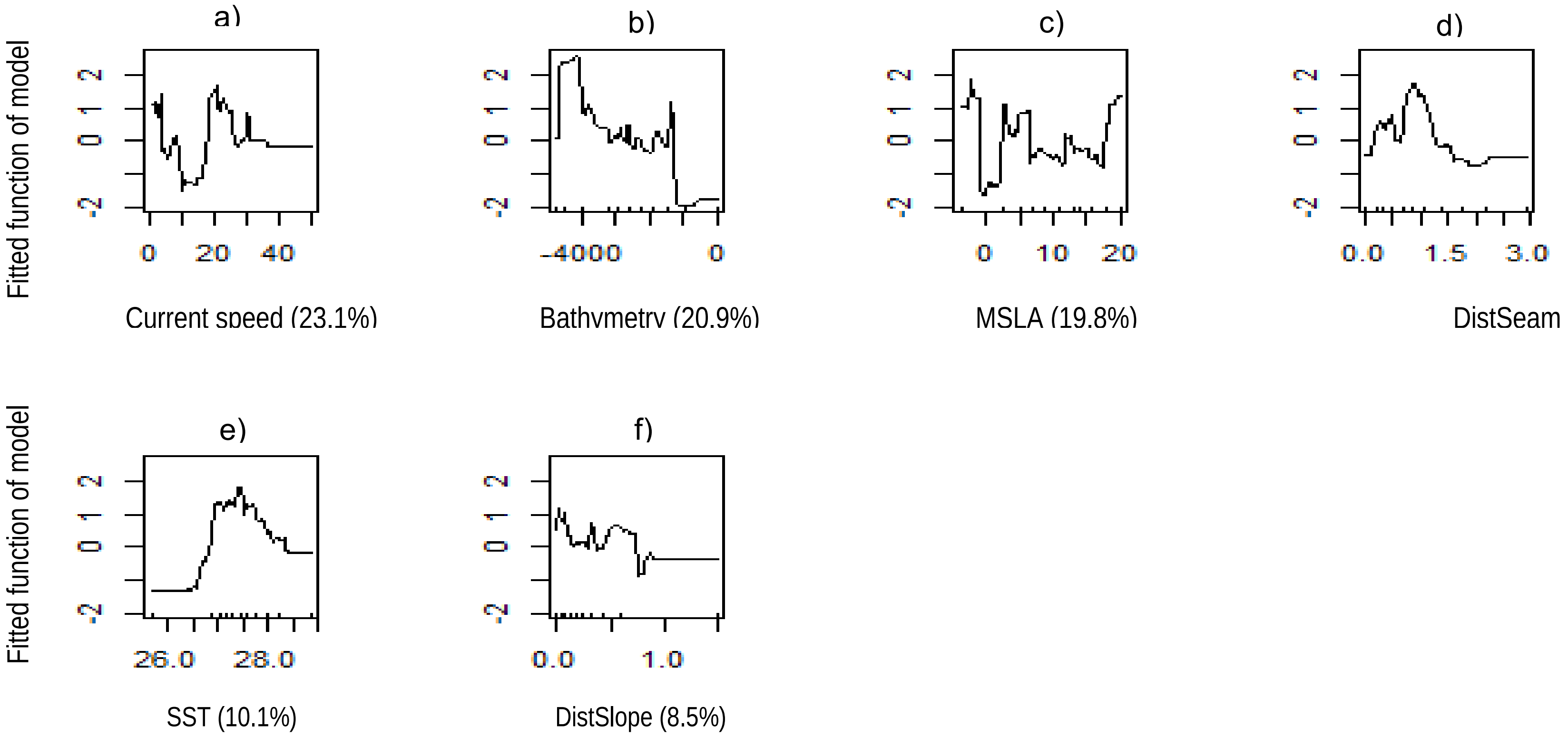


Figure 4.2: Results from BRT modelling of wedge-tailed shearwater PTT long foraging trips in 2013 for the final simplified model. These partial dependence plots represent the influence of each oceanographic variable on the binomial response (foraging/not foraging) after accounting for the average effects of all other variables in the model. Y-axes are on a logit transformed scale and the value of 0 is equivalent to a 50% probability of a bird foraging at that value of the predictor (X-axis). Hence, all values above 0 indicate a greater probability of foraging (peaks) while those below, a lesser probability of foraging (troughs). The percentages in parentheses represent the relative influence of each variable. Hence, all values above 0 indicate a greater probability of foraging (peaks) while those below a lesser probability of foraging (troughs). The percentages in parentheses represent the relative influence of each variable on the response. For descriptions of variables see Table 4.2.

4.4.3 2013 GPS

The 2013 GPS tracks, with increased data resolution, produced a better fit in the model. The simplified model showed a predictive deviance of 0.461 ± S.E. 0.035 and an AUC of 0.9659. The factors influencing bird foraging distribution were very similar to those seen in the PTT data for this same year (Figs. 4.2 & 4.3). SLAs and current speed were again important with a combined influence of ~32% (Fig. 4.3a & d). Most birds foraged in SLAs ~4-8cm (Table 4.3) with some occurring in higher levels above >20-26cm and >30cm and highly unlikely to forage in SLAs below ~4cm. Current speeds, while not as high on average at observed in PTT data (Fig. 4.2a) were higher, at 18-22 ms^{-1}, than those in non-foraging areas (Fig.4.3e – 14.5%). The greatest numbers of foraging birds occurred in weakly negative [Chl *a*] anomalies (Table 4.3; Fig. 4.3c – 16.6%). Bottom topography was important with bathymetry and distance to seamounts driving ~30% of the influence on the model. Shearwaters primarily foraged within 0.8-1.2° from seamounts, rarely farther than 1.5° (slightly farther than for PTT results of the same year), and in depths > 3000m (Fig. 4.3b & d).

The areas where SLAs of ~5cm, 20cm and 25cm at a distance of 1° from the seamounts attracted more foraging individuals. As SSTs increased, the probability of shearwaters foraging in those temperatures decreased with foraging mostly in < 26.25°C (Fig. 4.3g – 9.6%). Nevertheless, as results obtained from GPS tracking generally demonstrated similar patterns to those of the PTTs, it can be inferred that the use of PTT tracking and kernel density analysis, to define foraging and not-foraging, is accurate and appropriate.

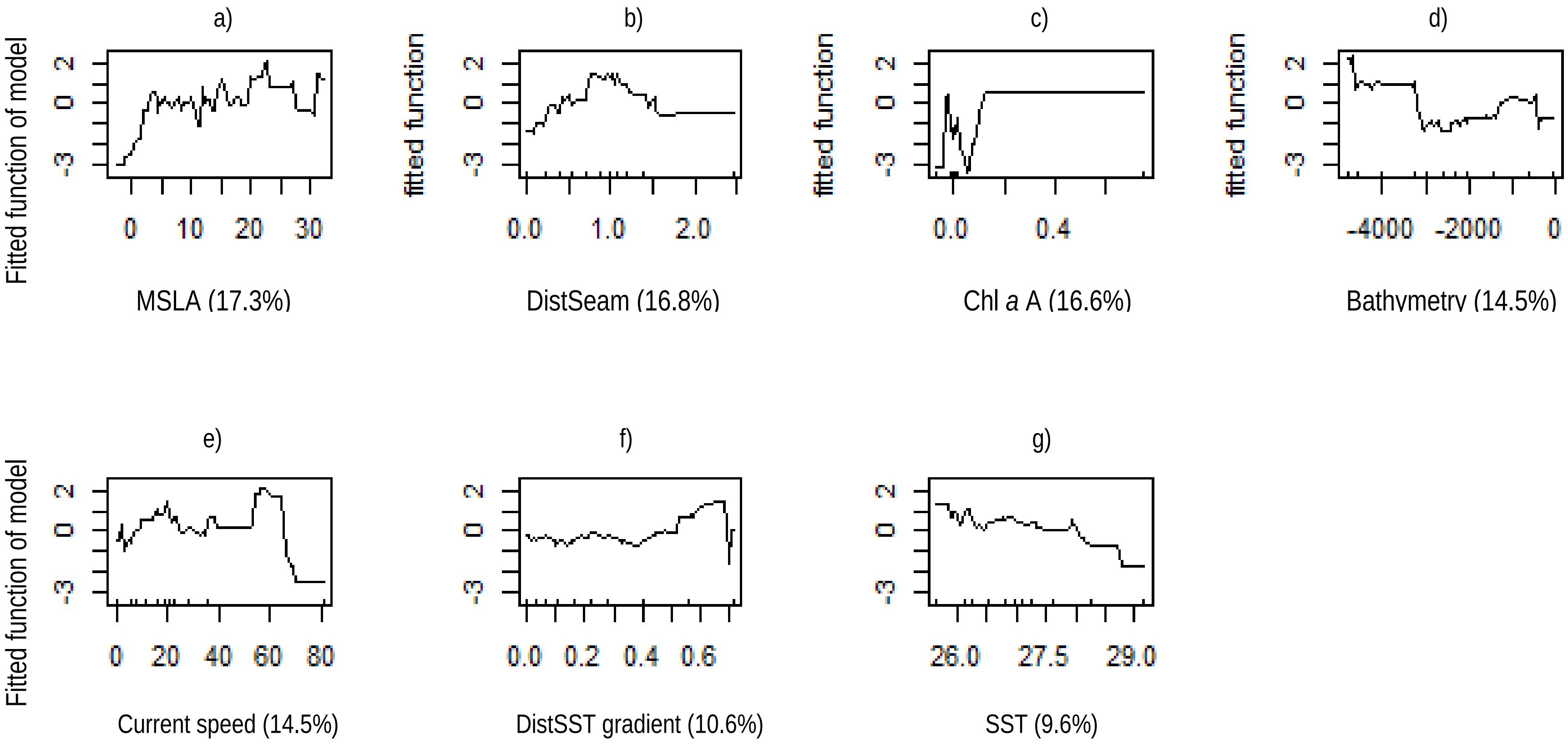
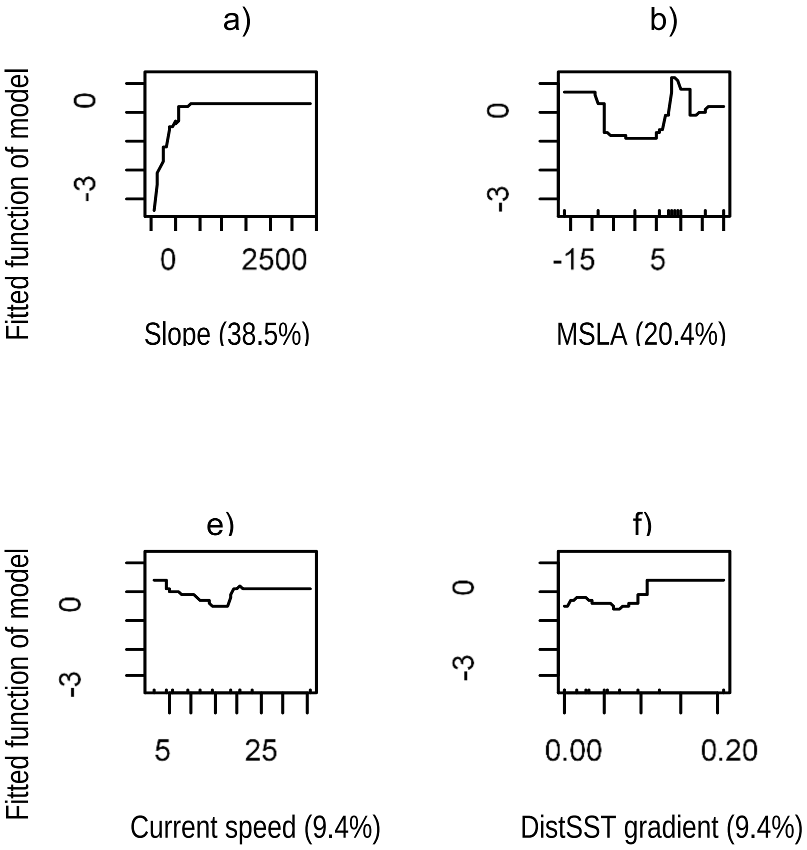


Figure 4.3: Results from BRT modelling of wedge-tailed shearwater long foraging trips tracked by GPS in 2013 for the final simplified model. These partial dependence plots represent the influence of each oceanographic variable on the binomial response (foraging/not foraging) after accounting for the average effects of all other variables in the model. Y-axes are on a logit transformed scale and the value of 0 is equivalent to a 50% probability of a bird foraging at that value of the predictor (X-axis). Hence, all values above 0 indicate a greater probability of foraging (peaks) while those below a lesser probability of foraging (troughs). The percentages in parentheses represent the relative influence of each variable. Hence, all values above 0 indicate a greater probability of foraging (peaks) while those below a lesser probability of foraging (troughs). The percentages in parentheses represent the relative influence of each variable on the response. For descriptions of variables see Table 4.2.

4.4.4 2012

The optimised model in 2012 retained 6 variables but was a comparatively weaker model with predictive deviance 0.777 ± S.E. 0.042 and an AUC of 0.8989. Shearwaters showed a clear preference for foraging over steeper slopes (600-700 m km^{-1}) compared to the non-foraging areas (few > 200m km^{-1}, Fig. 4.4a – 38.5%). This was the most important parameter influencing shearwater foraging in 2012 and these depths were always close (0.2°) from the steepest slope (Table 4.3, Fig. 4.4d – 9.6%). Again SLAs were significant in driving foraging behaviour, primarily in low to moderately positive anomalies of 8 cm and some in negative anomalies above -7cm (Fig. 4.4b – 20.4%). There was a limited effect of negative anomalies -8 to -16cm. The depth in which birds foraged was also important (Fig. 4.4c – 12.7%) with probability of foraging highest in depths of > 3000m. Current speeds in foraging locations peaked strongly at ~22 ms^{-1} (Table 4.3).



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4.4.5 2011

In 2011 PTT devices were set to a continuous schedule and attained considerably more location fixes than in other years (Table 4.1). This produced a more robust model with predictive deviance at 0.601 ± S.E. 0.089 and an AUC of 0.9476. Only four variables remained in the optimal model. SLAs had the strongest influence (Fig. 4.5a – 46.3%) on shearwater foraging with a very high proportion of foraging being observed in very weak negative and weak positive SLAs (2 to -2cm). 2011 was the only year which showed a fairly strong relationship between foraging and both SSTs and SSTAs. These relationships were evident at all bathymetric depths. Maximum foraging activity occurred at SSTs of ~28.25°C with most birds foraging at temperatures ranging between ~27.5-28.3°C (Fig. 4.5b – 26.5%). These temperatures were slightly lower (-0.2-0.5°C) and slightly higher (+0.25°C) than both the monthly climatologies and, than the SST anomalies that regularly occurred in the non-foraging zone (Fig. 4.5c – 14.3%). The birds primarily foraged in current speeds of ~5-15 ms^{-1} and were much less likely to forage in currents >15ms^{-1} (Fig. 4.5d – 12.9%). While relationship was seen between bathymetric parameters and foraging in the 2011 model, bathymetric values were very similar to those observed in other years. Foraging was always in close proximity to steepest slopes (0.05°) near seamounts (<1°, primarily at 0.4°), over deep bathymetry ~3000m and high slope gradients of ~250m km^{-1}.

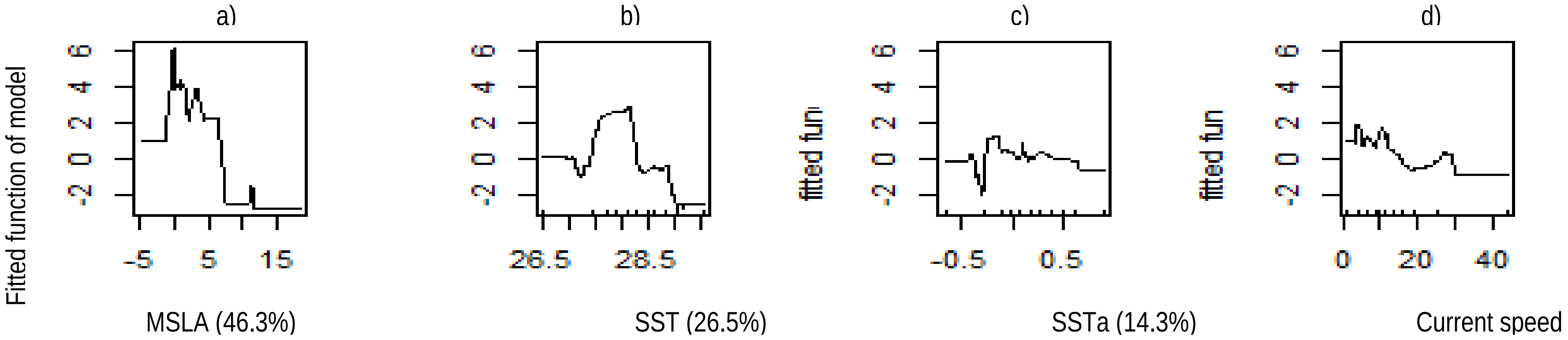

Figure 4.5: Results from BRT modelling of wedge-tailed shearwater long foraging trips in 2011 for the final simplified model. These partial dependence plots represent the influence of each oceanographic variable on the binomial response (foraging/not foraging) after accounting for the average effects of all other variables in the model. Y-axes are on a logit transformed scale and the value of 0 is equivalent to a 50% probability of a bird foraging at that value of the predictor (X-axis). Hence, all values above 0 indicate a greater probability of foraging (peaks) while those below a lesser probability of foraging (troughs). The percentages in parentheses represent the relative influence of each variable. Hence, all values above 0 indicate a greater probability of foraging (peaks) while those below a lesser probability of foraging (troughs). The percentages in parentheses represent the relative influence of each variable on the response. For descriptions of variables see Table 4.2.

4.4.6 2006

The paucity of data in 2006 (n tracks = 3; Table 4.1) resulted in the weakest model with a predictive deviance of 0.828 ± S.E. 0.081 and an AUC of 0.8931 for the 7 variables that remained after simplification (Fig. 4.6). However, while there were some obvious differences, results were broadly similar to those of other years (Table 4.3). The most important factor in 2006 was [Chl *a*] (Fig. 4.6a – 27.7%) showing that birds generally foraged in very low levels of productivity (<0.04 mg m^3), associated with very weakly negative [Chl *a*] anomalies (Fig. 4.6g – 5.3%; -0.004 mg m^3 less than long-term climatologies). In a similar way to other years (Fig. 4.1; Table 4.3), bathymetry and the bathymetric gradient were important influences. Birds always foraged in deep, but not the deepest waters (average -1550m Fig. 4.6b – 19.6%) and where the slope was steep (> ~200m/km; Fig. 4.6 – 14.2%; Table 4.3). An influence of SST was evident (Fig. 4.6d – 14.1%) with birds selectively foraging in a specific and narrow range of SSTs from ~27.75 – 28.75°C from within a potential range spanning ~26 to 29.25°C. These temperatures >~28°C were 0.2 - 0.7°C less than the usual climatologies for the area (Fig. 4.6e – 12.2%; Table 4.3).

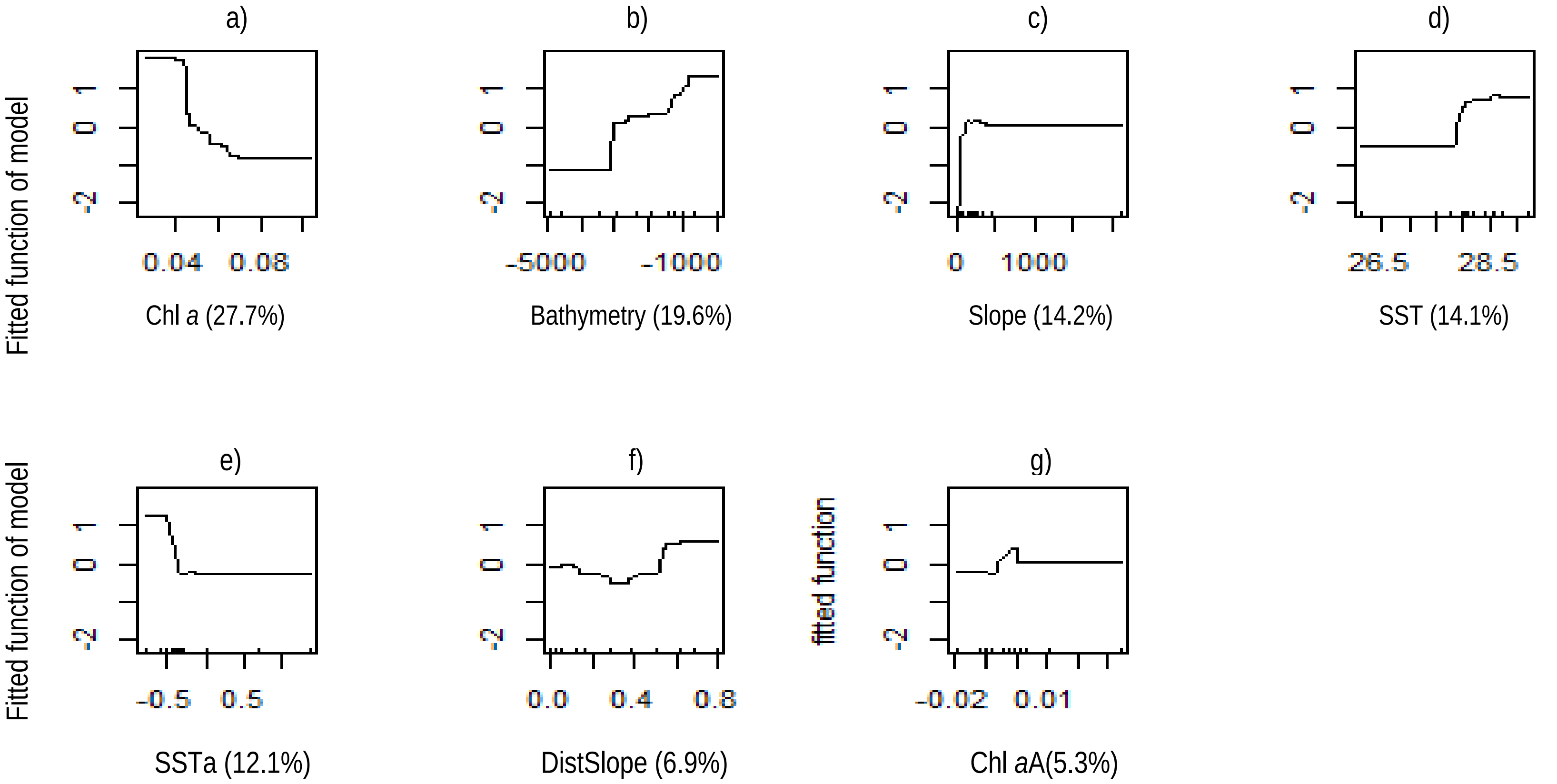

Figure 4.6 Results from BRT modelling of wedge-tailed shearwater long foraging trips in 2006 for the final simplified model. These partial dependence plots represent the influence of each oceanographic variable on the binomial response (foraging/not foraging) after accounting for the average effects of all other variables in the model. Y-axes are on a logit transformed scale and the value of 0 is equivalent to a 50% probability of a bird foraging at that value of the predictor (X-axis). Hence, all values above 0 indicate a greater probability of foraging (peaks) while those below a lesser probability of foraging (troughs). The percentages in parentheses represent the relative influence of each variable. Hence, all values above 0 indicate a greater probability of foraging (peaks) while those below a lesser probability of foraging (troughs). The percentages in parentheses represent the relative influence of each variable on the response. For descriptions of variables see Table 4.2.

4.5 DISCUSSION

4.5.1 Oceanography that influences foraging

Wedge-tailed shearwaters on ‘long’ foraging trips, foraged in spatially explicit locations in the Coral and northern Tasman Seas between 300 and 1400km from Heron Island. The specific locations used by individuals varied both within and among seasons and most individuals visited more than one location on any given long trip. No long trips occurred within 300km of the colony. Foraging sites were identifiable by specific oceanographic characteristics that included deep water in close proximity to rapidly changing bathymetric gradients. These sites also had strong associations with low to moderately positive sea level anomalies (SLAs) and were heavily influenced by current speeds.

This combination of characteristics unambiguously identifies the presence of local and mesoscale oceanographic features, in particular frontal convergences, eddies and zones of up- and down-welling, that were closely linked with foraging activity. These features are also known to be linked to interactions between large-scale oceanic currents and rapid changes in bottom topography (Burrage et al., 1996, Bograd et al., 1997, Song et al., 2001, Rennie et al., 2007). Bathymetry in the region where the shearwaters forage is complex, with large numbers of seamounts, the continental shelf edge and the Great Barrier Reef (GBR) itself. Interactions between this complex regional bathymetry and the South Equatorial Current that enters the north Coral Sea from the Pacific Ocean (Church, 1987, Ridgway and Dunn, 2003) almost certainly drive the patterns of oceanography observed at foraging sites in this study.

Not only are specific mesoscale oceanographic phenomena important, but it is also possible to identify particular features of these phenomena that are more attractive to foraging shearwaters. The associations between foraging activity and low to moderate sea level anomalies (SLAs; Fig. 4.7), suggest that the birds were most interested in foraging at the peripheries of eddies. Very positive or very negative SLAs denote areas at the centre of either warm or cold-core eddies respectively (Nel et al., 2001, Hyrenbach et al., 2006). These extreme values did not influence shearwater foraging in the present study implying that birds avoided eddy centres. Current velocities of around 20cm s^{-1}, which were usual in shearwater foraging sites, are indicative of the periphery of sea level highs such as at the edge of eddies (Kawai, 1972, Vastano and Borders, 1984). These results are in agreement with other studies which found associations between seabirds and eddy peripheries or convergence zones (Weimerskirch et al., 2004, Hyrenbach et al., 2006).

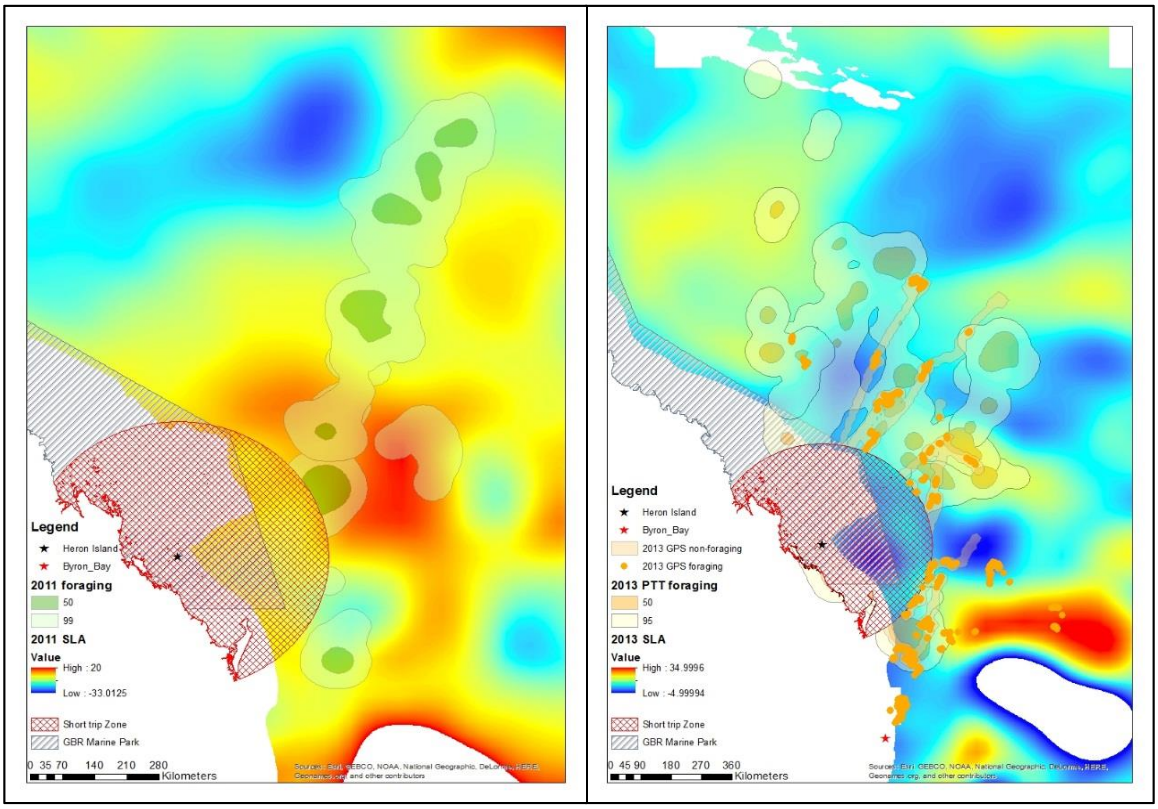

Figure 4.7: SLA and wedge-tailed shearwater foraging in 2011 (left panel) and 2013 (right panel, showing PTT and GPS). Darker blue areas show strongly negative SLAs while red show strongly positive SLAs. In general core-use (50% kernels) fall in the areas between or adjacent to these strongest anomalies rather than on top of them and in the positive upwelling convergence zones.

Interestingly, the oceanographic phenomena associated with shearwater foraging activity in the Coral Sea are remarkably similar to those associated with shearwater foraging at non-breeding migration end points in the northern hemisphere (chapter two). Both sets of foraging locations feature deep oceanic waters adjacent to seamounts and a strong influence of SLAs, thus implying that self-provisioning adult shearwaters forage over specific and identifiable oceanographic, independent of location or time of year. The preferential use of eddy peripheries implies that, in pelagic environments, these are areas of heightened prey availability that increase access to prey. This conclusion is supported by studies which assert that eddy peripheries are aggregation devices of micronekton (Sabarros et al., 2009, Drazen et al., 2011, Potier et al., 2014), a likely prey of shearwaters.

4.5.2 Thermal influences

My data show a general lack of influence of SST variables (SST, SST anomalies or fronts) on levels of foraging activity. In general, the range of SSTs available to shearwaters in the Coral Sea region was limited. The SST range actually exploited by foraging birds was even more narrowly bounded. Combined, these results suggest that the Coral Sea is a relatively thermally homogeneous environment, and that shearwaters non-randomly subsample this environment. However, the foraging areas preferred by shearwaters are not consistently characterised by specific SST values. This absence of thermal influence, combined with frequent occurrence of low SLAs in wedge-tailed shearwater foraging locations, infers that birds were not foraging directly over the convergences where SST fronts are most strikingly delineated (Yoder et al., 1994). It also supports the idea that they were not foraging in eddy centres, which are characterised by more extreme values of these variables (Nel et al., 2001).

In general these findings are contrary to those obtained by most other tropical studies which have consistently found that the thermal properties of the ocean exert a significant influence on seabird foraging (Haney, 1986, Spear et al., 2001). Strong SST effects found in other tropical systems were observed when seabirds foraged in association with very large-scale oceanic current or frontal systems such as those of the Gulf Stream or eastern tropical Pacific. These systems have more apparent temperature variations than occur in the Coral Sea region (Haney, 1986, Spear et al., 2001). Therefore, my results likely contrast because the Coral Sea does not experience these kinds of large-scale oceanographic phenomena (Scully-Power, 1973, Ridgway and Dunn, 2003). It is likely that the shearwaters' foraging strategy is not markedly different to those of other tropical species, but rather that temperature differences are less discernible in the Coral Sea.

4.5.3 Inter-annual variation

The factors that best predicted the distribution of foraging shearwaters varied among seasons. For example, during 2011, the influence of eddies on foraging activity was outweighed by that of elevated SSTs, and associated, slightly positive SST anomalies. There are a number of possible explanations for this type of inter-annual variation in site use and/or characteristics. Firstly, sea conditions were relatively warmer in 2011 (http://www.bom.gov.au/climate/enso/history/ln-2010-12/SST-records.shtml), suggesting that SST may become a more important determinant of prey availability under specific background climatic conditions. Such conclusions are consistent with prior evidence that both within and between season fluctuations in SST and variations in ENSO intensity impact prey availability and breeding participation in GBR seabirds (Smithers et al., 2003, Peck et al., 2004, Devney et al., 2009, Devney et al., 2010).

Alternatively, altered eddy dynamics, rather than the generally warmer temperatures, may have caused different foraging site use. Eddy intensity and stability can vary depending on scale. The smaller an eddy, the more ephemeral it is and conversely, the larger an eddy, the more permanent it is (Owen, 1981). Consequently, if eddies targeted by shearwaters in the Coral Sea are often small and transitory, this could explain inter-annual variation in location use. The oceanography and complex bathymetry of the region supports this possibility (Scully-Power, 1973, Andrews and Clegg, 1989). Many small-scale eddies and localised upwellings are generated by the multiple bifurcations of the South Equatorial Current (SEC) as it enters and moves through the Coral Sea – GBR region; the precise nature and duration of these phenomena being determined by the larger-scale dynamics (Andrews and Furnas, 1986, Andrews and Clegg, 1989, Ridgway and Dunn, 2003). Of course, these first two general explanations are not mutually exclusive, as the intensity and stability of eddies throughout the region in any one season will also be influenced by climatic-driven variation in oceanographic characteristics such as SST. Finally, some component of inter-annual variation in foraging location use is likely to result from individual variation in site choice by foraging adults. At present it is not possible to quantify the relative magnitude of this effect.

4.5.4 Oceanic productivity

Chlorophyll *a* concentration ([Chl *a*]), was used as an abiotic indicator of primary productivity in the present study (see Bost et al., 2009 for a review). In most years, [Chl *a*] exerted no influence on foraging. However, on some occasions foraging birds did appear to target negative [Chl *a*] anomalies. For example, in 2006, [Chl *a*] it was the strongest factor of influence with shearwaters foraging in the very lowest levels to be found. However, as only 3 birds were tracked in 2006, this result has to be interpreted with caution.

Combined, the results for the different oceanographic parameters examined in this study show that wedge-tailed shearwaters in the Coral Sea preferentially forage at the peripheries of mesoscale eddies, but that foraging activity has a limited relationship with SSTs or productivity. This general lack of influence of [Chl *a*] is in stark contrast to the results of numerous previous studies on seabird foraging that have found that seabirds target areas of elevated primary productivity; as indicated by high [Chl *a*] (e.g. Ballance et al., 1997, Baduini and Hyrenbach, 2003, Paiva et al., 2010, Cecere et al., 2013). For example, wedge-tailed shearwaters of the tropical Indian Ocean were reported to forage in areas of elevated primary productivity during both their breeding and non-breeding seasons (Catry et al., 2009b, Cecere et al., 2013). Furthermore, some studies that found seabirds foraging at the edges of eddies also found that the position of birds was strongly associated with either specific SSTs or elevated [Chl *a*] (e.g. Ainley et al., 2005, Hyrenbach et al., 2006). My study found the opposite effect, illustrating that, at least in this system, [Chl *a*] is not an ideal indicator of prey availability at these tropical foraging grounds.

This lack of association with [Chl *a*] enhancement could be explained by the strong decoupling that occurs between ocean dynamics and primary production in the Coral Sea region during the summer season (Menkes et al., 2014). This causes a time lag in the food chain between primary production and the upper trophic levels such as micronekton. This temporal mismatch would explain why shearwater foraging locations are not linked to elevated [Chl *a*]. Furthermore, it would also provide support for the hypothesis that eddy peripheries drive increased availability of prey such as micronekton (Sabarros et al., 2009, Drazen et al., 2011, Potier et al., 2014), which attracts shearwaters in this system.

4.5.5 Sub-surface predators

Shearwaters are not the only apex predators to be attracted to these kinds of ocean phenomena. Eddy-edge areas also attract sub-surface predators such as tuna (Mugo et al., 2010, Tew Kai and Marsac, 2010), the activity of which is well-known to influence the foraging of numerous seabirds in tropical environments (Au and Pitman, 1986, Au and Pitman, 1988, Ballance et al., 2006). Furthermore, the frontal regions at the periphery of eddies have also been directly linked with aggregations of micronekton on which both seabirds and other top-predators prey. For example, in the eastern tropical Pacific and Indian Ocean, both tuna (Fiedler and Bernard, 1987, Fonteneau et al., 2008) and seabirds (Au and Pitman, 1986, Ballance et al., 2006, Catry et al., 2009a) are known to aggregate at eddy periphery fronts, as are schools of micronekton (Bertrand et al., 2002, Sabarros et al., 2009).

GBR shearwaters may also interact with tuna in the east Philippine Sea during their winter migration (chapter two) but we currently lack evidence of these interactions. Furthermore, there is no direct observational evidence of shearwaters from southern GBR populations foraging in association with sub-surface predators during the breeding season. However, the Coral Sea foraging locations identified in this study overlap significantly with commercial tuna fisheries in the region (Evans et al., 2008, Farley and Clear, 2008, Young et al., 2011). This suggests that the interaction could be a strong and important one for enhancing prey availability to long-tripping shearwaters. Moreover, it highlights the fact that this potentially critical interaction needs to be confirmed and quantified to determine how important sub-surface predator interactions really are if foraging ecology in either group is to be fully understood.

4.5.6 Conservation

This research identifies locations that are consistently used by shearwaters on long, self-provisioning foraging trips during breeding. Inter-annual variation in location use suggests some flexibility in the system, but as all locations are beyond the short-trip range of the colony, these resources are essential to maintaining successful reproductive output at southern GBR colonies. Furthermore, most, if not all of these sites are not within the boundaries of current management zones, and have no special conservation status. My findings imply that the maintenance of these sites as viable and productive areas must be a priority in any future management strategies aimed at conserving GBR breeding shearwater populations.

However, due to the complex bathymetry and ocean dynamics in the region, the mesoscale mechanisms which drive resource availability at these locations tend to be small and transitory (Owen, 1981, Andrews and Clegg, 1989). This makes them more ephemeral and less predictable, or reliable as food aggregation mechanisms. Furthermore, ocean-scale currents entering the Coral Sea drive their presence, movement, position and intensity. This means that changes in the movement or flow of the SEC will have significant repercussions on local eddy and upwelling dynamics (Brinkman et al., 2002). For example, if ENSO events increase in frequency and severity as expected (IPCC, 2013), the speed and strength of the EAC would also increase, which could, in turn, result in reduced eddy formation, occurrence, size, frequency or position shifts (Weeks et al., 2010, Holbrook et al., 2011, Johnson et al., 2011). Such changes in ocean dynamics could reduce available foraging habitat and significantly impair the ability of shearwaters to successfully self-provision. Wedge-tailed shearwater chicks have minimal plasticity in their ability to deal with variation in food supplies (McDuie et al., 2013) and significant deleterious effects of climate and ENSO processes have previously been demonstrated (Smithers et al., 2003, Peck et al., 2004). Therefore, as chick survival depends on an adult’s ability to obtain sufficient resources for self-maintenance and chick-rearing, climatic or environmentally driven food reductions have the potential to negatively affect reproductive success. Future studies must determine how stable or ephemeral these phenomena are and how these dynamics affect shearwater reproductive success by analysing variation in food quality, acquisition and provisioning rates according to location. Only with this information is it possible to determine if it is more appropriate to manage seabirds according to location specific criteria or if a shift to ocean-scale criteria would be more effective.

Importantly, current management of the pelagic marine environment in the Coral Sea region is limited to the tuna and billfish fisheries, with little attention focused on other taxa such as seabirds. As it has now been demonstrated that Wedge-tailed shearwaters use the same region, it is very important that the goals and application of management in this fishery be integrated with conservation strategies and outcomes across a broader range of top-predators including seabirds.

4.5.7 Conclusion

Modelling the factors that influence seabird foraging location and habitat use has been crucial to advancing our understanding of the dynamics of food availability to seabirds and the trophic mechanisms that regulate prey availability and accessibility in tropical marine systems. The observed importance of upwelling and eddy convergences, combined with little influence of SST and productivity, highlights the disparity in mechanistic processes that influence prey availability in the Coral Sea compared with those seen in other regions. Such findings suggest that an understanding of local and regional scale dynamics and oceanography is essential for developing colony-specific conservation strategies.

The reproductive success of wedge-tailed shearwaters breeding in the southern GBR depends upon birds being able to access specific, pelagic foraging resources that are reliable, productive and likely to persist through time. Ultimately, the information derived from this study will aid in defining and predicting ‘good’ foraging locations for these and other tropical pelagic foraging seabirds, areas that may be indispensable, and should be prioritised for evaluation under management and conservation priorities. This kind of action that will vastly improve efficacy and efficiency of regional seabird management.

5. DRIVERS OF CRITICAL NEAR-COLONY FOOD AVAILABILITY FOR A TROPICAL BREEDING PROCELLARIIFORM: MESOSCALE EDDY AND TERRESTRIAL INPUT

This chapter is in preparation for submission to the Journal of Animal Ecology as: “A regional mesoscale eddy and terrestrial input rivers are major drivers of critical near-colony food availability for a tropical breeding Procellariiform.” by F McDuie, S. J. Weeks, M.G.R. Miller and B. C. Congdon.

The entire chapter was written by Fiona McDuie, with co-authors providing intellectual input to the design and implementation of the research and editorial contributions to the paper. Data collection, data analyses and production of tables and figures were conducted by Fiona McDuie.

5.1 ABSTRACT

Great Barrier Reef (GBR) wedge-tailed shearwaters obtain food for their chicks on short-trips near the breeding colony. Adult shearwaters were tracked with state-of-the-art GPS equipment in three breeding seasons (Feb-Apr) to identify the location of foraging grounds. Oceanographic characteristics of importance were identified and compared for foraging and non-foraging areas, to determine the mechanisms that drive prey availability.

Most trips were single day (70-85%) and all were within 300km from the colony. Foraging in general, was adjacent to the Capricorn shelf, where the largest oceanographic mechanism in the region, the mesoscale Capricorn Eddy, '*spins up*'. The eddy interacts with the bottom creating upwellings and fronts. Bathymetry was the most important explanatory variable of foraging (of 27 in the initial boosted regression tree model). Five bathymetrically and topographically distinct zones (hereafter referred to as zones 1-5) were identified, which were consistently revisited at varying levels of usage. The least used zone was most distant from the colony and exhibited characteristics more analogous to locations used by shearwaters on long foraging trips (deep sea level anomalies and currents). In 2013, strong sea-surface temperature (SST) fronts were generally influential on all foraging, indicating the dominance of the Capricorn Eddy. In 2014 the dominant factors varied among zones and were usually anomalous or absolute values of SST and chlorophyll *a,* suggesting a weakened effect of the eddy and elevated importance of fine-scale phenomena such as localised upwellings.

By contrast, a different mechanism influenced the zone nearest the colony. Foraging in this highly used zone was more strongly influenced by terrestrial input, demonstrated through foraging associations between birds and freshwater plumes as well as higher than average chlorophyll *a* levels. This is a complex system with two key mechanisms driving foraging of wedge-tailed shearwaters in the short-trip zone around Heron Island: terrestrial inputs and the Capricorn Eddy. Both are highly vulnerable to variations in climate processes and large-scale climatic phenomena. Consequently, predicted changes in these conditions, particularly driven by increased ENSO severity or frequency, could exacerbate the scarcity of prey and as such, seriously diminish the scale of profitable foraging locations and seabird foraging and reproductive success.

5.2 INTRODUCTION:

When breeding, the area in which seabirds can obtain food is constrained by the need to return to the colony at regular intervals to feed chicks (Weimerskirch et al., 1994, Weimerskirch, 1998). As a result, the specific environments or resources that can be used by adults to provision chicks are greatly reduced. This is one of the primary disadvantages of being a '*central-place'* forager (Orians and Pearson, 1979). As a consequence, the reproductive success and persistence of individual seabird colonies can be totally dependent on the continued stability and productivity of a relatively small number of near-colony foraging grounds. Therefore, to be able to effectively conserve seabirds requires protecting and managing these locations. This can only be done with detailed information on the locations of these sites and the oceanographic characteristics that have a direction influence on prey ability at each.

Near-colony foraging areas in temperate and sub-polar systems are generally characterised by enhanced primary productivity (Hyrenbach et al., 2002, Cecere et al., 2012). Cory's shearwaters (*Calonectris diomedea diomedea*) exploit shallow coastal areas of the Adriatic Sea that exhibited high net primary productivity (Cecere et al., 2012) and black-browed albatrosses (*Thalassarche melanophrys*) of the Kerguelen Archipelago forage at shelf-break areas known for elevated productivity (Cherel and Weimerskirch, 1995). These types of foraging areas can be seasonal and highly predictable, and are often related to large-scale oceanographic phenomena such as fronts, frontal convergences, upwellings or eddies (Hunt, 1991, Ainley et al., 2005, Yen et al., 2006a). For example, sooty shearwaters (*Puffinus griseus*) from New Zealand forage near the colony in shallow, neritic waters above the continental shelf that experience relatively high primary productivity and are characterised by seamounts and coastal upwelling (Shaffer et al., 2009). Fronts, convergences, eddies and upwellings, in turn are driven by wind, the interaction of currents or currents interacting with sea-floor topography (Andrews and Gentien, 1982, Bograd et al., 1997, Song et al., 2001). They are also strongly related to temperature (Becker and Beissinger, 2003, Ainley et al., 2005), the most important variable that structures marine ecosystems (Boehlert, 1988). Very strong temperature gradients are generally associated with large oceanic phenomena in temperate systems such as the Antarctic Convergence or the Kuroshio Current (King, 1974, Brown et al., 1975, Croxall and Prince, 1980).

Nevertheless, there are some similarities with temperate systems. Near-colony foraging areas are often associated with elevated productivity that is enhanced by frontal systems, eddies and upwellings (Le Corre, 2001, Weimerskirch et al., 2004, Cecere et al., 2013). For instance, in the Indian Ocean, sooty terns (*Sterna fuscata*) foraging is driven by seasonal blooms in primary productivity (Jaquemet et al., 2007), produced by currents in the Mozambique Channel in the western Indian Ocean (Lutjeharms and De Ruijter, 1996, de Ruijter et al., 2004, Quartly and Srokosz, 2004). Additionally, highly stable and predictable ocean-scale currents, which influence foraging in temperate systems (Croxall and Prince, 1980, Shaffer et al., 2009), also circulate throughout tropical regions, but associations with seabirds and prey enhancement to seabirds have not frequently been reported. One example of such a relationship exists in the eastern tropical Pacific, where seabird communities forage along the relatively stable Equatorial Front and associated ocean-scale currents (Spear et al., 2001, Mannocci et al., 2014). As with these kinds of systems in temperate regions, this front exhibits a recognisable and relatively strong sea-surface temperature (SST) gradient, infrequently seen in the tropics. Finally, frigatebirds (*Fregata minor*) of the Indian Ocean forage at the periphery of unpredictable mesoscale eddies that were loosely (Weimerskirch et al., 2004), but known to aggregate prey (Sabarros et al., 2009). However, these eddies tend to be unpredictable and only loosely correlated with productivity enhancement (Weimerskirch et al., 2004, Weimerskirch et al., 2010), possibly as a result of the high seasonality of eddy dynamics in the tropics caused by monsoonal and climatic influences (Stammer and Wunsch, 1999, Pullen et al., 2008). Therefore, while some drivers appear to be similar to those seen in temperate zones, they often differ in important ways such as size, predictability or level of productivity enhancement.

Physical differences in ocean mechanics means that tropical seabird/environment relationships often differ to those of temperate systems. There are no obvious large-scale upwellings, such as those seen in the Southern Ocean (Anderson et al., 2009), other than the Inter-tropical Convergence Zone (ITCZ) (Andrews et al., 2003). Therefore, links between seabird foraging and these types of predictable, larger-scale phenomena are much less common in tropical regions (Ashmole, 1971, Ainley and Boekelheide, 1984, Ballance et al., 2006). Instead, tropical seabirds primarily forage in association with smaller-scale upwelling systems. For example, wedge-tailed shearwaters (*Ardenna pacifica*) target mesoscale areas of upwelling induced productivity in the Indian Ocean, as do conspecifics in Hawaii (Baduini, 2002).

There is also evidence that other processes which are not commonly observed to influence foraging of seabirds in temperate systems may be important in the tropics. Interactions of numerous species of seabirds, with sub-surface predators such as tuna, have been seen in many tropical regions (Au and Pitman, 1988). For example, many species in the eastern tropical Pacific forage in association with fronts that aggregate predators (Au and Pitman, 1986, Ballance et al., 2006). Similarly, species in the Indian Ocean are commonly cited to associate with tuna, at fronts known to be favourable to them, including red-footed boobies (*Sula sula*) (Weimerskirch et al., 2005), great frigatebirds (Weimerskirch et al., 2010), sooty terns, Audubon's shearwaters (Le Corre, 2001) and wedge-tailed shearwaters (Catry et al., 2009b). Le Corre et al. (2005) even argue that seabird abundance in the Mozambique Channel could be used as indicators of tuna abundance, where numerous species are said to forage in association with tuna (Jaquemet et al., 2004). Many of these studies report overlap of areas of use by the relevant species with commercial fishing zones, rather than direct observations of interactions. Nevertheless, these relationships are more commonly in tropical systems.

So far, findings from seabird studies in tropical and temperate environments demonstrate both similarities and differences between factors that influence prey availability to seabirds. However, while the well-studied temperate zones generally demonstrate much the same patterns of influence, findings from tropical seabird studies indicate that there is greater variation and that they vary from one another. Although few studies have reported associations with macro or meso scale features, most have only been described in one study or for a single species or location. None have described or presented detail on the influence of finer-scale localised processes on tropical seabird foraging relationships, especially in near colony environments. For example, Australia's Great Barrier Reef (GBR) is not known for these kinds of larger-scale processes such as fronts or upwellings, or productivity enhancements (Kleypas and Burrage, 1994, Burrage et al., 1996, Brinkman et al., 2002). The distinctive topography of the region produces different oceanic effects that are less stable and predictable and drive smaller scale phenomena (Burrage et al., 1996, Brinkman et al., 2002, Choukroun et al., 2010).

In fact, finer-scale processes such as temperature effects may be more important than fronts and oceanic phenomena. For example, localised variations in SSTs have negatively impacted numerous seabird species of the GBR, within their breeding seasons. Erwin and Congdon (2007) found day-to-day SST variation affected both meal mass and feeding frequency to chicks of sooty terns (*Onychoprion fuscatus*), a declining species. Similarly, Peck et al. (2004) found that when SSTs increased over a 10 day period in the chick rearing season of wedge-tailed shearwaters, meal masses, chick growth and adult provisioning rates decreased correspondingly. Another species, black noddies (*Anous minutus)*, breeding on Heron Island also suffered food shortages from short-term SST increases (Devney et al., 2010). In all these cases, when SSTs increased, food disappeared, and conversely, when SSTs subsequently declined, food availability returned.

However, thermal dynamics can also influence seabird food resources through impacts of larger-scale processes such as climate change. The El Niño Southern Oscillation (ENSO) can cause SSTs to rise for extended periods and hence, drive much more deleterious food reductions for seabirds. Numerous negative impacts to seabirds of the GBR have been related to variation in the ENSO cycle. Effects are generally observed on longer-term time-scales such as between breeding season variations in seabird foraging or reproductive success. For example, Smithers *et al*. (2003) reported a significant reduction in wedge-tailed shearwater reproductive success when a strong season-scale ENSO event raised SSTs for an extended period, significantly decreasing food available to chick-provisioning birds. Indirect effects on regional dynamics have also been seen whereby ENSO precursors drove reduced breeding participation in Sooty and Common terns of the northern GBR through thermocline depth and intensity (Devney et al., 2009, but see crested terns, same study).

Further data from the GBR indicates that effects at different scales are not mutually exclusive but linked in some way (Smithers et al., 2003, Peck et al., 2004, Weeks et al., 2013). The Capricorn Eddy is a mesoscale oceanographic structure in the southern GBR that demonstrates links with both fine-scale temperature variations and large-scale ENSO conditions that impact foraging seabirds (Weeks et al., 2010, Weeks et al., 2013). The eddy is primarily driven by the speed and strength of the East Australian Current

(EAC), which varies under ENSO conditions (Weeks et al., 2010). The EAC interacts with areas of steep bathymetric change in the region and cold, nutrient-rich water is upwelled in the centre of the eddy and discharged to the edges, where it creates SST fronts that aggregate fish, nutrients and productivity. Short-term food reductions to wedge-tailed shearwaters occurred when the eddy moved westward and approached the GBR lagoon, forcing stratification that warmed surface layers via a deep, cold water intrusion (Weeks et al., 2013). Although this was a single event, the correlation suggests that shearwaters are influenced by the position, strength and movement of the Eddy, and hence, the factors that drive it (EAC, ENSO), as well as the conditions it, in turn, produces (localised upwelling). However, for this relationship to be true the birds must be both foraging in association with the Eddy, and impacted by the oceanography generated by it, which is currently not known. Such a relationship could be observed through variations in oceanographic parameters of the water column such as SST or Chlorophyll *a* [Chl *a*] anomalies and SST fronts, which are known to highlight the existence of fronts, convergences or upwellings (Oschlies and Garçon, 1998).

The processes that ultimately drive food availability in tropical systems are complex and relatively unknown. Tropical systems are generally more homogeneous, warmer and lower in productivity (Levinton, 2001), and do not generally experience the marked climate-driven seasonality, typical of temperate regions (Dickman et al., 2008). Therefore, results from tropical seabird studies do not agree as neatly as findings from studies of temperate seabirds. With multiple different factors reported to influence advantageous foraging for tropical seabirds, it is likely that the contrasting results have arisen from studies examining different parts of these processes independently.

Until now, there has not been a comprehensive study that simultaneously investigated all the possible influences on prey availability to tropical seabirds to determine the relative importance of different processes, and explore the reasons behind the inconsistent results from tropical systems. Consequently, processes responsible for increasing prey availability at tropical foraging grounds have yet to be quantified for tropical marine environments, and are not easily explained. Without a single study combining all this information, and a thorough exploration of all potential explanations, it is not possible to make any clear generalisations about tropical seabird foraging in near-colony grounds. This is the next most important step in tropical seabird research because until these conflicts have been resolved, it is not possible to generate a general model for the mechanisms that drive prey availability in tropical marine environments.

Wedge-tailed shearwaters are a Procellariiform (tube-nosed) seabird breeding in the southern GBR that have shown numerous observed impacts to their food resources from both fine and larger scale processes (Smithers et al., 2003, Peck et al., 2004, Weeks et al., 2013). This pelagic species dual-forages (Congdon et al., 2005) using longer foraging trips to reach distant foraging grounds (McDuie et al., 2015). Near-colony foraging grounds, used to obtain food for chicks, are likely to be within a maximum radius of 300km from the colony on Heron Island (McDuie et al., 2015, see chapters two and three). If so, foraging may occur in the same region as the Capricorn Eddy, and there should be readily identifiable oceanographic evidence (physio-chemical parameters of the water column) at foraging grounds that demonstrate a direct relationship with, or causality of, eddy dynamics. However, neither the locations of short-trip foraging, nor the mechanisms which drive prey availability to birds at those locations, have been documented to date. This severely limits our ability to effectively conserve and manage such seabird populations.

5.2.1 Aims:

I aimed to determine the trophic mechanism/s that drive food availability in near-colony foraging grounds used by wedge-tailed shearwaters of Australia's GBR for chick-provisioning. Through a high-resolution tracking study, I will identify the locations of critical, near-colony foraging grounds. A comprehensive set of oceanographic parameters will be examined in detail to accurately characterise these foraging areas, including how prey is enhanced and the way predators such as seabirds interact with this environment. Investigation will focus on parameters that have been considered in previous research of tropical systems (e.g. [Chl *a*], SST and bathymetry), as well as additional parameters specifically selected to highlight the presence of fine and mesoscale ocean dynamics (e.g. anomalous values of SST and [Chl *a*]) (Oschlies and Garçon, 1998, Palacios et al., 2006). With this information I can test the hypothesis that shearwaters forage in association with the small, mobile and variable Capricorn eddy. Furthermore, it will identify the optimal set of factors that define near-colony foraging grounds; facilitate generation of a model of trophic mechanisms influencing near-colony food resources of a tropical Procellariiform; and drive development of a method for accurately identifying the phenomena that are important to augmenting prey availability to pelagic foraging tropical seabirds.

Ultimately, it will be possible to map ideal foraging habitat and predict how changes in the oceanographic characteristics or phenomena would affect prey availability and the profitability of foraging in any given location. This is particularly important in locations where food is obtained to rear a chick, as it has direct repercussions on seasonal reproductive success. Finally, as the Heron Island colony is inside the GBR Marine Park, it is likely these chick-provisioning foraging grounds are also within the management zone. If so, detailing precise locations of foraging grounds would aid management of this population by identifying the most important areas to flag for protection.

5.3 **METHODS**

5.3.1 Study site and population monitoring:

Tracking in this study targeted the chick-provisioning or ‘near-colony’ foraging trips of wedge-tailed shearwaters breeding at Heron Island in the southern Great Barrier Reef (GBR), Australia (Congdon et al., 2005). Field work was conducted in the months of February and March, 2012, 2013 and 2014. Monitoring, trapping, and handling protocols followed those detailed previously (chapters two and three). During the 2012 season I monitored 30 active nests: 20 of these were experimental nests where at least one adult was tracked and 10 controls, where only chicks were handled. In 2013 I monitored 86 nests (66 tracked and 20 controls) and in 2014, 30 nests (20 tracked, 10 controls). Throughout the study period trip duration, provisioning cycles of adults, adult weight at the beginning and end of foraging trips and daily chick growth via meal masses were monitored at each experimental nest. These data can be used in future analyses to determine variation in food quality, acquisition and provisioning rates related to foraging location.

5.3.2 Electronic tracking

Electronic archival GPS (global positioning system) devices were deployed on adult wedge-tailed shearwaters for short, chick-provisioning trips. Short-trips are defined as those < 4 days (Congdon et al. 2005). All trips less than 4 days are included in the current analyses, although the majority of the trips observed were only 1 – 2 days.

In 2012 GPS tracking was undertaken using miniature Lotek GPSBugs™ (Lotek Wireless, St Johns, Canada) (10.4g, dimensions ~23x17x15 mm). GPSBugs were deployed on 30 individual adults, however high fail rates meant that 12 out of 30 deployments provided no data (Table 1). The remaining 18 provided a very limited number of position fixes, possibly as a result of poor battery life (~15hours) or poor signal acquisition.

Table 5.1: GPS deployment data for wedge-tailed shearwaters of Heron Island tracked on short foraging trips in years 2012-14. The number of individuals on which deployments were made for short-trips is indicated in parentheses. '*No data'* details logger failure or loss.

YEAR	# BIRDS	SHORT-TRIPS	LONG TRIPS	NO DATA	NO. FIX LOCATIONS	NO. OF FORAGING LOCATIONS	NO. OF NON-FORAGING LOCATIONS
2012	30	18	0	12	484	242	242
2013	78	79 (52)	18	8	9354	4015	5340
2014	38	34 (33)	0	4	3572	1947	1625

In 2013 and 2014, tracking data were acquired using modified, battery powered iGot-U™ GT-120 (Mobile Action Technology) GPS tracking devices (weight 10.2 g, dimensions ~44x22x5 mm after modification). My modification included reducing battery size (90-120 mAH and repackaging in 50mm clear heat shrink wrapping (Finishrink™ UK), to produce a slim, waterproof profile that reduced in-flight drag (Culik et al., 1994). Repackaging minimised size to fall within the accepted 3% of body weight limits for device deployment on seabirds (max weight. 10.5g and deployed only on adults weighing greater than 380g) (Kenward, 2001, Phillips et al., 2003).

In 2013, iGot-U™ devices were successfully deployed on 70 adult shearwaters that were rearing chicks. Of these, 18 remained away on long-trips (chapter four) and the remaining 52 produced 79 individual short-trips of various lengths between 1-3 days. In 2014, 33 shearwaters were tracked, producing 34 individual short-trips. No retrieved loggers failed to provide data. Some individuals were tracked on more than one foraging trip and multiple trips by the same individual are not statistically independent. If individuals visited the same foraging locations on multiple trips, the data would be biased to specific locations that were repeatedly visited by a smaller number of individuals. Therefore, I conducted a visual assessment of all foraging trips by mapping all tracks in Google Earth. In 2013, of the 19 birds which were tracked on multiple trips, none foraged along the same tracks or visited the same location on consecutive trips. Three individuals conducted trips that were in a similar direction from the colony but foraging locations (identified by ARS – see section 5.3.3.3) were never nearer 11-20km. In 2014, one individual was tracked on two foraging trips in the same direction from the colony but foraging locations were never within 6km of one another. Therefore, as no foraging locations were visited multiple times by any individual tracked on multiple trips and to preserve a robust sample size, all data were retained for the analyses.

Adult shearwaters depart the colony between 04:00-05:00h to forage at sea, and most returned in the early evening between ~19:00-20:00h. Therefore, GPS were set to record between 04:00h and 20:00h and programmed to record position fixes every 3 or 5 minutes depending on battery life identified during pre-season testing (4-6 days). GPS location accuracy is high (approx. ~4-50m) and, when obtaining very regular location fixes, provide very accurate information on the actual flight path of a bird during the hours of tracking. Devices were mounted at the base of an adult’s tail on three feathers with a single strip of TESA™ tape (Beiersdorf Germany). Temporary tail mounting was used as it considerably reduces disturbance to birds compared with back mounting and allows individual GPS devices to be reused on multiple individuals. Devices were deployed on adults upon their exit from the nest following chick feeding and removed at the conclusion of the subsequent short-trip. On some occasions, when birds were missed at the nest or did not return the following day, devices were retrieved at the first opportunity. No evidence of birds attempting to remove the tape, the device, or any damage to tail feathers was observed.

5.3.3 Data analysis

5.3.3.1 *Identifying foraging and non-foraging activity*

All GPS data were downloaded using the manufacturer's software, and tracks plotted using ArcGIS 10.2 for Desktop (©ESRI Inc.). In 2012, the GPS Bugs provided comparatively low numbers of fixes per track (3-28) and these were, in most cases, assumed to be at foraging locations. This conclusion was based on time of departure from the colony, time of first fix subsequent to departure and distance travelled in the interim, as well as on average flight speeds of 26-30 kmh^{-1} (*unpub. data*). Furthermore, Lotek technicians advised that the flight patterns of shearwaters likely prevented the GPSBugs from fixing on satellites only while they were in rapid flight. This conclusion was further supported by two GPSBug tracks that did provide positions for the birds in transit, confirming flight speed/distance travelled. By comparison, data obtained from iGot-U™ devices in 2013 and 2014 were of considerably higher resolution. Therefore, I used different methods to define foraging and non-foraging areas, for analyses comparing oceanography.

5.3.3.2 *Kernel density analysis*

The lowest resolution data from 2012 were considered accurate for foraging locations but with few non-foraging location data, a set of pseudo-non-foraging locations, to represent non-use areas, needed to be created to match the number of foraging locations. To do this I performed kernel density estimation (KDE) to estimate the core (50% UD kernel) and maximum use (95% UD kernel) areas (as detailed in chapter four). The data points within the core-use kernel (50%) are assumed to represent foraging, while the remaining kernel area represents non-foraging or non-use area (Hamer et al., 2007). The 50% kernel was clipped from the 95% kernel in ArcGIS 10.2 for Desktop and a set of pseudo-non-foraging points were generated from within the area that remained. These two sets of locations were combined to produce the binomial response variable (1/0 = foraging/non-foraging) that was used in modelling analyses to compare the oceanographic characteristics of foraging vs. non-foraging areas.

5.3.3.3 *First-passage time and Area-restricted search analysis*

For the 2013 and 2014 data, foraging and non-foraging locations were classified at the smallest scale possible. Foraging locations were defined by running the tracks through first-passage time (FPT) analyses to first identify area restricted search (ARS) locations (Fauchald and Tveraa, 2003, Pinaud and Weimerskirch, 2007). First-passage time (FPT) analysis calculates the time it takes an organism to cross a circle of a given radius (*r*) along the trajectory of its foraging track (Fauchald and Tveraa, 2003). This scale-dependent measure of search-effort is used to investigate foraging movements in animals, including seabirds (Pinaud and Weimerskirch, 2005, Pinaud and Weimerskirch, 2007, Pinaud, 2008, Sommerfeld et al., 2013). Using this analysis, ARS zones are placed along the track where turn angles (sinuosity) increase and flight speed decreases thus these areas are assumed to indicate the animal's foraging response to increases in prey density (Kareiva and Odell, 1987, Sommerfeld et al., 2013).

To prepare data for this analysis tracks were filtered by velocity, with all points exhibiting speeds greater than 75km h^{-1} removed, based on the ecology of wedge-tailed shearwaters and average flight speeds (McDuie and Congdon *unpub. data*). To deal with extant gaps in data from missing fixes, tracks were interpolated for location fixes at 10 minute intervals to obtain equal time intervals between fixes. No interpolation was done where points were > one hour apart. Filtering and analyses were conducted in R 3.03 (R Core Team, 2013), using the 'adehabitatLT' package (Calenge, 2006). Eleven individuals were sequentially tracked on >1 short trip (total of 27 trips), therefore these tracks were split into individual short trips by determining if birds either returned to the colony or were tracked to within 20km of the colony with the chick subsequently being fed. Some birds were not observed returning all the way to the colony on short trips due to loggers switching off at 20:00-21:00h.

First passage times (FPTs) were calculated for each location along the tracks using radii (*r*) that ranged between 1 and 80km, increasing incrementally by 1km. The (log) variance of the FPTs are plotted against the radii and the plot exhibits a maximum peak when there is ARS behaviour (Fauchald and Tveraa, 2003). This therefore, determines the ARS scale for that track which classifies the scale at which that individual is exhibiting ARS behaviour and this differs among individuals/tracks. Every location along foraging tracks are then allocated an ARS value of true (1) or false (0) all of which are used in the modelling analyses, as the required binomial response variable of 1/0, which represents foraging/not-foraging. FPT can be inaccurate if resting periods cannot be distinguished from foraging (Sommerfeld et al., 2013). I visually assessed each foraging track for periods of very low movement, often indicated by points that track very close together in a straight line, indicative of surface resting and easily visible in the data.

5.3.4 Oceanographic parameters

Once the status of foraging (ARS=1) or non-foraging (ARS=0) was defined for each latitude/longitude fix along all foraging tracks, the corresponding values for a set of oceanographic variables were extracted to each of these foraging and non-foraging location fixes in the data sets. The same high resolution, satellite derived oceanographic data were accessed as had been used previously in chapter two, pages 23-25 (Table 5.2) and downloaded as shapefiles to AcrGIS 10.2 for Desktop. However, due to the higher temporal and spatial resolution of the GPS data in the present study, and shorter trip duration, I also investigated a number of additional oceanographic parameters at higher resolution (3 day means in addition to the monthly climatologies). Sea-surface temperatures (SST), SST anomalies (SSTA), [Chlorophyll *a*] ([Chl *a*]), [Chl *a*] anomalies (ChlaA) and SST gradients (SSTG - hereafter called SST fronts).

Table 5.2: Definition of oceanographic variables and their measurements used in boosted regression modelling of GBR wedge-tailed shearwater short foraging trips.

Term	**Description**	**Measurement**
DistSSTG/25	Distance to nearest steep (25%) SST gradient or front	Degrees distance
ChlaMonth	[Chlorophyll *a*] ([Chl *a*]) monthly climatology	mg/m-3
Chla3dmean	[Chl *a*] 3 day means	mg/m-3
ChlaAmonth	[Chl *a*] Anomalies monthly climatology	mg/m-3
ChlaA3dmean	[Chl *a*] Anomalies 3 day means	mg/m-3
SSTmonth	Sea surface temperature (SST) monthly climatology	Degrees (°C)
SST3dmean	SST 3 day means	(°C)
SSTAmonth	SST Anomalies monthly climatology	(°C)
SSTA3dmean	SST Anomalies3 day means	(°C)

SSTGmonth	SST gradient (front) monthly climatology	(°C)/km
SSTG3dmean	SST front 3 day means	(°C)/km
Bathymetry	Depth of ocean floor	m
Bath_grad	Steepness of slope. Depth change in metres by distance	m/km
DistBathg	Distance to nearest steep (25%) bathymetric gradient	Degrees distance
Coldist	Distance to the colony	Degrees distance
Photic Depth	Transparency of water measured by Secchi disk	Metres depth
Distseam	Distance to the nearest seamount	Degrees distance
MSLA	Mapped sea level anomaly	mm
CDSP	Speed of currents in centimetres per second	cm/s

The complete set of oceanographic parameters used in this study were specifically selected for their capacity to more accurately and comprehensively characterise the marine environment throughout the foraging region. The values of SST or [Chl *a*] anomalies can reveal the presence, location and strength of oceanographic features like eddies, upwellings or oceanic fronts (Garvine, 1974, Oschlies and Garçon, 1998). Therefore, it was anticipated that they would be useful in revealing the Capricorn Eddy or frontal activity in the region. These variables are frequently overlooked by other studies but should be included as they are likely to be important in regional ocean dynamics.

I used two variables representing water quality to determine if fresh water or water clarity influenced foraging behaviour (and as such, prey availability). The first was photic depth, which is the transparency of water measured by Secchi disk depth (Weeks et al., 2012). The second was the presence of primary, secondary and tertiary freshwater plumes which begin nearest the coast and extend out to sea and are assessed at a weekly scale (da Silva et al., 2002-2014), for the 2013/14 data. Results of foraging frequency within these plumes are reported. ‘Central-place’ foraging limits distance that can be travelled from the colony so this factor was also investigated in the original full model analyses by year.

All data were imported to ArcGIS 10.2 for Desktop for mapping, assessment, manipulation and extraction of oceanographic variables (per chapter two pages 21-23). Three day and monthly means of all oceanographic data were matched by date to corresponding GPS track dates and subsequently collated into month and year of tracking, for analysis. These files were converted to CSV and modelled in R (R Core Team, 2013). Some of the environmental parameters selected for assessment are not available for shallow depths above the continental shelf (< ~200m), including mean sea level anomalies (MSLA) and current speeds (CDSP). Therefore, these data were only analysed for the bathymetrically deeper zones where they were available and reliable. In shallower coastal waters some oceanographic parameters derived from satellites can be unreliable due to turbidity, light refraction or presence of land in any given image pixel. For this reason, erroneous data points, which are generally excessively high or obviously inaccurate values (e.g. SST of 45.007°C or positive values for bathymetry) were assessed by comparing extracted values in the CSV files, identified and removed. Due to the higher prevalence of cloud cover during the summer months, which prevents satellites from obtaining data, there was a greater proportion of missing data in the variables for 3 day means. In the instances when there were too few data to be analysed, those parameters were automatically excluded so as not to exert a disproportionate influence on the model.

5.3.5 Statistical analysis and modelling

Boosted regression trees (BRT) were selected for these analyses due to the high number of environmental variables, the expectation of complex, non-linear relationships and because BRTs can easily deal with violation of statistical assumptions such as unequal variances (Elith et al., 2008, Buston and Elith, 2011) (see chapter two, pages 23-26 for detail). Default values and model runs followed recommendations by Elith et al. (2008) and used the Bernoulli (binomial) error distribution. Model parameters in this study used a tree complexity of one less than the number of predictor variables being considered in any analysis; began with a fast learning rate of 0.01; and a stepwise increase of trees beginning with 50 and increasing to a maximum of 10000. Randomness was introduced when necessary to improve model performance using bag fraction values between 0.5-0.75, the learning rate and tree complexity were adjusted until the model performance improved and the model was optimised.

Full models were run on all data by year, comparing foraging and non-foraging, with month as a factor. They were then simplified to produce the most parsimonious and accurate model defining the trophic mechanisms driving foraging intensity in shearwater foraging grounds. Finally, individual models were performed on each of the five separate sub-foraging-zones and results are presented for 2013 and 2014. However, due to the paucity of data from 2012, BRT models produced excessive over-fitting and spatial auto-correlation (SAC) when run on Zones 1, 2 and 4. Consequently, these models are omitted and results for the full model and zones three and five are reported.

5.4 **RESULTS**

Foraging shearwaters remained at-sea throughout the day departing before sunrise, between ~04:00 and 05:00h and returning to the colony after dark, between 19:00 and 21:00h, making most single day trips in the range of 14-17h. In 2012, 18 foraging trips were recorded for 18 individual birds and all were single day trips. Without complete tracks it was not possible to determine distance travelled from the colony. In 2013, 79 separate trips were obtained from 52 individual birds: 55 were single day trips (69.6%), 20 were two days (25.3%) and three trips were three days (3.8%). One bird remained away for four days (1.3%). Birds travelled on average 83.06 ± 9.13km from the colony (range 19.36 - 283.82km, n = 79; Table 5.3). In 2014, there were 34 separate trips from 33 tracked individuals: 28 single day trips (82.4%), five two day trips (14.7%) and one three day trip (2.9%). Birds travelled an average of 70.14km from the colony (range 16.42-212.73km, n = 34; Table 5.3). All trips were within 300km of Heron Island which was expected from analysis of shearwater long foraging trips (McDuie et al., 2015, chapter three). There was strong consistency of site use across the data-collection period and locations were characterised by different sets of oceanographic factors which varied by year.

Table 5.3: Summary of ARS data for GPS tracked wedge-tailed shearwaters. Values are mean ± 1 s.e. Range in parentheses beneath each.

	2013 (n=79)	**2014 (n=34)**
# tracked individuals	52	33
Single day trips	55 (69.6%)	28 (82.4%)
two day trips	20 (25.3%)	5 (14.7%)
>2 day trips	4 (5.1%)	1 (2.9%)
Max. distance from colony (km)	83.06 ± 9.13	70.14 ± 8.09
	(19.36 - 283.82)	(16.42 - 212.73)
# ARS per trip	2.42 ± 0.03	1.88 ± 0.02
	(0 - 215)	(7 - 159)
Scale of ARS (km)	6.62 ± 0.59	8.17 ± 0.10
	(2 - 19)	(2 – 28)
Distance of ARS from colony (km)	80.58 ± 0.78	67.27 ± 0.62
	(3.29 - 245.65)	(3.86 - 212.73)

5.4.1 Characteristics of area restricted search zones

In 2013, ARS behaviour was detected in 78 of the 79 trips. A total of 189 ARS events occurred with a mean of 2.42 ± 0.03 per trip. The average distance from the colony of ARS zones was 80.58 ± 0.78 km. ARS areas, where birds increased their search effort, had a mean scale of 6.62 ± 0.59 km. In 2014, ARS was detected in all trips providing a total of 60 ARS events with a mean of 1.88 ± 0.02 per trip. Mean distance of ARS zones from the colony was 67.27 ± 0.62 km and the mean scale of these zones was 8.17 ± 0.10 km (Table 5.3; Fig. 5.1).

5.4.2 Spatial separation of foraging regions

Discernible and separate areas of shearwater foraging activity were evident when foraging data were mapped (Fig. 5.1). Topography (reefs, slope, and unfeatured ocean floor) and bathymetry (depth) were observably different in five discrete locations that exhibited foraging activity. Bathymetry often influences foraging seabirds (Waugh et al., 1999, Jaquemet et al., 2004, Awkerman et al., 2005), so it was not surprising to find a strong influence of this parameter in first run 2012, 2013 and 2014 models. Furthermore, boosted regression tree (BRT) fitted function plots showed the existence of five identifiable peaks in distance from the colony (Fig. 5.1).

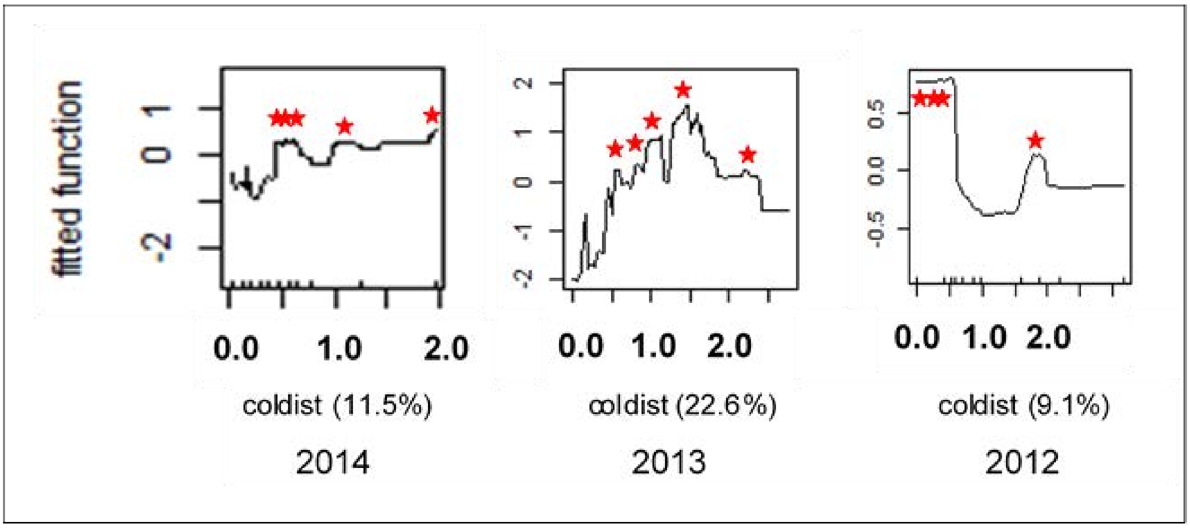

Figure 5.1: Fitted function plots from boosted regression model of 2014, 2013 and 2012, showing the influence of distance from the colony on the binomial response (foraging/not foraging). Y-axis is on a logit(P) transformed scale where the value of zero is equivalent to a 50% probability of a bird foraging at that value of the predictor (X-axis). The percentages in parentheses represent the relative influence of each variable on the response by year. Peaks which indicate fore likely bird foraging are indicated by red stars with five clear peaks in 2014 and 2013. Peaks in 2012 are less clear due to far fewer data.

The fitted function represents the logit(P) for foraging. Thus, the value of zero is equivalent to a 50% probability of a bird foraging at that value of the predictor (x axis). Hence, all values above 0 indicate a greater than 50% probability of foraging (peaks), while those below represent probability values less than 50% of foraging (troughs). These factors supported the division of data into five separate foraging zones which were mapped and delineated with polygons in ArcGIS 10.2 for Desktop (Fig. 5.1).

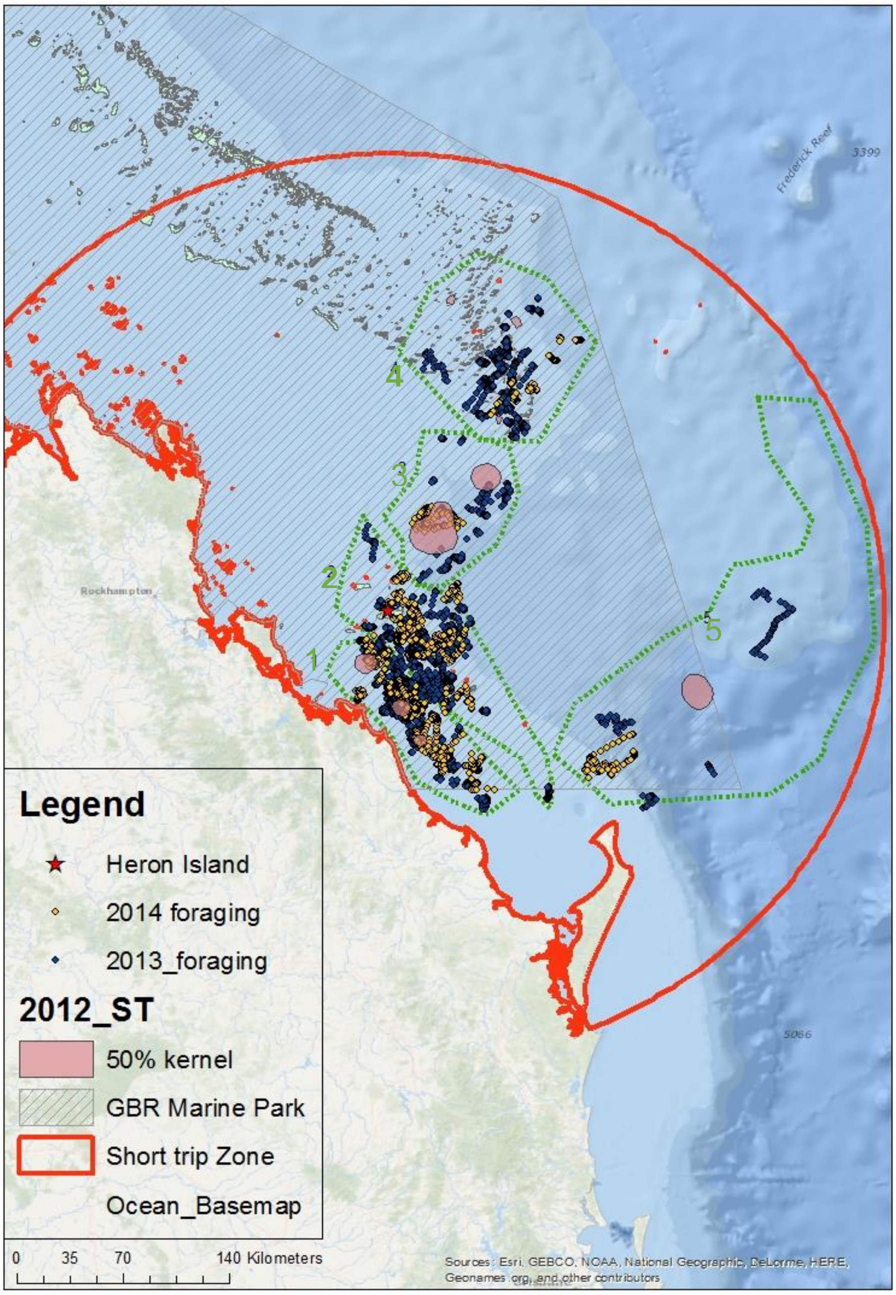

Figure 5.2: Regional map of short-trip foraging zone of wedge-tailed shearwaters. Outer buffer zone marks the maximum extent of the short-trip (ST) zone within which the five sub-regions are indicated by the green dotted outlines and numbered 1-5. Striped area is southern end of the GBR marine park. Actual foraging locations of shearwaters (ARS locations) are indicated for each year – light coloured points for 2014, dark points for 2013 and the 50% foraging kernels for 2012 (pink areas). The zones also include the 95% kernels which are not displayed on this map in order to highlight foraging areas in particular.

These foraging zones are (Fig. 5.2):

1. Inshore coastal area - most likely to be influenced by terrestrial input from runoff
2. Capricorn Bunker reefs - ‘*‘inter-reefal’’* area dominated by reef systems, islands, cays
3. Capricorn Channel - steeper bathymetry, nearest continental shelf edge, no reefs or cays
4. Swains reefs - ‘*‘inter-reefal’’* area dominated by reef systems, islands, cays
5. NE Fraser canyon - the deepest, most distant zone with very steep shelf edge

The most difficult foraging data to separate were those for zones one and two, being very close together (Fig. 5.2). However, these zones were clearly identifiable by topography (reefs in zone two) and were separated based on that parameter. Distances from the colony ranged from very near (~0.2°) to relatively far (~2.5°) and bathymetry from shallow (~34m) to deep (~800m). Zone one, the inshore area nearest the coast, was shallowest at 34m average depth where birds foraged. Foraging areas in *‘inter-reefal’* zones (two and four) were next shallowest at 40 and 60m, the Capricorn Channel (zone three) at the shelf edge deeper at ~130m and, finally, the deepest zone five where bathymetry at foraging sites was approximately 800m (Table 5.4).

Table 5.4: Depth and distance from the colony in the five separate foraging sub-zones identified as used by wedge-tailed shearwaters of the GBR during short-trips. The values represent the maximum value at which birds were most likely to be foraging.

	Zone 1	**Zone 2**	**Zone 3**	**Zone 4**	**Zone 5**
BATHYMETRY (~M)	34	40	135	60	800
DISTANCE FROM COLONY (~°)	0.2°	0.5°	0.6°	1.0°	2.5°

In each zone only data for birds which actually stopped and foraged within that zone were included, thus excluding tracks which overflew the zone without stopping within it. This was most relevant to zone three which had a number of tracks that traversed non-stop to zone four. Zones were analysed separately to determine spatial variation among drivers and trophic mechanisms by zone and by year to identify inter-annual variation.

5.4.3 Spatial/Auto correlation/Exclusions

Correlations, and associated excess VIF values were generally present between [Chl *a*] and [Chl *a*] anomalies; SST and SST anomalies at three day and monthly scales. Those with highest values were excluded from models in a step-wise approach until all variables exhibited values below accepted thresholds (see chapter two, Page 26, for detail). Distance to seamounts was consistently correlated with both distance to the colony and distance to the steepest bathymetric gradient (hereafter called slope), a variable which incorporates the presence of seamounts through their naturally steep sides (as well as other steep drop-offs and shelf edges). Therefore, it was fitting to exclude distance to seamounts from all analyses in favour of distance from the colony. Distance to land was consistently and strongly correlated with most or all bathymetric variables and exerted a limited influence on most models, hence it was also excluded from all analyses. Finally, as distance from the colony was used to define individual foraging areas within the short-trip zone and these areas were further defined by their distinct bathymetry, these factors were excluded with the exception of zone five which produced too weak a model with the exclusion of bathymetry. Modelling results presented are from simplified BRT models which best explain the trophic mechanisms operating at the various foraging scales of wedge-tailed shearwaters (Table 5.5).

5.4.4 Yearly tracking models

BRT models were conducted on tracking data for each year individually to determine the influence of regional-scale oceanographic processes and related inter-annual variation. As results with respect to bathymetry and distance from the colony from the first models run on 2012, 2013 and 2014 were used to identify the five separate foraging zones, they were ultimately excluded from the final annual BRT models. They were also excluded from analyses performed for each foraging zone.

5.4.4.1 *2014:*

In 2014, the model fit well when optimised (simplified) to seven factors with low predictive deviance of 0.475 ± S.E. 0.005. The high AUC of 0.9634 also indicates a strong, well-fitting model. Model results are presented in figure 5.3 which represents the influence of an oceanographic variable on the binomial response (foraging/non-foraging) after accounting for the average effects of all other variables in the model (Elith et al. 2008). Peaks above 0 represent the values (depths or distances) at which birds are more likely to be foraging (where 0 is a 50% probability that a bird will be foraging). The percentages in parentheses represent the relative influence of each variable in the total model fit, on the probability of foraging. For example, figure 5.3a represents the SST anomalies which exerted the strongest influence on this model (at 31.4%). This plot indicates a very low probability of birds foraging in SST anomalies between approximately 0 to -0.2°C less than the normal monthly climatology (where logit(P) values are strongly negative and equate to probabilities of foraging less than approx. 0.05), and there is a greater likelihood of birds foraging (than not-foraging) in SST anomalies of greater than -0.8°C (up to ~ -1.2°C) beneath the normal monthly climatologies. As SST anomalies become more negative the probability of birds foraging in those anomalous values increases signifying a strong relationship between foraging and intensely negative SST anomalies. Foraging was found to occur primarily in the higher values of the SST gradients (fronts) (Fig. 5.3d; 11.3%) but in specific SSTs (by month) of 27.2-27.4°C (Fig. 5.3e; 10.6%).Three daily means of SST indicated slightly higher average temperatures in foraging sites (up to ~28.1°C (Fig. 5.3g; 7.9%). Finally, foraging also mostly occurred in areas of low [Chl *a*] values (Fig. 5.3b; 14.9% influence) and weakly positive to more strongly negative [Chl *a*] anomalies (-0.1-0.2mg m^3) (Fig. 5.3c and f; 13.8% and 10.1% influence, respectively).

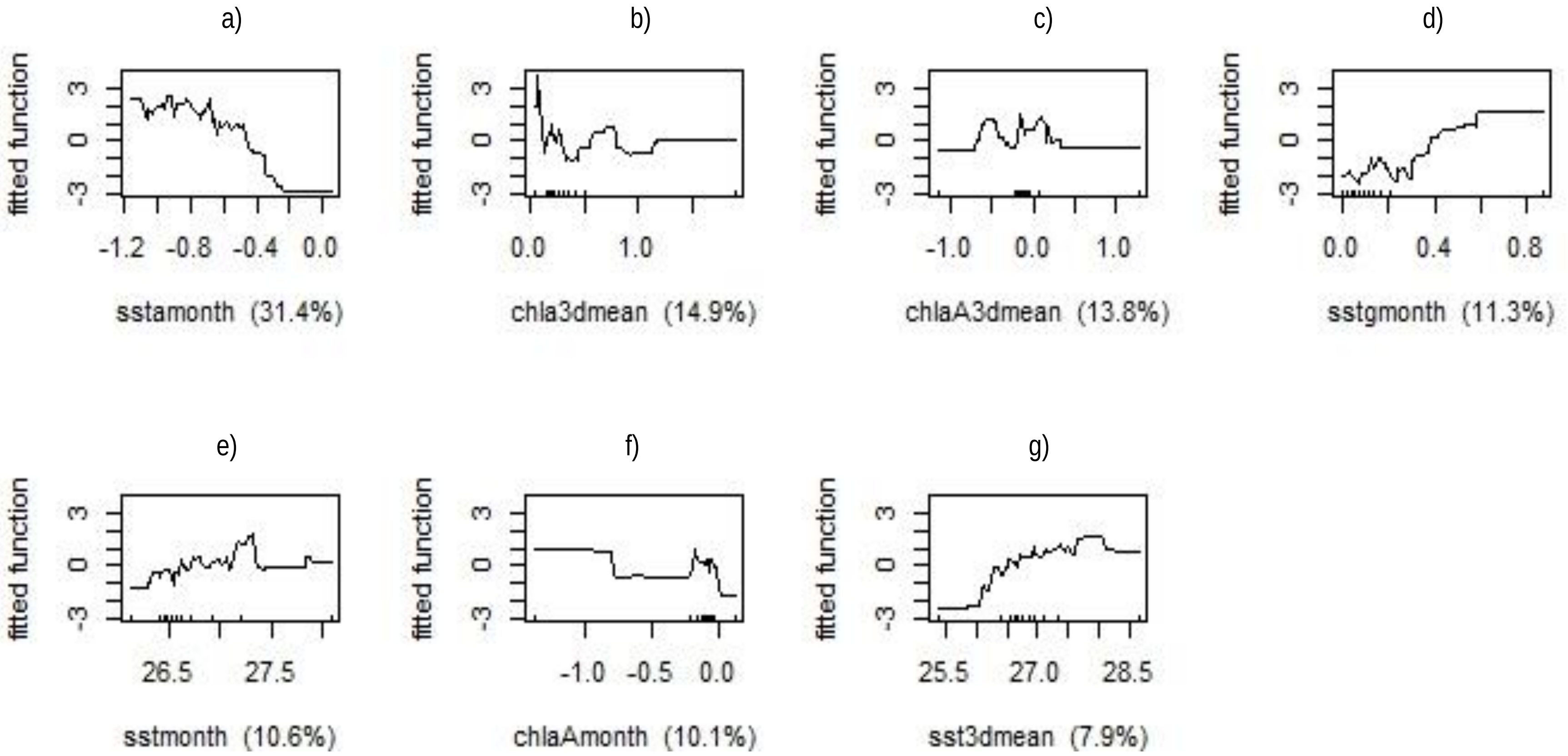

Figure 5.3: Results from BRT modelling of wedge-tailed shearwater short foraging trips in 2014 for the final simplified model. These partial dependence plots represent the influence of each oceanographic variable on the binomial response (foraging/not foraging) after accounting for the average effects of all other variables in the model. Y-axes are on a logit(P) transformed scale and the value of zero is equivalent to a 50% probability of a bird foraging at that value of the predictor (X-axis). The percentages in parentheses represent the relative influence of each variable on the response. For descriptions of variables see Table 5.2.

5.4.4.2 *2013:*

In 2013, proximity to the steep SST front exerted the strongest influence over shearwater foraging. The simplified model had 10 variables (Fig. 5.4 shows the top 8), a predictive deviance of 0.772 ± S.E. 0.013 and an AUC of 0.9082. The primary factor influencing foraging in 2013 was the proximity to the steepest SST fronts (Fig. 5.4a; 16%) with birds more likely to be foraging than not foraging in values between 0 and 0.3° distance (approx. 0 – 33km). In general, as distance from the front increased, probability of birds foraging decreased. Shearwaters generally foraged in areas with [Chl *a*] levels below 0.1 mg m^3 or greater than 4.2 mg m^3 (second plot – 15.1%). Foraging was associated with very weakly negative [Chl *a*] anomalies (peak -0.1mg $m^{3;}$ Fig. 5.4c; 13.6%). Foraging was more likely in SSTs around 26.5-27.3°C (Fig. 5.4d; 12.4%), and which were in either strongly negative anomalies (cooler than average by greater than -0.7°C) or slightly positive anomalies of 0.0.3°C (above monthly climatologies; Fig. 5.4f; 9.4%). Where a number of stronger peaks can be observed in the data it indicates that there are higher levels of foraging at different values of the predictor variable, (eg. distance to the SST front peaks at ~ 0, 0.05, 0.1, 0.2, 0.3° or 0, 5.5, 11, 22, 33km) which relates to variation among the foraging zones. This is detailed in the next section of results.

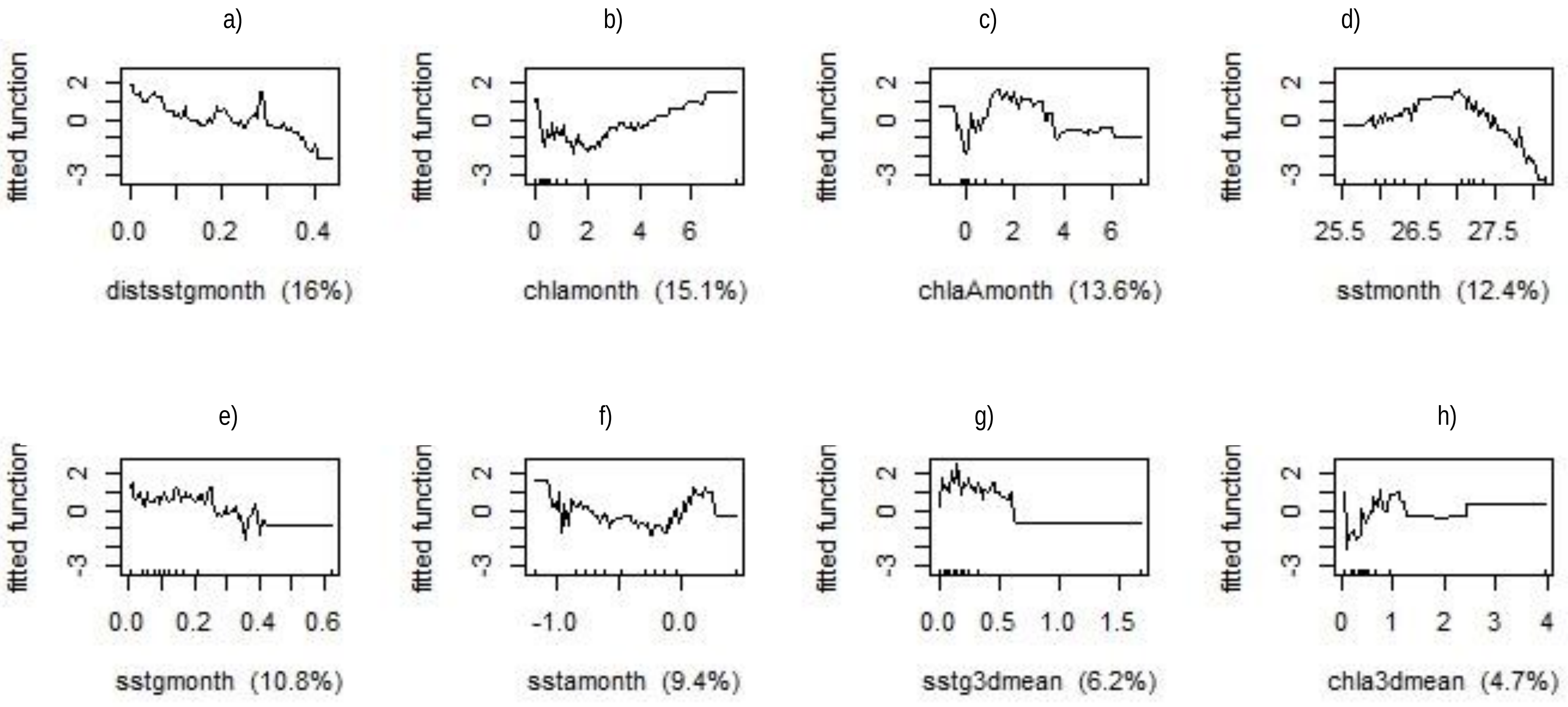

Figure 5.4: Results from BRT modelling of wedge-tailed shearwater short foraging trips in 2013 for the final simplified model. These partial dependence plots represent the influence of each oceanographic variable on the response (foraging/not foraging) after accounting for the average effects of all other variables in the model. Y axes are on a logit transformed scale where the value of zero is equivalent to a 50% probability of a bird foraging at that value of the x axis. The percentages in parentheses represent the relative influence of each variable on the response. For descriptions of variables see Table 5.2.

5.4.4.3 *2012:*

The paucity of data in 2012 resulted in the weakest of the annual models with a predictive deviance of 0.876 ± S.E. 0.037 and an AUC of 0.8816. However, results supported those of other years with birds visiting the same general locations. The most important factor, proximity to the SST front (Fig. 5.5a; 15.3%) shows two peaks where birds were more likely to be foraging (approx. 0.04 - 0.12° and >0.2° away, or ~4-14km and ~22km). Birds in this year generally foraged in the higher productivity waters ([Chl *a*] >~0.3 mg m^3; Fig. 5.5c; 10.6%) but this trend did not relate to the more positive anomalies of this parameter as birds were least likely to be foraging in [Chl *a*] values >0.2 mg m^3 (Fig. 5.5b; 12.7%). Foraging was focused on areas where the current speeds exceeded 17m^{-s} with foraging birds displaying a strong preference for the greatest speeds of >30m^{-s} (Fig. 5.5d; 10.3%) and primarily in temperatures of <27.75°C (sixth plot – 9%) which were in positive (0.8-1.2°C or strongly negative anomalies (>-0.6°C; Fig. 5.5h; 7.3%).

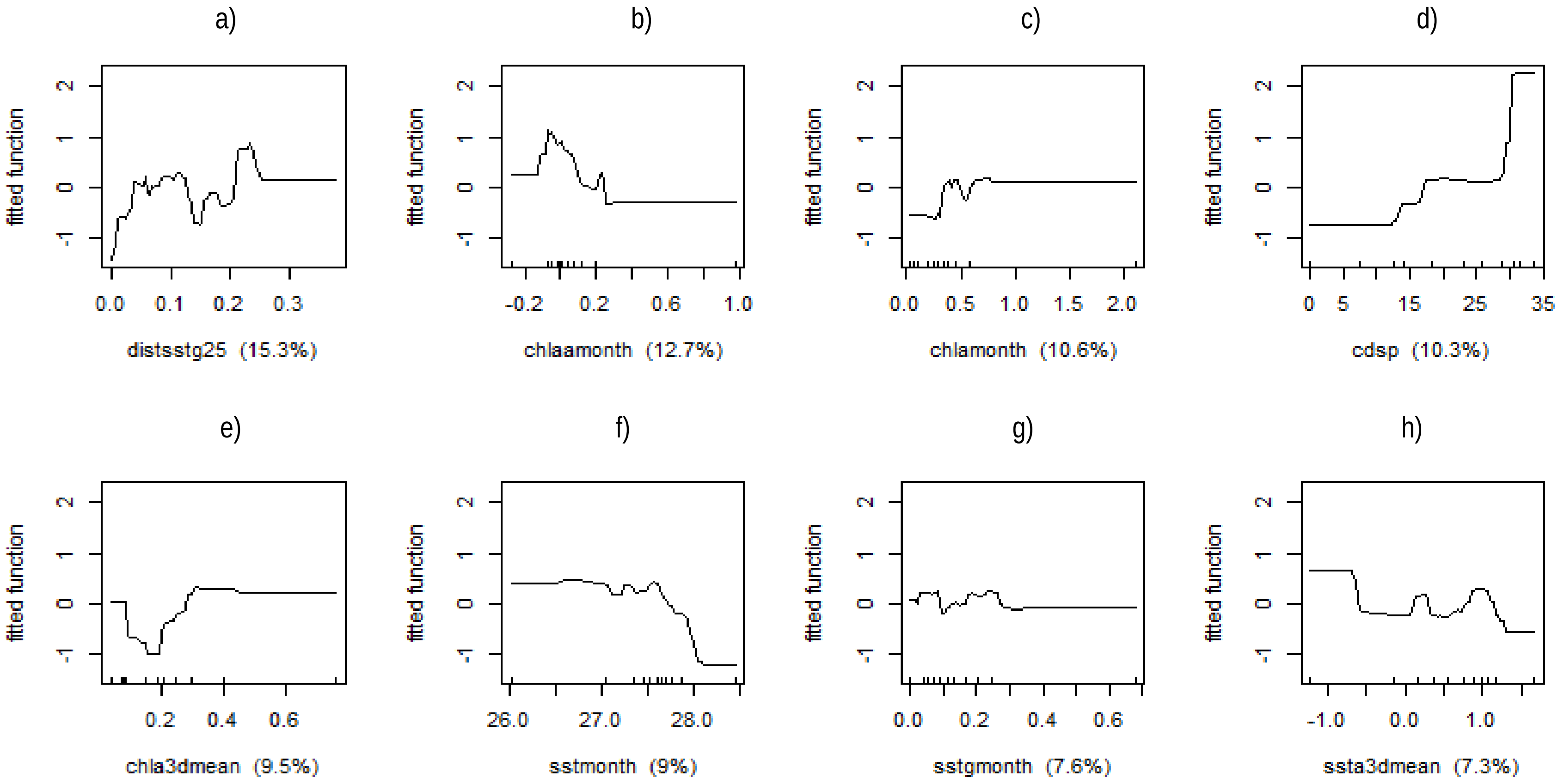

Figure 5.5: Results from BRT modelling of wedge-tailed shearwater short foraging trips in 2012 for the final simplified model. These partial dependence plots represent the influence of each oceanographic variable on the response (foraging/not foraging) after accounting for the average effects of all other variables in the model. Y axes are on a logit transformed scale where the value of zero is equivalent to a 50% probability of a bird foraging at that value of the x axis. The percentages in parentheses represent the relative influence of each variable on the response. For descriptions of variables see Table 5.2.

5.4.5 Zonal differentiation:

The five bathymetrically distinct foraging sub-zones were analysed independently to examine the relative importance of each oceanographic variable with increased precision. This also allowed me to look at the importance or influence of finer-scale local rather than regional processes. Results varied according to the amount of data in each zone. Zones three and five had fewer birds foraging within than zones one, two and four (Table 5.5). The combination of oceanographic factors of strongest influence on bird foraging differed for the various identified foraging zones (one to five) and these also differed within and between years of data collection. From visualising frequency distributions of each of the predictor variables, the values of the primary and, where applicable, secondary peaks and/or range of the data are presented for comparison among zones (Table 5.5). These values are taken from the partial dependence plots and histograms of data that very previously visualised. Means of predictor variables are not very informative due to the complex non-linear nature of the data and outputs. It is more revealing to examine the detail in the peaks and troughs of the outputs. There were too few data from 2012 to procure reliable BRT models of individual foraging zones but in general results supported those from 2013 and 2014.

Table 5.5: Simplified model results by zone of GPS tracking of wedge-tailed shearwaters in 2013 and 2014. Predictive deviance, S.E. and AUC are reported with proportion of birds foraging in each zone (prop.birds %). Approximate peak values of each of the oceanographic variables influencing foraging in the models. Peaks are taken from partial dependence plots and from frequency distributions. The values in parentheses represent the by those variables' positions in order of influence with the primary factor bolded. *2014 zone 5 - single bird. See table 5.2 for description of variables.

	2013					**2014**				
ZONES	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
Prop.birds	35.90%	36.20%	4.90%	19.70%	3.30%	46.30%	31.30%	11.20%	6.50%	4.70%
CV dev ± SE	0.837±0.018	0.687±0.068	0.622±0.075	0.696±0.006	0.356±0.04	0.375±0.031	0.541±0.023	0.417±0.047	0.312±0.068	0.555±0.159
AUC	0.8892	0.9269	0.9415	0.9148	0.979	0.9744	0.9549	0.9717	0.9803	0.9507
Relative influence of factors remaining in simplified models										
1	**Chlamonth**	**DistSSTG**	**DistSSTG**	**DistSSTG**	**Bathymetry**	**SSTAmonth**	**SSTGmonth**	**SSTmonth**	**ChlaAmonth**	**Bathymetry**
	0.3-0.5	0.15	0.1-0.15	0.17-0.21	800	-0.80	0.15-0.2	27.25	-0.06	*60
2	DistSSTG	SSTAmonth	SST3dmean	Chlamonth	MSLA	ChlaAmonth	SSTAmonth	SSTGmonth	SSTAmonth	SSTAmonth
	0-0.05	-0.90	26.8	0.2	4; -3	-0.10	-0.8	0.1-0.2	-0.5-0.6	-0.35- -0.4
3	SSTAmonth	Chlamonth	ChlaAmonth	SSTGmonth	Dist to slope	Photic Depth	Chla3dmean	ChlaA3dmean	SSTGmonth	Chlamonth
	-0.8	0.2	.-0.2--1.2	0.1	0.15	14.00	0.2	-0.07	0-0.15	0.05; 0.11
4	Chla3dmean	SSTGmonth	SSTmonth	SSTmonth	Slope	SSTmonth	DistSSTG	ChlaAmonth	SSTmonth	SSTA3dmean
	0.35	0.05-0.1	26.4	26.4	250; 1200	26.50	0.02-0.04	-0.06	27.1	-0.2
5	SSTGmonth	SSTmonth	Chlamonth	SSTAmonth	Photic Depth	DistSSTG	SST3dmean		DistSSTG	ChlaAmonth
	0.15	26.3	0.24	-0.8	30	0-0.02	26.3		0.02-0.04	-0.09
6				ChlaAmonth	Chlamonth	Chlamonth	SSTG3dmean			
				-0.1	0.25	0.30	0.10			
7				SSTG3dmean		SSTGmonth	ChlaA3dmean			
				0.1-0.2		0-0.05	-0.15			
8				Photic Depth						
				9 (8)						

In all years there were five identifiable peaks in the distance to the colony and bathymetry. These results were different and specific within each zone and, as such, supported the division of data into the five separate foraging zones (Fig. 5.2) that had been differentiated by topographic features (as described in methods). Distances from the colony ranged from very near (~0.2°) to relatively far (~2.5°) and bathymetry from shallow (~34m) to deep (~900m) (Table 5.5). Bathymetry often influences foraging seabirds (Waugh et al., 1999, Jaquemet et al., 2004, Awkerman et al., 2005) and was, unsurprisingly, shallowest in zone one, the inshore area nearest the coast at 34m where birds foraged. The reef foraging areas (zones two and four) were next shallowest at 40 and 60m, the Capricorn Channel (zone three) slightly deeper with birds foraging on a shallow slope at ~130m and, finally, the deepest zone five where bathymetry at foraging sites was approximately 800m (Table 5.5). Zone five exhibited the deepest and widest range of bathymetry and further differed from zones one to four being the only one influenced by the presence of the steepest bathymetric slope. Birds most often foraged in association with a slope of ~500m/km and were always much closer to the steepest slope (0.1° compared with 0.7-1.2°). SLA and current speed data were also available this region only, so this zone was analysed to include these data and as such, is not directly comparable with zones one to four.

Another variable which consistently influenced zonal models and showed multiple data peaks was the proximity to the steepest SST front, although the relative influence varied among zones and years (Table 5.5). The steepest SST front was represented by the upper 25% of frontal values, which were all those greater than 0.21°C/km. These areas represent the areas where the greatest rate of change in SST occurs over the narrowest horizontal distance.

5.4.5.1 *Zone 1: Coastal Inshore*

Zone one was expected to be directly influenced by terrestrial input such as freshwater from river outflow and floodwaters, as it was nearest the coast. This effect was demonstrated through a number of factors. Foraging in zone one usually occurred very near to or on top of (0-0.05°) the steepest SST front and this combined with comparatively high absolute frontal values (0.1-0.2°/km) suggests a stronger front in this zone. This influence was apparent in the strongly negative SST anomalies associated with foraging here (Table 5.5). Furthermore, primary, secondary and tertiary freshwater plumes (nearest to farthest from the coast) intruded on this zone throughout the season. Foraging occurred more frequently in tertiary than secondary plumes and never in primary plumes which are those nearest the coast. This influence was strongly evident in 2013 (Table 5.6; Fig. 5.6).

Table 5.6: Numbers of wedge-tailed shearwaters foraging (F) or not (NF) in freshwater plumes that occurred in zones 1, 2 & 3 in 2013 and 2014. Plumes are primary (1), secondary (2) and tertiary (3) which begin nearest the coast and extend various distances out to sea and are weekly measurements.

2013	**Zone 1**		**Zone 2**		**Zone 3**	
Plume	**NF**	**F**	**NF**	**F**	**NF**	**F**
Primary (1)	-	-	-	-	-	-
Secondary (2)	76	110	-	-	-	-
Tertiary (3)	216	262	1	31	-	-
2014						
Plume	NF	F	NF	F	NF	F
Primary (1)	-	-	-	-	-	-
Secondary (2)	0	25	2	0	-	1
Tertiary (3)	111	112	20	0	-	2

Potential coastal-driven eutrophication in this zone was evidenced by the highest average [Chl *a*] of all zones (averages of ~0.3-0.5 mg m^3 and with maximums up to 7 mg m^3) and this was true for each year. In 2013 it was the strongest factor influencing shearwater foraging with no influence of anomalous levels of this variable (Fig. 5.4; Table 5.5). By contrast, while [Chl *a*] was still the highest of all zones (those where it exerted an influence) in both 2014 and 2012, its influence was exceeded by other variables (Table 5.5). Concurrently, variations in [Chl *a*] anomalies were noted in both years. For example in 2014, the anomalies were weakly negative and this was the second most important driver of foraging (Table 5.5), while in 2012 the positive anomalies were the most important influence on foraging shearwaters (Fig. 5.5).

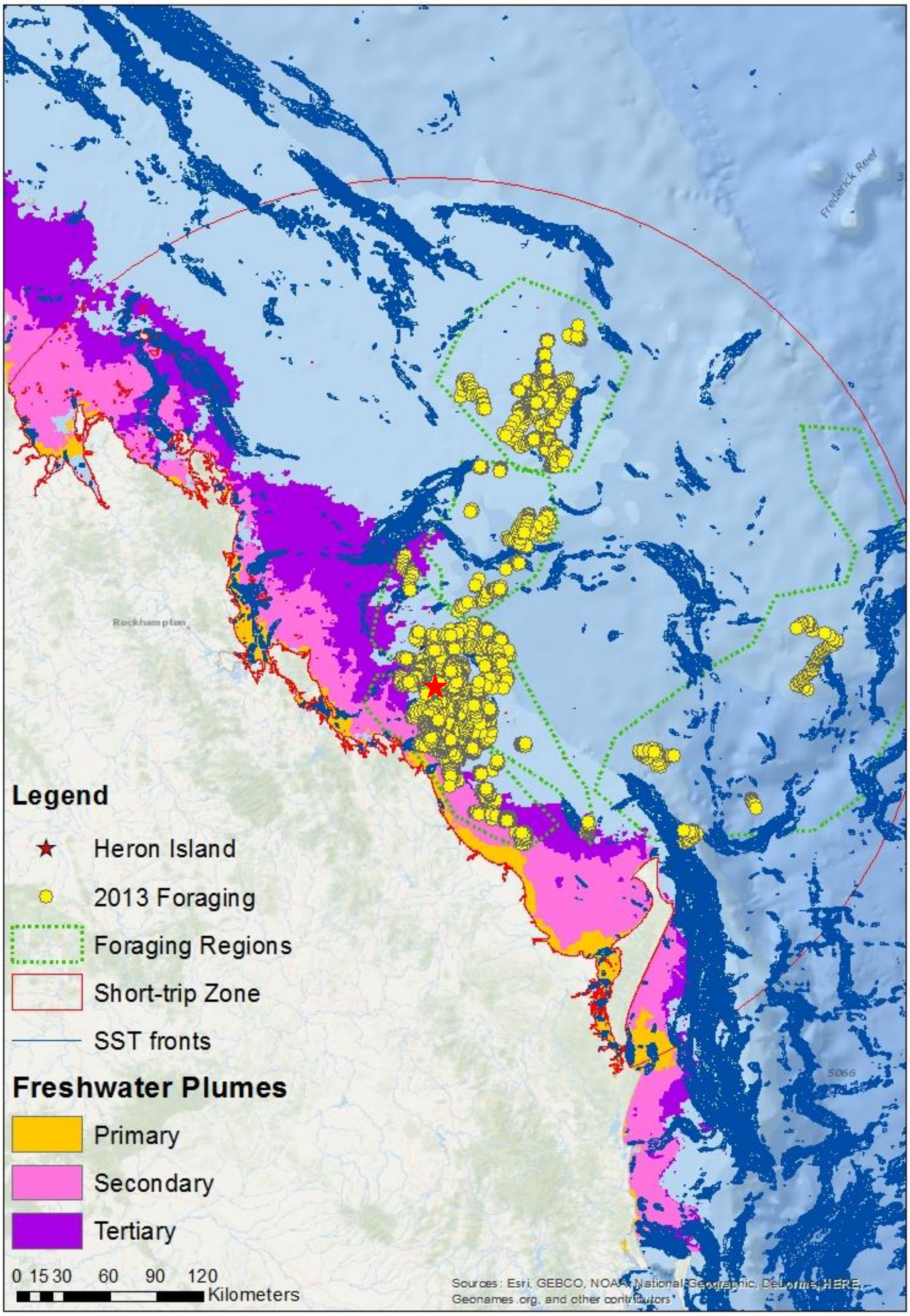

Figure 5.6: Freshwater Plumes in 2013 with wedge-tailed shearwater foraging locations overlaid. Foraging zones shown in green dotted outline, short-trip zone in red. Strongest SST fronts of the period are indicated by the dark blue areas which are more present in zones 2-5 and associated with foraging points.

5.4.5.2 *Zone 2: Capricorn Bunker Reefs*

This zone is characterised by the unique topography of numerous reefs and lagoons scattered throughout, around which shearwaters foraged (Fig. 5.7). It is a shallow area averaging 40m. In 2013, proximity to the steep SST front was the most important influence on foraging and they were slightly more distant than seen in zone one. This was combined with very weak frontal values in 2013 but in 2014 this effect was reversed. Actual frontal values were the highest of any zone in that year and the strongest influence on foraging (Fig. 5.3; Table 5.5). Shearwaters always selected anomalously negative SSTs, an important factor of influence in 2013 and 2014, with most foraging occurring in SSTs around 26.3°C (2013) and 26.9°C (2014). [Chl *a*] was important for its low values in foraging areas and, where anomalies were influential on foraging activity (2014), the birds avoided the positive anomalies and foraged in association with weakly negative anomalous [Chl *a*] (Table 5.5). The tertiary plume, which is the farthest from the coast, occasionally intruded to region 2. When that occurred, birds targeted these plume waters in 2013 but they were not found to forage in them in 2014 (Table 5.6; Fig. 5.6).

5.4.5.3 *Zone 3: Capricorn Channel*

The average depth in the shearwater foraging areas of the Capricorn Channel is 130m. This is the area between the two '*'inter-reefal"* foraging regions and the topography is unremarkable. Region three showed birds foraging relatively close to the SST front (~0.04° in 2013 and 0.12° in 2014), although SST gradients were never very strong, only exerting an influence in 2014. SSTs were cooler in foraging locations in 2013 (~26°C) but were much warmer in 2014 averaging >27°C and there was little effect of SST anomalies. There were slightly higher [Chl *a*] levels in this region than in the reef or deep areas, but this variable only influenced foraging activity in 2013. More important was the influence of [Chl *a*] anomalies in all years whereby the birds selectively foraged in weak negative anomalies (Table 5.5).

5.4.5.4 *Zone 4 – Swains Reefs*

The Swains reef systems exhibited similar influences over bird foraging as the other reef zone but they differed by year. This zone is slightly deeper at 60m, than the Capricorn Bunkers.

Again, proximity to the steepest SST front was the strongest factor in 2013, even with birds being at the greatest distance from the front, and again this was combined with low actual frontal values. This variable had the weakest influence in 2014. Rather the strongest effect came from [Chl *a*] anomalies which were consistently weakly negative where birds foraged. This was followed by the effect of SST anomalies which were also in the negative range. While these factors exhibited only a weak influence over foraging in 2013 the same relationships were observed. Actual SSTs were marginally important at ~26.4°C and 27.1°C in 2014 (Table 5.5).

5.4.5.5 *Zone 5: Fraser canyon/drop off*

Zone five, the deepest and most distant from the colony (Table 5.4)**,** was the least visited of all regions by short-tripping shearwaters and had relatively few data points (Table 5.5) with one bird in 2014, two in 2013 and four, with few data, in 2012, so results provide a general view and are interpreted with caution. Nevertheless, factors of influence were similar across all years. This region differs most markedly from the other four regions. It has unique topography and deep bathymetry resulting from the presence of the deep Fraser canyon and continental shelf drop off, creating areas of very steep slope. This meant that the region had the greatest range of depths available in any region. Even in first, complete models it was the only zone influenced by the presence of the steepest bathymetric slope. Birds most often foraged in association with a slope of ~500m/km and were always much closer to the steepest slope (0.1° compared with 0.7-1.2°). The exclusion of bathymetric variables created a very weak model so they were retained for the analyses performed for this zone.

Nevertheless, in both 2012 and 2013, the birds consistently avoided the very deep areas (>2000m), foraging in depths of ~800 to ~2000m and over steep slopes of ~500m depth change per km horizontal distance, providing a unique insight into the selection of foraging sites. The inclusion of bathymetric parameters produced a stronger model in 2013 (predictive deviance = 0.383; ± S.E. 0.023; AUC = 0.9759) than if excluded from the analysis (predictive deviance = 0.468, ± S.E.0.07; AUC = 0.968) so these variables were retained in the analysis of foraging in this zone. Ocean dynamics were also influential here with an effect of slightly positive and slightly negative SLAs in 2013, which was not apparent in 2014. These factors were not available in the other zones due to the inability of satellites to differentiate these parameters in the shallow depths above the continental shelf. Therefore, this zone is not directly comparable with those zones. Finally, when foraging, birds usually selected areas with the lowest [Chl *a*] available in the zone: ~0.05 mg m^3 in 2014; ~0.25 mg m^3 in 2013 and ~0.07-0.08 mg m^3 in 2012. An influence of [Chl *a*] anomalies was only apparent in 2014 at which time foraging was associated with weakly negative values. 2014 also differed in a limited influence of the bathymetric variables upon foraging activity. The single individual foraged in depths of ~60m at which there occurred negative SST anomalies (Table 5.5).

5.5 DISCUSSION

5.5.1 Location of foraging areas

Near-colony foraging locations used by GBR wedge-tailed shearwaters when provisioning chicks were always located within 300km of the Heron Island breeding colony. Often, sites were considerably closer to the island (mean 83.06 ± 9.13km). Furthermore, the same sites were consistently and repeatedly used over multiple years, underlining the importance of these specific locations for successful breeding.

For '*central-place foragers'* like wedge-tailed shearwaters the potential distance individuals can travel from the colony is constrained by the need to balance energy expenditure against the amount of food obtained whilst also returning frequently to feed the chick (Weimerskirch et al., 2003). Combined, these limitations can lead to breeding birds relying on only a few foraging locations relatively near the colony where the background environment provides sufficient return for the energy expended. For wedge-tailed shearwaters in the Capricorn-Bunker region of the GBR, there appear to be five such foraging areas. In resource-poor environments like the tropics, prey patches can be scarce (Weimerskirch et al., 2004). Nevertheless, they may also be predictable, particularly if there are consistent factors or oceanographic features that drive prey enhancement, such as fronts, convergences or upwelling (Weimerskirch et al., 2004, Weimerskirch, 2007). Therefore, once birds locate suitable foraging patches near the colony, it is logical that they would continue to return to those same areas if the food source is reliable. The consistent site-use by shearwaters of the GBR supports this hypothesis.

5.5.2 Foraging site characteristics

5.5.2.1 *Bathymetry*

Bathymetry was by far the most important feature characterising near-colony foraging sites used by breeding wedge-tailed shearwaters. Each of the five identifiable near-colony foraging zones had relatively specific and unique bathymetry. Furthermore, with the exception of zone one (nearest the coast) foraging activity in each zone was focused over areas of steep bathymetric change, such as at the edges of reefs and lagoons, along the continental shelf drop-off and along the fringes of submarine canyons (Fig. 5.7). Therefore, it is the presence of topographic features that cause steep bathymetric change, rather than any specific depth, that can most readily be used to identify foraging sites. The interactions of these types of topographic features with specific current flows are known to induce upwelling provide improved prey access to seabirds (Brown, 1979, Duffy, 1989, Yen et al., 2006b). My results imply such interactions occur at these GBR foraging locations.

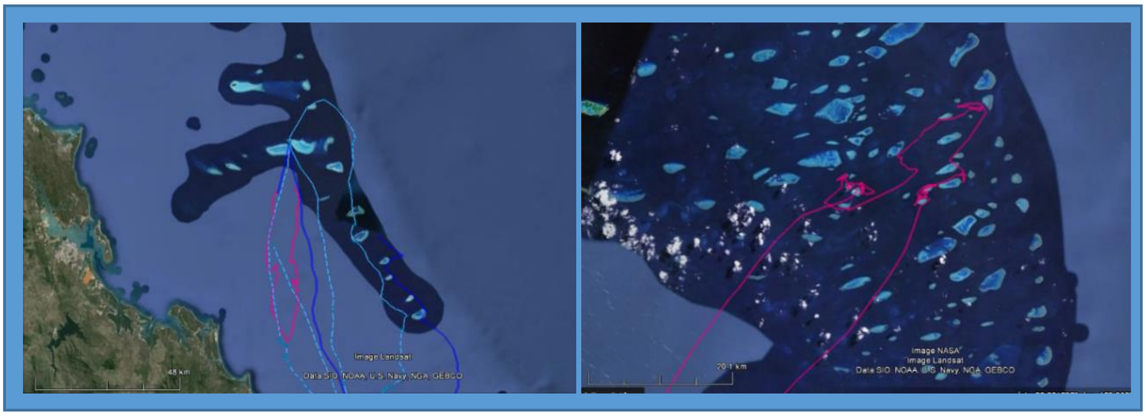

Figure 5.7: Small-scale maps of Capricorn Bunker reefs (left) and Swains Reefs (right) with shearwater GPS foraging tracks overlaid. Samples of tracks showing shearwaters following the edges of reef systems (light blue patches) on short-trips.

Zone five, farthest from the colony, was characterised by the greatest depth, steep drop-offs and the shelf-edge, as well as a submarine canyon of the sort often found along continental margins (Kämpf, 2006) (Fig. 5.2). Upwelling can develop over these types of canyons when favourable winds drive deep ocean water up over the shelf break (Hickey, 1995, Mirshak and Allen, 2005, Kämpf, 2006). Such upwelling is indicated in my data by the influence of sea level anomalies (SLAs) on shearwater foraging. In this region, prevailing winds generally drive coastward, parallel with the canyon, and probably contribute to generating this upwelling. Such upwelling can increase prey availability to seabirds in localised areas as reported in studies of wandering and black-browed albatrosses that forage over shelf slopes, breaks and places with steep drop-offs (Weimerskirch et al., 1993, Cherel and Weimerskirch, 1995). Therefore, prey accessibility for the GBR breeding wedge-tailed shearwaters is most likely enhanced in zone five by typical of those seen to influence the use of *at-distance* foraging locations in the Coral Sea, discussed previously (chapter four).

5.5.2.2 *Thermal and other influences on foraging*

Steep bathymetric change was also an important determinant of foraging activity in zones two to four. However, the way bathymetry interacted with other factors appeared to vary among these sites. The influence of bathymetry in zone one was minimal with other factors appearing more important. Therefore, to examine these interactions more closely the influence of multiple secondary oceanographic factors were investigate independent of bathymetry. Results identified the importance of finer-scale, zone-oriented processes such as SST parameters and identified how their influence varied among zones and years.

In most respects the short-trip foraging region for wedge-tailed shearwaters is a relatively homogeneous habitat exhibiting only small variations in SSTs. Despite this, shearwaters were consistently observed to forage within a narrow range of the temperatures available to them. Furthermore, they also targeted cooler elements of this range. Such results suggest that these lower than average SST values (SST anomalies) signify areas of improved prey accessibility. The strongest effect of SST anomalies was seen in zone one where this influence overshadowed all others.

SST fronts were one of the more important factors influencing foraging, especially in 2013. The importance of strong SST fronts in attracting foraging birds, indicates that the temperature differential across such fronts in some way generates a clear signal that attracts birds to those features. Despite the fact that temperature differentials across SST fronts in this study were not as pronounced as those seen across fronts in the higher latitudes (Shaffer et al. 2009), they were still a strong component impacting birds' behaviour. These kinds of temperature signals are often indicative of prey aggregations or enhancements (Spear et al., 2001, Cotté et al., 2007).

The multiple relationships between various SST parameters and near-colony foraging locations confirms expectations from previous studies of GBR seabirds that food availability is related to, and strongly influenced by, ocean temperatures (Smithers et al., 2003, Peck et al., 2004, Erwin and Congdon, 2007, Devney et al., 2010, Weeks et al., 2013). However, these previous studies demonstrate links with rapid changes in SSTs over short time periods while in the current study other variables more accurately and effectively revealed relationships with foraging activity. This suggests that combining both types of studies would produce better predictions of the influence of temperature on both prey availability and bird distributions.

5.5.2.3 *Upwellings and fronts*

The observed relationships between foraging activity and SST fronts also likely indicate the presence of localised small-scale upwellings that concentrate food items across smaller spatial scales (Uda, 1938). These phenomena intensify prey availability and potential prey interactions for predators. Such small-scale upwellings, oceanic fronts or eddies can be revealed by the presence of SST anomalies (Garvine, 1974). Therefore, these values can be used to highlight the presence of these oceanographic features. GPS tracking consistently showed shearwaters foraging around the edges of reef lagoons (Fig. 5.7). This, combined with a general and relatively strong effect of negative SST anomalies on foraging in zones two and four, suggests that reef topography drives minor upwellings of cooler water that the birds target (Garvine, 1974, Burrage et al., 1996, Choukroun et al., 2010). Consequently, these smaller scale upwellings may be an important, local-scale influence on prey accessibility. Small-scale upwellings can occur when ocean currents interact with reefs or areas of bathymetric change (Andrews and Gentien, 1982). This interaction is exemplified in the upwellings created by the East Australian Current (EAC) when it encounters these features (Andrews and Gentien, 1982, Oke and Middleton, 2000).

5.5.2.4 *Productivity*

Another driver of seabird foraging, which is frequently observed in temperate and sub-polar systems, is elevated primary productivity (measured by [Chl *a*]), particularly when enhanced by large or mesoscale phenomena like fronts, convergences, upwellings and eddies (Weimerskirch et al., 2002, Shaffer et al., 2003). Productivity has also been shown to influence foraging locations of chick-rearing wedge-tailed shearwaters of the tropical Indian Ocean, where it was enhanced by local upwelling (Cecere et al., 2013). However, in the southern GBR, whether shaped by upwelling or not, primary productivity was generally only remarkable for how low the measures were in wedge-tailed shearwater foraging habitat. The *'inter-reefal'* zones (two and four) occasionally exhibited slightly elevated [Chl *a*], but it was unusual and sporadic and only infrequently associated with fairly low levels of bird foraging.

Consequently, the general pattern across the entire region was that**,** regardless of background levels, wedge-tailed shearwaters exhibited their most active foraging in sites where [Chl *a*] exerted least influence. This directly contrasts with most previous seabird foraging studies that describe birds foraging in areas of elevated primary productivity. The reason for this discrepancy is unknown, however, the increased dynamics and unpredictable nature of the GBR/Coral Sea system means productivity may not persist for long periods in any single location. This would lead to a mismatch between [Chl *a*] and micronekton abundance. Such a temporal decoupling between ocean dynamics and primary productivity has previously been documented in this region (Menkes et al., 2014).

5.5.2.5 *Terrestrial inputs*

However, there was one notable exception to the general lack of influence of [Chl *a*]. Zone one, representing approximately 20% of foraging area and used by one third to half the foraging individuals, is arguably the most important foraging area. This region consistently exhibited consistently elevated [Chl *a*]. This was also the only area to receive significant inputs of freshwater from river discharge, suggesting that elevated [Chl *a*] could be directly attributed to coastal enrichment via nutrient runoff from the terrestrial environment**.**

Zone one was conspicuously different to the remaining zones in other ways as well, with multiple factors providing evidence that river discharge creates more intense oceanographic effects in this area. Firstly, shearwaters were found to forage in freshwater plumes in 2013 and 2014 (no data for 2012) that stretched seaward across the area. Secondly, this region had intensely negative SST anomalies which contributed strongly to shearwater foraging activity. Thirdly, birds were more closely associated with the SST front, particularly in 2013 when absolute frontal values were very high. They foraged either very close to, or directly over the front, rather than at some distance from it, as was more common in other zones. This front was particularly strong in 2013, probably due to the seasonally increased flooding in that year (BOM, 2014b). Combined, these factors suggest that the river discharge creates a sharp coastal temperature front where the colder flood waters merge with warmer oceanic water (Bowman and Iverson, 1978, Wolanski and Jones, 1981, Devlin et al., 2001, King et al., 2001). This also implies that the oceanographic phenomena created by these conditions are highly beneficial for prey enhancement and produce profitable foraging conditions for seabirds. The strong SST fronts in the region are likely driven by the meeting of freshwater outflows with coastal currents produced by larger-scale water movement, most likely due to the Capricorn Eddy (Kleypas and Burrage, 1994, Middleton et al., 1994, Weeks et al., 2010). This particular and unique combination of factors and the intense, repeated use of this zone by foraging birds suggests a strong influence of terrestrial input on foraging site choice by shearwaters. Such interactions have been seen in temperate and polar seabirds. For example, pelagic feeding species such as Northern fulmars (*Fulmarus glaciares*) and various gulls are known to forage in association with tidewater glaciers (McLaren and Renaud, 1982, Lydersen et al., 2014) while Southern giant petrels (*Macronectes giganteu*) and Balearic shearwaters (*Puffinus mauretanicus*) forage at freshwater river plumes (Louzao et al., 2011, Blanco et al., 2015). However, to my knowledge, such an effect of terrestrial outflows on foraging activity in a pelagic seabird has not previously demonstrated in a tropical system.

5.5.2.6 *Inter or Intra-specific competition*

Intra-specific and inter-specific competition is known to shape the distribution of seabird foraging activity (Ballance et al., 1997, Robertson et al., 2014). Without conducting similar tracking studies or at-sea surveys of different regional breeding shearwater colonies or other resident or breeding seabird species it is not possible to quantify these relationships. However, Wedge-tailed shearwaters are known to forage in mixed species flocks in other locations (Sealy, 1973, Mills, 1998), often with other seabird taxa, that have different demography and life history characteristics (Ballance et al., 2001). Wedge-tailed shearwaters in the Great Barrier Reef /Coral Sea region forage in association with other pelagic foraging species such as the sooty tern and common noddy (*Anous stolidus*) (Congdon et al., 2007). Foraging behaviour can also be influenced or regulated by competition with conspecifics (Lewis et al., 2001, Grémillet et al., 2004).

5.5.3 Large-scale processes

5.5.3.1 *The Capricorn Eddy*

The stability of oceanographic phenomena will directly determine the reliability of areas that provide enhanced prey availability to foraging seabirds. The Capricorn Eddy is driven by the EAC and '*spins up'* over the Capricorn shelf in the southern GBR (Fig. 5.8), and likely triggers upwellings or frontal convergences along the continental shelf edge and Capricorn Bunker reef system (Weeks et al., 2010). Its presence and influence on foraging activity in the current study appears as the importance of intense frontal areas (SST), primarily in foraging zones positioned along the edge of the continental shelf (two, three and four), adjacent to where the Eddy most commonly occurs. These foraging sites were also associated with slight [Chl *a*] enhancement, an effect that could also be driven by the Eddy as it is known to marginally enhance chlorophyll *a* in shelf waters (Kleypas and Burrage, 1994). The Eddy is dynamic and reliant upon regional and perhaps even ocean-scale currents and climatic processes, so its scale and intensity can be highly variable (Weeks et al., 2010). The complexity of oceanographic relationships and influences suggest that this eddy is the primary oceanographic feature driving variation in foraging site use by chick-rearing wedge-tailed shearwaters, as at least 80% of their near-colony foraging areas are concentrated in locations associated with the eddy (Fig. 5.8). However, prey availability to these birds is known to vary under different 'eddy conditions' (Weeks et al., 2013).

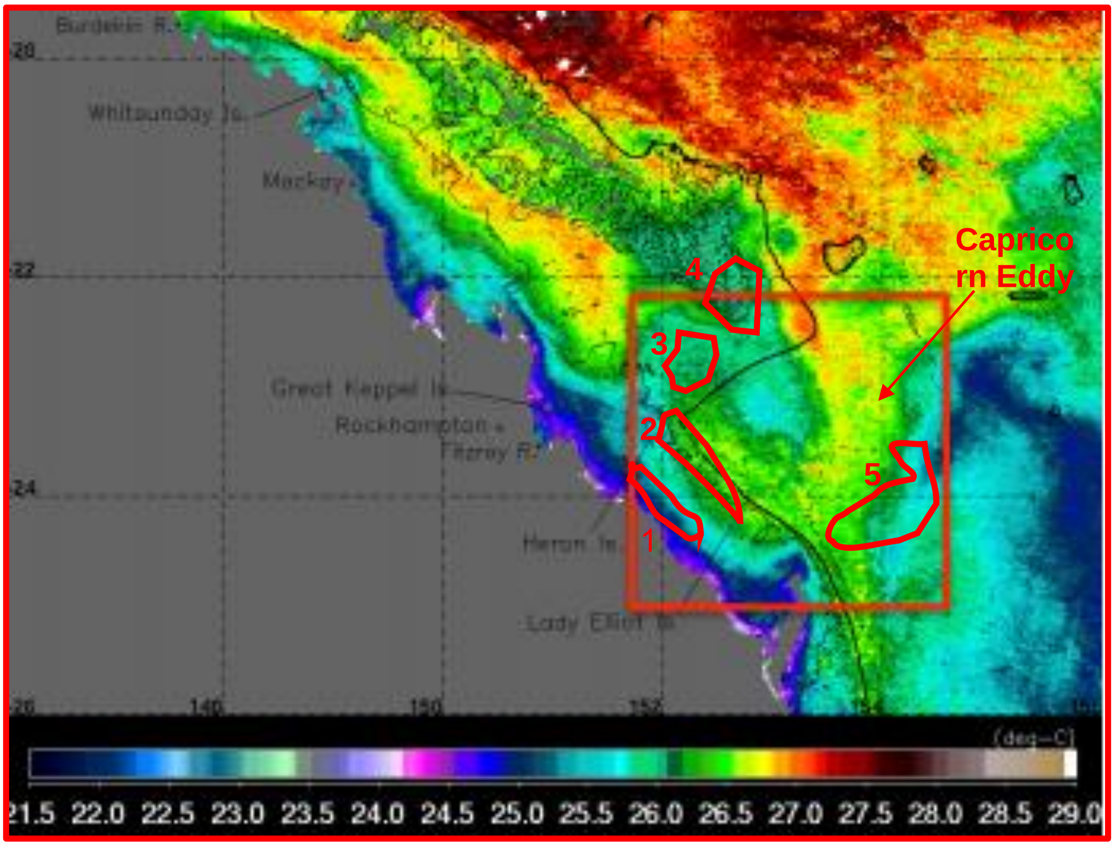

Figure 5.8: Five foraging zones (red outlines - zone one at left out to zone five farthest right) used by breeding wedge-tailed shearwaters of Heron Island in the southern GBR while short-tripping, overlaid on an image of the Capricorn Eddy. The colours in the image represent varying SSTs and clearly shows the presence of the eddy which is the green/yellow ‘J’ shaped feature identified within the red box. This figure shows the relationship with the identified foraging locations of shearwaters and the edge of the eddy.

Links have been found previously between food availability to wedge-tailed shearwaters and the intensity and movement of the Capricorn Eddy (Weeks et al., 2013), suggesting eddy dynamics not only determine foraging site use, but also prey availability. The Eddy is a mobile and unstable phenomenon which results in variable effects on ocean dynamics in the region; for example, when the eddy moves westward, closer to the reef edges, it forces an intrusion of cold water into the GBR lagoon. This causes intense stratification and traps warm water at the surface which reduces prey to seabirds (Weeks et al., 2013). Such a phenomenon could simultaneously weaken or eliminate SST fronts. Alternatively, the Eddy could shed southward under stronger movement of the EAC, or it could simply weaken, slow or reduce in size, all of which would likely weaken frontal intensity. This likely appears in the current data set via the seasonally variable influence of frontal intensity on foraging site use, with this being a potential explanation for the inter-annual variation seen in this study.

5.5.3.2 *Inter-annual regional variation*

While factors related to the Eddy appeared highly important to shearwater foraging environments in 2012 and 2013, this was not always the case. In 2014, there was a lack of developed sea-surface temperature (SST) fronts as demonstrated by relatively low frontal values and the limited influence that proximity to fronts exerted on foraging. Instead, the dominant influences on foraging were generally lower than average chlorophyll *a* ([Chl *a*]) and SSTs. These low SSTs indicate a weaker effect of eddy dynamics in 2014, likely replaced by the influence of minor upwellings occurring in the individual zones. These contrasting effects among seasons demonstrate the effect variability in oceanographic conditions can have on shearwater foraging activity. Inter-annual and inter-zonal disparity among factors of influence implies that, at times, the influence of the eddy diminishes and is replaced by phenomena operating on a finer, localised scale that contribute strongly to beneficial foraging for shearwaters.

Whether these seasonal inconsistencies did in fact drive variations in food levels, and how that affected food availability to foraging birds in different zones is not currently known. This study uses foraging intensity as a surrogate for prey availability however, the question as to what causes the inter-annual variation, remains. Do birds change where they forage to find specific background conditions and prey availability? Or, alternatively, do they forage in specific locations that sometimes experience different conditions that drive fluctuations in prey availability?

Combined, the cumulative results from these secondary oceanographic parameters highlight the importance of investigating multiple, specific variables to characterise foraging sites and areas of activity. In attempting to determine if any particular variables could be used to predict the distribution of chick provisioning birds, the investigation of factors beyond bathymetry revealed that the most important variables showed little spatial or temporal uniformity among zones or years. Foraging activity in any given year could be dominated by a single factor of influence or display considerable variation. For example, the strong influence of SST fronts at multiple sites in 2013, was a trend that was not apparent in 2014 when the most important factors varied among zones. This exemplifies the impracticality of using one or two oceanographic variables to predict foraging activity, or the rate thereof, in any given location at any particular time and suggests the influence of a larger-scale process that would explain most of the observed results.

5.5.3.3 *Climate-driven impacts*

Ultimately, foraging site selection and, presumably, prey availability to chick-provisioning wedge-tailed shearwaters is driven by two principal mechanisms operating in the southern GBR: terrestrial input and the Capricorn Eddy. Both of these phenomena are driven by local or regional scale weather and climatic conditions and thus are subject to impacts from changes in these conditions. Regional scale weather patterns are strongly influenced by the El Niño Southern Oscillation (ENSO) and there is evidence in this study, reflected by divergences in the most influential foraging predictor variables, that ENSO conditions affected both larger scale phenomena in the system and local oceanographic conditions. For example, the spinning of the Capricorn Eddy is regulated by the flow of the EAC (Weeks et al., 2010), which is strengthened by ENSO conditions (Burrage et al., 1994) that may cause the Eddy to shed southward (Weeks et al., 2010). 2013 was a neutral ENSO year and in that season Eddy influence was apparent in many zones, while zone one was heavily impacted by floodwater inundation from river discharge (BOM, 2014a). By comparison, 2014 exhibited stronger prevailing ENSO conditions, showing a less discernible influence of the Eddy and did not experience the extreme flood events of the previous year.

Climate-driven variations also affect the smaller, local-scale processes both directly and indirectly. ENSO variation affects global patterns of rainfall, storms and floods, causing variation in regional rainfall that directly determines levels of freshwater input in zone one. Additionally, ENSO or regional current influences on Eddy dynamics can produce a cascading effect that impacts the finer-scale functions within foraging zones by reducing the input of cooler water and nutrients into the GBR lagoon (Weeks et al., 2010). These kinds of variations would explain the slightly higher SSTs generally observed in 2014. Increased SSTs are known to be harmful to the reproductive success of wedge-tailed shearwaters, causing deleterious food reductions in the system (Smithers et al., 2003, Weeks et al., 2013). As such, advantageous foraging in all locations is potentially threatened by increasing SST and other changes predicted under current climate-change scenarios.

5.5.4 Conservation and management

The southern GBR, encompassing the Capricorn Bunker and Swains Reefs regions, host one of the world's largest breeding population of wedge-tailed shearwaters (Dyer and Hill, 1992, Hill et al., 1996). The region is also important for significant populations of other species including black noddies and brown boobies (BirdLife International, 2015). Consequently, Birdlife International has identified the area as an Important Bird Area (IBA). The foraging sites used by shearwaters fall primarily within the GBR Marine Park (GBRMP), but protection in the region is presently limited to that offered by Marine National Parks. Most protection is in the form of '*no-take*' fishing zones and is centred on islands or cays such as the Capricorn Bunkers, Lady Elliot Island and the Swains reefs (GBRMPA, 2011, BirdLife International, 2015).

Moreover, key foraging areas identified in this study, either lack protection specifically aimed at seabird conservation (particularly important for zone one), or lie outside currently managed areas (zone five). Therefore, the information obtained from this study serve to highlight the most important areas to be prioritised for assessment of threatening processes and improved management and/or protection. The identification of priority conservation sites for seabirds is a necessary first step towards promoting and implementing targeted conservation action. Birdlife International's Marine Important Bird Areas (MIBAs) specifically identify areas of importance to seabirds, including feeding areas of pelagic species, and the most important areas for site-based conservation efforts (Birdlife International, 2011). This includes threat assessment and identifying optimal conservation and management actions that need to be implemented to ensure protection of seabirds and their resources. This process is often accomplished on a large, ocean-scale but the results from the present study suggest that foraging areas on a smaller scale are equally important. Therefore, a similar threat assessment/conservation process should be applied in these areas for the improved management and conservation of this species.

If mesoscale upwelling and frontal dynamics in the region are critical to tropical seabird resource availability, it is essential to determine a method of identifying these phenomena. Knowing how and when these upwellings will occur will help to predict places that are most likely to provide consistently good foraging habitat for seabirds. To confirm this relationship with certainty I need evidence of the presence of the upwellings at any given time. An index that will identify the presence, location, strength and intensity of the Capricorn Eddy is current being developed. This will measure the Eddy itself, its presence, strength and intensity, as a factor to be included in studies in order to precisely define oceanographic relationships and, ultimately, allow confirmation of its regional influence in any given season at particular times. The index could then be linked to actual foraging activity and how prey aggregations are augmented. I could then clearly define the influence of this phenomenon over foraging and prey availability.

5.5.5 Conclusion

This in depth investigation identifies the most important oceanographic variables and mechanisms which drive the availability and accessibility of prey to pelagic, tropical breeding seabirds. The clear relationships indicate the variables that are the most informative proxies for prey availability, and the mechanisms that drive them, for use in future studies of pelagic foraging tropical seabirds. Ultimately, these findings provide a model of trophic mechanisms in tropical environments that can be used as a paradigm for comprehensive habitat modelling, particularly for tropical pelagic foraging seabirds, to develop global conservation efforts.

6. DISCUSSION

6.1 THESIS SYNTHESIS

This thesis presents research which significantly advances the understanding of tropical seabird foraging ecology. I detail precise locations, characteristics and spatial segregation of essential breeding and non-breeding foraging resources for a widespread, tropical breeding Procellariiform, the wedge-tailed shearwater. I also describe in depth the oceanographic mechanisms and drivers of prey availability to these upper level predators in tropical marine systems. I synthesise the results presented in the preceding four chapters to develop a comprehensive understanding of oceanographic relationships in tropical food resource environments and the trophic mechanisms that influence the availability and accessibility of prey. My data conclusively identify priority target areas to be flagged for threat assessment and thus can be effectively and readily applied to underpin improved conservation and management of pelagic foraging tropical seabirds. I highlight the broader implications and significance of my research and conclude by identifying future research priorities to advance knowledge in this field.

Sections are laid out as follows:

1. Spatial distribution of food resources
2. Non-breeding foraging grounds of the '*winter*' migration (Chapter 2)
3. Breeding season foraging grounds - long trips, adult resources (Chapters 3 & 4)
4. Breeding season foraging grounds - short trips, chick resources (Chapter 5)
5. Unexpected findings
6. Outcomes and Implications
7. Significance and conclusion

6.2 SPATIAL DISTRIBUTION OF FOOD RESOURCES

This extensive tracking study of wedge-tailed shearwaters of the Great Barrier Reef (GBR) has identified three spatially discrete food resource environments, each of which is essential to sustain this population and allow them to persist into the future. Of these critical foraging areas, one is used during the non-breeding period, and a further two are used independently for adult and chick resources during the breeding season (Fig. 6.1). The oceanographic and mechanistic characterisation of these locations demonstrates a general reliance upon regional, mesoscale phenomena, particularly eddies and frontal systems, that enhance prey and drive beneficial foraging associations.

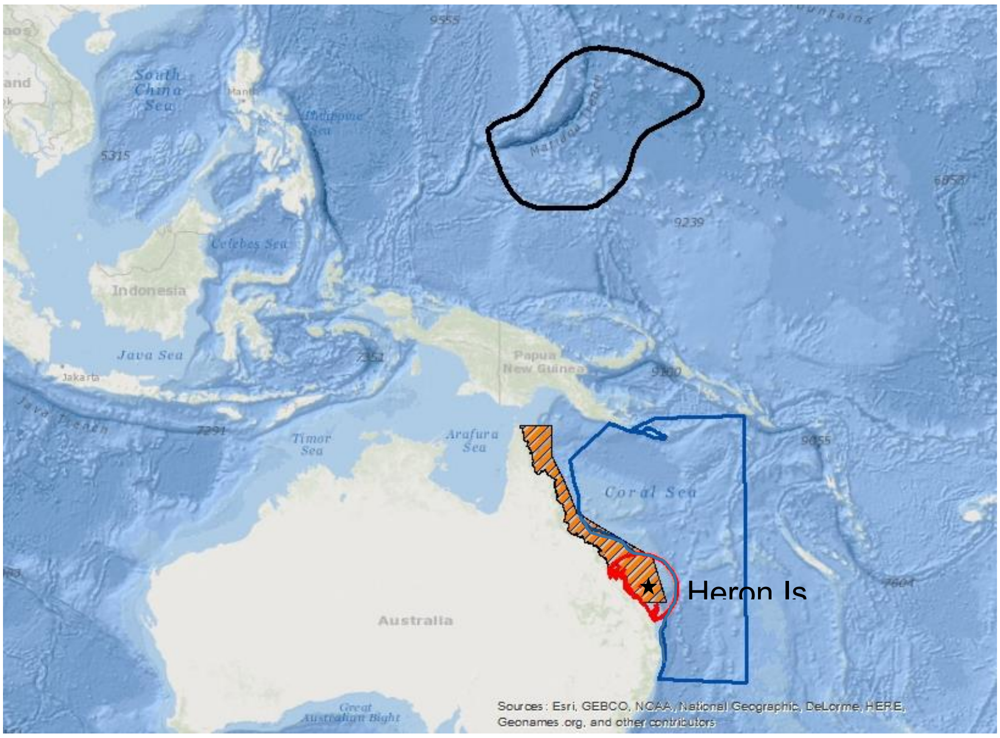

Figure 6.1: Map of the region used by wedge-tailed shearwaters that breed on Heron Island in the southern Great Barrier Reef (GBR) throughout the year. Black line denotes the non-breeding migratory foraging ground over the Mariana Trench; the blue line is the maximum area of the Coral Sea in which birds have been tracked on their long, self-provisioning foraging trips during breeding; and the red area is the short-trip foraging zone used by shearwaters when provisioning chicks. The yellow striped area is the GBR Marine Park and the black star shows the position of the colony on Heron Island.

6.3 NON-BREEDING FORAGING GROUNDS

Through my broadest-scale tracking study, I determined that adult wedge-tailed shearwaters conduct a trans-equatorial migration to a distant foraging ground during the non-breeding period, a strategy akin to that used by many temperate Procellariiformes (Shaffer et al., 2006, González-Solís et al., 2007, Reid et al., 2013). They are the first tropical Procellariiform known to do so. Wedge-tailed shearwater migration end points generally displayed markedly different characteristics and features to those of most previous studies, whether of temperate or tropical systems, migratory or dispersing species. Two phenomena presented as the most likely mechanisms that influenced foraging activity and prey availability in this system.

Firstly, oceanographic analysis presented mesoscale, warm-core eddies as the most likely oceanic mechanism driving foraging activity, indicated primarily by foraging associated with moderate sea-level anomalies (SLAs). More particularly, these measurements indicated that shearwaters were most strongly associated with the fronts at the peripheries of these eddies where sea-surface temperatures (SSTs) were high and Chlorophyll *a* ([Chl *a*] was low. Additionally, low wind speeds negated another potential explanatory variable proposed by Pinet et al. (2011), that high winds drive frontal systems which aggregate prey. Seabirds have known affinities with frontal formations, especially in temperate systems (Haney and McGillivary, 1985, Bost et al., 2009). However, few studies have directly associated migrating Procellariiformes with this habitat phenomenon (but see Sydeman et al., 2006, Yen et al., 2006a) and none have done so for non-breeding tropical species**.**

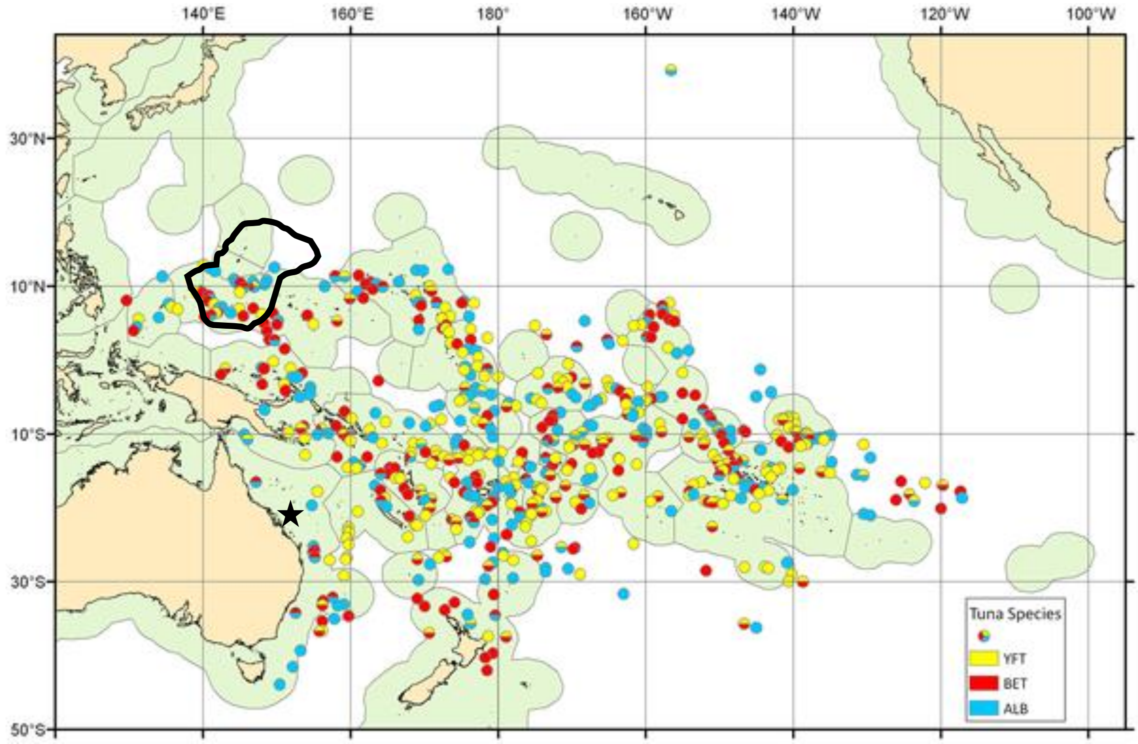

Figure 6.2: Map of Western Pacific Ocean catch rates of tuna in the WCPTF. Black line represents wedge-tailed shearwater core-use winger foraging ground and black star is the Heron Island colony. Green areas represent EEZs. From (Morato et al., 2010b) http://www.plosone.org/article/info:doi/10.1371/journal.pone.0014453.

Secondly, shearwater foraging grounds corresponded with the globally significant, commercial tuna fishery, the Western Central Pacific Tuna Fishery (WCPTF; Fig. 6.2). Interactions between tropical foraging seabirds and tuna are clear from the literature (e.g. Au and Pitman, 1986, Jaquemet et al., 2004, Le Corre and Jaquemet, 2005, Weimerskirch et al., 2005), as are links between seabirds, micronekton and oceanic phenomena and mesoscale eddies (Cotté et al., 2007, Sabarros et al., 2009, Santora et al., 2012). Therefore, these interactions are thought to drive advantageous foraging associations for tropical seabirds (Jaquemet et al., 2004, Le Corre and Jaquemet, 2005, Weimerskirch et al., 2005). Consequently, the spatial overlap with the WCPTF suggests that wedge-tailed shearwaters may experience a similar beneficial foraging relationship in '*winter'* foraging grounds.

6.4 BREEDING SEASON ADULT RESOURCES - LONG TRIPS

Congruence between PTT and the more accurate GPS tracking of shearwaters demonstrated that the former method efficiently identified and defined foraging locations. However, the generalisation that is inherent in kernel analyses used with PTT tracks, and the lower location accuracy of PTT means these results define habitat associations on a broader scale than the high resolution GPS study. Improvements to limited life of sufficiently small batteries will enable use of GPS to track long trips. Combined with appropriate pattern detection analyses (first passage time (FPT) to identify area restricted search (ARS) patterns), finer-scale habitat associations can be revealed.

As expected, wedge-tailed shearwaters always foraged at distant locations on long, self-provisioning trips, a pattern consistent with those of other dual-foraging seabirds (Weimerskirch, 1998, Magalhaes et al., 2008). However, the characteristics of those locations were not generally congruent with those of temperate dual-foragers, showing no evidence of enhanced [Chl a]. They were also dissimilar to those of the only other tropical Procellariiform known to dual-forage during chick-rearing, Barau's petrels, which prefer areas with high winds (Pinet et al., 2012). Instead, GBR shearwaters focused their foraging on deep water frontal systems and/or convergence zones generated at the peripheries of localised eddies that were closely linked to steep bottom topography. According to findings of other studies that found tropical seabird taxa foraging at eddy peripheries in the Mozambique Channel, these phenomena are said to enhance prey (Weimerskirch et al., 2004, Tew Kai and Marsac, 2010).

Another interesting observation from these long trips, was considerable spatial overlap between shearwater foraging locations and regional tuna fishing grounds. Therefore, sub-surface predator associations may also be important to shearwaters when breeding. Correspondence at this second shearwater foraging scale emphasises the potential importance of the interaction in driving enhanced prey accessibility at multiple foraging sites. However, in the absence of high resolution fisheries data or direct observation, it was beyond the scope of this study to conclusively confirm these associations. Therefore, the quantification of this relationship, its significance, and verification of direct interactions between GBR shearwaters and sub-surface predators, as well as the importance of the association, should be a priority for future research.

6.5 BREEDING SEASON CHICK RESOURCES - SHORT-TRIPS

Shearwaters foraged at five distinct zones (1-5) within 300km of their colony and consistently associated with the mesoscale Capricorn Eddy, the primary mechanism that influences the southern GBR. The Eddy drives local oceanography and evidence of its presence was observable in various oceanographic factors that that were associated with shearwater foraging grounds. For example, steep SST fronts and lower than average SSTs and [Chl a] values are factors that distinguish the presence of identifiable oceanographic frontal systems. The relationship between shearwaters, the Eddy and SSTs fits with expectations from prior studies that demonstrated consistent correlations between prey reductions and changes in Eddy dynamics and/or increased SSTs (Smithers et al., 2003, Peck et al., 2004, Weeks et al., 2013).

Such an affinity for foraging in association with mesoscale oceanic phenomena is not particularly unusual in seabirds (Weimerskirch et al., 2004, Hyrenbach et al., 2006). However, again the marked lack of influence of elevated [Chl *a*] conflicts with other studies that quantified short-trip foraging areas of Procellariiformes (e.g. Baduini and Hyrenbach, 2003, Magalhaes et al., 2008, Cecere et al., 2013). In the present study, elevated [Chl *a*] was only observed in GBR shearwater foraging zones in one instance. In the near shore zone (zone one), input from the terrestrial environment entered the system and freshwater interacting with the Capricorn Eddy produced strong SST fronts and coastal enrichment (elevated [Chl *a*]). As this kind of enrichment is constant along the coast (Devlin et al., 2001, Devlin and Brodie, 2005), this would nullify the trophic time-lag (Hutchings et al., 1995, Grémillet et al., 2008, Menkes et al., 2014) and explain a co-occurrence in these foraging grounds of [Chl *a*] and pelagic forage-fish from higher trophic levels which are prey of shearwaters. The high levels of foraging activity, which were clearly associated with the strong physiochemical gradients created by the convergence of water bodies, suggests that significant enhancement of prey availability is associated with these combined phenomena.

Inter-annual variation among predominant oceanographic factors of influence suggests variation in the location and/or intensity of the Capricorn Eddy. However, despite this, wedge-tailed shearwaters repeatedly used the same foraging areas. This implies that tropical environments are more predictable than has been supposed (Weimerskirch, 2007); that areas outside these sites are not predictably abundant; or, prey availability in these zones is usually sufficient to sustain chick provisioning, except under the most dire of circumstances such as severe ENSO conditions (Smithers et al., 2003). Nonetheless, the implication is that these sites are essential to sustaining chick-rearing for breeding GBR shearwaters, and none currently experience any seabird-specific protection.

Shearwater foraging at this near-colony scale is clearly associated with and influenced by the Capricorn Eddy. However, it is not currently possible to directly measure the intensity of this mesoscale phenomenon at any given time. Algorithms are currently being developed that can be used to determine the presence and intensity of the Eddy. Forthcoming research should utilise this algorithm to directly quantify the relationship between Eddy dynamics and both foraging activity and prey availability. Further research could also determine differences in the amount of food obtained from the different foraging grounds, to identify whether any given foraging ground or zone provides consistently reliable foraging and/or '*better*' food supplies for shearwaters.

6.6 UNEXPECTED LACK OF ENHANCED PRODUCTIVITY

In almost all previous seabird foraging studies, that aimed in some way to quantify the foraging environment, areas of elevated primary productivity ([Chl *a*]) were found to be important (e.g. Guinet et al., 1998, Weimerskirch et al., 2001, Inchausti et al., 2003). As a result, [Chl *a*] is routinely used to validate seabird foraging habitat as it is readily available via remotely sensed satellite data. However, elevated [Chl *a*] does not necessarily correlate with increased prey availability. For example, Grémillet et al. (2008) found that overlap of Cape gannet (*Morus capensis*) foraging habitat with highly productive ocean in the Benguela upwelling zone did not correspond to increased prey availability. Additionally, Sommerfeld et al. (2015), in a study of boobies, found that the size of prey patches decreased when associated with locally elevated [Chl a]. These findings provide evidence for a spatial and temporal mismatch between elevated [Chl *a*] and higher trophic levels, like the pelagic fish which are prey of seabirds (Hutchings et al., 1995, Menkes et al., 2014).

In fact, other phenomena may be considerably more important. Becker and Beissinger (2003) argue that the influence of oceanic, prey-aggregating features at finer-scales of foraging (<10km) eclipse [Chl *a*]. My findings, demonstrating recurrent associations with local frontal systems and eddy peripheries, provide support for this assertion, especially given that elevated [Chl a] was rarely a prominent characteristic of shearwater foraging locations**.** These results add weight to the suggestion that [Chl *a*] is not necessarily an appropriate indicator of seabird foraging habitat (Grémillet et al., 2008, Sommerfeld et al., 2015), and that this may be especially true for more homogeneous tropical environments.

Another possibility is that prey availability at these eddy peripheries is not defined by [Chl a] measurements taken from the ocean's surface (Hutchings et al., 1995, Grémillet et al., 2008). Rather, shearwater foraging may be related to some other as yet undetermined parameter that might be a more appropriate measure of prey availability, such as sub-surface [Chl a] or the deep chlorophyll maxima (DCM) (Cullen, 1982, Banse, 1987, Miller and Wheeler, 2012). Measurements of the DCM are not readily available and as such, their effects on ‘productivity’, prey enhancement and foraging of apex predators are largely unknown. Nevertheless, they could well be contributing to bottom-up processes which result in aggregations of prey items (micronekton etc.) that are important to seabirds (Lebourges-Dhaussy et al., 2000). Therefore, the study of this factor, in the context of drivers of seabird foraging activity, would be an interesting step forward in this field of research.

In addition, these relationships could be investigated in further depth with development of an efficient algorithm to measure and identify productivity gradients and their intensity. This may prove to be a further layer of understanding regarding beneficial frontal systems through new [Chl *a*] measurement. This would help to more clearly and accurately quantify the true nature of the relationship between foraging and productivity. In the present study, effects of strong fronts or eddies may have masked other, less obvious effects.

6.7 OUTCOMES & IMPLICATIONS

6.7.1 Defining foraging habitat

Tracking data from this study will be added to the ‘*Tracking Ocean Wanderers’* database, the largest seabird tracking database, contributing to global knowledge of habitat used by seabirds. There are currently very few data for tropical species/regions and none for the tropical south-western Pacific Ocean where I have identified the most important foraging grounds for GBR wedge-tailed shearwaters. In addition, habitat mapping via predictive modelling using these data can identify both ‘*good*’ foraging habitat and other potential locations based on identified oceanographic parameters that define known foraging grounds.

Comparing and contrasting these findings with previous research draws attention to both similarities and divergences and identifies weaknesses, strengths and potentially missing elements in oceanographic characterisation and defining of food resource habitat. These results should be used to guide decisions regarding ideal variables for modelling marine environments. For example, anomalous values of [Chl *a*] and SSTs, have primarily been used to measure ENSO conditions and responses in previous work (Wilson, 1991, Velarde et al., 2004, Devney et al., 2009). However, my results indicate their suitability for clearly identifying important mesoscale phenomena and discriminating finer-scale processes that influence seabird foraging. Additionally, the efficacy of SLAs for revealing mesoscale eddies, as seen herein, has been observed in previous research (see Chaigneau et al., 2009 for a description of eddy activity in major upwelling zones), but seldom used to define tropical seabird habitat. Specifically, links have been made with some seabirds in the Mozambique Channel (Weimerskirch et al., 2004, Tew Kai and Marsac, 2010). The detailed description of oceanography and dynamics produced by this study underscores the utility and value of using an extensive, explicitly selected set of parameters in pelagic habitat modelling studies to reveal regional oceanographic processes (Palacios et al., 2006).

6.7.2 A model of tropical seabird foraging ecology

This study has identified a number of environmental/oceanographic correlates of Wedge-tailed shearwater foraging activity across three spatial scales. Eddies and their peripheries are clearly identified as a vital component in driving beneficial foraging associations, at all spatial scales. Furthermore, my results have distinguished finer-scale processes and identified terrestrial outflow as an important mechanism driving foraging, which has not previously been documented for a tropical pelagic seabird. Finally, my research implies that these shearwaters have foraging links with sub-surface predators in at least two foraging scales. If these are important, as also suggested by previous tropical seabird studies (e.g. Au and Pitman, 1988, Jaquemet et al., 2004, Le Corre and Jaquemet, 2005), this relationship should be directly confirmed and quantified. Combined, these data inform future studies as to the optimal set of parameters that best identify mechanisms in tropical environments at various spatial scales. These findings are not only useful for identifying important foraging areas for Wedge-tailed shearwaters but may be applicable to other populations and species of pelagic foraging seabirds in this and other tropical regions. To determine the generality of these findings, additional tracking studies and environmental modelling of foraging locations used by other tropical pelagic foraging seabird populations and species are required.

6.7.3 Conservation

The comprehensive data set generated in this study on the foraging ecology of GBR wedge-tailed shearwaters will underpin and guide the conservation and management of this population. In important areas flagged for assessment, it may also be advisable to implement the process for defining candidate Marine Important Bird Areas (Birdlife International, 2011), which are globally recognised management zones. The Heron Island shearwater colony forms part of one of the largest wedge-tailed shearwater populations worldwide (~ 2 million birds across the Coral Sea/GBR region) (Congdon et al., 2007). It is therefore, an important component of the GBR ecosystem, the Australian seabird community and global shearwater populations. Consequently, this has significant pan-tropical conservation implications for a widespread and abundant Procellariiform which is considered to be in decline, and threatened by anthropogenic processes (primarily overfishing and climate change) (IUCN, 2013).

These data can be developed to define optimal management strategies for multiple species throughout the tropics. Most of these shearwater foraging locations overlap with, or are used by, a variety of marine life, implying that these areas offer favourable conditions and/or reliable prey interactions and heightens the significance of these locations. For example, other seabirds are known to attend the same foraging grounds. Streaked shearwaters (*Calonectris leucomelas*) of Japan (Takahashi et al., 2008), and various species of terns and boobies (Birdlife International, 2014) use the same '*winter*' foraging grounds; while in the southern GBR, shearwater foraging grounds correspond with those of tracked masked and brown boobies (*Sula dactylatra and leucogaster*) (McDuie et al. *unpub. data*). Additionally, these locations are not exclusive to seabirds. Many locations across the world's oceans have been found to support numerous taxa (Croxall et al., 1992, Spear et al., 2001, Morato et al., 2010a, Santora et al., 2012), and my results point toward a co-occurrence of seabirds with other upper level taxa and the species they predate; specifically micronekton and sub-surface predatory tuna. Such associations have been recorded by numerous previous studies, especially in tropical regions, with well-demonstrated interactions among seabirds, tuna and micronekton (e.g. Bertrand et al., 2002, Le Corre and Jaquemet, 2005, Sabarros et al., 2009, Tew Kai and Marsac, 2010). Therefore, the health of these areas may govern both the longevity of this shearwater population, and potentially multiple other species.

Knowing important food resource locations highlights priority target areas for threat assessment and evaluation. As a result, management strategies in place in specific locations can be scrutinised, developed or improved. In this way, I would be able to determine if it is possible to conduct location specific management or if a shift to ocean specific strategies would be more effective. This is significant as the spatial segregation of breeding and non-breeding foraging grounds into three discrete regions means that each habitat is likely to be threatened by different processes and require different protection and management. The lack of protection currently offered to any of these locations underscores the need for a strong conservation focus in the management of this GBR seabird population. Addressing threatening processes which can be managed (such as human extraction practices) would help mitigate other impacts, particularly those resulting from declining oceanic conditions. These tenets have considerable global conservation significance, particularly in tropical marine ecosystems. Threatening processes must be minimised to mitigate the potentially disastrous effects of global warming and climate-change which could decimate marine species and ecosystems.

6.7.4 Climate change impacts

Climate change is potentially the most prevalent threat to marine ecosystem function with far-reaching implications for all tropical organisms (Hoegh-Guldberg and Bruno, 2010, IPCC, 2013). Climate-change is also one of the two most significant threats to seabirds globally (Croxall et al., 2012). Numerous prior studies demonstrate the dangers posed by changing climate-driven processes to seabird communities and prey availability (e.g. Schreiber and Schreiber, 1984, Piatt et al., 1999, Devney et al., 2009). Additionally, increases in SSTs, particularly those related to climate-change processes such as El Niño Southern Oscillation (ENSO), deleteriously impact wedge-tailed shearwaters (Smithers et al., 2003, Peck et al., 2004, Weeks et al., 2010). My results add another layer to this dynamic by demonstrating that seasonal variations in climatic patterns and regional or localised oceanography, produce disparate patterns of foraging activity. Such relationships can be explained by processes related to climatic variation. For instance, if the currents that produce eddies characteristic of shearwater foraging locations alter, shift or reduce (as is predicted under certain climatic conditions), these eddies could fail to occur. This would likely result in reduced prey availability, but until these phenomena are directly linked to amounts of food entering the seabird colony, this cannot be conclusively confirmed. As such this is an ideal next step and should be a focus of forthcoming research.

6.8 SIGNIFICANCE AND CONCLUDING REMARKS

This research underscores the need to design effective and region-appropriate management and conservation strategies for seabirds. This is particularly important in light of marked differences identified between temperate and tropical regions. Importantly, assumptions based on trophic mechanisms in temperate environments are clearly unsuitable for modelling patterns and processes in tropical systems. The theories generated and conclusions reached in my study have significant implications for future research on tropical seabird foraging ecology and trophic mechanisms in tropical marine systems.

Well-defined relationships between prey availability and ocean dynamics are indispensable in strategic planning for effective management and conservation of a species. The improved understanding of oceanographic mechanisms provided by my research could potentially be applied to pelagic foraging seabirds in tropical systems, especially when habitats and requirements are similar. Accordingly, they may contribute to the global management of seabird populations. For example, one approach would be to use the findings herein to implement the development of global procedures for identifying and proposing candidate MIBAs (Birdlife International, 2011), particularly when species habitats and requirements are similar.

Another important consideration is the apparent significance of associated fisheries and sub-surface predator interactions. Commercial fisheries threaten multiple species, locations and ecosystems, and overfishing is another strong contributory factor to global seabird declines (Croxall et al., 2012). If reductions are not addressed, the global decline of seabirds will likely continue unabated. Large aggregations of sub-surface predatory tuna, a prime target of commercial fisheries, may be important to enhancing pelagic foraging of shearwaters, especially when considering the considerable overlap of shearwaters and sub-surface predator foraging grounds. Current management strategies tend to be single-species focused and, where there are commercially important fisheries, these are generally the chief focus. However, inter-species interactions, especially between seabirds and tuna, indicate that integrated management may be more suitable and beneficial in the longer term. It seems certain that management of fisheries may be pivotal in ensuring their long-term sustainability and safeguarding continued access to beneficial prey aggregations for shearwaters and other seabirds. Ultimately, the research presented in this thesis provides a foundation on which detailed oceanographic and trophic studies of tropical marine ecosystems and seabird foraging ecology can be based and further explored in future studies.

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APPENDICES

Appendix 1: Acronyms used in this thesis

BAS	British Antarctic Survey
BOM	Bureau of Meteorology
GBR	Great Barrier Reef
GBRMP	Great Barrier Reef Marine Park
GBRMPA	Great Barrier Reef Marine Park Authority
ITCZ	Inter Tropical Convergence Zone
MIBA	Marine Important Bird Area
MTSRF	Marine and Tropical Sciences Research Facility
NCCARF	National Climate Change Adaptation Research Facility
NERP	National Environmental Research Program
WCPTF	Western Central Pacific Tuna Fishery

Appendix 2: Abbreviations used in this thesis

Analyses

ARS	Area Restricted Search
AUC	Area Under the Curve
BRT	Boosted Regression Tree (analysis)
FPT	First Passage Time (analysis)
ROC	Receiver Operating Curve
SAC	Spatial Auto-Correlation
VIF	Variance Inflation Factor

Oceanographic data types

Bath_grad	bathymetric gradient
[Chl *a*]	Chlorophyll A concentration
ChlaMonth	Chlorophyll A, monthly average
Chla3dmean	Chlorophyll A, 3 day average
ChlaAmonth	Chlorophyll A anomaly, monthly average
CDSP	Current speed
ChlaA3dmean	Chlorophyll A, monthly average
Coldist	Distance from colony

DCM	Deep Chlorophyll Maxima
DistBathg	Distance from the steepest bathymetric gradient
Distseam	Distance from nearest seamount
DistSSTG/25	Distance from steepest sea-surface temperature gradient
MSLA	mean sea-level anomaly
SSTmonth	sea-surface temperature, monthly average
SST3dmean	sea-surface temperature, 3 day average
SSTAmonth	sea-surface temperature anomaly, monthly average
SSTA3dmean	sea-surface temperature anomaly, 3 day average
SSTGmonth	sea-surface temperature gradient, monthly average
SSTG3dmean	sea-surface temperature gradient 3 day average
SLA	sea-level anomaly
SSS	sea-surface salinity

Electronic tracking

GLS	Geolocator System
GPS	Geographic Positioning System
KDE	Kernel Density Estimation
PTT	Platform Terminal Transmitter satellite telemetry data logger
UD	Utilisation Distribution