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Diversity and Distributions

Identifying predictable foraging habitats for a wide-ranging marine predator using ensemble ecological niche models

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ABSTRACT

Aim Ecological niche modelling can provide valuable insight into species' environmental preferences and aid the identification of key habitats for populations of conservation concern. Here, we integrate biologging, satellite remote-sensing and ensemble ecological niche models (EENMs) to identify predictable foraging habitats for a globally important population of the grey-headed albatross (GHA) *Thalassarche chrysostoma*.

Location Bird Island, South Georgia; Southern Atlantic Ocean.

Methods GPS and geolocation-immersion loggers were used to track at-sea movements and activity patterns of GHA over two breeding seasons ($n = 55$; brood-guard). Immersion frequency (landings per 10-min interval) was used to define foraging events. EENM combining Generalized Additive Models (GAM), MaxEnt, Random Forest (RF) and Boosted Regression Trees (BRT) identified the biophysical conditions characterizing the locations of foraging events, using time-matched oceanographic predictors (Sea Surface Temperature, SST; chlorophyll *a*, chl-*a*; thermal front frequency, *TFreq*; depth). Model performance was assessed through iterative cross-validation and extrapolative performance through cross-validation among years.

Results Predictable foraging habitats identified by EENM spanned neritic (<500 m), shelf break and oceanic waters, coinciding with a set of persistent biophysical conditions characterized by particular thermal ranges (3–8 °C, 12–13 °C), elevated primary productivity (chl-*a* > 0.5 mg m^{-3}) and frequent manifestation of mesoscale thermal fronts. Our results confirm previous indications that GHA exploit enhanced foraging opportunities associated with frontal systems and objectively identify the APFZ as a region of high foraging habitat suitability. Moreover, at the spatial and temporal scales investigated here, the performance of multi-model ensembles was superior to that of single-algorithm models, and cross-validation among years indicated reasonable extrapolative performance.

Main conclusions EENM techniques are useful for integrating the predictions of several single-algorithm models, reducing potential bias and increasing confidence in predictions. Our analysis highlights the value of EENM for use with movement data in identifying at-sea habitats of wide-ranging marine predators, with clear implications for conservation and management.

Keywords

albatross, biologging, Boosted Regression Trees, front map, generalized additive models, habitat model, Random Forest, satellite remote sensing.

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INTRODUCTION

Ecological niche modelling (also referred to as *species-habitat, predictive habitat, habitat-based* and *species distribution modelling*) provides a framework for understanding species' distributions as a function of their environmental preferences. Understanding the mechanisms that underlie environmental preference is particularly challenging for wide-ranging species with complex life histories, especially in the marine realm where conditions are highly dynamic. Recent efforts to integrate animal tracking ('biologging'), satellite remote-sensing and ecological niche modelling have generated valuable insights into the interactions between wide-ranging marine species and their oceanic environment (e.g. Howell *et al.*, 2015; Raymond *et al.*, 2015; Torres *et al.*, 2015). However, most studies utilize a single modelling framework with its specific biases, reducing the comparability of results and potentially limiting predictive capacity. An alternative is to adopt an ensemble ecological niche modelling approach (EENM; Araújo & New, 2007), which combines the output of multiple algorithms into one predictive surface and has been used successfully for identifying key habitats of marine predators, including sea turtles (Pikesley *et al.*, 2013) and seabirds (Oppel *et al.*, 2012).

Predicting the locations of suitable foraging habitats for wide-ranging pelagic species such as procellariiform seabirds (albatrosses, petrels and shearwaters) is non-trivial, given the complex and scale-dependent interactions between oceanographic processes and prey field dynamics, and the diverse aspects of bird physiology, energetics, reproductive and other constraints that govern foraging behaviour. The spatial ecology of pelagic seabirds appears to be influenced by processes both extrinsic and intrinsic to each individual. For example, habitat preferences of Southern Ocean seabirds vary among species (Commins *et al.*, 2014), populations (Nel *et al.*, 2001; Louzao *et al.*, 2011; Joiris & Dochy, 2013) and individuals (Phillips *et al.*, 2006; Patrick & Weimerskirch, 2014); between sexes (Phillips *et al.*, 2004); between life history stages (Phillips *et al.*, 2005); through the annual cycle (Phillips *et al.*, 2006; Wakefield *et al.*, 2011); and in response to changes in oceanographic conditions (Xavier *et al.*, 2013). Ecological niche modelling must be conducted with an awareness of the multifaceted influences on habitat selection if it is to be informative for identifying and managing priority areas for conservation (Lascelles *et al.*, 2012).

The energetic demands of reproduction are known to strongly influence habitat selection by pelagic seabirds during breeding phases. The constraints of incubation and chick provisioning impose a central place foraging mode, as trips are restricted to waters within an accessible range of the colony (Weimerskirch *et al.*, 1993). Individuals face trade-offs between the costs of flight and the necessity for reliable acquisition of prey of sufficient quality to meet the demands of chick provisioning in addition to their own energetic requirements, including for self-maintenance (Weimerskirch *et al.*, 1997). These constraints are particularly pronounced during the brood-guard period, when chicks require continual attendance by a parent to avoid chilling, are at their most vulnerable to predation and have a small stomach volume so they require frequent meals (Weimerskirch *et al.*, 1988; Xavier *et al.*, 2003; Wakefield *et al.*, 2011).

Breeding success is therefore conditional upon the abilities of each bird to predict the locations of suitable foraging habitats within a commutable distance of the colony. The oceanic seascapes over which pelagic seabirds search for food are highly heterogeneous (Fauchald *et al.*, 2000; Weimerskirch, 2007). Suitable foraging habitats that include prey of sufficient number and quality accessible within the diving capabilities of the species are formed by stochastic biophysical processes; hence, the locations of exploitable prey aggregations are usually unpredictable at fine spatial scales (Hazen *et al.*, 2013). However, there is evidence to suggest that some species, particularly albatrosses, may target or track regions in which the availability of prey resources is related to persistent oceanographic conditions and hence predictable over broad- to mesoscales, thus optimizing foraging success (Piatt *et al.*, 2006; Weimerskirch, 2007; Kappes *et al.*, 2010; Louzao *et al.*, 2011).

Grey-headed albatrosses (GHA) *Thalassarche chrysostoma*, in common with many Southern Ocean predators, have been shown to exploit predictable foraging opportunities generated through biophysical coupling along ocean fronts – physical interfaces between contrasting water masses (Belkin *et al.*, 2009; Bost *et al.*, 2009). The Antarctic Polar Frontal Zone (APFZ), an extensive, dynamic region that marks the northern boundary of the Antarctic Circumpolar Current (ACC), is known to be an important feature for seabirds and marine mammals in this sector of the Southern Ocean (Catry *et al.*, 2004; Wakefield *et al.*, 2011; Scheffer *et al.*, 2012). Within the broadscale APFZ, intense oceanographic dynamics lead to the generation of chaotic eddies and the manifestation of mesoscale (10s-100s of kilometres) or submesoscale (~1 km) thermohaline fronts. Aggregations of prey, such as the mesopelagic fish and cephalopods often targeted by GHA, can be concentrated within this zone, both through processes of mechanical entrainment and bottom-up forcing (Rodhouse & White, 1995; Reid *et al.*, 1996; Catry *et al.*, 2004; Rodhouse & Boyle, 2010). Areas of frequent or persistent frontal activity, such as the APFZ, may therefore constitute predictable foraging habitats for regional populations of wide-ranging predators.

Here, a novel application of EENM is developed, using high-resolution data tracking the movements and activity patterns of GHA from the largest global colony, to identify persistent oceanographic conditions that characterize foraging habitats within the area accessible to breeding birds. We use a suite of remotely sensed oceanographic data, including the first regional application of a thermal front frequency index, in an iterative presence–availability model framework, with the following aims: (i) to identify the biophysical conditions that characterize the locations of observed foraging events; (ii) to model the spatial distribution of predictable

foraging habitats, (iii) to explore the comparative utility of EENM and single-algorithm models in the context of using movement data to define foraging habitats of wide-ranging species over broad- to mesoscales and (iv) to evaluate the extrapolative performance of EENM through time.

METHODS

Device deployment

Birds were tracked from Colony B at Bird Island, South Georgia (54°00′S 38°03′W) over December–January of two austral breeding seasons, during the brood-guard phase (total $n = 55$ birds; $n = 25$ in 2009/2010; $n = 30$ in 2011/2012; Fig. 1). GPS loggers used were i-gotU (MobileAction Technology; http://www.i-gotu.com; 25 g mass), earth & Ocean Technology (e&O-Tec) MiniGPSlog (25 g) or e&O-Tec MicroGPSlog (10 g) and were attached using Tesa® marine cloth tape (total 5 g) to mantle feathers. Devices were programmed to record fixes at 10- or 15-min intervals and were recovered after one complete foraging trip. Birds were also equipped with geolocation-immersion loggers (British Antarctic Survey; Mk 13; ~1.5 g mass), attached to a standard British Trust for Ornithology metal or plastic ring. Birds were restrained on the nest only during device deployment, and handling time during deployment and retrieval was minimized (5–10 min).

Behavioural classification

Landing rate (number of landings per 10-min interval) derived from the immersion data was used to identify foraging bouts (following Dias *et al.*, 2011). Take-off from the water surface is energetically costly for albatrosses, so we assumed that immersion events indicated prey capture attempts (following Wakefield *et al.*, 2011). Empirical evidence from previous work on this population shows that birds frequently catch prey in rapid directed flight without any obvious area-restricted search (ARS) behaviour (Catry *et al.*, 2004), so we used landing rate in preference to identifying ARS.

Locations of immersion events were derived through temporal matching of GPS and immersion data. As birds rest on the water surface overnight (Catry *et al.*, 2004), only locations recorded in daylight hours were used (bounded by civil dawn and dusk; solar zenith of −6°). All locations within a 50 km radius of the colony were excluded from analysis to remove rafting behaviour. GPS tracks were interpolated to regular 10-min intervals. Landing rate was derived using a sliding window that summed the immersion events in the 10-min preceding each GPS location. Interpolated point locations along each track were then classified as either foraging – associated with at least one immersion event– or transit.

The study area was defined as the region enclosed by a radius corresponding to the whole data set absolute maximum displacement from the colony (1185 km). To resolve the spatial distribution of foraging events, a two-dimensional regular grid of the study area (71°S to 32°S; 55°W to 21°W) was created at 0.5° resolution. Grid cells in which foraging events were recorded were designated as 1, and grid cells that contained transit locations, or no bird presence, were designated as 0. All analyses were conducted in R version 3.1.

Oceanographic data

Remotely sensed oceanographic data were obtained for a matching time span (late December–end January) for each
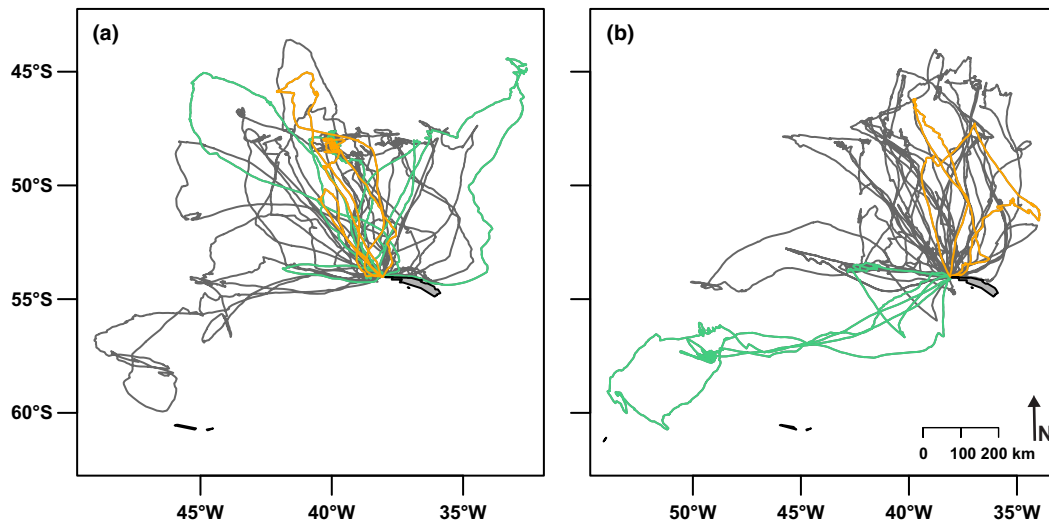

Figure 1 GPS tracking of grey-headed albatrosses (GHA) from Bird Island, South Georgia. Trips used to identify the spatial distribution of foraging events during the (a) 2009/2010 ($n = 25$) and (b) 2011/2012 ($n = 30$) breeding seasons (brood-guard phase). Birds for which sexes are known are highlighted in orange for female ($n = 3$, 2009/2010, $n = 2$, 2011/2012) and green for male ($n = 5$, 2009/2010; $n = 3$, 2011/2012).

tracking period (2009/2010; 2011/2012). Daily NASA Multi-Sensor Merged Ultra-High Resolution (MUR) Sea Surface Temperature (SST) imagery was downloaded via OpenDAP, and daily chlorophyll-*a* (chl-*a*) imagery was processed from MODIS-Aqua data; both were mapped to the study area in geographic projection at 1.2-km resolution. Daily images were used to generate monthly median SST and chl-*a* (log scaling) composites. Bathymetric data were obtained for a matching spatial extent from the General Bathymetric Chart of the Oceans (GEBCO_08 grid; http://www.gebco.net) and used to derive depth at 30 arc second resolution.

Thermal composite front maps (Miller, 2009) were generated from MUR SST data, over rolling 7-day periods

spanning the tracking period. Thermal fronts were detected in each MUR SST scene using single-image edge detection (SIED; Cayula & Cornillon, 1992; front detection threshold = 0.4 °C). Successive 7-day composites were used to prepare monthly front frequency (*TFreq*) layers, which quantify the frequency with which a front is detected in each pixel as a ratio of the number of positive detections to the number of cloud-free observations. All environmental data layers were standardized at 0.5 degree resolution through bilinear interpolation ('raster' package for R; Hijmans & Etten, 2012; Fig. 2). Oceanographic data layers were selected on the basis of availability, coverage and previously demonstrated influence on habitat selection by GHA and sympatric seabird
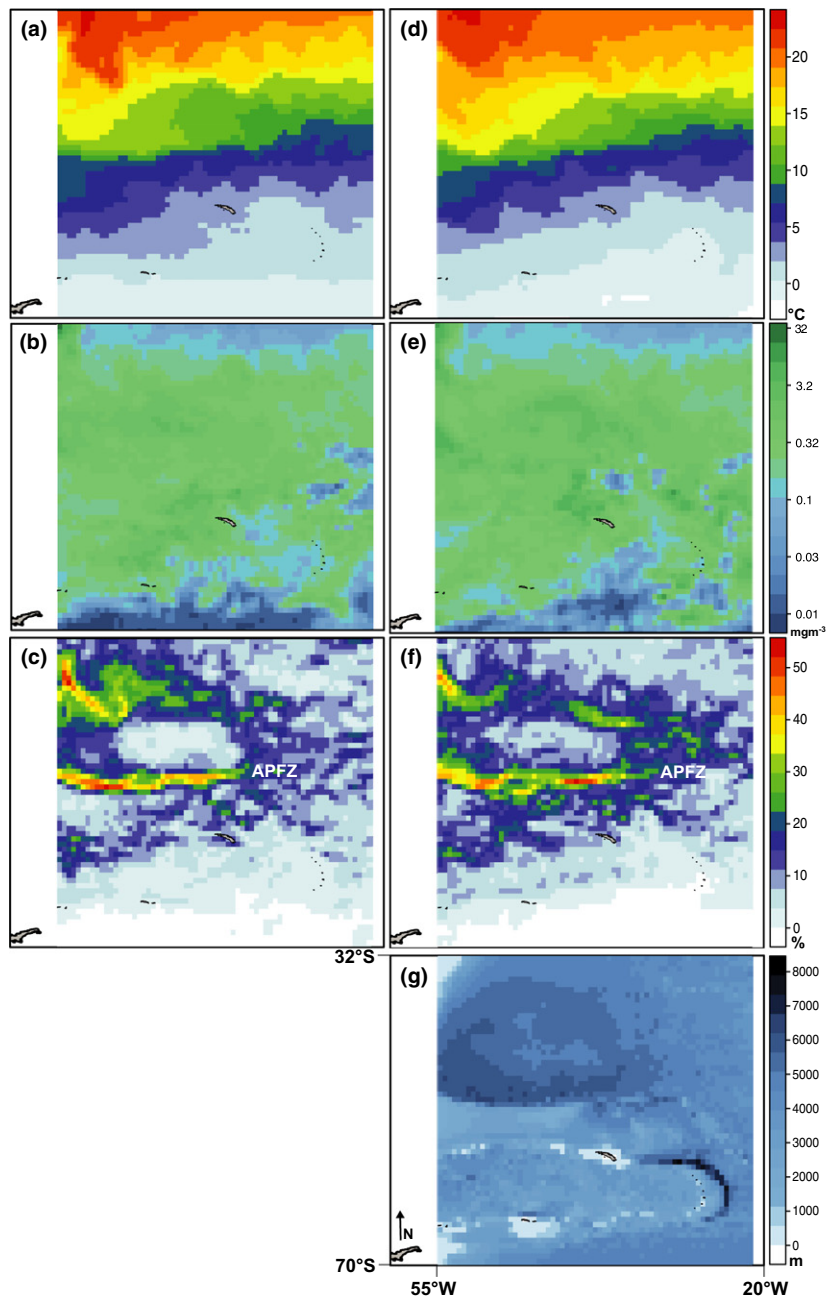

Figure 2 Environmental data layers for brood-guard period (end December–end January). Dynamic variables, (a) Sea Surface Temperature (SST, °C; monthly median composite) for 2009/2010, (b) chlorophyll-*a* (chl-*a*, mg m^{-3}; monthly median composite; log transformed), for 2009/2010 and (c) thermal front frequency (*TFreq*, % time; 0.4°C front detection threshold; monthly synoptic composite) for 2009/2010. (d–f) Dynamic variables for 2011/2012. (g) GEBCO Depth (30 arc-second resolution).

species (e.g. Xavier *et al.*, 2003; Phillips *et al.*, 2006; Wakefield *et al.*, 2011; Ballard *et al.*, 2012).

Ensemble ecological niche modelling (EENM)

Previous work concluded that an ensemble approach is preferable to the use of single-algorithm models for predicting seabird habitat affinities (Oppel *et al.*, 2012). However, the technique has not, to our knowledge, yet been used to identify predictable foraging habitats using movement data. We used EENM with movement data to identify the biophysical conditions characterizing the locations of foraging events. Ecological niche models were fitted using the Generalized Additive Models (GAM), Maximum Entropy (MaxEnt), Random Forest (RF) and Boosted Regression Tree (BRT) algorithms within the biomod2 package for R (Thuiller *et al.*, 2009, 2014).

The package 'biomod2' uses a presence–availability framework to model habitat suitability. As grid cells in which no foraging events were detected cannot be classified as true absences, control locations (pseudo-absences) were iteratively resampled from within the study area. Five iterations of 1000 randomly selected control locations were used over successive model runs (Barbet-Massin, 2012). Each model run involved 10-fold cross-validation, with data randomly apportioned to a 75%/25% split for model calibration and testing phases.

Relative importance of environmental variables was determined using the built-in method in biomod2, which overcomes difficulties associated with comparing model-specific outcomes through a randomization procedure (Thuiller *et al.*, 2009, 2014). This protocol fits a Pearson correlation between fitted values and predictions, where each variable has been randomly permutated. If the two are correlated, the variable is considered of little importance. This procedure was repeated 10 times for each variable within each model run. The relative importance of each environmental variable (relative importance of the contribution to the model coefficients, RICC) was then scaled by subtracting the mean correlation coefficient from 1. The overall explanatory power of the environmental variables was derived using the mean-of-means of standardized variable importance over all iterations per algorithm (Table S1).

Outputs of each single-algorithm model were evaluated over both model calibration and testing data sets for each model iteration. A triad of performance metrics (AUC, TSS and Boyce Index) was generated for each iteration per algorithm, and we calculated the mean of each metric over each iteration of control locations and mean of each metric over all models fit per algorithm ($n = 50$; 10-fold cross-validation for each of 5 iterations of control locations; Tables S3 and S4). Only those with a True Skill Statistic (TSS) equal to or greater than 0.7 were included in the final ensemble. Ensemble projections were created using a weighted average across all single-algorithm models, based on TSS, and accounting for differences in algorithm performance. EENM projections

were based on a habitat suitability index (HSI), scaled between 0 and 1, where 1 represents greatest suitability.

Resultant EENMs were then evaluated, using AUC, TSS and Boyce Index (Boyce *et al.*, 2002; Hirzel *et al.*, 2006). We calculated all performance metrics for each EENM fitted to the full data set from each year. AUC and TSS were calculated using in-built biomod2 functionality. Boyce Index was calculated through projection of each model on to the full data set for each year ('ecospat' package for R; Broenniman *et al.*, 2014) to obtain a value comparing model predictions of HSI with the input presence data set in each case.

EENM extrapolative performance

EENM extrapolative performance was assessed through cross-validation between the two years for which we had data. We projected each model on to the combined synoptic environmental data surfaces for the contrasting year to that upon which the model was constructed. Performance metrics (AUC, TSS and Boyce Index) were calculated for each of these projected models. Spatial concordance between predictions of models extrapolated across time and year-specific models was quantitatively compared using Mantel tests (ade4 package for R; Dray & Dufour, 2007).

RESULTS

Foraging trips

Maximum displacement from the colony ranged between 153 km and 1185 km, with a mean ± SD of 744 ± 249 km. Trip duration ranged between 0.6 and 6.1 days, with a mean of 2.9 ± 1.3 days. All trips involved at least one foraging event (based on landing rate derived from the immersion data), with a mean of 6.1 ± 3.7 foraging events per trip (range 2–17). Sex was available for a small subsample of tracked birds ($n = 8$, 2009/2010; $n = 5$, 2011/2012), in which no differences in foraging trips between sexes were detected (Fig. 1). Given the small sample of known sex, sex effects were not included in further population-level analyses.
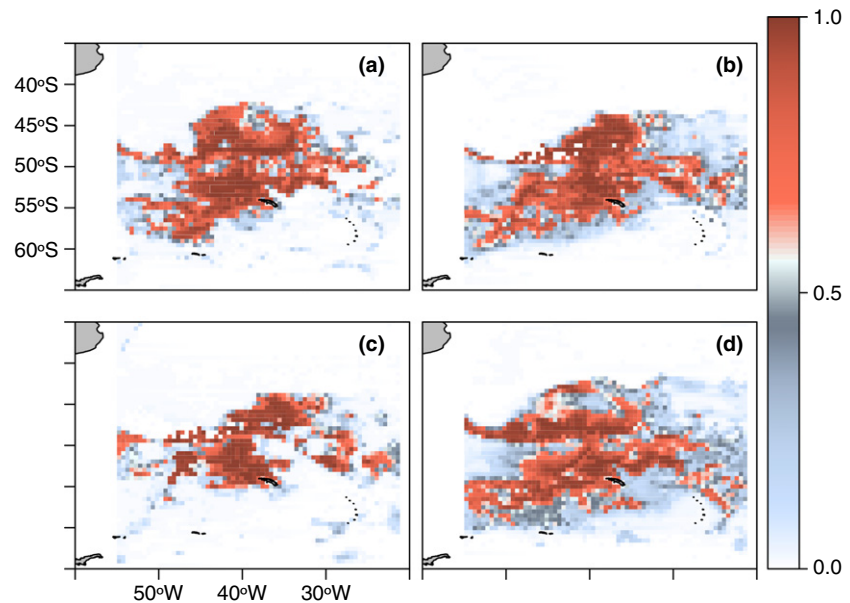
Predictable foraging habitats

Median SST and chl-*a* concentration were important contributory variables to EENMs constructed for both years of the study, suggesting these biophysical variables influence albatross foraging habitat selection over the scales investigated by our models (Table 1). However, the overall explanatory contribution of chl-*a* to the 2011/2012 EENM (RICC = 0.150) was lower than its contribution to the 2009/2010 EENM (RICC = 0.585), and the inverse was observed for the contribution of SST to each EENM (RICC, 2009/2010 = 0.577; RICC, 2011/2012 = 0.744). The relative contributions of water depth and the frequency of mesoscale thermal front manifestation (*TFreq*) to the explanatory capabilities of the EENM were lower than that of SST and

Table 1 Variable importance (mean over all model sets per algorithm), scaled as relative importance of contribution to model coefficients (RICC), from 0 to 1. Variable importance rankings in brackets

	Variable importance, 2009/2010				Variable importance, 2011/2012			
	SST	Chl-*a*	*TFreq*	Depth	SST	Chl-*a*	*TFreq*	Depth
GAM	0.61396 (1)	0.4570 (2)	0.06512 (4)	0.17284 (3)	0.92174 (1)	0.09860 (3)	0.07752 (4)	0.16574 (2)
MaxEnt	0.45498 (2)	0.48992 (1)	0.06060 (4)	0.12338 (3)	0.55658 (1)	0.21478 (3)	0.31830 (2)	0.18928 (4)
RF	0.46120 (2)	0.52012 (1)	0.08466 (4)	0.16598 (3)	0.51792 (1)	0.27812 (2)	0.24914 (3)	0.20358 (4)
BRT	0.5644 (1)	0.56014 (2)	0.01672 (4)	0.05316 (3)	0.59350 (1)	0.29776 (2)	0.22872 (3)	0.0805 (4)
EENM	0.577 (2)	0.585 (1)	0.037 (4)	0.086 (3)	0.744 (1)	0.150 (3)	0.155 (2)	0.100 (4)

Figure 3 Spatial predictions of ensemble ecological niche models (EENMs) and cross-validation among years. Spatial predictions of final EENM (weighted mean, removal of MaxEnt predictions) for (a) 2009/2010 and (b) 2011/2012. Cross-validation of (c) 2009/2010 EENM onto 2011/2012 environmental conditions and (d) 2011/2012 EENM onto 2009/2010 environmental conditions. Spatial predictions displayed as habitat suitability index (HSI) per grid cell, scaled from 0 to 1. Greater similarity between (a, b) and (c, d) indicates better EENM transferability among years.

chl-*a* across both years, although *TFreq* and depth were more important to the 2011/2012 model set (RICC, *TFreq* = 0.155, RICC, depth = 0.100) than for 2009/2010 (RICC, *TFreq* = 0.037; RICC depth = 0.086).

Spatial predictions of EENMs identified suitable foraging conditions across neritic (<500 m depth), shelf break and oceanic regions, reflecting the variety of foraging locations used by birds tracked in both breeding seasons (Fig. 3). EENM-derived spatial predictions of habitat suitability were similar in extent, distribution and scaling among years (Fig. 3a,b). Regions of high habitat suitability were associated with particular SST ranges (3–8 °C, 12–13 °C) and productive regions (median chl-*a* > 0.5 mg m^{-3}). The APFZ (Fig. 2e,f) was also identified as an area highly suitable for foraging in both years (Fig. 3), although this zone lies at the extremes of the area accessible to birds during brood-guard (Fig. 1).

EENM vs. single-algorithm models

Model predictions

The ranking of environmental variables (mean over 50 runs per algorithm) was broadly comparable among single-algorithm models, although some variability was evident

(Table 1). For example, ranking of variable importance was similar among GAM, RF and BRT models in both years, but notably different for MaxEnt models. EENM rankings smoothed over the algorithm-specific variability. However, explanatory contributions of environmental variables were ranked differently by year-specific EENMs (Table 1).

Model response curves for each variable were comparable among algorithms. GAM, RF and BRT in particular generated model sets with very similar response curves for SST, *TFreq* and depth, although less consistency among algorithms is evident in chl-*a* response curves (Fig. 4). MaxEnt models were subject to greater inconsistency in predicted responses (Figs S1–S3).

Similarly, spatial predictions of models fitted using the GAM, RF and BRT algorithms were comparable in the extent and distribution of predicted high suitability habitats, and in the scaling of the habitat suitability index (HSI) in these regions (Fig. 5). MaxEnt models, however, generated more spatially restricted predictions with overall lower HSI throughout the accessible area. For these reasons, we did not include MaxEnt in the final EENMs. The distribution, extent and scaling of suitable habitats identified in EENM predictions integrated the predictions of GAM, RF and BRT, smoothing over algorithm-specific variation (Fig. 3). EENM
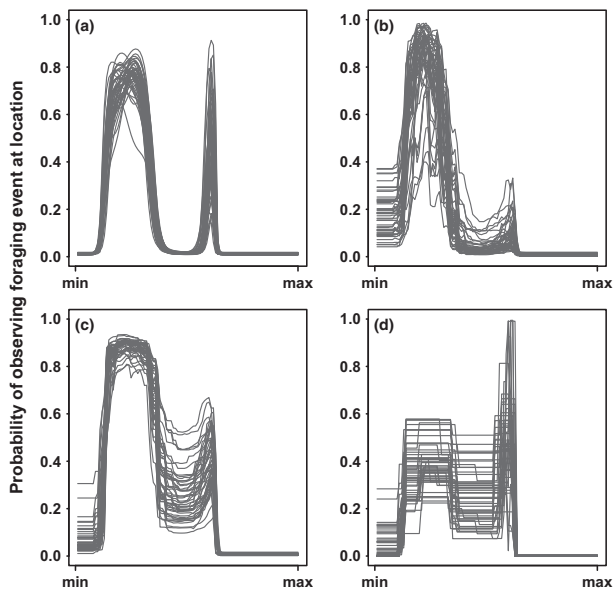
Figure 4 Model Response Curves for SST in 2011/2012 model sets, per algorithm, (a) GAM, (b) RF, (c) BRT, (d) MaxEnt.

predictions showed a strong spatial concordance in the location and extent of suitable habitats identified in each year (Fig. 3; HSI, Mantel r = 0.9599).

Model performance

EENMs were highlighted by AUC and Boyce Index as the best performing models in comparison with all single-algorithm models, in both years. However, the True Skill Statistic (TSS) selected Random Forest (RF) as the best performing in both years (Table 2).

Evaluation metrics indicated similar performance of single-algorithm models across model sets (variance, AUC = 0.0002; TSS = 0.001; Boyce Index = 0.002; Table 2) and for each of these single-algorithm models among years (correlation, AUC r = 0.999; TSS = 0.935; Boyce Index = 0.884; Table 2). AUC and TSS ranked single-algorithm models in a similar order in both years (e.g. AUC = RF, BRT, GAM, MaxEnt; Table 2), but there was little concordance between rankings of single-algorithm models among the three performance metrics used (AUC, TSS and Boyce Index). The weighted mean EENM including predictions of GAM, RF and BRT models was retained as the final model for each year.

EENM extrapolative performance

EENMs extrapolated across years to predict suitable foraging habitats over contrasting mesoscale oceanographic conditions performed well according to AUC and Boyce Index scores. All model performance metrics (AUC, TSS and Boyce Index) reveal the extrapolative performance of the 2011/2012 EENM to be superior to that of the 2009/2010 EENM.

Spatial predictions of EENMs extrapolated across years were broadly comparable to the predictions of each year-specific EENM, highlighting the suitable foraging conditions located to the north and west of the colony. Extrapolation of the 2011/2012 EENM to the 2009/2010 combined environmental data surface exhibited strong similarity with the 2009/2010 EENM (HSI, Mantel r = 0.9437), but extrapolation of the 2009/2010 EENM on to 2011/2012 conditions predicted more spatially restricted regions of high habitat suitability than those predicted by the year-specific model (HSI, Mantel r = 0.8740; Fig. 3). The proportion of the area accessible to the population during this breeding phase in which suitable foraging habitats were predicted to occur was comparable among years (Fig. 6).

DISCUSSION

Predictable foraging habitats for the grey-headed albatross population breeding at Bird Island, South Georgia, appear to coincide with a set of persistent biophysical conditions. Over the spatial and temporal scales investigated by our models, EENM performed better than single-algorithm models in predicting the distribution of observed foraging events. These insights highlight the potential of EENM as a tool for use with movement data in identifying at-sea habitats of marine predator populations of conservation concern and for guiding mitigation of spatially explicit anthropogenic threats in high suitability habitats.

Predictable foraging habitats

Our ensemble ecological niche models (EENMs) highlight SST and median surface chl-*a* concentration (monthly synoptic fields) as important determinants of habitat suitability for foraging grey-headed albatrosses during brood-guard. SST has been found to be a useful predictor of habitat preference for other albatross species at South Georgia and elsewhere (Awkerman *et al.*, 2005; Kappes *et al.*, 2010; Wakefield *et al.*, 2011; Deppe *et al.*, 2014). GHA also appeared to respond to the frequency of mesoscale thermal front manifestation (*TFreq*), which characterized the APFZ, and to water depth, although these predictors had a lesser influence in models.

SST is a proxy for the spatial structuring of biophysical conditions over the vast ranges utilized by these ocean-wandering seabirds. Different foraging guilds of pelagic predators exploit prey types that associate with particular temperature regimes (Commins *et al.*, 2014). GHA are known to seize prey from the ocean surface (<2–3 m depth; Huin & Prince, 1997) and to feed predominantly on ommastrephid squid, including *Martialia hyadesi*, crustaceans, including Antarctic krill *Euphausia superba* and, less commonly, lamprey *Geotria australis*, mesopelagic fish and gelatinous zooplankton (Rodhouse *et al.*, 1990; Reid *et al.*, 1996; Xavier *et al.*, 2003; Catry *et al.*, 2004). Although the diet of tracked birds was not determined, their distribution was broadly comparable with previous years when all these prey types were recorded (Xavier
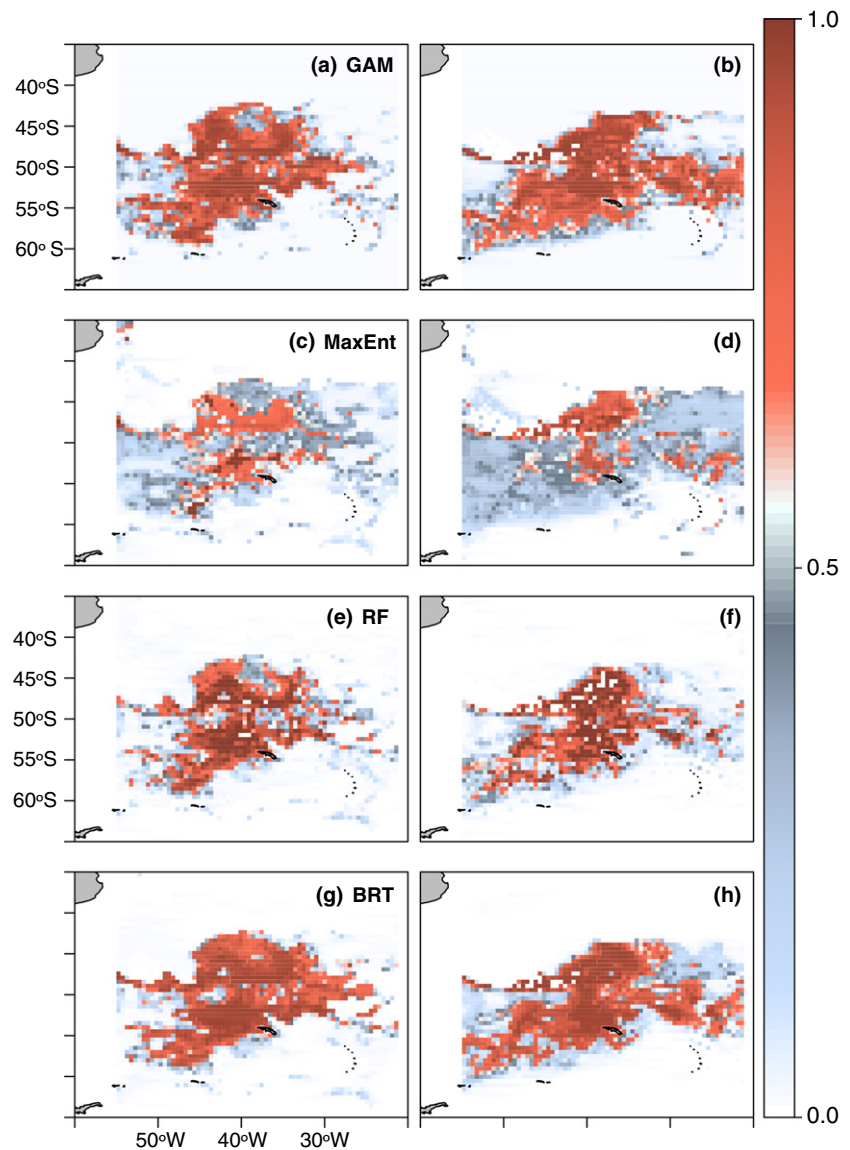
Figure 5 Spatial predictions of ecological niche models per algorithm, (a) Generalized Additive Models, GAM, 2009–2010 (b) GAM, 2011/2012; (c) Maximum Entropy, MaxEnt, 2009/2010, (d) 2011/2012; (e) Random Forest, 2009/2010, (f) 2011/2012; (g) Boosted Regression Trees, 2009/2010, (h) 2011/2012. Spatial predictions displayed as habitat suitability index (HSI) per grid cell, scaled from 0 to 1 (mean over all model runs, n = 50 per algorithm).

Table 2 Model performance metrics (mean over all model sets per algorithm). Area under receiver operating characteristic curve (AUC) scaled 0 to 1; True Skill Statistic (TSS) scaled 0 to 1; and Boyce Index scaled −1 to +1. Highest scoring model for each performance metric highlighted in bold. EENM rows have metrics for final EENM, without MaxEnt (black), and EENM with MaxEnt (grey). Performance rankings per metric in brackets

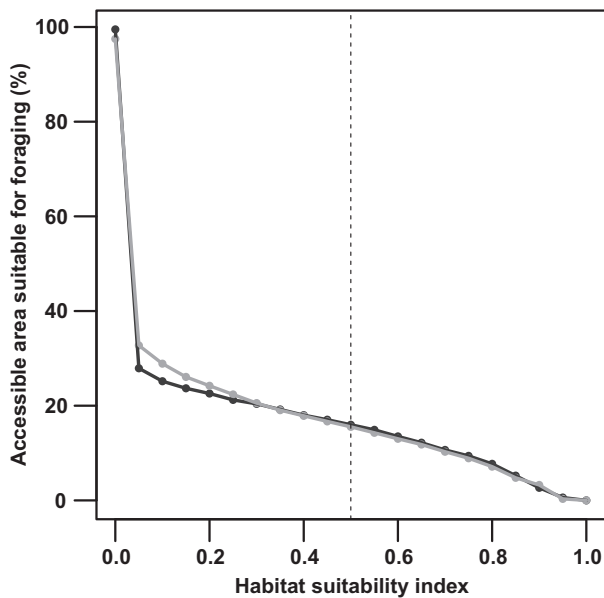| Model Set	Model evaluation, 2009/2010			Model evaluation, 2011/2012		
	AUC	TSS	Boyce index	AUC	TSS	Boyce index
GAM	0.9421 (3)	0.8237 (2)	0.9213 (2)	0.9372 (3)	0.7835 (3)	0.8943 (3)
MaxEnt	0.9276 (4)	0.7740 (4)	0.9300 (1)	0.9101 (4)	0.7184 (4)	0.9051 (1)
RF	0.9523 (1)	**0.8277** (1)	0.8329 (3)	0.9563 (1)	**0.8283** (1)	0.8998 (2)
BRT	0.9444 (2)	0.8176 (3)	0.7130 (4)	0.9418 (2)	0.7843 (2)	0.8615 (4)
EENM	**0.9547**	0.7914	**0.9512**	**0.9610**	0.7871	**0.9656**
	0.9479	0.7514	0.8990	0.9591	0.7791	0.9626
EENM extrapolation	0.9107	0.5194	0.8536	0.9281	0.6630	0.9358
	0.9038	0.5188	0.7138	0.9267	0.6208	0.9540

Figure 6 Percentage of area accessible during brood-guard phase (estimated using whole data set maximum displacement from colony) containing oceanographic conditions suitable for foraging against EENM-predicted habitat suitability index (HSI). 2009/2010 EENM (weighted mean) as black line; 2011/2012 in grey.

et al., 2003; Catry *et al.*, 2004). This suggests that the environmental conditions identified through this modelling procedure reflect the key habitats and main prey that are targeted by grey-headed albatrosses at South Georgia, which represent c. 50% of the global breeding population (ACAP, 2009).

Chl-*a* was also identified as a predictor of the spatial distribution of foraging events. Overall, foraging activity was more likely in productive regions. Chl-*a* concentrations (monthly median) were highest on-shelf, with peak values recorded to the south-west of the colony. The APFZ was not characterized by elevated productivity over the spatial and temporal scales investigated in this model. Birds foraging in productive shelf waters around South Georgia are likely to be targeting Antarctic krill and icefish *Champsocephalus gunnari*, which are more closely tied to bottom-up forcing mechanisms than the squid and mesopelagic fish found in the APFZ (Wakefield *et al.*, 2012).

High *TFreq* values and narrow SST contours characterize the APFZ, which was identified by the EENM as a region of high habitat suitability for GHA. Plunge-diving GHA have been observed in association with large aggregations of *M. hyadesi* at the ocean surface within the APFZ (Rodhouse & Boyle, 2010). Although few foraging events were observed in the APFZ during the tracking period, it is likely that those birds foraging in the APFZ were targeting ommastrephid squid. The APFZ lies at the northernmost extreme of the observed foraging range during brood-guard, which might suggest that reproductive constraints influenced the strength of the association with this region. Regardless, the high spatial overlap between the APFZ and the distribution of GHA during other breeding stages and in the non-breeding period

(Phillips *et al.*, 2004; Croxall *et al.*, 2005) suggest it is a key foraging area for this species, year-round.

In previous studies in the region, the spatial extent of the APFZ has been estimated using historical or averaged data, which did not match the temporal resolution of animal movement data. For example, Xavier *et al.* (2003) used the position of the polar front (PF) derived from survey data in 1997 to investigate habitat preference of birds tracked in 2000. However, the APFZ is a highly dynamic feature, characterized by intense mesoscale variability, and the PF can vary in position by as much as 100 km in 10 days (Trathan *et al.*, 1997). Detecting fronts in a temporally averaged SST composite can also mask the dynamic nature of these features. The *TFreq* index, used here for the first time in the Southern Ocean, is an objective, synoptic product that enables incorporation of mesoscale oceanographic dynamics in broad-scale ecological niche models (Scales *et al.*, 2014).

In addition to the selection of environmental data layers, analytical scale is a key aspect of the construction of ecological niche models. Matching the spatial resolution of remotely sensed data sets with the scales over which animals locate key foraging areas remains a major challenge in habitat modelling (Storch, 2002; Luoto *et al.*, 2007), particularly in the marine realm (Araújo & Guisan, 2006; Hirzel *et al.*, 2006). In our study, environmental data layers were interpolated to a standard 0.5 degree grid resolution, which was deemed appropriate given the extent of the area over which tracked birds roamed. To ensure scale match of the research question, response and environmental data sets, we also restricted temporal averaging of environmental data layers to one month, matching the duration of the brood-guard phase for the focal population.

EENM vs. single-algorithm models

Model predictions

Single-algorithm ecological niche models fitted on the same data set can perform differently and generate contrasting predictions (Guisan & Zimmerman, 2000; Thibaud *et al.*, 2014).

Single-algorithm models used here ranked the relative importance of environmental variables differently in both years, yet overall concordance was observed in estimated variable importance between algorithms. Relative variable importance in final EENMs for each year broadly echoes the consensus in variable ranking among GAM, RF and BRT model sets. Year-specific EENMs conflicted in the ranking of environmental variable importance. SST, *TFreq* and Depth were ascribed greater importance in the 2011/2012 ensemble, whereas the importance of chl-*a* dropped from 2009/2010 to 2011/2012. This could be attributable to non-stationary processes that govern the responses of grey-headed albatrosses to oceanographic conditions (Jenouvrier *et al.*, 2005), or indicative of the need for additional environmental data to enhance the capacity of our models to capture the mechanisms underlying foraging habitat selection.

Concordance in model response curves per environmental variable from single-algorithm models increases confidence in the capacity of these models to detect responses to environmental conditions. We observed strong concordance between model response curves resulting from GAM, RF and BRT across all environmental variables in both years and so included these model sets in final EENMs. EENM predictions integrating outputs of several single-algorithm models predicting broadly similar responses could be regarded as preferable to any single-model output in terms of confidence in predictions. Similarly, broadly matching spatial predictions, such as those predicted by GAM, RF and BRT in our analysis, increase confidence in these single-algorithm model outputs and in the spatial predictions of the final EENMs. This is a key aspect of the utility of the EENM process in enabling the construction of more reliable predictive habitat-based models.

Model performance

We observed notable differences in model performance rankings using alternative metrics (i.e. AUC, TSS and Boyce Index). There is, to our knowledge, no current consensus on which metric is preferable in this context, although the reliability of AUC has been heavily criticized (Boyce et al., 2002; Lobo et al., 2008). The TSS is independent of sample size (prevalence; Allouche et al., 2006), so we chose this metric over AUC for model selection. We also implemented the Boyce Index as a comparative measure of model performance (Boyce et al., 2002; Hirzel et al., 2006). As with all movement data sets, our response variable is strictly presence-only, and so a presence-only model evaluation metric is likely the most appropriate. However, we note that the use of multiple performance metrics in EENM construction and evaluation is clearly preferable to any single metric (Allouche et al., 2006; Jiménez-Valverde, 2012; Thibaud et al., 2014). EENMs were selected as the best performing models in both years using the Boyce Index and AUC methods, confirming that averaging the outputs of several single-algorithm models into an ensemble improved predictive capacity in our test case.

Our exploration of the utility of EENM in this context highlights the capacity of the technique for comparing among the predictions of single-algorithm models and selecting the best performing models on a case-by-case basis. For example, taking a conservative approach, we excluded MaxEnt from final EENMs, improving performance and increasing confidence in predictions. EENM is useful for excluding strong bias and smoothing over weaker biases in different model predictions. Our results exemplify the potential of EENM for use with movement data in identifying predictable foraging habitats for wide-ranging marine vertebrates over broad scales.

EENM extrapolative performance

Ecological niche models constructed and validated over the same extent can show limited transferability in space and time (Randin et al., 2006; Torres et al., 2015). While we did not have sufficient data to investigate transferability through space, the extrapolative performance of our EENMs across the two years of this study was good, although the 2011/2012 ensemble performed considerably better than that constructed for 2009/2010 (2009/2010, AUC = 0.9107, TSS = 0.5194, Boyce Index = 0.8536; 2011/2012, AUC = 0.9281, TSS = 0.6630, Boyce Index = 0.9348). Changes in the performance of ensembles extrapolated across years are indicative of poor transferability through time, because of variation in animal–environment interactions or, more probably, the failure of models to fully capture the drivers of these interactions.

Further tests of EENM extrapolative performance, for example to other populations of the same species (e.g. Torres et al., 2015), or through multiple years in the same region, are necessary to ascertain true extrapolative capabilities. Moreover, the multiscale periodicity of oceanographic variability in the region (e.g. decadal-scale Southern Ocean Oscillation Index) is likely to influence extrapolative capability (e.g. Jenouvrier et al., 2005). Some key questions remain: for example, After how many years is the extrapolative performance of a year-specific model likely to fade? How do predictable habitats over short-term time-scales align with predictable habitats on interannual or decadal time-scales? Future work should investigate variability in oceanographic conditions within and among years if these techniques are to prove useful for predicting population-level responses to climate-mediated ecosystem change.

Nevertheless, multi-model ensembles can increase confidence in model predictions, where they are implemented with awareness of technical limitations (Marmion et al., 2009; Oppel et al., 2012). By better incorporating uncertainty, the output of EENMs provides a robust basis for recommendations relating to the management of threats to marine vertebrate populations of conservation concern.

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REFERENCES

Agreement on the Conservation of Albatrosses and Petrels (ACAP) (2009) *ACAP Species assessment: Grey-headed*

Albatross Thalassarche chrysostoma. Available at: http://www.acap.aq (accessed 17 November 2014).

Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.

Araújo, M.B. & Guisan, A. (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 677–1688.

Araújo, M.B. & New, M. (2007) Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, **22**, 42–47.

Awkerman, J.A., Fukuda, A., Higuchi, H. & Anderson, D.J. (2005) Foraging activity and submesoscale habitat use of waved albatrosses *Phoebastria irrorata* during chick- brooding period. *Marine Ecology Progress Series*, **291**, 289–300.

Ballard, G., Jongsomjit, D., Veloz, S.D. & Ainley, D.G. (2012) Coexistence of mesopredators in an intact polar ocean ecosystem: The basis for defining a Ross Sea marine protected area. *Biological Conservation*, **156**, 72–82.

Barbet-Massin, M., Jiguet, F., Albert, C.H. & Thuiller, W. (2012) Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*, **3**, 327–338.

Belkin, I.M., Cornillon, P.C. & Sherman, K. (2009) Fronts in large marine ecosystems. *Progress in Oceanography*, **81**, 223–236.

Bost, C.A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J.B., Guinet, C., Ainley, D.G. & Weimerskirch, H. (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, **78**, 363–376.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. & Schmiegelow, F.K. (2002) Evaluating resource selection functions. *Ecological Modelling*, **157**, 281–300.

Broenniman, O., Petitpierre, B., Randin, C., Engler, R., Breiner, F., D'Amen, M., Pellissier, L., Pottier, J., Pio, D., Garcia Mateo, R., Di Colla, V., Hordijk, W., Dubuis, A., Scheerer, D., Salamin, N. & Guisan, A. (2014) ecospat: Spatial ecology miscellaneous methods. R package version 1.0. http://CRAN.R-project.org/package=ecospat.

Catry, P., Phillips, R.A., Phalan, B., Silk, J.R.D. & Croxall, J.P. (2004) Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Marine Ecology Progress Series*, **280**, 261–273.

Cayula, J.-F. & Cornillon, P.C. (1992) Edge detection algorithm for SST images. *Journal of Atmospheric and Oceanic Technology*, **9**, 67–80.

Commins, M.L., Ansorge, I. & Ryan, P.G. (2014) Multi-scale factors influencing seabird assemblages in the African sector of the Southern Ocean. *Antarctic Science*, **26**, 38–48.

Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V. & Briggs, D.R. (2005) Global circumnavigations: tracking year-round ranges of non-breeding albatrosses. *Science*, **307**, 249–250.

Deppe, L., McGregor, K.F., Tomasetto, F., Briskie, J.V. & Scofield, R.P. (2014) Distribution and predictability of foraging areas in breeding Chatham albatrosses *Thalassarche eremita* in relation to environmental characteristics. *Marine Ecology Progress Series*, **498**, 287–301.

Dias, M.P., Granadeiro, J.P., Phillips, R.A., Alonso, H. & Catry, P. (2011) Breaking the routine: individual Cory's shearwaters shift winter destinations between hemispheres and across ocean basins. *Proceedings of the Royal Society of London B: Biological Sciences*, **278**, 1786–1793.

Dray, S. & Dufour, A.B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, **22**, 1–20.

Fauchald, P., Erikstad, K.E. & Skarsfjord, H. (2000) Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology*, **81**, 773–783.

Guisan, A. & Zimmerman, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.

Hazen, E.L., Suryan, R.M., Santora, J.A., Bograd, S.J., Watanuki, Y. & Wilson, R.P. (2013) Scales and mechanisms of marine hotspot formation. *Marine Ecology Progress Series*, **487**, 177–183.

Hijmans, R.J. & vanEtten, J. (2012) *raster: Geographic analysis and modelling with raster data. R package vzrersion 20-08.* http://CRANR-projectorg/package=raster

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, **199**, 142–152.

Howell, E.A., Hoover, A., Benson, S.R., Bailey, H., Polovina, J.J., Seminoff, J.A. & Dutton, P.H. (2015) Enhancing the TurtleWatch product for leatherback sea turtles, a dynamic habitat model for ecosystem-based management. *Fisheries Oceanography*, **24**, 57–68.

Huin, N. & Prince, P. (1997) Diving behaviour of the grey-headed albatross. *Antarctic Science*, **9**, 243–249.

Jenouvrier, S., Weimerskirch, H., Barbraud, C., Park, Y.H. & Cazelles, B. (2005) Evidence of a shift in the cyclicity of Antarctic seabird dynamics linked to climate. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 887–895.

Jiménez-Valverde, A. (2012) Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography*, **21**, 498–507.

Joiris, C.R. & Dochy, O. (2013) A major autumn feeding ground for fin whales, southern fulmars and grey-headed albatrosses around the South Shetland Islands, Antarctica. *Polar Biology*, **36**, 1649–1658.

Kappes, M.A., Shaffer, S.A., Tremblay, Y., Foley, D.G., Palacios, D.M., Robinson, P.W., Bograd, S.J. & Costa, D.P. (2010) Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. *Progress in Oceanography*, **86**, 246–260.

Lascelles, B.G., Langham, G.M., Ronconi, R.A. & Reid, J.B. (2012) From hotspots to site protection: identifying marine

protected areas for seabirds around the globe. *Biological Conservation*, **156**, 5–14.

Lobo, J.M., Jiménez-Valverde, A. & Real, R. (2008) AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, **17**, 145–151.

Louzao, M., Pinaud, D., Peron, C., Delord, K., Wiegand, T. & Weimerskirch, H. (2011) Conserving pelagic habitats: seascape modelling of an oceanic top predator. *Journal of Applied Ecology*, **48**, 121–132.

Luoto, M., Virkkala, R. & Heikkinen, R.K. (2007) The role of land cover in bioclimatic models depends on spatial resolution. *Global Ecology and Biogeography*, **16**, 34–42.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, **15**, 59–69.

Miller, P. (2009) Composite front maps for improved visibility of dynamic sea-surface features on cloudy SeaWiFS and AVHRR data. *Journal of Marine Systems*, **78**, 327–336.

Nel, D.C., Lutjeharms, J.R.E., Pakhomov, E.A., Ansorge, I.J., Ryan, P.G. & Klages, N.T.W. (2001) Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Marine Ecology Progress Series*, **217**, 15–26.

Oppel, S., Meirinho, A., Ramírez, I., Gardner, B., O'Connell, A.F., Miller, P.I. & Louzao, M. (2012) Comparison of five modelling techniques to predict the spatial distribution and abundance of seabirds. *Biological Conservation*, **156**, 94–104.

Patrick, S.C. & Weimerskirch, H. (2014) Consistency pays: sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird. *Biology Letters*, **10**, 20140630.

Phillips, R.A., Silk, J.R.D., Phalan, B., Catry, P. & Croxall, J.P. (2004) Seasonal sexual segregation in two Thalassarche albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society B: Biological Sciences*, **271**, 1283–1291.

Phillips, R.A., Silk, J.R., Croxall, J.P., Afanasyev, V. & Bennett, V.J. (2005) Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology*, **86**, 2386–2396.

Phillips, R.A., Silk, J.R., Croxall, J.P. & Afanasyev, V. (2006) Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biological Conservation*, **129**, 336–347.

Piatt, J.F., Wetzel, J., Bell, K., DeGange, A.R., Balogh, G.R., Drew, G.S., Geernaert, T., Ladd, C. & Byrd, G.V. (2006) Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: Implications for conservation. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**, 387–398.

Pikesley, S.K., Maxwell, S.M., Pendoley, K., Costa, D.P., Coyne, M.S., Formia, A., Godley, B.J., Klein, W., Makanga-Bahouna, J., Maruca, S., Ngouessono, S., Parnell, R.J.,

Pemo-Makaya, E. & Witt, M.J. (2013) On the front line: integrated habitat mapping for olive ridley sea turtles in the southeast Atlantic. *Diversity and Distributions*, **19**, 1518–1530.

Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M. & Guisan, A. (2006) Are niche-based species distribution models transferable in space? *Journal of Biogeography*, **33**, 1689–1703.

Raymond, B., Lea, M.A., Patterson, T. et al. (2015) Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography*, **38**, 121–129.

Reid, K., Croxall, J. & Prince, P. (1996) The fish diet of black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. Chrysostoma* at South Georgia. *Polar Biology*, **16**, 469–477.

Rodhouse, P.G. & Boyle, P.R. (2010) Large aggregations of pelagic squid near the ocean surface at the Antarctic Polar Front, and their capture by grey-headed albatrosses. *ICES Journal of Marine Science*, **67**, 1432–1435.

Rodhouse, P.G. & White, M.G. (1995) Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic Polar Frontal Zone. *The Biological Bulletin*, **189**, 77–80.

Rodhouse, P., Prince, P., Clarke, M. & Murray, A. (1990) Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. *Marine Biology*, **104**, 353–362.

Scales, K.L., Miller, P.I., Embling, C.B., Ingram, S.N., Pirotta, E. & Votier, S.C. (2014) Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of The Royal Society Interface*, **11**, 20140679.

Scheffer, A., Bost, C.A. & Trathan, P.N. (2012) Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia. *Marine Ecology Progress Series*, **465**, 281–297.

Storch, I. (2002) On spatial resolution in habitat models: can small-scale forest structure explain capercaillie numbers? *Conservation Ecology*, **6**, 6.

Thibaud, E., Petitpierre, B., Broennimann, O., Davison, A.C. & Guisan, A. (2014) Measuring the relative effect of factors affecting species distribution model predictions. *Methods in Ecology and Evolution*, **5**, 947–955.

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M.B. (2009) BIOMOD–a platform for ensemble forecasting of species distributions. *Ecography*, **32**, 369–373.

Thuiller, W., Georges, D. & Engler, R. (2014) biomod2: Ensemble platform for species distribution modeling. R package version 3.1-64. http://CRAN.R-project.org/package=biomod2

Torres, L.G., Sutton, P., Thompson, D.R., Delord, K., Weimerskirch, H., Sagar, P.M., Sommer, E., Dilley, B.J., Ryan, P.G. & Phillips, R.A. (2015) Poor transferability of species distribution models for a pelagic predator, the Grey Petrel, indicates contrasting habitat preferences across ocean basins. *PLoS ONE*, **10**, e0120014.

Trathan, P., Brandon, M. & Murphy, E. (1997) Characterization of the Antarctic Polar Frontal Zone to the north of

South Georgia in summer 1994. *Journal of Geophysical Research: Oceans (1978–2012)*, **102**, 10483–10497.

Wakefield, E.D., Phillips, R.A., Trathan, P.N., Arata, J., Gales, R., Huin, N., Robertson, G., Waugh, S.M., Weimerskirch, H. & Matthiopoulos, J. (2011) Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. *Ecological Monographs*, **81**, 141–167.

Wakefield, E.D., Phillips, R.A. & Belchier, M. (2012) Foraging black-browed albatrosses target waters overlaying moraine banks-a consequence of upward benthic-pelagic coupling? *Antarctic Science*, **24**, 269–280.

Weimerskirch, H. (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography*, **54**, 211–223.

Weimerskirch, H., Bartle, J.A., Jouventin, P. & Stahl, J.C. (1988) Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor*, **90**, 214–219.

Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. (1993) Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *The Auk*, **110**, 325–342.

Weimerskirch, H., Mougey, T. & Hindermeyer, X. (1997) Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology*, **8**, 635.

Xavier, J., Croxall, J., Trathan, P. & Wood, A. (2003) Feeding strategies and diets of breeding grey-headed and wandering albatrosses at South Georgia. *Marine Biology*, **143**, 221–232.

Xavier, J., Louzao, M., Thorpe, S., Ward, P., Hill, C., Roberts, D., Croxall, J.P. & Phillips, R.A. (2013) Seasonal changes in the diet and feeding behaviour of a top predator indicate a flexible response to deteriorating oceanographic conditions. *Marine Biology*, **160**, 1597–1606.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Model Response Curves for Chl-*a* in 2011/12 model sets, per algorithm, (a) GAM, (b) RF, (c) BRT, (d) MaxEnt.

Figure S2 Model Response Curves for *TFreq* in 2011/12 model sets, per algorithm, (a) GAM, (b) RF, (c) BRT, (d) MaxEnt.

Figure S3 Model Response Curves for depth in 2011/12 model sets, per algorithm, (a) GAM, (b) RF, (c) BRT, (d) MaxEnt.

Table S1 Variable importance per iteration of control locations, 2009/10.

Table S2 Variable importance per iteration of control locations, 2011/12.

Table S3 Model performance metrics per iteration of control locations, 2009/10.

Table S4 Model performance metrics per iteration of control locations, 2011/12.

Table S5 Model Parameterization settings.

BIOSKETCH

Kylie L. Scales is a marine spatial ecologist, with particular interest in the mechanistic linkages between mesoscale oceanography and marine predator habitat use. This research was carried out by an interdisciplinary, multi-institution team of authors, combining expertise in biologging, physical oceanography, habitat-based modelling and remote sensing.