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Final Report

## Critical seabird foraging locations and trophic relationships for the Great Barrier Reef



Bradley C. Congdon, Fiona McDuie, Mark G.R. Miller,  
Scarla J. Weeks and Craig Steinberg



Australian Government  
Department of the Environment

 **Reef &  
Rainforest**  
RESEARCH CENTRE

# **NERP Project 6.3 Final Report December 2014**

## ***Critical seabird foraging locations and trophic relationships for the Great Barrier Reef***

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## Acronyms Used In This Report

<b>GBR</b>	.....	Great Barrier Reef
<b>NERP</b>	.....	National Environmental Research Program
<b>JCU</b>	.....	James Cook University
<b>NCCARF</b>	.....	National Climate Change Adaptation Research Facility
<b>MTSRF</b>	.....	Marine and Tropical Sciences Research Facility
<b>PNG</b>	.....	Papua New Guinea
<b>RRRC</b>	.....	Reef and Rainforest Research Centre Limited
<b>TSRA</b>	.....	Torres Strait Regional Authority

## Abbreviations Used In This Report

<b>SST</b>	.....	Sea-surface temperature
<b>GLS</b>	.....	Geolocator System
<b>GPS</b>	.....	Geographic Positioning System
<b>PTT</b>	.....	Platform Terminal Transmitter satellite telemetry data logger
<b>UD</b>	.....	Utilisation Distribution

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Research at Lord Howe Island is in collaboration with N. Carlile, Office of Environment & Heritage, NSW, and I. Hutton. Lord Howe Island Tours, Lord Howe Island.

Research at Bramble Cay is in collaboration with J. Rainbird and staff, Torres Strait Regional Authority, Thursday Island/Cairns and J. Lavers, Monash University, Melbourne.

## Executive Summary

Core foraging areas and associated oceanographic characteristics for Great Barrier Reef (GBR) breeding shearwaters have been identified and mapped at three spatial scales across multiple years. The compilation of data across years confirms previous preliminary findings. During breeding adults use only near-colony foraging grounds (<300km) for chick provisioning. Foraging activity and prey availability at these sites is linked to both meso-scale eddy dynamics in the Capricorn channel and river flood-plume characteristics adjacent to the coast.

Foraging locations used by masked boobies during breeding correspond to, and broadly overlap with areas used by wedge-tailed shearwaters. Foraging site use by these two species is out of phase by ~6 months and each species is known to use different foraging techniques and to take prey of different types and sizes. Consistent prey availability in these areas is driven by the dynamics of the Capricorn Eddy and associated oceanographic phenomena. The observed overlap in foraging distributions highlights the potential year round importance of these sites and phenomena for providing prey to a range of top-predators.

Adults shearwaters on longer self-provisioning trips routinely travel up to 1000km and forage in association with seamounts of the Coral Seas. Foraging occurs in waters characterised by strong physiochemical gradients typical of large-scale eddies and frontal systems associated with steep bathymetric change. Foraging at these sites overlaps significantly with known commercial fishing activity. Most at-distance sites are outside the management zone of the GBRMP.

When not breeding GBR shearwaters are trans-equatorial migrants that overwinter in Micronesia. In general, over-wintering areas have oceanographic features associated with poor foraging habitat. However, foraging site use is strongly linked to positive sea-level anomalies. This indicates the presence of intense anti-cyclonic eddies and frontal systems at foraging locations that likely enhance prey availability to shearwaters beyond levels expected based on standard indices of primary production. Importantly, both shearwater migration routes and over-winter grounds overlap significantly with areas used by the world's largest tuna fishery. This finding raises significant previously undocumented conservation concerns for this GBR breeding species.



## Introduction

Seabird are marine apex predators whose foraging and reproductive success is explicitly linked to both local and large-scale oceanographic variation. Previously, we have shown that intense El Niño events cause almost total nesting failure of impacted seabird colonies on the Great Barrier Reef (GBR) (Smithers *et al.* 2003) and that significant decreases in prey availability occur in direct association with small-scale increases in sea-surface temperature (SST), independent of prevailing El-Niño conditions (Peck *et al.* 2004, Erwin & Congdon 2007, Devney *et al.* 2010).

As sea-surface temperatures continue to rise with global climate-change, these results predict substantial detrimental impacts on seabird populations of the GBR. This finding has important implications for both seabird and coral reef ecosystem management in the region. Specifically, it means that effective conservation of GBR breeding seabirds requires detailed information on foraging areas, resource use and links to oceanography. Without this information it is not possible to identify or manage anthropogenic threats outside of nesting colonies. Previous results also suggest that seabirds are sensitive indicators of changes in forage-fish availability/accessibility associated with oceanographic variation that can be used to develop models of, and monitor for, these potential impacts.

Therefore, this project aimed to use state-of-the-art data logging equipment attached to foraging seabirds to identify core foraging areas for GBR breeding seabirds and to investigate the relationships between prey availability/accessibility and physiochemical oceanographic parameters at these locations. Specific project objectives were 1) to obtain detailed information on the distribution, stability and physiochemical characteristics of critical seabird foraging habitat used by GBR breeding seabirds; 2) for the first time identify and characterise non-breeding foraging habitats used by GBR shearwaters, 3) Quantify how foraging activity at these sites varies with climate driven changes in oceanography, both within and among breeding seasons; 4) establish potential linkages and interactions between these areas/processes and other anthropogenic activities, specifically long-line tuna and other commercial fishing activity.

The ability of seabirds to cope with climate variation is also dependent on the flexibility of different life-history characteristics. Therefore, this project also aimed to further assess both behavioral and developmental plasticity of specific seabird species under fluctuating resource availability.

Combined these two project components provide substantial new insight into the factors determining forage-fish distribution and abundance in tropical reef ecosystems and enable us to determine the likely range of oceanographic and climatic conditions within which seabird reproduction on the GBR will remain viable. Thus, they provide a basis for informed seabird management decisions, as well as for predicting how climate variation and/or other anthropogenic stressors may influence breeding success into the future.

## Methodology

This study mapped core foraging areas used by GBR breeding seabirds at multiple spatial over a three to four year period. Foraging tracks were obtained for three species, wedge-tailed shearwaters (x4 seasons), masked boobies (x3 seasons) and brown boobies (x2 seasons), each species breeding in a different region of the GBR.

Wedge-tailed shearwaters breeding in the southern GBR at Heron Island were used as the principal model for pelagic foraging species. This was because we had previously shown shearwaters at this site to be the most sensitive indicator of changes in forage-fish distribution and accessibility associated with oceanographic variation (Smithers et al. 2003, Peck et al. 2004). For Heron Island shearwaters, we identified i) near-colony foraging locations used for chick provisioning, ii) at-distance locations used by adults for self-provisioning during breeding, and iii) non-breeding locations used by overwintering adults. As a model for larger more inshore forager species we examined foraging habitat use by boobies during chick provisioning; masked boobies in the Swains Reefs of the southeastern GBR and brown boobies at Raine Island in the far northern GBR.

At each colony seabird foraging tracks were obtained using a combination of different Geolocator System (GLS, Figure 1), Geographic Positioning System (GPS) and ARGOS Platform Terminal Transmitter (PTT) satellite telemetry data loggers. For shearwaters, GLS loggers were used to locate over-wintering areas and so establish potential overlap between breeding and non-breeding resources and the oceanographic conditions associated with attaining breeding condition. During breeding, as well as mapping foraging locations, data were also obtained on the success of each foraging trip via comparison of chick and adult weights pre and post logger deployment. Tracking and foraging success data were then combined with high-resolution satellite image and other *in-situ* physical oceanographic information to explicitly link patterns of foraging activity to oceanography and to explore functional relationships.

The project concentrated on analyses of foraging behaviour in GBR breeding seabirds but also located core foraging habitat used by wedge-tailed shearwaters breeding in other areas, Lord Howe Island and Western New Caledonia, so as to establish possible overlap in feeding resource use among colonies and to establish the generality of relationships seen for GBR breeding birds.



**Figure 1.** GLS data logger used to track wedgetailed shearwaters to non-breeding overwinter foraging locations

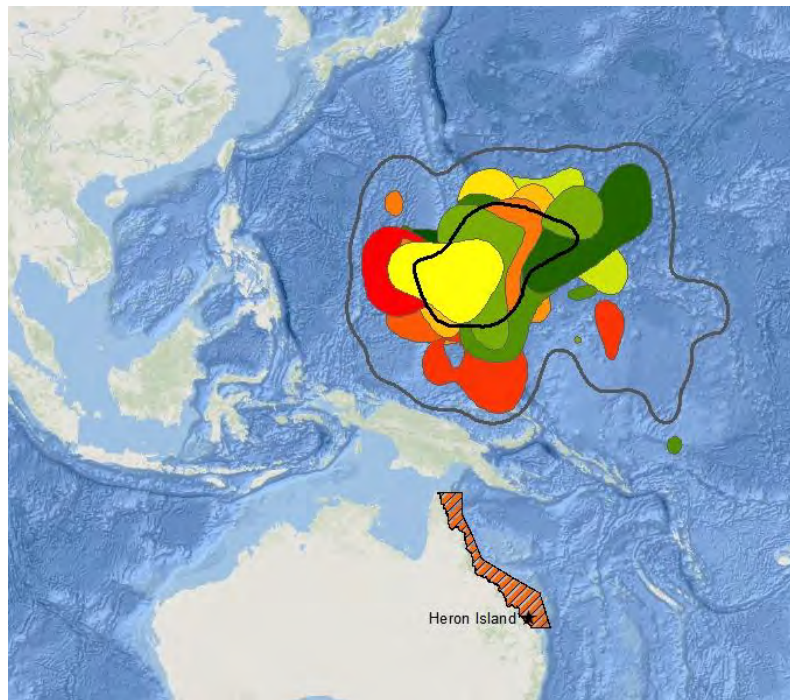
## ***Wedge-tailed Shearwaters***

This project defined core foraging areas for southern Great Barrier Reef (GBR) breeding wedge-tailed shearwaters using foraging track kernel analysis at three spatial scales.

### ***Overwinter non-breeding foraging areas***

Wedge-tailed shearwaters breeding in the southern GBR migrate ~6000km north to a single, core-use foraging area to the east of Guam in Micronesia (Figure 2). These are the first tropical tube-nosed seabirds (Procellariiformes) known to conduct a lengthy, trans-equatorial winter migration. The migration pattern is similar to that observed for temperate Procellariiformes shearwaters, but non-breeding foraging ground characteristics are significantly different; analogous to those of tropical species in the Indian Ocean that do not undertake trans-equatorial migrations. Migratory patterns and non-breeding foraging-site use are highly consistent between years. Core-use areas have notably high sea-surface temperatures, very low wind speeds and low primary productivity. These are oceanographic features normally thought to produce poor foraging habitat.

However, intensity of foraging site use was also very strongly associated with positive sea-level anomalies. These anomalies indicate the presence of intense anti-cyclonic eddies at foraging locations that generate frontal systems and likely aggregate prey. Documented frontal activity in this area is associated with the 'Western Pacific Warm Pool' and is linked to high levels of sub-surface predator feeding. For example, this region is a focus of the Western Central Pacific Tuna Fishery. Consequently, our results suggest that feeding associations with sub-surface predators considerably enhance prey availability to shearwaters beyond levels expected based on standard oceanographic indices of primary production. If so, any significant reduction in sub-surface predator stocks could be a serious threat to the non-breeding survivorship and long-term persistence of this seabird population.

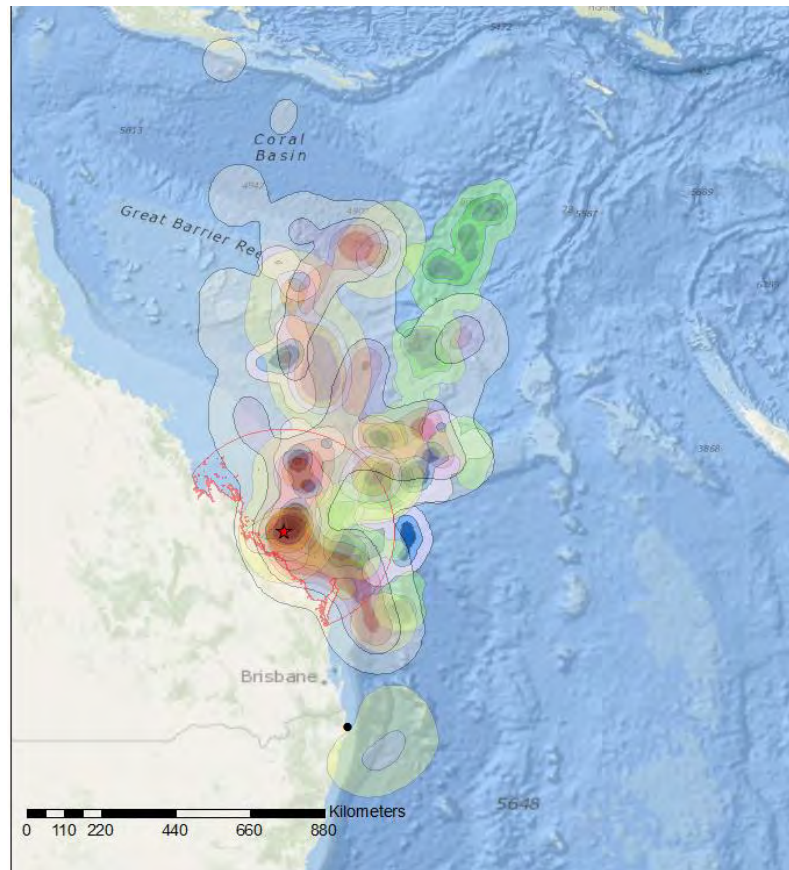


**Figure 2.** Individual core-use non-breeding foraging kernels (50% Utilisation Distribution, UD) for adult wedge-tailed shearwaters from Heron Island on the southern Great Barrier Reef (GBR), from May to October/November 2012. The area inside the dark black line represents the pooled 50% UD core-use area while the outer grey line represents the 95% UD maximum extent of use kernel for all birds. The star indicates the breeding site at Heron Island and the striped area shows the Great Barrier Reef Marine Park.

### ***Adult self-provisioning foraging areas during breeding***

During breeding adult shearwaters undertake 'at-distance' self-provisioning trips of ~10 days during which they do not return to the colony but remain at-sea to replenish their own body reserves. On self-provisioning trips adults routinely travel up to 1000km and forage in association with the Tasmanid Seamounts of the Coral and northern Tasman Seas (Figure 3). At-distance foraging locations vary among years but specific locations are reused both within and among seasons. Foraging sites are characterized by deep water in close proximity to rapidly changing bathymetric gradients near seamounts. They also have strong associations to both positive and negative sea level anomalies and steep sea-surface temperature gradients.

Combined these characteristics unambiguously describe local to meso-scale upwellings, downwellings, eddies and frontal systems adjacent to seamounts and highlight their importance for enhancing prey availability to shearwaters. 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 increased absolute measures of primary productivity. Importantly, most frequently used at-distance foraging sites are outside the management zone of the GBRMP.



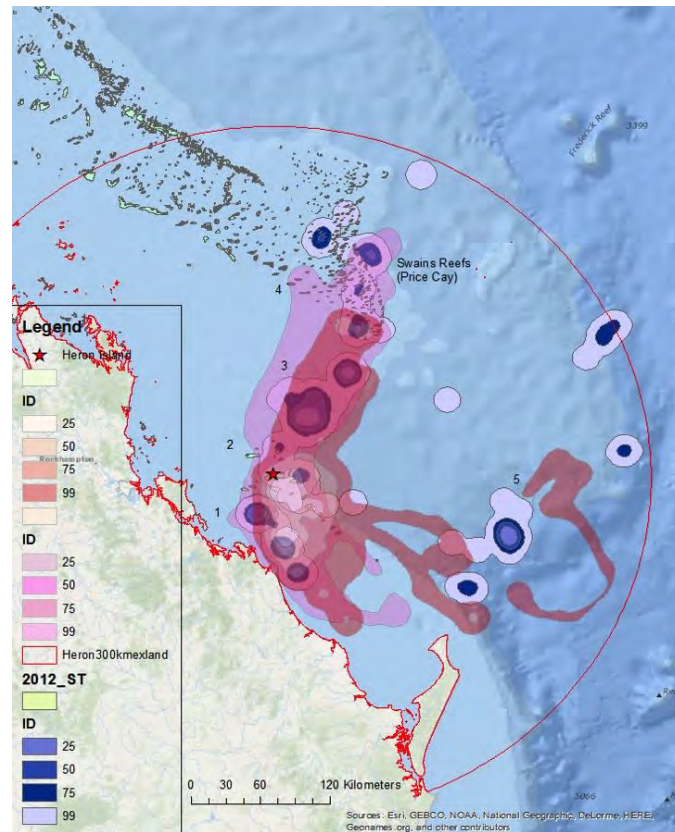
**Figure 3.** Adult at-distance self-provisioning foraging locations 2006-2013 for southern GBR wedge-tailed shearwaters during breeding. Different colours represent individual years, while the four levels of intensity per colour represent increasing foraging kernel densities of 99, 75, 50 & 25% UD, 25% being the most intensely used area. The star indicate the location of the breeding colony at Heron Island and the solid red line shows the maximum foraging range of adults when collecting food to provisioning chicks. Adults on self-provisioning trips often also foraged in this near-colony region while in transit to, or from, more distant foraging sites.

### ***Chick-provisioning foraging areas during breeding***

During breeding, adults use only near-colony foraging grounds (<300km) to provision chicks. Most chick provisioning trips are of one-day duration. Near-colony foraging locations varied among years and individuals, but specific locations were consistently reused both within and among years (Figure 4).

Near-colony foraging occurred in five principal and topographically distinct regions within 300km of the colony: 1) inshore adjacent to the mainland coast; 2) within the Capricorn-Bunker Reefs and along the associated continental slope; 3) in the Capricorn Channel between the Capricorn and Swains Reefs; 4) within the Swains Reefs and along the associated continental slope; and 5) over the submarine canyon system dissecting the continental slope to the north-east of Fraser Island (Figure 5).

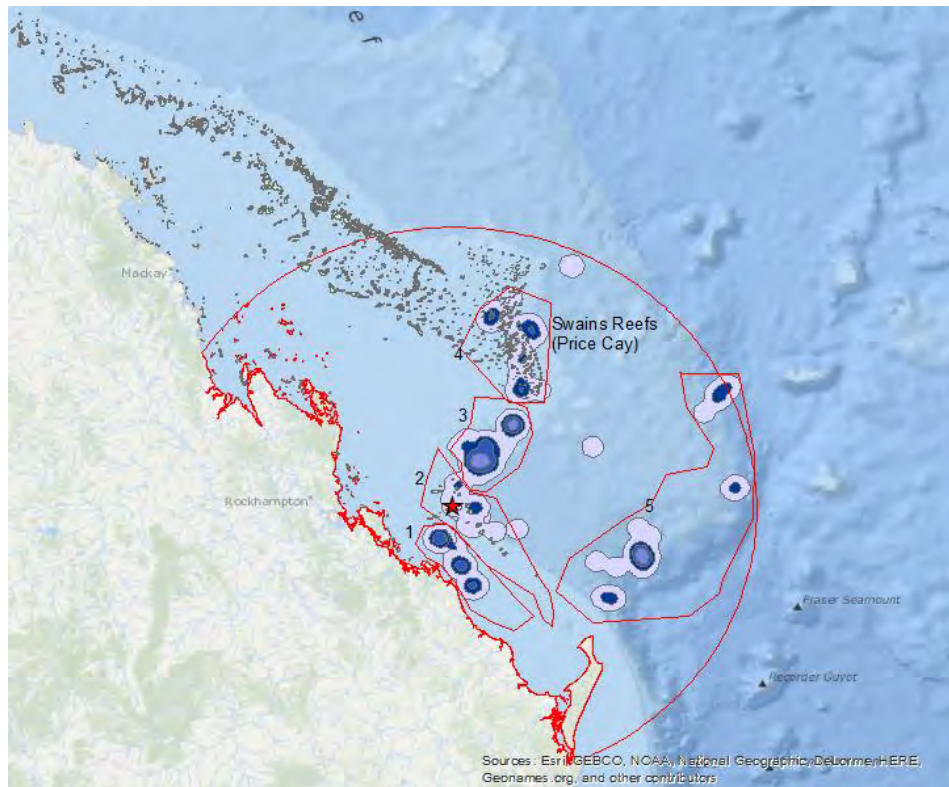




**Figure 4.** Foraging locations for southern GBR breeding wedge-tailed shearwaters when obtaining food to provision chicks 2012-2013. Different colours represent individual years/months (Blue-February/March 2012, Red-February 2013, Purple-March 2013), while the increasing levels of intensity per colour represents foraging kernel densities of 99, 75, 50 & 25% UD respectively, 25% UD being the smallest and most intensely used area. The solid red line indicates the maximum foraging range observed for adults during chick provisioning trips.

Areas 1-4 were used each season with the intensity of use varying between seasons. Area 5 was used infrequently for chick provisioning, but is a region included often in many adult self-provisioning trips (Figure 3).

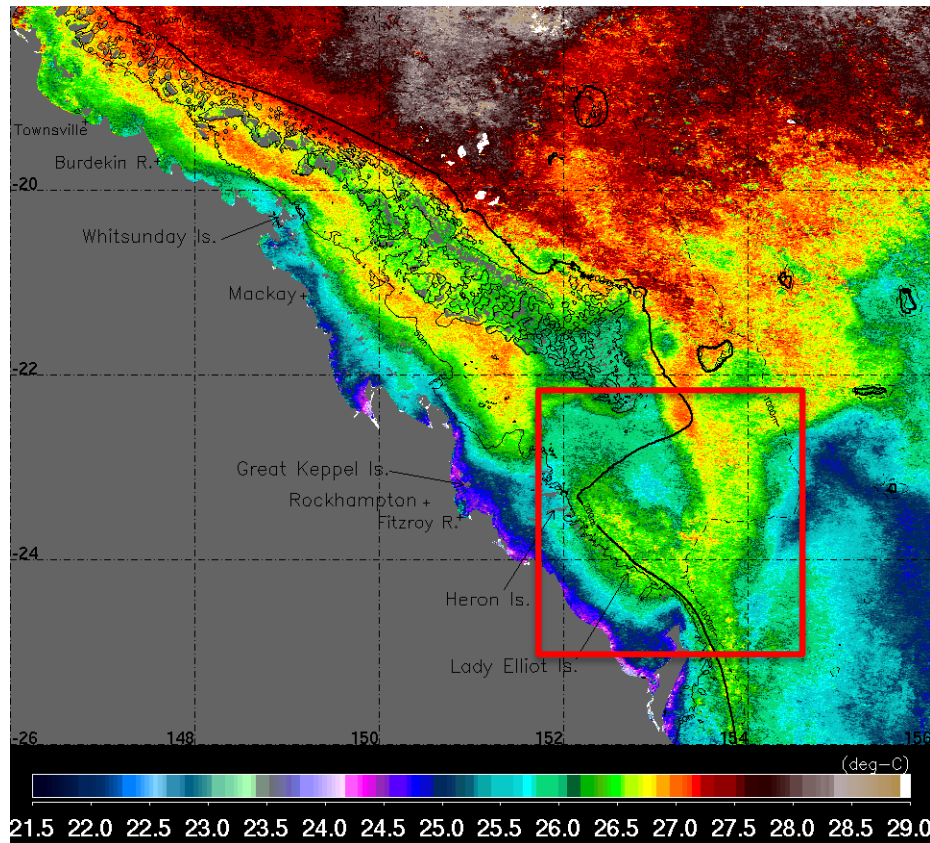
We identified a range of oceanographic parameters as important in defining foraging habitat within these regions, with the relative importance of particular variables differing between years and regions. In general, foraging activity was most strongly related to 'rates of change' in oceanic parameters rather than absolute values. For example, in all regions foraging was more likely to occur nearer to steep sea-surface temperature (SST) gradients. Positive foraging associations were also observed with lower than average SSTs at particular sites. As with at-distance foraging sites, in general foraging activity was not related to higher than average chlorophyll-a levels. Birds often foraged in areas having lower than average chlorophyll-a values. Importantly, in the inshore zone (1) we also saw a strong association between foraging activity and the location of secondary and tertiary freshwater plumes, as well as links with higher than average chlorophyll-a levels. These associations were not apparent in other regions.



**Figure 5.** Delineation of the five principal foraging regions used by southern GBR breeding wedge-tailed shearwaters when obtaining food to provision chicks overlaid on 2012 foraging kernel densities (as per Figure 4).

We have previously shown the influence of the ‘Capricorn Eddy’ on chick provisioning rates and meal sizes in wedge-tailed shearwaters independent of information on foraging site use (Weeks *et al.* 2013). Results from the tracking and oceanographic analyses presented here further confirm the importance of this phenomena in determining year to year variation in reproductive success of wedge-tailed shearwaters breeding in the southern GBR. Foraging areas 2-5 are all regions where the edge of the Capricorn eddy interacts with steep bathymetric change (figure 6). Therefore, these areas are likely upwelling zones or frontal convergence zones where cooler oceanic waters entrained in the eddy are brought into contact with the warmer shallower waters of the GBR lagoon; the intensity and scale of the eddy in any one season determining it’s likely influence on food availability.

Importantly, foraging area (1) is where oceanic waters from the Capricorn Eddy interact with freshwater river plumes carrying terrestrial inputs. High levels of foraging activity are clearly associated with the strong physiochemical gradients created by the convergence of these water bodies, suggesting significant enhancement of prey availability associated with these combined phenomena. These findings highlight the additional, and previously unrealised, importance of river dynamics and terrestrial inputs on year-to-year reproductive success.



**Figure 6.** Sea-surface temperature (SST) satellite image demonstrating the activity of the 'Capricorn Eddy' (enclosed within the red box) interacting with steep bathymetry along the continental shelf edge adjacent to the Capricorn-Bunker and Swains Reef regions in the southern GBR.

### ***Foraging at non-GBR shearwater colonies***

Examining the overlap between foraging grounds used by GBR breeding shearwaters and those at other colonies fringing the Coral Sea was begun after initial results indicated the extent of self-provisioning trips undertaken by adults. These comparisons were not an original component of the project. Consequently, final analyses defining core breeding and non-breeding foraging areas for non-GBR breeding wedge-tailed shearwaters and the overlap in habitat use by GBR and non-GBR breeding colonies are preliminary.

Current data suggest that at-distance foraging ranges for birds from Heron Island, Lord Howe Island and New Caledonian breeding colonies do not overlap significantly in the central or southern Coral Sea. This lack of overlap implies foraging resources accessed by each colony during breeding are distinct and that reproductive success at each location is independently determined by local oceanographic conditions. This finding also enables each colony to be used as a replicate in analyses examining the relationship between oceanography and foraging activity, thus substantially increasing our ability to generalize findings from the GBR to other systems. Confirmation of these findings and identification of oceanographic phenomena associated with the foraging areas of non-GBR colonies is ongoing.

On Lord Howe Island a combined data set for the entire 3.5-month chick-rearing period has been used to highlight the influence of the lunar cycle on food availability and provisioning rates at this breeding location.



## ***Overlap of foraging sites with commercial fisheries***

Shearwater foraging locations and activity at the intermediate and larger spatial scales significantly overlaps and potentially interacts with a number of important commercial fisheries.

- 1) The Western and Central Pacific Tuna Fishery, which provides some of the highest commercial tuna catch rates globally (GBR breeding colonies)
- 2) The Eastern (Australian) Billfish & Tuna Fishery (GBR breeding colonies)
- 3) The New Caledonia Tuna and Billfish fisheries (New Caledonia breeding colonies)
- 4) The (Australian) Small Pelagic Fishery (Lord Howe Island breeding colonies).
- 5) The Southern (Australian) Squid Jig Fishery (Lord Howe Island breeding colonies).

Associations with the first two of these fisheries have been demonstrated at low resolution using long-term multiyear catch data from these fisheries. Due to difficulty and subsequent delays in obtaining high-resolution fisheries catch per unit effort data more detailed quantification of overlap is ongoing.

Despite only low-resolution analyses being undertaken so far these findings raise significant previously undocumented conservation concerns for seabirds foraging in these waters. However, they also suggest that the data we are obtaining on prey dynamics can be used to aid predictions on the likely consequences of changing oceanography on prey availability to other top predators in these fisheries.

## ***Boobies***

This project aimed to establish core foraging areas used by two booby species at two locations; the Swains Reefs in the southern GBR and at Raine Island in the far northern GBR. Tracking of masked boobies in the Swains Reefs was undertaken consistently over three-years during the winter breeding period in July-August. In general, field trip logistic and weather constraints meant that sampling occurred over a short 5-7 day period.

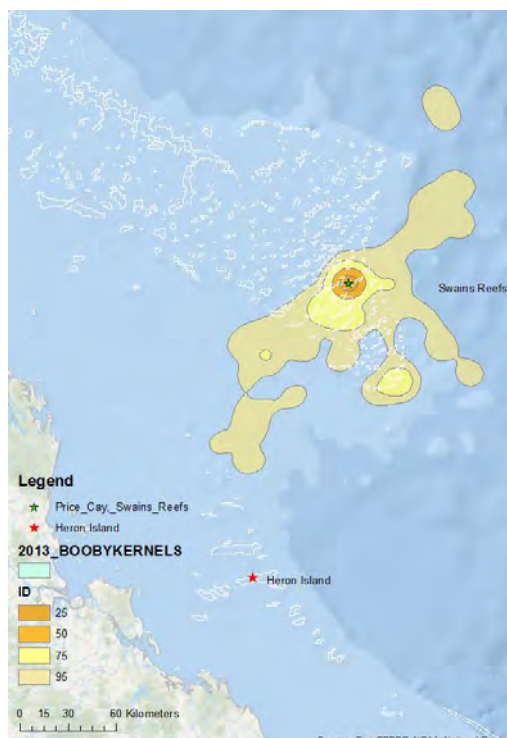
Tracking of brown boobies at Raine Island was hampered significantly by lack of access to the island in 2012 and 2013. A small number of tracks had been obtained prior to 2012 and access to the island in December 2014 allowed a significant number of new foraging tracks to be obtained over the ~10-day sampling period. Consequently, the analysis of brown booby foraging behaviour at this location is ongoing.

### ***Masked boobies - Swains Reefs***

In general, masked boobies provisioning chicks in the Swains Reefs undertake a single 6-8 hour foraging trip each day. Adults alternated, with one foraging from dawn to approximately mid-day and the second foraging from mid-day until dusk. All foraging trips occur within a ~150km radius of breeding colonies. Across 2012 to 2014, foraging activity was concentrated in two main areas; i) within inshore reef waters and along the associated continental slope, and ii) in the Capricorn Channel between the Capricorn and Swains Reefs (Figure 7).

Foraging locations used by masked boobies correspond to, and broadly overlap with foraging areas (3) and (4) used by wedge-tailed shearwaters breeding at Heron Island (Figure 4). Foraging site use by these two species is out of phase by ~6 months and each species is known to use different foraging techniques and to take prey of different types and sizes. Although prey type and densities likely change, consistent prey availability in these areas appears driven by the dynamics of the Capricorn Eddy and associated oceanographic phenomena, as described previously. Therefore, the observed overlap in foraging distribution between species highlights

the potential year round importance of these sites and the associated oceanographic phenomena for providing prey across a range of top-predators in this system.

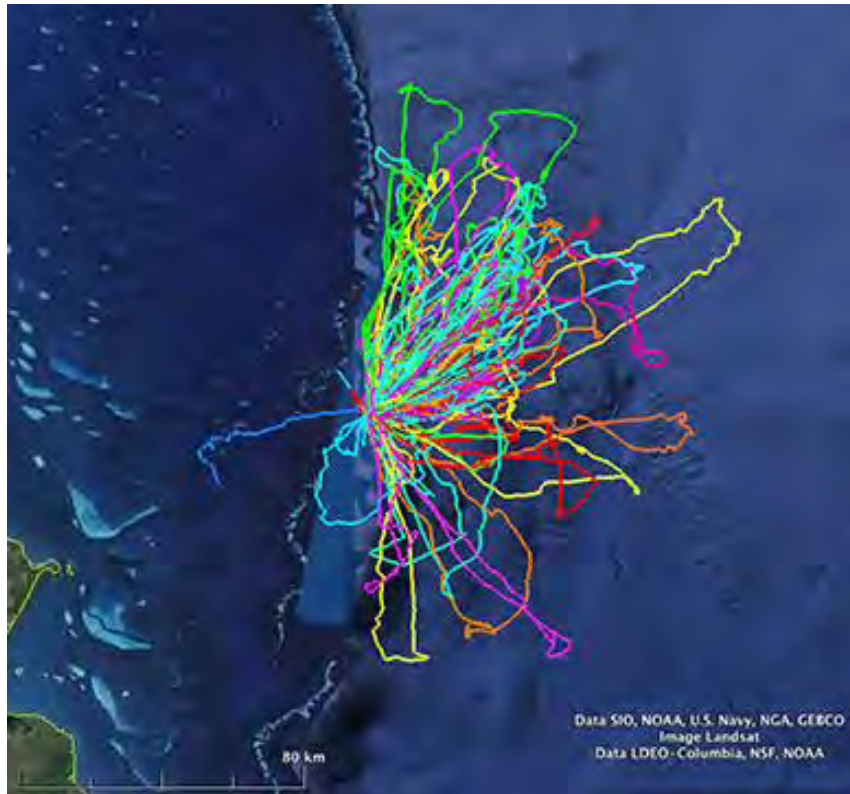


**Figure 7.** Example foraging Kernels for Swains Reefs (GBR) breeding masked boobies when provisioning chicks, generated from 2013 foraging tracks. Increasing levels of colour intensity represents foraging kernel densities of 99, 75, 50 & 25% UD's respectively, 25% UD being the smallest and most intensely used area. Note this kernel also includes within colony activity of tagged individuals at nest sites.

### ***Brown boobies - Raine Island & Bramble Cay***

Assess to Raine Island in December 2014 allowed a significant number of foraging tracks to be obtained, but an analysis of these tracks is ongoing. Example tracks are provided to demonstrate the current extent of observed foraging activity at this site (Figure 8).

These preliminary results suggest that the foraging behaviour of brown boobies at Raine Island is very similar to that of masked boobies in the Swains Reefs. All foraging occurred within a relatively short distance of the colony (~100-150 km), primarily over deep oceanic waters, rather than on the continental shelf in inter-reefal areas. Foraging activity was focused along the continental slope edge to the north, northeast and south of the colony in areas of steep bathymetric change (Figure 8). In general males and females undertook a single half-day foraging trip each day. Adults alternated, with one, usually the male, foraging from dawn to approximately mid-day and the second usually female foraging from mid-day until dusk. Analyses of the interactions of these tracks with significant oceanographic features in the region are on going.



**Figure 8.** Example foraging tracks for Raine Island (GBR) breeding brown boobies when provisioning chicks, December 2014

Breeding seabird populations were surveyed and mapped at Bramble Cay during a Torres Strait Regional Authority (TSRA) - James Cook University (JCU) collaborative field trip in November - December 2013. Given the ongoing logistic difficulties accessing Raine Island, Bramble Cay was assessed as an excellent potential alternative tracking location for brown boobies, with foraging birds potentially feeding in waters influenced by both oceanic waters at the continental shelf edge and the Fly River (PNG) flood plume.

Globally, the evidence of the significant negative impacts of plastics on seabird breeding success is increasing. Consequently, the quantity, distribution and use of plastics and other rubbish by nesting brown boobies at Bramble Cay was also mapped. The data we obtained at Bramble Cay suggest this is a high incidence site. These data are currently being incorporated into comparative analyses of the incidence of plastics in booby breeding colonies throughout the East Indian and Western Pacific Oceans.



**Figure 9.** Example of plastics in a breeding brown booby nest at Bramble Cay, Torres Strait.

## Changing Oceanography and adaptability

Previously for seabirds breeding in the southern GBR, we have quantified the influence of regional changes in sea-surface temperature (SST) on shearwater provisioning rates and meal sizes across multiple years (Smithers et al. 2003, Peck et al. 2004). We have also identified similar impacts of SST on prey availability to other species (Erwin & Congdon 2007, Devney et al. 2010). More recently we have quantified direct links between shearwater prey availability, SST and patterns of water stratification driven by the dynamics of the Capricorn Eddy during a single breeding season (Weeks et al. 2013). Additional analyses now demonstrate that the Capricorn Eddy influences prey availability to provisioning shearwaters similarly across multiple seasons. Direct links can be seen between incursions of cooler waters at depth in the Capricorn channel and changes to shearwater prey availability in multiple years. These results further highlight the significant role the Capricorn Eddy plays in mediating forage-fish dynamics in this system. They also provide a direct measure linking prey availability and chick growth/survival to oceanographic indices that can be used to identify potential tipping points in this system.

However, both the intensity and predictive power of the relationships change substantially between years. This highlights both the dynamic nature of these phenomena and the likely influence of other important driving factors. Further analyses provide the first quantitative evidence that freshwater flood plumes also influence shearwater foraging behaviour at a subset of foraging locations accessed by southern GBR breeding seabirds. This new understanding provides an opportunity to further improve the predictive power of current models linking prey availability and ocean dynamics by including more detailed river outflow data and associated measures of sediment and nutrients loads in these analyses.

In addition, the survival of chicks into the future is not just dependent on changing oceanography, but also on the ability of chicks to compensate for changes in prey availability via plasticity of growth patterns and/or the ability of adults to compensate by altered foraging behaviour. Previously the adaptability of chick development has been assessed for two species breeding on the southern GBR. Results demonstrate chicks have only a limited capacity to alter

growth patterns in response to rapid changes in food availability (Deveny *et al.* 2010, McDuire *et al.* 2013).

A detailed analysis of the ability of adult wedge-tailed shearwaters at Heron Island to compensate for rapid changes in food availability by altering foraging behaviour is now complete. Findings demonstrate that adults also have a limited capacity to respond to rapid changes in chick requirements or demands and that during periods of poor food availability adults preferentially maintain their own condition at the cost of chick growth and survival.

Combined, the lack of facultative response in both chick development and adult foraging behaviour highlights possible adaptive evolutionary links between these phenomena and patterns of local resource availability; implying they would be similarly unable to adjust to any rapid reductions in food availability as expected under existing climate-change scenarios. This would, lead to detrimental impacts on overall chick survival, colony reproductive output and long-term breeding success.

Overall, this project has quantified links between seabird reproductive success and oceanography in the GBR and greater Coral Sea region. Importantly, it has demonstrated the large-scale and dynamic nature of oceanic features that are important to these wide-ranging taxa. Thus, highlighting the need for future research that quantitatively assesses the relative effectiveness of traditional versus alternative Marine Protected Areas Design strategies at capturing and conserving these features.

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