

# Using habitat models for chinstrap penguins *Pygoscelis antarctica* to advise krill fisheries management during the penguin breeding season

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## Abstract

**Aim:** To predict the at-sea distribution of chinstrap penguins across the South Orkney Islands and to quantify the overlap with the Southern Ocean krill fishery.

**Location:** South Orkney Islands, Antarctica.

**Methods:** Penguins from four colonies across the South Orkney Islands were tracked using global positioning systems (GPSs) and time depth recorders (TDRs). Relationships between a variety of environmental and geometric variables and the at-sea distribution of penguins were investigated using general additive models for the three main phases of the breeding season. Subsequently, the final models were extrapolated across the South Orkney archipelago to predict the at-sea distribution of penguins from colonies where no tracking data are available. Finally, the overlap between areas used by chinstrap penguins and the krill fishery was quantified.

**Results:** The foraging distribution of chinstrap penguins can be predicted using two simple and static variables: the distance from the colony and the direction of travel towards the shelf-edge, while avoiding high densities of *Pygoscelis* penguins from other colonies. Additionally, we find that the chinstrap penguins breeding on the South Orkney Islands use areas which overlap with frequently used krill fishing areas and that this overlap is most prominent during the brood and crèche phases of the breeding season.

**Main conclusions:** This is the first step in understanding the potential impacts of the krill fishery, for all colonies including those where no empirical tracking data are available. However, with the available data, it is not currently possible to infer an impact of the krill fisheries on penguins. With this in mind, we recommend the implementation of monitoring schemes to investigate the effects of prey depletion on predator populations and to ensure that management continues to follow a precautionary approach and is addressed at spatial and temporal scales relevant to ecosystem operation.

## KEYWORDS

Antarctica, chinstrap penguin, fisheries overlap, habitat modelling, krill fishery, management, marine predator, *Pygoscelis antarctica*

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## 1 | INTRODUCTION

There is now a widespread concern and a growing understanding of threats facing marine systems across the globe (Halpern et al., 2012). In particular, Southern Ocean ecosystems are facing a number of significant challenges (Gutt et al., 2015; Trathan & Agnew, 2010), especially at those locations where some of the fastest rates of warming on our planet have been recorded (Gille, 2002, 2008; Hauck, Hoppema, Bellerby, Völker, & Wolf-Gladrow, 2010; Turner et al., 2009). In addition to these signals of regional climate change, there is now also growing interest in the commercial harvesting of Antarctic krill (*Euphausia superba*), a species which is prey for many Antarctic marine predators and potentially one of the last major underdeveloped sources of marine protein. Potential threats posed by the fishery include reductions in krill abundance, disturbance of krill swarm structure that may alter foraging opportunities (Alonzo, Switzer, & Mangel, 2003), or accidental mortality and by-catch (Trathan et al., 2015). Harvesting in the Southern Ocean is increasingly taking place at small spatial scales, often in close proximity to predator breeding colonies (Hinke Jefferson et al., 2017). However, despite decades of research, the impacts on predator populations of harvesting key forage species such as krill and small pelagic fish remain poorly understood (Cury et al., 2011; Hilborn et al., 2017; Sherley et al., 2017). Understanding the factors that influence the distribution of marine predators is fundamental to mitigate these potential impacts (Louzao et al., 2011; Manly, McDonald, Thomas, McDonald, & Erickson, 2002).

Many marine predators target areas of high prey predictability, often in association with physical features or oceanographic processes such as areas of upwelling, frontal systems, eddies and shelf breaks (Pinaud & Weimerskirch, 2002; Scales et al., 2014; Weimerskirch, 2007). These associations occur as a result of increased primary production or aggregation of marine organisms in these areas (Bertrand et al., 2008). However, the accessibility of these hotspots to predators must also be considered (Aarts, MacKenzie, McConnell, Fedak, & Matthiopoulos, 2008; Matthiopoulos, 2003). For example, some species of marine predator are central place foragers during the breeding season, constrained to return to land frequently to provision offspring (Orlans Gordon & Pearson Nolan, 1979). Thus, the distance from their breeding colony is an important constraint limiting their at-sea distribution and the habitats available to them (Raymond et al., 2015). Additionally, competition for resources from other krill-eating predators will impact on both the quantity of prey available (Barlow et al., 2002; Lewis, Sherratt, Hamer, & Wanless, 2001) and the accessibility of these areas to predators from different colonies (Wakefield et al., 2013). These constraints are likely to vary on a temporal scale as the foraging range of many seabirds is highly variable between incubation, chick-rearing, premoult and overwintering. Impacts from reduced krill availability are likely to be highest during periods where individuals may be limited in their foraging range, while requiring increased energy for offspring provisioning, potentially resulting in lower breeding success (Forcada & Trathan, 2009). These impacts are likely to vary between predator

populations, according to species and location (Klein, Hill, Hinke, Phillips, & Watters, 2018).

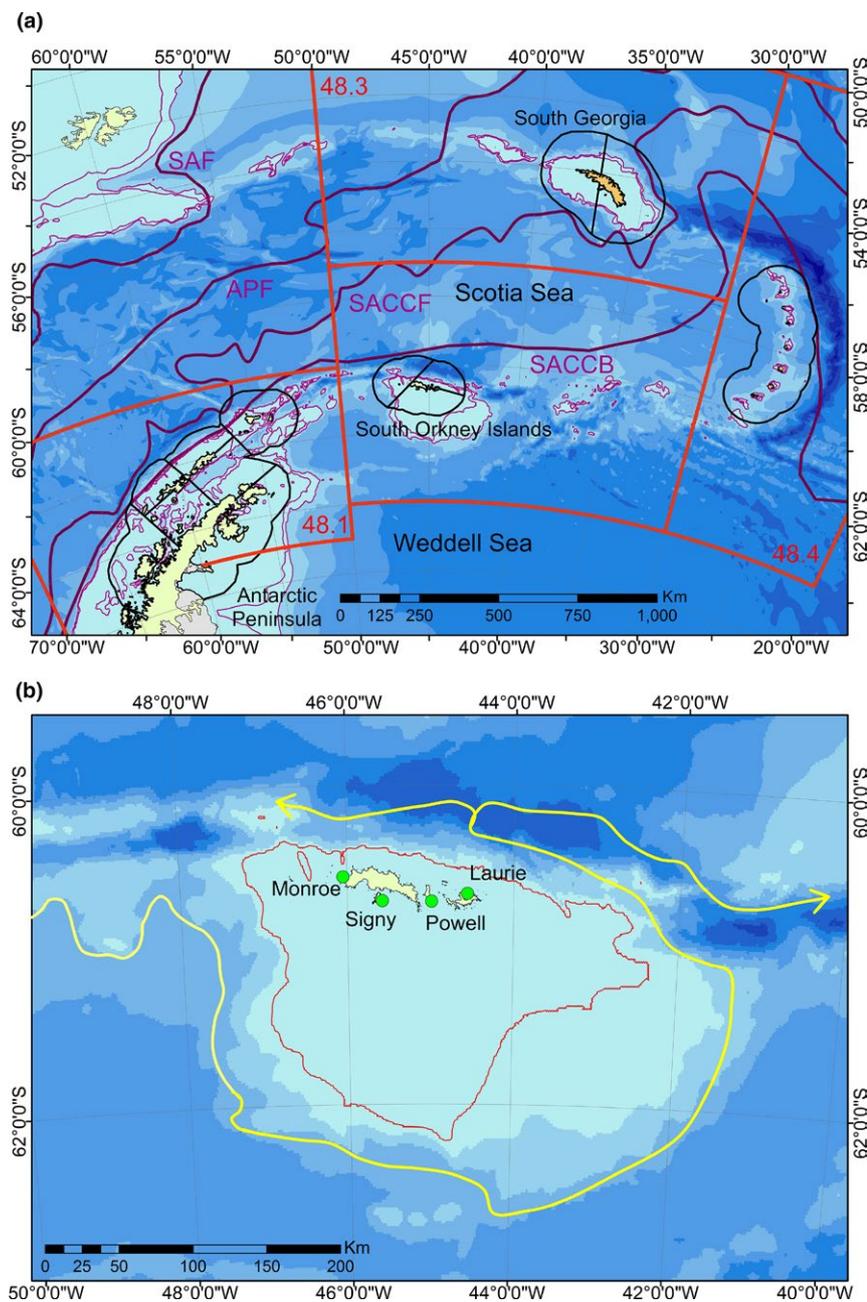
Concern about the rapid expansion of the fishery in the 1980s and the potential impact on nontarget species were two of the principal factors that led to the establishment in 1982 of the Commission for the Conservation of Antarctic Marine Living Resources (SC-CAMLR 2016, see Supporting Information). A key issue for CCAMLR is how to manage the krill fishery at small spatial scales, so that it does not threaten krill-dependent predators (Hilborn et al., 2017; Sherley et al., 2017). The fishery is currently managed in a precautionary manner, with low catch limits relative to the stock size, coupled with rules to distribute the catch spatially to minimize any effects on predators (Hill et al., 2016). However, CCAMLR is working to revise the spatial and temporal distributions of catches to accommodate potential future expansion of the fishery. Consequently, without a better understanding of how predators might be impacted at greater catch levels, CCAMLR will be unlikely to reach an agreement about how the fishery should develop. With this in mind, the CCAMLR Ecosystem Monitoring Programme (CEMP) was established to monitor predator, prey and environmental indicators with the aim of detecting and understanding ecosystem changes (Agnew, 1997). However, the location of CEMP monitoring effort at many localities has little spatial or temporal overlap with areas of increased fishery usage; thus, evidence of any impacts on the fishery is unavailable. With no evidence of current impacts, yet with the proposed expansion of the fishery, it is important to gain insight into which predator populations may be most vulnerable and to devise targeted management at the appropriate spatial and temporal scales for protection (Klein et al., 2018). For example, Klein et al. (2018) showed how penguins are the most vulnerable krill predators to changes in krill growth as a result of climate change and that reducing fishing effort may moderate these impacts in some locations. Limiting the overlap between vulnerable predator colonies and the krill fishery, during the breeding season, could then allow constraints surrounding more robust populations, or at other times of the year, to be relaxed (Klein et al., 2018). Consequently, quantifying the overlap between the at-sea distribution of predators and the krill fishery is a first step in identifying important areas for management. Further understanding of the temporally explicit drivers behind the distribution of marine predators can be gained via the implementation of habitat preference models (e.g., Block et al., 2011).

Recent developments in habitat preference models have enabled us to predict the distribution of predators in relation to environmental features and accessibility (Aarts et al., 2008; Wakefield et al., 2011). Additionally, the increasing availability of remote sensing data, and the miniaturization and affordability of biologging devices, has resulted in many large-scale tracking studies across multiple species and populations (Grecian et al., 2016; Raymond et al., 2015). Despite this, many populations and entire species remain untracked, as many breeding colonies are impractical to access due to logistical constraints. Thus, when empirical tracking data are not available, the ability to predict the distributions of marine predators as a function of their physical environment, accessible habitat and competition

is essential to their protection (Wakefield et al., 2011). Predictions of habitat utilization can be used to inform marine spatial planning, including the identification of priority areas for conservation or fisheries management (Grecian et al., 2016; Oppel et al., 2012; Ratcliffe et al., 2015).

In this context, our study develops a series of habitat preference models for one of the most abundant CEMP-monitored avian species breeding in the Atlantic sector of the Southern Ocean, the chinstrap penguin (*Pygoscelis antarctica*). We sought to identify the preferred habitats used by this species during the times of year when animals are constrained to return to land to provision their offspring. Our study focused on the South Orkney Islands (Figure 1a), one of the principal archipelagos in the Atlantic sector and one of the main areas of intense krill fishing activity. Our

intention was to identify how habitat preferences vary on a temporal scale, to highlight where management objectives should be critically evaluated. Thus, our primary aim was to identify the most parsimonious models to predict the foraging locations of chinstrap penguins during the main phases of their breeding season: incubation, brood and crèche. Secondly, we aimed to use these models to extrapolate predicted distributions around other colonies for which no tracking data are available and thus to apply a novel methodology to quantify overlap between predators and the fishery, using predicted distribution output from habitat models, instead of empirical tracking data. Such outputs would contribute to quantifying the potential for competition between penguins and the fishery, resulting in plausible options for a revised management framework in these near-shore habitats.



**FIGURE 1** (a) The boundaries of FAO statistical subareas 48.1, 48.2, 48.3 and 48.4 (red), and the boundaries of the CCAMLR small-scale management units (SSMU) for the krill fishery (black). The major fronts of the Antarctic Circumpolar Current (ACC); Southern ACC Boundary (SACCB); Southern ACC Front (SACCF); Antarctic Polar Front (APF); and Sub-Antarctic Front (SAF). (b) The four chinstrap penguin colonies from which telemetry data were obtained. The 500-m isobath representing the shelf-edge is indicated in red. The front along the shelf-edge (the Weddell Front), in yellow, based on Heywood et al. (2004) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

## 2 | METHODS

### 2.1 | Study site and species

We tracked breeding birds from Cape Geddes on Laurie Island in 2011/2012, from the south of Powell Island in 2013/2014, from Gourlay Point on Signy Island in 2013/2014 and 2015/2016, and from the southwest of Monroe Island in 2015/2016 (Figure 1b). Birds were instrumented during incubation, brood and crèche (Powell, Signy 2015 and Monroe only) (Supporting information Table S1; Supporting information Figure S1).

### 2.2 | Device deployment and data processing

All animal handling procedures were approved by the joint British Antarctic Survey and University of Cambridge Animal Ethics Committee. Individuals were captured at the nest and instrumented with a global positioning system (GPS) and time depth recording

(TDR) device (see Supporting Information). GPS data from each individual were allocated to separate foraging trips, and each trip was processed using the *trip* (Sumner, 2012) and *crawl* (Johnson, 2013) packages in R (R version 3.3.1; The R Foundation for Statistical Computing) using RStudio (version 1.0.136; RStudio, Inc.). The package *diveMove* (Luque, 2007) was used to calculate dive statistics (see Supporting Information). Subsequently, the processed TDR and GPS data were integrated using the *crawl* movement model to estimate locations of dives along the track.

### 2.3 | Tracking data

The concept of area-restricted search behaviour (ARS, the time taken to cross a circle of a given radius), as a proxy for foraging behaviour, is well developed in the literature for some species of flying seabird (Fauchald & Tveraa, 2003). For penguins however, ARS is less commonly used, and metrics such as dive depths of >5 m (Bengtson, Croll, & Goebel, 1993; Kokubun, Lee, Kim, &

**TABLE 1** The environmental variables used in model selection

Covariate type	Predictor	Resolution (km)	Source
Geometric	Bearing	0.3	Calculated using bespoke code in R
	Distance to colony (km)	0.3	Calculated using <code>gridDistance</code> function in R package <i>Raster</i>
	Distance to shelf break (km)	0.3	Calculated using cost-distance tool in ArcMap 10.4.1
Static	Bathymetry	0.3	Dickens et al. (2014)
	Slope	0.3	Calculated from bathymetry in ArcMap 10.4.1
	Rugged	0.3	Calculated from bathymetry in ArcMap 10.4.1
	Aspect	0.3	Calculated from bathymetry in ArcMap 10.4.1
	Density of <i>Pygoscelis</i> penguins from other colonies	0.3	Calculated using Equation 1
Dynamically variable	Mean sea-level anomaly (MSLA)	17.5	AVISO <a href="http://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/msla.html">http://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/msla.html</a>
	Mean primary productivity (PP)	11.7	MODIS <a href="http://orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.vgpm.m.chl.m.sst4.php">http://orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.vgpm.m.chl.m.sst4.php</a>
	Mean current velocity (OSC)	33.5	Podaac <a href="https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg">https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg</a>

Takahashi, 2015; Kokubun, Takahashi, Mori, Watanabe, & Shin, 2010; Takahashi et al., 2003) and dive wiggle behaviour (Bost et al., 2007; Kokubun, Kim, Shin, Naito, & Takahashi, 2011; Takahashi et al., 2004) are preferred; a wiggle is a sudden decrease in depth, unrelated to final ascent, which probably indicates the penguin is pursuing prey. As it would be counterintuitive for penguins to perform deep dives unless they were actively searching for prey, that is foraging, hereafter, we refer to foraging dives as any dive >5 m deep with >2 wiggles. We cannot determine whether penguins were successful in prey capture attempts, but this approach does allow us to model the important foraging habitat of chinstrap penguins and identify the overlap between chinstrap foraging areas and krill fisheries.

## 2.4 | Covariate data

All telemetry data and all covariate data were projected using the South Pole Lambert azimuthal equal area projection, centred at 58°W and 62°S, to limit distortion. Covariate values at each foraging dive location, and at a constant time interval of 4 min along the track, were extracted using the R package *Raster* (Hijmans & van Etten, 2014).

## 2.5 | Environmental variables

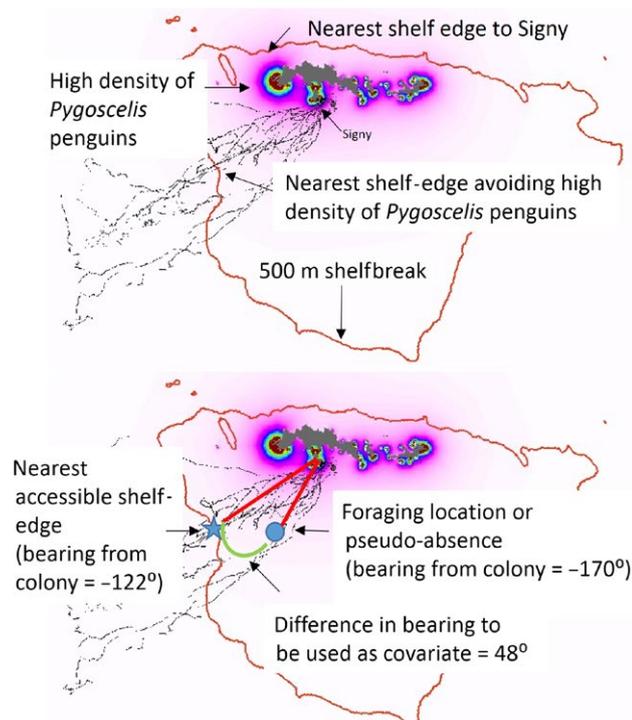
Both static and dynamic environmental covariate data were used in the analysis. The static covariates were based on the high-resolution

bathymetric data (Dickens et al., 2014; Table 1) from which slope, aspect and ruggedness (variation in three-dimensional orientation) were calculated using the spatial analyst toolset in ArcGIS (ESRI version 10.4.1). The dynamic covariates were based on daily, or 5-day mean, values of biologically meaningful remotely sensed oceanographic data (Table 1). Unfortunately, the scale of the dynamic covariate data available in this region is very coarse in comparison with the scale of the tracking data. Additionally, cloud cover and sea-ice result in gaps in many of these data layers. For this reason, the environmental data were averaged across various scales, and the layers with missing data were excluded (see Supporting Information).

## 2.6 | Geometric variables

Geometric covariates consisted of the distance of each point from the colony without crossing land, the distance of each point from the shelf-edge (500 m), the distance from the shelf-edge taking into account whether the point was inside or outside the shelf-edge (i.e., points inside the 500-m isobath were assigned a positive value, and points outside the 500-m isobath were assigned a negative value) and at-sea density of *Pygoscelis* penguins from other colonies (Figure 2) and were calculated using R package *gdistance* (van Etten, 2012).

Initial data exploration indicated that penguins showed directional movement towards the shelf-edge (depth >500 m). However, this movement appeared to be influenced by the density of *Pygoscelis* penguins from other colonies (see Figure 2). We therefore calculated



### Calculating geometric covariates

1. A raster of the *geographic distance* from the colony, avoiding land, was created for each colony using R package *gdistance*. This was used as the covariate *distance from colony* in the model.
2. The equation  $Density = population/distance\ to\ breeding\ colony^2$  (Wakefield et al., 2011) was used to create individual rasters of the at-sea *density* of birds from each colony of *Pygoscelis* penguins.
3. For each study colony, the at-sea *density* rasters of birds from all other colonies (excluding the focal colony) were summed together to create a raster of the density of *Pygoscelis* penguins from all other colonies. This was used as the covariate *density* in the model.
4. A *cost-distance* raster was created using R package *gdistance*. This increases the cost of travelling through cells which have higher densities of *Pygoscelis* penguins from other colonies.
5. For each colony a *distance-sum* raster was created by adding together the *cost-distance* raster and the *geographic distance* raster.
6. The point on the shelf-edge with the lowest value on the *distance-sum* raster was identified and defined as the *nearest accessible shelf-edge*.
7. The bearing to this point from the colony was calculated.
8. The bearing of each tracking location and pseudo-absence location from the colony was calculated.
9. The difference between the bearing of each point from the colony and the bearing of the *nearest accessible shelf-edge* from the colony was calculated. This was used as the covariate *bearing* in the model.

**FIGURE 2** Calculating the geometric variables for use in the GAM model [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

a covariate *bearing* which was the difference between the bearing of each foraging dive from the colony and the bearing of the nearest point of the shelf-edge from the colony, while taking into account the density of penguins from all other colonies of *Pygoscelis* penguins across the South Orkney archipelago.

## 2.7 | Model fitting and selection

Our study area was defined for each colony of tracked birds as the maximum distance travelled from the colony, while avoiding land, as this limited the analysis to include only those areas accessible to the penguins. For each study colony in turn, three control points (pseudo-absences, Aarts et al., 2008) for each foraging dive location were randomly selected within the study area and values of each covariate calculated for all points. The probability of foraging dive occurrence was calculated as a function of each of the covariates modelled using GAMs in the R package *mgcv* (Wood, 2006). The smooth of each covariate was taken, and the maximum number of knots was initially set to 3 and only increased if the model response curve did not fit the raw data. Additionally, model overfitting was further reduced using cubic regression splines with shrinkage which penalize variables during fitting (Wood, 2006). Semivariograms produced using the R package *gsta* (Pebesma, 2004) showed some autocorrelation in our data; however, the cross-validation method for model selection, described below, provides a cautious approach to achieve a parsimonious model, and thus, this is unlikely to affect our final model (Aarts et al., 2008).

Model selection followed the forward stepwise approach, using *k*-fold cross-validation, where *k* is the number of tracked populations (Laurie, Powell, Signy (2013/2014), Signy (2015/2016) and Monroe). For each variable, models were constructed using data from four of the five tracked site-year groups and evaluated by predicting the distribution around the excluded population. Models were evaluated using the area under the curve (AUC), sensitivity (correctly predicted presences) and specificity (correctly predicted absences), which were calculated by generating a ROC curve using R package *pROC* (Robin et al., 2011). Values may range from 0.5 to 1.0, where a value of 0.5 is no better than random and 1.0 indicates a perfect model. Each of the covariates was ranked according to the AUC value, and the highest ranking covariate was selected. The remaining covariates were added to the model in turn in order of AUC, retaining the resulting model if the AUC value increased. In cases where two covariates scored similar AUC values, each combination of the highest scoring covariates was evaluated. Those predictors that resulted in small increases to predictive power were included, given the aim of the analysis was to make the best predictive model. This process continued until there was no increase in AUC. Correlation between the covariates was considered; however, our aim was to create the model with the highest predictive power, rather than to identify which variables were more important ecologically; thus, given that the forward stepwise approach only retains covariates which improve model performance, correlation between covariates was disregarded.

The final GAM model was used to predict the at-sea distribution of foraging chinstrap penguins around every colony in the South Orkney archipelago (see Supporting Information). To allow for the sampling probabilities of available and used units, we estimated predicted values which are proportional to the probability of use, for a vector *x* of *p* predictor covariates, using the equation (Manly et al., 2002):

$$\tau(x_i) = \frac{\exp\{\log_e[(1-P_a)P_u/P_a] + \beta_0 + \beta_0x_{i1} + \dots + \beta_px_{ip}\}}{1 + \exp\{\log_e[(1-P_a)P_u/P_a] + \beta_0 + \beta_0x_{i1} + \dots + \beta_px_{ip}\}}$$

where  $P_a$  = proportion of absences,  $P_u$  = proportion of presences and  $\beta_0 \dots \beta_p$  are model coefficients.

These predictions were then multiplied by the size of the population to predict at-sea areas of high penguin density. Subsequently, the overlap between the percentages of chinstrap penguins using an area which is also used by the krill fishery was quantified using CCAMLR catch and effort data (see Supporting Information). Finally, as many tracking studies deploy only GPSs (and not TDRs), we created models using solely GPS data, to test model performance based on the positional data alone.

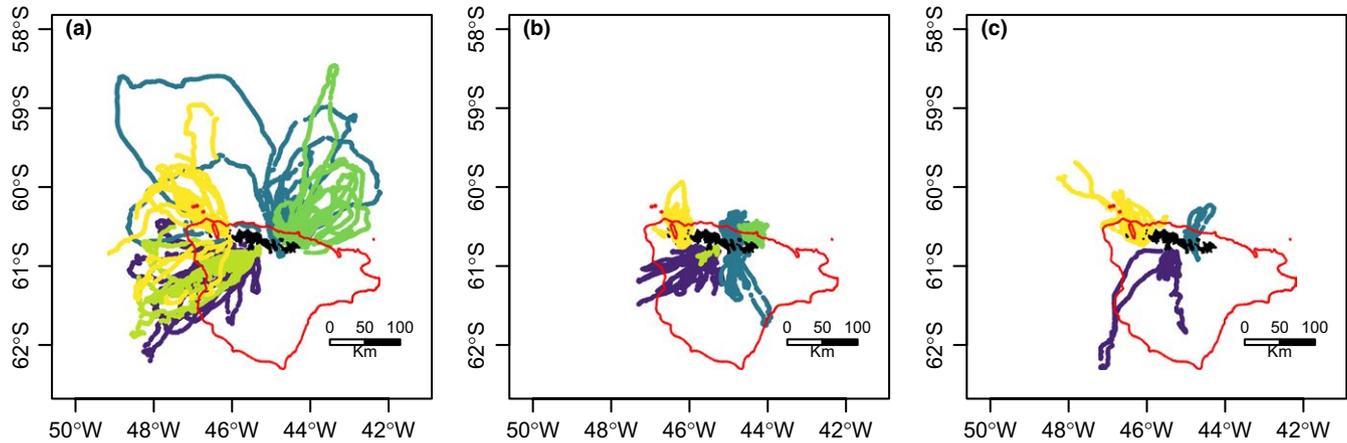
## 3 | RESULTS

### 3.1 | Spatial distribution of foraging locations

Based on the combined GPS position data and associated dive behaviour data, we collated information from a total of 116 trips from 79 individuals during incubation, 309 trips from 101 individuals during brood and 36 trips from 19 individuals during crèche (Supporting information Table S1). Birds travelled a greater maximum distance (with associated trip duration and path length) during incubation than during brood and crèche (Supporting information Table S1). Linear mixed-effects models showed that path length differed between the phases of the breeding season (likelihood ratio = 31.4,  $p < 0.001$ ), and the Holm–Bonferroni post hoc test showed significant differences in path length between incubation and brood (adjusted  $p < 0.01$ ), between brood and crèche (adjusted  $p = 0.02$ ), but not between incubation and crèche (adjusted  $p = 0.38$ ). Birds from all colonies tended to dive throughout the trip (Supporting information Figure S3), rather than commuting to specific areas in which they then foraged (dives >5 m deep with more than two wiggles); this was true during all phases of the breeding season (Figure 3).

### 3.2 | Model selection and evaluation

AUC values indicated that of the 15 individual predictor variables tested during the initial stages of model selection, the models containing *bearing* best described the foraging locations of incubating chinstrap penguins, and *distance from the colony* best described those in the brood and crèche phases (Table 2). In most cases, there was a considerable decline in model performance between those including the first or second highest scoring variables and those using other predictor variables (Supporting information Table S2). In the



**FIGURE 3** The location of foraging dives made by chinstrap penguins breeding on the South Orkney Islands during (a) incubation, (b) brood and (c) crèche based on GPS and TDR data. Colours represent different sites/years: Powell (blue), Monroe (yellow), Laurie (dark green), Signy 2013 (light green), Signy 2015 (navy). The 500-m isobath representing the shelf-edge is indicated in red [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

case of the brood model, *density* and *bearing* scored similarly, and thus, models using all combinations of the top three variables were evaluated. The final models used only *bearing* and *distance from the colony* to predict the location of foraging dives at any point during the breeding season, and adding additional covariates did not improve predictive power. The sensitivity and specificity indicated that the models performed well for predicting both the presences and absences of foraging locations.

### 3.3 | Performance across models

Models were validated by excluding each tracking site in turn and subsequently making spatial predictions into the excluded site. There was little difference in predictive power between models excluding different groups (Figure 4; Supporting information Table S3). This suggests that model predictions are applicable to all colonies of chinstrap penguins breeding on the South Orkney Islands (Figure 5) and might perform well across other sites.

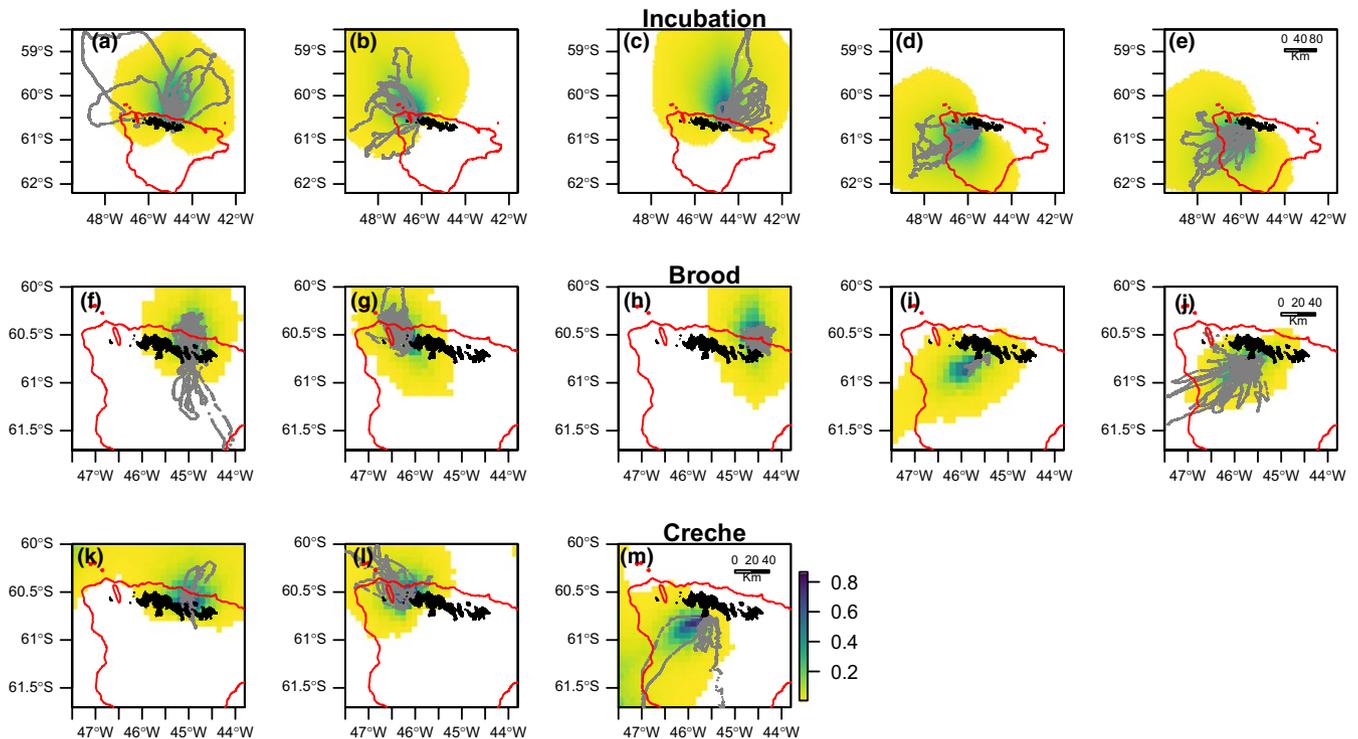
### 3.4 | Response curves

We found that as the difference between the bearing of a point from the colony and the bearing of the nearest available shelf-edge increased, the probability of occurrence of foraging dives decreased in all stages of the breeding season (Figure 6; Supporting information Figure S4). This suggests that individuals are moving directionally towards the nearest part of the shelf-edge avoiding high densities of *Pygoscelis* penguins from other colonies. Additionally, as the distance from the colony increased, the probability of foraging dives decreased during all phases of the breeding period (Figure 6). However, during brood and crèche when the distance from the colony >100 km, the probability of foraging increased again. This suggests that penguins may be less constrained by *Pygoscelis* penguins from other colonies as distance from the colony increases. We

**TABLE 2** Model performance metrics from GAM models to predict the at-sea foraging distribution of chinstrap penguins breeding on the South Orkney Islands

	Variable	AUC	Specificity	Sensitivity
Foraging locations (GPS and TDR)				
Incubation	Bearing	0.83	0.74	0.81
	Distance	0.80	0.73	0.80
	Distance and bearing	<b>0.88</b>	<b>0.81</b>	<b>0.86</b>
	Distance and bearing and density	0.88	0.80	0.85
	Distance and bearing and density	0.88	0.80	0.85
Brood	Bearing	0.82	0.77	0.81
	Distance	0.94	0.87	0.92
	Density	0.84	0.76	0.86
	Distance and bearing	<b>0.95</b>	<b>0.91</b>	<b>0.92</b>
	Distance and bearing and density	0.93	0.87	0.92
Crèche	Bearing	0.82	0.73	0.86
	Distance	0.86	0.77	0.82
	Distance and bearing	<b>0.91</b>	<b>0.79</b>	<b>0.93</b>
Travel locations (GPS only)				
Incubation	Distance and bearing	<b>0.90</b>	<b>0.82</b>	<b>0.86</b>
Brood	Distance and bearing	<b>0.96</b>	<b>0.91</b>	<b>0.94</b>
Crèche	Distance and bearing	<b>0.94</b>	<b>0.80</b>	<b>0.96</b>

Note. The highest scoring models for each phase are highlighted in bold.



**FIGURE 4** Predicted distributions of chinstrap penguins for individual colonies using models created excluding the colony for which predictions were made, during the incubation phase (a) Powell, (b) Monroe, (c) Laurie, (d) Signy (2013/2014) and (e) Signy (2015/2016); during the brood phase (f) Powell, (g) Monroe, (h) Laurie, (i) Signy (2013/2014) and (j) Signy (2015/2016); and during the crèche phase (k) Powell, (l) Monroe and (m) Signy (2015/2016) with empirical foraging dive locations overlaid. The 500-m isobath representing the shelf-edge is indicated in red. The study area during incubation is larger than during brood or crèche, representing the difference in foraging range between the phases [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

note, however, that most foraging trips were <100 km in distance (Supporting information Figure S2) and therefore that responses at this distance were based on very few observations.

### 3.5 | Foraging locations versus travelling locations

When models were created using just GPS data, instead of GPS and TDR data, the model performance metrics were as good as the models created with both GPS and TDR data (Table 2), and distribution maps were also almost identical. The same predictor variables were important when modelling dive locations as when modelling GPS positions.

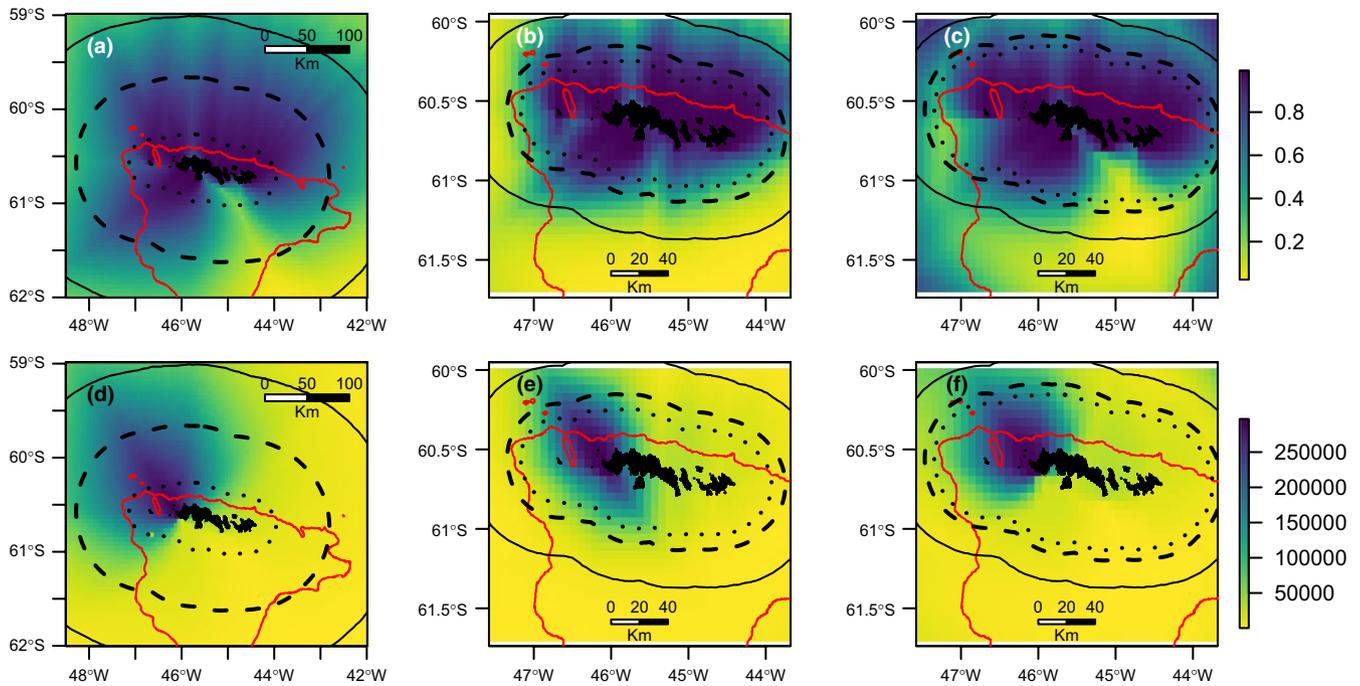
### 3.6 | Estimated spatial distribution and overlap with fisheries

The most intense fishing activity has been located along the shelf-edge to the north-west of the South Orkney Islands both historically (Figure 7a) and during the past six years (Figure 7b). This area is located in CCAMLR management area South Orkney West, the location of 36% of the summer krill catch (Table 3). This locality coincides with predictions of areas of high-density chinstrap foraging distributions (Figure 5). The percentage of the bird distribution in intensively used area (50% of area used) that overlaps with areas used historically by the fishery is 27%, 63% and 70% during incubation, brood and crèche, respectively

(Figure 8, Table 4). Additionally, during the same periods, 16%, 50% and 51% of the bird distribution home range areas (95% of area used) of the South Orkney population of chinstrap penguins overlaps with areas used historically by the fishery (Table 4).

## 4 | DISCUSSION

Many studies have utilized seabird tracking data to understand and predict the at-sea distribution of seabirds from a single colony (Lynnes, Reid, Croxall, & Trathan, 2002; Trathan et al., 2006); however, most models perform poorly when extrapolating predicted distributions into new locations (Torres et al. 2015). We present the first study that combines the effects of availability, competition and directional travel towards the shelf-edge to describe and make robust predictions about the at-sea distribution of chinstrap penguins breeding on the South Orkney Islands. Furthermore, this is the first study to quantify the overlap between the fishery and birds from all colonies, not just those from which tracking data were available. Using tracking data from just 204 individuals, <0.00017% of the estimated chinstrap penguin breeding population at the South Orkney Islands (600,000 pairs; Poncet & Poncet, 1985), we were able to create generic models which were powerful in their ability to predict the habitat utilization across all tracked populations during the three main phases of the breeding season.



**FIGURE 5** Predictions of the probability of occurrence for all chinstrap penguins breeding on the South Orkney Islands during (a) incubation, (b) brood and (c) crèche; predictions weighted by population size during (d) incubation, (e) brood and (f) crèche. The 500-m isobath representing the shelf-edge is indicated in red. The 95% percentile of trip distance (Figure S2) is shown in black. Predictions were only made in the study area for each colony (maximum distance from the colony recorded by tracked birds); thus, the scale varies between incubation, where the maximum distance was further from the colony than during brood or crèche [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

#### 4.1 | Habitat preferences of chinstrap penguins

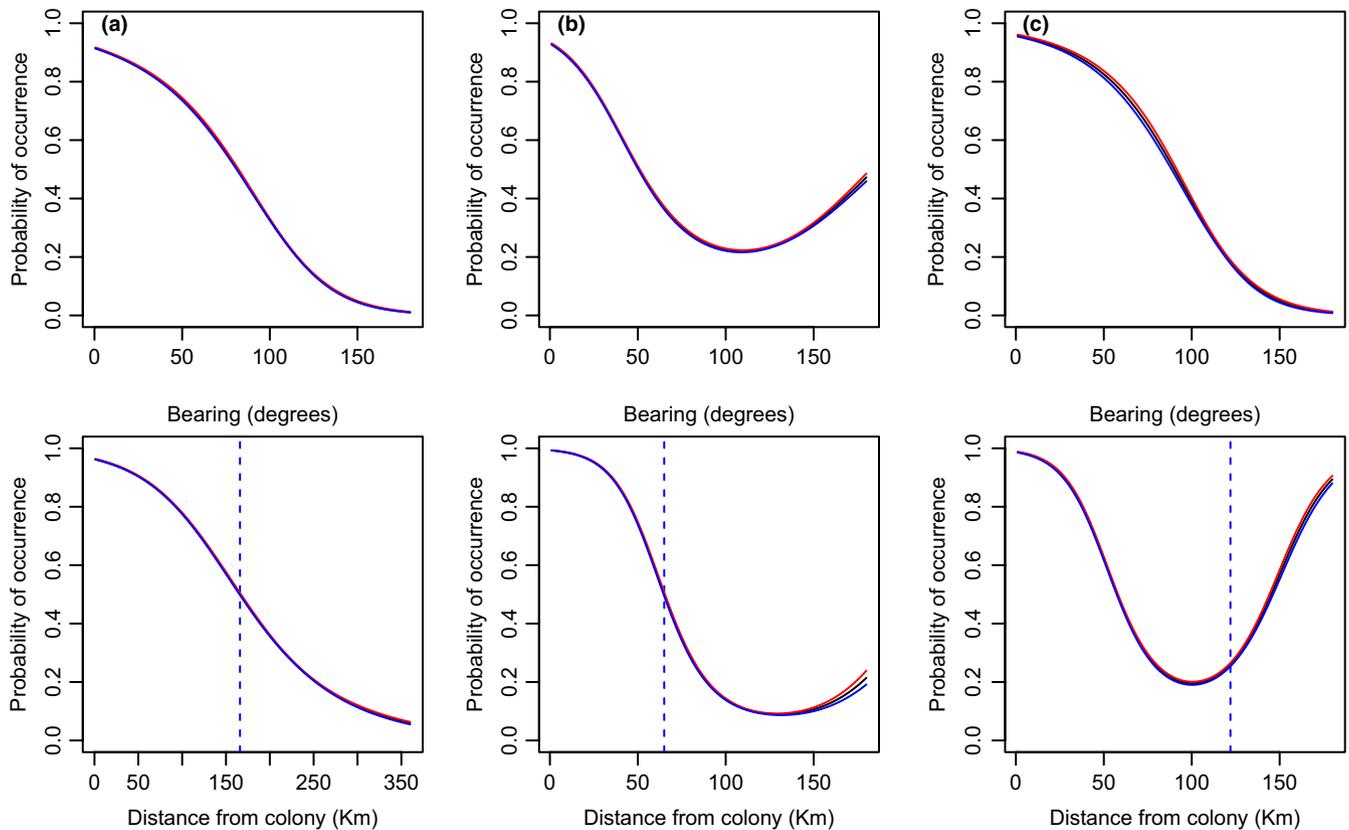
The distance from the colony and the difference in bearing from the colony between dive locations and the nearest accessible shelf-edge (adjusting for the density of *Pygoscelis* penguins) were predictors in the most parsimonious models describing the distribution of foraging chinstrap penguins.

Previous studies provide strong evidence that habitat availability and competition are major drivers in the at-sea distribution of central place foragers (Ainley, Nur, & Eric, 1995; Raymond et al., 2015; Trathan et al., 2006; Wakefield et al., 2017). Optimal foraging theory suggests that animals will forage in areas abundant in resources, while minimizing the costs associated with travelling from the colony (MacArthur & Pianka, 1966). Zones of resource depletion may surround large colonies of breeding seabirds (Ashmole, 1963) requiring birds to travel further to encounter abundant prey areas, whereas the cost of travelling from the colony (in terms of both energetic cost to the adult and fasting time for the chick) increases with distance from the colony. Thus, it is not surprising that as the distance from the colony increases, the probability of occurrence decreases. However, habitat utilization is often not distributed uniformly within the maximum distance travelled from the colony, and inter- or intra-specific competition with birds from neighbouring colonies may also affect the distribution of seabirds at sea (Pianka, 1981; Raymond et al., 2015; Wakefield et al., 2013). An important element of our habitat models is the at-sea density of birds from other *Pygoscelis* colonies, implying that prey depletion or interference competition in

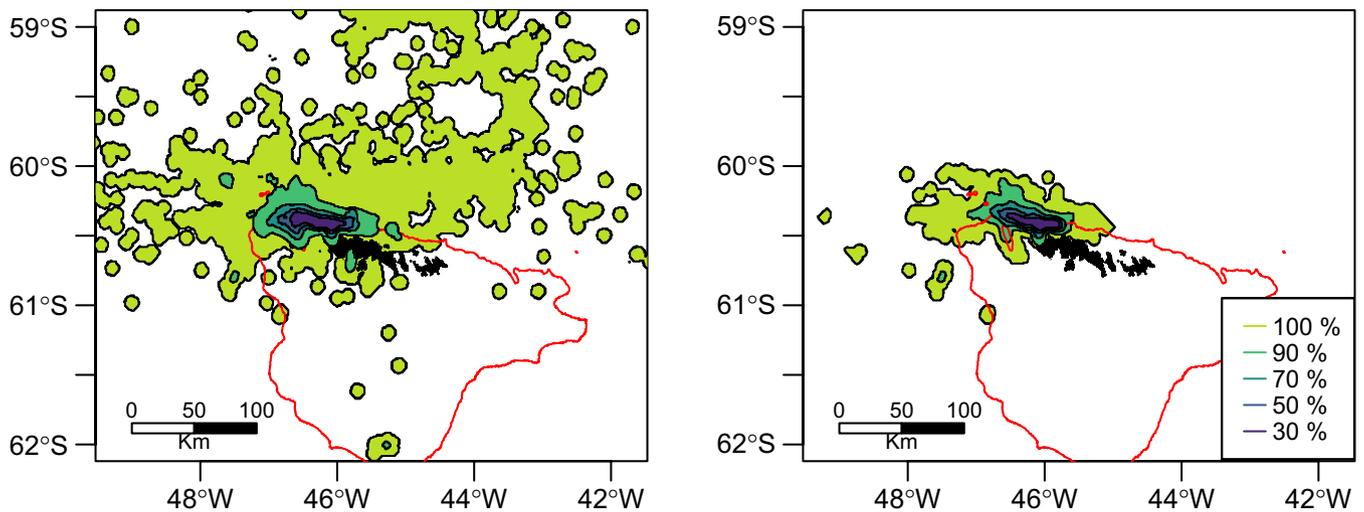
the proximity of our study colonies is important. Certainly, our cost-distance analysis suggests that it is important to consider the impacts of nearby colonies when attempting to understand the direction of travel of birds during foraging. Spatial segregation in the at-sea distribution of seabirds via prey depletion or disturbance has been observed in other species of seabird (Catry, Ramos, Catry, Monticelli, & Granadeiro, 2013; Wakefield et al., 2013), and it is hypothesized that this may be culturally sustained, in part, via information transfer among conspecifics (Wakefield et al., 2013). Niche theory suggests that animals segregate in space, time or diet, to avoid competition (Pianka, 1981). Thus, neighbouring colonies of seabirds, which utilize common prey species, are likely to exhibit spatial segregation in foraging locations to avoid competition (Masello et al., 2010).

When considered independently, the density of *Pygoscelis* penguins from other colonies was in the top three predictor variables for all models. However, when combined with *distance from the colony*, the predictor *bearing*, which included directional movement to the shelf-edge, in addition to the density of *Pygoscelis* penguins from other colonies, was more powerful in all cases. This indicates that chinstrap penguins breeding on the South Orkney Islands are exhibiting directional movement towards the shelf-edge in addition to influences of competition from other colonies of *Pygoscelis* penguins and distance from the colony.

Bathymetric features, such as shelf-edges or seamounts, are associated with upwelling, increased primary productivity and aggregations of marine organisms such as krill and higher predators (Bertrand et al., 2008; Ichii, 1990; Scales et al., 2014; Weimerskirch,



**FIGURE 6** Response curves (95% confidence intervals) for a model using distance and bearing to predict the foraging (GPS and TDR) locations during (a) incubation, (b) brood and (c) crèche, and the GPS locations during (d) incubation, (e) brood and (f) crèche, for chinstrap penguins breeding at the South Orkney Islands. The 95% percentile of trip distance (Figure S2) is shown in blue [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



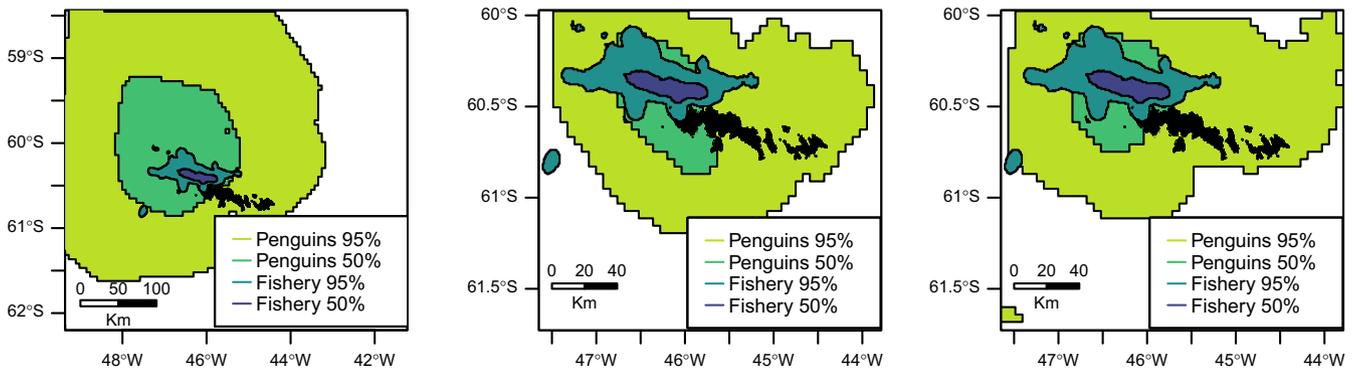
**FIGURE 7** Kernel density estimation of summed krill catch in subarea 48.2 during the *Pygoscelis* penguin breeding season (October to March) between (a) 1980/1981 and 2015/2016 and (b) 2010/2011 and 2015/2016. The 500-m isobath is highlighted in red [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

2007). Although krill can move autonomously (Hamner & Hamner, 2000), they also depend upon ocean currents for distribution on a larger scale (Hunt et al., 2016; Murphy et al., 1998) and have been associated with hydrographic flows at the shelf-edge (Trathan et al., 2003). Correspondingly, the shelf-edge is an important habitat for

some penguins (Kokubun et al., 2011; Lynnes et al., 2002), and chinstraps in this study were also observed travelling towards this feature. During incubation, when penguins are less constrained, they travelled beyond the shelf-edge, perhaps in search of abundant areas with reduced competition from conspecifics. However, during brood

**TABLE 3** Overall krill catch for each of the management units used by CCAMLR, South Orkney West (SOW), South Orkney Northeast (SONE), South Orkney Southeast (SOSE) and South Orkney Pelagic (SOPA) in subarea 48.2 (CCAMLR C1 catch and effort dataset, 2016)

	All months		Summer (October–March)		Winter (April–September)	
	Catch in tonnes	Proportion of annual total	Catch in tonnes	Proportion of annual total	Catch in tonnes	Proportion of annual total
SOW	1,365,335.80	0.80	604,295.90	0.36	761,039.90	0.45
SOSE	40,477.00	0.02	24,733.00	0.01	15,744.00	0.01
SONE	75,002.60	0.04	62,132.60	0.04	12,870.00	0.01
SOPA	218,176.50	0.13	181,217.10	0.11	36,959.40	0.02
Total	1,698,991.90	1.00	872,378.60	0.51	826,613.30	0.49



**FIGURE 8** The predicted at-sea distribution of chinstrap penguins overlaps with the krill fishery at the 50% intensively used area and the 95% home range area during (a) incubation, (b) brood and (c) crèche [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Bird area	Historical fishery		Recent fishery (last 6 years)	
	Intensively used area (%)	Full area (%)	Intensively used area (%)	Full area (%)
<b>Incubation</b>				
Intensively used area (%)	4	27	3	15
Full area (%)	2	16	2	3
<b>Brood</b>				
Intensively used area (%)	17	63	14	49
Full area (%)	11	50	9	35
<b>Crèche</b>				
Intensively used area (%)	20	70	15	56
Full area (%)	11	51	8	36

**TABLE 4** The quantified overlap between the population of chinstrap penguins breeding on the South Orkney Islands and the krill fishery

Note. The intensively used areas comprise the top 50% of penguin or fishery locations, and the full area encompasses 95% of the penguin or fishery locations.

when penguins are most constrained, near-shore foraging areas are particularly important (Lynnes et al., 2002). Near-shore waters are slow-moving; thus, replenishment of prey on the shelf is likely to be restricted. This suggests that chinstrap penguins may travel towards areas with a faster replenishment rate of prey (Trathan et al., 2003), as local resources became depleted.

#### 4.2 | Adding environmental variables to the model

The addition of environmental variables did not improve the predictive performance of any of the models. The scale of dynamic covariate data and data gaps due to cloud or sea-ice cover may have led to ecologically significant mismatches with the scale of

tracking data. Additionally, the relative availability of habitats may vary between sites. This would result in variation in habitat selection between colonies and lead to models with poor predictive power (Matthiopoulos, 2003; Wakefield et al., 2017). Previous studies where habitat models for central place foragers maintained high predictive power when extrapolated into new locations frequently include availability (e.g., distance from the colony) and competition as important predictor variables (Raymond et al., 2015; Wakefield et al., 2011), and environmental variables were often less important.

### 4.3 | Model performance and limitations

High AUC, specificity and sensitivity indicated that our models performed well when predicted across colonies within the South Orkney archipelago. However, deviations from the model both within and across sites, because of either individual behaviour, variation in habitat preference or availability, or interannual variability, are to be anticipated (Lynnes et al., 2002; Trathan et al., 2006). At three of the four colonies in this study, data were available for 1 year only, with different colonies visited in different years. Thus, although interannual variation in foraging range is likely to occur, the models perform well in all years; thus, the main signals that we have detected are likely to reflect the general patterns of foraging behaviour. Deviations from our model were most evident at Powell, where 8% of birds headed towards the southern shelf-edge during brood, instead of to the north of the island as the model predicted. One of the limitations of the model is that only one position for the nearest shelf-edge is identified for each colony. Thus, for colonies such as Powell, where birds travel to two different areas of the shelf-edge, the model will only make predictions towards one of these locations. Foraging in more than one direction might be associated with multiple areas of prey predictability, for example over submarine canyons as well as at the shelf-edge. Future studies could incorporate such aspects, allowing predictions to be made in multiple directions from the colony, if the proportion of animals preferring one feature over another were known. This may impact the predictions made for untracked colonies, if features such as submarine canyons occur within the foraging range of the colony, in which case birds may frequent these areas in addition to, or instead of, the shelf-edge, deviating from model predictions. Birds from Laurie also diverged from model predictions by travelling further east than predicted. This is likely to be due to spatial segregation from colonies to the west and may be due to inaccurate population estimates from nearby colonies. In this context, improving the future accuracy of colony population data (Humphries et al., 2017) might help to improve our models.

Using just GPS data, we were also able to build robust models that have the potential to be extrapolated elsewhere, where tracking data and/or diving data are not available. This is unsurprising, given that chinstrap penguins dive throughout their foraging trips,

and supports the use of GPS data alone to predict important penguin habitats.

### 4.4 | Penguin–fishery overlap

Our models highlight that for chinstrap penguins, near-shore areas are vital for foraging; during incubation, brood and crèche, more than 75% of their trips, respectively, occur within 90, 37 and 44 km of the colony. At the South Orkney Islands, krill harvesting is concentrated into a small number of locations, with 75% of krill catches taken from within 80 km of land, mostly (67%) from the area to the west of Monroe Island (CCAMLR Krill Fishery Report, 2016), which coincides with the highest at-sea density of chinstrap penguins. The overlap between chinstrap penguins and fisheries is highest during brood and crèche. This coincides with periods that birds are the most constrained in their foraging ranges and thus unable to greatly extend their ranges to compensate for potential prey depletion by the fishery. Our models demonstrate that the overlap between chinstraps and the krill fishery corresponds with the different scales of incubation, brood and crèche, over time-scales of approximately 30 days and spatial scales of 10 to 100 km.

### 4.5 | Wider implications for management

Ongoing changes within the Antarctic marine ecosystem are anticipated, as marine mammal populations continue to recover following their overexploitation (Trathan, Ratcliffe, & Masden, 2012; Trathan & Reid, 2009) and climate change proceeds (Gille, 2008). Predicted changes in krill biomass as a result of ocean warming (e.g., Hill, Phillips, & Atkinson, 2013) are likely to have varying impacts on predator populations, and penguins are likely to be the most vulnerable group (Klein et al., 2018; Plagányi & Butterworth, 2012). Reducing fishing impact at some penguin colonies may partially negate these impacts (Klein et al., 2018). Additionally, impacts observed at small scales are likely to be lost when effects are considered over larger scales (Klein et al., 2018); thus, it is vital to identify the appropriate spatial scale for management of the krill fishery in these areas. Currently, catch limits are apportioned into FAO statistical subareas (Figure 1a), but fishing is increasingly condensed within these units (Figure 7), and the foraging areas of some penguin colonies overlap considerably with fisheries operating in these condensed areas. With this in mind, we recommend that CCAMLR prioritizes the identification of an appropriate scale for management to address the mismatch between the scale at which the fishery is managed and that which occurs in practice. This could be achieved following a risk assessment approach (CCAMLR 2016).

Determining whether krill fisheries are impacting marine predators is vital and requires monitoring data to be collected, which in many places is not happening, or at least not in some locations where the fisheries are operating most intensively, for example to the northwest of Monroe Island. Developing reference control sites

for comparison with fished sites is now vital for disentangling the confounding effects of climate change, fishing and changes in recovering marine mammal populations. Attempts to experimentally determine how fisheries deplete forage fish stocks and therefore impact dependent species have shown that fishing near-shore can increase the range of foraging trips and impact chick survival, leading to considerable change in population size (Bertrand et al., 2012; Pichegru et al., 2009; Sherley et al., 2015). Additionally, the foraging efficiency of breeding seabirds may be significantly affected by not only the regional quantity, but also the temporal and spatial patterns of prey removals.

In this context, we suggest that CCAMLR might consider three options for improving the scientific basis for management of the krill fishery: (a) Develop appropriate penguin population monitoring (Fretwell et al., 2012; Rees, Brown, Fretwell, & Trathan, 2017), and measure krill biomass and distribution under variable levels of krill harvesting, to separate fishing effects from natural variability; (b) develop a series of depletion observations to explore how large penguin colonies deplete the prey stock throughout the breeding season and to investigate the rates of krill replenishment in the absence of harvesting; and (c) create precautionary management zones in proximity to large *Pygoscelis* penguin breeding colonies, within which the fishery is restricted during the penguin breeding season, at least until such time that further information is available on krill depletion and replenishment rates. For example, for the South Orkney Islands, restricting the catch limit within 60 km of the coast of Monroe Island during January and February would reduce any potential impacts on chinstrap penguins in this region. Such restrictions should be considered in the context of increased research effort, directed towards understanding the competition for krill. To compensate for these limitations, catch limits in other areas, or at other times, may be increased (Hewitt et al., 2004; Klein et al., 2018; Watters, Hill, Hinke, Matthews, & Reid, 2013). However, the potential impacts on other krill-eating predators would need to be investigated fully before catch limits could be increased (Constable, 2011).

## 5 | CONCLUSION

We present habitat models which rely on simple, and available, variables to predict the at-sea distribution of chinstrap penguins breeding across the South Orkney Islands, including for colonies where no empirical tracking data are available. This is the first step in understanding the potential impacts of the krill fisheries, at spatial and temporal scales relevant to ecosystem operation. With the available data, it is not currently possible to infer an impact of the krill fishery on penguins. However, should the fishery increase or become more spatially concentrated, then such impacts may become evident. As such, we recommend that GPS and TDR telemetry data are collected from a range of sites to further test the efficacy of our models and that similar models are applied to other krill-eating predators.

Coupling telemetry studies with long-term demographic studies would increase their value. Thus, it is vital that monitoring occurs in areas where large predator colonies overlap with intensively fished areas and that an appropriate scale is identified at which to manage the fishery in these locations. Until these issues are addressed, we recommend that krill catch limits are restricted in areas of intensive use by penguins during their breeding season, and these restrictions should vary on a temporal basis associated with life history processes.

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## DATA ACCESSIBILITY

The tracking data used in this analyses can be accessed at [www.seabirdtracking.org](http://www.seabirdtracking.org)

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## 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>
- Agnew, D. J. (1997). Review—the CCAMLR ecosystem monitoring programme. *Antarctic Science*, 9, 235–242.
- Ainley, D. G., Nur, N., & Eric, J. W. (1995). Factors affecting the distribution and size of pygoscelid penguin colonies in the Antarctic. *The Auk*, 112, 171–182. <https://doi.org/10.2307/4088776>
- Alonso, S.H., Switzer, P.V., & Mangel, M. (2003). An ecosystem-based approach to management: Using individual behaviour to predict the indirect effects of Antarctic krill fisheries on penguin foraging. *Journal of Applied Ecology*, 40, 692–702. <https://doi.org/10.1046/j.1365-2664.2003.00830.x>
- Ashmole, N. P. (1963). The regulation of numbers of tropical oceanic birds. *Ibis*, 103, 458–473.
- Barlow, K., Boyd, I., Croxall, J., Reid, K., Staniland, I., & Brierley, A. (2002). Are penguins and seals in competition for Antarctic krill at South Georgia? *Marine Biology*, 140, 205–213.
- Bengtson, J. L., Croll, D. A., & Goebel, M. E. (1993). Diving behaviour of chinstrap penguins at Seal Island. *Antarctic Science*, 5, 9–9.
- Bertrand, A., Gerlotto, F., Bertrand, S., Gutiérrez, M., Alza, L., Chipollini, A., ... Quesquén, R. (2008). Schooling behaviour and environmental forcing in relation to anchoveta distribution: An analysis across multiple spatial scales. *Progress in Oceanography*, 79, 264–277. <https://doi.org/10.1016/j.pocean.2008.10.018>
- Bertrand, S., Joo, R., Arbulu Smet, C., Tremblay, Y., Barbraud, C., & Weimerskirch, H. (2012). Local depletion by a fishery can affect seabird foraging. *Journal of Applied Ecology*, 49, 1168–1177. <https://doi.org/10.1111/j.1365-2664.2012.02190.x>

- Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A., Bograd, S. J., ... Harrison, A. (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*, 475, 86. <https://doi.org/10.1038/nature10082>
- Bost, C.-A., Handrich, Y., Butler, P., Fahlman, A., Halsey, L., Woakes, A., & Ropert-Coudert, Y. (2007). Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 248–255. <https://doi.org/10.1016/j.dsr2.2006.11.007>
- Catry, T., Ramos, J. A., Catry, I., Monticelli, D., & Granadeiro, J. P. (2013). Inter-annual variability in the breeding performance of six tropical seabird species: Influence of life-history traits and relationship with oceanographic parameters. *Marine Biology*, 160, 1189–1201. <https://doi.org/10.1007/s00227-013-2171-2>
- CCAMLR (2016). SC-CAMLR-V, Report of CSC. Hobart, Australia: CCAMLR.
- Constable, A. J. (2011). Lessons from CCAMLR on the implementation of the ecosystem approach to managing fisheries. *Fish and Fisheries*, 12(2), 138–151. <https://doi.org/10.1111/j.1467-2979.2011.00410.x>
- Cury, P. M., Boyd, I. L., Bonhommeau, S., Anker-Nilssen, T., Crawford, R. J., Furness, R. W., ... Paleczny, M. (2011). Global seabird response to forage fish depletion—one-third for the birds. *Science*, 334, 1703–1706. <https://doi.org/10.1126/science.1212928>
- Dickens, W. A., Graham, A. G., Smith, J. A., Dowdeswell, J. A., Larter, R. D., Hillenbrand, C.-D., ... Kuhn, G. (2014). A new bathymetric compilation for the South Orkney Islands region, Antarctic Peninsula (49 degrees-39 degrees W to 64 degrees-59 degrees S): insights into the glacial development of the continental shelf. *Geochemistry Geophysics Geosystems*, 15, 2494–2514. <https://doi.org/10.1002/2014GC005323>
- Fauchald, P., & Tveraa, T. (2003). Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology*, 84, 282–288. [https://doi.org/10.1890/0012-9658\(2003\)084\[0282:UFPTIT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0282:UFPTIT]2.0.CO;2)
- Forcada, J., & Trathan, P. N. (2009). Penguin responses to climate change in the Southern Ocean. *Global Change Biology*, 15(7), 1618–1630. <https://doi.org/10.1111/j.1365-2486.2009.01909.x>
- Fretwell, P. T., LaRue, M. A., Morin, P., Kooyman, G. L., Wienecke, B., Ratcliffe, N., ... Trathan, P. N. (2012). An emperor penguin population estimate: The first global, synoptic survey of a species from space. *PLoS One*, 7, e33751. <https://doi.org/10.1371/journal.pone.0033751>
- Gille, S. T. (2002). Warming of the Southern Ocean since the 1950s. *Science*, 295, 1275–1277. <https://doi.org/10.1126/science.1065863>
- Gille, S. T. (2008). Decadal-scale temperature trends in the Southern Hemisphere ocean. *Journal of Climate*, 21, 4749–4765. <https://doi.org/10.1175/2008JCLI2131.1>
- Grecian, W. J., Witt, M. J., Attrill, M. J., Bearhop, S., Becker, P. H., Egevang, C., ... Kopp, M. (2016). Seabird diversity hotspot linked to ocean productivity in the Canary Current Large Marine Ecosystem. *Biology Letters*, 12(8), 20160024. <https://doi.org/10.1098/rsbl.2016.0024>
- Gutt, J., Bertler, N., Bracegirdle, T. J., Buschmann, A., Comiso, J., Hosie, G., ... Tournadre, J. (2015). The Southern Ocean ecosystem under multiple climate change stresses—an integrated circumpolar assessment. *Global Change Biology*, 21, 1434–1453. <https://doi.org/10.1111/gcb.12794>
- Halpern, B. S., Longo, C., Hardy, D., McLeod, K. L., Samhour, J. F., Katona, S. K., ... Ranelletti, M. (2012). An index to assess the health and benefits of the global ocean. *Nature*, 488, 615. <https://doi.org/10.1038/nature11397>
- Hamner, W. M., & Hamner, P. P. (2000). Behavior of Antarctic krill (*Euphausia superba*): Schooling, foraging, and antipredatory behavior. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 192–202. <https://doi.org/10.1139/f00-195>
- Hauck, J., Hoppema, M., Bellerby, R. G. J., Völker, C., & Wolf-Gladrow, D. (2010). Data-based estimation of anthropogenic carbon and acidification in the Weddell Sea on a decadal timescale. *Journal of Geophysical Research*, 115, C03004. <https://doi.org/10.1029/2009JC005479>
- Hewitt, R. P., Watters, G., Trathan, P. N., Croxall, J. P., Goebel, M. E., Ramm, D., ... Watkins, J. L. (2004). Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia Sea. *CCAMLR Science*, 11, 81–97.
- Heywood, K. J., Locarnini, R. A., Frew, R. D., Dennis, P. F., & King, B. A. (1998). Transport and water masses of the Antarctic Slope Front system in the eastern Weddell Sea. *Ocean, Ice, and Atmosphere: Interactions at the Antarctic Continental Margin, Antarctic Research Series*, 75, 203–214. <https://doi.org/10.1029/ar075p0203>
- Hijmans, R. J., & van Etten, J. (2014). raster: Geographic data analysis and modeling. *R Package Version*, 2, 15.
- Hilborn, R., Amoroso, R. O., Bogazzi, E., Jensen, O. P., Parma, A. M., Szuwalski, C., & Walters, C. J. (2017). When does fishing forage species affect their predators? *Fisheries Research*, 191, 211–221.
- Hill, S., Atkinson, A., Darby, C., Fielding, S., Krafft, B. A., Godo, O., ... Watkins, J. L. (2016). Is current management of the Antarctic krill fishery in the Atlantic sector of the Southern Ocean precautionary? *CCAMLR Science*, 23, 31–51.
- Hill, S. L., Phillips, T., & Atkinson, A. (2013). Potential climate change effects on the habitat of Antarctic krill in the Weddell quadrant of the southern ocean. *PLoS One*, 8(8), e72246. <https://doi.org/10.1371/journal.pone.0072246>
- Hinckley, T., Cossio, M., Goebel, M., Reiss, S., Trivelpiece, W., & Watters, G. (2017). Identifying risk: Concurrent overlap of the Antarctic krill fishery with krill-dependent predators in the Scotia Sea. *PLoS One*, 12, e0170132. <https://doi.org/10.1371/journal.pone.0170132>
- Humphries, G., Naveen, R., Schwaller, M., Che-Castaldo, C., McDowall, P., Schrimpf, M., & Lynch, H. (2017). Mapping application for penguin populations and projected dynamics (MAPPPD): Data and tools for dynamic management and decision support. *Polar Record*, 53, 160–166. <https://doi.org/10.1017/S0032247417000055>
- Hunt, G. L. Jr, Drinkwater, K. F., Arrigo, K., Berge, J., Daly, K. L., Danielson, S., ... Karnovsky, N. (2016). Advection in polar and sub-polar environments: Impacts on high latitude marine ecosystems. *Progress in Oceanography*, 149, 40–81. <https://doi.org/10.1016/j.pocean.2016.10.004>
- Ichii, T. (1990). Distribution of Antarctic krill concentrations exploited by Japanese krill trawlers and minke whales. *Proc. NIPR Symp. Polar Biology*, 36–56.
- Johnson, D. (2013). Crawl: fit continuous-time correlated random walk models to animal movement data. R package version 1.4-1.
- Klein, E. S., Hill, S. L., Hinke, J. T., Phillips, T., & Watters, G. M. (2018). Impacts of rising sea temperature on krill increase risks for predators in the Scotia Sea. *PLoS One*, 13(1), e0191011. <https://doi.org/10.1371/journal.pone.0191011>
- Kokubun, N., Kim, J.-H., Shin, H.-C., Naito, Y., & Takahashi, A. (2011). Penguin head movement detected using small accelerometers: A proxy of prey encounter rate. *Journal of Experimental Biology*, 214, 3760–3767. <https://doi.org/10.1242/jeb.058263>
- Kokubun, N., Lee, W. Y., Kim, J.-H., & Takahashi, A. (2015). chinstrap penguin foraging area associated with a seamount in Bransfield Strait, Antarctica. *Polar Science*, 9, 393–400. <https://doi.org/10.1016/j.polar.2015.10.001>
- Kokubun, N., Takahashi, A., Mori, Y., Watanabe, S., & Shin, H.-C. (2010). Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. *Marine Biology*, 157, 811–825. <https://doi.org/10.1007/s00227-009-1364-1>
- Lewis, S., Sherratt, T., Hamer, K., & Wanless, S. (2001). Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, 412, 816. <https://doi.org/10.1038/35090566>

- 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. <https://doi.org/10.1111/j.1365-2664.2010.01910.x>
- Luque, S. P. (2007). diveMove: Dive analysis in R. *R News*, 7, 8–14.
- Lynnes, A., Reid, K., Croxall, J., & Trathan, P. (2002). Conflict or co-existence? Foraging distribution and competition for prey between Adélie and chinstrap Penguins. *Marine Biology*, 141, 1165–1174.
- MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, 100, 603–609. <https://doi.org/10.1086/282454>
- Manly, B., McDonald, L., Thomas, D., McDonald, T., & Erickson, W. (2002). *Resource selection by animals: Statistical analysis and design for field studies*. Dordrecht, The Netherlands: Kluwer.
- Masello, J. F., Mundry, R., Poisbleau, M., Demongin, L., Voigt, C. C., Wikelski, M., & Quillfeldt, P. (2010). Diving seabirds share foraging space and time within and among species. *Ecosphere*, 1, 1–28.
- Matthiopoulos, J. (2003). The use of space by animals as a function of accessibility and preference. *Ecological Modelling*, 159, 239–268. [https://doi.org/10.1016/S0304-3800\(02\)00293-4](https://doi.org/10.1016/S0304-3800(02)00293-4)
- Murphy, E. J., Watkins, J., Reid, K., Trathan, P., Everson, I., Croxall, J., ... Hofmann, E. (1998). Interannual variability of the South Georgia marine ecosystem: Biological and physical sources of variation in the abundance of krill. *Fisheries Oceanography*, 7, 381–390. <https://doi.org/10.1046/j.1365-2419.1998.00081.x>
- 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. <https://doi.org/10.1016/j.biocon.2011.11.013>
- Orians Gordon, H., & Pearson Nolan, E. (1979). *On the theory of central place foraging. Analysis of ecological systems* (pp. 155–177). Columbus, OH: Ohio State University Press.
- Pebesma, E. J. (2004). Multivariable geostatistics in S: The gstat package. *Computers & Geosciences*, 30, 683–691. <https://doi.org/10.1016/j.cageo.2004.03.012>
- Pianka, E. R. (1981). Competition and niche theory. *Ariel*, 128, 205–172.
- Pichegru, L., Ryan, P., Le Bohec, C., Van der Lingen, C., Navarro, R., Petersen, S., ... Grémillet, D. (2009). Overlap between vulnerable top predators and fisheries in the Benguela upwelling system: Implications for marine protected areas. *Marine Ecology Progress Series*, 391, 199–208. <https://doi.org/10.3354/meps08283>
- Pinaud, D., & Weimerskirch, H. (2002). Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos*, 99, 141–150. <https://doi.org/10.1034/j.1600-0706.2002.990114.x>
- Plagányi, É. E., & Butterworth, D. S. (2012). The Scotia Sea krill fishery and its possible impacts on dependent predators: Modeling localized depletion of prey. *Ecological Applications*, 22(3), 748–761. <https://doi.org/10.1890/11-0441.1>
- Poncet, S., & Poncet, J. (1985). A survey of penguin breeding populations at the South Orkney Islands. *British Antarctic Survey Bulletin*, 68, 71–81.
- Ratcliffe, N., Hill, S. L., Staniland, I. J., Brown, R., Adlard, S., Horswill, C., & Trathan, P. N. (2015). Do krill fisheries compete with macaroni penguins? Spatial overlap in prey consumption and catches during winter. *Diversity and Distributions*, 21, 1339–1348. <https://doi.org/10.1111/ddi.12366>
- Raymond, B., Lea, M. A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J. B., ... Gales, R. (2015). Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography*, 38, 121–129. <https://doi.org/10.1111/ecog.01021>
- Rees, W., Brown, J., Fretwell, P., & Trathan, P. (2017). What colour is penguin guano? *Antarctic Science*, 29, 417–425. <https://doi.org/10.1017/S0954102017000190>
- Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., & Müller, M. (2011). pROC: An open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*, 12, 77. <https://doi.org/10.1186/1471-2105-12-77>
- Scales, K. L., Miller, P. I., Embling, C. B., Ingram, S. N., Pirota, 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. <https://doi.org/10.1098/rsif.2014.0679>
- SC-CAMLR (2016). *Report of the thirty-fifth meeting of the scientific committee. Scientific committee for the conservation of Antarctic marine living resources*. Hobart, Australia: CCAMLR.
- Sherley, R. B., Ludynia, K., Dyer, B. M., Lamont, T., Makhado, A. B., Roux, J.-P., ... Votier, S. C. (2017). Metapopulation tracking juvenile penguins reveals an ecosystem-wide ecological trap. *Current Biology*, 27, 563–568. <https://doi.org/10.1016/j.cub.2016.12.054>
- Sherley, R. B., Winker, H., Altwegg, R., van der Lingen, C. D., Votier, S. C., & Crawford, R. J. (2015). Bottom-up effects of a no-take zone on endangered penguin demographics. *Biology Letters*, 11, 20150237. <https://doi.org/10.1098/rsbl.2015.0237>
- Sumner, M. (2012). trip: spatial analysis of animal track data. R package version 1.1-12.
- Takahashi, A., Dunn, M., Trathan, P., Croxall, J., Wilson, R. P., Sato, K., & Naito, Y. (2004). Krill-feeding behaviour in a chinstrap penguin compared to fish-eating in Magellanic penguins: A pilot study. *Marine Ornithology*, 32, 47–54.
- Takahashi, A., Dunn, M., Trathan, P., Sato, K., Naito, Y., & Croxall, J. (2003). Foraging strategies of chinstrap penguins at Signy Island, Antarctica: Importance of benthic feeding on Antarctic krill. *Marine Ecology Progress Series*, 250, 279–289. <https://doi.org/10.3354/meps250279>
- Torres, L. G., Sutton, P. J., Thompson, D. R., Delord, K., Weimerskirch, H., Sagar, P. M., ... 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(3), e0120014. <https://doi.org/10.1371/journal.pone.0120014>
- Trathan, P. N., & Agnew, D. (2010). Climate change and the Antarctic marine ecosystem: An essay on management implications. *Antarctic Science*, 22, 387–398. <https://doi.org/10.1017/S0954102010000222>
- Trathan, P., Brierley, A., Brandon, M., Bone, D., Goss, C., Grant, S., ... Watkins, J. (2003). Oceanographic variability and changes in Antarctic krill (*Euphausia superba*) abundance at South Georgia. *Fisheries Oceanography*, 12, 569–583. <https://doi.org/10.1046/j.1365-2419.2003.00268.x>
- Trathan, P. N., García-Borboroglu, P., Boersma, D., Bost, C. A., Crawford, R. J., Crossin, G. T., ... De La Puente, S. (2015). Pollution, habitat loss, fishing, and climate change as critical threats to penguins. *Conservation Biology*, 29, 31–41. <https://doi.org/10.1111/cobi.12349>
- Trathan, P., Green, C., Tanton, J., Peat, H., Poncet, J., & Morton, A. (2006). Foraging dynamics of macaroni penguins *Eudyptes chrysolophus* at South Georgia during brood-guard. *Marine Ecology Progress Series*, 323, 239–251. <https://doi.org/10.3354/meps323239>
- Trathan, P., Ratcliffe, N., & Masden, E. (2012). Ecological drivers of change at South Georgia: The krill surplus, or climate variability. *Ecography*, 35, 983–993. <https://doi.org/10.1111/j.1600-0587.2012.07330.x>

- Trathan, P. N., & Reid, K. (2009). Exploitation of the marine ecosystem in the sub-Antarctic: historical impacts and current consequences. *Papers and Proceedings of the Royal Society of Tasmania*, 9–14.
- Turner, J., Bindschadler, R., Convey, P., Di Prisco, G., Fahrbach, E., Gutt, J., ... Summerhayes, C. (2009). Antarctic climate change and the environment.
- van Etten, J. (2012). *gdistance*: Distances and routes on geographical grids. R package version 1.1–4. Available at CRAN. [R-project.org/package=gdistance](http://R-project.org/package=gdistance).
- Wakefield, E. D., Bodey, T. W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., ... Jackson, A. L. (2013). Space partitioning without territoriality in gannets. *Science*, 341, 68–70. <https://doi.org/10.1126/science.1236077>
- Wakefield, E. D., Owen, E., Baer, J., Carroll, M. J., Daunt, F., Dodd, S. G., ... Miller, P. I. (2017). Breeding density, fine-scale tracking and large-scale modeling reveal the regional distribution of four seabird species. *Ecological Applications*, 27(7), 2074–2091. <https://doi.org/10.1002/eap.1591>
- Wakefield, E. D., Phillips, R. A., Trathan, P. N., Arata, J., Gales, R., Huin, N., ... Matthiopoulos, J. (2011). Habitat preference, accessibility, and competition limit the global distribution of breeding Black-browed Albatrosses. *Ecological Monographs*, 81, 141–167. <https://doi.org/10.1890/09-0763.1>
- Watters, G. M., Hill, S. L., Hinke, J. T., Matthews, J., & Reid, K. (2013). Decision-making for ecosystem-based management: Evaluating options for a krill fishery with an ecosystem dynamics model. *Ecological Applications*, 23(4), 710–725. <https://doi.org/10.1890/12-1371.1>
- Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 211–223. <https://doi.org/10.1016/j.dsr2.2006.11.013>
- Wood, S. N. (2006). *Generalized additive models: An introduction with R*. New York: CRC press.

## BIOSKETCH

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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