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Using habitat models for chinstrap penguins, *Pygoscelis antarctica,* to inform marine spatial management around the South Sandwich Islands during the penguin breeding season

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ABSTRACT

If not carefully managed, harvesting of Antarctic krill risks disturbing the ecological balance of many Antarctic and sub-Antarctic sites where krill-dependent predators feed. One of the least disturbed sites anywhere within the Southern Ocean and one where krill fishing has so far been virtually non-existent is the South Sandwich Islands volcanic archipelago. Some of the main krill predators breeding at the South Sandwich Islands are penguins, with five species breeding on the islands, the dominant species of which is the chinstrap penguin. In this paper we report on the results of ARGOS PTT deployments during the chinstrap penguin chick-rearing period, using the recorded foraging trips to develop habitat models. Foraging habitats used by chinstrap penguins during this period were best characterised by distance from the colony and sea surface temperature and, using these two covariates, we predicted the chick-rearing foraging habitat use around all islands. We show that the provisions of the South Georgia and South Sandwich Islands Marine Protected Area ensure that chinstrap penguins, and other krill-dependent predators with similar foraging ranges, likely have robust protection during the summer. During the winter, when krill predators are likely to forage further offshore, seasonal sea ice provides a physical barrier to exclude the fishery, again ensuring the islands' unique biodiversity receives strong protection. However, to the north of the marginal sea ice zone, competition between krill predators and the fishery could exist if the fishery were ever to explore new locations for resource extraction. We make a number of conclusions, including the need for winter tracking data to inform future management options.

1. Introduction

The South Sandwich Islands are a major ecological hotspot for penguins in the southwest Atlantic sector of the Southern Ocean, yet there has been limited scientific study of the islands. This is due to their remote location, steep, rocky coastlines, and lack of protection from the prevailing winds and ocean swells. The island arc spans a latitudinal range from approximately 56°S to 60°S (Fig. 1). All 11 islands are south of the Antarctic Polar Front and experience a maritime Antarctic climate, however winter pack ice only reaches the northernmost islands during late winter (August and September), while the southernmost islands are ice-bound from as early as May (see Fig. 1 and Thorpe and Murphy, this issue). This climatic gradient is reflected in the distribution of penguins found on the islands. The northern islands support a large population of macaroni penguins (*Eudyptes chrysolophus,* ~95,000 pairs, Lynch et al., 2016), a species typical of sub-Antarctic climates, while the southerly islands support greater numbers of Adélie penguins (*Pygoscelis adeliae,* ≥ 125,000 pairs, Lynch et al., 2016), a species more typical of Antarctic and maritime Antarctic climates. Chinstrap penguins (*Pygoscelis antarctica*) are the most abundant penguin species breeding at the South Sandwich Islands, with a minimum population size of 1.3 million pairs across all islands (Lynch et al., 2016). Similar to macaroni penguins, chinstrap penguin numbers are concentrated towards the northern islands, with the largest colony on Zavodovski Island with an estimated 600,000 breeding pairs. Other large colonies of chinstrap penguins are also found on the northern islands (Visokoi = 185,000 pairs, Candlemas = 205,000 pairs, Vindication = 95,000 pairs, Saunders = 155,000 pairs), although Thule Island at the very southern end of

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the archipelago is the breeding site of at least 47,000 pairs (Lynch et al., 2016). Gentoo penguins (*Pygoscelis papua*) are found in small colonies on many of the islands, with a total breeding population of just ~2000 pairs (Lynch et al., 2016).

At almost all sites so far examined within the southwest Atlantic, macaroni penguins and all three *Pygoscelis* penguin species have a high dependence upon Antarctic krill (*Euphausia superba*) during their summer breeding season. Of these species, gentoo penguins have a more generalist diet, taking more fish than either chinstrap or Adélie penguins (Ratcliffe and Trathan, 2012). Krill is also thought to be a major dietary item for penguins breeding across the South Sandwich Islands archipelago based on the colour of guano deposits (Rees et al., 2017; GVC pers. obs.).

Despite being such an important hotspot for chinstrap penguins, with over one third of the global population nesting across the archipelago (Strycker et al., 2020), the inaccessibility of the South Sandwich Islands has so far prevented studies of breeding and foraging behaviour.

At a few locations elsewhere, however, the foraging behaviour of chinstrap penguins has been well studied. For example, at the South Orkney Islands, around 600 nm to the south-west of the South Sandwich Islands (Fig. 1), Warwick-Evans et al. (2018) used telemetry data from chinstrap penguins breeding at four colonies from across the islands to develop habitat models. They found that distance to the colony and the bearing to the nearest area of continental shelf-break, whilst avoiding high densities of penguins from other colonies, were the most important factors explaining habitat selection. This suggests that around the South Orkney Islands, the rapid change in seafloor topography at the peri-insula shelf-edge may act to concentrate or replenish krill stocks, while inter- and intra-specific competition between neighbouring penguin colonies leads to segregation of foraging habitats. The importance of the shelf-edge and inter-colony competition has been identified previously at the South Orkney Islands (Lynnes et al., 2002) and was further validated by Trathan et al. (2018) with chinstrap tracking data from the South Shetland Islands. In both the South Orkney and South Shetland Islands, chinstrap penguins were found to move towards the shelf-break while exhibiting a relatively limited foraging range during the chick-rearing period. During this time, chinstrap penguins are central place foragers and, therefore, long foraging trips would be energetically costly to the adults (Moreno and Sanz, 1996) while chicks would be forced to fast for longer periods between feeds. Habitat models from the

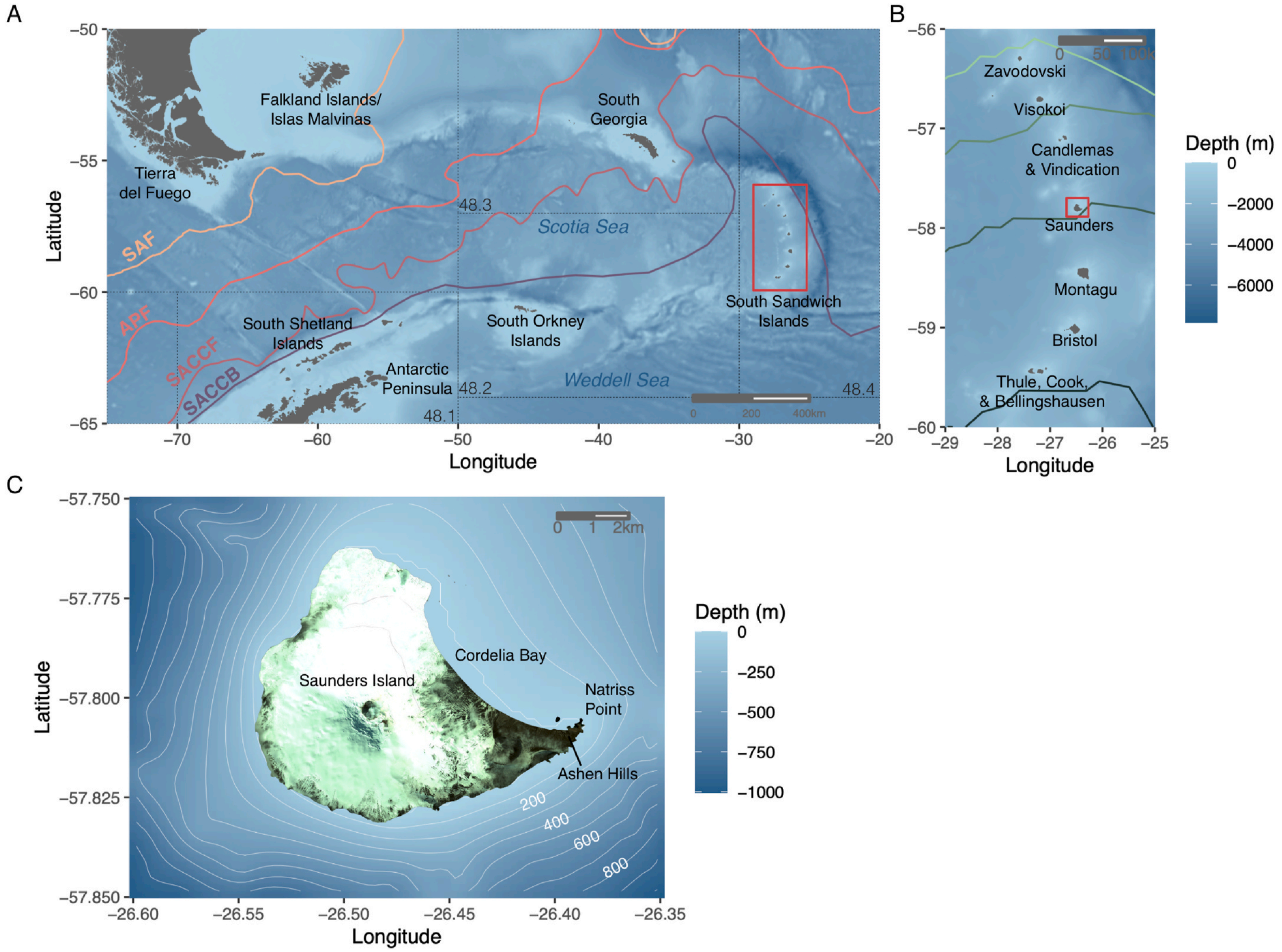

Fig. 1. Location and details of the South Sandwich Islands. A) The South Sandwich Islands are located in the eastern Scotia Sea, south of the main flow of the Antarctic Circumpolar Current (ACC), in CAMLR Convention Subarea 48.4 (blue boxes). The ACC has multiple fronts: the sub-Antarctic Front (SAF), the Antarctic Polar Front (APF), the Southern ACC Front (SACCF), and the Southern ACC Boundary (SACCB). The area bounded by the red box is expanded in B. B) The 11 islands in the South Sandwich Islands form a volcanic island arc. Saunders Island (red box) is in the middle of the island chain. The 15% median sea ice extent (1981–2010, green lines) is shown for September (light green, top) - December (dark green, bottom), as it retreats south (median (1981–2010) position of sea ice extent >15%, monthly mean concentration from https://nsidc.org/data/seaice_index/). C) Chinstrap penguins tagged in this study were nesting at the base of the Ashen Hills, near Natriss Point. Satellite image: Maxar Products. WorldView-2 image. Acquisition date: November 6, 2010 © 2021 Maxar Technologies.

South Orkney Islands and South Shetland Islands predicted that the highest at sea densities of chinstrap penguins would be close to colonies in relatively slow-moving shelf waters. As such, these models have been used to predict the foraging habitat use of unstudied chinstrap colonies across the Antarctic Peninsula and South Orkney Islands with a high degree of confidence (Trathan et al., 2018; Warwick-Evans et al., 2018).

More recently, Phillips et al. (2021) showed that for chinstrap penguins breeding at the South Orkney Islands, foraging distances varied between breeding stages, and that prey patch quality was lower near the colony than at more distant foraging patches, consistent with "Ashmole's halo" (Ashmole, 1963, 1971); however, patch quality near the colony improved over the breeding season. Phillips et al. (2021) suggested that chinstrap penguin foraging strategies are influenced by both breeding stage and prey distribution, and that low patch quality near the colony may be due to a combination of depletion by intraspecific competition but compensated for by natural variation in prey abundance.

Compared to the South Orkney Islands and South Shetland Islands, the South Sandwich Islands have a very limited area of continental shelf, being formed by volcanic cones that fall off steeply on all sides (Fig. 1). This, and the isolated nature of the islands, both from one another and from the Antarctic continental landmass, could result in differences in the foraging behaviour and habitat use of chinstrap penguins in the region.

Krill are advected to the South Sandwich Islands from the southern Scotia Sea and Antarctic Peninsula region by the Antarctic Circumpolar Current (ACC; Hofmann and Murphy, 2004; Thorpe et al., 2007). It is unknown whether krill reproduce and form a self-sustaining population across the South Sandwich Islands archipelago, but based on the limited area of shelf and the flow of the ACC, this is unlikely; work on krill reproduction suggests most production occurs much further south (Hofmann and Hüsrevoğlu, 2003; Perry et al., 2019). As such, advection of krill must be sufficient to support the large, krill-dependent penguin populations on the South Sandwich Islands, together with demands from pelagic predators such as humpback whales (e.g. Trathan et al., 2022; see also Baines et al., 2021; Bamford et al., this issue).

Understanding krill consumption by predators is important, as krill are not only prey to a diverse guild of predators (Trathan and Hill, 2016), but also the target of the largest commercial fishery in the Antarctic, including at nearby South Georgia (Trathan et al., 1997; Trathan et al., 2021). Catches around the Antarctic peaked at 528,331 t in 1981/1982 (of which 373,656 t were taken from the southwest Atlantic), but then declined with the breakup of the former Soviet Union (CCAMLR, 2021).

Over 99% of all catches are now taken in the southwest Atlantic (Fig. 1), where the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) interim catch limit is 620,000 t, though this has never been reached. No incidence of illegal krill fishing has ever been reported to CCAMLR. CCAMLR has spatially partitioned the catch limit with only 93,000 t apportioned to FAO Subarea 48.4, the area surrounding the South Sandwich Islands (Fig. 1). Nevertheless, krill harvesting around the South Sandwich Islands is extremely infrequent, most recently reaching just ~50 t (<0.01%) in the 1991/1992 fishing season.

Over the past decade, catches in the southwest Atlantic have slowly increased and are now more than historical maximum levels. The catch in 2019/2020 was 450,731 t (approximately 73% of the CCAMLR limit; CCAMLR, 2021). As global demand for krill continues to increase (Nicol et al., 2012), understanding the foraging behaviour of krill-dependent predators is key to preventing competition with the expanding krill fishery (Trathan et al., 2018; Trathan et al., 2021). This is especially important during the breeding season, when penguins are highly dependent on local krill stocks around the colony; areas which often overlap with those targeted by commercial fishing activities. However, identifying and protecting these hotspots is challenging if telemetry data are lacking (Lascelles et al., 2012).

In this study, we determine the foraging habitat use of chinstrap penguins around the South Sandwich Islands, by deploying ARGOS Platform Transmitter Terminal (PTT) satellite trackers to sample foraging activities of chick-rearing adults during the breeding season. The primary objective was to compare the distribution of foraging habitat use with the management provisions of the Marine Protected Area (MPA) implemented by the Government of South Georgia and the South Sandwich Islands (GSGSSI). The GSGSSI follows the CCAMLR approach for managing the krill fishery, but it imposes additional, more robust domestic management measures to safeguard and protect the marine ecosystem.

2. Methods

2.1. Study location and tag deployment

We deployed 20 KiwiSat® K2G 173A ARGOS PTTs on breeding chinstrap penguins at Natriss Point, Saunders Island in the South Sandwich Islands archipelago on January 6th, 2020 (Fig. 1). The population of chinstrap penguins on Saunders Island was previously estimated at 155,000 pairs, making this representative of the colony sizes typically found throughout the South Sandwich Islands (Lynch et al., 2016). Note, however, that there is some evidence that this colony may have declined recently (Hart et al., this issue).

To deploy the devices, we first identified nests where both adults were present and appeared to be in good condition through visual inspection. We then captured one of the adults while ensuring that the other was still attending the nest. As far as possible, we also chose nests with two eggs or chicks, such that if one chick was lost, the adults would continue to provision the second. Chinstrap penguins typically lay two eggs, and so we were not artificially selecting for higher-quality parents through this method. The PTTs weighed 34g and were attached to the lower back of the bird to limit drag using Tesa® tape and two-part epoxy resin applied over the tape (modified after Wilson, 1997). After attachment, we released each bird and observed them to ensure that they returned to the nest. To prolong battery-life, the PTTs were only programmed to switch on when wet (haul-out mode) and so would only transmit positional data while the birds were at sea. The deployment period ended when the bird moulted approximately two months later, resulting in the PTT falling off and transmissions ceasing.

Ethical review of the tracking was conducted by Oxford University Local Animal Welfare Ethical Review Board and included the justification for the study, the numbers of animals involved, training and protocols. An environmental risk assessment was also carried out as part of the GSGSSI permit application. The visit was carried out under permit to Pelagic Expeditions, and the tracking conducted under Regulated Activity Permit 2019/024-ammended, issued to TH. No unexpected welfare issues were observed post-release, although we could not continue to observe the birds for long after tag attachment.

2.2. Data filtering

All ARGOS PTT location data and their associated error estimates were downloaded using the CLS interface (https://www.argos-system.org/) and analysed using R v3.6.2 (R Core Team, 2019). Chinstrap penguins have been shown to dive continuously throughout foraging trips during all stages of breeding (Warwick-Evans et al., 2018), and so we did not attempt to partition the data into active foraging versus travel in this study. However, fixes that would have required an average swimming speed greater than 12 km h^{-1} were removed from the dataset using the speedfilter() function from the package *trip* v1.6.0 (Sumner, Wotherspoon and Hindell, MA, 2009). This speed threshold was chosen given the reported swimming speed of chinstrap penguins is 8.6 km h^{-1} (Culik and Wilson, 1994), making apparent sustained travelling speeds greater than 12 km h^{-1} most likely the result of inaccurate positional data. We used the crwMLE() function from the *crawl* v2.2.1 package

(Johnson et al., 2008; Johnson and London, 2018) to fit continuous-time correlated random walk models to the data and interpolated the tracks from each individual at 5 min intervals using the crwPredict() function. Since movement data is often incomplete and imprecise, these models allow uncertainty to be taken into account, including a prior distribution for the ARGOS error classes (0, 1, 2, 3, A, B) associated with each fix.

Next, we removed fixes that were over land or within 1 km of land (to further allow for inaccuracy in the fixes) and split the track data into individual foraging trips, defining the start and end of a trip to be when the bird spent more than 10 min within the 1 km buffer around the island. Trips with fewer than two observed fixes were removed. Visual inspection of each trip showed that this correctly split the majority of tracks into individual foraging trips. However, a subset of trips did not start or end at the colony and could not be separated by this method. This was because a position fix was not obtained when the bird exited the water and before the tag went into haul-out mode. In these cases, a long period of low-speed movement at sea was incorrectly inferred to have occurred, when, in fact, the bird was most likely attending the nest. Plotting the rolling average speed across a 3-h window over the entire deployment period highlighted these erroneous periods of low-speed movement. Removal of the parts of the trips when the speed was less than 1.2 km h^{-1} for more than 3 h was, in most cases, sufficient to remove these erroneous sections and correctly split the tracks into individual foraging trips. Trips that were not split correctly by this method were further split by hand. Given the lack of position data at the start and end of these trips, there may be some inaccuracy in the start and end times of a small subset of trips in our dataset.

To ensure that our data represented only the chick-provisioning period and did not include any pre-moult foraging trips, we plotted the maximum distance from the colony for each trip. During pre-moult foraging, the adults are no longer constrained to central place foraging since their chicks have fledged, allowing the birds to travel much greater distances away from the colony (Warwick-Evans et al., 2019). We did not record enough pre-moult trips for habitat suitability modelling of the pre-moult period, and so we discarded these long foraging trips, which were greater than 100% longer than previous trips and always the last trip before the transmission ended (when the tag was moulted).

2.3. Environmental covariates

To determine chinstrap penguin foraging habitat use around Saunders Island, we first defined our study area as the maximum and minimum longitudes and latitudes recorded from our tagged birds during the chick-rearing period. This represents a reasonable area that the penguins could move within, forming a biologically realistic null-model, while allowing our model to characterise variation between the habitats that they selectively travelled to or avoided (Wakefield et al., 2011). To form our background dataset (pseudo-absence dataset), we randomly selected points across this area, excluding land, using the randomPoints() function from the *dismo* v1.3-3 package (Hijmans et al., 2020). We picked the same number of background points as the number of observed or interpolated fixes for each PTT (presences) in our dataset, since our presence dataset was large and the background dataset therefore covered the study area with high density.

We selected several biologically meaningful environmental and spatial covariates to use in our models (Table 1). We selected sea surface temperature (SST), sea surface height, and northward- and eastward-water velocities since krill are thought to be advected into this region by currents (Hofmann and Murphy, 2004). These variables could therefore indicate the locations of these currents and, thus, areas of high krill availability. Similarly, we selected surface chlorophyl concentration as a proxy for local productivity, which could also indicate areas of high krill abundance. We also chose to model features of the seabed, including depth, slope, and distance to the shelf break, since previous work at South Georgia showed that the highest densities of krill were found in shelf waters and particularly at the shelf-edge (Trathan et al., 2003). Finally, we included distance to the colony, since chinstrap penguins are central place foragers during the breeding season and previous studies have shown this to be an important factor in determining chinstrap penguin foraging habitat use (Trathan et al., 2018; Warwick-Evans et al., 2018). Since our study period spanned January and February, with 64% of the observations in January and 36% in February, we calculated the weighted average of the January and February monthly means for all time-varying physical and biological covariates. We did not include bearing to the shelf-break as a covariate, because visual inspection of the data showed that most foraging occurred to the east of the colony whereas the nearest area of shelf-break was almost due south of the colony, suggesting that the birds were not moving directionally towards the nearest area of shelf-break. Finally, we tested for correlations among covariates with the *correlations* v0.6.0 package (Makowski et al., 2019). Distance to the shelf break was correlated with both distance to the colony and with depth (Pearson's correlation coefficient = 0.78 and −0.80, respectively) and so we excluded distance to the shelf break while we retained distance to the colony and depth to retain the maximum number of covariates. None of the other covariates had correlation coefficients greater than |0.7|. We used the package *raster* v3.4-5 (Hijmans, 2020) to extract the values of the environmental covariates for each data point in our presence and pseudo-absence datasets.

Table 1
Environmental variables considered for habitat suitability modelling.

Covariate	Resolution	Source
Distance to colony	200 m × 200 m	Calculated using raster::gridDistance()
Distance to shelf break	200 m × 200 m	Calculated from bathymetry using raster::rasterToContour() and raster::distance()
Depth	200 m × 200 m	British Antarctic Survey Geodata Portal
Slope	200 m × 200 m	Calculated from bathymetry using raster::terrain()
Sea surface temperature	5 km × 9 km	CMEMS global-analysis-forecast-phy-001-024-monthly[a]
Sea surface height	5 km × 9 km	CMEMS global-analysis-forecast-phy-001-024-monthly[a]
Northward surface water velocity	5 km × 9 km	CMEMS global-analysis-forecast-phy-001-024-monthly[a]
Eastward surface water velocity	5 km × 9 km	CMEMS global-analysis-forecast-phy-001-024-monthly[a]
Surface chlorophyll concentration	14 km × 27 km	CMEMS global_analysis_forecast_bio_001_028-monthly[b]

[a] https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=GLOBAL_ANALYSIS_FORECAST_PHY_001_024

[b] https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=GLOBAL_ANALYSIS_FORECAST_BIO_001_028

2.4. Habitat suitability modelling

Foraging habitat use was determined using a General Additive Modelling (GAM) approach within the package *mgcv* v1.8-31 (Wood, 2017), following Warwick-Evans et al. (2018). We used forward stepwise model selection with cross-validation to evaluate model performance. In practice, for each of our eight covariates, we ran models that withheld the presence and pseudo-absence points for each PTT in turn, thus using data from 19 of the 20 individuals for each model run. We then evaluated each model by predicting into the individual that was withheld and averaging the area under the curve (AUC) across all 20 of these runs. We calculated the AUC, sensitivity, and specificity from the receiver operating characteristic (ROC) curve, using the package *pROC* v1.17.0.1 (Robin et al., 2011). When AUC = 1, model predictions are 100% correct. AUC = 0.5 represents a model that has no better predictive ability than chance. Sensitivity measures the number of true positives, while specificity measures the number of true negatives. For each covariate, we also varied the number of knots from three to six, capping at six knots to prevent overfitting (total number of models tested = 640 in the first round). We identified the combination of covariate and knots with the highest AUC value, and then repeated the process by adding additional covariates, until the increase in the AUC was marginal with the addition of further covariates. We plotted all response curves using the draw() function from the R package *gratia* (https://gavinsimpson.github.io/gratia/index.html) and checked for overfitting.

We used the model that best predicted foraging habitat selection around Saunders Island to predict the probability of occurrence of chinstrap penguins around all other islands in the South Sandwich Islands using the predict() function from *mgcv*. For each island, we took the locations of all colonies from Convey et al. (1999) and predicted the probability of occurrence at a 1 × 1 km resolution around the island. We chose this relatively fine-scale resolution as a trade-off between the varying spatial scales of the covariates included in our final model. We set all probabilities greater than 100 km from the colony to zero since prior studies (Lynnes et al., 2002; Kirin et al., 2010; Kokubun et al., 2015; Hinke et al., 2017; Lowther et al., 2018; Warwick-Evans et al., 2018) and our own data show that chinstraps are highly unlikely to forage this far from the colony while provisioning chicks. We calculated the predicted number of individuals in each 1 km^2 cell by dividing the probability of occurrence by the sum of the probability of occurrences across the entire study area, multiplying the importance values by the estimated number of breeding individuals on each island, using population estimates from Lynch et al. (2016). All code used in the analysis of this data is available at https://github.com/GemmaClucas/CHPE_Tracking_South_Sandwich_Islands.

3. Results

Out of the 20 PTT tags that we deployed on chinstrap penguins, the average duration of deployment was 65 days (range = 7–103) with 11 of the devices recording through to the end of the chick-rearing period. We recorded 388 chick-rearing provisioning trips, with an average of 19.4 recorded per bird, and a mean duration of 20 h. The mean maximum distance that the birds travelled from the colony was 28.9 km (range: 2.38–124 km) and few trips extended more than 50.0 km offshore (Fig. 2).

The model that best predicted chinstrap penguin foraging habitat around Saunders Island included distance from the colony and sea surface temperature as covariates and had AUC = 0.927, sensitivity = 0.848, specificity = 0.904 (Fig. 3, Table 2). Adding a third covariate only resulted in marginal increases in AUC (Table 2) and so the model with two covariates was chosen as the most parsimonious.

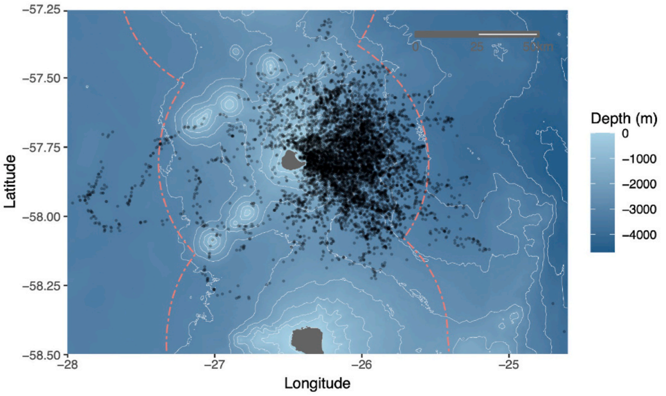

Fig. 2. Locations of the fixes obtained from the 20 PTT tags deployed on chinstrap penguins. Only observed fixes are shown (black dots) from the chick-rearing period. Dashed red line denotes the boundary of the 50 km pelagic no-take zone around the islands.

Predicting the probability of occurrence around other islands identified areas up to ~40 km offshore from all islands as important chinstrap penguin foraging habitat (Fig. 4a), although a non-zero probability of occurrence did extend more than 50 km offshore from the islands in some areas i.e. outside of the pelagic no-take zone. By weighting the probability of occurrence by the number of individuals breeding on each island, we predicted higher densities of chinstrap penguins in the waters around Zavodovski Island, with much lower densities around the other islands that have smaller populations of chinstrap penguins (Fig. 4b).

4. Discussion

Our analyses provide the first insight into the foraging behaviour of penguins breeding at the South Sandwich Islands, an isolated archipelago where five species of penguin breed, including approximately one third of the world population of chinstrap penguins. Using satellite-linked PTT devices to track chinstrap penguins during the chick-rearing period from Saunders Island, midway along the island chain, we found birds made short foraging trips, with an average maximum distance travelled from the colony of 28.9 km and with most trips not exceeding 50 km from the colony. This contrasts with trips from other chinstrap breeding sites in the southwest Atlantic, where trips during the chick-rearing period extend 40–70 km from the colony on average (Lowther et al., 2018; Trathan et al., 2018; Warwick-Evans et al., 2018; Phillips et al., 2021). The shorter foraging range in the South Sandwich Islands may (partially) be the result of difference in bathymetric topography. At the South Orkney and South Shetland islands, the shelf regions and particularly the shelf-break appears to play a key role in determining chinstrap foraging habitat, whereas at the South Sandwich Islands, the steep sides of the islands means the shelf-break is relatively close and undefined.

We identified distance from the colony and sea surface temperature as the best predictors of foraging habitat use and, using these two covariates, we predicted foraging habitat use around the other islands. Distance from the colony had the greatest influence on habitat use, and, as Saunders Island is small relative to the distance travelled by birds, our models predicted a relatively high probability of occurrence in all directions around the island. The influence of sea surface temperature was mainly apparent in the easterly direction of the observed (Fig. 3) and predicted (Fig. 4a) habitat use. Extrapolation of our habitat model to other islands in the archipelago provided similar results, with the influence of sea surface temperature most apparent around Saunders Island and Montagu Island (Fig. 4a).

Extrapolation of our model to the rest of the archipelago also highlighted the relative importance of some of the islands compared to others. The very large population of chinstrap penguins found on Zavodovski dominates the distribution (Fig. 4b). Yet, it is important to note that our density estimation method does not consider the number of individuals transiting through cells, but rather represents an instantaneous snapshot of potential foraging activity. Therefore, an even higher density of individuals would be expected to utilise cells close to the island than is represented in Fig. 4.

The high density of individuals around Zavodovski could result in prey depletion close to the colony, a phenomenon known as “Ashmole’s halo.” Ashmole (1963, 1971) hypothesised that competition for food would result in prey depletion around seabird colonies, which could ultimately limit population size. While Ashmole (1963) noted that at high latitudes, the seasonal abundance of prey, and the ability of seabirds to time their breeding with peaks in prey availability may not result in severe competition for food, a decline in patch quality close to chinstrap penguin colonies has been observed elsewhere (Phillips et al., 2021), resulting in increasing foraging ranges over the course of the breeding season (Kokubun et al., 2015). Depletion of prey resources near to the colony could lead to longer foraging trips being more energetically advantageous since the cost of travelling further to a higher density

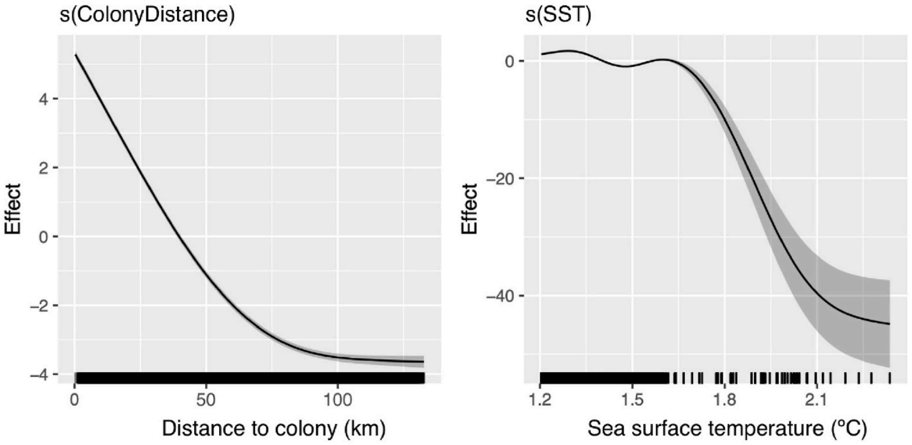

Fig. 3. Response curves (with 95% credibility interval) for the model that best predicted chinstrap penguin foraging presence around Saunders Island. The final model included distance to the colony with three knots and sea surface temperature with six knots. The black bars show the distribution of the data.

prey patch could be offset by higher prey encounter rates (Phillips et al., 2021), but this is also likely to vary between and within years, depending upon resource availability (Lowther et al., 2018; Phillips et al., 2021). Santora et al. (2020) found that the foraging ranges of Adélie penguins from colonies with ~1000s of pairs was significantly shorter than those from colonies with ~100,000s of pairs, while Warwick-Evans et al. (2018) and Warwick-Evans et al.,(in press) evaluated the impact of population size on the foraging range of chinstrap penguins and did not find any effect. The populations investigated in these studies, however, were smaller than those found on Zavodovski. Therefore, collecting tracking data from Zavodovski should be a high priority for future studies. It would also be advantageous to track for multiple years, to determine whether there is inter-annual variability in foraging range at these islands.

The distance to the colony has previously been found to be an important explanatory variable in chinstrap penguin foraging habitat at the South Orkney Islands and South Shetland Islands (Trathan et al., 2018; Warwick-Evans et al., 2018) and can be explained by the adults' need to return to the colony regularly to provision their growing chicks. Interestingly, we did not observe directional movement towards the nearest part of the shelf-break in our study. The nearest part of the shelf break lies directly south of the colony on Saunders Island (Fig. 1c), whereas foraging was concentrated to the east of the colony (Fig. 2). It is likely that the topography of the seabed, which rises steeply around the island, does not lead to predictable aggregations of krill in the same way as is observed at the South Orkney Islands and South Shetland Islands (Warwick-Evans et al., 2018; Trathan et al., 2018). Further, as the islands are the tips of volcanic cones, the available shelf area is minimal and krill may not be able to aggregate over the shelf as observed elsewhere (Trathan et al., 2003). Rather, foraging appeared to be concentrated in cooler, deep waters to the east of the island, perhaps because these cooler waters supported higher krill biomass (Siegel et al., 2004).

Krill advected to the South Sandwich Islands in the austral summer likely originate from areas that were covered with sea ice as late as November in the south-eastern Scotia Sea or northern Weddell Sea (Thorpe and Murphy, this issue; Hofmann and Murphy, 2004; Murphy et al., 2004; Siegel et al., 2004). The Southern ACC Boundary (SACCB), a region of rapid water movement, may be responsible for much of this transport (Hofmann and Murphy, 2004). The SACCB flows to the north of the South Sandwich Islands before it meanders south and passes east of the islands (Fig. 1a). Thus, cold water currents around the islands may be the result of mesoscale interactions between the flow of the SACCB, Weddell Sea water, and bottom topography, and could be responsible for entraining krill around the South Sandwich Islands. Chinstrap penguins may therefore be preferentially foraging in these areas of cooler water if they are associated with high krill biomass.

Taken in combination with previous habitat models for the species, our models highlight how chinstrap penguins may forage adaptively depending upon breeding site location and the surrounding environment, with different environmental cues predicting foraging activity in different locations. Large colonies exist at the South Shetland Islands, at the South Orkney Islands, and at the South Sandwich Islands, each with differing amounts of available foraging habitat and oceanographic conditions. It is therefore interesting that they do not exist at other sub-Antarctic locations and there are only small populations at South Georgia, Bouvetøya, and at the Balleny Islands (Trivelpiece and Trivelpiece, 2013).

Moreno and Sanz (1996) estimated that chinstrap penguins raising chicks during the brood stage will require 2.04 kg day^{-1} of krill to remain in energy balance, with this requirement decreasing to 1.68 kg day^{-1} during the crèche phase (during which adults spend less time at the nest guarding young and can more easily self-provision). With a population of 1.3 million breeding pairs of chinstrap penguins on the South Sandwich Islands (Lynch et al., 2016), the breeding adults alone will consume approximately 5,300 tonnes day $^{-1}$ of krill during the brood stage, and 4, 400 tonnes day $^{-1}$ of krill during the crèche phase. This amounts to 258, 000 tonnes of krill required to sustain the adults over the chick-rearing period and does not account for the requirements of non-breeding adults or chicks, making this likely to be an under-estimate of the true biomass consumed. In addition to chinstrap penguins, the islands also support large populations of krill-dependent macaroni and Adélie penguins and a recovering population of humpback whales that migrates from Brazil to the area each austral summer (IWC Breeding Stock A; Zerbini et al., 2011). Other cetaceans that feed around the islands (Reilly et al., 2004) are also krill consumers. Thus, the advection of krill to the South Sandwich Islands must be substantial.

Despite these large populations of krill predators, historical surveys of krill biomass have recorded comparatively low densities of krill around the South Sandwich Islands (Hewitt and Watkins, 2004). During the CCAMLR, 2021 survey, total krill biomass in FAO Area 48, which encompasses the Scotia Sea from the Antarctic Peninsula north to South Georgia and east to the South Sandwich Islands, was estimated to be 60.3 million tonnes (SC-CAMLR-XXIX, 2010, Annex 5) but with relatively low krill biomass around the South Sandwich Islands (although see Siegel et al., 2004; Krafft et al., 2021). This low biomass of krill is difficult to reconcile with the abundance of krill predators at the islands and could indicate that there is a high rate of replenishment of the krill stock from sources further south, but with a low standing stock at any given time. However, there is considerable heterogeneity in the distribution and abundance of krill in the Scotia Sea that occurs intra- (Reid et al., 2010) and inter-annually (Watkins et al., 1990; Siegel et al., 1998; Brierley et al., 1999; Trathan et al., 2003; Siegel et al., 2004; Fielding

Table 2
Results from our model selection procedure. The top 10 models with one, two, and three covariates are shown, ordered according to AUC. The number of knots used in the smooth is denoted by k. The model that best predicted foraging habitat use is shown in bold.

Top 10 models with 1 covariate	AUC	Sensitivity	Specificity
s(ColonyDistance, k = 3)	0.9096	0.8271	0.8898
s(ColonyDistance, k = 4)	0.9091	0.8271	0.8898
s(ColonyDistance, k = 5)	0.9090	0.8271	0.8898
s(ColonyDistance, k = 6)	0.9085	0.8271	0.8898
s(NorthVelocity, k = 4)	0.8321	0.8144	0.7675
s(NorthVelocity, k = 3)	0.8318	0.8144	0.7675
s(NorthVelocity, k = 5)	0.8317	0.8144	0.7675
s(NorthVelocity, k = 6)	0.8315	0.8144	0.7675
s(SST, k = 5)	0.8033	0.7080	0.8489
s(SST, k = 6)	0.8032	0.7012	0.8488
Top 10 models with 2 covariates			
s(ColonyDistance, k = 3) + s(SST, k = 6)	**0.9273**	**0.8476**	**0.9036**
s(ColonyDistance, k = 3) + s(SST, k = 5)	0.9273	0.8468	0.9052
s(ColonyDistance, k = 3) + s(chlorA, k = 5)	0.9270	0.8489	0.8960
s(ColonyDistance, k = 3) + s(chlorA, k = 6)	0.9270	0.8483	0.8969
s(ColonyDistance, k = 3) + s(chlorA, k = 3)	0.9270	0.8481	0.9029
s(ColonyDistance, k = 3) + s(SST, k = 4)	0.9266	0.8469	0.9000
s(ColonyDistance, k = 3) + s(SST, k = 3)	0.9265	0.8506	0.8998
s(ColonyDistance, k = 3) + s(chlorA, k = 4)	0.9263	0.8471	0.8991
s(ColonyDistance, k = 3) + s(Height, k = 3)	0.9242	0.8542	0.8970
s(ColonyDistance, k = 3) + s(Height, k = 5)	0.9234	0.8514	0.8980
Top 10 models with 3 covariates			
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(North, k = 4)	0.9298	0.8566	0.8915
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(Bathymetry, k = 6)	0.9296	0.8548	0.9004
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(NorthVelocity, k = 6)	0.9295	0.8578	0.8916
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(NorthVelocity, k = 5)	0.9295	0.8579	0.8899
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(Bathymetry, k = 5)	0.9294	0.8558	0.9005
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(NorthVelocity, k = 3)	0.9293	0.8597	0.8875
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(chlorA, k = 5)	0.9290	0.8541	0.9007
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(chlorA, k = 3)	0.9289	0.8524	0.9013
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(chlorA, k = 4)	0.9289	0.8555	0.8947
s(ColonyDistance, k = 3) + s(SST, k = 6) + s(chlorA, k = 6)	0.9286	0.8565	0.8937

ColonyDistance = Distance to colony.
NorthVelocity = Northward surface water velocity.
SST = Sea surface temperature.
chlorA = Surface chlorophyll concentration.
Height = Sea surface height.

et al., 2014). This suggests a complex and dynamic system, making the estimation of krill abundance challenging (Trathan et al., 2022). The requirement to understand the drivers of krill abundance and distribution at scales relevant to krill-dependent species highlights the need for precautionary management of the commercial krill fishery, at least until such time that we can accurately measure krill biomass and set catch limits at scales relevant for ecosystem function and operation (Watters et al., 2020).

Within the South Georgia and the South Sandwich Islands MPA (SGSSI MPA), fishery quotas are set through international agreement by CCAMLR, although GSGSSI imposes additional, more robust management measures as a further precaution. Currently, there is no krill fishery in operation around the South Sandwich Islands, although CCAMLR has set a catch limit of 93,000 tonnes within Subarea 48.4. CCAMLR and GSGSSI recognise the need for careful management around the islands to avoid unsustainable resource competition between krill predators and any future krill fishing activity. CCAMLR has therefore defined a series of small-scale management units (SSMUs; Hewitt, Watters, et al., 2004) to provide options for the subdivision of regional catch quotas to prevent concentration of fishing effort in certain areas. Subarea 48.4 is divided into two SSMUs: the South Sandwich Islands SSMU, which includes the islands and region up to 85 km offshore; and the South Sandwich Islands pelagic SSMU, which includes the rest of Subarea 48.4 (see Lynnes et al., 2002; Trathan et al., 2008). While our data suggests that the inshore SSMU sufficiently encompasses the main foraging habitat during chick-rearing, the collection of tracking data during incubation for chinstrap penguins and during all breeding periods for other species would be beneficial. More recently, CCAMLR has also endorsed (SC-CAMLR-38, 2019) a new management strategy for krill (see also Trathan et al., 2021; Trathan et al., 2022), whilst GSGSSI has implemented other spatial and temporal management measures to ensure that the unique biodiversity of the archipelago is protected.

The SGSSI MPA was declared in 2012, with further enhancements in 2013 (Trathan et al., 2014) and 2018 (https://www.gov.gs/wp-content/cache/all/32110-2/index.html; accessed 23-June-2021). The SGSSI MPA is a sustainably managed MPA, including a strict no-take zone extending 3 nm around each of the South Sandwich Islands, and a ban on commercial midwater fishing (i.e. krill fishing) within 50 km of each of the islands. This latter measure was designed to further protect the foraging areas of krill-dependent predators, even though at the time, no data existed to confirm their foraging ranges (Hart and Convey, 2018). Temporal restrictions on krill fishing activities are also in place, such that the krill fishery can only operate between May and September, that is, in the winter, when populations of krill predators have finished breeding and many cetaceans have migrated north to their calving grounds. The SGSSI MPA also restricts vessels from carrying heavy fuel oil in the vicinity of the South Sandwich Islands, as a precautionary measure to prevent potential pollution should a vessel encounter uncharted rocks in this volcanically active area.

The chinstrap penguin foraging habitat that we predicted from our habitat model aligns well with the 50 km pelagic no-take zone around the islands (Fig. 4a). Most foraging activity is predicted to occur within the bounds of the no-take zone during the chick-rearing period, and this, combined with the seasonal closure of the krill fishery, should prevent resource competition from occurring during this sensitive period. During the incubation period, prior to chick-rearing, chinstrap foraging ranges are likely to be larger, since adults typically spend longer at sea and have a larger foraging range (e.g. Warwick-Evans et al., 2018). Nevertheless, the seasonal closure of the krill fishery should still protect prey resources even if preferred foraging habitat extends outside of the no-take zone during incubation and pre-moult foraging trips. However, if a large winter fishery were to operate just prior to the start of the breeding season, local depletion could result in carry-over effects and limit krill-availability (Trathan et al., 2022).

During winter, the northward progression of the seasonal sea ice through the archipelago is likely to force chinstrap, macaroni, and gentoo penguin populations to move north as the surface waters cool. In contrast, Adélie penguins, whose winter foraging habitat includes the marginal ice zone and loose pack ice (Fraser and Trivelpiece, 1996; Clarke et al., 2003; Ballard et al., 2010; Dunn et al., 2011; Hinke et al., 2015) would probably stay within the sea ice as it moves northwards. Thus, the winter foraging areas of Adélie penguins would likely remain protected from a winter krill fishery, which cannot operate in the marginal ice zone. However, the populations of chinstrap, macaroni and gentoo penguins from the islands would probably stay north of the ice edge (Wilson et al., 1998; Trivelpiece et al., 2007; Ratcliffe and Trathan, 2012; Hinke et al., 2015; Ratcliffe et al., 2015) and high penguin densities might occur to the north of the South Sandwich Islands in winter.

Winter mortality may explain recently observed changes in population size of chinstrap penguins on the Antarctic Peninsula and South Shetland Islands (Barbosa et al., 2012; Strycker et al., 2020), but there is still little data on the winter movements of this species. Some individuals tracked in winter from the South Shetland Islands stayed close to their

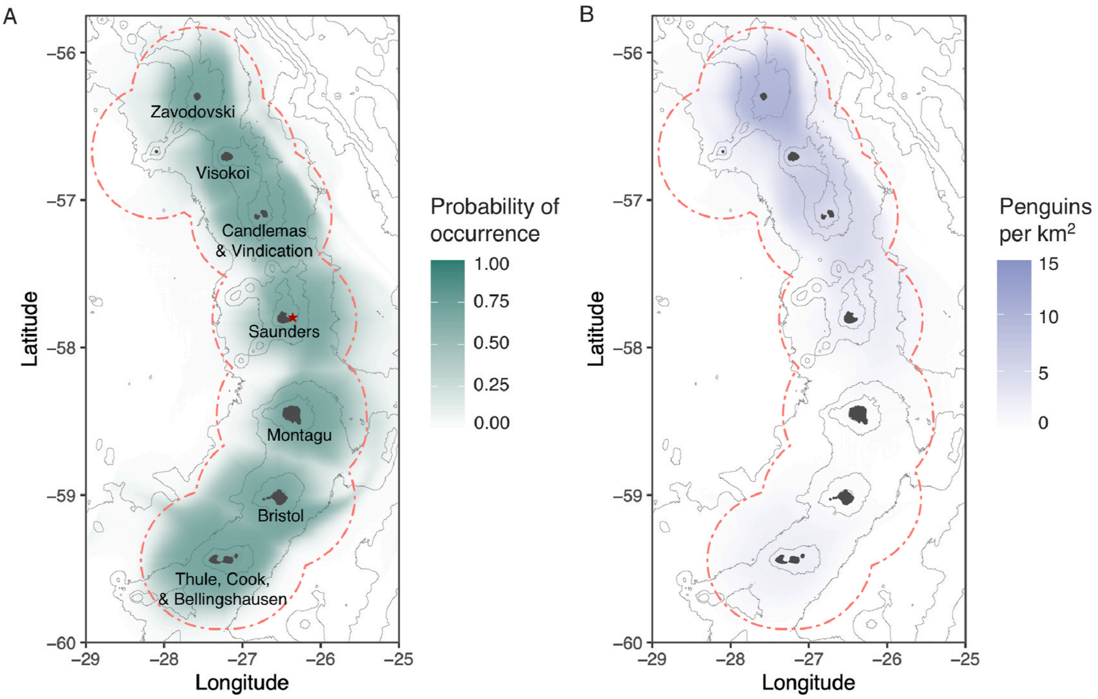

Fig. 4. Results from our habitat suitability modelling, extrapolated to all the islands in the South Sandwich Islands. A) A high probability of occurrence of chinstrap penguins is predicted within the bounds of the 50 km no-take zone. The red marker indicates where the penguins were tagged on Saunders Island in this study. B) Weighting the probability of occurrence by population size highlights the higher density of penguins predicted around Zavodovski Island.

colonies in shelf waters (Trivelpiece et al., 2007), while others made long-distance pelagic migrations into the Scotia Sea (Hinke et al., 2015). A couple of individuals have been tracked migrating to the South Sandwich Islands from the South Shetland Islands as well as from Bouvetøya (Trivelpiece et al., 2007; Biuw et al., 2010) potentially adding to the penguin numbers likely to be found to the north of the islands in winter. Collecting data on the winter movements of the resident chinstrap penguins should therefore be a priority to avoid resource competition during the months when the krill fishery is open.

5. Conclusions

We show that the management provisions of the SGSSI MPA appear to protect chinstrap penguin foraging habitat during the breeding season through the exclusion of krill fishing activities within 50 km of all coastlines and the seasonal closure of the krill fishery across the SGSSI Maritime Zone from October–April. This protection is likely to extend to other krill-dependent predators with similar foraging ranges and breeding seasons, although future studies are necessary to confirm this.

We highlight that during winter, when the area outside the South Sandwich Islands 50 km pelagic no-take zone is open to the krill fishery, the fishery is unlikely to operate because of seasonal sea ice forming a physical barrier to fishing operations. However, to the north of the sea ice, krill predators may still be vulnerable to competition if the fishery were to operate in these open water areas. At present, the risk of such operations are minimal, as the fishery has never operated in this area previously and preferentially only operates close to shelf and shelf slope areas where krill are predictable. These areas will mainly be ice-covered at the South Sandwich Islands in winter (Fig. 1, see also Thorpe and Murphy, this issue), protecting them from fishery operations. Nevertheless, information about the distribution and abundance of krill predators in open water areas in the winter would help inform future management options and determine the likely effect of changing sea ice conditions.

A key consideration for future management should be the sources of krill that supply the South Sandwich Islands. If the islands are dependent upon the movement of krill in the ACC, then CCAMLR must regulate harvesting so that more-southerly parts of the krill population are not depleted prior to their arrival at the South Sandwich Islands. Close cooperation between CCAMLR and scientists interested in the South Sandwich Islands is therefore critical for informing management and protecting biodiversity at the archipelago.

CRediT authorship contribution statement

Gemma V. Clucas: Conceptualization, Investigation, Formal analysis, Methodology, Visualization, Writing – original draft. **Victoria Warwick-Evans:** Methodology, Formal analysis, Writing – review & editing. **Tom Hart:** Conceptualization, Resources, Funding acquisition, Writing – review & editing. **Philip N. Trathan:** Conceptualization, Methodology, Funding acquisition, Resources, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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