Trans-equatorial migration and non-breeding habitat of tropical shearwaters: implications for modelling pelagic Important Bird Areas

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ABSTRACT: Declining prey availability drives many seabirds to migrate following breeding. While long-distance, latitudinal migrations are common in temperate-breeding species (including temperate-breeding Procellariiformes), regional dispersal or longitudinal migration is more common in tropical-breeding species. We used geolocators to track adult, tropical-breeding wedge-tailed shearwaters *Ardenna pacifica* from the Great Barrier Reef, Australia, through a ~6000 km migration to non-breeding grounds in Micronesia. This lengthy, trans-equatorial migration was similar to that undertaken by temperate-breeding Procellariiformes, but contrasted with patterns previously observed for tropical-breeding species. However, the oceanographic characteristics of tropical non-breeding habitats differed significantly from those of temperate sites. Core-use habitat had high sea-surface temperatures, very low wind speeds and low primary productivity, features normally associated with poor foraging habitat. However, activity was strongly linked to positive sea-level anomalies, indicating the presence of anti-cyclonic eddies at foraging sites. Such eddies are often associated with oceanic fronts and are known to aggregate micronekton and facilitate sub-surface predator feeding. Consequently, our 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 is the first tropical study to simultaneously assess the full set of oceanographic features considered important for modelling pelagic Important Bird Areas (IBA). Our findings demonstrate 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 framework for better predicting candidate Marine IBAs throughout tropical regions.

KEY WORDS: Overwinter · Tropical Procellariiform · Sea-level anomalies · Sub-surface predator · Electronic tracking · Marine Important Bird Areas (MIBAs) · Habitat modelling

INTRODUCTION

In the pelagic marine environment, prey availability is strongly influenced by oceanographic or other environmental factors and 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 temperate 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 under-

standing 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 shearwaters *Puffinus puffinus* and flesh-footed shearwaters *Ardenna carneipes* consistently use the same non-breeding locations over multiple years (Guilford et al. 2009, Reid et al. 2013). Populations of other species, such as Cory's shearwaters *Calonectris diomedea* and sooty shearwaters *Ardenna 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, 2006, Shaffer et al. 2006, Hedd et al. 2012). At the same time of year, productivity in the 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*, or Christmas shearwaters *Puffinus nativitatis*, which migrate longitudinally across the Pacific (Everett & Pitman 1993, Priddel et al. 2014). However, 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).

We know of only 2 previous tracking studies of tropical Procellariiformes that considered the physical oceanography of non-breeding foraging grounds.

Both were in the Indian Ocean and each has revealed species-specific non-breeding dispersal and/or migratory behaviour. They suggest that for tropical species, the mechanisms driving the choice of non-breeding foraging habitat differ to those driving the choice for 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 *Ardenna pacifica* that breed in the Seychelles disperse to various locations throughout the Central Indian Ocean basin, between 1000 and 3700 km from breeding colonies (Catry et al. 2009b).

Importantly, regardless of the pattern of dispersal or the distance travelled, in all non-breeding areas identified in these 2 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 with 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 to locations having high commercial catch of yellowfin tuna *Thunnus albacares* and skipjack tuna *Katsuwonus pelamis* (Catry et al. 2009b). Both are predatory tuna 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 these locations as critical foraging areas for tropical species.

Foraging associations between breeding seabirds and sub-surface predators have been observed for many species in tropical environments. This has led to these associations being considered more important in tropical than temperate systems (Au & Pitman 1986, Jaquemet et al. 2004, 2005, Weimerskirch et al. 2006). The 2 tracking studies (Catry et al. 2009b, Pinet et al. 2011) 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, where these shearwaters overwinter and the characteristics of their non-breeding habitat have, until now, remained unknown. Therefore, this study aimed to establish where wedge-tailed shearwaters of the southern GBR spend the 5 to 6 mo non-breeding period, to determine the physical oceanographic characteristics of these non-breeding foraging grounds, and to 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 characterized 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.

MATERIALS AND METHODS

Geolocator tracking

This study was conducted at Heron Island (23° 26′ S, 151° 51′ E), in the Capricorn and Bunker Group of islands of the southern Great Barrier Reef (GBR) Marine Park, Australia. To ascertain migratory routes and overwinter foraging locations, we deployed 30 British Antarctic Survey (BAS) MK19 (weight 2.5 g) global location sensing (GLS) loggers (Biotrack) on wedge-tailed shearwaters *Ardenna pacifica* that also carried 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 in order to identify the optimal parameters for obtaining accurate locations upon data download. However, for logistical reasons our 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, we completed a post-retrieval calibration (>5 d) at Heron Island in addition to the pre-deployment calibration.

Adult shearwaters were caught by hand on their return to the burrow at night or when they exited the nest. We optimized GLS device deployment and retrieval by selecting individuals known to have nested in the same burrow or area for >2 concurrent seasons. The GLS device 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 4.6 g, representing approximately 1.3% of the birds' weight. This is well below the recommended maximum weight for GLS device deployments (~3–5%; Kenward 2001).

Geolocators calculate geographic position via readings of ambient light that are used to estimate both local day-length (latitude) and to compare the timing of local midday to Greenwich Mean Time (longitude) (Wilson et al. 1992, Phillips et al. 2004). Ambient light level was measured and logged every minute and the maximum level recorded every 5 min. This provided an estimated latitude and longitude for each bird twice daily. The wet or dry status of the logger was sampled every 3 s and the internal temperature (representing sea temperature) was recorded if the logger was continuously wet for 25 min. A logger remaining dry at night indicates the bird may be on land or at the breeding colony, so we could derive departure and return dates to the colony from immersion data. This information coincided with position data retrieved from the loggers that showed clear and lengthy north and southbound migratory movements from, and returning to, the colony.

The GLS logger deployments did not deter the birds from returning to feed their chick on subsequent days, indicating no desertion as a result of handling or deployment. Furthermore, on retrieval of the loggers after 7 to 10 mo, we observed no injury to birds' legs, with the exception of 1 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).

GLS data analysis

Data were downloaded using BAStrak software Communicate and Decompressor. Light data curves were edited in the BASTra Transedit2 program, using a threshold setting of 16 and a sun elevation

correction of −3.5, based on the analysis of the calibration data. This process calculates the latitude and longitude position of the logger at noon and midnight GMT. During editing, all data points were individually assessed and 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 excluded (in accordance with 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, the 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 periods of heavy 'shading'. Therefore, data were excluded for a minimum of 10 to 15 d 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 at 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 a return to the colony. 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 devices proved to have malfunctioning temperature switches that made temperatures derived from logger readings unreliable.

Kernel analysis

Locations obtained from GLS data 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) where utilization distribution (UD) contours represent areas of use at different densities (25, 50, 75, 95%). We focused on the 95 and 50% kernel density contours, as they are generally considered to represent the maximum-use extent and core-

use areas, respectively, for foraging seabirds (Hamer et al. 2007). As wedge-tailed shearwaters of the Indian Ocean disperse to multiple core foraging locations in their non-breeding period, we also produced 50 and 95% UDs for all birds individually. This allowed us to visualize the overlap among individuals and to 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 we used the pooled data for analysis. KDEs and UDs were produced for 2 periods: (1) the entire non-breeding period (May–November), and (2) the Southern Hemisphere winter months only (June, July and August), so as to determine the core-use area without including migration (May and October–November) or the period of low logger accuracy (September).

All kernel analyses were performed in R v.3.0.3 (R Core Team 2013) using the 'adehabitat' LT (long term) and HR (home range) packages (Calenge 2006, 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.

Bird foraging and non-foraging areas

For our selected analyses (boosted regression, see 'Statistical analysis and modelling' below) it was necessary to compare oceanographic characteristics between places where birds were likely foraging and not foraging during the austral winter months (June–August). The likely 'foraging area' was defined as the core-use 50% kernel, as per Hamer et al. (2007). We then extracted this 50% kernel from the maximum-extent 95% kernel and classified the remaining area as 'non-foraging'. Wedge-tailed shearwaters did in fact occur in this 'non-foraging area', but in densities low enough to suggest that foraging activity was either unlikely or limited (Hamer et al. 2007). To obtain the comparative data set needed for the boosted regression analysis, we generated a random set of geographic sampling locations within the 'non-foraging area' equivalent to the number of observed GLS points in the corresponding core-use 50% kernel or 'foraging area'. Generating equal sample sizes for each of the binomial response outcomes in this way is thought to produce the most reliable results

and highest predictive accuracy from boosted regression analyses (Barbet Massin et al. 2012). The random 'non-foraging' sampling locations were generated in ArcGIS 10.2 for Desktop.

Oceanographic parameters

We extracted data for 7 environmental and oceanographic parameters (Table 1) from both the 'foraging' and 'non-foraging' areas. We used the parameters suggested by BirdLife International as those most appropriate for assessing and modelling 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, m s^{-1}), sea-surface temperatures (SST, °C), presence of seamounts, and chlorophyll *a* (chl *a*, mg m^{-3}). Data on these variables are readily available for the region.

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. We used monthly composite images for all parameters to minimise data loss resulting from cloud cover. The data for the 3 boreal summer months (winter months for shearwaters — June, July and August) were then combined into a single file.

Shearwater 'foraging' and 'non-foraging' locations were overlaid onto these oceanographic rasters and environmental/oceanographic predictor variable data extracted from the corresponding pixels by month for the period June, July and August. 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 data in any given pixel of a satellite image can be affected by light refraction, shallow water or the presence of land, so erroneous data points were identified, assessed and removed.

Statistical analysis and modelling

We used boosted regression trees (BRT) to evaluate the combined influence of environmental variables on the presence of foraging birds. BRT is a predictive modelling technique that is considered to have supe-

Table 1. Oceanographic variables, resolution and sources used in the environmental analyses of winter migratory foraging areas of wedge-tailed shearwaters *Ardenna pacifica* of the Great Barrier Reef (GBR)

Variable (abbrev.)	Unit	Description	Resolution	Data source
Sea-level anomaly (SLA)	mm	Mapped monthly mean sea-level anomaly; 0.25 × 0.25° resolution	0.25 × 0.25°	Ssalto/Duacs – DT MSLA, AVISO Satellite Altimetry Data (http://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/msla-uv.html)
Summary wind speed (Wind)	m s^{-1}	Monthly mean wind speed	1 × 1°	NOAA Aquarius Scatterometer L2_EVSCI_V1.3.5; NOAA Oceancolor Web (http://oceancolor.gsfc.nasa.gov)
Bathymetry (Bath)	m	Ocean bathymetry		NODC www.ngdc.noaa.gov
Sea surface salinity (SSS)	psu	Monthly mean sea-surface salinity	1 × 1°	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 temperature	4 km	Aquarius Sea Surface Temperatures (SST) 4 µ night time (http://oceandata.sci.gsfc.nasa.gov/search/file_search.cgi)
Distance to seamount (Distseam)	°	Distance to the nearest seamount		Undersea feature names (www.gebco.net/data_and_products/undersea_feature_names). Deep Reef Explorer high resolution depth model GBR/Coral Sea (Beaman 2010); (www.deepreef.org/projects). List of Pacific Seamounts; (www.ldeo.columbia.edu/~small/PacificSmts/). Seamount Biogeosciences Network Catalog (http://earthref.org/SC/)
[chl *a*]	mg m^{-3}	Monthly mean [chl *a*]	4 km	Aqua MODIS Chlorophyll *a* concentrations ([chl *a*]) (http://oceandata.sci.gsfc.nasa.gov/search/file_search.cgi)

rior predictive performance when compared with traditional regression models (Desalegn & Beierkuhnlein 2010, Oppel et al. 2012). BRT can cope with random and missing data, the potential for numerous interactions, numerous variables of different classes, including binomial response variables such as presence/absence (or core-use vs. maximum-use in the present case) and the sort of non-linear relationships that may be expected when investigating environmental variables in marine ecosystems (Elith et al. 2008, Elith & Leathwick 2013). Modelling was conducted in R v.3.0.3 (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).

The suite of environmental characteristics that best predict the response variable (foraging activity) is optimised 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). Once an optimal model is selected, variable interactions are queried and the most important factors identified by way of variable ranks (Elith et al. 2008, Elith & Leathwick 2013).

The minimum number of trees recommended to optimise these models is 1000 (Elith et al. 2008), so in the current analysis we used a step-wise approach, incrementally increasing by 50 trees to a maximum of 5000 (Ridgeway 2007), allowing the model to identify the optimal number of trees. We used a fast learning rate of 0.01, tree complexities of 7 and 5 (1 less than the total number of variables) and the Bernoulli (binomial) error distribution. Optimal model predictive performance is indicated by minimum CV (predictive cross-validation) deviance, and standard error. The best model is indicated by the highest 'area under the receiver operating characteristic (ROC) curve' (AUC) values (Fielding & Bell 1997, Elith et al. 2008). Partial dependence plots, that are used to visualise the influence of a variable after accounting for the average effects of all other variables in the model (Elith et al. 2008), were produced in R (R Core Team 2013) with the 'gbm.plot' and 'gbm.plot.fits' functions.

Models were run through a simplification process in R with 'gbm.simplify', analogous to backward selection in regression. This process drops non-informative predictor variables that degrade model performance, to produce the most parsimonious model (Elith et al. 2008). Although regression trees are quite resilient to highly correlated predictors, multicollinearity can confound the model's ability to identify the optimal set of explanatory variables (Ridgeway 2007, Elith et al. 2008, Elith & Leathwick 2013). Correlation was assessed with multicollinearity scatterplot matrices, correlation coefficients and Variance Inflation Factors (VIFs) in R using the 'car', 'usdm', 'MASS' and 'clusterGeneration' packages (Venables & Ripley 2002, Fox & Weisberg 2011, Naimi 2013, Qiu & Joe 2013) and conservative threshold values of 0.7 (correlation) and 4 (VIF) (Rogerson 2001, O'Brien 2007, Dormann et al. 2013). Spatial autocorrelation (SAC) can also affect model predictive performance (Crase et al. 2012). This was assessed with spline correlograms, using the 'ncf' package (Bjørnstad 2013) in R (R Core Team 2013) using moderate and generally acceptable values between approximately −0.3 to +0.3 (Cohen 1988). Finally, data in BRT must be cross-validated to optimise the model's predictive ability and estimate the optimal number of iterations. Geographic exclusion has been found to yield the most reliable results in BRT (Barbet Massin et al. 2012). Therefore, we divided our data into 3 geographic subsets for cross-validation in R using 'gbm. step'. BRT results presented are the CV (predictive) deviance and its standard error (±1 SE), AUC values, the factors of strongest influence and notable interactions.

RESULTS

Analyses and errors

Many of our GLS tracks showed considerable shading and data errors in late July and August 2012. The month of August is the main monsoon season in the northern hemisphere (Martinez et al. 1998, Qu & Lukas 2003). Consequently, these shading events may have been associated with an extreme storm event — Typhoon Hakui — which tracked through the area between 1 and 7 August 2012 (RSMC Tokyo 2012), causing heavy cloud cover. There were no excessively strong correlations (>0.70) or VIF values >4 in the analysis.

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. 1). KDE-UD of the entire migration (May–November) was used to visualise the broad movement patterns of the birds
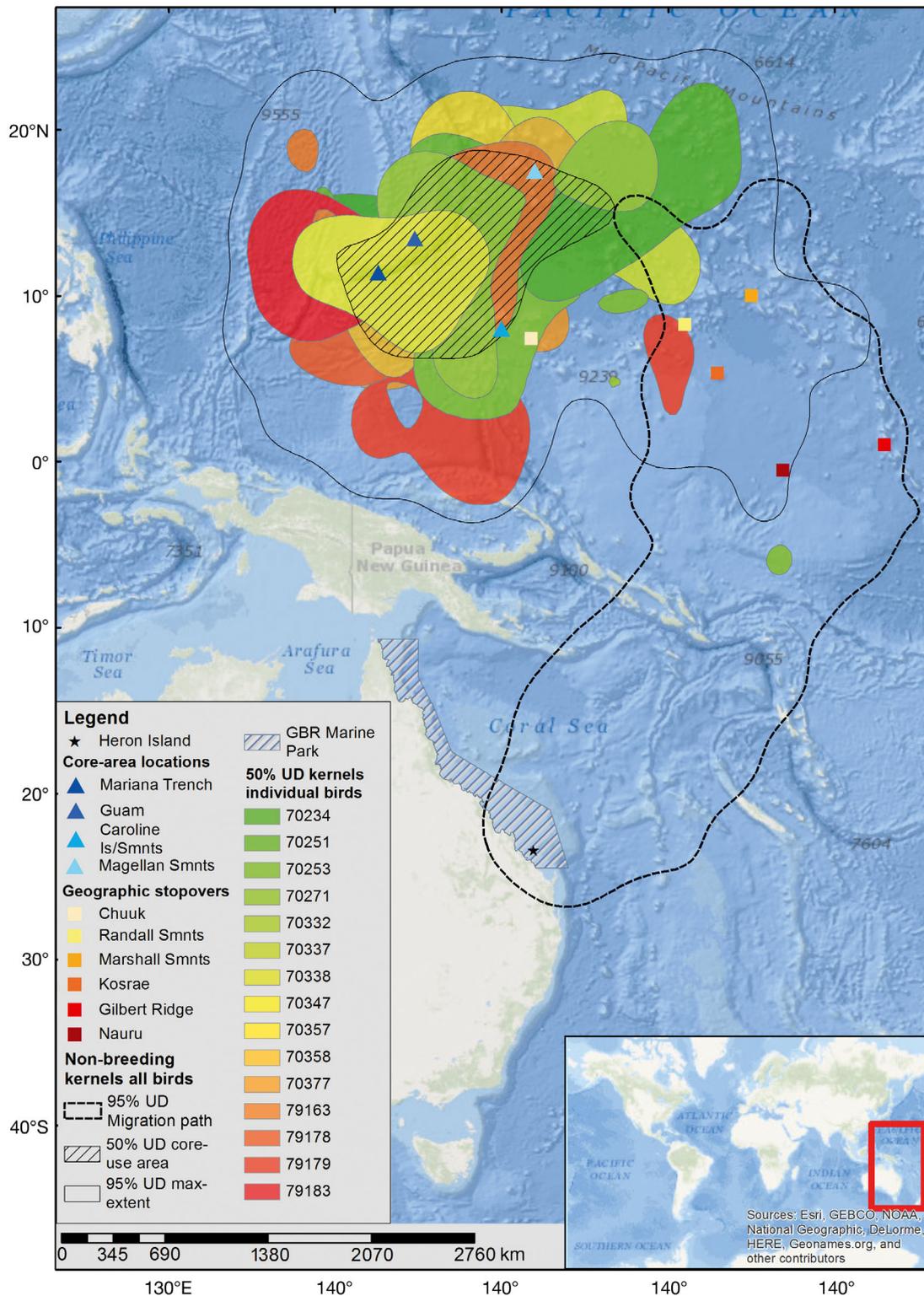
Fig. 1. Non-breeding season migration data for 15 adult wedge-tailed shearwaters *Ardenna pacifica* from Heron Island (★) on the Great Barrier Reef (GBR) tracked from May to October/November 2012. Core-use (50% utilization distribution [UD]) and maximum-use (95% UD) kernels for the winter months only (June through September) and the migration pathway kernel (95% UD — used during May, June, September, October and November) for all birds are indicated. Core-use kernels (50% UD) for each of the 15 birds are shown by orange and green shades. Geographic stopovers and core-area locations are shown by coloured squares and triangles, respectively

Table 2. Summary of Heron Island wedge-tailed shearwater winter non-breeding migration data in 2012. Timing and duration of overwinter migration, outbound migration and time spent in the core (50%) areas. *Values uncertain or unknown due to equinox data loss (see 'Materials and methods: GLS data analysis')

Bird ID	Date of departure from Heron Is.	Date of return to Heron Is.	Migration duration (d)	Date of arrival in 50% core-use area	Duration from colony to core-use area (d)	Time spent in core-use area (d)
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	21 May	29 Oct	161.9	11 Jun	21.5	117.6
± SE	1.1	2.5	2.1	3.4	2.9	10.8

throughout the non-breeding period (1392 locations). Further KDE-UD were produced for the migration pathway and the winter months (June, July and August) (Fig. 1).

Wedge-tailed shearwaters remained within the tropics during the non-breeding period. They conducted a northwards migration from Heron Island in the southern GBR, to non-breeding grounds in the area of the Caroline Islands and associated with seamounts in the Federated States of Micronesia, the Magellan Seamounts and the Mariana Trench. The migration crossed the equator and exceeded a distance of 6000 km. The area of maximum-use (the 95% kernel) and the core-use area (50% kernel bound by ~140°E–160°E and 7°N–20°N) were centred on and to the southeast of the Mariana Trench over latitude 12°N and longitude 148°E. Combined, they covered an area of approximately 2500 × 1600 km. The average duration of the entire non-breeding period away from Heron Island was 161.9 (152–178) d.

Wedge-tailed shearwaters showed striking temporal consistency of departure from the breeding colony (Table 2) with most individuals departing the colony within a 7 d period beginning May 16. Only 2 individuals departed after May 22. There was an average outbound migration length of 21.5 d (range 14–53 d) to reach the core-use non-breeding area. Initially birds moved in a northeasterly 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 to 19 d to arrive in core-use non-breeding areas (50% kernel; Table 2).

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, causing 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.

Stopovers

Most birds migrated relatively continuously and reached core-use non-breeding grounds in less than 20 d (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 (Federated States of Micronesia) were important 'stopover' destinations, with all but 2 individuals spending time

Table 3. Environmental predictor variables (see Table 1), their measured range and mean ± SE for core-use and maximum-use areas, and the relative influence (rel. infl.) on the final, simplified boosted regression model of shearwater presence in the over-winter foraging grounds

| Variable | Core-use area | | Maximum-use area | | Rel. infl. |
	Mean ± SE	Range	Mean ± SE	Range	(%)
SLA (mm)	1551 ± 314	749 to 2079	877 ± 771	−1759 to 2642	46.6
Wind (m s^{-1})	5.0 ± 0.5	4.0 to 6.4	5.3 ± 0.9	3.5 to 7.3	15.2
Bath (m)	−4558 ± 6 43	−214 to −9174	−4319 ± 1118	−278 to −6625	10.5
SSS (psu)	34.4 ± 0.2	33.9 to 34.9	34.5 ± 0.4	33.7 to 35.6	9.1
SST (°C)	29.0 ± 0.2	28.0 to 29.5	28.8 ± 0.3	27.7 to 29.5	8.5
Distseam (°)	0.35 ± 0.30	0 to 1.78	0.67 ± 0.71	0 to 3.36	6.1
[Chl a] (mg m^{-3})	0.026 ± 0.010	0.005 to 0.090	0.040 ± 0.030	0.008 to 0.160	4.0

in these locations prior to reaching the 50% core-use area. This highlights some temporal inconsistency among individual migratory patterns. The 3 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.

Non-breeding core-use area

Most birds spent the greater portion of their time during the non-breeding period in the 50% kernel, mostly during the months of June, July and August. The 50% 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. 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 we began to lose tracking accuracy in early to mid-August, and were still there when it was regained in early October.

Oceanography of winter core-use area

We analysed the influence of a set of explanatory oceanographic variables (Table 3), on bird foraging (n = 568) and non-foraging (n = 568) locations. The CV deviance of the BRT model was 0.40 ± 0.01 (mean ± SE) and resulted in a high AUC value of 0.98 using 1550 trees (Fig. 2). Model simplification retained all variables in the model. When circles occur at the top of the probability graphs (value = 1, Fig. 2b), it indi-

cates foraging birds are more likely to occur at those specific values of that factor and conversely, where circles occur at the bottom (value = 0), foraging birds are not predicted to occur at those values.

The strongest determinant of occurrence of shearwaters in the core-use (foraging) area was sea-level anomalies (SLA). The mean SLA in the core-use area was considerably higher than that in the 95–50% maximum-use (non-foraging) area (Table 3, Fig. 2). Further, the birds used only areas with positive SLAs between 1000 and 2000 mm, which was a narrow subset of those available to them during the non-breeding months (Fig. 3).

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

The ocean depth of the region was also an important predictor 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 3). Furthermore, birds were always most likely to occur over the greatest depths (>6000 m; Fig. 2), and were often found in association with intermediate depths (4000–6000 m; Fig. 2).

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).

Absolute sea-surface temperatures (SSTs) were relatively unimportant in the model but were gener-
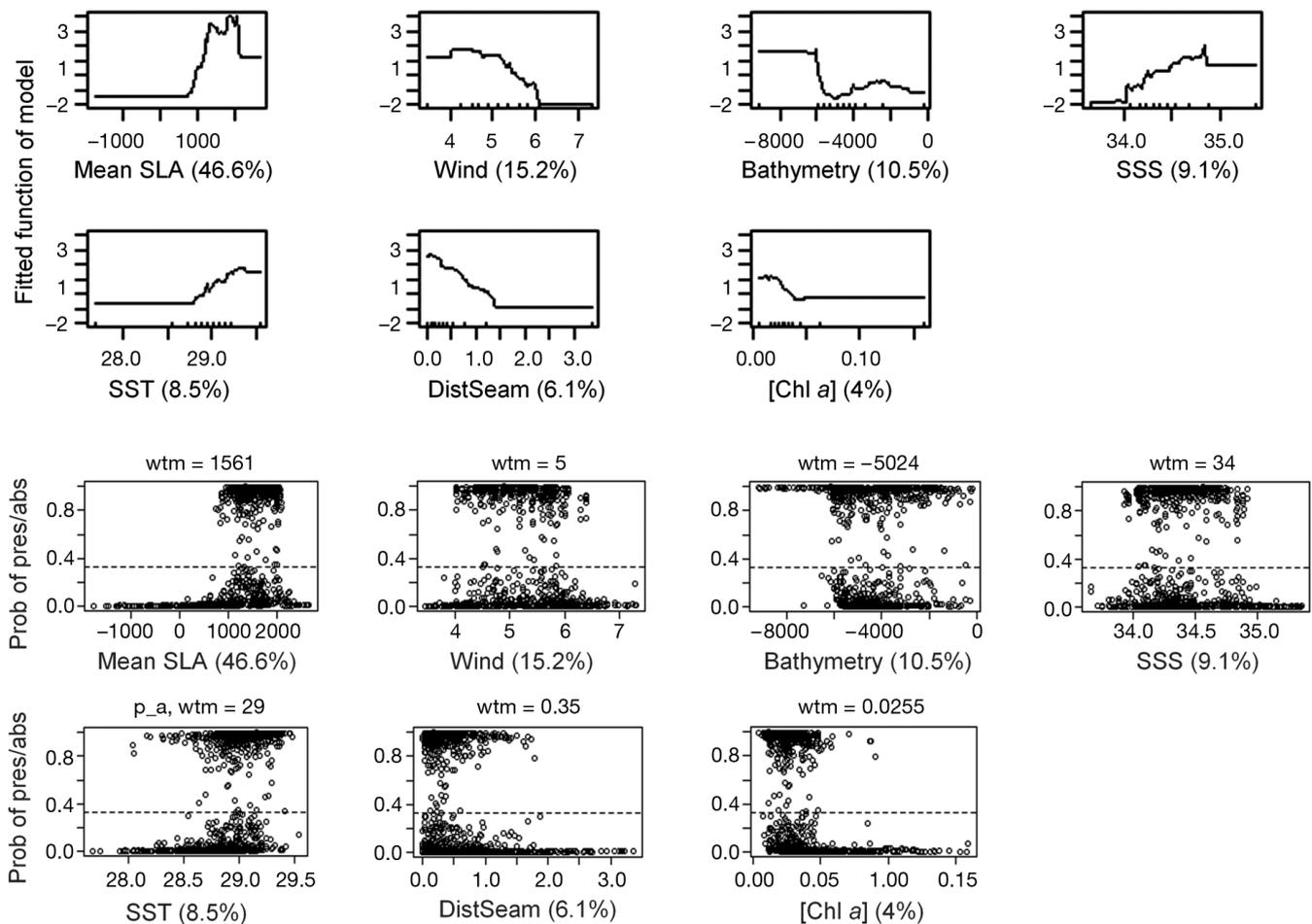
Fig. 2. Boosted regression tree (BRT) model results of influential oceanographic parameters in wedge-tailed shearwater non-breeding foraging areas. (a) Partial dependence plots show the relative influence of each factor on the activity of birds (core-use area in which birds are more likely to be foraging versus maximum-use area where birds are most likely transiting) after accounting for the influence of all other factors (fitted functions of the model range from −2, which is the 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 more information on the variables, see Table 1. (b) Fitted Value (FV) plots 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. Occurrences above the dotted horizontal line, which represents the algorithm threshold (0.35), are considered 'foraging'. The weighted means (wtm) of each are indicated at the top of the plots. SLA: sea-level anomaly; SSS: sea-surface salinity; SST: sea-surface temperature; DistSeam: distance to seamount

ally high across the total region, with minimal variation (27.7–29.5°C; Table 3). However, shearwaters were never predicted to occur at high densities in water below ~28.3°C (Fig. 2).

While primary productivity ([chl a]) had the weakest influence on the model overall, the core-use non-breeding area was characterised by very low primary productivity compared with the maximum-use area (Table 3, Fig. 2). Across the range of values, foraging shearwaters were most likely to occur at the lowest, below 0.05 mg chl a m^{-3} (Fig. 2). In addition, wedge-tailed shearwaters were not predicted to occur in regions where [chl a] values were consistently high

(>0.1 mg chl a m^{-3}). Nevertheless, the low level of influence of this variable in the model means this factor does not contribute to explaining the increased occurrence of shearwaters in core-use areas.

Seamounts are prolific throughout the entire non-breeding region, and while proximity to seamounts had a negligible influence on the model, birds were nevertheless always predicted to be considerably nearer to seamounts in the core-use than maximum-use area (Table 3). In the core-use area most birds were <1° from seamounts and were never predicted to be >2° away (Fig. 2). Nevertheless, because the average distance to seamounts in the maximum-use
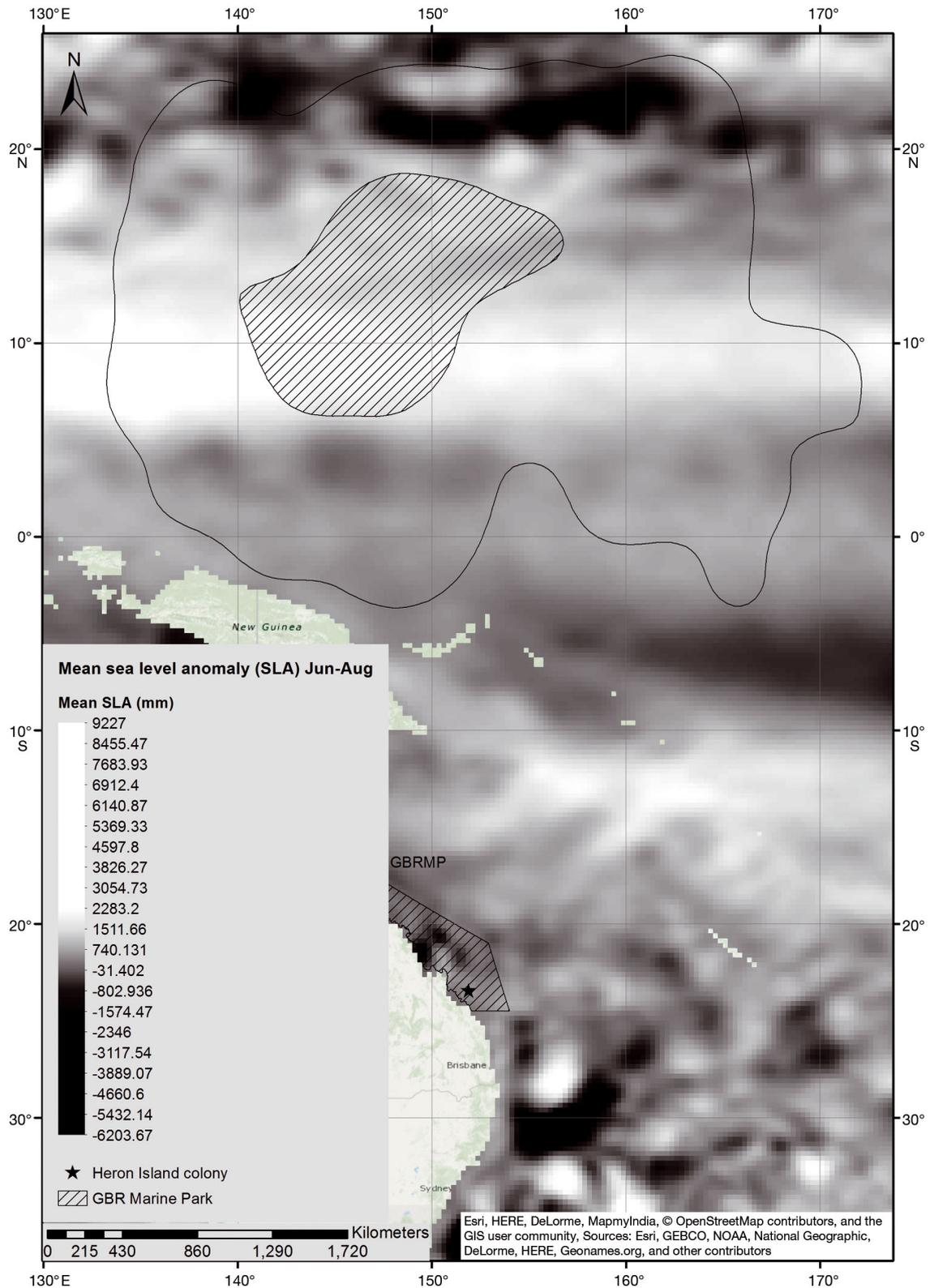
Fig. 3. Mean sea level anomaly (SLA) map of the wedge-tailed shearwater non-breeding region showing the mean SLA of the winter months (June to August) overlaid with core-use and maximum-use winter kernels. The lighter shades within the core-use area are indicative of the moderately positive SLAs (~1000–2000 mm) that occur in the region where shearwaters are more likely to be foraging

region was also relatively small (Table 3), this factor had little predictive power.

In interpreting these BRT models it is also important to consider pairwise interactions (Elith et al. 2008). Only 2 such interactions were observed in the model. The first one was a strong interaction between SLA and bathymetry that showed increasing bird activity predicted over very deep bathymetry (>6000 m) at SLA of 1000 to 2000 mm. SLA also strongly interacted with wind speeds in this model where the occurrence of birds at 1500 to 2000 mm SLA mostly occurred at wind speeds of 3 to 5 m s^{-1}.

DISCUSSION

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, *Pterodroma leucoptera caledonica*. However, rather than migrating northward, this population moves to the Eastern Tropical Pacific, dispersing to multiple core-use foraging areas which are in fact, primarily south of the Equator (Priddel et al. 2014).

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 ele-

vated [chl a] levels, wedge-tailed shearwater wintering areas were typically characterised by very low primary productivity. Importantly, the non-breeding distribution of this species could not be predicted using indices of primary production.

Similarly, other factors known to influence tropical species non-breeding distributions, such as consistent strong prevailing winds (Pinet et al. 2011), were not found to be important in our study. Instead, wind speeds in wedge-tailed shearwater non-breeding habitat were very low (4–6 m s^{-1}; 7.7–11 knots) with non-breeding areas being located in the Inter-Tropical Convergence Zone (ITCZ or 'the doldrums') (Soloviev & Lukas 1997) where there is a weakening of regional prevailing winds (Wyrtki & Meyers 1976, Philander et al. 1987). Therefore, unlike Barau's petrel (Pinet et al. 2011), it is unlikely that strong winds contribute significantly to wedge-tailed shearwater prey availability.

The parameter that exerted the strongest influence over the distribution of wedge-tailed shearwaters in the present study was 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). From the distribution of positive SLAs through time it can be seen that anticyclonic mesoscale eddies 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 (<500 or >3000 mm 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 presence of shearwaters in core-use non-breeding areas.

Currently, precisely what oceanic processes concentrate prey at the edges of eddies is unclear (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), but elevated productivity was a poor predictor of habitat use in our model. However, satellites only perceive [chl *a*] at the surface and currently the role of sub-surface productivity in stratified environments is not clearly understood. For example, *in situ* sampling has shown that significant primary productivity at the thermocline can be associated with nutrient depleted surface layers (Herbland et al. 1983). This phenomenon, called the Typical Tropical Structure (TTS; Herbland et al. 1983), 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 uncoupling between measures of primary production ([chl *a*]) and the biomass of species at higher trophic levels, such as micronekton, may also 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 (Lehodey et al. 1998). 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 (low [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).

Association with sub-surface predators

Despite performing a trans-equatorial migration, in general, the oceanographic characteristics of core-use 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-use 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 facilitated foraging with sub-surface predators may be important to the overwinter 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 is 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).

CONCLUSIONS

This study identifies the non–breeding foraging areas that are important to migratory wedge-tailed shearwaters of the GBR. In addition, we 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. We see clear and strong associations with moderate positive SLAs linked to 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.

Furthermore, being the first study of a tropical system to simultaneously assess the full set of oceanographic features considered important for modelling pelagic Important Bird Areas (IBAs) (BirdLife International 2011), our findings have implications for tropical seabird conservation and management. They suggest that IBA modelling in the tropics should extend beyond standard indices of productivity and highlight the importance of including measures of oceanographic or eddy and frontal dynamics and assessments of sub-surface predator interactions. Consequently, this study provides a basis for improving the identification and management of candidate Marine IBAs throughout tropical regions.

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