DOI: 10.1111/ddi.12702

BIODIVERSITY RESEARCH

WILEY Diversity and Distributions

Habitat modelling of tracking data from multiple marine predators identifies important areas in the Southern Indian Ocean

Ryan R. Reisinger[1,2,3] | Ben Raymond[4,5,6] | Mark A. Hindell[5,6] | Marthán N. Bester[7] | Robert J. M. Crawford[8,9] | Delia Davies[10] | P. J. Nico de Bruyn[7] | Ben J. Dilley[10] | Stephen P. Kirkman[8,9] | Azwianewi B. Makhado[8,10] | Peter G. Ryan[10] | Stefan Schoombie[10] | Kim Stevens[10] | Michael D. Sumner[4,6] | Cheryl A. Tosh[7] | Mia Wege[7] | Thomas Otto Whitehead[10] | Simon Wotherspoon[4,5] | Pierre A. Pistorius[1]

[1]DST/NRF Centre of Excellence at the FitzPatrick Institute of African Ornithology, Department of Zoology and Coastal and Marine Research Institute, Nelson Mandela University, Port Elizabeth, South Africa

[2]Centre d'Etudes Biologiques de Chizé, UMR 7372 du CNRS-Université de La Rochelle, Villiers-en-Bois, France

[3]CESAB-FRB, , Aix-en-Provence, France

[4]Australian Antarctic Division, Kingston, TAS, Australia

[5]Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS, Australia

[6]Antarctic Climate and Ecosystems Cooperative Research Centre, University of Tasmania, Hobart, TAS, Australia

[7]Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Hatfield, South Africa

[8]Department of Environmental Affairs, Branch Oceans and Coasts, Cape Town, South Africa

[9]Animal Demography Unit, Department of Biological Sciences, University of Cape Town, Rondebosch, South Africa

[10]DST/NRF Centre of Excellence, FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa

Correspondence
Ryan R. Reisinger, Centre d'Etudes Biologiques de Chizé, UMR 7372 du CNRS-Université de La Rochelle, Villiers-en-Bois, France.
Email: ryan.r.reisinger@gmail.com

Funding information
National Research Foundation, Grant/Award Number: 94916, SNA103359 and SNA2005060800001; South African Department of Environmental Affairs; Scientific Committee on Antarctic Research; Fondation pour la Recherche sur la Biodiversité

Editor: David Schoeman

Abstract

Aim: The distribution of marine predators is driven by the distribution and abundance of their prey; areas preferred by multiple marine predator species should therefore indicate areas of ecological significance. The Southern Ocean supports large populations of seabirds and marine mammals and is undergoing rapid environmental change. The management and conservation of these predators and their environment relies on understanding their distribution and its link with the biophysical environment, as the latter determines the distribution and abundance of prey. We addressed this issue using tracking data from 14 species of marine predators to identify important habitat.

Location: Indian Ocean sector of the Southern Ocean.

Methods: We used tracking data from 538 tag deployments made over a decade at the Subantarctic Prince Edward Islands. For each real track, we simulated a set of pseudo-tracks that allowed a presence-availability habitat modelling approach that estimates an animal's habitat preference. Using model ensembles of boosted regression trees and random forests, we modelled these tracks as a response to a set of 17 environmental variables. We combined the resulting species-specific models to evaluate areas of mean importance.

Results: Real tracking locations covered 39.75 million km^2, up to 7,813 km from the Prince Edward Islands. Areas of high mean importance were located broadly from the Subtropical Zone to the Polar Frontal Zone in summer and from the Subantarctic to Antarctic Zones in winter. Areas of high mean importance were best predicted by factors including wind speed, sea surface temperature, depth and current speed.

Main conclusions: The models and predictions developed here identify important habitat of marine predators around the Prince Edward Islands and can support the large-scale conservation and management of Subantarctic ecosystems and the marine predators they sustain. The results also form the basis of future efforts to predict the consequences of environmental change.

KEYWORDS

areas of ecological significance, distribution, distribution models, hotspots, marine mammals, marine protected areas, seabirds

1 | INTRODUCTION

The distribution and life history traits of marine predators are influenced by the distribution and abundance of their prey, which are themselves affected by physical and biological factors. Therefore, marine top predators are touted as sentinels of marine ecosystems, which potentially integrate diverse and complex environmental signals (e.g., Boyd & Murray, 2001; Durant et al., 2009; Moore, 2008). Accordingly, areas with a high abundance or diversity of foraging top predators are regarded as representing ecologically important areas (Block, Costa, Boehlert, & Kochevar, 2003; Hazen et al., 2013). Predators may also have significant top-down effects on ecosystems (Baum & Worm, 2009; Heithaus, Frid, Wirsing, & Worm, 2008). Quantitative information on the spatial distribution of marine predator assemblages is therefore required to better understand and manage marine systems. This is particularly so given the increasing anthropogenic impacts on the oceans (Halpern et al., 2015; Maxwell et al., 2013). While the distributions of many marine predator species are becoming well-known, there is an increasing emphasis on considering species assemblages to identify important ecological areas and common drivers of distribution and habitat use (e.g., Block et al., 2011; Patterson et al., 2016; Raymond et al., 2015; Thiers, Delord, Bost, Guinet, & Weimerskirch, 2017).

The Southern Ocean is a vast area interspersed with very few terrestrial sites where seabirds and seals can breed. One such island group is the Prince Edward Islands, comprising Marion Island and Prince Edward Island. At least 29 seabird species and three seal species breed there—collectively numbering millions of individuals—making the Prince Edward Islands a globally significant site for seabirds and seals (Ryan & Bester, 2008). In 2013, South Africa declared a 180,633 km^2 marine protected area in the exclusive economic zone (EEZ) surrounding the islands, partly to protect this biodiversity (Lombard et al., 2007). A number of seabird species breeding at the islands have a threatened or near-threatened conservation status (Table S1). Wide-scale environmental changes in the southern Indian Ocean have influenced the population sizes of several seal and seabird species breeding at Subantarctic islands (Weimerskirch, Inchausti, Guinet, & Barbraud, 2003). At the Prince Edward Islands, mean sea surface temperatures increased by 1.4°C from 1949 to 1998 (Mélice, Lutjeharms, Rouault, & Ansorge, 2003) and such changes, coupled with changes in prey abundance and distribution, are thought to affect the abundance and life history parameters of several top predators breeding there (Crawford, Dyer, Upfold, & Makhado, 2014; Wege, Etienne, et al., 2016).

Seabirds and marine mammals at the Prince Edward Islands have been studied since the 1950s (Bester et al., 2011; Cooper & Brown, 1990), with the first studies using tracking devices to investigate their at-sea distribution conducted in the early 1990s (Bester & Pansegrouw, 1992). Despite decades of research, most studies have focussed on individual species and no study has considered the distribution of an assemblage of top predators from the Prince Edward Islands. Thus, there is a significant gap in our understanding of the common patterns and drivers of marine predator distribution, and therefore the ecologically significant areas, in this region.

In this study, we collate tracking data for 14 species, including 10 seabirds, 3 seals and 1 cetacean from the Prince Edward Islands, to contribute to a broader understanding of the distribution and habitat use of marine top predators in the Southern Indian Ocean. Specifically, we build habitat preference models for each species, based on a set of environmental covariates, and predict areas of high habitat preference. We then combine these preference scores for all species to identify common areas of high preference. We focus on overlap and commonality at meso-scales (10 s–100 s of km), at which oceanographic and environmental features are likely to impact the foraging distribution of marine top predators.

2 | METHODS

The Prince Edward Islands (46.9°S, 37.7°E) are situated in the southwest Indian Ocean sector of the Southern Ocean (Figure 1). The

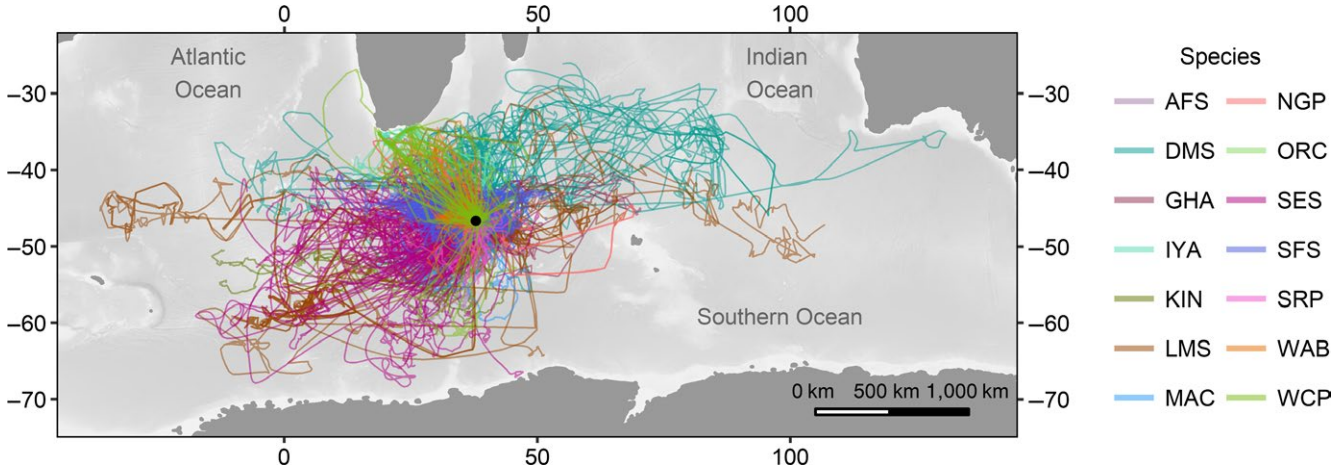

FIGURE 1 Location estimates for 538 tracking deployments on 14 species of marine predators at the Prince Edward Islands (filled black point), used to model important habitat around the islands. Utilization distributions for each species are shown in Figure 2. AFS, Antarctic fur seal; DMS, sooty albatross; GHA, grey-headed albatross; IYA, Indian yellow-nosed albatross; KIN, king penguin; LMS, light-mantled albatross; MAC, macaroni penguin; NGP, northern giant petrel; ORC, killer whale; SES, southern elephant seal; SFS, Subantarctic fur seal; SRP, rockhopper penguin; WAB, wandering albatross; WCP, white-chinned petrel. [Colour figure can be viewed at wileyonlinelibrary.com]

islands are the summit of a volcano which rises ~5,000 m from the surrounding seafloor. Oceanographically, the region is dominated by the east-flowing Antarctic Circumpolar Current and three associated fronts: the Subtropical, Subantarctic and Antarctic Polar Fronts (from north-south) (Lutjeharms & Ansorge, 2008).

We collated published and unpublished tracking data for 14 predator species tracked from the Prince Edward Islands from 2003 to 2014 (Table 1; additional details in Table S1). Animals were tracked using a variety of satellite-linked (Argos) and global positioning system (GPS) tags. Details of animal capture and restraint, tags used, tag attachment methods, ethics approval and permitting are contained in the references cited in Table 1. After removing tracks with fewer than 30 at-sea locations and those flagged based on visual inspection, the dataset contained 538 individual tracks. Complete as well as incomplete tracks were retained.

All analyses were conducted in the R environment (R Core Team, 2017). First, we pre-processed tracks using the "argosfilter" package (Freitas, 2012) to remove position estimates that created location spikes (turning angles <15 and 25 degrees in conjunction with displacements >2.5 and 5 km, respectively) and high movement speeds (Freitas, Lydersen, Ims, Fedak, & Kovacs, 2008). We estimated animal locations at regular time intervals by fitting a continuous-time correlated random walk model (Johnson, London, Lea, & Durban, 2008) to each track using the "crawl" 1.5 package (Johnson, 2015). This model accounts for errors around Argos location estimates, but we also fit the model to GPS tracks, assuming the same accuracy as the highest Argos location quality class. The time interval chosen was the whole number nearest the median time interval in the unprocessed tracking data for the given species and tag type (Table S1). While the tracks therefore had different inherent accuracies, these differences are negligible with respect to the spatial scale of variation of the environmental data and the scale of the study. The tracking data were classified into "summer" tracks and "winter" tracks. The dates defining these two putative seasons for each species were the two minima of tracking effort in approximately April and October (Figure S1). Where a track comprised dates in both seasons, we assigned the whole track to the season with the larger proportion of locations.

We assessed the representativeness of the tracking data for each species in each season by drawing curves of the cumulative number of grid cells visited against the number of individuals tracked. The order in which individuals were sampled was randomly shuffled to generate 1000 curves in each case. The mean of these curves was then modelled as a nonlinear asymptotic regression, and the cumulative number of cells visited as a percentage of the estimated number of cells at the asymptote was used as a measure of the representativeness (cf. Hindell, Bradshaw, Sumner, Michael, & Burton, 2003; Lascelles et al., 2016).

To characterize the environment potentially available to individuals, and thus allowing a case–control design for habitat preference modelling (Aarts, MacKenzie, McConnell, Fedak, & Matthiopoulos, 2008), we simulated random or pseudo-tracks. For each real track, we simulated 20 pseudo-tracks by fitting a first-order vector autoregressive model characterized by the step lengths and turning characteristics of the real track—estimated from the random walk model—as detailed in Raymond et al. (2015). This maintains characteristics of the real tracks relevant for estimating the space available to an individual if it had no habitat preferences. This also means that characteristics of the tracking data due to the tag type (e.g., sampling frequency) are reflected in both the real and pseudo tracks for each individual animal, thereby minimizing any biases in the final results due to different tag types used on different species. The number of pseudo-tracks was chosen, as in Raymond et al. (2015), as a compromise between adequately characterizing the available environment and limiting the dataset size for computation. Pseudo-locations falling on land were rejected and re-sampled.

TABLE 1 Tracking data from 14 top predator species used to model important habitat around the Prince Edward Islands. Further details in Table S1

Family	Species	Common name	Abbreviation	Tracks (*n*)	Start date	End date	Location estimates (*n*)	Reference/data source
Birds								
Albatrosses	*Phoebetria palpebrata*	Light-mantled albatross	LMS	23	2008/04/13	2014/01/15	7,845	DEA unpubl. data FIAO unpubl. data
Albatrosses	*Phoebetria fusca*	Sooty albatross	DMS	41	2008/04/02	2013/12/31	16,072	DEA unpubl. data Schoombie, Dilley, Davies, Glass, & Ryan, 2017;
Albatrosses	*Thalassarche chrysostoma*	Grey-headed albatross	GHA	47	2012/12/16	2014/12/29	23,860	FIAO unpubl. data
Albatrosses	*Thalassarche carteri*	Indian yellow-nosed albatross	IYA	24	2008/12/18	2011/03/31	1,813	DEA unpubl. data
Albatrosses	*Diomedea exulans*	Wandering albatross	WAB	26	2009/04/15	2014/03/30	8,453	FIAO unpubl. data
Penguins	*Aptenodytes patagonicus*	King penguin	KIN	16	2008/04/03	2013/07/31	14,451	Pistorius et al., 2017;
Penguins	*Eudyptes chrysocome*	Southern rockhopper penguin	SRP	60	2008/04/19	2014/03/26	9,772	DEA unpubl. data FIAO unpubl. data Whitehead, Kato, Ropert-Coudert, & Ryan, 2016;
Penguins	*Eudyptes chrysolophus*	Macaroni penguin	MAC	57	2008/04/01	2013/12/24	22,123	DEA unpubl. data FIAO unpubl. data Whitehead et al., 2016;
Petrels	*Procellaria aequinoctialis*	White-chinned petrel	WCP	19	2012/12/05	2013/03/09	11,240	FIAO unpubl. data
Petrels	*Macronectes halli*	Northern giant petrel	NGP	10	2008/04/07	2010/10/26	2,962	DEA unpubl. data
Mammals								
Dolphins	*Orcinus orca*	Killer whale	ORC	10	2012/04/28	2013/05/21	1,991	Reisinger et al., 2015;
Eared seals	*Arctocephalus gazella*	Antarctic fur seal	AFS	41	2009/12/10	2014/08/05	31,245	Wege, 2017;
Eared seals	*Arctocephalus tropicalis*	Subantarctic fur seal	SFS	76	2009/04/26	2013/09/06	62,119	De Bruyn, Tosh, Oosthuizen, Bester, & Arnould, 2009; Kirkman, Yemane, Lamont, Meÿer, & Pistorius, 2016; Wege, Tosh, de Bruyn, & Bester, 2016; Wege, 2017;

(Continues)

TABLE 1 (Continued)

Family	Species	Common name	Abbreviation	Tracks (*n*)	Start date	End date	Location estimates (*n*)	Reference/data source
True seals	*Mirounga leonina*	Southern elephant seal	SES	88	2003/11/03	2013/01/08	30,330	Mcintyre, Bornemann, Plötz, Tosh, & Bester, 2012; Tosh et al., 2012; Tosh et al., 2015 MRI unpubl. data
Total	14			538			244,276	

DEA, Department of Environmental Affairs; MRI, Mammal Research Institute; FIAO, FitzPatrick Institute for African Ornithology; AFS, Antarctic fur seal; DMS, sooty albatross; GHA, grey-headed albatross; IYA, Indian yellow-nosed albatross; KIN, king penguin; LMS, light-mantled albatross; MAC, macaroni penguin; NGP, northern giant petrel; ORC, killer whale; SES, southern elephant seal; SFS, Subantarctic fur seal; SRP, rockhopper penguin; WAB, wandering albatross; WCP, white-chinned petrel.

At each real and pseudo-location, we extracted a set of 17 environmental covariates—mainly remotely-sensed by satellites—using the "raadtools" (Sumner, 2016) and "raster" (Hijmans, 2016) packages (Table 2; additional details in Table S2). For dynamic environmental covariates, we matched the date and time of the location to the nearest environmental data in space and time. We chose widely available environmental covariates which are commonly used to model the habitat of marine predators (Table S2). They are assumed to represent bio-physical factors influencing predators and/or their prey directly or indirectly; however, some covariates may be proxies for unknown or unmeasured environmental factors.

We assessed habitat preference by modelling the relationship between the space use of animals and environmental covariates. We adopted the aforementioned case–control design (Aarts et al., 2008), where location estimates from a real track were treated as presences (1) and the pseudo-locations from the 20 simulated tracks were treated as habitat potentially available to an individual (0). Classification models were used to discriminate these two sets of points based on their environmental covariates (Table 2).

These habitat preference models do not explicitly account for habitat accessibility—an important constraint for central place foragers (such as breeding seabirds and female fur seals provisioning pups). We therefore constructed separate accessibility models for each species for prediction purposes. Here, the response was whether a given cell contained any real or pseudo-locations (1) (i.e., it was potentially accessible) or did not contain any location estimates (0); the sole predictor variable was distance from colony, as we assumed accessibility to be a function of distance. Predictions from the habitat preference models were then weighted by the predictions from the accessibility models, yielding a prediction surface of preference, given availability. The habitat preference predictions are not absolute estimates of the probability that a habitat is preferred and are not directly comparable between different species (e.g., Beyer et al., 2010). To enable comparisons between species, we therefore transformed each prediction map by percentile to give a habitat importance (hereafter percentile habitat) score (Raymond et al., 2015).

Habitat preference scores were calculated from ensemble models (combination or set of models) which combined boosted regression trees (Friedman, 2001) and random forests (Breiman, 2001). These constituent models were fitted through the "caret" (Kuhn, 2016) package (Table S3). Models were tuned by compiling sets of candidate models with different parameter combinations and then comparing the average area under the receiver operating characteristic curve (AUC) scores—calculated from 10-fold cross-validation—of these candidate models (Tables S3 and S4). Cross-validation folds were created by randomly dividing individuals into 10 groups containing an approximately equal number of individuals. The real and simulated tracks from any one individual were always kept together in the same fold. AUC scores calculated from random cross-validation are usually overoptimistic due to spatial autocorrelation (Hijmans, 2012), but our cross-validation scheme should result in AUC scores which reflect the generalized model performance more accurately. Indeed, AUC scores calculated using this cross-validation scheme were on average 0.19

TABLE 2 Environmental variables used as predictors in habitat selectivity models for 14 top predator species tracked from the Prince Edward Islands. Further details in Table S2

Abbreviation	Description	Type	Unit	Spatial resolution	Temporal resolution	Source
DEP	Ocean depth	Static	m	0.02°	—	General Bathymetric Chart of the Oceans hosted by the British Oceanographic Data Centre
TRI	Terrain ruggedness index (Wilson et al. 2007)	Static	—	0.02°	—	Derived from DEP
SLOPE	Ocean floor slope	Static	°	0.02°	—	Derived from DEP
SST	Sea surface temperature	Dynamic	°C	0.25°	Monthly	NOAA/OAR/ESRL
SSTgrad	Sea surface temperature gradient	Dynamic	°	0.25°	Monthly	Derived from SST
SSHa	Sea surface height anomaly	Dynamic	m	0.12°	Daily	SSALTO/DUACS, produced and distributed by the Copernicus Marine and Environment Monitoring Service
SSHgrad	Sea surface height gradient	Dynamic	°	0.25°	Daily	Produced by SSALTO/DUACS, distributed by Aviso with support from CNES
CURRU	Horizontal (zonal) geostrophic velocity	Dynamic	cm/s	0.25°	Weekly	Produced by SSALTO/DUACS, distributed by Aviso with support from CNES
CURRV	Vertical (meridional) geostrophic velocity	Dynamic	cm/s	0.25°	Weekly	Produced by SSALTO/DUACS, distributed by Aviso with support from CNES
EKE	Eddy kinetic energy	Dynamic	cm^2/s^2	0.25°	Weekly	Derived from CURRU and CURRV
MLD	Mixed layer depth	Climatology	m	1°	Monthly	Scripps Institution of Oceanography/UCSD
CHLA	Chlorophyll-a concentration	Climatology	mg/m^3	9 km	Monthly	NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group
PROD	Net primary production	Dynamic	mg C/m^2/day	0.08°	Monthly	Ocean Productivity Web
ICE	Sea ice concentration	Dynamic	%	25 km	Monthly	National Snow and Ice Data Center
DISTICE	Distance from sea ice concentration >15%	Dynamic	km	25 km	Monthly	Derived from ICE
WINDU	Horizontal (zonal) wind	Dynamic	m/s	1.9°	Daily	NOAA/OAR/ESRL PSD
WINDV	Vertical (meridional) wind	Dynamic	m/s	1.9°	Daily	NOAA/OAR/ESRL PSD

lower (range = −0.31 to −0.08) than those calculated using random stratified cross-validation during preliminary model runs. We then created ensembles (or combinations) of these models by "stacking" them using the "caretEnsemble" package (Deane-Mayer & Knowles, 2016). The weight of each model in the ensemble (or "stack") is its coefficient in a logistic regression of the model predictions (probability of being a real location estimate) against the original outcome (real or pseudo-location estimate) (Zhou, 2012). Model performance in all cases was evaluated using AUC scores. To generate prediction maps, we calculated the mean of each environmental covariate for the study period (summer and winter separately) based on input data at the same spatio-temporal resolution as that used to model habitat preference. We used ordinary Kriging to interpolate any missing values. Values of these variables were then sampled on a new 0.1° × 0.1° grid which was used for prediction. By predicting to the mean environmental conditions over the study period while matching the locations used in the models to the spatio-temporally nearest environmental covariates, the interannual variation typical of this dynamic marine system should be accounted for to some extent. However, this assumes that the correlation between animal behaviour and environmental covariates holds across years, and interannual variation will likely still have some unquantified influence on our output.

To evaluate which species showed similar habitat preferences, we used affinity propagation clustering (Frey & Dueck, 2007) to identify the number and composition of clusters ("apcluster" package; Bodenhofer, Kothmeier, & Hochreiter, 2011). For visualization, we calculated kernel utilization distributions (Worton, 1989) for each species ("adehabitatHR" package; Calenge, 2006), with *h*-values selected using the ad hoc method (Silverman, 1986). Finally, we calculated mean habitat importance; first, as the mean of all percentile habitat scores in each cell. However, because the diverse suite of species in this study can be expected to use the environment in different ways, we also calculated mean habitat importance scores using the top 8 percentile habitat scores for each cell and using only the top four scores—a more lenient overlap measure (*cf*. Raymond et al., 2015).

For mapping and further modelling, we used only cells with mean habitat importance in the 95th percentile. To identify the environmental variables associated with these areas of high mean importance, we also modelled the relationship between mean importance scores and the set of environmental covariates using a model ensemble (as above). In this case, models were regression rather than classification models, as the response values are continuous, and models were evaluated using root mean square error (RMSE) and the coefficient of determination (R^2).

3 | RESULTS

We analysed 538 tracks from 14 species, which yielded 244,276 at-sea location estimates, covering an area of 39.75 million km^2. Location estimates were up to 7,813 km from the deployment location (Figure 1). More than half the location estimates (126,835; 52%) were in the EEZ around the Prince Edward Islands, but most location estimates (152,265; 62%) were outside the Prince Edward Islands marine protected area. Few locations were in the EEZ around mainland South Africa (3,181 locations; 1.3%). The estimated representativeness of the tracking data for each species ranged from 32.7% (killer whales) to 96.5% (Subantarctic fur seals) during summer and from 45.0% (killer whales) to 97.4% (Subantarctic fur seals) during winter (Table S5).

Many species showed strong directional tendency in their movement, as well as having marked differences between summer and winter distributions (Figure 2). Based on the kernel utilization distributions, species fell into several groups with similar patterns of space use. In summer, these were species with (1) core areas south of the islands (Antarctic fur seal, macaroni penguin and rockhopper penguin), (2) around the islands and to the north (wandering albatross, sooty albatross, killer whale, Subantarctic fur seal and grey-headed albatross), (3) north of the islands, particularly near South Africa (white-chinned petrel and Indian yellow-nosed albatross), and (4) to the south-west of the islands (southern elephant seal and light-mantled albatross) (Figure 2). In winter, four core use areas were identified: (1) to the southwest of the islands (macaroni penguin, Antarctic fur seal, rockhopper penguin, king penguin and southern elephant seal), (2) around the islands (Subantarctic fur seal, northern giant petrel and killer whale), (3) broadly distributed (light-mantled albatross and sooty albatross), and (4) near South Africa (Indian yellow-nosed albatross) (Figure 2). Overlap was generally lower in winter than in summer.

Model performance (AUC) ranged from 0.54 to 0.85. Boosted regression trees generally had the highest AUC scores, but scores were nearly always within one standard deviation of each other (Figure S2). The predictions of models used in the ensemble generally showed strong correlation (mean = 0.83, range = 0.44–0.99).

The predictor variables differed in their importance rank across species and seasons, but during summer the variables sea surface temperature (SST), distance to the ice edge (DISTICE), depth (DEP) and primary productivity (PROD) (ranked by mean variable relative importance across species) were often the most important predictors of habitat preference (Figure S3). These four predictors had combined importance of 28.2–84.2 (mean = 43.1) across the species. During winter, the same four variables were generally most important, but ranked DISTICE, DEP, PROD, SST. Their combined importance across species was 28.7–58.0 (mean = 38.2) (Figure S3).

Cluster analysis of the percentile habitat scores indicated four species clusters in summer and in winter. Nine species comprised a single large cluster in summer and five species a single cluster in winter. In summer, light-mantled sooty albatross, macaroni penguins and white-chinned petrels each formed their own independent clusters, while in winter killer whales, sooty albatross and Indian yellow-nosed albatross each formed an independent cluster (Figure S4). The hierarchical clustering did not match taxonomic relationships among the species.

Prediction maps for each species are shown in Figure 3. In this figure, we mapped predictions only above an arbitrarily chosen threshold of 95, but generally, cells with predicted habitat importance in the 99th percentile showed good agreement with kernel utilization distributions. In summer, cells with the highest mean habitat importance

generally ranged from the approximate location of the Antarctic Polar Front to north of the approximate location of the Subtropical Front (Figure 4). Mean habitat importance for all species indicated the highest value areas around the Subantarctic Front. In contrast to the mean importance calculated for four and eight species, the mean importance for all species did not identify as many important cells in proximity to the Prince Edward Islands (Figure 4). In winter, the highest mean importance areas (four and eight species) included cells slightly further south than in summer and areas south and south-west of the islands in the Polar Frontal Zone were important (Figure 4). Mean importance for all species highlighted some far-lying areas, including small patches nearer the Antarctic continent. Waters surrounding the Crozet Islands to the east of the Prince Edward Islands were included among important areas. Cells with high mean habitat importance for all species were generally more patchily distributed than cells with high mean importance for four and eight species (Figure 4).

Areas with the highest mean habitat importance were often situated outside the Prince Edward Islands EEZ (Figures 4 and S5). Within the EEZ, the proportion of important grid cells inside versus outside the marine protected area was relatively even across mean habitat importance values (Figure S5) and the marine protected area often encompassed cells with very high mean habitat importance (Figure S6). Virtually all cells in the EEZ around the Prince Edward Islands met the 95th percentile threshold (see methods), and therefore, the proportion of important cells in the marine protected area matched the proportion of the EEZ represented by the marine protected area (~34%).

Ensemble models of mean habitat importance indicated that wind (WINDV and WINDU), SST, DEP, SST gradient (SSTgrad) and

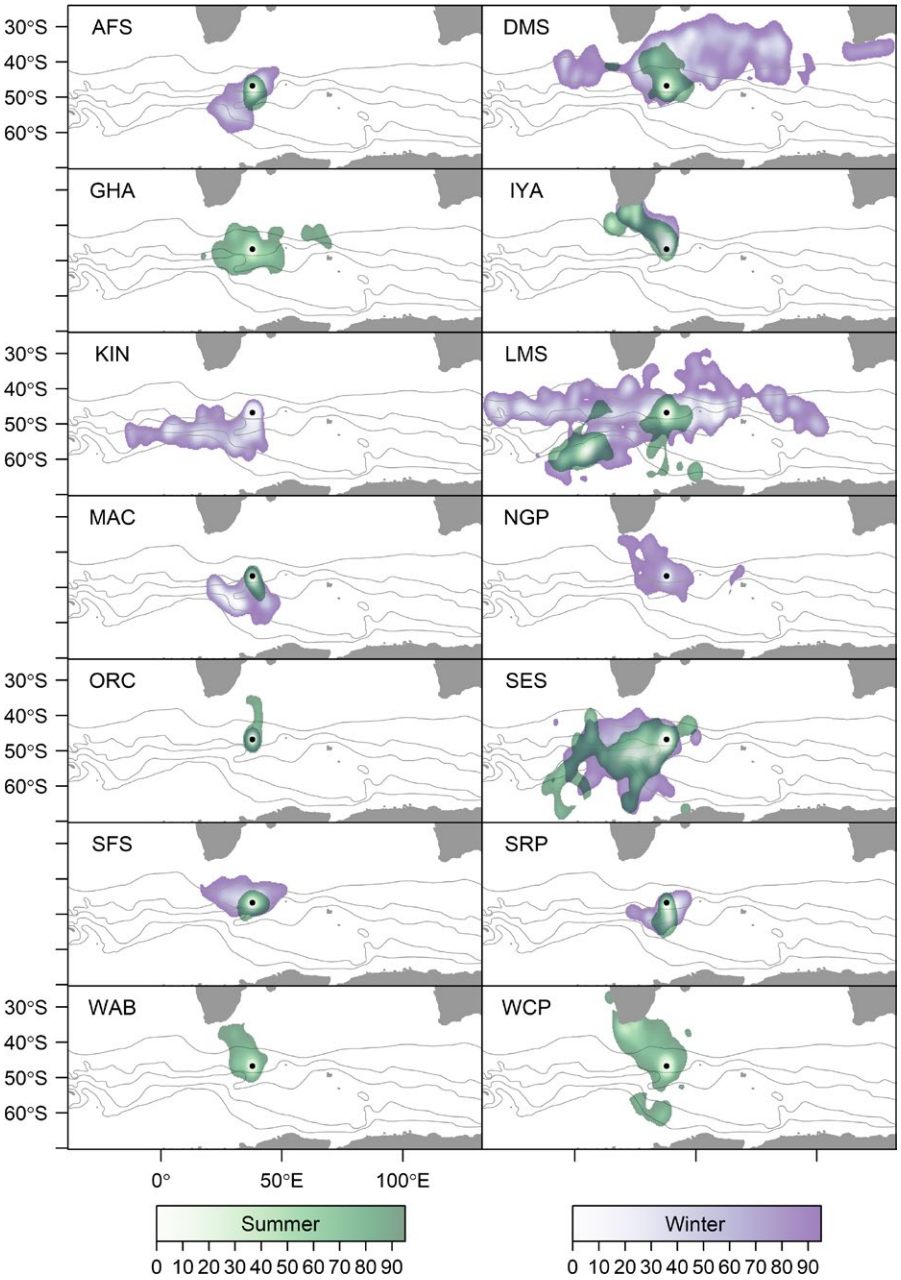

FIGURE 2 Kernel utilization distributions of 14 predator species tracked from the Prince Edward Islands during summer (green) and winter (purple). Lower utilization distribution values, typically below 50%, indicate the core areas. Grey lines indicate positions of major fronts after Orsi et al. (1995); from north to south: the Subtropical Front, Subantarctic Front, Antarctic Polar Front, Southern Antarctic Circumpolar Front and the southern boundary of the Antarctic Circumpolar Current. AFS, Antarctic fur seal; DMS, sooty albatross; GHA, grey-headed albatross; IYA, Indian yellow-nosed albatross; KIN, king penguin; LMS, light-mantled albatross; MAC, macaroni penguin; NGP, northern giant petrel; ORC, killer whale; SES, southern elephant seal; SFS, Subantarctic fur seal; SRP, rockhopper penguin; WAB, wandering albatross; WCP, white-chinned petrel. [Colour figure can be viewed at wileyonlinelibrary.com]

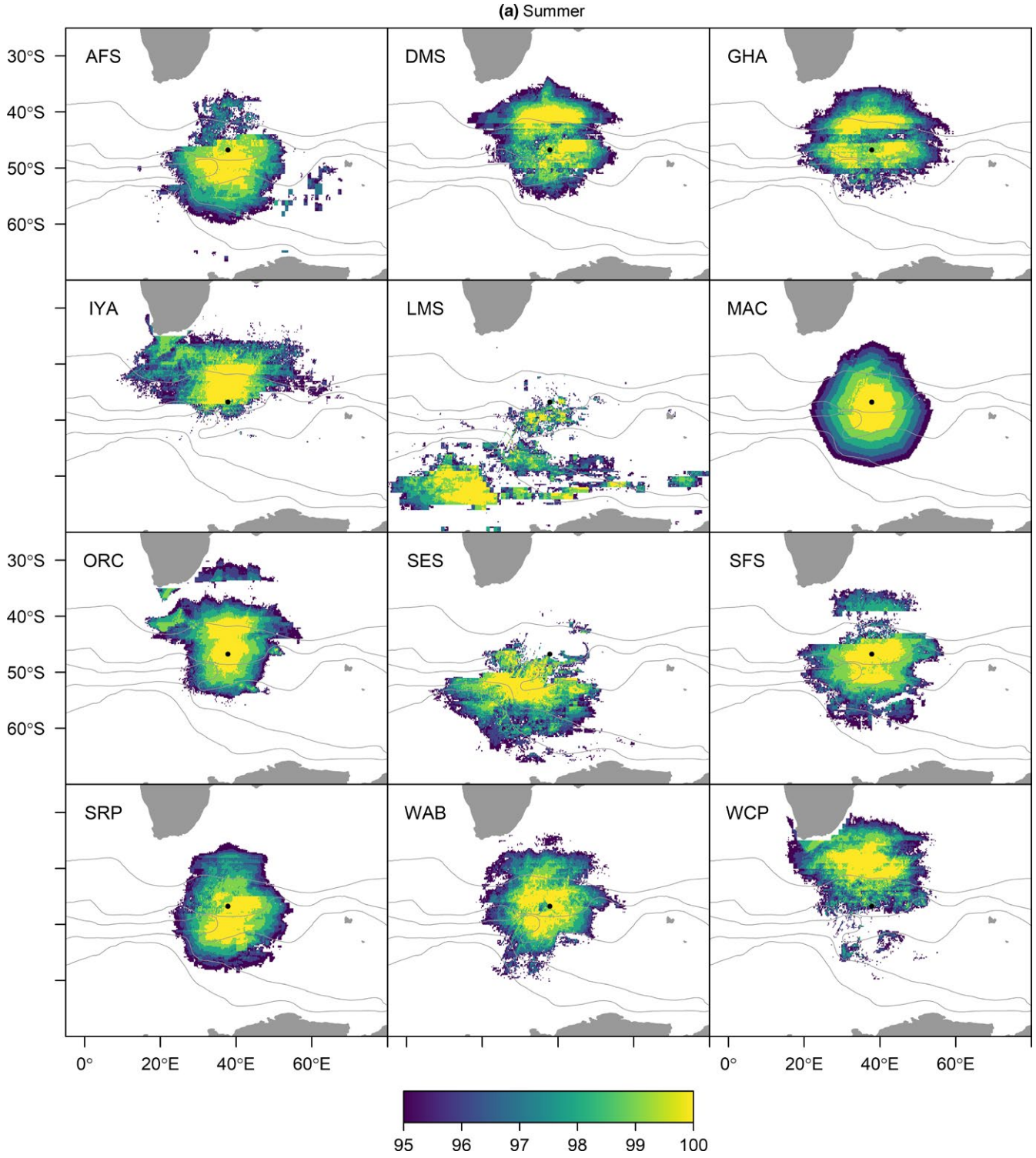

FIGURE 3 Habitat preference predictions of ensemble models for 14 predator species tracked from the Prince Edward Islands during (a) summer and (b) winter. Predictions have been percentile-transformed to yield a habitat importance score which is comparable among species, and only cells with values >95 are shown (representing 5% of the most important cells in the study area). Grey lines show the positions of oceanographic fronts, as in Figure 2. AFS, Antarctic fur seal; DMS, sooty albatross; GHA, grey-headed albatross; IYA, Indian yellow-nosed albatross; KIN, king penguin; LMS, light-mantled albatross; MAC, macaroni penguin; NGP, northern giant petrel; ORC, killer whale; SES, southern elephant seal; SFS, Subantarctic fur seal; SRP, rockhopper penguin; WAB, wandering albatross; WCP, white-chinned petrel. [Colour figure can be viewed at wileyonlinelibrary.com]

meridional current (CURRV) were generally important environmental predictors during summer and winter (Figure S7). Partial plots of the predictions (Figure S8) show similar relationships between mean importance and environmental variables across seasons and models. During summer, areas of high mean importance are characterized by high SST, negative WINDV (i.e., northerly wind),

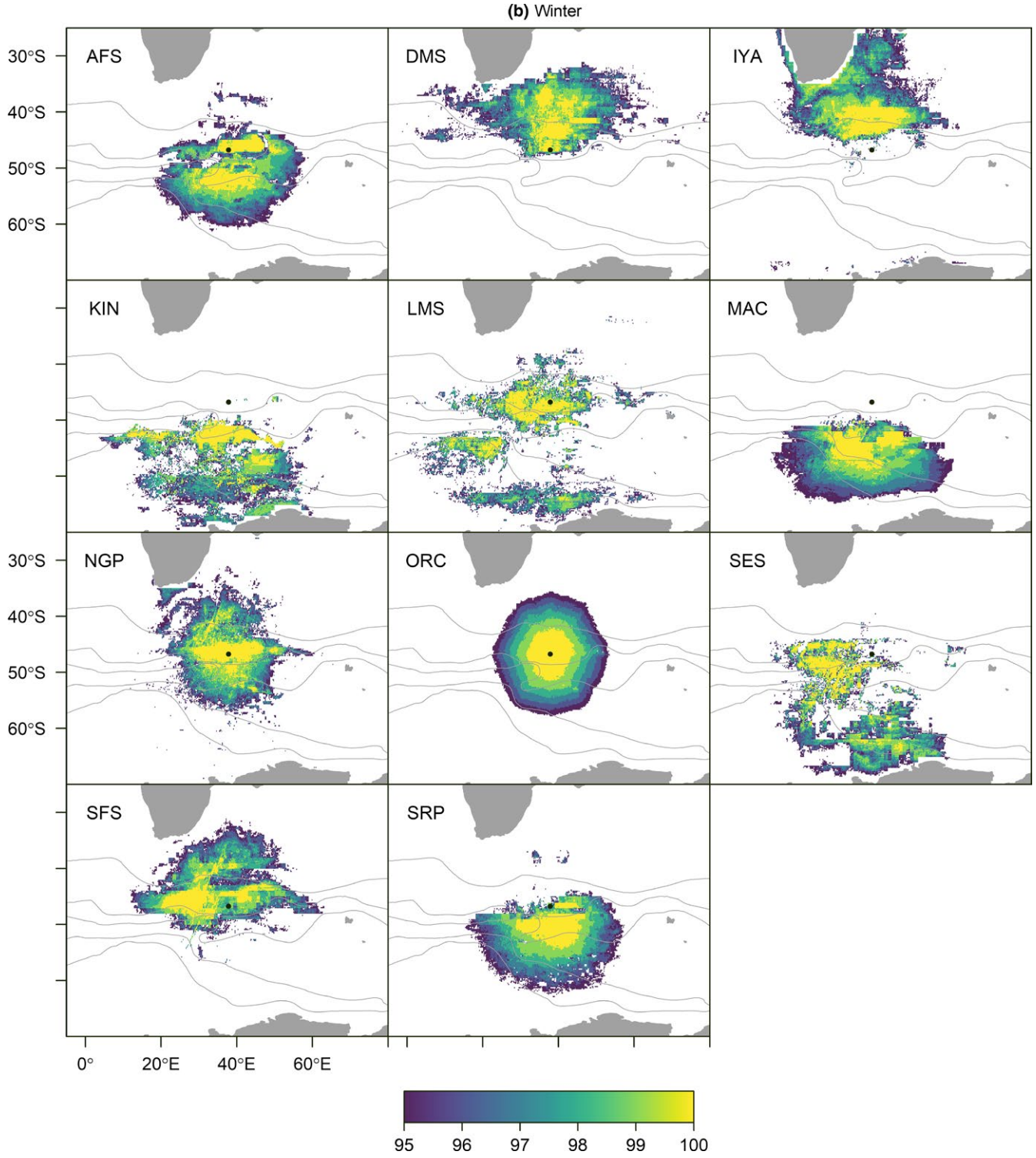

FIGURE 3 (Continued)

positive WINDU (i.e., westerly wind), shallower DEP and lower SSTgrad. These relationships were similar during winter; however, SST of important areas showed a lower peak, mean habitat importance was high in very shallow and very deep areas, and distance to sea ice (DISTICE) of ~1,000 km was related to important areas (Figure S8).

4 | DISCUSSION

Using tracking data from 14 species and an ensemble modelling approach, this is the first study that quantitatively describes important habitats for an assemblage of marine top predators around the Prince Edward Islands in the Southern Indian Ocean. The study illustrates

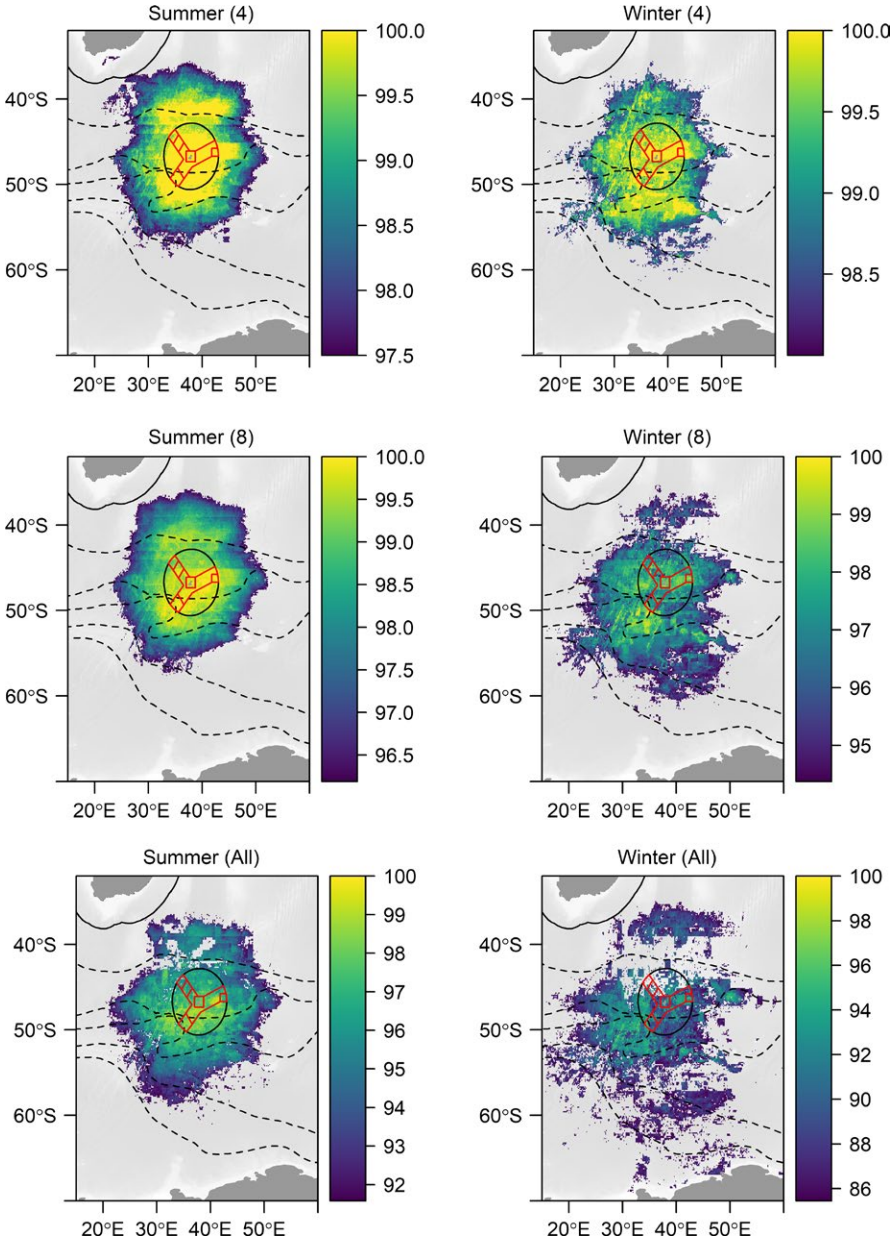

FIGURE 4 Maps showing mean habitat importance scores for top predators tracked from the Prince Edward Islands during summer (left panels) and winter (right panels). Habitat importance was calculated as the mean of the four highest scores in each cell (upper panels), eight highest scores in each cell (middle panels) and of all scores in each cell (bottom panels). Only cells with scores in the 95th percentile are shown. Solid black lines show the South African Exclusive Economic Zone, solid red lines show the Prince Edward Islands Marine Protected Area, and dashed black lines show average locations of important oceanographic fronts (Orsi et al. 1995). From north to south these are the Subtropical Front, Subantarctic Front, Antarctic Polar Front, Southern Antarctic Circumpolar Current Front and the southern boundary of the Antarctic Circumpolar Current. [Colour figure can be viewed at wileyonlinelibrary.com]

the extensive at-sea distribution of predators breeding at the islands. Tracking locations covered nearly 40 million km^2, with animals travelling nearly 8,000 km from the islands; almost half of the location estimates were outside of the South African EEZ. Cluster analysis of the habitat preference model predictions shows different habitat use among the species, which is unsurprising considering their taxonomic diversity. However, habitat use did not necessarily follow taxonomic similarities. Important areas were situated from subtropical waters north of the Subtropical Front to Antarctic waters south of the Polar Front (Figure 4). During winter, important areas were more broadly distributed. Seabirds and seals are, in general, less constrained by dependent offspring during this time and can search for prey more extensively. More extensive search areas may also be required by seasonal changes in the abundance and distribution of prey, including possible prey depletion following more concentrated summer foraging.

The Marine Protected Area in South Africa's EEZ around the Prince Edward Islands was designed during a systematic conservation planning study, with the aim of conserving biodiversity patterns and processes around the islands, while minimizing constraints of an existing fishery (Lombard et al., 2007). Kernel utilization distributions for three species—southern elephant seals, wandering albatrosses and grey-headed albatrosses—were among the data layers used to define pelagic "flexible processes". These data identified several of the important areas identified in the present study—including areas to the south-west and north-west of the islands—but inadequately represented the broader top predator community. Lombard et al. (2007) recommended that new information, such as presented here, be used to reassess the spatial plan. The authors also pointed to the importance of a management framework beyond the Prince Edward Islands EEZ, and our results show that this is indeed necessary. The latter point was also

highlighted in a study that used tracking data from 10 seabird species at the Crozet, Kerguelen and Amsterdam islands to identify Important Bird Areas using criteria set out by BirdLife International (Delord et al., 2014). The authors identified 19 candidate Important Bird Areas in the southern Indian and southern Atlantic Oceans, several of which include important habitat identified in our study. An analysis of global tracking data from 60 seabird species also identified a high concentration of IBAs in the southwest Indian Ocean, including many in the high seas (Lascelles et al., 2016).

Tracking data for nine species of seabirds and marine mammals has similarly been used to identify important habitat for top predators around the Kerguelen Archipelago, ~2,300 km east southeast of the Prince Edward Islands (Thiers et al., 2017). The authors of that study developed habitat models for four of the nine species included, which they considered representative of the top predator community at the islands. Using these models, they predicted that the shallow Kerguelen/Heard plateau and its shelf-break was important to the community (Thiers et al., 2017), echoing the findings of an earlier effort to identify areas of ecological significance based on tracking data for five species from Kerguelen and Heard islands (Hindell et al., 2011). The Prince Edward Islands, in contrast, have a small (~1,000 km^2) shelf between the two islands, limiting shelf and shelf-break habitats for predators. Some species made use of distant shelf and shelf-break habitats off South Africa (Indian yellow-nosed albatross and white-chinned petrel), but high mean importance areas were generally pelagic. This has two notable implications. Firstly, much of the important area is in the high seas, beyond the jurisdiction of any nation, which presents a conservation and management challenge (Game et al., 2009). Secondly, the processes and features associated with favourable pelagic foraging habitat for meso- and apex predators are often dynamic (Hazen et al., 2013). It is therefore important to explicitly link predator distributions with environmental data to accurately predict the spatial occurrence of such areas for any management actions (Game et al., 2009; Hyrenbach, Forney, & Dayton, 2000). Our habitat models were primarily predictive but the environmental covariates in the models have mechanistic links with biological productivity and therefore the distribution and abundance of prey. The relative importance of environmental covariates in our habitat models offers some insight into the factors that influence top predator distributions. However, it is critical to note that our models allow interactions among covariates, and that these interactions are themselves likely to be very important (Dormann, 2007).

In species-specific models, sea surface temperature, primary productivity and depth were often important predictors of habitat preference. In a tagging study of 23 top predator species in the Pacific Ocean, Block et al. (2011) showed a positive relationship between SST and predator abundance. Similarly, a global analysis of marine species richness showed that SST was the best predictor of species richness across diverse taxa (Tittensor, Mora, Jetz, & Lotze, 2010). In the same study, however, primary productivity was a better predictor of species richness in cetaceans and pinnipeds (Tittensor et al., 2010). In our species-specific models, productivity was also of high importance. SST and productivity are linked and are among the main factors influencing ocean ecosystems (Garrison, 2009; Kaiser et al., 2005). While these predictors may be decoupled in time and space, and from prey availability at higher trophic levels (e.g., Grémillet et al., 2008), we might expect that they broadly indicate profitable foraging areas for marine top predators (e.g., Block et al., 2011). Depth is also an important predictor in both species-specific and mean habitat importance models and bottom slope was important in a winter mean habitat importance model. Bathymetric characteristics have often been linked to predator diversity (Bouchet, Meeuwig, Salgado Kent, Letessier, & Jenner, 2015; Morato, Hoyle, Allain, & Nicol, 2010), as the seafloor has a fundamental influence on biophysical processes (Garrison, 2009; Kaiser et al., 2005). For example, features like seamounts and shelf breaks can interact with currents to increase vertical mixing and upwelling, which increases productivity and in turn may attract higher order predators (Bouchet et al., 2015; Morato et al., 2010).

SSTgrad, SSHA and SSHgrad are linked to ocean fronts and eddies, which are considered important to a range of marine top predators (Nel et al. 2001, Bost et al., 2009; Scales et al., 2014). While these had moderate influence for some species (e.g., light-mantled albatross in summer), only SSTgrad was an important predictor in the mean habitat importance models, and the direction of this relationship was contrary to expectation, with lower SSTgrad in high mean importance areas. Eddy kinetic energy was a poor predictor even in species-specific models. It may be that such associations will only be detected at finer spatio-temporal scales, or if along-track behaviour of the animals is modelled rather than using a case–control design.

In terms of mean habitat importance, SST was influential but wind typically had a greater influence. Wind affects the depth of the mixed layer (MLD), which in turn affects primary productivity and chlorophyll-a concentration (Sallée, Speer, & Rintoul, 2010), but it is interesting that these variables themselves (CHL, PROD, MLD) were not of higher importance than wind for predicting mean importance (although both PROD and CHL were generally more influential in species-specific models). Our use of monthly climatologies (MLD and CHL) and coarse resolution data (MLD) may have masked this relationship, as well as the secondary nature of the mean habitat importance model. Response curves for the environmental variables, particularly SST and WINDU, illustrate the seasonal southward shift of important areas, from the Subtropical and Subantarctic Zones in summer to a more Polar Frontal Zone distribution in winter.

Given the diverse space use and foraging strategies of predators included in this study, it is possible that these factors identified as most influential for mean habitat importance only correlate with high mean importance areas, rather than being the mechanistic cause thereof. This should have been alleviated somewhat using only the 4 or 8 highest species scores for each cell, which should select sets of predators with similar responses to environmental conditions (as identified in the cluster analysis). However, different sets of predators will be selected in each case which may preclude broad inference in this study. The dataset we assembled may be used to further explore such mechanistic links. However, our results show that there is unlikely to be a simple relationship linking areas of high top predator overlap with environmental predictors in this region.

The results underscore the utility of predictive modelling for management and conservation purposes. Along with other studies around French and Australian islands in the Indian Ocean sector of the Southern Ocean (Delord et al., 2014; Hindell et al., 2011; Patterson et al., 2016; Thiers et al., 2017), we show the advantages of analysing multi-species tracking data to identify important marine habitat for top predators, but also illustrate diverse foraging areas and space use patterns for Subantarctic top predators breeding at different archipelagos.

4.1 | Limitations and future research

The study makes a significant contribution to our knowledge of marine top predator distribution in the Southern Ocean. However, some caveats should be noted.

The tracking data available for the study are not representative of all top predators breeding at the Prince Edward Islands. Although we included a broad range of taxa with varied foraging strategies, smaller seabirds are not represented due to the logistical challenges of tracking them. Inshore-feeding species—Gentoo penguins (*Pygoscelis papua*) and Crozet shags (*Phalacrocorax [atriceps] melanogenis*)—were also not included. However, the inter-island shelf and inshore areas typically used by the latter species (e.g., Carpenter-Kling et al., 2017) represent a very small number of grid cells in our study, and most of these cells are already highlighted. Therefore, the inclusion of tracking data for these species would be unlikely to significantly change our findings.

Not all life history stages of each species are represented in our study: data are primarily from adult individuals, and breeding phases are better represented. Although our analysis suggests that tracking data are representative of the population of each species, these results apply only to the life history stage during tracking. Moreover, representativeness can only be estimated and, in our method, the representativeness score was dependent on the nonlinear regression used.

We compared environmental covariates along observed tracks to those along simulated tracks to estimate broad-scale habitat preferences. Alternatively, we could calculate indices of foraging behaviour (or "area-restricted search") along each track and compare characteristics of putative foraging locations with those of putative non-foraging locations (e.g., Reisinger, Keith, Andrews, & de Bruyn, 2015). While this may reveal environmental features related to foraging specifically, the selected indices of foraging behaviour may show weak correspondence with actual foraging (e.g., Ramasco, Barraquand, Biuw, McConnell, & Nilssen, 2015; Weimerskirch, Pinaud, Pawlowski, & Bost, 2007) and a single index might not be appropriate across species with different foraging modes. Furthermore, this approach typically does not account for environments that were available but not used by the animals, which may underestimate habitat preference.

The data and results presented here form the basis of future efforts to predict the consequences of environmental change (e.g., Hazen et al., 2013), and it would be useful to identify species representative of the distribution of the broader suite of marine predators. Explicitly identifying specific priority areas requires choosing thresholds for habitat percentile and mean habitat importance values, and further work is required in this regard. Further effort should also be directed towards exploring alternative approaches for modelling the distribution and overlap of this set of marine top predators, including multivariate models (e.g., Elith & Leathwick, 2007; Warton et al., 2015).

ACKNOWLEDGEMENTS

We are grateful to the numerous field biologists who assisted with fieldwork at the Prince Edward Islands. This work was supported by a National Research Foundation (NRF) SANCOR grant to R.R.R. (94916), NRF SANAP grants to M.N.B., R.J.M.C. (SNA103359), P.J.N.d.B., P.G.R. and P.A.P. (SNA2005060800001), and a Scientific Committee on Antarctic Research (SCAR) Fellowship to R.R.R. Data were collected through various research programmes funded by the NRF and the South African Department of Environmental Affairs, which also provided logistical support. This work benefitted from the activities of the SCAR Retrospective Analysis of Antarctic Tracking Data project, funded by the Centre de Synthèse et d'Analyse sur la Biodiversité of the Fondation pour la Recherche sur la Biodiversité.

DATA ACCESSIBILITY

Individual locations, pseudo-locations and environmental covariates extracted at these locations, as well as predictions and overlap scores, are deposited in Reisinger et al. (2017): https://doi.org/10.6084/m9.figshare.5613016

ORCID

Ryan R. Reisinger http://orcid.org/0000-0002-8933-6875

REFERENCES

Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., & Matthiopoulos, J. (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, *31*, 140–160. https://doi.org/10.1111/j.2007.0906-7590.05236.x

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, *78*, 699–714. https://doi.org/10.1111/j.1365-2656.2009.01531.x

Bester, M. N., de Bruyn, P. J. N., Oosthuizen, W. C., Tosh, C., McIntyre, T., Reisinger, R., … Wege, M. (2011). The marine mammal programme at the Prince Edward Islands: 38 years of research. *African Journal of Marine Science*, *33*, 511–521. https://doi.org/10.2989/1814232X.2011.637356

Bester, M. N., & Pansegrouw, H. M. (1992). Ranging behaviour of southern elephant seal cows from Marion Island. *South African Journal of Science*, *88*, 574–575.

Beyer, H. L., Haydon, D. T., Morales, J. M., Frair, J. L., Hebblewhite, M., Mitchell, M., & Matthiopoulos, J. (2010). The interpretation of habitat preference metrics under use-availability designs. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*, 2245–2254. https://doi.org/10.1098/rstb.2010.0083

Block, B. A., Costa, D. P., Boehlert, G. W., & Kochevar, R. E. (2003). Revealing pelagic habitat use: The tagging of Pacific pelagics program. *Oceanologica Acta*, *25*, 255–266.

Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., … Costa, D. P. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, *475*, 86–90. https://doi.org/10.1038/nature10082

Bodenhofer, U., Kothmeier, A., & Hochreiter, S. (2011). APCluster: An R package for affinity propagation clustering. *Bioinformatics*, *27*, 2463–2464. https://doi.org/10.1093/bioinformatics/btr406

Bost, C. A., Cotté, C., Bailleul, F., Cherel, Y., Charrassin, J. B., Guinet, C., … Weimerskirch, H. (2009). The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *Journal of Marine Systems*, *78*, 363–376. https://doi.org/10.1016/j.jmarsys.2008.11.022

Bouchet, P. J., Meeuwig, J. J., Salgado Kent, C. P., Letessier, T. B., & Jenner, C. K. (2015). Topographic determinants of mobile vertebrate predator hotspots: Current knowledge and future directions. *Biological Reviews*, *90*, 699–728. https://doi.org/10.1111/brv.12130

Boyd, I. L., & Murray, A. W. A. (2001). Monitoring a marine ecosystem using responses of upper trophic level predators. *Journal of Animal Ecology*, *70*, 747–760. https://doi.org/10.1046/j.0021-8790.2001.00534.x

Breiman, L. (2001). Random forests. *Machine Learning*, *45*, 5–32. https://doi.org/10.1023/A:1010933404324

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Carpenter-Kling, T., Handley, J. M., Green, D. B., Reisinger, R. R., Makhado, A. B., Crawford, R. J. M., & Pistorius, P. A. (2017). A novel foraging strategy in gentoo penguins breeding at sub-Antarctic Marion Island. *Marine Biology*, *164*, 33.

Cooper, J., & Brown, C. R. (1990). Ornithological research at the sub-Antarctic Prince Edward Islands: A review of achievements. *South African Journal of Antarctic Research*, *20*, 40–57.

Crawford, R., Dyer, B., Upfold, L., & Makhado, A. (2014). Congruent, decreasing trends of gentoo penguins and Crozet shags at sub-Antarctic Marion Island suggest food limitation through common environmental forcing. *African Journal of Marine Science*, *36*, 225–231. https://doi.org/10.2989/1814232X.2014.926293

De Bruyn, P. J. N., Tosh, C. A., Oosthuizen, W. C., Bester, M. N., & Arnould, J. P. Y. (2009). Bathymetry and frontal system interactions influence seasonal foraging movements of lactating subantarctic fur seals from Marion Island. *Marine Ecology Progress Series*, *394*, 263–276. https://doi.org/10.3354/meps08292

Deane-Mayer, Z. A., & Knowles, J. E. (2016). *caretEnsemble: Ensembles of caret models*. R package version 2.0.0. Retrieved from https://CRAN.R-project.org/package=caretEnsemble

Delord, K., Barbraud, C., Bost, C. A., Deceuninck, B., Lefebvre, T., Lutz, R., … Weimerskirch, H. (2014). Areas of importance for seabirds tracked from French southern territories, and recommendations for conservation. *Marine Policy*, *48*, 1–13. https://doi.org/10.1016/j.marpol.2014.02.019

Dormann, C. F. (2007). Promising the future? Global change projections of species distributions. *Basic and Applied Ecology*, *8*, 387–397. https://doi.org/10.1016/j.baae.2006.11.001

Durant, J., Hjermann, D., Frederiksen, M., Charrassin, J., Le Maho, Y., Sabarros, P., … Stenseth, N. (2009). Pros and cons of using seabirds as ecological indicators. *Climate Research*, *39*, 115–129. https://doi.org/10.3354/cr00798

Elith, J., & Leathwick, J. (2007). Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity and Distributions*, *13*, 265–275. https://doi.org/10.1111/j.1472-4642.2007.00340.x

Freitas, C. (2012). *argosfilter: Argos locations filter*. R package version 0.63. Retrieved from https://CRAN.R-project.org/package=argosfilter

Freitas, C., Lydersen, C., Ims, R. A., Fedak, M. A., & Kovacs, K. M. (2008). A simple new algorithm to filter marine mammal Argos locations. *Marine Mammal Science*, *24*, 315–325. https://doi.org/10.1111/j.1748-7692.2007.00180.x

Frey, B. J., & Dueck, D. (2007). Clustering by passing messages between data points. *Science*, *315*, 972–977. https://doi.org/10.1126/science.1136800

Friedman, J. H. (2001). Greedy function approximation: A gradient boosting machine. *Annals of Statistics*, *29*, 1189–1232. https://doi.org/10.1214/aos/1013203451

Game, E. T., Grantham, H. S., Hobday, A. J., Pressey, R. L., Lombard, A. T., Beckley, L. E., … Richardson, A. J. (2009). Pelagic protected areas: The missing dimension in ocean conservation. *Trends in Ecology and Evolution*, *24*, 360–369. https://doi.org/10.1016/j.tree.2009.01.011

Garrison, T. (2009). *Essentials of Oceanography*, 5th ed. Belmont, CA: Brooks/Cole Cengage Learning.

Grémillet, D., Lewis, S., Drapeau, L., van der Lingen, C. D., Huggett, J. A., Coetzee, J. C., … Ryan, P. G. (2008). Spatial match-mismatch in the Benguela upwelling zone: Should we expect chlorophyll and sea-surface temperature to predict marine predator distributions? *Journal of Applied Ecology*, *45*, 610–621. https://doi.org/10.1111/j.1365-2664.2007.01447.x

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., … Walbridge, S. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications*, *6*, 7615. https://doi.org/10.1038/ncomms8615

Hazen, E., Suryan, R., Santora, J., Bograd, S., Watanuki, Y., & Wilson, R. (2013). Scales and mechanisms of marine hotspot formation. *Marine Ecology Progress Series*, *487*, 177–183. https://doi.org/10.3354/meps10477

Heithaus, M. R., Frid, A., Wirsing, A. J., & Worm, B. (2008). Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution*, *23*, 202–210. https://doi.org/10.1016/j.tree.2008.01.003

Hijmans, R. J. (2012). Cross-validation of species distribution models: Removing spatial sorting bias and calibration with a null model. *Ecology*, *93*, 679–688. https://doi.org/10.1890/11-0826.1

Hijmans, R. J. (2016). *raster: Geographic data analysis and modeling*. R package version 2.5-8. Retrieved from https://CRAN.R-project.org/package=raster

Hindell, M. A., Bradshaw, C. J. A., Sumner, M. D., Michael, K. J., & Burton, H. R. (2003). Dispersal of female southern elephant seals and their prey consumption during the austral summer: Relevance to management and oceanographic zones. *Journal of Applied Ecology*, *40*, 703–715. https://doi.org/10.1046/j.1365-2664.2003.00832.x

Hindell, M. A., Lea, M., Bost, C., Charrassin, J., Gales, N., Goldsworthy, S., … Guinet, C. (2011). Foraging habitats of top predators, and areas of ecological significance, on the Kerguelen Plateau. In G. Duhamel, & D. Welsford (Eds.), *The Kerguelen Plateau: Marine ecosystem and fisheries* (pp. 203–215). Paris, France: Societe Francaise d'Ichtyologie.

Hyrenbach, K. D., Forney, K. A., & Dayton, P. K. (2000). Marine protected areas and ocean basin management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *10*, 437–458. https://doi.org/10.1002/(ISSN)1099-0755

Johnson, D. S. (2015). *crawl: Fit continuous-time correlated random walk models to animal movement data*. R package version 1.5. Retrieved from https://CRAN.R-project.org/package=crawl

Johnson, D. S., London, J., Lea, M., & Durban, J. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology*, *89*, 1208–1215. https://doi.org/10.1890/07-1032.1

Kaiser, M. J., Attrill, M. J., Jennings, S., Thomas, D. N., Barnes, D. K. A., Brierley, A. S., … Williams, P. J. le. B. (2005). *Marine ecology: Processes, systems, and impacts*. New York, NY: Oxford University Press.

Kirkman, S. P., Yemane, D. G., Lamont, T., Meÿer, M. A., & Pistorius, P. A. (2016). Foraging behavior of subantarctic fur seals supports efficiency of a marine reserve's design. *PLoS ONE*, *11*, e0152370.

Kuhn, M. (2016). *caret: Classification and regression training*. R package version 6.0-73. Retrieved from https://CRAN.R-project.org/package=caret

Lascelles, B. G., Taylor, P. R., Miller, M. G. R., Dias, M. P., Oppel, S., Torres, L., … Small, C. (2016). Applying global criteria to tracking data to define important areas for marine conservation. *Diversity and Distributions*, *22*, 422–431. https://doi.org/10.1111/ddi.12411

Lombard, A. T., Reyers, B., Schonegevel, L. Y., Cooper, J., Smith-Adao, L. B., Nel, D. C., … Chown, S. L. (2007). Conserving pattern and process in the Southern Ocean: Designing a Marine Protected Area for the Prince Edward Islands. *Antarctic Science*, *19*, 39–54.

Lutjeharms, J. R. E., & Ansorge, I. J. (2008). Oceanographic setting of the Prince Edward Islands. In S. L. Chown, & P. W. Froneman (Eds.), *The Prince Edward Islands: Land–sea interactions in a changing ecosystem* (pp. 17–38). Stellenbosch, South Africa: Sun Press. https://doi.org/10.18820/9781928357063

Maxwell, S. M., Hazen, E. L., Bograd, S. J., Halpern, B. S., Breed, G. A., Nickel, B., … Costa, D. P. (2013). Cumulative human impacts on marine predators. *Nature Communications*, *4*, 1–9.

Mcintyre, T., Bornemann, H., Plötz, J., Tosh, C. A., & Bester, M. N. (2012). Deep divers in even deeper seas: Habitat use of male southern elephant seals from Marion Island. *Antarctic Science*, *24*, 561–570. https://doi.org/10.1017/S0954102012000570

Mélice, J.-L., Lutjeharms, J. R. E., Rouault, M., & Ansorge, I. J. (2003). Sea-surface temperatures at the sub-Antarctic islands Marion and Gough during the past 50 years. *South African Journal of Science*, *99*, 363–366.

Moore, S. (2008). Marine mammals as ecosystem sentinels. *Journal of Mammalogy*, *89*, 534–540. https://doi.org/10.1644/07-MAMM-S-312R1.1

Morato, T., Hoyle, S. D., Allain, V., & Nicol, S. J. (2010). Seamounts are hotspots of pelagic biodiversity in the open ocean. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 9707–9711. https://doi.org/10.1073/pnas.0910290107

Nel, D. C., Lutjeharms, J. R. E., Pakhamov, 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.

Orsi, A. H., Whitworth, T. III, & Nowlin, W. D. Jr (1995). On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Research Part I*, *42*, 641–673.

Patterson, T. A., Sharples, R. J., Raymond, B., Welsford, D. C., Andrews-Goff, V., Lea, M. A., … Hindell, M. (2016). Foraging distribution overlap and marine reserve usage amongst sub-Antarctic predators inferred from a multi-species satellite tagging experiment. *Ecological Indicators*, *70*, 531–544. https://doi.org/10.1016/j.ecolind.2016.05.049

Pistorius, P., Hindell, M., Crawford, R., Makhado, A., Dyer, B., & Reisinger, R. (2017). At-sea distribution and habitat use in king penguins at sub-Antarctic Marion Island. *Ecology and Evolution*, *7*, 3894–3903. https://doi.org/10.1002/ece3.2833

R Core Team (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Ramasco, V., Barraquand, F., Biuw, M., McConnell, B., & Nilssen, K. T. (2015). The intensity of horizontal and vertical search in a diving forager: The harbour seal. *Movement Ecology*, *3*, 15. https://doi.org/10.1186/s40462-015-0042-9

Raymond, B., Lea, M. A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J. B., … Goldsworthy, S. D. (2015). Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography*, *38*, 121–129.

Reisinger, R. R., Keith, M., Andrews, R. D., & de Bruyn, P. J. N. (2015). Movement and diving of killer whales (*Orcinus orca*) at a Southern Ocean archipelago. *Journal of Experimental Marine Biology and Ecology*, *473*, 90–102. https://doi.org/10.1016/j.jembe.2015.08.008

Ryan, P. G., & Bester, M. N. (2008). Pelagic predators. In S. L. Chown, & P. W. Froneman (Eds.), *The Prince Edward Islands: Land–sea interactions in a changing ecosystem* (pp. 121–164). Stellenbosch, South Africa: Sun Press. https://doi.org/10.18820/9781928357063

Sallée, J.-B., Speer, K. G., & Rintoul, S. R. (2010). Zonally asymmetric response of the Southern Ocean mixed-layer depth to the Southern Annular Mode. *Nature Geoscience*, *3*, 273–279. https://doi.org/10.1038/ngeo812

Scales, K. L., Miller, P. I., Hawkes, L. A., Ingram, S. N., Sims, D. W., & Votier, S. C. (2014). On the front line: Frontal zones as priority at-sea conservation areas for mobile marine vertebrates. *Journal of Applied Ecology*, *51*, 1575–1583. https://doi.org/10.1111/1365-2664.12330

Schoombie, S., Dilley, B. J., Davies, D., Glass, T., & Ryan, P. G. (2017). The distribution of breeding Sooty Albatrosses from the three most important breeding sites: Gough, Tristan and the Prince Edward Islands. *Emu-Austral Ornithology*, *117*, 160–169. https://doi.org/10.1080/01584197.2017.1289804

Silverman, B. W. (1986). *Density estimation for statistics and data analysis*. Boca Raton, FL: Chapman & Hall/CRC. https://doi.org/10.1007/978-1-4899-3324-9

Sumner, M. D. (2016). *raadtools: Tools for synoptic environmental spatial data*. R package version 0.3.2.9004. Retrieved from https://github.com/AustralianAntarcticDivision/raadtools

Thiers, L., Delord, K., Bost, C.-A., Guinet, C., & Weimerskirch, H. (2017). Important marine sectors for the top predator community around Kerguelen Archipelago. *Polar Biology*, *40*, 365–378. https://doi.org/10.1007/s00300-016-1964-4

Tittensor, D., Mora, C., Jetz, W., & Lotze, H. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, *466*, 1098–1101. https://doi.org/10.1038/nature09329

Tosh, C. A., de Bruyn, P. J. N., Steyn, J., Bornemann, H., van den Hoff, J., Stewart, B. S., … Bester, M. N. (2015). The importance of seasonal sea surface height anomalies for foraging juvenile southern elephant seals. *Marine Biology*, *162*, 2131–2140. https://doi.org/10.1007/s00227-015-2743-4

Tosh, C. A., Steyn, J., Bornemann, H., van den Hoff, J., Stewart, B., Plötz, J., & Bester, M. (2012). Marine habitats of juvenile southern elephant seals from Marion Island. *Aquatic Biology*, *17*, 71–79. https://doi.org/10.3354/ab00463

Warton, D. I., Blanchet, F. G., O'Hara, R. B., Ovaskainen, O., Taskinen, S., Walker, S. C., & Hui, F. K. C. (2015). So many variables: Joint modeling in community ecology. *Trends in Ecology and Evolution*, *30*, 766–779. https://doi.org/10.1016/j.tree.2015.09.007

Wege, M. (2017). *Population trend and foraging ecology of Antarctic and Subantarctic fur seals at Marion Island*. PhD Thesis, University of Pretoria.

Wege, M., Etienne, M. P., Oosthuizen, W. C., Reisinger, R. R., Bester, M. N., & de Bruyn, P. J. N. (2016). Trend changes in sympatric Subantarctic and Antarctic fur seal pup populations at Marion Island, Southern Ocean. *Marine Mammal Science*, *32*, 960–982. https://doi.org/10.1111/mms.12306

Wege, M., Tosh, C. A., de Bruyn, P. J. N., & Bester, M. N. (2016). Cross-seasonal foraging site fidelity of subantarctic fur seals: Implications for marine conservation areas. *Marine Ecology Progress Series*, *554*, 225–239. https://doi.org/10.3354/meps11798

Weimerskirch, H., Inchausti, P., Guinet, C., & Barbraud, C. (2003). Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Science*, *15*, 249–256. https://doi.org/10.1017/S0954102003001202

Weimerskirch, H., Pinaud, D., Pawlowski, F., & Bost, C.-A. (2007). Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the wandering albatross. *American Naturalist*, *170*, 734–743.

Whitehead, T. O., Kato, A., Ropert-Coudert, Y., & Ryan, P. G. (2016). Habitat use and diving behaviour of macaroni *Eudyptes chrysolophus* and eastern rockhopper *E. chrysocome filholi* penguins during the critical pre-moult period. *Marine Biology*, *163*, 19. https://doi.org/10.1007/s00227-015-2794-6

Wilson, M. F. J., O'Connell, B., Brown, C., Guinan, J. C., & Grehan, A. J. (2007). Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Marine Geology*, *30*, 3–35.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, *70*, 164–168. https://doi.org/10.2307/1938423

Zhou, Z.-H. (2012). *Ensemble methods: Foundations and algorithms*. Boca Raton, FL: CRC Press.

BIOSKETCH

Ryan R. Reisinger is a post-doctoral research fellow, presently at the Centre d'Etudes Biologiques de Chizé. His research focuses on the ecology of marine predators with an emphasis on their movement and foraging.

Author contributions: R.R.R., B.R., M.A.H. and P.A.P. conceived and designed the research. R.R.R., B.R., M.A.H., M.D.S. and S.W. conducted analyses and contributed to analytical tools and methods. R.R.R., M.N.B., R.J.M.C., D.D., P.J.N.d B., B.J.D., S.P.K., A.B.M., P.G.R., S.S., K.S., C.A.T., M.W., T.O.W. and P.A.P. contributed to tracking data. R.R.R. wrote the manuscript with contributions from all other authors.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Reisinger RR, Raymond B, Hindell MA, et al. Habitat modelling of tracking data from multiple marine predators identifies important areas in the Southern Indian Ocean. *Divers Distrib*. 2018;24:535–550. https://doi.org/10.1111/ddi.12702