

Oceanographic drivers of near-colony seabird foraging site use in tropical marine systems

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ABSTRACT: Wedge-tailed shearwaters of Australia's southern Great Barrier Reef (GBR), obtain food for their chicks on short trips adjacent to the breeding colony. GPS tracking (from February to April in 2013 and 2014) indicated that most trips were of 1 d duration (70 to 85 %) and that all were within 300 km of the colony. Oceanographic characteristics of foraging and non-foraging areas were compared to identify mechanisms driving prey availability. Foraging generally occurred adjacent to the Capricorn Shelf, where the largest oceanographic feature in the region, the Capricorn Eddy, creates increased frontal activity and upwellings. Shearwaters consistently revisited 4 bathymetrically and topographically distinct foraging zones influenced by this mesoscale eddy. In 2013, strong sea surface temperature (SST) fronts associated with relatively intense eddy activity influenced foraging activity in all foraging zones. In 2014 the dominant oceanographic factors influencing foraging were SST and chlorophyll *a* concentration ([chl *a*]) or their anomalies. However, these influences varied among zones, suggesting a weakened effect of the eddy and elevated importance of fine-scale phenomena such as localised upwellings. Foraging in the coastal foraging zone was also significantly influenced by terrestrial inputs: specifically, birds foraged in association with freshwater flood plumes with higher [chl *a*]. The oceanographic mechanisms underlying prey availability to shearwaters in this system are tightly linked to variations in climatic conditions. Consequently, predicted changes associated with climate change, such as increased frequency or severity of El Niño events, are likely to seriously diminish the profitability of identified foraging locations and the reproductive output of impacted colonies. Currently, most identified foraging areas are without specific management or protection status.

KEY WORDS: Seabird foraging · Trophic relationships · Capricorn Eddy · Terrestrial run-off · Chick provisioning · GPS tracking · Oceanographic characteristics · Wedge-tailed shearwater · *Ardenna pacifica*

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INTRODUCTION

When breeding, seabirds are 'central-place' foragers (Orians & Pearson 1979) that must return to the colony at regular intervals to feed chicks. This requirement constrains the area in which they can obtain food (Lack 1954, Ashmole 1963, Weimerskirch et al. 1994, Weimerskirch 1998). As a consequence, reproductive success and viability of seabird colonies

can be totally dependent on the continued stability and productivity of a small number of near-colony foraging grounds.

Management and conservation initiatives (e.g. marine protected areas) seeking to protect foraging grounds are often applied to relatively large areas of ocean surrounding colonies. However, from a conservation and management perspective, it may not be sufficient or appropriate to focus on areas that have

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not been unambiguously identified as important foraging locations. Instead, specific identifiable areas characterised by explicit oceanographic processes may be appropriate targets for protection and/or management. Therefore, to enable the development of higher-resolution, more effective management options it is important to identify both the particular areas that are most frequented by foraging birds and the oceanographic conditions that characterise these areas.

In temperate and sub-polar systems, foraging areas close to breeding colonies are generally characterised by enhanced primary productivity, as shown, for example, by studies of Cory's shearwaters *Calonectris diomedea diomedea* (Cecere et al. 2013b) and black-browed albatrosses *Thalassarche melanophrys* (Cherel & 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. 2006). These same phenomena are also strongly related to ocean temperature and temperature gradients (Becker & Beissinger 2003, Ainley et al. 2005), that are in turn linked to larger oceanic features such as the Antarctic Convergence, or the Kuroshio Current (King 1974, Brown et al. 1975, Croxall & Prince 1980).

Highly stable and predictable large-scale currents similar to those that influence prey availability in temperate systems (Croxall & Prince 1980, Shaffer et al. 2009) also circulate throughout the tropics. However, in tropical regions, documented links between seabird foraging, prey availability and these large-scale phenomena are much less common (Ashmole 1971, Ainley & Boekelheide 1984, Ballance et al. 2006). Instead, tropical seabirds primarily forage in association with smaller-scale frontal systems, eddies and upwellings (Le Corre 2001, Weimerskirch et al. 2004, Tew Kai et al. 2009, Cecere et al. 2013a; but see Rayner et al. 2016). Therefore, while drivers of foraging activity at some tropical locations appear to be similar to those seen in temperate zones (Baduini 2002, Jaquemet et al. 2007, Cecere et al. 2013a), in other areas they often differ in important ways (Weimerskirch et al. 2004, 2010, Sabarros et al. 2009).

Australia's Great Barrier Reef (GBR) is not known for high levels of productivity associated with larger-scale fronts or upwellings (Kleypas & Burrage 1994, Burrage et al. 1996, Brinkman et al. 2002). However, the distinctive topography of the region produces a range of smaller, less stable, and unpredictable oceanographic effects that enhance productivity at local

scales (Burrage et al. 1996, Brinkman et al. 2002, Choukroun et al. 2010). Specific changes in these phenomena have also been shown to negatively impact food availability to seabirds breeding on the GBR (Smithers et al. 2003, Peck et al. 2004).

The Capricorn Eddy is a mesoscale oceanographic structure in the southern GBR, the position and intensity of which is primarily driven by the speed and strength of the East Australian Current (EAC); which in turn varies under different El Niño Southern Oscillation (ENSO) conditions (Weeks et al. 2010). The activity of the Capricorn Eddy has demonstrated links to both fine-scale temperature variation and short-term food availability to foraging shearwaters (Weeks et al. 2010, 2013). This suggests it is a local-scale phenomenon capable of significantly influencing the longer-term reproductive success of seabirds in the region. However, the currently documented links have only been observed over a single breeding season (Weeks et al. 2013). Importantly, it is not known if shearwaters actually forage in association with this eddy, or are impacted by oceanographic processes generated by it that affect prey availability.

Wedge-tailed shearwaters *Ardenna pacifica* that breed in the southern GBR use a dual foraging strategy (Congdon et al. 2005). Long foraging trips allow adults to reach distant foraging grounds for self-provisioning, while shorter trips are used to obtain food for chicks (McDuie et al. 2015). Consequently, food availability at short-trip foraging locations is critical to chick survival and overall reproductive success. By definition, short trips must necessarily be nearer the colony and are likely to be within a maximum radius of 300 km (McDuie et al. 2015). Therefore, short-trip foraging sites have the potential to be directly associated with the location and intensity of oceanographic features generated by the Capricorn Eddy.

Through the use of high-resolution GPS tracking this study aimed to identify the near-colony foraging grounds used for chick provisioning by wedge-tailed shearwaters of the southern GBR and establish the oceanographic characteristics influencing foraging site choice and intensity of use. Specifically, we aimed to determine whether shearwaters forage in direct association with the Capricorn Eddy. We examined a comprehensive set of oceanographic parameters in order to accurately characterise foraging grounds. Our investigation focused on parameters that have been considered in previous research of tropical systems, such as chlorophyll *a* concentrations ([chl *a*]), sea surface temperature (SST) and bathymetry, as well as additional parameters specifically selected to highlight the presence of fine and meso-

scale ocean dynamics (e.g. SST and [chl a] anomalies) (Oschlies & Garçon 1998, Palacios et al. 2006). Consequently, we were able to (1) identify the optimal set of oceanographic factors defining near-colony foraging grounds, for comparison with other tropical and temperate studies; (2) develop best practice for accurately identifying the oceanographic phenomena that are most important for augmenting prey availability to tropical seabirds in general; and (3) generate a model of the trophic mechanisms influencing near-colony food availability to seabirds of the Southern GBR that forage in mixed species flocks in association with wedge-tailed shearwaters.

MATERIALS AND METHODS

Study site and population monitoring

Tracking in this study targeted the near-colony foraging trips of wedge-tailed shearwaters breeding on Heron Island in the southern GBR, Australia (Congdon et al. 2005). Field work was conducted in the months of February and April in 2013 and 2014. Monitoring, trapping, and handling protocols followed those detailed in McDuie & Congdon (2016). In 2013 we monitored 86 nests (66 tracked and 20 controls) and in 2014, 30 nests (20 tracked, 10 controls). At control nests, adult birds were not handled, but chick meal masses were monitored in order to test for any effects of GPS logger deployment on patterns of adult provisioning.

Electronic tracking

Electronic archival GPS devices were deployed on chick-rearing adult wedge-tailed shearwaters during short, chick-provisioning trips, defined as <4 d (Congdon et al. 2005). All trips <4 d are included in the current analyses, although the majority of the trips observed were only 1 to 2 d. Devices were mounted at the base of an adult's tail on 3 feathers

with a single strip of Tesa™ tape (Beiersdorf). Temporary tail mounting was used as it considerably reduces disturbance to birds compared with back mounting, and allows 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.

Tracking data were acquired using modified, battery powered iGot-U™ GT-120 (Mobile Action Technology) GPS tracking devices (weight 10.2 g, dimensions ~44 × 22 × 5 mm after modification). Modification included reducing battery size (90 to 120 mA) and repackaging in 50 mm clear heat shrink wrapping (Finishrink™), to produce a slim, waterproof profile that reduced in-flight drag (Culik et al. 1994). Repackaging reduced weight such that it fell within the accepted limit (3 % of body weight) for device deployment on seabirds; devices were deployed only on adults weighing greater than 380 g (Kenward 2001, Phillips et al. 2003). GPS were set to record position fixes every 3 or 5 min (depending on individual battery life as determined during pre-season testing, giving 4 to 6 d total tracking), between 04:00 h and 20:00 h, which corresponds to the approximate colony departure and return times for most birds. GPS location accuracy is high (~4 to 50 m) and frequent location fixes provide very accurate flight path information.

In 2013, GPS devices were successfully deployed on 78 adult shearwaters. Of these, 18 remained away on long trips (McDuie et al. 2015), 8 produced no data or were lost and the remaining 52 provided data on 79 individual short trips (Table 1). In 2014, 33 shearwaters were tracked, producing data on 34 individual short trips. No retrieved logger failed to provide data. Some individuals were tracked on multiple sequential short trips during a single deployment; these

Table 1. GPS deployment data for wedge-tailed shearwaters breeding on Heron Island in the southern Great Barrier Reef (GBR) tracked on foraging trips in 2013 and 2014. The number of tracked individuals making short trips is indicated in parentheses. 'No data' indicates logger failure or loss

Year	No. of birds	Short trips	Long trips	No data	No. of locations		
					Fixed	Foraging	Non-foraging
2013	78	79 (52)	18	8	9355	4015	5340
2014	38	34 (33)	0	4	3572	1947	1625

trips may not be statistically independent. Therefore, all trips were mapped and visually assessed in Google Earth to determine if any individuals visited the same foraging locations on multiple trips, thereby biasing the data to specific locations. Only 20 birds in total (2013 to 14) were tracked on multiple trips (19 in 2013 and 1 in 2014). Of these, none foraged along the same tracks or visited the same location on consecutive trips and no foraging locations, identified by area restricted search (ARS) locations (see below), were within 6 to 11 km of one another. Therefore, all 79 individual short trips were retained for the analyses with individual as a random factor, preserving a more robust sample size.

Identifying foraging and non-foraging activity

Foraging and non-foraging locations in the data obtained from iGot-U™ devices in 2013 and 2014, were classified at the smallest scale possible. Foraging locations were identified by running the tracks through first passage time (FPT) analyses and identifying ARS locations (Fauchald & Tveraa 2003, Pinaud & Weimerskirch 2007). ARS zones are a standard measure used to indicate an animal's foraging response to increases in prey density (Kareiva & Odell 1987, Sommerfeld et al. 2013).

To prepare data for this analysis tracks were filtered by velocity, with all points exhibiting speeds greater than 75 km h^{-1} removed as likely to be erroneous positions (based on wedge-tailed shearwater average flight speeds; F. McDuie & B. Congdon unpubl. data). Tracks were interpolated at 10 min intervals to obtain equal time periods between fixes and to account for any gaps due to missing fixes. No interpolation was done where points were greater than 1 h apart. Filtering and analyses were conducted in R 3.03 (R Core Team 2013), using the 'adehabitatLT' package (Calenge 2006). Eleven individuals were tracked on >1 short trip (total of 27 trips). These tracks were split into individual short trips by determining if birds returned to, or approached within 20 km of the colony, with their chick subsequently being fed. This procedure was followed because on occasion, birds which returned late were not observed returning all the way to the colony due to loggers switching off at between 20:00 and 21:00 h.

We used radii for FPT from 1 to 80 km in increments of 1 km to find the peak in the (log) variance, which represents the ARS scale for that individual (Fauchald & Tveraa 2003). Every location along each foraging track was allocated an ARS value of either

true (1) or false (0) to denote foraging or non-foraging, the binomial response variable used in the modelling. FPT can be inaccurate if resting periods cannot be distinguished from foraging (Sommerfeld et al. 2013), so following FPT categorization, tracks were visually assessed for periods of very low movement. Points tracking very close together in a straight line were defined as surface resting and categorized as non-foraging.

Oceanographic parameters and rationale

Once the status (foraging or non-foraging) of each GPS fix on each foraging track had been defined, the corresponding values for a set of oceanographic variables were extracted for each. Raw oceanographic data, with the exception of distance parameters, were obtained as monthly climatologies from high resolution satellite imagery at 1.5 (www.gpem.uq.edu.au/oceanography) or 4 km (SST/[chl a] variables) resolution (Table 2).

The complete set of oceanographic parameters used in this study were specifically selected for their capacity to accurately and comprehensively characterise the marine environment within foraging sites. In particular, the values for SST gradients (hereafter 'fronts'), and SST and [chl a] anomalies, can reveal the presence, location and strength of oceanographic features like eddies, upwellings or oceanic fronts (Garvine 1974, Oschlies & Garçon 1998). The Aqua MODIS SST and [chl a] data (3 d and monthly means for absolute and anomalous values) were assessed. Anomalies indicate the difference between monthly and long-term (2002 to 2012) climatologies. Contours at intervals of 0.02°C of change in SST ($^\circ\text{C km}^{-1}$ horizontal distance) were created for the strongest SST gradients (the upper 25% of SST frontal values; $>0.21^\circ\text{C km}^{-1}$), which indicate the presence of oceanic fronts (Moore et al. 1999)

Bathymetry and specific topographic features such as steep slopes, reefs and islands were also identified as they are likely to influence seabird prey availability (Hyrenbach et al. 2002, Yen et al. 2004, Palacios et al. 2006, Morato et al. 2008, McDuie & Congdon 2016). Etopo 1 Ice surface bathymetry data set was used with change of depth (m km^{-1}) calculated to represent the bathymetric gradient or slope. Subsequently, contours were created at 100 m intervals to identify the areas of steepest slope (top 20%). Distance between foraging/non-foraging points and the nearest steep bathymetric slope was calculated using the Euclidian distance tool in ArcGIS 10.2 for Desktop. We also did the

Table 2. Definitions and sources of oceanographic variables used in boosted regression tree modelling of GBR wedge-tailed shearwater short foraging trips in the southern GBR

Model variable	Description	Unit	Source(s)
Chla(month)	[chl a] monthly climatology	mg m ⁻³	NASA OceanColor Aqua MODIS (oceancolor.gsfc.nasa.gov)
Chla(3dmean)	[chl a] 3 d means		
ChlaA(month)	[chl a] anomalies, monthly climatology		
ChlaA(3dmean)	[chl a] anomalies, 3 d means		
SST(month)	Sea surface temperature (SST) monthly climatology	°C	NASA OceanColor Aqua MODIS; Aquarius Sea Surface Temperatures 4 µ nighttime (https://oceancolor.gsfc.nasa.gov/cgi/l3)
SST(3dmean)	SST 3 d means		
SSTa(month)	SST anomalies, monthly climatology		
SSTa(3dmean)	SST anomalies, 3 d means		
SSTG(month)	SST gradient (front)	°C km ⁻¹	NASA OceanColor Aqua MODIS; Aquarius Sea Surface Temperatures 4 µ nighttime
SSTG(3dmean)	SST gradient (front), 3 d means	°C km ⁻¹	
DistSSTG	Distance to nearest steep (25 %) SST gradient (front)	Degrees distance	Calculated using ArcGIS 10.2 for Desktop
Bathymetry	Depth of ocean floor		NOAA National Centres for Environmental Information - ETOPO1 Global Relief Model (https://www.ngdc.noaa.gov/mgg/global/global.html)
Bath.grad	Steepness of slope: bathymetric depth change over distance	m km ⁻¹	Biophysical Oceanography Group, University of Queensland (www.gpem.uq.edu.au/oceanography)
DistSlope	Distance to nearest steep (25 %) bathymetric slope	Degrees distance	Calculated using ArcGIS 10.2 for Desktop
Coldist	Distance to the colony	Degrees distance	Calculated using ArcGIS 10.2 for Desktop
Photic Depth	Water transparency (Secchi disk depth)	m	Biophysical Oceanography Group, University of Queensland (www.gpem.uq.edu.au/oceanography)

same distance calculations for other oceanographic features known to influence behaviour: SST front, nearest land and distance to the colony (Kitaysky et al. 2000, Yen et al. 2004, Amorim et al. 2009).

We used 2 variables representing water quality to determine if water clarity or fresh water influenced foraging behaviour. This was because turbidity may offer protection to prey items while clarity can enhance the ability of visual predators like seabirds to detect prey (Ainley 1977, Haney & Stone 1988, Henkel 2006). 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 extend out to sea from the coast and are assessed at a weekly scale (da Silva et al. 2002–2014).

Shape files were exported to ArcGIS 10.2 for Desktop with the OGR Shapefiles package and maps projected in the World Geodetic System (WGS) 1984 geoid. 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 that can be associated with bird positions. These layers were overlaid on the GPS tracks and values for each oceanographic variable were matched to the corresponding bird foraging and non-foraging points (latitude/longitude locations by date), collated into month and year of tracking for analysis and modelling in R (R Core Team 2013). Oceanographic parameters in any given image pixel can be affected by turbidity, light refraction, cloud cover, shallow water (<200 m depth), or the presence of land and so produce excessive val-

ues (e.g. SST above 45°C or positive values for bathymetry). These erroneous data were identified and removed. Due to the high 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 d means, and when too few data were available these were excluded.

Statistical analysis and modelling

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 elucidating complicated relationships among numerous variables and can provide powerful ecological insights (Elith et al. 2008, Buston & Elith 2011). Therefore, to evaluate the combined influence of environmental variables on the foraging activity of shearwaters we used boosted regression trees (BRTs). BRT is a machine learning, predictive modelling technique that is currently considered to have superior predictive performance over traditional regression models (Desalegn & Beierkuhnlein 2010, Opper et al. 2012). This is due to a lack of assumptions about the type of functions or interactions being modelled (Buston & Elith 2011) and because of the ability of BRT to deal with random and missing data, binomial response variables and violations of traditional statistical assumptions such as independence of data and unequal variances (Leathwick et al. 2006, Elith et al. 2008, Buston & Elith 2011). Finally, BRT improves performance by combining many models for prediction and includes stochasticity to reduce variance in the model and improve accuracy. Modelling was conducted in R version 3.0.3 (Hijmans & 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 values for 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 & 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).

Default values and model runs followed recommendations by Elith et al. (2008) and used the Bernoulli (binomial) error distribution and were conducted in R as described above. In this study we used a tree complexity of 3 to 6, began with a fast learning rate of 0.01, and employed a flexible, stepwise increase of trees from 50 to 10 000. If the minimum number of trees (1000, as recommended by Elith et al. 2008) was not reached, or the maximum (10 000, as determined by Ridgeway 2007) exceeded, the learning rate and tree complexity were adjusted until the model performance was optimised. Data in BRT are cross-validated to optimise the model predictive ability and estimate the optimal number of iterations. Randomness was introduced when necessary to improve model performance using bag fraction values between 0.5 and 0.75, which give the best results for binomial responses. Full models were run on all data by year, comparing foraging and non-foraging, with month as a factor and accounting for individual birds. Models were run through a simplification process in R using `gbm.simplify`, a process 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) defining the characteristics driving foraging intensity in shearwater foraging grounds. Optimal models are indicated by the highest area under the receiver operating characteristic (ROC) curve (AUC) values (Fielding & Bell 1997, Elith et al. 2008). Partial dependence plots, 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. 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) which negatively affects the ability to interpret the model (Kuhn 2008). BRT results presented are the cross-validation (CV) predictive deviance and its standard error (± 1 SE), AUC values, the factors exerting the strongest influence on foraging locations, and notable interactions among them.

Finally, we tested for effects of GPS logger deployments on adult foraging activity (short and long-trip duration) or provisioning patterns (chick mass; chick meal masses before and after deployment) with Mann-Whitney *U* tests.

Auto correlation and exclusions

The main concern when dealing with species distribution data, particularly where distribution is mainly affected by environmental factors, is spatial autocorrelation (SAC) (Elith & Leathwick 2009). It can affect model predictive performance (Crane et al. 2012) and residuals, causing bias in parameter estimates and increasing Type I errors (Dormann et al. 2007, Miller et al. 2018). We assessed SAC using the *ncf* package (Bjornstad 2013) in R (R Core Team 2013), accepting customarily acceptable Moran's *I* values, i.e. <0.22 (McDuie & Congdon 2016) and moderate values between approximately -0.3 and $+0.3$ for spline correlograms (Cohen 1988).

Correlation and collinearity among predictors were assessed with correlation coefficients, variance inflation factors (VIFs) and multicollinearity scatterplot matrices in R using the *car*, *usdm*, *MASS* and *clusterGeneration* packages (Venables & Ripley 2002, Fox & Weisberg 2011, Naimi 2013, Qiu & Joe 2013). Any variables that exceeded the conservative threshold values of 0.7 (correlation) and 4 (VIF) (Rogerson 2001, O'Brien 2007, Dormann et al. 2013) were removed prior to analysis. When collinearity and associated excess VIF values, assessed per McDuie & Congdon (2016), were present we excluded those with highest VIF values from models in a step-wise approach until all variables exhibited values below accepted thresholds. Collinearity was generally present between [chl *a*] and [chl *a*] anomalies and SST and SST anomalies at 3 d and monthly scales; so for the annual models we excluded absolute SST and

[chl *a*], which had the highest VIFs, in favour of their anomaly values. 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 importance of predictors and detail in the peaks and troughs of the BRT outputs and empirical data histograms. Visualisation of frequency distributions of each predictor variable allowed us to identify the values of the primary and, where applicable, secondary peaks and/or range of the data which are presented for comparison.

RESULTS

Trip characteristics

Foraging shearwaters remained at sea throughout the day. They departed before sunrise (between ~04:00 and 05:00 h) and returned to the colony after dark (between 19:00 and 21:00 h). Most single day trips lasted between 14 and 17 h. In 2013, 79 separate trips were obtained from 52 individual birds: 69.6% were 1 d trips, 25.3% were 2 d trips, and 3.8% were 3 d trips. Only 1 bird remained away for 4 d (1.3%). Birds travelled on average 83.06 km from the colony ($n = 79$; Table 3). In 2014, there were 34 separate trips from 33 tracked individuals: 82.4% were 1 d trips, 14.7% were 2 d trips, there was only a single 3 day trip (2.9%), and no trip lasted 4 d. Birds travelled an average of 70.14 km from the colony ($n = 34$; Table 3). All trips were within 300 km of Heron Island, which was expected from analysis of shearwater long foraging trips (McDuie et al. 2015). There was strong consistency of site use among individuals and locations.

Table 3. Summary of area restricted search (ARS) data for GPS tracked wedge-tailed shearwaters in the southern GBR in 2013 and 2014. Values are mean \pm 1 SE. Values in parentheses indicate percentage or range

	2013 ($n = 79$)	2014 ($n = 34$)
No. of tracked individuals	52	33
1 day trips	55 (69.6%)	28 (82.4%)
2 day trips	20 (25.3%)	5 (14.7%)
>2 day trips	4 (5.1%)	1 (2.9%)
Total no. of ARS locations	4015	1947
Max. distance from colony (km)	83.06 \pm 9.13 (19.36–283.82)	70.14 \pm 8.09 (16.42–212.73)
No. of ARS locations per trip	2.42 \pm 0.03 (0–215)	1.88 \pm 0.02 (7–159)
Scale of ARS (km)	6.62 \pm 0.59 (2–19)	8.17 \pm 0.10 (2–28)
Distance of ARS from colony (km)	80.58 \pm 0.78 (3.29–245.65)	67.27 \pm 0.62 (3.86–212.73)

GPS logger effects

There were no differences between our control and GPS groups in meal masses provided to chicks by adults carrying GPS loggers on the day before device attachment (CTRL $n = 43$, GPS $n = 48$; $U = 865$, $p < 0.18$) or on the day of detachment (CTRL $n = 43$, GPS $n = 49$; $U = 1003.5$, $p = 0.70$). Likewise there were no differences in chick mass ($t_{49} = -1.699$, $p = 0.10$) or duration of subsequent long trips (>4 d) (CTRL $n = 28$, GPS $n = 35$; $U = 371.5$, $p = 0.10$). However, on average

GPS carrying adults on short trips stayed away from the colony slightly longer (1.71 d, $n = 49$) than controls (1.28 d, $n = 43$; $U = 688$, $p < 0.01$).

Characteristics of area restricted search zones

In 2013, ARS behaviour was detected in 78 of the 79 trips. A total of 189 ARS events where birds increased their search effort occurred, with a mean of 2.42 ± 0.03 events per trip. The average distance (\pm SE) from the colony of ARS zones was 80.58 ± 0.78 km. ARS areas 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 3, Fig. 1).

Spatial separation of areas of foraging activity

When ARS foraging activity was mapped, discernibly discrete areas were evident that differed in bathymetry (depth) and topography (reefs, slope, and featureless ocean floor). The first run of the BRT model showed bathymetry and distance from the colony to be the principal factors influencing foraging. Foraging activity peaks were associated with 5 identifiable bathymetric depths ranging from shallow (~ 34 m) to deep (~ 800 m), and with 5 distances from the colony ranging from very near ($\sim 0.2^\circ$) to relatively far ($\sim 2.5^\circ$). Combined, these results supported the division of the data into 5 separate foraging zones (Fig. 1). Zones were delineated with polygons in ArcGIS 10.2 for Desktop (Fig. 1). The proximity of Zones 1 and 2 made them more difficult to separate spatially, but they were clearly identifiable by their distinct topography (reefs in Zone 2). Following this first analysis, bathymetry and distance from the colony were excluded from further models to test the relative

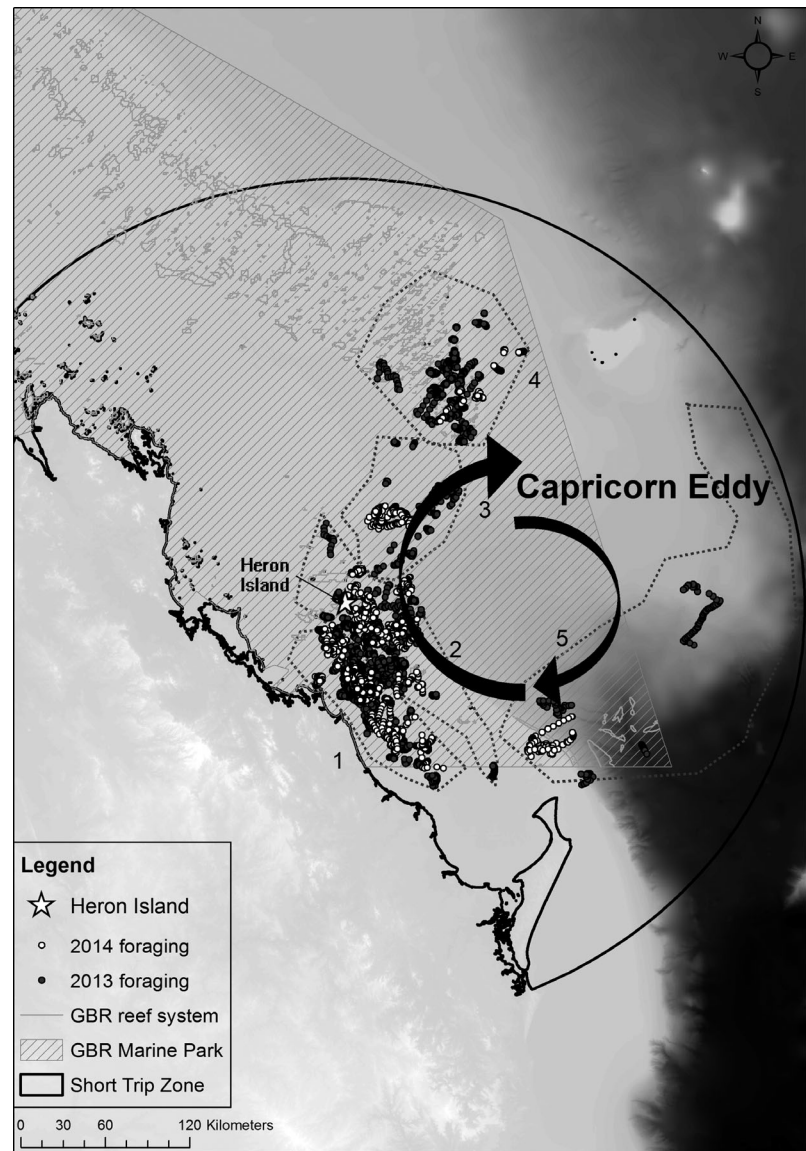


Fig. 1. Short-trip foraging zones of wedge-tailed shearwaters in the southern Great Barrier Reef (GBR). Foraging locations of tracked birds (area restricted search locations) are shown for (○) 2014 and (●) 2013, with foraging zones delineated by dotted outlines and numbered 1 to 5. Primary foraging zones were Zone 1 (inshore), Zone 2 (Capricorn Bunker), Zone 3 (Capricorn Channel) and Zone 4 (Swains Reefs). Few individuals foraged in Zone 5. The solid black semicircle marks the maximum extent of the short-trip zone. The striped area is the southern end of the GBR marine park. The approximate position of the Capricorn Eddy is indicated by the black arrows. Darker shading indicates deepest bathymetry and lighter area is above the continental shelf

importance of other oceanographic variables. In these analyses, only data for birds that actually stopped and foraged in any given zone were included in analyses for that zone. Tracks that overflowed a zone en route to a different foraging zone were included as non-foraging points for the destination zone. This was most relevant to Zone 3, which was traversed by a number of non-

stop tracks en route to Zone 4. Zones were analysed separately to identify spatial variation among oceanic drivers by zone. Modelling results presented are from the simplified BRT models that best explain the influences operating at the various spatial scales.

Inter-annual and fine-scale variation

BRT modelling was first conducted on tracking data for each year separately in order to test for inter-annual variation in the influence of regional-scale oceanographic processes. We identified the importance or influence of finer-scale, rather than regional, oceanographic processes by examining the relative importance of oceanographic variables in 4 distinct foraging sub-zones independently by year. The combination of oceanographic factors of strongest influence on shearwater foraging differed among zones and between years of data collection and the increased precision highlighted local variation in trophic processes.

In 2014, the simplified BRT model had 6 variables and fitted well with a low predictive deviance of 0.612 ± 0.023 SE and high AUC of 0.942. The primary factor influencing foraging was the strength of the SST front, based on 3 d average values, with 25.1% influence on total model fit (Fig. 2a). In this case, foraging

was concentrated at the intermediate fronts (values of >0.45 to 0.6 , where the predicted probability of occurrence is $>50\%$), with limited foraging predicted to occur over the strongest fronts (>0.6) or where fronts were lacking (<0.3). Water clarity was the next strongest influence (18.4%), with foraging predicted to occur when the clarity was >10 m and more often 25–30 m (Fig. 2b). This was followed by [chl a] anomalies (17.1%), with foraging predicted to occur in strongly negative to weakly positive anomalies (-0.6 to 0.2 mg m^{-3} ; Fig. 2c). The average (\pm SD) [chl a] in foraging areas was low (0.3 ± 0.003 mg m^{-3}), reflecting the generally oligotrophic nature of tropical oceans.

Proximity to the SST front had some influence on foraging activity (17%), with most foraging predicted to occur within 4–6 km of the strongest locally occurring SST front, and another peak at 11–22 km (Fig. 2d), reflecting variation among foraging zones (Table 4). Monthly average SST front values had 11.2% influence on model fit and the pattern of predicted foraging activity (Fig. 2e) was similar to that for 3 d values (Fig. 2a). Finally, the model generally predicted foraging to be in water that was cooler than climatological averages, when SST anomalies were between -0.3 and -1°C (Fig. 2f). The average SST of foraging areas, calculated from our empirical data, was $26.8 \pm 0.006^\circ\text{C}$. There were no strong interactions between variables in the model.

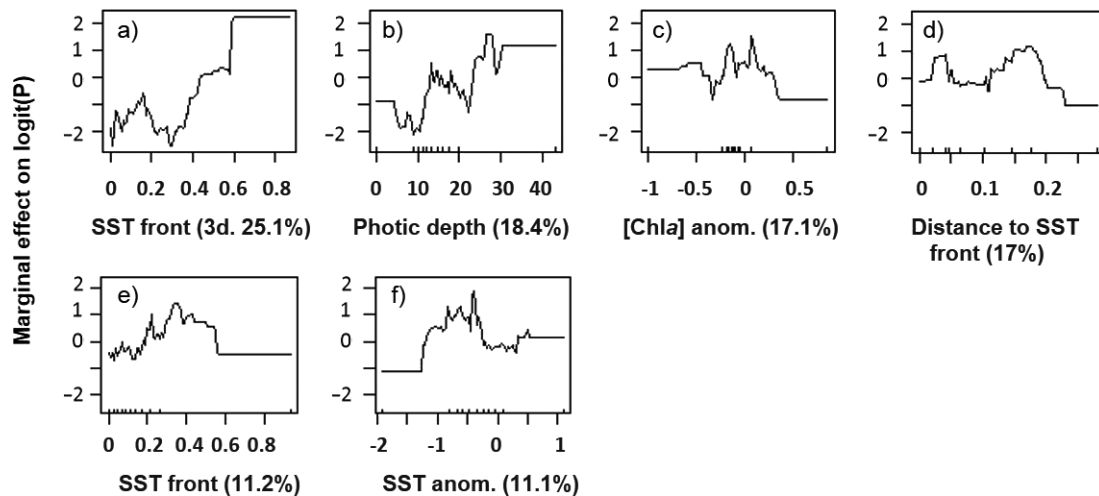


Fig. 2. Simplified model results for 2014 from the final, simplified boosted regression tree (BRT) model of wedge-tailed shearwater short foraging trips in the southern GBR, showing the influence of oceanographic variables on the binomial response (foraging/non-foraging) after accounting for the average effects of all other variables in the model (Elith et al. 2008). For descriptions of variables see Table 2. *y*-axis values show the probability on a logit(*p*)-transformed scale that a bird will be foraging at the value of the predictor shown on the *x*-axis. A value of 0 indicates a 50% probability that a bird will be foraging at values of the predictor shown; thus peaks above 0 represent the values (e.g. SST front strengths, distances to SST fronts or anomalies of [chl a] and SST) at which birds are more likely to be foraging. The flat portion at the right end of the effect lines indicates 0 data at these values. The percentages in parentheses represent the relative influence of each variable in the total model fit on the probability of foraging. For example, 3 day averages of the SST front, shown in panel (a), exerted the strongest influence on this model (25.1%)

Table 4. Simplified model results of GPS tracking of wedge-tailed shearwaters in the southern GBR in 2013 and 2014. Results are shown for the 4 main foraging zones (see Fig. 1), listing the top 4 factors in order of influence from the most (1) to least (4) influential factor. For each zone, the proportion (%) of birds foraging in the zone is shown, as well as the cross-validation (CV) predictive deviance and its standard error (± 1 SE), and the area under the receiver operating characteristic (ROC) curve (AUC). Approximate peak values of each of the oceanographic variables influencing foraging in the models are shown, taken from partial dependence plots, frequency distributions and calculated means. Double peaks are indicated by 2 values, separated by a semi-colon. See Table 2 for description of variables

	2013				2014			
	Zone 1	Zone 2	Zone 3	Zone 4	Zone 1	Zone 2	Zone 3	Zone 4
% foraging	27.9%	46.4%	4.90%	13.9%	36.7%	4%	11.80%	6.79%
CV dev. \pm SE	0.813 \pm 0.031	0.696 \pm 0.007	0.772 \pm 0.037	0.773 \pm 0.008	0.55 \pm 0.024	0.646 \pm 0.039	0.466 \pm 0.057	0.356 \pm 0.049
AUC	0.897	0.898	0.9332	0.9033	0.9324	0.9347	0.9676	0.9772
Relative influence of factors remaining in simplified models								
1	DistSSTG 0 to 0.05	ChlaA(month) <0; 0.8 to 1	DistSSTG 0.07 to 0.25	DistSSTG 0.01 to 0.1	SSTa(month) <-0.7	SSTG(month) 0.1 to 0.2	ChlaA(month) <0	ChlaA(month) <-0.06
2	ChlaA(month) <0; >2	DistSSTG 0.05; 0.22	ChlaA(month) 0.2	SSTG(month) >0.15; 0.35	ChlaA(month) <-0.1	SSTa(month) <-0.4	SSTG(month) >0.12	SSTa(month) -0.5 to 0.6
3	SSTa(month) -0.2 to -1	SSTa(month) <0; 0.05	SSTa(month) <-1.5	SSTa(month) <-0.2; 0.2	DistSSTG <0.05; 0.15 to 0.2	ChlaA(month) <0	DistSSTG >0.09	SSTG(month) 0 to 0.15
4	SSTG(month) >0.05 to 0.25	SSTG(month) 0 to 0.1	SSTG(month) 0.08; 0.25	ChlaA(month) >-0.15	SSTG(month) >0.15	DistSSTG >0.15	SSTa(month) <-0.4	DistSSTG >0.1

In 2013 the simplified BRT model had 6 variables (Fig. 3) and fitted well with a predictive deviance of 0.665 ± 0.024 SE and an AUC of 0.9258. The primary factor influencing foraging in 2013 was proximity to the steepest SST fronts (24.8% influence; Fig. 3a), with more birds likely to be foraging nearer the front (at distances between 0 and ~8 km). Another peak at 19–25 km distance reflects variation among foraging zones (Table 4). This factor was a much stronger

influence on foraging in 2013 than in 2014 and, in general, as distance from the front increased, probability of birds foraging decreased. With regard to water clarity (22.6% influence), as in 2014, shearwaters were most likely to forage in clearer water, at photic depths of 18–24 m and ~30 m, but with some foraging also predicted in more turbid water, at photic depths of ~2 m and 7–11 m (Fig. 3b). The model predicted that shearwaters were more likely

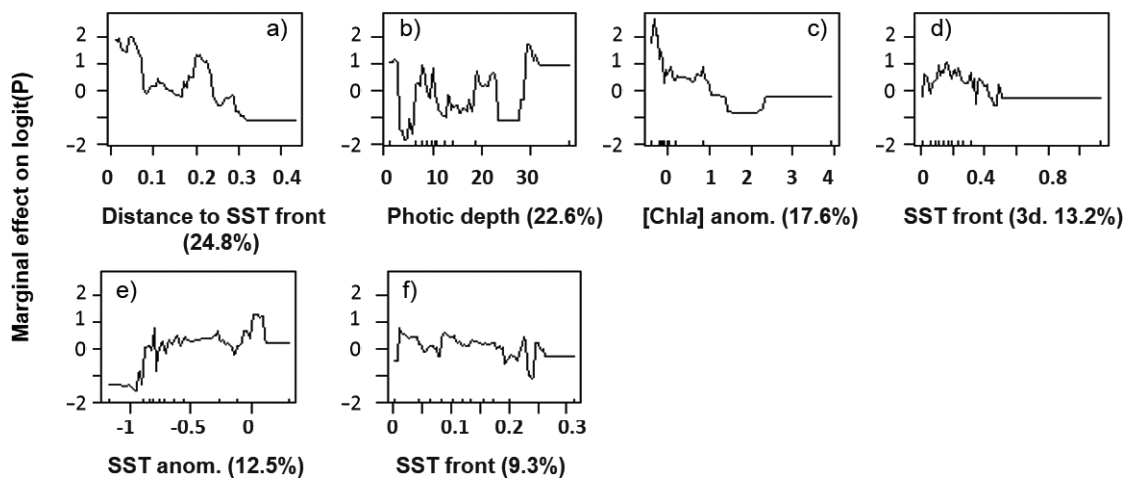


Fig. 3. Simplified model results for 2013 from the final, simplified boosted regression tree (BRT) model of wedge-tailed shearwater short foraging trips, showing the influence of oceanographic variables on the binomial response (foraging/non-foraging) after accounting for the average effects of all other variables in the model (Elith et al. 2008). See Table 2 for descriptions of variables and Fig. 2 legend for an explanation of the content of diagrams

to forage in areas with negative [chl a] anomalies and showed a weak association between foraging and positive anomalies up to 1 mg m^{-3} greater than long-term averages (17.6% influence; Fig. 3c). The average [chl a] in which shearwaters foraged (from empirical data) was slightly higher in 2013 than in 2014 at $0.81 \pm 0.01 \text{ mg m}^{-3}$.

The presence of weaker SST fronts was important with 3 d (13.2% influence; Fig. 3d) and monthly means (9.3% influence; Fig. 3f) predicting foraging at 0.05–0.5 and 0.25 respectively, which was less than 2014. Finally, SST anomalies had 12.5% influence on total model fit; anomalies that were either strongly negative (lower than -0.5°C) or slightly positive ($+0.01^\circ\text{C}$) were most often associated with foraging activity (Fig. 3e). The average SST of foraging grounds was $26.7 \pm 0.006^\circ\text{C}$. The peaks in the annual model outputs indicate higher levels of foraging at those values of the predictor variables. This relates to variation among the foraging zones which is detailed in the next section of results.

Variation among foraging zones

Inshore foraging and terrestrial run-off. Birds foraging in the shallowest ($\sim 34 \text{ m}$) zone near the coast (Zone 1) were directly influenced by terrestrial freshwater input from river outflow. This effect was demonstrated by links between foraging activity and a number of environmental factors. Most obvious was the influence of primary, secondary and tertiary freshwater plumes. These are defined by their distance from the coast, with primary and tertiary plumes being closest to and furthest from the coast, respectively. Foraging occurred more frequently in tertiary than secondary plumes and never in primary plumes. This influence was more strongly evident in 2013 (Table 5, Fig. 4). In addition, foraging usually occurred very near to or on top of the steepest SST front (0 to $0.05^\circ \text{ km}^{-1}$) in this zone. This, combined with comparatively high absolute frontal values (0.1 to $0.2^\circ \text{ km}^{-1}$), especially in 2013, suggests a strong SST front in this zone associated with the flood plumes. This influence was also apparent in the more strongly negative SST anomalies associated with foraging (Table 4). Finally, [chl a] was highest in this zone and more strongly anomalous: in 2013 foraging was characterised by weakly negative and strongly positive anomalies, but by more strongly negative anomalies in 2014.

Reef topography. Numerous reefs and lagoons are scattered throughout the region and this distinct topography typifies Zones 2 (Capricorn Bunker Reefs)

Table 5. Numbers of wedge-tailed shearwaters foraging (F) or not (NF) in freshwater plumes that occurred in foraging zones (Zones 1, 2 and 3; see Fig. 1) in the southern GBR in 2013 and 2014. Plumes are defined as primary, secondary or tertiary by their distance from the coast, with primary and tertiary plumes being closest to and furthest from the coast, respectively, and are assessed at a weekly scale

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

and 4 (Swains Reefs), which have average depths of 40 and 60 m respectively. These 2 reef areas were notable for the inter-annual variation in factors of influence, with more parity in values in 2014 than in 2013. Foraging had a stronger relationship with the SST fronts in 2013, when proximity to the front was always one of the more influential factors, than in 2014. In 2014, foraging effort in these reef zones was generally focused farther from the SST front, than in Zones 1 and 3. A minor influence of weakly positive SST anomalies was predicted in 2013 but, in general, shearwaters consistently selected more negatively anomalous values in both years. Finally, foraging was mostly associated with negative anomalies of [chl a] in 2014 in both reef zones. In 2013, foraging was associated with positive anomalies in Zone 2 and with more negative values in Zone 4 (Table 4).

The tertiary freshwater flood plume, which is the farthest from the coast, occasionally intruded to the Capricorn Bunker reefs. Birds targeted these plume waters in 2013 but not 2014 (Table 5, Fig. 4).

Deeper waters. Outside the reefs, a smaller amount of foraging occurred in bathymetrically deeper areas (Zones 3 and 5; Fig. 1). The Capricorn Channel (Zone 3), with average depth of 130 m, is topographically unremarkable and demonstrated somewhat less inter-annual variability than the shallower zones. In 2013, foraging was most strongly influenced by proximity to the SST front, when shearwaters were much more likely to forage nearer the SST front although the front was not particularly strong. This coincided with foraging consistently associated with stronger negative SST anomalies and positive [chl a] anomalies, which contrasted with the influence of negative [chl a] anomalies in this zone in 2014

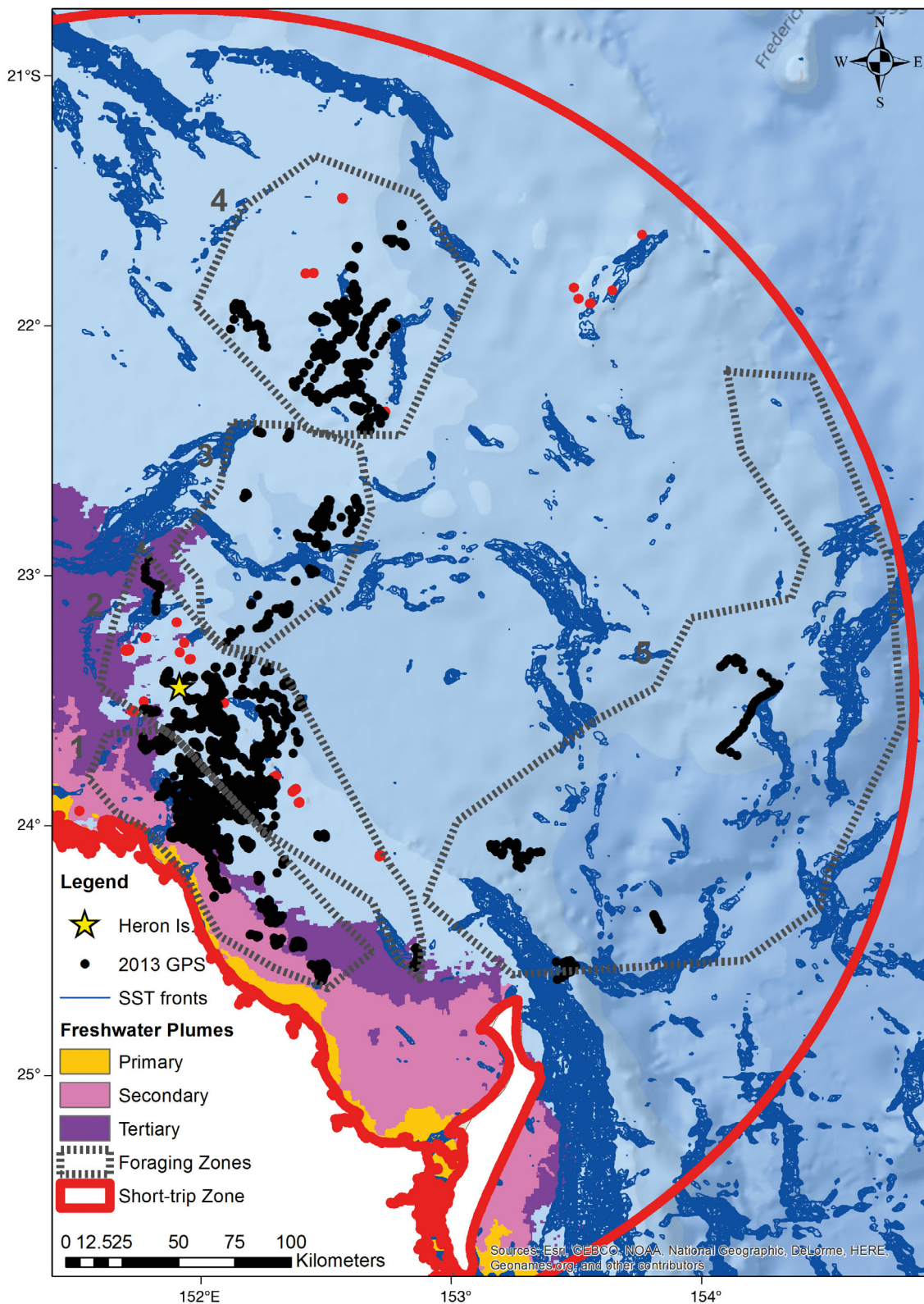


Fig. 4. Freshwater plumes in the southern GBR in 2013 with wedge-tailed shearwater foraging locations overlaid. Black dots mark foraging locations of tracked birds (area restricted search locations) in 2013. Foraging zones are delineated by dotted outlines (see Fig. 1); the solid red circular line marks the maximum extent (300 km from the breeding site on Heron Island) of the short-trip foraging zone. Strongest SST fronts of the period are indicated by the dark blue patches

(Table 4). The deepest foraging zone (Zone 5) was farthest from the colony, and the least visited by birds on short trips (1 bird in 2014 and 2 in 2013) so we were unable to analyze these data for comparison and cannot draw any inferences.

DISCUSSION

Location and characteristics of foraging areas

Near-colony foraging locations used by GBR wedge-tailed shearwaters when provisioning chicks were always located within 300 km of the Heron Island breeding colony. Often, sites were considerably closer to the island (83.06 ± 9.13 km, mean \pm SE). Furthermore, the same sites were consistently and repeatedly used over both years of the study, underlining the importance of these specific locations for successful breeding. Constraints imposed by the need to balance energy expenditure against food obtained, whilst also provisioning chicks, can lead to a reliance on only a few suitable near-colony foraging locations (Weimerskirch et al. 2003). For wedge-tailed shearwaters in the Capricorn Bunker region of the GBR, there appear to be 5 such foraging areas.

In resource-poor tropical environments, prey patches can be scarce (Weimerskirch et al. 2004). Nevertheless, they may also be predictable, particularly if there are oceanographic features that consistently drive prey enhancement, such as fronts, convergences or upwelling (Weimerskirch et al. 2004, Weimerskirch 2007). The consistent use of sites by shearwaters of the GBR supports this hypothesis.

Each of the 5 identifiable near-colony foraging zones had distinct bathymetry and, with the exception of Zone 1 (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. Therefore, it is the presence of steep bathymetric change, rather than any specific depth, that can most readily be used to identify foraging sites. Such topographic features are known to facilitate prey aggregation for seabirds (Haney et al. 1995). Further, the interactions of these types of topographic features with specific current flows are known to induce upwelling and provide improved prey access to seabirds (Brown 1979, Duffy 1989, Yen et al. 2006). Our results imply such interactions occur at these GBR foraging locations. However, the short-trip foraging region used by wedge-tailed shearwaters is a relatively oligotrophic and homogeneous habitat,

exhibiting very low primary productivity and only small variations in SST. Despite this, shearwaters consistently foraged within a specific narrow and cooler range of the SST than those generally available. This suggests that, in the southern GBR, lower than average SST and/or negative SST anomalies are consistently associated with improved prey availability

Similar relationships have been seen elsewhere (Spear et al. 2001, Cotté et al. 2007). Links between foraging activity and SST fronts/anomalies also indicate the presence of localised upwellings and frontal systems that concentrate food items at small spatial scales (Uda 1938). The influence of SST on foraging was strongest in Zone 1, where intensely negative SST anomalies contributed strongly to foraging activity. The relationships confirm expectations based on previous regional GBR studies (Smithers et al. 2003, Peck et al. 2004, Erwin & Congdon 2007, Devney et al. 2010, Weeks et al. 2013) that near-colony food availability is related to, and strongly influenced by ocean temperatures, despite the SST gradients observed in our study not being as pronounced as those at higher latitudes (Shaffer et al. 2009).

In general, wedge-tailed shearwaters exhibited most foraging activity at sites where [chl *a*] was lowest. This directly contrasts with most previous foraging studies, including those of wedge-tailed shearwaters, that describe seabirds foraging in areas of elevated primary productivity (Cecere et al. 2013a). The reason for this discrepancy is currently unknown; however, the increased dynamism and inherent unpredictability 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 prey (e.g. micronekton) abundance. Such a temporal decoupling between ocean dynamics and primary productivity has previously been documented in this region (Menkès et al. 2015). There was one exception to the lack of influence of [chl *a*]. Zone 1, adjacent to the coast, consistently exhibited elevated [chl *a*]. This was the only foraging area that received significant freshwater input from river discharge, suggesting that elevated [chl *a*] in this zone is likely due to coastal enrichment via nutrient runoff from the terrestrial environment.

The Capricorn Eddy

The Capricorn Eddy is a mesoscale eddy driven by the East Australian Current (EAC) that 'spins up' over the Capricorn shelf in the southern GBR, and likely triggers upwelling or frontal convergence along

the continental shelf edge and Capricorn Bunker reef system (Weeks et al. 2010). Fine-scale oceanographic parameters such as SST or [chl a] anomalies or gradients are frequently overlooked by other studies but they are likely to be important in regional ocean dynamics and their inclusion here demonstrates their utility in revealing the Capricorn Eddy or frontal activity in the region. Previously, the dynamics of the Capricorn Eddy have been proposed as a major driver of food availability for breeding shearwaters in this region (Weeks et al. 2013). Zones 2, 3 and 4 are located precisely where this eddy encounters the continental shelf edge, thus confirming its importance. In addition, Zone 1 is located where oceanic waters entrained by the Capricorn Eddy encounter freshwater flood plumes from coastal rivers. This interaction creates more intense gradients in the oceanographic parameters and favourable conditions for foraging shearwaters, which suggests that foraging in this zone was also heavily influenced by eddy dynamics. Consequently, at least 80% of shearwater near-colony foraging areas in the southern GBR are influenced by this eddy.

The Capricorn Eddy is an ephemeral, mobile and unstable phenomenon, that is influenced by climate-driven processes, and which can have varying effects on ocean dynamics and trophic relationships in the region. For example, varying ENSO conditions can cause the eddy to shift westward, closer to the reef edges, forcing an intrusion of cold water into the GBR lagoon. This causes intense stratification and traps warm water at the surface, which reduces availability of prey to seabirds (Weeks et al. 2013). Such a phenomenon could simultaneously weaken or eliminate SST fronts. Alternatively, the eddy can shift southward under stronger movement of the EAC, or it can simply weaken, slow or reduce in size, all of which would likely weaken frontal intensity. Such variability is apparent, evidenced in our results through the seasonal variation we have seen in the influence of SST fronts on foraging sites used. This inter-annual and inter-zonal variation implies that, at times, the importance of the eddy diminishes and is replaced by phenomena operating on a finer, more localised scale.

Device-handling effects

A slightly higher proportion of adults carrying GPS devices conducted 2 d rather than 1 d trips on the day after logger deployment compared to the controls. We cannot unequivocally confirm whether this was a response to handling during deployment or to the

device itself. Importantly, these effects did not influence our comparative tests to determine the oceanographic characteristics of foraging versus non-foraging grounds chosen by individual birds, as these were pair-wise comparisons. That birds carrying GPS loggers returned the same sized meals to their chicks both prior to and during logger deployment (results not shown) is evidence that they successfully foraged in the locations to which we tracked them. Whether these were the same places used by control birds is impossible to know. However, the fact that multiple individuals used and reused our identified locations within and across two seasons is suggestive of the importance of these locations to the colony as a whole.

CONCLUSION

This in-depth investigation identified the most important oceanographic variables and likely mechanisms driving near-colony availability/accessibility of prey to pelagic, tropical breeding seabirds in this system and highlights that, in order to fully characterise foraging sites and activity, it is important to investigate multiple, specific oceanographic variables at both fine and regional scales across multiple seasons. Knowing how these phenomena vary with changes in large-scale climate systems will enable us to further predict the impact of climate change or climate-driven variation on foraging habitat for seabirds. This can be used to inform future studies and to improve the management and conservation of seabirds in the region and elsewhere. Although Birdlife International has identified the Southern GBR as an Important Bird Area (IBA), the key foraging areas identified in this study either lack protection specifically aimed at seabird conservation (particularly important for Zone 1), or lie outside currently managed areas (Zone 5). Therefore, the information obtained from this study serves to prioritise these areas for assessment of threatening processes and improved management and/or protection. Ultimately, these findings can be used as a paradigm for comprehensive habitat modelling, particularly for tropical pelagic foraging seabirds, that can be used to aid regional and global conservation efforts.

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LITERATURE CITED

- Ainley D (1977) Feeding methods in seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. In: Llano G (ed) Adaptations within Antarctic ecosystems. Smithsonian Institution, Washington, DC, p 664–685
- Ainley D, Boekelheide R (1984) An ecological comparison of oceanic seabird communities of the South Pacific Ocean. *Stud Avian Biol* 8:2–23
- ✦ Ainley DG, Spear LB, Tynan CT, Barth JA, Pierce SD, Glenn Ford R, Cowles TJ (2005) Physical and biological variables affecting seabird distributions during the upwelling season of the northern California Current. *Deep Sea Res II* 52:123–143
- ✦ Amorim P, Figueiredo M, Machete M, Morato T, Martins A, Santos RS (2009) Spatial variability of seabird distribution associated with environmental factors: a case study of marine Important Bird Areas in the Azores. *ICES J Mar Sci* 66:29–40
- Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103:458–473
- Ashmole N (1971) Seabird ecology and the marine environment. In: Farner D, King J (eds) Avian biology, Vol 1. Academic Press, New York, NY, p 224–286
- ✦ Baduini C (2002) Parental provisioning patterns of wedge-tailed shearwaters and their relation to chick body condition. *Condor* 104:823–831
- ✦ Ballance L, Pitman R, Fiedler P (2006) Oceanographic influences on seabirds and cetaceans of the eastern tropical Pacific: a review. *Prog Oceanogr* 69:360–390
- ✦ Becker BH, Beissinger SR (2003) Scale-dependent habitat selection by a nearshore seabird, the marbled murrelet, in a highly dynamic upwelling system. *Mar Ecol Prog Ser* 256:243–255
- Bjornstad ON (2013) ncf: spatial nonparametric covariance functions. <https://cran.r-project.org/packages=ncf>
- ✦ Brinkman R, Wolanski E, Deleersnijder E, McAllister F, Skirving W (2002) Oceanic inflow from the Coral Sea into the Great Barrier Reef. *Estuar Coast Shelf Sci* 54:655–668
- ✦ Brown R (1979) Seabirds of the Senegal upwelling and adjacent waters. *Ibis* 121:283–292
- ✦ Brown R, Cooke F, Kinnear P, Mills EL (1975) Summer seabird distributions in Drake Passage, the Chilean fjords and off southern South America. *Ibis* 117:339–356
- ✦ Burrage DM, Steinberg CR, Skirving WJ, Kleypast JA (1996) Mesoscale circulation features of the Great Barrier Reef region inferred from NOAA satellite imagery. *Remote Sens Environ* 56:21–41
- ✦ Buston PM, Elith J (2011) Determinants of reproductive success in dominant pairs of clownfish: a boosted regression tree analysis. *J Anim Ecol* 80:528–538
- ✦ Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519
- ✦ Cecere JG, Calabrese L, Rocamora G, Catoni C (2013a) Movement patterns and habitat selection of wedge-tailed shearwaters (*Puffinus pacificus*) breeding at Aride Island, Seychelles. *Waterbirds* 36:432–437
- ✦ Cecere JG, Catoni C, Maggini I, Imperio S, Gaibani G (2013b) Movement patterns and habitat use during incubation and chick-rearing of Cory's shearwaters (*Calonectris diomedea diomedea*) (Aves: Vertebrata) from Central Mediterranean: influence of seascape and breeding stage. *Ital J Zool* 80:82–89
- ✦ Cherel Y, Weimerskirch H (1995) Seabirds as indicators of marine resources: black-browed albatrosses feeding on ommastrephid squids in Kerguelen waters. *Mar Ecol Prog Ser* 129:295–300
- ✦ Choukroun S, Ridd PV, Brinkman R, McKinna LI (2010) On the surface circulation in the western Coral Sea and residence times in the Great Barrier Reef. *J Geophys Res Oceans* 115:C06013
- Cohen J (1988) Statistical power analysis for the behavioral sciences. Routledge Academic, New York, NY
- ✦ Congdon BC, Krockenberger AK, Smithers BV (2005) Dual-foraging and co-ordinated provisioning in a tropical Procellariiform, the wedge-tailed shearwater. *Mar Ecol Prog Ser* 301:293–301
- ✦ Cotté C, Park YH, Guinet C, Bost CA (2007) Movements of foraging king penguins through marine mesoscale eddies. *Proc R Soc B* 274:2385–2391
- ✦ Crase B, Liedloff AC, Wintle BA (2012) A new method for dealing with residual spatial autocorrelation in species distribution models. *Ecography* 35:879–888
- ✦ Croxall J, Prince P (1980) Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol J Linn Soc* 14:103–131
- ✦ Culik B, Bannasch R, Wilson R (1994) External devices on penguins: How important is shape? *Mar Biol* 118:353–357
- Desalegn W, Beierkuhnlein C (2010) Plant species and growth form richness along altitudinal gradients in the southwest Ethiopian highlands. *J Veg Sci* 21:617–626
- ✦ Devney CA, Caley MJ, Congdon BC (2010) Plasticity of noddy parents and offspring to sea-surface temperature anomalies. *PLOS ONE* 5:e11891
- ✦ Dormann CF, McPherson JM, Araújo MB, Bivand R and others (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628
- ✦ Dormann CF, Elith J, Bacher S, Buchmann C and others (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46
- ✦ Duffy D (1989) Seabird foraging aggregations: a comparison of two southern upwellings. *Colon Waterbirds* 12: 164–175
- Elith J, Leathwick J (2013) Boosted Regression Trees for ecological modeling. <http://cran.r-project.org/web/packages/dismo/vignettes/brt.pdf>
- Elith J, Leathwick J (2009) Species distribution models: ecological explanation and prediction across space and time. *Ann Rev Ecol Evol Syst* 40:677–697
- ✦ Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *J Anim Ecol* 77:802–813
- ✦ Erwin CA, Congdon BC (2007) Day-to-day variation in sea-surface temperature reduces sooty tern *Sterna fuscata* foraging success on the Great Barrier Reef, Australia. *Mar Ecol Prog Ser* 331:255–266

- Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environ Conserv* 24:38–49
- Fox J, Weisberg S (2011) *An R companion to applied regression*, 2nd edn. Sage, Thousand Oaks, CA
- Garvine RW (1974) Dynamics of small-scale oceanic fronts. *J Phys Oceanogr* 4:557–569
- Haney JC, Stone AE (1988) Seabird foraging tactics and water clarity: Are plunge divers really in the clear? *Mar Ecol Prog Ser* 49:1–9
- Haney JC, Haury LR, Mullineaux LS, Fey CL (1995) Seabird aggregation at a deep North Pacific seamount. *Mar Biol Lett* 123:1–9
- Henkel LA (2006) Effect of water clarity on the distribution of marine birds in nearshore waters of Monterey Bay, California. *J Field Ornithol* 77:151–156
- Hijmans RJ, Elith J (2013) Species distribution modeling with R. CRAN R Project
- Hijmans RJ, Phillips S, Leathwick J, Elith J, Hijmans MRJ (2013) 'dismo': species distribution modeling. <https://cran.r-project.org/web/packages/dismo/> (accessed on 24 May 2014)
- Hunt GL Jr (1991) Occurrence of polar seabirds at sea in relation to prey concentrations and oceanographic factors. *Polar Res* 10:553–560
- Hyrenbach KD, Fernández P, Anderson DJ (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Mar Ecol Prog Ser* 233:283–301
- Jaquemet S, Le Corre M, Quartly G (2007) Ocean control of the breeding regime of the sooty tern in the southwest Indian Ocean. *Deep Sea Res I* 54:130–142
- Kareiva P, Odell G (1987) Swarms of predators exhibit 'prey-taxis' if individual predators use area-restricted search. *Am Nat* 130:233–270
- Kenward R (2001) *A manual for wildlife radio tagging*. Academic Press, London
- King W (1974) *Pelagic studies of seabirds in the central and eastern Pacific Ocean*. Smithsonian Institution Press, Washington, DC
- Kitaysky AS, Hunt GL Jr, Flint EN, Rubega MA, Decker MB (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar Ecol Prog Ser* 206:283–296
- Kleypas J, Burrage D (1994) Satellite observations of circulation in the southern Great Barrier Reef, Australia. *Int J Remote Sens* 15:2051–2063
- Kuhn M (2008) Building predictive models in R using the caret package. *J Stat Softw* 28:1–26
- Lack D (1954) *The natural regulation of animal numbers*. Clarendon Press, Oxford
- Le Corre M (2001) Breeding seasons of seabirds at Europa Island (southern Mozambique Channel) in relation to seasonal changes in the marine environment. *J Zool* 254: 239–249
- Leathwick JR, Elith J, Francis MP, Hastie T, Taylor P (2006) Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. *Mar Ecol Prog Ser* 321:267–281
- McDuire F, Congdon BC (2016) Trans-equatorial migration and non-breeding habitat of tropical shearwaters: implications for modelling pelagic Important Bird Areas. *Mar Ecol Prog Ser* 550:219–234
- McDuire F, Weeks SJ, Miller MGR, Congdon BC (2015) Breeding tropical shearwaters use distant foraging sites when self-provisioning. *Mar Ornithol* 43:123–129
- Menkès C, Allain V, Rodier M, Gallois F and others (2015) Seasonal oceanography from physics to micronekton in the south-west pacific. *Deep Sea Res II* 113:125–144
- Miller MGR, Carlile N, Phillips JS, McDuire F, Congdon BC (2018) The importance of tropical tuna for seabird foraging over a marine productivity gradient. *Mar Ecol Prog Ser* 586:233–249
- Moore JK, Abbott MR, Richman JG (1999) Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *J Geophys Res Oceans* 104: 3059–3073
- Morato T, Varkey DA, Damaso C, Machete M and others (2008) Evidence of a seamount effect on aggregating visitors. *Mar Ecol Prog Ser* 357:23–32
- Naimi B (2013) usdm: uncertainty analysis for species distribution models. <https://cran.r-project.org/web/packages/usdm/usdm.pdf> (accessed on 2 Jun 2014)
- O'Brien RM (2007) A caution regarding rules of thumb for variance inflation factors. *Qual Quant* 41:673–690
- Oppel S, Meirinho A, Ramírez I, Gardner B, O'Connell AF, Miller PI, Louzao M (2012) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biol Conserv* 156:94–104
- Orians G, Pearson N (1979) On the theory of central place foraging. In: Horn D, Mitchell R, Stairs G (eds) *Analysis of ecological systems*. Ohio State University Press, Columbus, OH, p 155–177
- Oschlies A, Garçon V (1998) Eddy-induced enhancement of primary production in a model of the North Atlantic Ocean. *Nature* 394:266–269
- Palacios DM, Bograd SJ, Foley DG, Schwing FB (2006) Oceanographic characteristics of biological hot spots in the North Pacific: a remote sensing perspective. *Deep Sea Res II* 53:250–269
- Peck DR, Smithers BV, Krockenberger AK, Congdon BC (2004) Sea surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons. *Mar Ecol Prog Ser* 281:259–266
- Petus C, da Silva ET, Devlin M, Wenger AS, Álvarez-Romero JG (2014) Using MODIS data for mapping of river types within river plumes in the Great Barrier Reef, Australia: towards the production of river plume risk maps for reef and seagrass ecosystems. *J Environ Manag* 137:163–177
- Phillips RA, Xavier JC, Croxall JP, Burger A (2003) Effects of satellite transmitters on albatrosses and petrels. *Auk* 120: 1082–1090
- Pinaud D, Weimerskirch H (2007) At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *J Anim Ecol* 76:9–19
- Qiu W, Joe H (2013) clusterGeneration: random cluster generation (with specified degree of separation). <http://cran.r-project.org/web/packages/clusterGeneration/index.html> (accessed on 2 Jun 2014)
- R Core Team (2013) *R: a language and environment for statistical computing*. R: Foundation for Statistical Computing, Vienna
- Rayner MJ, Carlile N, Priddel D, Bretagnolle V and others (2016) Niche partitioning by three *Pterodroma* petrel species during non-breeding in the equatorial Pacific Ocean. *Mar Ecol Prog Ser* 549:217–229

- Ridgeway G (2007) gbm: generalized boosted models. <https://cran.r-project.org/web/packages/gbm/> (accessed on 8 Jun 2014)
- Robin X, Turck N, Hainard A, Tiberti N, Lisacek F, Sanchez JC, Müller M (2011) Package pROC. <http://cran.r-project.org/web/packages/pROC/pROC.pdf> (accessed on 28 May 2014)
- Rogerson P (2001) Statistical methods for geography. Sage, London
- Sabarros PS, Ménard F, Lévénéz JJ, Tew-Kai E, Ternon JF (2009) Mesoscale eddies influence distribution and aggregation patterns of micronekton in the Mozambique Channel. *Mar Ecol Prog Ser* 395:101–107
- Shaffer SA, Weimerskirch H, Scott D, Pinaud D and others (2009) Spatiotemporal habitat use by breeding sooty shearwaters *Puffinus griseus*. *Mar Ecol Prog Ser* 391: 209–220
- Smithers B, Peck D, Krockenberger A, Congdon B (2003) Elevated sea-surface temperature, reduced provisioning and reproductive failure of wedge-tailed shearwaters (*Puffinus pacificus*) in the southern Great Barrier Reef, Australia. *Mar Freshw Res* 54:973–978
- Sommerfeld J, Kato A, Ropert-Coudert Y, Garthe S, Hindell MA (2013) Foraging parameters influencing the detection and interpretation of area-restricted search behaviour in marine predators: a case study with the masked booby. *PLOS ONE* 8:e63742
- Spear LB, Ballance LT, Ainley DG (2001) Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the Equatorial Front. *Mar Ecol Prog Ser* 219:275–289
- Tew Kai E, Rossi V, Sudre J, Weimerskirch H and others (2009) Top marine predators track Lagrangian coherent structures. *Proc Natl Acad Sci USA* 106:8245–8250
- Uda M (1938) Researches on 'siome' or current rip in the seas and oceans. *Geophys Mag* 11:302–372
- Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York, NY
- Weeks SJ, Bakun A, Steinberg CR, Brinkman R, Hoegh-Guldberg O (2010) The Capricorn Eddy: a prominent driver of the ecology and future of the southern Great Barrier Reef. *Coral Reefs* 29:975–985
- Weeks S, Werdell PJ, Schaffelke B, Canto M, Lee Z, Wilding JG, Feldman GC (2012) Satellite-derived photic depth on the Great Barrier Reef: spatio-temporal patterns of water clarity. *Remote Sens* 4:3781–3795
- Weeks SJ, Steinberg C, Congdon BC (2013) Oceanography and seabird foraging: within-season impacts of increasing sea surface temperatures on the Great Barrier Reef. *Mar Ecol Prog Ser* 490:247–254
- Weimerskirch H (1998) How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in sooty shearwaters. *J Anim Ecol* 67: 99–109
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res II* 54:211–223
- Weimerskirch H, Chastel O, Ackermann L, Chaurand T, Cuenot-Chaillet F, Hindermeyer X, Judas J (1994) Alternate long and short foraging trips in pelagic seabird parents. *Anim Behav* 47:472–476
- Weimerskirch H, Ancel A, Caloin M, Zahariev A, Spagiari J, Kersten M, Chastel O (2003) Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *J Anim Ecol* 72:500–508
- Weimerskirch H, Le Corre M, Jaquemet S, Potier M, Marsac F (2004) Foraging strategy of a top predator in tropical waters: great frigatebirds in the Mozambique Channel. *Mar Ecol Prog Ser* 275:297–308
- Weimerskirch H, Le Corre M, Tew Kai E, Marsac F (2010) Foraging movements of great frigatebirds from Aldabra Island: relationship with environmental variables and interactions with fisheries. *Prog Oceanogr* 86:204–213
- Yen P, Sydeman W, Hyrenbach K (2004) Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *J Mar Syst* 50:79–99
- Yen P, Sydeman W, Bograd S, Hyrenbach K (2006) Spring-time distributions of migratory marine birds in the southern California Current: oceanic eddy associations and coastal habitat hotspots over 17 years. *Deep Sea Res II* 53:399–418

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