

# Distribution and predictability of foraging areas in breeding Chatham albatrosses *Thalassarche eremita* in relation to environmental characteristics

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**ABSTRACT:** The analysis of environmental characteristics to explain the distribution of endangered seabirds can aid in the identification of important areas at sea and lead to more effective conservation. We used high resolution Global Positioning System (GPS) tracking data to study the at-sea patterns of chick-rearing Chatham albatrosses *Thalassarche eremita* across 3 years (2007, 2008 and 2009) in relation to bathymetry, slope, sea surface temperature (SST) and chlorophyll *a* (chl *a*) concentration. Birds mostly foraged within 400 to 600 km of their colony, located within the southeastern part of New Zealand's continental shelf, the Chatham Rise. Despite little spatial overlap across years, foraging areas were predominantly associated with waters of less than 2500 m depth, slopes of 1 to 4°, SST between 15 and 16°C, and chl *a* concentrations >1 mg m<sup>-3</sup> in all years. According to boosted regression tree models, no single habitat variable particularly explained the spatial occurrence of foraging areas. However, bathymetry was of higher relative importance in 2008 and 2009, while chl *a* was relatively more important in 2007, a year of increased primary productivity. Our results suggest that chick-rearing Chatham albatrosses rely on resources that are generally predictable in location, but that they also respond to fine-scale changes within their foraging environment. Incorporating such dynamics into conservation planning might be best addressed by mitigating incidental bycatch in fishing operations, as well as implementing a protected area southeast of the breeding site, which we identified as a key foraging zone.

**KEY WORDS:** Habitat selection · Chatham Rise · GPS · BRT analysis · Important marine areas · Conservation planning

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## INTRODUCTION

Foraging seabirds are thought to respond to spatial heterogeneity in food abundance and availability, which in turn is subject to physical and biological processes linked to oceanic features such as bathymetric relief, sea surface temperature and primary productivity (Croxall & Wood 2002, Weimers-

kirch et al. 2005, Weimerskirch 2007). Exploitable food resources at sea can be patchy and ephemeral, and their predictability via environmental characteristics varies with geographic region and spatial scale (Pinaud & Weimerskirch 2007, Trathan et al. 2008, Phillips et al. 2009). Species such as albatrosses, shearwaters and petrels (Procellariiformes) can cover large distances in comparatively little

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time and are known to target large and meso-scale phenomena like oceanic frontal zones, eddies, seamounts or continental shelf areas as potential foraging areas (e.g. Waugh et al. 1999, Piatt et al. 2006, Raymond et al. 2010). Within such predictable structures, area-restricted search behaviour is commonly applied in order to locate prey which can be scattered at finer scales (Weimerskirch 2007, Miramontes et al. 2012). The detection of potential foraging areas by seabirds may result from prior experience based on recurring prey aggregations, local enhancement or through the recognition of ocean colours or odours (Grünbaum & Veit 2003, Weimerskirch et al. 2007, Nevitt et al. 2008, Kappes et al. 2010).

Variation in foraging behaviour across and within species had led researchers to characterise 2 different 'modes of exploitation' in seabirds depending on preferences for either pelagic (open oceanic) or neritic (shelf region) foraging habitats, often in the context of resource partitioning through different search and prey detection patterns (Waugh & Weimerskirch 2003, Elliott et al. 2009, Miramontes et al. 2012). Such patterns can be species-specific, but mostly depend on temporal (e.g. stages in the annual cycle) and spatial (e.g. location of breeding colony) factors as well as interactions between species (Paiva et al. 2010a,b, Wakefield et al. 2011). Generally, the accessibility of foraging habitats varies over time and is more restricted during the breeding season when birds become central place foragers (Pinaud & Weimerskirch 2005, Wakefield et al. 2009, Kappes et al. 2010), with spatial confinement being most pronounced during early chick-rearing (e.g. Hedd et al. 2001, Huin 2002, Phalan et al. 2007). In many species, the extent of the foraging range varies with breeding stage, being most restricted during early chick-rearing (Hedd et al. 2001, Huin 2002, Phalan et al. 2007). Moreover, foraging patterns and habitat choice can be subject to inter-annual variation according to species-specific responses to changing environmental conditions around their breeding sites (Xavier et al. 2003, 2004).

Here, we studied foraging patterns and habitat use in a rare New Zealand endemic breeder, the Chatham albatross *Thalassarche eremita*. The species is listed as 'vulnerable' by the IUCN ([www.iucnredlist.org](http://www.iucnredlist.org), version 2012.2.) with its entire population breeding on a single rock stack (The Pyramid) located in the east of New Zealand's extended continental shelf, the Chatham Rise. The area is characterised by steep shelf slopes within a transition zone of subtropical and subantarctic frontal

systems, and is currently subject to a high level of commercial fishing activities (Nicholls et al. 2002), which pose a threat to breeding Chatham albatrosses due to competition for the same resource as well as incidental bycatch of birds during fishing operations (Robertson et al. 2003). Based on annual observed fatalities in relation to population productivity, Chatham albatrosses were assessed to be at 'very high' risk of being killed in both trawl and longline fisheries within the Chatham Rise (Richard & Abraham 2013).

Effective conservation of highly mobile species such as albatrosses requires an understanding of the factors that influence their habitat use patterns, locally and within a wider oceanographic context, in order to assess and mitigate risks (Michael et al. 2013), especially during the chick-rearing period when energy requirements and foraging effort are thought to be highest (Weimerskirch et al. 2005). Preliminary satellite tracking studies of Chatham albatrosses in 1997 found that brooding birds remained within the shelf region of the Chatham Rise (Robertson & Nicholls in BirdLife International 2004), despite other predictable meso-scale features like frontal zones as well as seamounts being within their reach. This suggests that the species relies on continental shelf features when raising small chicks. However, information is lacking on whether such distributional patterns are consistent over time and thus could inform conservation planning. It is also unknown whether spatially and temporally stable common foraging areas exist, and to what degree the foraging distribution (and its potential annual variation) responds to environmental conditions at finer spatial scales than addressed in previous studies.

In the present study, we used high resolution Global Positioning System (GPS) tracking data from adult breeding Chatham albatrosses during early chick-rearing over 3 consecutive years to investigate: (1) the overall extent and variation in their annual foraging range and (2) the annual distribution of foraging areas in relation to environmental characteristics. Specifically, we assess the performance of 4 habitat parameters commonly studied as proxies for prey availability (bathymetry, slope, sea surface temperature [SST] and chlorophyll *a* [chl *a*] concentration) as explanatory variables for the spatial and temporal occurrence of foraging areas. We then discuss the potential of those parameters for the identification or even prediction of key foraging areas for Chatham albatrosses and the applications of our results in conservation planning.

## MATERIALS AND METHODS

### Logger deployment

Chatham albatrosses were studied at The Pyramid (44° 25' S, 176° 14' W; 1.7 ha, 174 m a.s.l.), the southernmost islet of the Chatham Islands archipelago, New Zealand, where ca. 4500 pairs breed annually. Eggs are laid from September to October and hatch during November and December, with chicks fledging from March to April (ACAP 2009). We studied the foraging distribution of adult breeders during early chick-rearing (i.e. November–December) across 3 consecutive years by fitting miniaturized GPS data loggers to 12 birds in 2007, 29 birds in 2008 and 27 birds in 2009. Each GPS device (type 'GiPSy', TechnoSmArt; 45 × 24 × 3 mm with integrated antenna) was attached to a rechargeable battery (53 × 35 × 5 mm). The combined weight of 28 g was equivalent to 0.8% of the average body mass of Chatham albatrosses and thus was below the recommended threshold of 3%, above which adverse behavioural effects could be expected (Phillips et al. 2003). Birds were monitored after data loggers were fitted, with the majority returning to their nests immediately. The data loggers were set to take one positional fix every 5 min to allow for high resolution track recordings while maintaining battery power for about 10 d, in correspondence to the estimated maximum foraging trip length of 8 d in brooding Chatham albatrosses (Robertson & Nicholls in BirdLife International 2004). The devices were waterproof sealed and attached with Tesa® tape to the back feathers of study birds. All birds fitted with devices were identifiable by both metal and black-on-white numbered Darvic sight bands. To account for the limited life span of the GPS batteries, we recaptured birds upon their first return to their nest by monitoring individually marked nest sites on a daily basis. With annual retrieval rates of 80 to 90%, and the number of failed nests amongst study birds not exceeding levels observed within the remaining colony, we could rule out any deleterious effects of the GPS loggers.

### Data processing and identification of foraging areas

Positional data downloaded from the GPS devices was processed in ArcGIS 9.3.1 (ESRI 2008). We excluded all locations on land as well as within a buffer of 0.5 km around the colony to account for on-shore bird locations erroneously located at sea due to

spatial deviations in the GPS recordings. We chose to also include incomplete foraging trips in subsequent analyses, as we could rule out biases towards near-colony locations: in all cases of premature device failure the bird had already covered above average distances from the colony.

The comparatively high spatial resolution of our tracking data allowed for foraging range description (i.e. maximum north/south and east/west extent) based on the actual distribution of tracks. We assessed variation in the extent of annual foraging ranges by calculating home range sizes as minimum convex polygons (mcp) using the 'adehabitatHR' package (Calenge 2011) implemented in R version 3.0.1 (R Development Core Team 2013). To account for differences in the number of birds tracked each year, we created random subsamples of the 2008 and 2009 datasets based on the smaller sample from 2007 ( $n = 10$  individuals) for comparison, using bootstrapping procedures. As both the 2008 and 2009 datasets yielded one trip reaching far beyond the range of all other trips, we ran our analyses with mcp's based on both 100% and 95% of the 2008 data and 100% and 90% of the 2009 data, to determine whether excluding 'extremes' (Calenge 2011) affected the results.

We used kernel density estimation (KDE), applying Hawth's Tools (Beyer 2006) in order to identify core areas in the foraging distribution for further analysis in relation to environmental characteristics. Density estimates were based on the quartic kernel function (Silverman 1986) which calculates point densities within a specified neighbourhood around each point. The resulting density estimates correspond to the amount of time the birds spent in any given area (Seaman et al. 1999), and can be used as a proxy measure for the intensity with which certain parts of the foraging range were frequented (Wood et al. 2000). KDE does not require serial independence of observations, and the use of constant time intervals increases the accuracy and precision of the estimate (De Solla et al. 1999), which makes it a convenient method given the nature of GPS tracking data. It has also been recommended as useful when interactions with the marine environment are investigated (Wood et al. 2000). When applied to data from multiple tracks, the method has been found to perform equivalent to alternative methods such as first-passage-time or state-space modelling in the identification of important areas (i.e. areas of intensified use) within the foraging range of breeding albatrosses (Tancell et al. 2013). The 50% volume contours (PVC) of the KDE are commonly regarded as descriptors of core

foraging areas (e.g. Hedd et al. 2001, Neves et al. 2012, Paiva et al. 2013). Similar to Brothers et al. (1998), we pooled individual tracking data to estimate and evaluate annual foraging zones at the population level. As suggested by several authors (e.g. Beyer 2006, Calenge 2011, Tancell et al. 2013), we based the choice of the smoothing parameter ( $h$ ) used in the KDE on successive trials and visual assessment of the effectiveness of resulting PVC in order to determine the most appropriate value for our analytical purposes and according to the nature of our data.

For all 3 years of our study we found a comparatively small smoothing parameter of  $h = 5$  km as the best fit for our data, as it prevented over-smoothing within high resolution spatial datasets of relatively widespread or scattered distribution, and enabled us to identify areas of intensified use during foraging on a fine spatial scale. Based on the assumption that these areas were correlated spatially with higher exploitation of the environment (Tancell et al. 2013), we used the resulting 50 PVC to select potential foraging areas for further analysis with respect to environmental characteristics of the foraging habitat. We acknowledge that this method could include concentrations of non-foraging locations resulting from birds repeatedly passing through the same area (overlapping tracks) or 'resting' (i.e. drifting or sleeping), where the latter in visual foragers like albatrosses might particularly bias density estimates from night time locations. However, bias towards potential 'resting' locations during darkness was minimised by applying KDE to pooled data (Tancell et al. 2013). Moreover, based on positional data alone, 'resting' locations cannot be reliably distinguished from locations resulting from foraging by a 'sit and wait' strategy, which may occur when feeding on squid that are available to pelagic foragers only at night (Imber 1973, Weimerskirch et al. 2007). It is also possible that 'resting' locations during both day and night result from birds prospecting for potential prey captures (Miramontes et al. 2012), such as sitting on the water while waiting for refuse from commercial fishing operations or following other prey cues. As albatrosses have been found to also forage along a straight path (Catry et al. 2004, Weimerskirch et al. 2007), we assumed that overlapping tracks within potential foraging habitat should not be excluded by default when identifying foraging areas. Considering this, and in concordance to other authors (e.g. Hedd et al. 2001, Neves et al. 2012, Paiva et al. 2013), we regarded the term 'foraging areas' as warranted to describe the areas we identified via 50 PVC.

## Analysis of environmental characteristics in relation to foraging areas

### Environmental data and sampling design

To investigate whether the occurrence and spatial distribution of foraging areas of Chatham albatrosses was linked to environmental characteristics, we obtained data on 2 static and 2 dynamic habitat parameters for the region of the Chatham Rise. Raster data sets of bathymetry and seafloor slope were sourced from the New Zealand Institute of Water and Atmosphere (NIWA), at a grid size of  $1.2 \times 1.2$  km and  $0.25 \times 0.25$  km, respectively. Information on SST and chl  $a$  was downloaded from online servers (<ftp://podaac-ftp.jpl.nasa.gov/oceanTemperature/modis/L3/aqua> and <http://oceansci.gsfc.nasa.gov/SeaWiFS/L3SMI>), available at spatial resolutions of  $4 \times 4$  km and  $9 \times 9$  km, respectively. We chose monthly composites of SST and chl  $a$  to minimise data loss caused by cloud cover, approximating the time periods within which most foraging trips were recorded (November for 2007 and 2008 and December for 2009 study periods).

To minimise bias when correlating the distribution of foraging areas with environmental characteristics (Zandbergen 2010), we standardised the spatial resolution of bird tracking data and environmental data by designing a customised grid as a common sampling unit for 'presence' or 'absence' of foraging areas (i.e. bird locations identified via the 50 PVC of our KDE) and respective habitat variables across the foraging range. To avoid disproportionately inflating the number of 'absence' grid cells, we based the spatial extent of our sampling grid on the 'range of normal activities' during foraging (Calenge 2011), which in our case was the area within which 96 % of all bird locations had been recorded during the 3 years of the study. This excluded 2 trip sections reaching approximately 300 km and 600 km beyond this area, which were considered to be 'occasional large moves to unusual places outside the normal home range' (Calenge 2011). For computational reasons we considered a grid cell size of  $9 \times 9$  km as appropriate, which corresponded to the spatial scale of the coarsest habitat variable (chl  $a$ ). Values of the remaining habitat variables of finer spatial resolution were averaged per grid cell to ensure unique values per sampling unit. 'Presence' of foraging areas was assigned to 2.8 % of all grid cells in 2007, 6.1 % in 2008 and 2.6 % in 2009. We estimated annual overlap between foraging areas via the percentage of shared 'presence' grid cells between each year, in addition

to visual inspection of potential clusters of overlapping cells in order to identify common or key foraging zones (i.e. spatially and temporally consistent presence of foraging areas).

### Statistical analysis

We tested whether annual frequency distributions of bathymetry, slope, SST and chl *a* values within grid cells of foraging area 'presence' differed from those within grid cells of foraging area 'absence', using a 2-sided Kolmogorov-Smirnov test. The same test statistics were used to determine whether the environmental characteristics in foraging areas were consistent across years, by comparing the annual frequency distributions of habitat variables within grid cells of 'presence' only.

To quantify the relative importance of the different habitat variables in explaining the annual distribution of foraging areas, we used boosted regression tree (BRT) models with foraging area 'presence/absence' across the spatial grid as the response variable (coded 1 or 0). A BRT model is a form of regression that uses a boosting algorithm to linearly combine up to several thousand trees into one model, improving overall model accuracy (e.g. Elith et al. 2008). BRTs perform well in model discrimination (Elith et al. 2006, Keller et al. 2011, Schmidt & Drake 2011) and can incorporate some colinearity between explanatory variables as well as non-linear relationships and potential interactions among explanatory variables (Elith et al. 2008). Machine learning approaches such as BRT have also been shown to provide the best discrimination between areas of seabird presence and absence and the smallest bias in previous tests (Oppel et al. 2012).

Our gridded sampling design increased the possibility of spatial autocorrelation altering the parameter estimates and error probabilities of the statistical model by influencing the variance-covariance matrix (Kühn 2007). Therefore, we tested for spatial autocorrelation using a Moran's *I* test (calculated in relation to the first nearest neighbour of each observation) in the 'spdep' package (Bivand et al. 2011) using R version 2.13.1 (R Development Core Team 2011). We found low but significant autocorrelation in the residuals for foraging area 'presence/absence' (Moran's *I* = 0.409,  $p < 0.001$ ). To account for this, we integrated our models with a spatial component (i.e. spatial auto-covariate term; SAC) that expressed how much the response variable at any one site reflects response values at spatially adjacent and surround-

ing sites (Dormann et al. 2007). This method effectively allowed us to create a new explanatory variable which was included in addition to the habitat variables (i.e. bathymetry, slope, SST and chl *a*) in each model (Diniz-Filho et al. 2008). The SAC term is intended to capture spatial autocorrelation originating from the movement of Chatham albatrosses between sampling sites (i.e. grid cells). We computed the SAC term for each grid cell following the method of Augustin et al. (1996), using a neighbourhood boundary of 200 km for the 'presence/absence' model, weighted by inverse distances among neighbouring observations.

We fitted a BRT model for each year of the study (2007, 2008 and 2009) using the `gbm.step` function in the 'dismo' R package (Hijmans et al. 2012) with evaluation functions from the 'gbm' package (Ridgeway 2010). We applied a tree complexity of 5 (which automatically detects and fits up to 5-way interactions among explanatory variables), a learning rate of 0.01, and a Bernoulli error structure. Because using the same data for model testing and validation leads to over-fitting and deflates the estimated error rate, the optimal number of trees was determined using 10-fold cross-validation (CV) with a bag fraction of 0.5. The relative contribution (i.e. 'relative importance') of the explanatory variables was estimated in the 'gbm' package based on the number of times the variable was selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees (Friedman & Meulman 2003). The contribution of each variable was scaled so that the sum added up to 100, with higher numbers indicating stronger influence on the response. Model performance was assessed using CV deviance. Lower CV deviances indicate better performance than higher CV deviances. An additional measure of model performance was calculated during cross-validation, using the area under the receiver operating curve (AUC), which provides a measure of the degree to which the fitted values discriminate between observed outcomes (Hanley & McNeil 1982). An AUC value of 1 indicates that the model perfectly discriminates between outcome 1 (presence) and outcome 0 (absence), while a value of 0.5 indicates that the model performs no better than chance.

## RESULTS

We retrieved recordings of at least one complete foraging trip from 48 of 50 birds recaptured. Six individuals completed multiple trips before recapture,



Table 1. *Thalassarche eremita*. Overview of annual sample sizes, trip parameters and range description via maximum north-south and east-west extent and minimum convex polygons (mcp) for foraging birds during 3 consecutive chick-rearing periods (November/December 2007, 2008, and 2009)

Year	No. ind. tracked	Bird locations	Foraging trip		— Trip duration — (days)				Max. distance from colony (km)	Range extent <sup>a</sup>		Home range (km <sup>2</sup> )	
			Com- plete	Incom- plete	Min.	Max.	Mean	SE		N/S	E/W	mcp (100%)	Extremes excluded
2007	10	3264	12	0	2	3	2.5	0.1	406	41.8°S / 46.2°S	177.7°W / 171.3°W	149	N/A
2008	20	13 182	22	7	1	6	3.5	0.3	652	41.5°S / 46.3°S	175.7°E / 169.3°W	417	289 (95 %)
2009	18	7464	18	6	1	5	2.3	0.3	1260	41.6°S / 46.6°S	179.7°W / 161.6°W	548	351 (90 %)

<sup>a</sup>Note that the study area crosses the dateline. Coordinates are given in decimal degrees

while battery or device failure resulted in incomplete trip recordings in 13 cases. The dataset for subsequent analyses comprised 12 complete trips from 10 individuals in 2007, 22 complete and 7 incomplete trips from 20 individuals in 2008, and 18 complete and 6 incomplete trips from 18 birds in 2009 (Table 1). Despite similar numbers of individuals tracked and number of foraging trips, almost twice as many bird locations were recorded in 2008 as in 2009. Moreover, birds spent on average 1 d longer on a foraging trip in 2008 than in either 2007 or 2009 chick-rearing periods (Table 1). Unlike in subsequent years, birds tracked in 2007 never ventured out to sea for more than 3 d and showed little variation in trip length.

#### Spatial and temporal patterns in foraging range and distribution of foraging areas

Chatham albatrosses reached a maximum distance of 405 km from their colony in 2007, 651 km in 2008 and 1260 km in 2009 (Table 1). The overall foraging range of chick-rearing birds stretched from 41.5°S to 46.6°S and 175.7°E to 161.6°W with little annual variation in the N/S extent of foraging ranges but clear differences in the E/W extent (Table 1). Nevertheless, the majority of birds did not leave the continental shelf area (Chatham Rise), and most remained within a radius of 400 km from the colony. In 2009, this range was only exceeded by one individual venturing to the east to forage around the Louisville Ridge (Fig. 1). During the 2008 season, however, birds were observed to forage more often up to 600 km off their breeding island, predominantly frequenting the southern and eastern parts of the Chatham Rise (Fig. 1).

Home range size according to mcp's appeared more restricted in 2007 than in either 2008 or 2009, even if individuals that ranged beyond the common distributional range were excluded (Table 1). Bootstrap sampling of subsets from 2008 and 2009 data showed that this was not due to tracking larger numbers of birds in these years compared to 2007. We found that 100% of the simulated home range sizes for 2008 and 83% of simulated home range sizes for 2009 were larger than the 2007 home range, at a significance level of  $p < 0.01$ . Excluding 'extreme' data (Calenge 2011), we obtained the same result for simulations run on 95% of the 2008 tracking dataset. However, for simulations on 90% of the 2009 tracking dataset, only 64% of the simulated home ranges were larger than in 2007. Home range size, trip duration and the number of bird locations indicated a more widespread distribution and more intense use of the foraging range during 2008.

Foraging areas (as identified via KDE and transferred onto our generalised sampling grid) were relatively widespread across the general foraging range, occurring both on the shelf and along shelf edges but only occasionally in deeper waters north and south of the Chatham Rise (Fig. 2). Birds appeared to forage in roughly similar regions across years, although actual overlap of 'presence' grid cells was rare, being largest between 2007 and 2009 (9.4%) and between 2008 and 2009 (9.3%), compared to only 6.7% overlap between 2007 and 2008 and over all 3 years (2.2%). Extensive overlap was obvious only to the west of the main Chatham Island as well as south and east of the breeding colony (Fig. 2). The latter was the only region where foraging area 'presence' from all 3 years overlapped and this area also yielded the largest number of adjacent

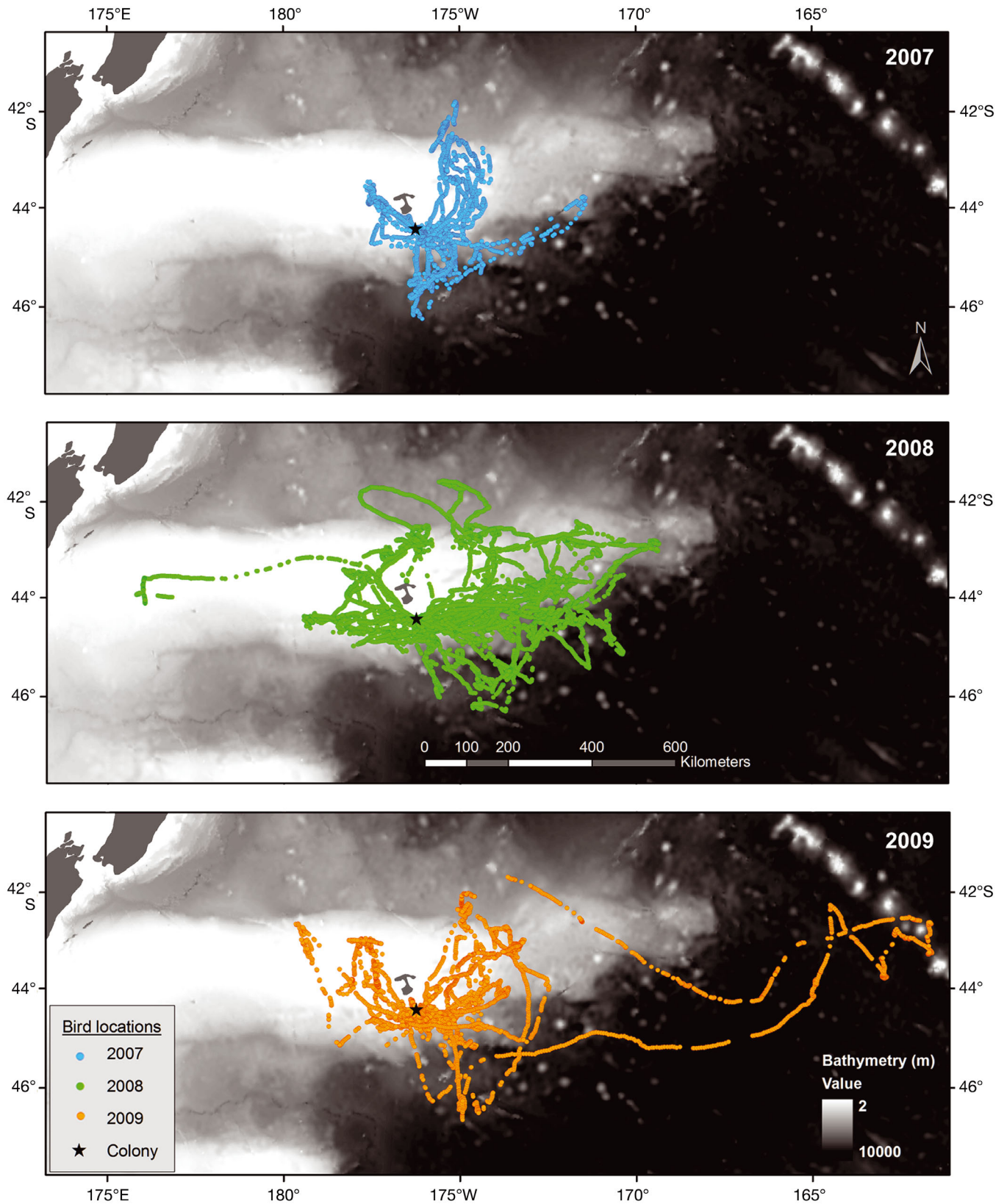


Fig. 1. *Thalassarche eremita*. Foraging range and distribution during early chick-rearing in November/December 2007, 2008 and 2009. Shown are annual distributions of bird locations as retrieved from GPS tracking devices at a setting of 1 fix per 5 min

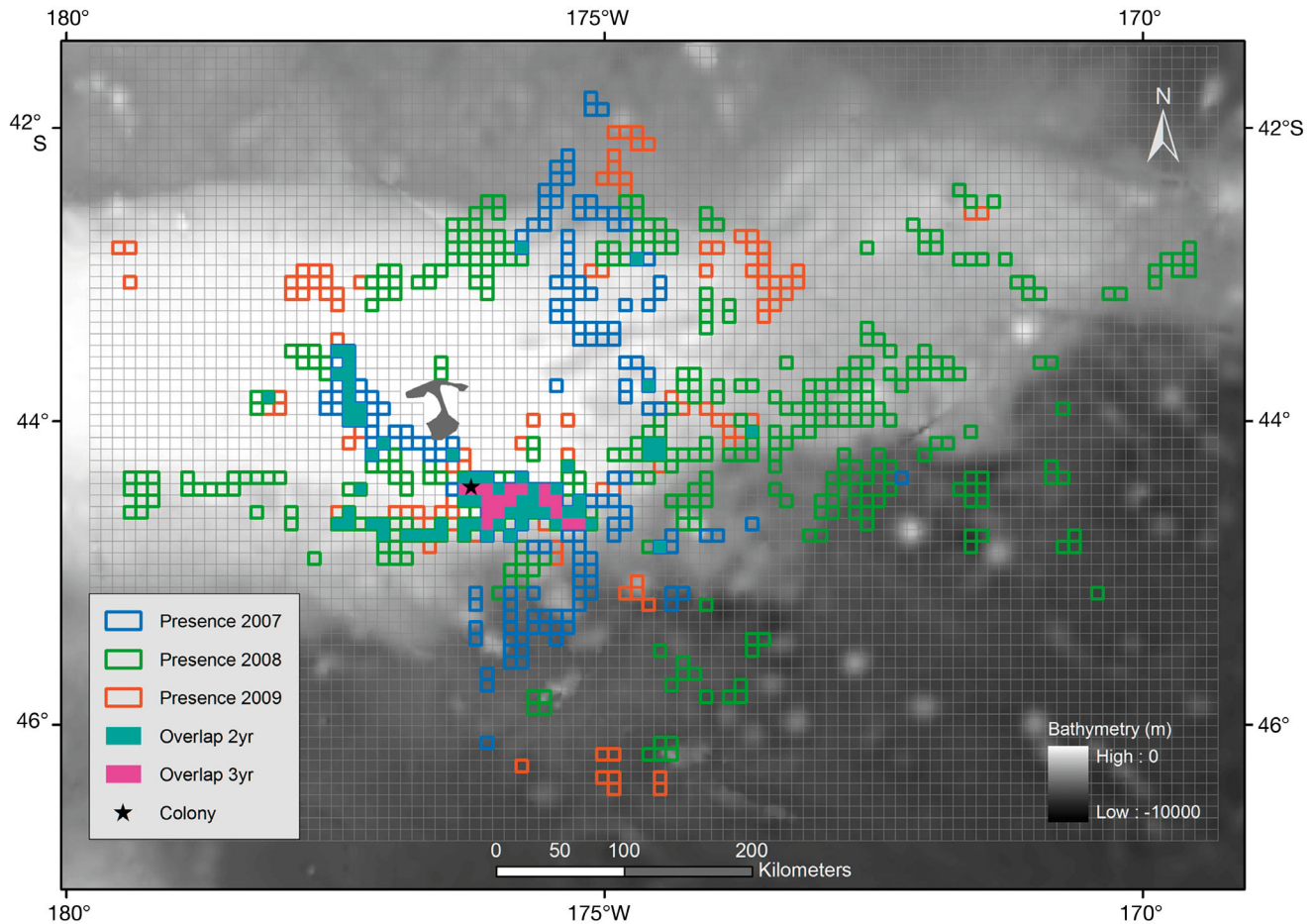


Fig. 2. *Thalassarche eremita*. Overview of 'presence' (coloured grid cells) and 'absence' (plain grid cells) of foraging areas across a customised grid (cell size  $9 \times 9$  km) covering the general foraging range during early chick-rearing over 3 consecutive years (November/December 2007, 2008 and 2009). Annual distributions of foraging areas (i.e. 'presence' grid cells) and spatial overlap between cells occupied in 2 as well as all 3 years are colour coded

overlap cells (Fig. 2). Other than this, no major common foraging zones (i.e. spatially and temporally consistent occurrence of foraging areas) could be identified.

#### Environmental characteristics in relation to foraging areas

The frequency distributions of bathymetry, slope, SST and chl *a* values within foraging areas ('presence' across grid) were significantly different ( $p < 0.001$ ) from the frequency distributions within areas where foraging activity was 'absent'. This was true for all 3 years of the study, except for chl *a* concentrations in 2009 ( $p = 0.2$ ). This suggests that foraging areas occurred in relation to the environmental characteristics of the general foraging range, and not simply by chance. Within foraging areas only, the

characteristics of slope did not vary significantly between years ( $p > 0.1$ ), while annual differences in the characteristics of bathymetry and chl *a* concentration were significant ( $p < 0.001$ ). Variation in the annual distributions of SST within foraging areas was significant between both the 2007 and 2009 as well as 2008 and 2009 seasons ( $p < 0.001$ ) but non-significant between 2007 and 2008 seasons ( $p = 0.07$ ).

Overall, the range of values for bathymetry, slope, SST and chl *a* within foraging areas was more restricted compared to that sampled across grid cells where foraging areas were absent (Fig. 3A–D). Foraging areas were absent from the deepest waters as well as the steepest slopes within the general foraging range in all years, but at the same time were more likely to occur in areas with comparatively steeper slopes of 1 to  $4^\circ$  and within comparatively shallower waters ( $< 2000$  m; Fig. 3A,B). Foraging areas rarely occurred at SST below  $12^\circ\text{C}$  and above



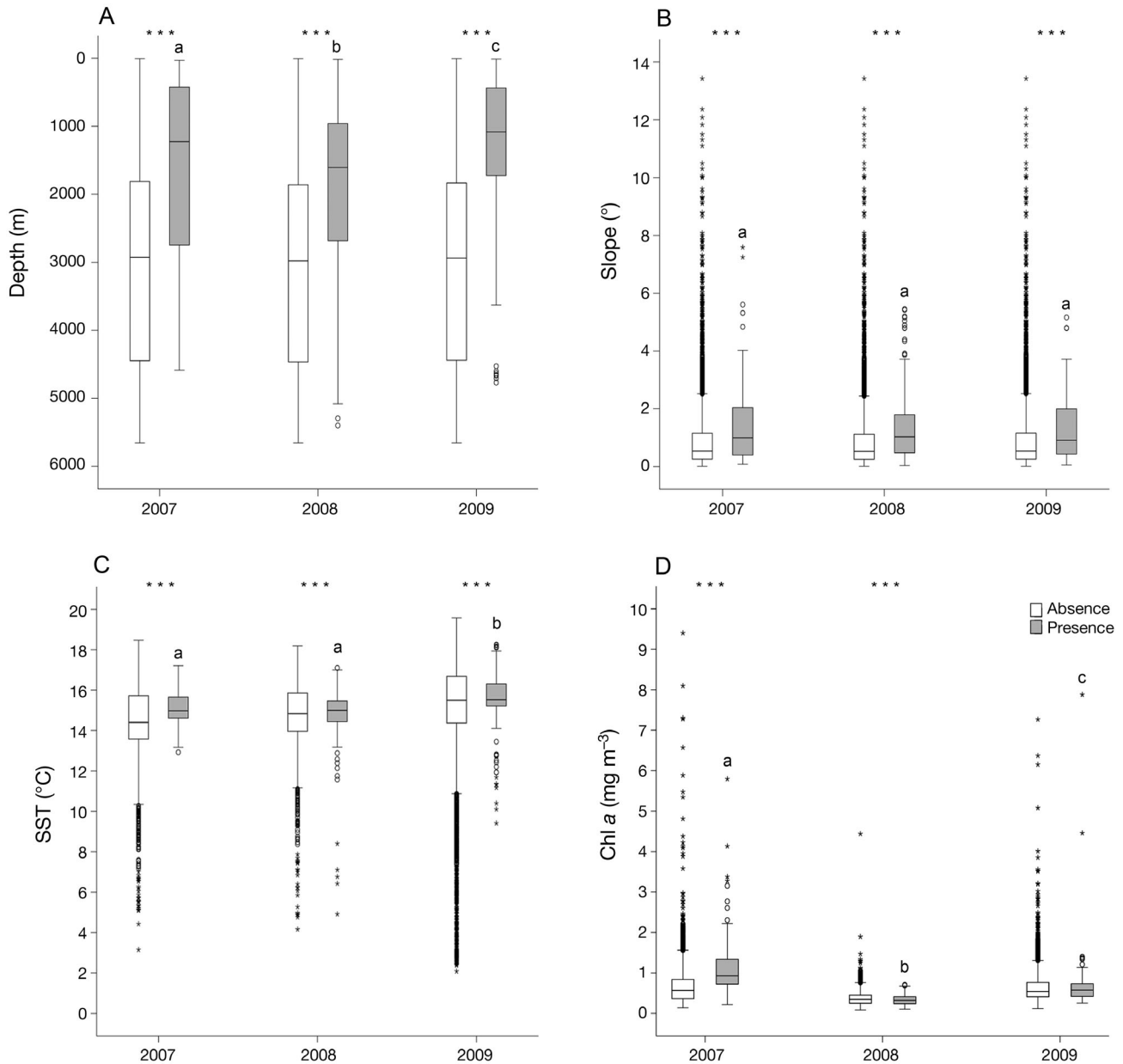


Fig. 3. *Thalassarche eremita*. Distribution of (A) bathymetry, (B) slope, (C) sea surface temperature (SST) and (D) chlorophyll *a* (chl *a*) concentration values within grid cells of foraging area 'presence' (filled box plots) versus 'absence' (blank box plots) across the general foraging range during early chick-rearing in November/December 2007, 2008 and 2009. Displayed are median, quartiles, extremes and outliers of the environmental data sets. Asterisks [\*\*\*] indicate significant differences ( $p < 0.001$ ) between habitat characteristics within grid cells of foraging area 'presence' versus 'absence' within years, while different letters (a, b, c) illustrate significant differences ( $p < 0.001$ ) amongst years within grid cells of foraging 'presence' only (i.e. same letters = no difference)

18°C, and were most commonly associated with SST ranges of 15 to 16°C in all years (Fig. 3C). The tendency of foraging areas to occur in association with comparatively higher chl *a* concentrations ( $>1 \text{ mg m}^{-3}$  to  $2.5 \text{ mg m}^{-3}$ ), however, only appeared obvious in 2007 (Fig. 3D).

Low CV deviance ( $<0.3$ ) in combination with high ( $>0.9$ ) cross-validated AUC values within our boots-

ted regression tree analysis indicated that the annual BRT models explained nearly all the variation in foraging area 'presence/absence' across the general foraging range. However, no single environmental variable stood out as particularly powerful in explaining the observed distribution of foraging areas, with individual contributions not exceeding 20.5% (Table 2). In comparison, the SAC term consistently

contributed ca. 50 % each year. Accounting for SAC, chl *a* concentration was of highest relative importance in 2007, contributing 20.5%; while in 2008 and 2009 bathymetry was the strongest explanatory variable with contributions of 13.9% and 15.2%, respectively (Table 2). The relative contributions of bathymetry, slope and SST remained similar across years, while chl *a* explained comparatively less in 2008 and 2009 (Table 2).

## DISCUSSION

### General foraging patterns and range

During early chick-rearing, we found Chatham albatrosses concentrated their foraging efforts within shelf and shelf-break areas of the Chatham Rise and only rarely ventured into deeper pelagic waters. This pattern was consistent across all 3 years of our study, and has also been observed by Robertson & Nicholls (in BirdLife International 2004) in preliminary satellite-tracking studies of brooding Chatham albatrosses in 1997, suggesting that this behaviour is typical for the species. Remaining within continental shelf and slope areas while raising chicks (neritic foraging) has been found in several other albatross species breeding on islands located on a shelf (e.g. Hedd et al. 2001, Awkerman et al. 2005, Waugh et al. 2005). Such

species typically have relatively small foraging ranges and short foraging trips, which corresponds with what we found for Chatham albatrosses. This contrasts with a more pelagic foraging pattern found in many procellariiform species breeding on islands with little or no shelf region. Birds in this environment often have to cover considerable distances to exploit regions where prey availability is enhanced due to physical processes like frontal systems, eddies or seamounts, as well as continental shelf regions (Catry et al. 2004, Xavier et al. 2004, Freeman et al. 2010). Interestingly, Rayner et al. (2012) found that Chatham petrels *Pterodroma axillaris*, which breed on a neighbouring island to the Chatham albatrosses within the Chatham Rise, concentrated their foraging efforts during chick-rearing within pelagic waters about 1300 km to the south of their colony. Such observations indicate that it could be species-specific foraging strategies (i.e. prey preferences), rather than the location of the breeding site which determines the location of marine areas used for foraging during breeding. Different foraging patterns and spatial segregation due to resource partitioning in species using the same geographical region has been observed in several studies (e.g. Nicholls et al. 2002, Waugh & Weimerskirch 2003, Kappes et al. 2011).

Trip durations recorded for brooding Chatham albatrosses in our study never exceeded 6 d and can be classified as 'short' trips according to Baduini & Hyrenbach (2003). In other albatross species, short trips have been related to the need to provide chicks with regular meals (Brothers et al. 1998, Hedd et al. 2001, Catry et al. 2004). Based on studies in *Pterodroma* petrels, Rayner et al. (2012) even suggested that the time available at sea might determine distance travelled more than habitat selection. However, as Chatham albatrosses can reach flight speeds of 85 km h<sup>-1</sup> (Nicholls & Robertson 2007) and have been recorded to be able to cross the South Pacific within 11 d (Robertson & Nicholls in BirdLife International 2004), they should be capable of venturing beyond the continental shelf area within 6 d if it were advantageous. The rare occurrence of long distance trips during our study provides evidence that Chatham albatrosses actively limited the extent of their foraging range during chick-rearing. This receives further affir-

Table 2. *Thalassarche eremita*. Results of annual boosted regression tree (BRT) models to explain 'presence/absence' of foraging areas across the general foraging range during 3 consecutive chick-rearing periods (November and December 2007 through 2009). For an individual tree created in the BRT model, a variable's relative importance is the sum of squared improvements at all splits determined by it. A variable's overall relative importance (shown here) is the average of these values over all trees, expressed as a percentage. Variables given include a spatial autocorrelation term (SAC), bathymetry, slope, sea surface temperature (SST), and chlorophyll *a* (chl *a*). The top 2 most important variables in each model are highlighted in bold. Area under the receiver operating curve (AUC;  $\pm$ SE) and cross-validation (CV) deviance ( $\pm$ SE) values indicate model performance, where high AUC values and low CV deviances indicate better performance

Variable	Relative importance (%)		
	2007	2008	2009
SAC	<b>44.8</b>	<b>54.5</b>	<b>51.6</b>
Bathymetry	14.4	<b>13.9</b>	<b>15.2</b>
Slope	10.5	10.7	10.7
SST	10.4	10.8	11.8
Chl <i>a</i>	<b>20.5</b>	7.6	11.5
AUC ( $\pm$ SE)	0.954 (0.005)	0.933 (0.005)	0.941 (0.009)
CV deviance ( $\pm$ SE)	0.145 (0.009)	0.270 (0.007)	0.139 (0.004)

mation by the observation that the majority of birds remained within 400 to 600 km of their colony, and thus did not even exploit the full extent of the Chatham Rise. The restriction of the foraging range when brooding chicks has been found in many procellariiform species, and is assumed to occur in response to spatial and temporal constraints of central place foraging being strongest during this stage (Brothers et al. 1998, Fernández et al. 2001, Phalan et al. 2007). Due to a lack of data from other stages of the breeding season, we cannot confirm whether Chatham albatrosses would extend their foraging range during incubation or when attending larger chicks, and whether such ranges would reach beyond the continental shelf. Brothers et al. (1998) observed that shy albatrosses *Thalassarche cauta*, despite having a larger foraging range during incubation compared to chick-rearing, remained within shelf areas during both stages. Further studies are needed to determine whether it is the constraints of chick-rearing which likewise cause Chatham albatrosses to limit their foraging range extent. Our results suggest there is a sufficient availability of prey resources close to the colony in most cases, and that the Chatham Rise region can sustain adults and their offspring during periods of increased energy demands. However, this also indicates that bathymetric features and a neritic foraging pattern cannot entirely explain the observed foraging range extent of Chatham albatrosses.

#### **Potential of environmental characteristics in explaining the distribution of foraging areas**

Foraging within a region of comparatively high prey predictability such as the Chatham Rise might imply the existence of spatially defined and re-occurring foraging areas, possibly coinciding with physical features like the shelf break, where upwelling processes may enhance prey availability (Croxall & Wood 2002, Garcia et al. 2008). However, within meso-scale structures like continental shelves, the distribution of prey might be scattered at a finer scale (Miramontes et al. 2012). The relatively widespread distribution and low overlap of foraging areas we found for chick-rearing Chatham albatrosses across years, with no clear preference for either on-shelf or shelf break regions, appears to correspond to spatially scattered resources. Nevertheless, an area of overlapping foraging across all years of the study was identified at the southern shelf break of the Chatham Rise, indicating com-

paratively more predictable recurrence of prey resources within that region. Relatively inconsistent foraging locations have also been observed in chick-guarding white-capped albatrosses *Thalassarche steadi* (Torres et al. 2011), although birds in this case foraged within both neritic and pelagic habitats. In shy albatrosses, an exclusively neritic species during breeding, Hedd et al. (2001) reported foraging zones to be consistent across years, and they concluded that foraging birds were not distributed randomly within shelf regions. They associated this pattern with the observation of SST within foraging zones being similar each year, and assumed this indicated relatively stable and predictable prey availability within those zones. We too found evidence that foraging Chatham albatrosses were not distributed simply at random, as we could identify significant relationships between foraging areas and local bathymetry, slope, SST and chl *a* concentration. Foraging areas predominantly occurring within shallower waters but also at steeper slopes confirms the overall shelf-bound (neritic) foraging pattern of chick-rearing Chatham albatrosses. Wakefield et al. (2011) found similar relationships in chick-rearing black-browed albatrosses *Thalassarche melanophrys*, where foraging birds also showed no preference for either on-shelf or shelf break areas while at the same time tended to forage at comparatively steeper slopes and within a comparatively small band of SST. This suggests that the habitat associations we observed might be common in neritic foragers.

In the BRT models, none of the 4 habitat variables we tested stood out as being particularly powerful in explaining the observed distribution of foraging areas, while the relatively most important variable in all years was the SAC. This might be partly due to our gridded design in which a single foraging area could incorporate >1 grid cells or sampling units, but possibly also reflects the general pattern of chick-rearing Chatham albatrosses foraging within a spatially confined area. In all habitat variables except for chl *a*, the 'relative importance' values (i.e. the measure for how well each habitat parameter explained the distribution of foraging areas in relation to other parameters within the model) showed little change across years. This indicates that bathymetry, slope and SST remained consistent in their respective explanatory performance despite annual inconsistencies in the occurrence of foraging areas. Although weak, these habitat variables hold some predictive value for the foraging distribution of Chatham albatrosses.

Within the annual models, bathymetry performed comparatively better than slope, SST and chl *a* in 2 out of 3 years (2008 and 2009) while chl *a* had the comparatively strongest effect on the distribution of foraging areas in 2007. This was possibly related to a persisting La Niña weather pattern in 2007 ([www.niwa.co.nz/climate/nzcu/climate-update-101-november-2007/global-setting-and-climate-outlook](http://www.niwa.co.nz/climate/nzcu/climate-update-101-november-2007/global-setting-and-climate-outlook)), which caused lower water temperatures and increased chl *a* concentrations within the Chatham Rise region (O'Driscoll et al. 2011). Accordingly, a potentially enhanced local prey availability during that time might have led to a stronger relationship between foraging areas and chl *a*. Similarly, in another neritic forager, the waved albatross *Phoebastria irrorata*, Awkerman et al. (2005) found that both SST and chl *a* partly explained habitat use during foraging but were less consistent in predicting foraging location than bathymetry. Louzao et al. (2012) identified chl *a* as the most important variable characterising the distribution of chick-rearing Balearic shearwaters *Puffinus mauretanicus* foraging in continental shelf areas. It appears that for dynamic habitat parameters such as SST or chl *a*, the time frame for which data is retrieved from satellite recordings might influence their explanatory as well as predictive potential (e.g. Suryan et al. 2012). That chl *a* concentration is possibly a poor proxy for prey abundance was illustrated by Freeman et al. (2010), who found significant spatial overlap of foraging movements of chick-rearing black petrels *Procellaria parkinsoni* with shelf break regions (supposedly indicating enhanced prey availability), but relationships with chl *a* did not prove to be significant. On the other hand, Grémillet et al. (2008) found a strong match of seabird at-sea foraging habitat and zones of high primary productivity, but at the same time a spatial mismatch between seabirds and pelagic fish.

The lack of a clear single main explanatory habitat variable suggests we might be observing an interaction of equally important parameters affecting foraging distribution in the Chatham albatross. Hence, the foraging pattern of the species may be partly opportunistic (e.g. scanning an overall predictable area for foraging opportunities rather than specifically targeting distinct areas), resulting in little spatial repeatability in foraging areas and similar preferences for both on-shelf and shelf-break foraging environments. However, the comparatively scattered distribution of foraging areas and little overlap across years may also be due to annual variation in the spatial distribution of SST and chl *a* concentration and thus associated potential prey resources. Such spatial

and temporal dynamics within the environmental conditions might also have been causing the annual differences in home range size (i.e. most confined in 2007 and most widely spread in 2008) we found for foraging Chatham albatrosses. Our results thus mirror Cherel et al. (2000), who concluded that albatrosses rely on resources that are roughly predictable in location, but whose availability nevertheless varies from one year to the next.

The variance we encountered between the occurrence of foraging areas and 4 oceanographic habitat parameters suggests that other extrinsic factors such as ecosystem shifts, spatial dynamics of food webs and even the presence of commercial fishing operations (Waugh et al. 2005, Grémillet et al. 2008, Hipfner 2008, Torres et al. 2011) might need consideration when explaining habitat choice during foraging. For Chatham albatrosses, it is likely that the observed distribution of foraging areas is not only related to prey items made available by certain environmental conditions, but also to increased food availability due to fishing operations in the Chatham Rise area as individuals have repeatedly been recorded to fall victim to fisheries bycatch (Robertson et al. 2003, Richard & Abraham 2013). The overlap of foraging birds and fisheries has been observed in other albatross species by both Waugh et al. (2005) and Torres et al. (2011), suggesting that birds may target fishing vessels regularly. Moreover, regional prey depletion due to fisheries (Bertrand et al. 2012) can cause variation in suitable foraging areas or a mismatch between explanatory variables and bird distribution.

The potential of also including non-foraging behaviours within the identified foraging areas, such as resting or commuting, might mask relationships with environmental characteristics and thus increase the 'noise' in our analysis. However, such locations (i.e. slow movement along a straight line) could not reliably be assigned unequivocally to a specific foraging or non-foraging behaviour, and we did not see any benefit by trying to exclude them. As Miramontes et al. (2012) pointed out, albatrosses might even select resting areas in the context of prospecting for potential prey capture. We also assumed that during periods of strong time and energy constraints like early chick-rearing, foraging birds would not have much time to rest or sleep until returning to the nest in order to relieve their partner. Moreover, given the scope of our study, we considered it reasonable to include all areas where birds spent increased amounts of their time as such areas may be critical for conservation even if not exclusively used for foraging.



### Applications in conservation planning

Ensuring a safe and sustainable foraging environment for breeding birds is important for the conservation of any seabird species. Our study suggests that since the entire population of Chatham albatrosses is concentrated at a single breeding site within the Chatham Islands, the conditions of the Chatham Rise and in particular its southern and eastern parts will be critical for both adult survival and reproductive success of the species.

One management approach to protect the species from detrimental impacts of commercial fisheries would be to minimise overlap between fishing operations and bird distributions (Żydelis et al. 2011). This would imply the exclusion of fishing operations in areas that Chatham albatrosses primarily use for foraging. The foraging zone we identified on the shelf and shelf-break southeast of the breeding colony as consistently frequented by foraging birds has the potential to warrant the enforcement of strict conservation measures, including closure to fisheries. The comparatively small extent and spatio-temporal consistency of this area would make it feasible to be used as a protected area for Chatham albatrosses. However, considering that much of the remaining foraging areas were scattered and less predictable in location across the eastern Chatham Rise, it will also be crucial to enforce effective mitigation of incidental seabird bycatch for all fishing operations frequenting this region. This would ensure protection of foraging birds across their whole range and also reduce losses of albatrosses when they follow fishing boats into unprotected areas. The implementation of ecosystem-based fishery quotas and fisheries management to limit the risk of local prey depletion around seabird breeding colonies, as suggested by Bertrand et al. (2012), would also be a desirable measure.

It might be argued that studying only one stage of the breeding season, as well as a time frame of 3 years, might not be sufficient to identify a key foraging area for the species for the purposes of limiting fisheries from a productive area. However, as we found similar results as an older study (Robertson & Nicholls in BirdLife International 2004), and since we focused on the early chick-rearing period where breeding birds are supposedly the most vulnerable due to increased energy demands, we believe our study provides a reliable basis to recommend and implement the conservation measures needed for long-term protection of the species.

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