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Changes in prey fields increase the potential for spatial overlap between gentoo penguins and a krill fishery within a marine protected area

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Abstract

AIM: Management of competition with predators is an important consideration for fisheries, particularly within marine protected areas (MPAs) where conservation is a primary objective. We aimed to test whether static no-take zones within a large, sustainable-use MPA prevented overlap between gentoo penguins and a krill fishery during two winters with contrasting prey fields.

LOCATION: South Georgia, Southwest Atlantic Ocean.

METHOD: We used satellite tracking ($N = 16$, June–September 2018) to describe gentoo penguin movements and distribution and quantified their overlap with the MPA's no-take zone (NTZ) and the krill fishing grounds. DNA metabarcoding of scats ($N = 220$, April–September 2018) was used to quantify diet.

RESULTS: When krill were at moderate densities and evenly distributed in 2001, gentoo penguins would have spent all of their time within the 12 NM NTZ, but when availability was low in 2018, they spent 46.3% of their time outside the NTZ and 9.6% within the krill fishing grounds. The extension of the NTZ to 30 km in response to this finding would have produced a 14.9% increase in protection for penguins and displaced 4% of fishery hauls. Gentoo penguin diet comprised 25.8% krill, which is lower than in the late 1980s but more than in 2009.

MAIN CONCLUSIONS: Gentoo penguins extend their foraging range when krill is scarce, which increases the potential for spatial overlap with the krill fishery during periods of nutritional stress. Current regulations allow for expansion of both extent and catches by the krill fishery and, should this occur, gentoo penguins may face heightened risks from competition. A dynamic ocean management framework, that extends closed areas in response to near real-time data on penguin movements and krill density estimates, may reduce the potential for competition in this sustainable-use MPA while allowing a profitable krill fishery.

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KEYWORDS
DNA metabarcoding, dynamic ocean management, fishery competition, gentoo penguin, krill, MPA, prey field, satellite tracking, spatial overlap

1 | INTRODUCTION

Forage fish or crustacean species are important in predator diets and fishery harvests, which may lead to competition for food (Cury et al., 2011). Forage stocks are driven by natural variability in recruitment that makes the effects of environment and fisheries upon stocks and predators difficult to disentangle (Hilborn et al., 2017). Nonetheless, evidence is emerging that fishery mortality can have effects upon prey stocks and dependent predators independently of natural variability (e.g. Carroll et al., 2017; Sherley et al., 2018; Watters et al., 2020). Impacts upon predators are most likely where their spatial, temporal and dietary overlap with the fishery is high, alternative prey are scarce and when stocks are at naturally low levels (Hilborn et al., 2017). Fisheries can be managed in an ecologically sensitive manner by setting catch limits that reserve predator food requirements (Hill et al., 2020) or restricting the timing or locations of fishing to minimize overlap with foraging predators (Sherley et al., 2018). Marine protected areas (MPAs) are a form of spatially defined management unit where fishing and other anthropogenic threats are prohibited or tightly regulated (Agardy, 1994). Fishery managers face heightened expectations to minimize ecological impact within shared-use MPAs, given the conservation of biodiversity is a primary objective (McCay & Jones, 2011).

Antarctic krill *Euphausia superba* is an important forage species in the South Georgia food web that exhibits pronounced environmentally induced fluctuations in biomass though time (Fielding et al., 2014). South Georgia hosts globally important populations of seabirds (Handley et al., 2020), and variability in the krill stock has strong effects upon the diets, breeding success and population trends of several species (Reid et al., 2005). A fishery within South Georgia's maritime zone operates over the shelf during winter (Grant et al., 2013) and is managed by the Government of South Georgia and the South Sandwich Islands (GSGSSI) within the framework of regulations set by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). A precautionary catch limit of 279,000 t is allocated to subarea 48.3 that contains South Georgia, although only a fraction of this was caught over the past 18 years (mean = 43,000 t, max = 75,200 t; CCAMLR, unpubl. data).

GSGSSI designated the entire 200 NM maritime zone around South Georgia as a sustainable-use MPA in 2012, and minimizing competition between predators and fisheries is among the key management considerations (GSGSSI, 2013; Handley et al., 2020). The original MPA regulations included a no-take zone (NTZ) extending 12 NM (22.2 km; hereafter NTZ1) from shore to segregate fishing and nearshore predator aggregations, and an open season for the krill fishery between 1 April to 31 October when most predator species disperse away from the maritime zone (GSGSSI, 2013; Handley et al., 2020; Ratcliffe et al., 2015). These limits were revised in May 2019 following the five-yearly MPA review process: the open season was shortened by two months (1 May to 30 September) and the NTZ was extended to 30 km (16.2 NM; hereafter NTZ2), the latter in response to the preliminary findings of this study.

Gentoo penguins *Pygoscelis papua* are distributed across the Falklands, subantarctic islands and Antarctic Peninsula, and the 25% of the world population that breeds at South Georgia (Lynch, 2013) has been proposed as a cryptic species *P. poncetii* (Tyler et al., 2020). Poor krill availability during winter at South Georgia can reduce gentoo penguin breeding numbers in the following breeding season by lowering survival and breeding propensity (Croxall & Rothery, 1995). If krill recruitment later in spring fails, gentoo penguins experience complete breeding failures, as observed in five out of the past 38 years (Waluda et al., 2017; BAS, unpubl. data).

As residents, gentoo penguins share the South Georgia shelf with the krill fishery during winter, but NTZ1 was believed to prevent their spatial overlap (Handley et al., 2020) based on limited tracking data from a single year that showed birds remain within 17 km of shore (Tanton et al., 2004). However, breeding macaroni penguins *Eudyptes chrysolophus* at South Georgia extend their foraging ranges when krill is scarce (Horswill et al., 2017). If gentoo penguins respond in a similar way during winter, then low krill availability might elevate the risk of them overlapping with the krill fishery, potentially exacerbating reductions in foraging success in years when food is scarce.

This study uses tracking data from a larger sample of gentoo penguins from two different study sites in 2018 to evaluate seasonal variation in their overlap with NTZ1 and the krill fishing grounds and explore how movement patterns emerge from changes in the birds' time budgets and trip durations. Simultaneously, DNA metabarcoding of scats was used to quantify diet. We compare the results with previous studies at South Georgia in winter and interpret the differences in terms of annual and seasonal changes in the krill prey field. We also quantify the improvement in the protection that NTZ2 would have afforded gentoo penguins, and how this would have changed the distribution of krill fishery hauls. We evaluate the potential for competition between the krill fishery and gentoo penguins and make recommendations for future management.

2 | METHODS

2.1 | Field methods

We tracked adult gentoo penguins using Kiwisat K2G 273C satellite tags (Lotek NZ) that transmit locations for 67 days. Tags' dimensions were 125 × 43 × 20 mm, 107 g or 1.67% of the average weight of the equipped birds (6.4 kg, *SD* = 0.49). Tags were deployed on randomly selected birds roosting at Maiviken (Lat −54.24, Lon −36.49, 11 June 2018, *N* = 8) and Ocean Harbour (−54.34, −36.27, 18 June 2018, *N* = 8; Figure 1), which are 27 km apart by the shortest sea journey. These sites were chosen for their proximity to the krill fishing grounds, which maximized the likelihood of detecting spatial overlap. The tags were attached to the lower back using waterproof tape and epoxy resin. Tags of a similar size had no effects on the foraging behaviour of gentoo penguins in a previous study (Ratcliffe et al., 2018).

We used prey DNA in scats to quantify diet to a high taxonomic resolution while avoiding the intrusion of sampling stomach contents (Deagle et al., 2007). Visits to Maiviken were made weekly between 3 April and 19 September 2018 (avalanche risk prevented one visit in June). During each of the 24 visits, 25 scats were collected, producing a total of 600 samples. Samples were scooped into a 2 ml plastic screw-top tube containing 80% ethanol with a clean spatula and frozen at −20°C (McInnes, Alderman, et al., 2017).

2.2 | Diet analysis using DNA metabarcoding

A diagrammatic overview and details of the diet analysis are presented in Appendix S1. DNA was extracted from roughly 30 mg of scat material using the Maxwell RSC Tissue DNA Kit (Promega) and processed on the Maxwell RSC 48 nucleic acid purification instrument (Promega). To obtain material for DNA extraction, 500 µl of scat/ethanol slurry was pipetted to a new 1.5 ml tube, centrifuged briefly and the supernatant poured off. The pellet was re-suspended and homogenized in 120 µl of STAR buffer (Roche Diagnostics); 100 µl was loaded into the cartridge on the extraction instrument, and DNA was eluted in 100 µl of Tris-EDTA buffer.

Three DNA markers providing different taxonomic information were amplified from the scat DNA and characterized using high-throughput DNA sequencing. Initially, all samples were analysed using a highly conserved metazoan primer set that amplifies a region of the nuclear 18S gene (18S_Metazoan; McInnes, Alderman, et al., 2017). Its taxonomic resolution is relatively poor (class level), but it recovers DNA from all animal lineages and

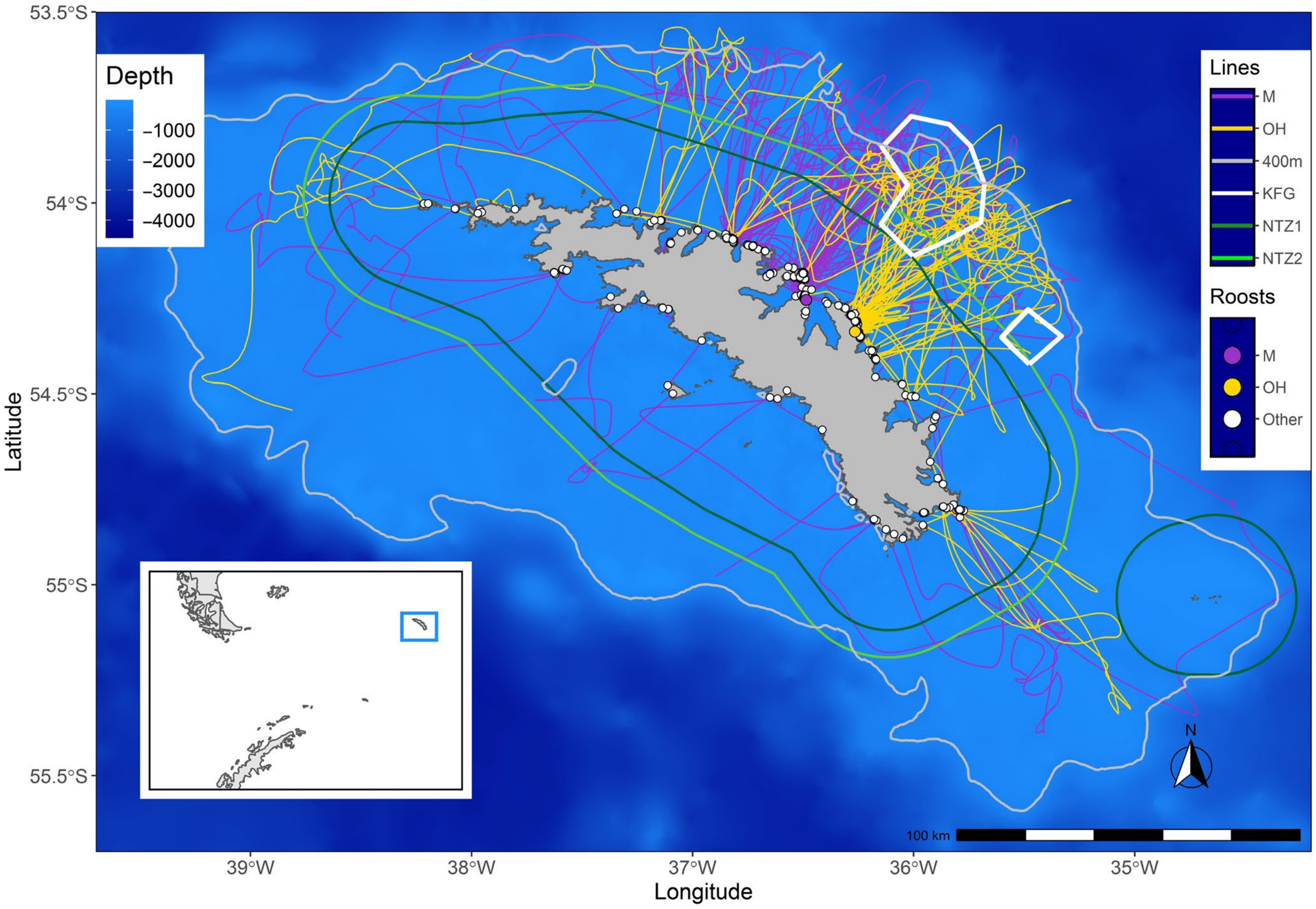

FIGURE 1 Gentoo penguin tracks around South Georgia (Projection EPSG 3,762), coloured according to deployment location (M: Maiviken, OH: Ocean Harbour). The legend abbreviations are NTZ1—12 NM NTZ boundary, NTZ2—30 km NTZ boundary (note the boundary around Clerke Rocks, the isolated dark green circle to the east, remained at 12 NM), KFG—krill fishing grounds (95% isopleth of locations where the krill fishery hauled nets), 400m—the 400 m isobath representing the shelf edge and Other—roost sites other than the deployment locations where penguins spent time ashore. The inset map shows the location of the main map within the Scotia Sea

provides a broad dietary overview. The samples containing sequences based on the 18S analysis (see Section 3) were characterized with two other group-specific primer pairs that amplify a region of the mtDNA 16S gene. These PCR primers amplify markers allowing species or genus level identification of fish (16S_degenerate; Deagle et al., 2007) and krill (16S_Krill; designed for this study). Sequencing of the PCR amplification products was performed in two runs on a MiSeq Genome Sequencer (Illumina), using the MISEQ V2 reagent kits (300 cycles).

Sequences were processed using a bioinformatics pipeline according to McInnes, Jarman, et al. (2017) with minor modifications (Appendix S1). For each marker, the sequences were de-multiplexed based on unique identifiers incorporated on both primers. Fastq files were processed using USEARCH v11.0.667 (Edgar, 2010). Paired-end sequences were merged using the fastq_mergepairs function, and primer sequences were trimmed. Reads from all samples were pooled and dereplicated using the fastx_uniques function. Sequencing errors and chimeras were filtered out using the unoise3 function to create a zOTU (zero-radius operational taxonomic unit) list of unique sequences (Edgar & Flyvbjerg, 2015). Each sequence in each sample was then matched to these zOTU sequences (usearch_global -id 0.90), providing a table with zOTU read numbers from each sample.

To assign taxonomy, each zOTU was searched against the NCBI nucleotide collection using BLASTN and taxonomic assignation performed with MEGAN, version 5.11.3 (Huson et al., 2007) and the Lowest Common Ancestor (LCA) assignment algorithm. LCA parameters were set at a top per cent of 5% minimum score of 250, 300 and 100 for the 18S_SSU, 16S_degenerate and 16S_Krill marker, respectively. In MEGAN, zOTUs derived from the 18S_SSU primer set were conservatively assigned to class, whereas zOTUs derived from the two other markers were initially classified at the lowest level possible (usually genus or species). Taxonomic assignments for the 16S_degenerate and 16S_Krill were then curated manually based on expert knowledge of prey species in the region and known reference database deficiencies (McInnes, Jarman, et al., 2017). For these markers, only prey in the targeted groups (Actinopterygii and Euphausiidae, respectively) were included in the final dataset. For the 18S marker, samples were only retained if they had >40 sequences matching the potential prey group; this threshold was increased to >1,000 sequences for samples to be included in the krill and fish datasets. Diet summaries were calculated as the mean of the percentage composition within individual scats rather than the proportions of sequences read across all scats, to ensure equal weighting across samples (Deagle et al., 2019). The sex of birds that produced each scat was determined by CHD-1 gene amplification in scat DNA (Faux et al., 2014; Appendix S2).

2.3 | Tracking data processing

Gentoo penguins often spend time roosting ashore during winter (Williams, 1991), which must be excluded from analyses that quantify the proportions of time at sea within management areas. The satellite tags used did not collect wet-dry data, so ARGOS fixes were plotted on a high-resolution map of the South Georgia coastline and their intervals were classed as occurring on land or at sea (Appendix S3).

ARGOS locations were projected as South Georgia Lambert Conformal Conic (EPSG 3762). Tracks were modelled using the R package CRAWL, which fits a continuous correlated random walk model that accounts for observation errors in the ARGOS fixes and uncertainty in the path of the animal in-between them (Johnson et al., 2008). The model was used to sample the most likely locations of each penguin at hourly intervals. The paths during short day trips were poorly characterized by the ARGOS data: the implications of this for the study are explained in Appendix S3.

2.4 | Tracking data analysis

The proportion of time ashore in relation to daylight and date was modelled using a generalized additive model (GAM). The R package oce was used to estimate the solar elevation for each position, and the following interval was classed as night if it was below −6°. The number of land and sea intervals was summed across individuals within each day and night–daylight combination to form a binomial response variable. Data were summarized across individuals as mixed models at the individual level experienced problems with convergence and over-dispersion in the model residuals due to birds switching between single- and multi-day trips.

The GAM was fitted with night–daylight as a factor and date as a smooth term using a logit link and binomial errors in the mgcv package. As the data were time series, a two-day autocorrelation term was fitted in all models. Model selection was conducted using the lowest value of AIC. Goodness-of-fit of the models was assessed by inspection of residual plots using the gam.check function within mgcv.

The proportions of time at sea spent within 10 and 17 km buffers from the coast (those used in Tanton et al., 2004), bathymetric features, management units and fishing grounds were calculated by removing time spent ashore and quantifying the number of points that fell inside and outside the polygons. The continental shelf around South Georgia was defined by a polygon of the 400 m isobath. The location of the krill fishing grounds was delimited using of the coordinates of all krill fishery net haul locations during the 2018 season, sourced from data held by GSGSSI. A 95% isopleth of the kernel density of haul locations was extracted using the package adehabitatHR with a smoothing parameter of 1.8 km, which was selected because it produced an isopleth that tightly enclosed the observed points and ensured the fishing grounds did not extend into NTZ1.

To investigate seasonal variation in the use of the two NTZs and fishing grounds, the number of points inside and outside of the polygons for each day was used as the binomial response variables in a GAM, again summed across individuals. The factor for

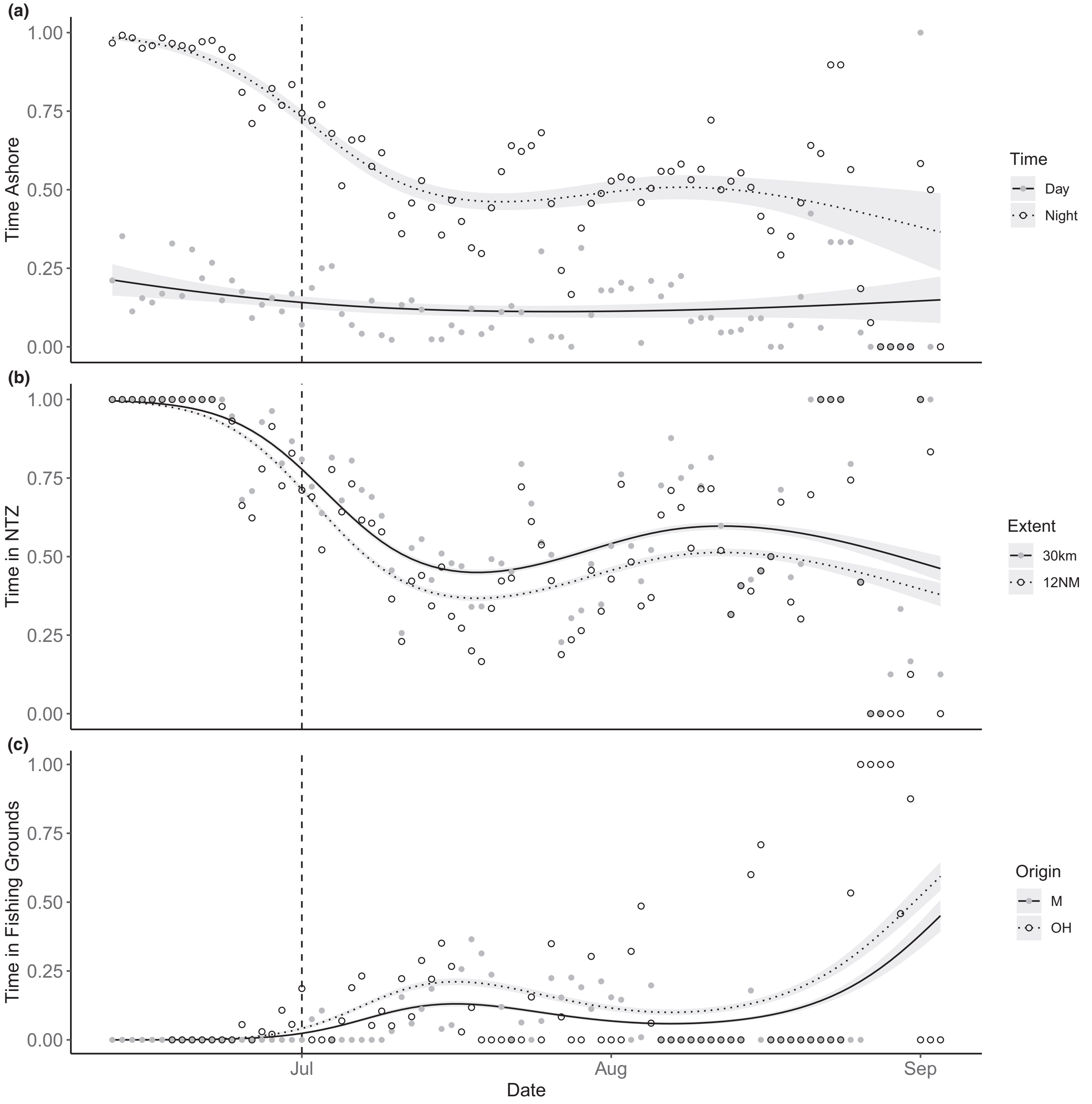

FIGURE 2 Seasonal change in the proportion of time spent by South Georgia gentoo penguins for (a) total time ashore during the day and night, (b) at-sea time spent within the 12 NM and 30 km NTZ and (c) at-sea time spent in the krill fishing grounds according to the deployment location (*M* = Maiviken, OH = Ocean Harbour). Lines represent smooths from the GAMs, ribbons the 95% confidence intervals of the smooths, and points the raw daily proportions combined across all individuals. The day that the krill fishery started is shown by the dashed vertical line

the NTZ analysis was whether the boundary was 12 NM or 30 km from shore, while that for the fishing ground analysis was the deployment site (Maiviken or Ocean Harbour). Modelling proceeded as described above for the proportion of time ashore. The percentage of net hauls falling within NTZ2 was also calculated to quantify the effect the extension would have had upon the distribution of catches.

3 | RESULTS

3.1 | Deployment summary

The satellite tags transmitted for 25 to 76 days and produced 18,164 locations (Table S1). The cause of six tags ceasing transmission much earlier than expected is unknown, but premature device failure or the tag sinking at sea (following detachment from, or death of, the bird) are the possible explanations. This will have underestimated the utilization distribution of the sample compared to a situation where all tags had transmitted for 67 days. The total distance individual penguins travelled ranged between 364 km and 1,812 km (Table S1), which correlated with the duration of their tags' operation (Pearson correlation: $r = 0.678$, $t = 3.54$, $df = 14$, $p = 0.003$). This meant is was not possible to make meaningful comparisons of movement distances and spatial use among individuals as differences were largely determined by tag life span.

3.2 | Time budgets and trip durations

The average proportion of time gentoo penguins spent ashore was 0.446 ($SE = 0.004$). A GAM with different intercepts and smooth terms of date for day and night periods received most support (AIC 906.7 vs. >1,463.3 for simpler models). The proportion of time ashore at night was 1.0 for the first two weeks of deployment, followed by a decline during the following 25 days to approximately 0.5, after which it fluctuated around this level (Figure 2a). The proportion of time ashore during the day was lower than that at night with little seasonal pattern (Figure 2a). Of the 545 trips to sea, 87% were completed in less than one day, 6% were between one and three days in duration, and 7% were longer (maximum 9.9 days). The proportion of the total time spent at sea was 0.385 for trip durations of less than one day, 0.274 for those between one and three days and 0.341 for longer trips.

3.3 | Penguin movements

Gentoo penguin distribution was confined to the continental shelf: the proportion of locations within the 400 m isobath was 0.934 and none of the tracks extended over the abyssal plain (Figure 1). Penguins utilized the area of shelf 25 km either side of the two deployment locations most intensively (Figure 1). Birds originating from Maiviken had a more westerly distribution than those from Ocean Harbour although there was some overlap (Figure 1). Some penguins travelled around the entire coast of South Georgia, typically making a series of multi-day trips that ended in widely spaced roost sites, such that they progressed along the coastline in a series of hops (Figure 1; Figure S1). Of the trips under 24 hr in duration, the proportion of at-sea locations within the 10 and 17 km coastal buffers were 0.974 and 0.998, respectively. Simulation models of movement patterns confirmed that gentoo penguins are rarely able to travel over 17 km from shore during day trips in winter (Appendix S3), so our results relating to the use of the NTZs are robust to the poor characterization of day trips by the satellite tags.

3.4 | Overlaps with management units and fishing grounds

The proportion of time that gentoo penguins spent within the NTZ1 and NTZ2 was 0.537 ($SE = 0.011$) and 0.617 ($SE = 0.009$), respectively, so the extension afforded a 14.9% increase in protection. A GAM with different intercepts for NTZ extent and parallel smooths for date received more support (AIC = 1,451.8) than the interactive model (1,473.3) and the one without NTZ extent (1621.0). During the first two weeks of the study (up to the 23 June), the birds spent all their time within the two NTZs but this declined over the next 25 days to fluctuate around the average thereafter (Figure 2b). The seasonal patterns of the decline in the use of the NTZs and time spent ashore at night are strikingly similar (Figure 2a vs. b), indicating that movements beyond the NTZ boundary occur during multi-day trips. Daily change in NTZ use will arise on days when tags fail but, as this will only have affected 1.9% of bird-days across the entire study, the majority of the variation can be attributed to bird movements.

Four krill fishing vessels operated within the MPA and caught 23,174 t between the first haul on 1 July and the last on 8 September 2018. The 95% isopleth of net hauls was localized to the NW of the Barff Peninsula (Figure 1). The proportion of time at sea that gentoo penguins spent within the krill fishing grounds was 0.096 ($SE = 0.003$), and differences among deployment sites were evident (0.073, $SE = 0.003$ for Maiviken birds and 0.129, $SE = 0.005$ for Ocean Harbour birds). A GAM with differences in intercepts for deployment site and parallel smooths of date received more support than the interactive model (AIC = 1,388.7 vs. 1,480.1, respectively) or that with no site effect (1,535.7). No birds visited the krill fishing grounds before 24 June, but the proportion of time spent there increased to the average value thereafter (Figure 2c). The marked increase in time spent in the fishing grounds after 26 August is caused by the movements of the single bird from Maiviken whose tag was still transmitting at that time. The extension of the no-take zone from 12 NM to 30 km from shore would have displaced 92 (4%) of the krill fishery's net hauls observed during the 2018 fishing season.

3.5 | Diet

Only 220 (36.7%) of the 600 scats yielded sufficient prey DNA sequences for quantifying diet. Recovery was particularly poor in the early season (single scats in weeks 1 and 2, none in week 3 and three in week 4), so these data were pooled for the weekly analysis. Gentoo penguin diets across the season, based on the 18_S Metazoan analysis, were dominated by teleost fish (59.5%) and Malacostraca crustaceans (39.1%), with small amounts of cephalopod (0.7%) and the remainder comprising assorted taxa (Table S2). The Malacostraca component comprised 78.4% Euphausiids, 7.3% Decapods, 5.7% Amphipods, 0.5% Isopods and a remainder that could not be assigned to a lower level.

Of the scats, 114 were produced by females, 91 by males and 15 could not be assigned to sex. The diets of the two sexes were similar; fish comprised 61.6% in females versus 56.5% in males, crustaceans 36.9% versus 43.0% and cephalopods 1.0% versus 0.3%, respectively. The weekly diet composition fluctuated markedly (Figure 3a) and crustaceans only dominated the diet in five of the 21 sampling occasions. There was substantial variability in the

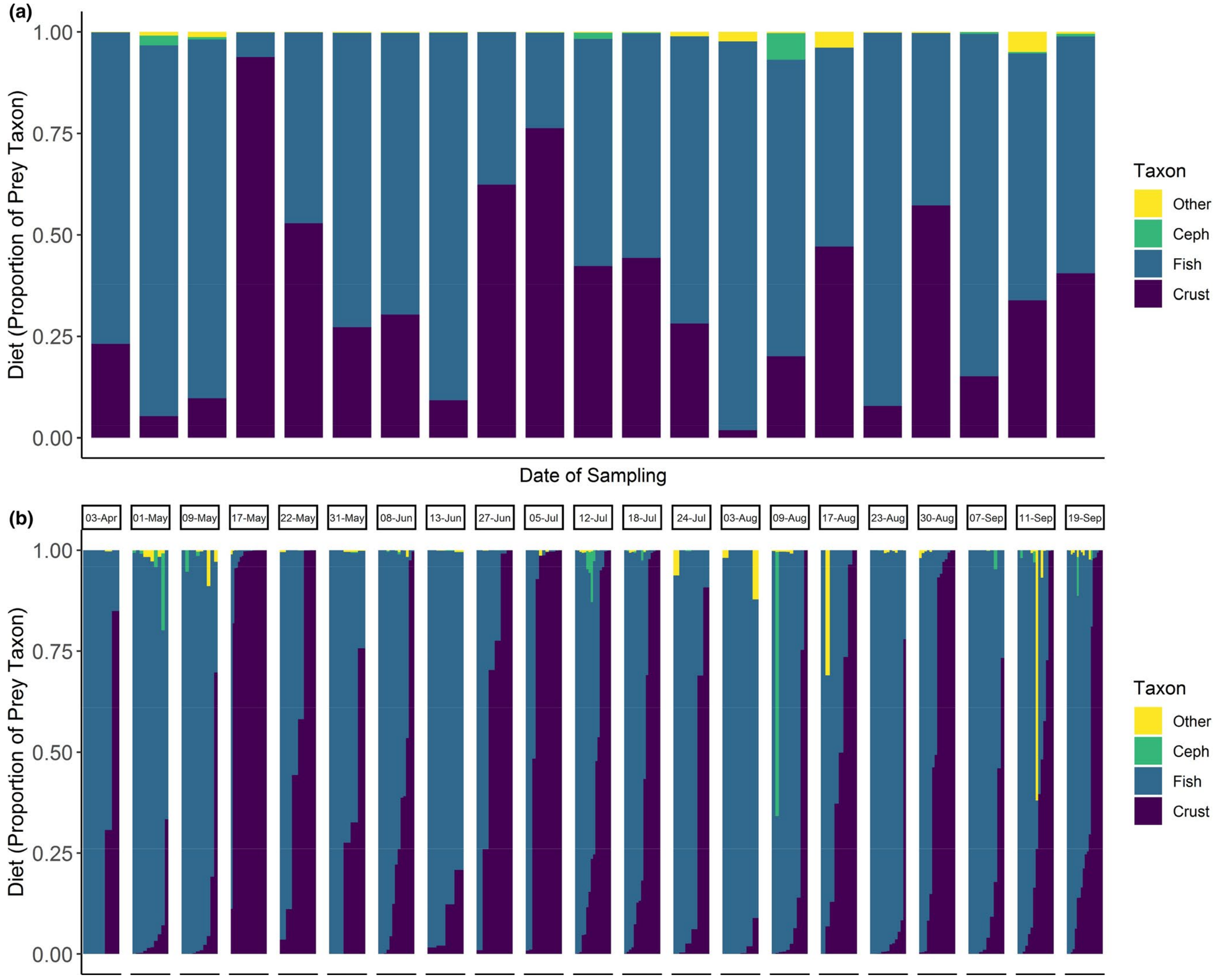

FIGURE 3 Weekly variation in the diet composition of gentoo penguins at Maiviken, South Georgia, based on proportions of 18S DNA marker sequences recovered from scats. Data are summarized by averages across sampling dates (a) and by individual within sampling dates (b). The weekly bar widths are standardized even though they are based on varying sample sizes of scats. Data from all four visits in April are pooled owing to small sample sizes and no sampling occurred in the third week of June

proportions of fish and crustacean among individual scats within weeks (Figure 3b).

The 16_S krill analysis showed that the Euphausiid component of the diet comprised 84.5% *E. superba*, 10.9% *Thysanoessa macrura*, 3.5% *E. vallentini* and ~0.5% of both *E. frigida* and *E. tricantha*. *E. superba* therefore accounted for 25.8% of the total gentoo penguin diet. The fish component of the diet based on the 16_S degenerate analysis comprised painted notie *Lepidonotothen larseni* (32.1%), mackerel icefish *Champsocephalus gunnari* (28.2%), 19 other bentho-demersal taxa (34.9%) and four mesopelagic taxa (4.8%; Table S3).

4 | DISCUSSION

The closure of the krill fishery during summer is an important management measure for reducing spatiotemporal overlap with migratory predator species that disperse away from the maritime zone during winter (GSGSSI, 2013; Handley et al., 2020; Ratcliffe et al., 2015). However, our study confirmed previous observations that gentoo penguins remain in the shelf waters that adjoin their breeding localities throughout the winter (Clausen & Putz, 2003; Hinke et al., 2017; Tanton et al., 2004). Therefore, the closed season does not prevent the krill fishery from overlapping temporally with gentoo penguins, and achieving segregation relies on the spatial protection afforded by the NTZ.

Gentoo penguins in our study initially showed fidelity to the area of shelf offshore of their deployment locations before dispersing along the coastline in a series of hops during multi-day trips, staging at roost sites along the way. Similar patterns of movement have been observed elsewhere in the species' range (Clausen & Putz, 2003; Hinke et al., 2017). The overlap of tracked penguins with the NTZs is likely to be broadly representative of the whole South Georgia population since the NTZs surround the entire archipelago, and multi-day trips extended over similar ranges from shore irrespective of their departure location. However, the krill fishing grounds are highly localized, and so the likelihood of gentoo penguins overlapping with these will depend on the proximity of the roost site from which they departed. Birds tracked from Ocean Harbour were almost twice as likely to overlap with the krill fishery as those at Maiviken, even though these roosts are only 27 km apart. Since we deliberately selected roost sites close to the fishing grounds to quantify overlap, our estimates will be biased high compared to that for the South Georgia gentoo penguin population as a whole.

In 2001, 96% and 100% of gentoo penguin locations were within 10 and 17 km of shore, respectively (Tanton et al., 2004), which led to the conclusion that NTZ1 would prevent overlaps of their foraging distribution with the krill fishery during winter (Handley et al., 2020). Williams et al. (1992) calculated a foraging range of 27 km (14 NM) during the 1989 winter based on trip durations and simplified assumptions about movement patterns. However, 98% of these were trips of less than a day's duration that were unlikely to have extended over 17 km from shore (Appendix S3). Our study found similar use of the 10 and 17 km coastal buffers as Tanton et al. (2004) and our day trips starting from Bird Island show a striking similarity to those from deployments there in 2001 (Appendix S3). This shows that the ranges of day trips in 1989, 2001 and 2018 have not changed, which is to be expected given the short day-length at South Georgia in winter and slow travel speeds of penguins.

Although short distance day trips are typical for gentoo penguins during winter (Hinke & Trivelpiece, 2011; Tanton et al., 2004; Williams, 1991; Williams et al., 1992), those at South Georgia in 2018 also performed multi-day trips. During these trips, birds made longer distance movements out to the shelf edge, which resulted in them spending almost half their at-sea time outside NTZ1 and 9.6% within the krill fishing grounds (see Section 3). The fact that birds roosting in the vicinity of Bird Island in 2018 performed such long trips offshore, while those in 1989 and 2001 did not, shows that the change from day trips to multi-day trips arise from the year, rather than the different deployment locations, sampled in these studies.

These differences in gentoo penguin movements and time budgets between years probably arise from contrasting prey fields. Winter krill stock assessments are not available, but patterns can be inferred from surveys over the shelf during the preceding and following summers. In January 2001, krill density averaged 36.7 g m^2 (CV = 27.5%) and length frequencies were multimodal, while in January 2002, density increased to 137.0 g m^2 (CV = 30.1) and length frequencies were dominated by small individuals (Fielding et al., 2014). This indicates that winter krill densities were moderate and evenly distributed across the shelf in January 2001, transitioning to higher abundance due to recruitment by January 2002. During January 2018, krill density was high at 250 g/m^2 but the CV was 98.6% due to krill being absent from the survey area outside of one enormous swarm, and the size frequencies were dominated by a single peak of large krill (BAS, unpubl. data). In January 2019, krill densities were 21.2 g m^2, distribution was more even (CV = 26.1%) and small krill predominated (BAS, unpubl. data). A fixed acoustic mooring on the shelf revealed krill swarms were scarce throughout the winter of 2018 (BAS, unpubl. data) and the small krill did not appear in Antarctic fur seal *Arctocephalus gazella* diets until November 2018 (J. Forcada, pers. comm.). This indicates a highly aggregated distribution of an old cohort of large krill in January 2018 that disappeared through the winter, transitioning to a moderate density and more even distribution following recruitment in Nov 2018.

Winter conditions in 2018 carried over to affect predator performance at Bird Island and Maiviken in the following spring. The number of nesting gentoo penguins at Maiviken in 2018 declined by 31% compared to the previous year, while laying dates at Bird Island were delayed by two weeks compared to the 30-year average (BAS, unpubl. data). Antarctic fur seal numbers at Bird Island were low, abortion rates were high, and pup birth weights were the lowest in 35 years of monitoring (J. Forcada, pers. comm.). These are all indicators of low krill availability over the South Georgia shelf during late winter and early spring (Croxall & Rothery, 1995; Ried et al., 2005). However, the recruitment of krill in November 2018 salvaged the breeding season for the income-breeding gentoo penguins, which experienced high productivity (1.59 chicks per pair) at Maiviken later that summer (BAS, unpubl. data).

These lines of evidence show that krill availability in 2001 was sufficient for gentoo penguins to meet their nutritional requirements during short-range day trips, but low abundance and patchy distribution of krill in 2018 forced them to perform multi-day trips that extended out to the shelf edge. Similarly, female macaroni penguins at South Georgia extended their foraging ranges and durations in a year of poor krill availability (Horswill et al., 2017) and African penguins *Spheniscus demersus* in South Africa performed longer duration trips as prey abundance within 40 m of the surface declined (McInnes et al., 2019).

Gentoo penguins performed longer foraging trips as the season progressed, which increased the probability of them remaining at sea overnight, leaving the NTZs and overlapping with the krill fishing grounds. Bertrand et al. (2012) found an increase in the foraging range of seabirds after the opening of the Peruvian anchovy *Engraulis ringens* fishery that depleted prey in waters close to the colony. The change of behaviour we observed in gentoo penguins at South Georgia runs contrary to such a pattern of avoidance: long trips started prior to the fishery opening while the overlap with the fishing grounds increased afterwards. The seasonal increase in foraging range may instead be associated with the seasonal vertical migration of krill below 200 m (Saunders et al., 2007; Taki et al., 2005), placing them at the limits of gentoo penguin dive depths (Ratcliffe et al., 2018; Williams et al., 1992). This is supported by the finding that resident female Antarctic fur seals at South Georgia dived deeper and switched to diurnal foraging during mid-winter (I. J. Staniland, pers. comm.).

The findings of our study changed policy and management within the SGSSI MPA by extending the NTZ to 30 km which would have produced a 14.9% increase in the protection afforded to gentoo penguins and prevented 4% of the net hauls observed in 2018.

The relative benefits of the change in policy for conservation are therefore greater than the relative loss to the fishery. The fishery previously occupied a greater area of the northern shelf (Grant et al., 2013) so the NTZ extension will prevent it returning to its former spatial extent. The NTZ would need to be extended to the 400 m depth contour (~55 km from shore) to fully encompass the gentoo penguin distribution observed in 2018. This may be unnecessary given the limited spatial overlap of gentoo penguins with the current fishing grounds and the fact they are more likely to remain within NTZ2 in years of higher krill availability. Closing the shelf to the krill fishery would have a major impact on its performance owing to low and unpredictable krill densities in off-shelf waters (Hill et al., 2009).

Gentoo penguins are generalist predators and their diets switch between krill and demersal fish depending on their relative availability (Waluda et al., 2017). Krill comprised only 26% of the diet in 2018, which suggests that krill was scarce compared to winters in the late 1980s (60%–98% of the diet; Williams, 1991), but more abundant than that during 2009 (13.5%; Xavier et al., 2017). Similarly, Antarctic fur seal diets at Bird Island contained no krill in the winter of 2009 and the second lowest amount in 12 years in 2018 (J. Forcada, pers. comm.). During 2018, there was evidence for substantial variation in diet through time and among individuals which probably reflects short-term variability in the local abundance of krill and fish (Kato et al., 1991), but little difference among sexes which contrasts with previous studies where males ate more fish and females more crustaceans (Williams, 1991; Xavier et al., 2017). The ability of gentoo penguins to switch from krill to fish gives the impression that they can avoid competition with the fishery through dietary segregation. However, the masses of fish meals are lower than those of krill, suggesting that the availability of fish during winter may be inadequate to compensate for the loss of krill from the diet (Kato et al., 1991; Williams, 1991). This reduction in foraging success, combined with an increase in energy consumption associated with birds spending less time roosting ashore (Bevan et al., 2002), will result in gentoo penguins finding it more difficult to meet their nutritional requirements in winters when krill availability is low.

5 | CONCLUSIONS

NTZ1 was designed to segregate the foraging areas of gentoo penguins from overlap with the krill fishery using the best data available at the time. Our findings show that, during years and times of the season when krill availability is low, gentoo penguins extend their foraging ranges beyond NTZ1 and across the entire South Georgia shelf. This shortfall in protection may increase the risk of competition during periods when birds are already experiencing challenges in meeting their nutritional requirements, which elevates the risk of competition from the fishery within the areas of overlap. The results emphasize the importance of designing NTZs using predator tracking data collected across a range of prey abundances and distributions, particularly in highly variable environments such as those found at South Georgia and in upwelling systems, where several prominent examples of predator–fishery interactions occur (Hill et al., 2020).

While the overlap of gentoo penguins with the krill fishing grounds was low during 2018, the current regulations allow for significant increases in both the spatial extent and catches by the fishery that have the potential to heighten the risk of overlap in the future. NTZ2 will segregate gentoo penguin foraging from the fishery, irrespective of expansion in the area fished, during years when krill availability is sufficient to allow birds to meet their nutritional requirements during day trips. However, overlap will increase with the spatial extent of the fishing grounds when krill availability is low and birds make longer trips that take them beyond the NTZ2 boundary. Preventing such overlap using static boundaries would require closure of the whole shelf: this would render the krill fishery uneconomical (see above), even though the patterns of krill abundance and distribution that cause gentoo penguins to leave NTZ2 may only occur during one in ten years (Fielding et al., 2014; BAS unpubl. data).

Dynamic Ocean Management may offer an alternative approach: closed area boundaries are adjusted through time in response to near real-time information on environmental and biological variability, which achieves equivalent protection to static boundaries within smaller areas (Dunn et al., 2016; Hazen et al., 2018; Lewison et al., 2015). One variant is the flexible closure management framework proposed by McInnes et al. (2019) for African penguin and anchovy–sardine (*Engraulis capensis*–*Sardinops sagax*) fisheries in South Africa. Its implementation at South Georgia would require real-time collection of gentoo penguin satellite tracking data and rapid, automated krill density estimates from acoustic arrays installed on fishing or patrol vessels (Azira et al., 2019). Repetition of this across years would allow quantification of the relationship between penguin movements and krill prey fields, and the recognition of reference points at which NTZ2 would be extended (Hill et al., 2020; McInnes et al., 2019). Once the krill densities that lead to gentoo penguins leaving the NTZ are sufficiently well quantified, management can proceed using krill density alone, saving the expense of tracking penguins *in perpetuity*.

Since the interactions between penguin behaviour and the fishery occur in winter, they provide a leading indicator that could inform adjustments to fishing prior to it impacting upon gentoo penguin breeding performance in the following spring. This would not only reduce the risk of the krill fishery causing reductions in breeding success but also avert it being implicated in naturally-induced breeding failures, which are a feature of gentoo penguin demography even in locations where no fishery competition occurs (Crawford et al., 2003). The implementation of Dynamic Ocean Management presents technical and political challenges, but there are a growing number of examples that show it can be effective in mitigating non-target bycatch by fisheries (Lewison et al., 2015), instilling confidence that it can be extended to manage fishery competition. Successful implementation of Flexible Closure Management would be an important step towards the achievement of wider ecosystem based feedback management of the krill fishery within this sustainable-use MPA, which is a long-standing aspiration of CCAMLR and the SGSSI government (Hill et al., 2020).

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AUTHORS' CONTRIBUTIONS

NR designed the study, analysed the data and drafted the paper. BD and AP analysed the scat samples. KL collected the data. All authors contributed data analysis, interpretation and writing the manuscript and approved the final version for publication.

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DATA AVAILABILITY STATEMENT

Tracking data are accessible from the NERC Polar Data Centre (https://doi.org/10.5285/01E8E674-0403-4CCA-8271-415B63130C3D) and diet data from the Australian Antarctic Division (https://doi.org/10.26179/5eafa8a6bcf22).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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