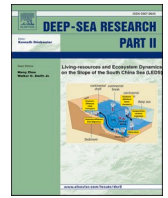




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Humpback whale (*Megaptera novaeangliae*) distribution and movements in the vicinity of South Georgia and the South Sandwich Islands Marine Protected Area

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ABSTRACT

Humpback whales (*Megaptera novaeangliae*) are showing strong recovery from commercial whaling in the western South Atlantic. In this region, humpback whales migrate annually from their winter breeding grounds off the coast of Brazil to their summer feeding grounds near to the Polar Front, an area that includes the waters of South Georgia and the South Sandwich Islands (SGSSI). This latter region includes a Marine Protected Area (MPA), which has been developed to ensure sustainable management of fisheries, and protection of foraging predators. To date, management measures within the MPA have primarily been concerned with foraging predators that rely upon Antarctic krill, including for a number of previously over-exploited species. With humpback whales increasing in the western South Atlantic, understanding their spatiotemporal distribution within the MPA is important as it will help inform management particularly in respect of interactions between humpback whales and the regional fishery for Antarctic krill. Here we develop habitat models from the distribution and movement patterns of 16 individuals at their high-latitude feeding grounds, south of 50°S. We show that whale habitat use varies throughout the foraging period. Upon reaching their feeding ground, whales use the area to the east of the South Sandwich Islands, moving westward into the centre of the Scotia Arc and towards South Georgia during the high summer, and then expanding back towards the east in the winter. Based on these findings, we discuss the implications for the future, including necessary research required for underpinning management.

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1. Introduction

Industrialised commercial exploitation of whales saw populations of various species collapse globally, almost to the point of extinction (Clapham et al., 1999; Thomas et al., 2016). During the 20th Century, in the Southern Hemisphere alone, over two million whales were killed (Rocha et al., 2015). In the South Atlantic, the focal hub of this exploitation was the Sub-Antarctic Island of South Georgia, a summertime feeding area for many migratory whale species. Whaling from shore at South Georgia began in 1904 when the first station was founded at Grytviken. In its early days, whaling at South Georgia was coastal, which was, in part, driven by an abundance of whales in coastal embayments, particularly humpback whales (*Megaptera novaeangliae*), and the fact catches had to be towed to shore for processing (Hart, 2021). However, technological advancements in the mid-1920s and the advent of at-sea factory ships (Clapham and Baker, 2009) meant that whaling at South Georgia could expand into the pelagic realm (Trathan and Reid, 2009). Between 1904 and 1965 over 176,000 animals were caught within a day's sailing of South Georgia (Allison, 2016), and after such intense hunting whales became rare in these waters for the remainder of the 20th Century. Here we focus on humpback whales, but a similar story also played out for other rorqual whales of commercial interest landed at South Georgia (Calderan et al., 2021; Clapham et al., 1999; Jackson et al., 2020; Kennedy et al., 2020; Thomas et al., 2016).

In the western South Atlantic (Fig. 1), humpback whales migrate annually from their breeding grounds in coastal Brazilian waters to their feeding grounds, near to the Polar Front, 10°–50°W (Horton et al., 2011, 2020; Zerbini et al., 2006, 2011). The feeding ground encompasses an area which includes South Georgia and the South Sandwich Islands (SGSSI). Humpback whales typically remain feeding in the SGSSI region until autumn (Engel and Martin, 2009; Stevick et al., 2005; Zerbini et al., 2006, 2011).

Since the closure of shore based whaling activity at South Georgia in

the mid-1960s, and the cessation of all commercial whaling in the mid-1980s, this western South Atlantic population of humpback whales is believed to be nearly recovered (Zerbini et al., 2019). In the years after whaling ceased through to the turn of the new century (1979–2000), humpback whales were sighted infrequently around South Georgia (Hedley et al., 2001; Moore et al., 1999; Reilly et al., 2004). It was not until surveys carried out in Brazil between 2006 and 2015 that the population was found to be steadily increasing in the region (Ward et al., 2011; Wedekin et al., 2017), and more recently still, new models suggest that the population in the western South Atlantic is close to 93% of pre-exploitation levels (Zerbini et al., 2019).

Management of whale populations globally, including within the Southern Ocean, falls under the remit of the IWC. This intergovernmental organisation oversees efforts to measure population abundance and connectivity; assess recovery rates post whaling; and develop conservation management plans for whale populations (Punt and Donovan, 2007). However, in addition to the IWC, environmental management of the Southern Oceans also falls under the jurisdiction of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). CCAMLR has the primary remit of safeguarding Antarctica's marine living resources, including harvested species such as Antarctic krill (*Euphausia superba*) which are a key dietary item for many baleen whale species (Reilly et al., 2004). However, under the CAMLR Convention, management of whales is not explicitly considered, other than generically, as part of generic marine living resources. As such, CCAMLR's management efforts have not included whales as direct beneficiaries, with such benefits only arising indirectly from the holistic nature of CCAMLR's Conservation Measures that safeguard krill stocks and other krill-dependent predator species. Until recently, CCAMLR monitoring has only focused on land-breeding krill predators, as these are constrained by their foraging range and are most vulnerable to change. These species are also more readily accessible to researchers (CCAMLR, 2013).

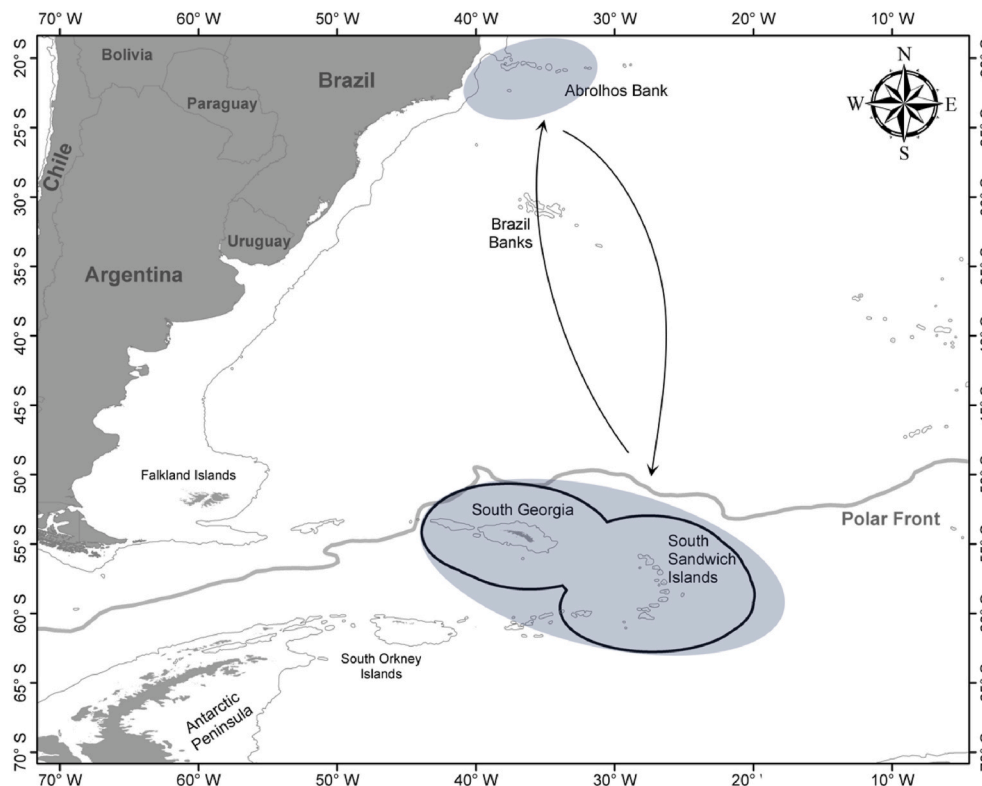


Fig. 1. Migratory links (arrows) between humpback whale winter breeding grounds near to the Abrolhos Bank in Brazil (northerly shaded area) and the summer feeding grounds south of the Polar Front near South Georgia and the South Sandwich Islands (southerly shaded area). Thin grey line indicates the 1,000 m bathymetric contour, thick labelled grey line indicates the position of the Polar Front, and the SGSSI MPA is indicated by the thick black line.

The United Kingdom’s Overseas Territory of SGSSI falls within the CAMLR Convention Area, and, as such, the Government of SGSSI (GSGSSI) implements all internationally agreed CCAMLR Conservation Measures within the archipelago’s Maritime Zone. However, GSGSSI has also established additional conservation and protective measures to enhance those mandated by CCAMLR. A key measure around SGSSI was the establishment of a Marine Protected Area (MPA) in 2012, which extends from the coastline out to the outer extent of the Maritime Zone of the islands.

All of the management measures established under the SGSSI MPA were set-up with conservation in mind (GSGSSI, 2019; Trathan et al., 2014) and regulate human activities within the marine system (Fig. 2). These measures aim to protect habitats and species, including: (i) the exclusion of bottom trawling throughout the entire MPA; (ii) the implementation of no-take zones, which prohibit commercial fishing vessels from operating in ecologically sensitive areas, including close to land; (iii) the prohibition of demersal longline fishing in waters shallower than 700 m and in waters deeper than 2250 m; (iv) the prohibition of all fishing in the pelagic closed areas around the South Sandwich Islands; (v) the closure of several regions to all fishery activity with the aim of protecting benthic communities; and (vi) the annual closure of the krill fishery from October to April, which prevents resource competition during the breeding season of many krill-dependent land-breeding species, and the summer feeding season for many species of krill-eating migratory baleen whales (GSGSSI, 2019). As whales remain a research priority for the GSGSSI as a recovering over-exploited species (GSGSSI, 2021), understanding their distribution in relation to the SGSSI MPA, particularly for the most abundant species, humpback whales (Baines et al., 2021), will provide useful insights and better inform the management of this MPA. Given the recovery of whales, particularly humpback whales (Zerbini et al., 2019), in the western South Atlantic; the contribution of whales to the Antarctic ecosystem (Ratnarajah et al., 2016; Reilly et al., 2004); and the overlap between the IWC’s remit to conserve whale populations in the Southern Ocean and CCAMLR’s focus towards ecosystem-based management of krill and krill-dependent predators, it now is timely to assess ecosystems more holistically in

order to understand how whales use the Southern Ocean.

The SGSSI MPA is subject to reviews every five years, during which the existing provisions of the MPA are assessed. Further, if agreed, new management measures are also implemented, based on any newly acquired objective scientific evidence. For example, during the next review in 2023, identified Important Marine Mammal Area (IUCN Marine Mammal Protected Areas Taskforce, 2020) should be considered, as should information from the use of modern approaches to assessing whale habitat use patterns, such as satellite telemetry, which, until recently, have not been used in SGSSI waters (Kennedy et al., 2020).

Models of animal habitat use provide an important means of evaluating areas of habitat importance for management (Gregr et al., 2013). Models built from satellite telemetry-based tracking of individual animals provide high resolution, time-stamped location information, which can provide information both during periods accessible for fieldwork and during less accessible periods (Curtice et al., 2015; Friedlaender et al., 2009, 2011; Raymond et al., 2015; Zerbini et al., 2015). Such insights are valuable for remote locations, such as SGSSI, where sighting surveys have typically been conducted during the austral summer (Baines et al., 2021; Branch, 2011; Reilly et al., 2004).

Given their strong recovery relative to pre-exploitation levels (Zerbini et al., 2019), and current high estimated abundance of southwest Atlantic humpback whales (Baines et al., 2021; Bortolotto et al., 2017), it is now timely to examine their habitat use in relation to high latitude ecosystem management. This enables assessment of the efficacy of relevant management measures, and provides information for future improvements. Broad basin-scale studies of humpback whale habitat use in the wider southwest Atlantic (Bombosch et al., 2014; El-Gabbas et al., 2021; Hindell et al., 2020; Reisinger et al., 2021), combined with identification of their south-bound migration routes (Horton et al., 2020; Zerbini et al., 2006, 2011), have led us to expect that humpback whales are currently making use of large areas of the SGSSI MPA. Furthermore, return migration from the feeding to the breeding grounds is not synchronous; whales leave high latitudes over several months, and humpback sex ratios on the winter breeding grounds are biased towards males (Barlow et al., 2011). This raises the possibility that some females

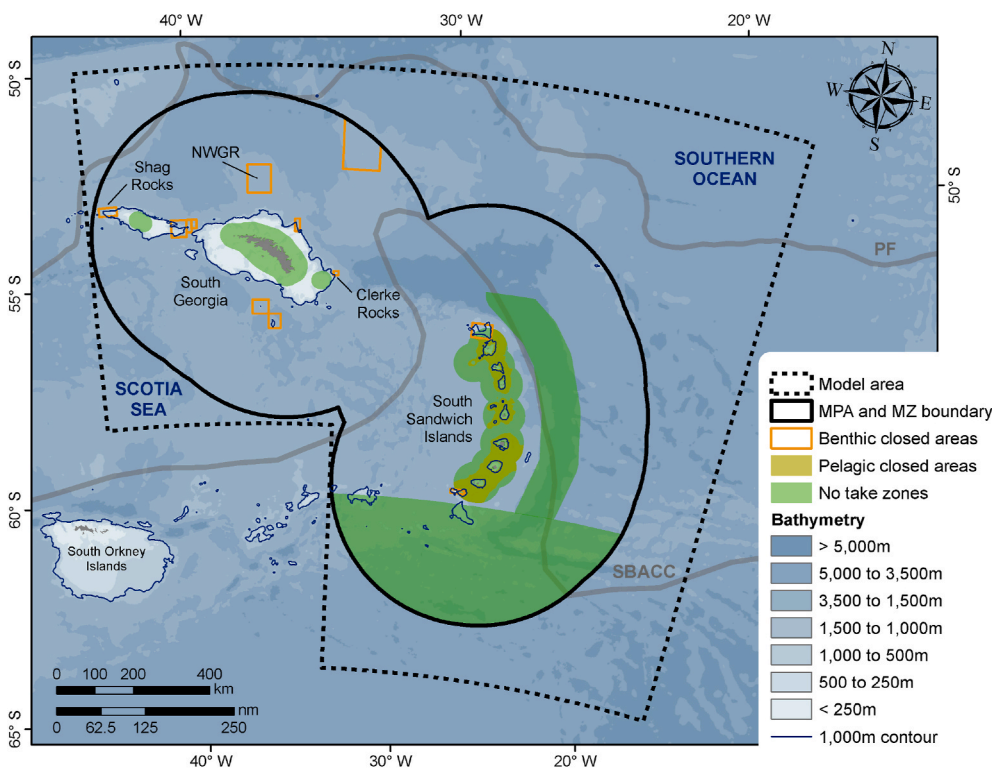


Fig. 2. The South Georgia and South Sandwich Island region depicting the extent of the South Georgia and South Sandwich Islands Marine Protected Area (MPA) and Maritime Zone (MZ) in black, along with the management measures implemented by GSGSSI (2019) – benthic (orange boxes) and pelagic (kaki green shading) closed areas and no take zones (green shading). The hashed black box defines the extent of the models applied here, and the grey lines the two primary frontal features in the region, which are, from north to south, the Polar Front (PF) and the Southern Boundary of the Antarctic Circumpolar Current (SBACC). Northwest Georgia Rise indicated (NWGR).

remain in the higher latitudes in years when they are not breeding, and that, at least for some members of the population, a larger component of their annual energetic requirements comes from higher latitudes (Baines et al., 2021); this occurs during a period where fishery resource competition may exist. In order to determine whether existing management measures protect Antarctic krill in places where humpback whales feed, finer resolution studies are required. Here, we use predictive habitat models based on telemetry data to describe the likely habitat use patterns of humpback whales across their feeding grounds. We investigate the level of overlap with the current provisions of the SGSSI MPA, and make management recommendations in light of these findings.

2. Methods

2.1. Collection of satellite telemetry data

Between 2003/2004 and 2019/2020, 138 location-only and archival radio-frequency platform transmitting terminal (PTT) tags were deployed on humpback whales wintering off the coast of Brazil; details of programming, deployment methods for these tags, and ethical approvals are found in Horton et al. (2020) and Zerbinini et al. (2006, 2011). Here we analyse these already published Brazilian data, supplemented by new data from two additional location only PTT tags, which were deployed on the SGSSI feeding grounds on the 19th and January 22, 2019. Tags were obtained from Wildlife Computers (Redmond, WA, United States) and were sterilised with ethylene oxide prior to deployment. Deployment of these satellite tags was conducted in accordance with the approvals and conditions from relevant Animal Ethics Committees (BAS Animal Welfare and Ethical Review Board application #1040) and of the GSGSSI Regulated Activity Permit 2018/035.

At both tagging sites, PTT tags were transdermally implanted into the posterior flank of each whale, near to the base of the dorsal fin using either a carbon-fiber pole (Brazil), or a modified pneumatic line-thrower (ARTS; Air Rocket Transmitter System) see Heide-Jørgensen et al. (2001) for details (both Brazil and South Georgia). All tags were deployed from rigid hulled inflatable boats. Tags from two individuals (one each in 2004 and 2009) were duty cycled for transmission every other day to maximise tag battery life.

2.2. Telemetry data processing

To examine activity on the feeding grounds we considered only data south of 50°S, a latitude approximately indicative of the position of the Antarctic Polar Front (Orsi et al., 1995; Trathan et al., 2000) and the general availability of krill (Siegel et al., 2013). A subsample of the deployed 138 PTT tags ($n = 20$), which corresponded to those tags that provided location information south of 50°S, were used in the current study. PTT uplink locations were estimated by the Argos satellite system and a measure of locational accuracy, defined by a location class (3, 2, 1, 0, A, B and Z in order of decreasing accuracy), was assigned to each estimated location (Argos, 2016). Z locations represent an invalid uplink (Argos, 2016), and were removed. To remove other implausible locational fixes, the remaining raw Argos locational data were processed with the R package 'argosfilter' v.0.63 (Freitas et al., 2008). To identify any implausible locations on the feeding grounds south of 50°S, we used a maximum travel speed of 5.56 m s⁻¹ to filter locations that would have required unrealistic swim speeds, and thus more likely represent location fix errors. This estimate was based on previously published humpback whale swim speeds (Derville et al., 2020; Gales et al., 2009; Garrigue et al., 2010, 2015; Riekkola et al., 2019; Ropert-Coudert et al., 2020; Weinstein and Friedlaender, 2017).

To limit erroneous linear interpolations between locations, gaps in uplink frequency greater than 72 h (three days) were separated and assigned unique identifiers; these sub-tracks were then modelled separately (after Pirota et al., 2018). Data were processed in the R package

'crawl' v.2.2.1 (Johnson and London, 2018; Johnson et al., 2008), where continuous-time correlated random walk models (CTCRW) were used to estimate and regularise the time interval between observed satellite uplinks. The fitting of these models allowed the frequency of estimated locations along the tracks to be regularised into a defined time interval, standardising sampling between tags whilst maintaining the inherent properties of each individual track. Drift models, which allow for long-term directional trends in the tracking data, were fitted, and locations were estimated at 6 h intervals. CTCRW models could not be fitted for one whale due to high proportions of low precision location class uplinks. This individual was removed from subsequent analyses.

2.3. Environmental covariates and model selection

To examine the distribution of humpback whales in the SGSSI region we used habitat models developed within a commonly used Generalised Additive Model (GAM) framework (e.g. Bamford et al., 2021; Raymond et al., 2015; Warwick-Evans et al., 2018). These models enable non-linear responses to environmental covariates to be accounted for, and, based on the covariate responses, facilitate the prediction of the likelihood of a whale being present in a given area. Models of this type can take into account individuality or temporality expressed within the data (Wood, 2006). However, accounting for individual variation by using mixed models can lead to issues with model convergence, and is particularly problematic for smaller datasets (Raymond et al., 2015). Therefore, we applied standard GAMs.

Our models allowed for the modelling of both the presence and the absence of a whale. To do this, for each observed presence of a whale, three-independent background locations were randomly generated using the 'random point' tool in the spatial analyst toolbox of ArcMap v10.6. These random locations were confined to occur within the modelled area, which was defined linearly at 50°S on the northern extent, which is approximately the position of the Polar Front (Orsi et al., 1995; Trathan et al., 2000), by available telemetry data to the east and south (17°W and 64°S, respectively); and to include the extent of the SGSSI Maritime Zone to the west (Fig. 2). A ratio of 3:1 random to presence locations was chosen as to balance between data provision to the model, covariate resolution, the impact of pseudo-replication in the model, and processing speed. Environmental covariate data were then extracted for all locations, random and observed. Here we opted to use both static and dynamic variables to parameterise the habitat available to humpback whales (Table 1). Candidate environmental variables were chosen that are commonly used to represent oceanic habitats (Hindell et al., 2020; Raymond et al., 2015; Reisinger et al., 2021). Our covariates included silica concentration, to describe latitudinal patterns in the western South Atlantic (Post et al., 2014) and iron concentration due to its positive relationship with primary productivity (Holm-Hansen et al., 2004; Korb et al., 2005). Where possible contemporaneous data were used to capture finer resolution environmental features (e.g. sea level anomaly and eddy kinetic velocity) that would be lost if all covariates were applied as climatologies. However, in some instances, data availability dictated that we used climatologies of covariates (e.g. sea surface temperature, chlorophyll *a* concentration, etc.) where these were also informative. When climatologies were calculated, or when spatial or temporal averaging calculations were performed on the underlying environmental data (e.g. slope from bathymetry data), standard deviations were also input as covariates during model selection.

Both satellite derived chlorophyll and satellite derived sea surface temperature data are impacted by cloud cover, which results in patchy data availability. We therefore tested bi-linear (a weighted average produced from the values of the nearest four raster cells), and 1.5 times the raster resolution as extraction buffers for these covariates. However, all resulted in unacceptable data gaps. To reduce the effect of gaps in these data layers, for both chlorophyll and sea surface temperature data, we created monthly climatologies between 2004 and 2020, and extracted such monthly data. The R package 'rerddapXtracto' v.1.0

Table 1

Environmental variables used during model selection and their standard deviations (sd) where applicable.

Variable	Resolution	Processing	Source
Depth (m)	Fixed at	None	(GEBCO Bathymetric
Bathymetric	0.001° ×	Calculated	Compilation Group, 2020)
slope (°) + sd	0.001° (15-arc second)	from depth layer in ArcGIS	
Sea Level Anomaly (m) + sd	Daily at 0.25° × 0.25°	None	AVISO + altimetry data - https://www.copernicus.eu/en
Eddy Kinetic Velocity (m s ⁻¹) + sd		None	
Chlorophyll-a concentration (mg m ⁻²) + sd	Monthly composites at 0.17° × 0.17°	Log transformed - monthly climatologies	MODIS imagery (Behrenfeld and Falkowski, 1997) from http://sites.oregonstate.edu/ocean.productivity/index.php
Sea surface temperature (°C) + sd	Monthly at 0.17° × 0.17°	Level 3 monthly climatologies	MODIS-aqua https://oceancolor.gsfc.nasa.gov/v13/
Mixed layer depth (m) + sd	Monthly at 0.083° × 0.083°	2004–2018 monthly climatologies	Global Reanalysis PHY 001 030: https://www.copernicus.eu/en
Salinity (PSU, 1e ⁻³) + sd			
Sea surface height (m) + sd			
Silica concentration (mmol m ⁻³)	Monthly at 0.25° × 0.25°	None	Global ocean biogeography hindcast for January through October 2004 to 2019 and the Global Ocean biogeography analysis and forecast for November 2019 to 2020: https://www.copernicus.eu/en
Iron concentration (mmol m ⁻³)			
Wind stress curl (MPa m ⁻¹) × 1	Monthly at 1 × 1	None	R package v. 1.0 'rerddapXtracto' (Mendelssohn, 2020) NOAA SWFSC ERDDAP dataset ID: erdlasFnWPr_LonPM180
Frontal position estimates from Sea surface temperature and chlorophyll a	Monthly at 0.17° × 0.17°	Based on the above log transformed Chlorophyll a data.	Based on Sea surface temperature and chlorophyll a data calculated using R package 'grec' v.1.4.1 (Lau-Medrano, 2020)
Distance to sea ice edge	Monthly (m)	None	Euclidean distance calculated in ArcGIS v10.6 to the average monthly position of the Antarctic sea ice: https://nsidc.org/data/seaice_index/archives

(Mendelssohn, 2020) was used to extract wind stress curl data. This package accesses the National Oceanic and Atmospheric Administration (NOAA) Southwest Fisheries Science Centre (SWFSC) ERDDAP data server and extracts values (ID: erdlasFnWPr_LonPM180). Estimates of frontal positions were derived from chlorophyll and sea surface temperature data using the R package 'grec' v.1.4.1 (Lau-Medrano, 2020). This package applies a Contextual Median Filter algorithm to discern fine-scale gradients in these covariates, which are indicative of the presence of a frontal feature (Belkin and O'Reilly, 2009), and were extracted at monthly intervals. Prior to model selection, whale locations that were affected by covariate data gaps were removed from the analysis.

Small intra-year samples dictated the pooling of data across all years (2004–2020). However, we expected that, due to the dynamic nature of the oceanic currents in the southwest Atlantic (Young et al., 2014), and

the importance of currents in transporting krill from the Antarctic Peninsula into the South Georgia system (Hofmann and Murphy, 2004; Murphy et al., 1998), whale use of the SGSSI MPA would likely vary through the season. In response to this, we modelled three distinct periods within the year, which divided the austral season into three approximately equal periods. The first of these was the early summer period (October to December), which corresponds to the arrival period for the whales on the feeding grounds; this period contains data from nine whales. The second period, high summer (January to March), represents a probable period of maximum habitat usage; this period contains data from 12 whales. The final period represents autumn and early-winter (April to July) habitat usage and is constrained temporally by data availability in the winter months, which is either a consequence of whale migration out of the modelled area, or tag longevity (likely the dislodgment and loss of the implantable tags); this period contains data from three whales. In some instances, data from an individual whale spanned one or more modelled periods; such data were therefore subset for use in each model period.

Due to limited availability of humpback whale tracking data in the Austral autumn/winter, we were unable to match the model periods to that of the licensed krill fishery. Defining a contemporaneous winter model period for the krill fishery (i.e. from May onwards) would have resulted in too little data to accurately parameterise humpback whale habitat use. Therefore, we defined the winter model period as beginning in April, which corresponds to the decrease in ambient air temperatures and the onset of typically winter weather (Whitehouse et al., 2008). This model period, at least in part, offers the ability to assess the distribution of humpback whales during a proportion of the krill fishing season. This provides information that could inform management measures, and is timely given that a portion of the humpback whale population might be remaining in the high latitudes through winter (Clark and Clapham, 2004; Moore et al., 1999).

We examined collinearity between the environmental variables using Variance Inflation Factors (VIFs) in the R package 'usdm' 1.1.18 (Naimi et al., 2014). Using a threshold of 0.7 (Dormann et al., 2013) pairs of variables were examined and the higher of the two scoring variables were removed. Semi-variograms produced in the R package 'gstat' v.2.0.6 (Pebesma, 2004) showed that spatial autocorrelation was present to some extent in the data (between ~5 and 8 km). Within 'mgcv', structures can be added to GAMs to help account for spatio-temporal autocorrelation (Dormann et al., 2007), which is intrinsically associated with tracking data (Reisinger et al., 2018). However, in this instance, we opted not to, as despite aiding with explanatory power, these structures would hinder the ability to extrapolate from the model (Dormann et al., 2007), likely biasing predictions to areas with tracking data, and hindering the primary objective of this study.

To predict the likelihood of occurrence, here also referred to as habitat, of a whale we applied GAMs with a binomial error structure in the R package 'mgcv' 1.8.31 (Wood, 2006). Smooths of each covariate were taken and we fitted cubic regression splines with shrinkage and with the number of knots set to four to minimise overfitting of the data (Wood, 2006). To select candidate variables for the final model a forward stepwise approach applying *K*-fold cross validation was used to evaluate model performance. Here *K* equalled the number of months in each modelled period. Variable performance was assessed by reviewing area under the curve (AUC), sensitivity and specificity (correct predictions of presence and absence locations, respectively) produced in the R package 'pROC' v.1.16.2 (Robin et al., 2011). Values range from 0.5 to 1.0, with scores closer to the lower bound implying performance no better than random, and those with a score closer to 1 implying a model with outstanding performance (Mandrekar, 2010). Additionally, our applied cross-validation approach provided a conservative means of selecting modelled covariates, and thus autocorrelation is unlikely to affect the selection of the final model (Aarts et al., 2008).

Models were projected across the study area at a resolution of 0.1° × 0.1° (approx. 11 km × 6.5 km at this latitude) and standardised for ease

of comparison between modelled periods. Using visualisations of these predictive models the spatial overlap between the current SGSSI MPA management measures and predicted humpback whale habitats were estimated.

2.4. Spatial overlaps

Overlaps between humpback whale spatial predictions and the management measures implemented under the SGSSI MPA were calculated at three threshold levels; >95%, >50%, and >33% likelihood of humpback whale occurrence. The upper thresholds were chosen to identify important (>95%) and core (>50%) habitat used by humpback whales. In addition, the lower threshold (>33%) was selected to account for the wide-ranging behaviour of whales and the likely lower percentage occurrence predictions associated with such a cosmopolitan species. Overlaps were calculated using the extent of the SGSSI MPA shapefiles (available at: <https://www.sggis.gov.gs/>) and the lower resolution predictive model raster layers subsampled using the above selection thresholds. Layers were reprojected using a Lambert Azimuthal Equal Area projection centred on 54.01°S 36.3°W, and measurements reported to the nearest km².

3. Results

3.1. Tagging success

A total of 140 whales were tagged between 2004 and 2019, of which, 20 transmitted from locations south of 50°S, and for modelling purposes 16 whales provided sufficient information to be included in the present

analyses (Table 2, Fig. S2). Data transmission continued on average for 46 ± 40 days south of 50°S (Table 2), and in total the modelled data corresponded to 738 days of whale feeding activity.

3.2. Model performance and visualisation

Telemetry data were pooled and modelled using GAMs to predict the likelihood of occurrence across the study area for the defined seasonal periods. Whale locations and random background points, hereafter positions, which were affected by covariate data gaps and removed from the analysis corresponded to a removal of 19% (n = 542 positions) from the early summer model; 21% (n = 1,152 positions) from the high summer model; 27% (n = 402 positions) from the winter model; and 21% (n = 2,096 positions) from the all data model. VIFs indicated that in the early summer model, six variables exhibited collinearity; in the high summer model three variables exhibited collinearity; in the winter model four variables exhibited collinearity; and in the all data model, four variables exhibited collinearity. Details of the VIF values are available in Table S1. Models of each period produced acceptable AUC, specificity and sensitivity values (Table 3), with visualisations of these models displaying shifts in spatial occupancy between the three time periods.

The early summer model (October to December) indicated that the distribution of humpback whales was best described by three covariates (Table 3): (i) bathymetric depth, where deeper water suggested a greater likelihood of whale occurrence, along with a slight increase in occurrence in regions >2,000 m deep; (ii) sea-level anomaly, which was negatively linked to occurrence, with a slight peak between 0.1 and 0.2 m; and (iii) eddy-kinetic energy, where occurrence was positively

Table 2

Deployment durations for the tagged humpback whales used in the habitat models with data south of the 50°S threshold used to differentiate between migratory and feeding grounds. Total is inclusive of the random background locations. Whether or not a whale provided data to each modelled period is indicated by the final three columns, where a cross indicates inclusion of data from a whale in the modelled period (Early summer, ES, n = 9; high summer, HS, n = 12; winter, W, n = 3).

Whale ID	Modelled locations south of 50°S	Tag deployed	Date south of 50°S	Date of transmission end/north of 50°S	Duration (days)	Model period contributed to		
						ES	HS	W
24642	145	October 27, 2003	February 02, 2004	April 29, 2004	87		×	×
87771	74	September 14, 2009	October 19, 2009	November 13, 2009	25	×		
87783 ^{aa}	119	September 18, 2009	December 31, 2009	February 01, 2010	32	×	×	
121189	159	October 20, 2012	March 21, 2013	July 27, 2013	128		×	×
121203	287	September 25, 2017	November 22, 2017	February 04, 2018	74	×	×	
120937	213	September 23, 2017	November 24, 2017	January 18, 2018	55	×	×	
111870	258	October 07, 2017	December 01, 2017	February 06, 2018	67	×	×	
84484	31	September 27, 2018	January 07, 2018	January 14, 2018	7		×	
112696	25	September 27, 2018	November 29, 2018	December 06, 2018	7	×		
171994	87	September 26, 2018	November 30, 2018	December 22, 2018	22	×		
84485	79	September 27, 2018	January 04, 2019	January 24, 2019	20		×	
121191	24	September 27, 2018	January 09, 2019	January 15, 2019	6		×	
81123 ^{bb}	142	January 19, 2019	January 19, 2019	May 23, 2019	124		×	×
174065 ^{bb}	133	January 22, 2019	January 22, 2019	March 13, 2019	50		×	
194601	37	October 13, 2019	December 01, 2019	December 10, 2019	9	×		
194591	100	October 10, 2019	December 16, 2019	January 10, 2020	25	×	×	
Pseudo-absence data	5957		–	–	–			
Totals	7870		–	–	738	9	12	3

^a 87783 tag duty cycled for every other day transmission.

^b tags deployed on the SGSSI feeding ground.

Table 3

Contribution of covariates to the final GAM models selected through a forward step-wise cross-validation approach. Contribution was assessed in terms of area under the curve (AUC), specificity (correctly predicted absences), and sensitivity (correctly predicted presences) values. Covariate acronyms are as follows: Sea level anomaly (SLA); Eddy-kinetic energy (EKV); Salinity (SAL); frontal features detected in SST data (SSTF); wind stress curl (CURL); chlorophyll-a concentration (CHL); iron concentration (FE); silica concentration (SI); and sea-surface height (ZOS); and the standard deviation of the named covariate (SD). Bold indicates the covariate combination with the highest AUC value, and the covariates of the final model for each modelled time period.

	Variable	AUC	Specificity	Sensitivity
Early Summer (Oct–Dec)	DEPTH	0.708	0.607	0.776
	SLA	0.634	0.529	0.742
	EKV	0.617	0.557	0.687
	DEPTH + SLA + EKV	0.734	0.607	0.814
High summer (Jan–Mar)	SAL.SD	0.679	0.483	0.878
	FE	0.543	0.424	0.691
	SAL	0.511	0.686	0.476
	SSTF	0.550	0.689	0.409
	SI	0.640	0.600	0.711
	SAL.SD + FE + SAL + SSTF + SI	0.684	0.685	0.661
Winter (Apr–Jul)	CURL	0.880	0.766	1.000
	CHL.COMP.SD	0.723	0.727	0.802
	CHL.COMP	0.687	0.784	0.646
	SSTF	0.571	0.689	0.589
	ZOS.SD	0.788	0.807	0.847
	CURL + CHL.COMP.SD + CHL.COMP + SSTF + ZOS.SD	0.896	0.847	0.886
All data	ZOS.SD	0.637	0.615	0.737
	FE	0.574	0.443	0.775
	SLA	0.595	0.600	0.688
	ZOS.SD + FE + SLA	0.660	0.576	0.788

correlated with higher eddy kinetic velocities (Fig. 3a).

The high summer model (January to March) showed that humpback whale distribution was characterised by five covariates (Table 2): (i) the standard deviation of salinity showed that humpback whale occurrence peaked 0.2 units above the mean; (ii) iron concentration showed an overall positive, yet sigmoidal relationship with occurrence; (iii) salinity showed a peak at 33.85 PSU; (iv) frontal gradients detected in sea surface temperature showed an initial positive correlation up until $\sim 0.4\text{C km}^{-1}$, with stronger frontal detections leading to a decrease in occurrence; (v) silica concentration peaked in its influence on occurrence at $\sim 40\text{ mmol m}^{-3}$ (Fig. 3b).

The winter distribution (April to July, excluding June due to telemetry disruption) was characterised by five covariates (Table 3): (i) wind-stress curl showed a peak in humpback whale occurrence with slight negative values; (ii and iii) the standard deviation of chlorophyll concentration and chlorophyll concentration itself both showed that occurrence was at its highest as chlorophyll concentration also peaked, and remained within ~ 100 units; (iv) frontal gradients detected in sea surface temperature data showed a strong correlation between occurrence and frontal activity; and (v) the standard deviation of sea surface height where occurrence peaked in response to values < 0.05 above the mean (Fig. 3c). For this model, both the standard deviations of chlorophyll concentration and sea surface height were subject to wide ranging standard errors at higher values; this stemmed from there being fewer data points corresponding to these high values ($n = 18$, $1.64\% > 0.12\text{ m}$ and $n = 15$, 1.37% , $> 150\text{ mg m}^{-3}$, see Fig. S1).

Finally, a model using all data best described whale habitat use with three covariates (Table 3): (i) the standard deviation of sea surface height showed that humpback whale occurrence peaked with values greater than 0.15 above the mean; (ii) increases in iron concentration were positively correlated with occurrence; and (iii) sea-level anomaly, which had a broadly consistent influence on occurrence throughout (Fig. 3d) was included in the final model as it marginally increased the

AUC of the model (+0.002).

3.3. Model visualisations over the SGSSI MPA region

Our habitat models describe the likely distribution of humpback whales throughout the year based on multiple years of pooled data. The first of these models predicted that during the early summer period humpback whales mainly used areas to the north and east of the South Sandwich Islands, with a particular focus on the vicinity of the South Sandwich Trench (Fig. 4a). As the season progressed into the high summer, model visualisations displayed a westward shift in where whales were likely to be located compared to the early-summer period. The tracked whales appeared to be moving west into the Scotia Arc, to the south and south-east of South Georgia, as well as onto the South Georgia shelf. The east of the South Sandwich Islands was still used to some extent, but far less so than in previous months (Fig. 4b). Winter habitat utilisation in our models showed that humpback whales expanded their footprint over the majority of the South Georgia shelf and beyond into the wider Scotia Sea, but with a notable increase in their predicted occurrence around the South Sandwich Islands, and further south towards the latitudes where the winter sea-ice reforms. Humpback whales had a low likelihood of occurrence to the west of mainland South Georgia (Fig. 4c). The combined model showed that humpback whales were likely using large areas of the modelled area, with the lower predictions occurring due north of the South Sandwich Islands; mid-range predictions throughout the arc between South Georgia and the South Sandwich Islands, and due south of the South Sandwich Islands; and with higher predictions over the shelf of South Georgia (Fig. 4d). Model visualisations display both latitudinal and longitudinal shifts through the seasons. Between the early and high summer, whale habitat shifted westwards, with a shift back to the south-east as winter progressed. However, when all data are modelled together, these seasonal patterns and regions of higher habitat use are smoothed, and only the shelf of mainland South Georgia (to the coast from the shelf break; $< 1,000\text{ m}$) remains highly significant.

3.4. Spatial overlap with the SGSSI MPA

We used model visualisations at a resolution of $0.1^\circ \times 0.1^\circ$ to calculate the spatial overlap with the SGSSI MPA. The overlap with the SGSSI MPA/SGMZ equates to approximately $1.27 \times 10^6\text{ km}^2$ or 57% of the total modelled area of $2.2 \times 10^6\text{ km}^2$. Within the MPA, our models show that humpback whale distribution varies through the feeding season. Visually, during the early summer period, humpback whales concentrated to the east of the SGSSI MPA, focussing to the east of the South Sandwich Islands within the MPA, and their likelihood of presence was influenced by bathymetric features, and shelf break dynamics. As the season progresses, whale distribution shifted, and became more homogenous throughout the SGSSI MPA, particularly to the west of the South Sandwich Islands, and onto the shelf of mainland South Georgia. During the winter, humpback whale distribution saw an eastwards expansion towards the South Sandwich Islands and 60°S , but whales also maintained a presence near to South Georgia. More generally, the all data model showed that humpback whale habitat use over all seasons is focussed on the shelf of South Georgia, with lower levels of occurrence throughout the SGSSI MPA than compared to the individually modelled time periods.

An initial examination of the overlap between the available tracking data and the SGSSI MPA revealed that at all times of the year humpback whales use habitats within the MPA more than they use areas outside the MPA. Overlap is at its lowest during the early summer where 68.6% of the tracking data occurred within the MPA, and peaks during the winter period where 96% of the data were within the boundaries of the MPA (Table 4).

Overlaps between the MPA and the predicted whale habitat show that the MPA provides a high level of overlap at multiple threshold

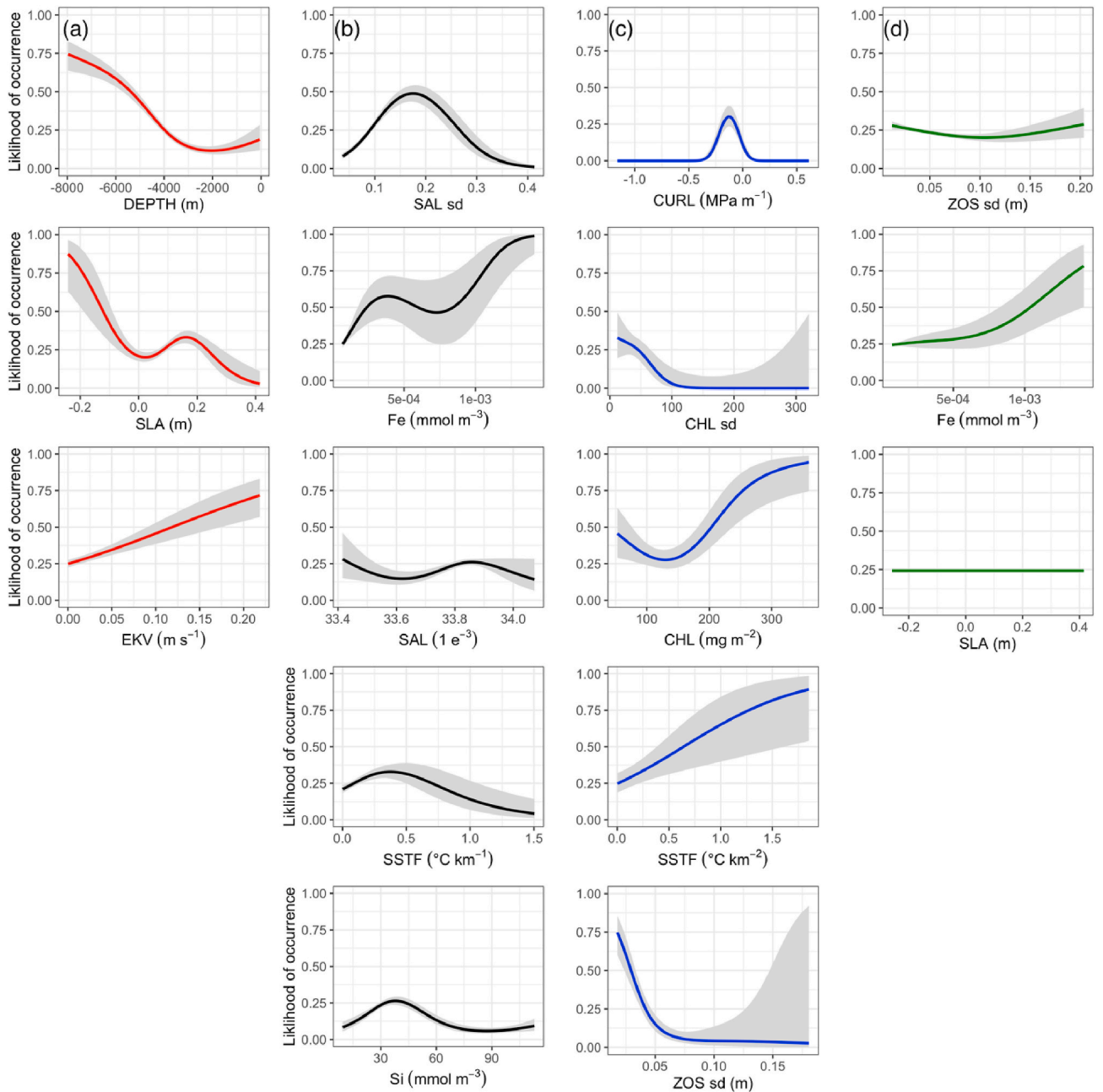


Fig. 3. Covariate response curves for the four modelled time periods: (a) early-summer (Oct to Dec) in red; (b) high-summer (Jan–Mar) in black; (c) winter (Apr–Jul, excluding June) in blue; and (d) all data model in green. Grey shading indicates 2 standard error bounds for the modelled covariates. Plot produced in the R package ‘visReg’ (Breheny and Burchett, 2017). Covariate acronyms are as follows: Sea level anomaly (SLA); Eddy-kinetic energy (EKV); Salinity (SAL); frontal features detected in SST data (SSTF); wind stress curl (CURL); chlorophyll-a concentration (CHL); iron concentration (FE); silica concentration (SI); and sea-surface height (ZOS); and the standard deviation of the named covariate (sd).

levels, over multiple time periods. At the highest threshold level of >95%, during the high summer, 100% of predicted habitat used by modelled humpback whales was within the boundaries of the SGSSI MPA (Table 4, column c). This pattern of overlap between humpback whale activity within the MPA was also seen in other modelled time periods, where the overlap was between 50% and 96% within the MPA at >50% threshold, and between 35% and 100% at the >33% threshold (Table 4, column c). At the >50% and >33% thresholds the total overlap between predicted humpback whale distribution and the SGSSI MPA increased as the season progresses from early summer to winter (Table 4, column b). The all data model predicts a more homogenous likelihood of occurrence across the modelled area, with the range of the percentage predictions reaching a lower maximum percentage compared to the

other modelled time periods (Fig. 4). Consequently, the overlap between the all data model and the SGSSI MPA is lower than that of the individually modelled time periods (Table 4, column b). In relation to the modelled area, the largest predicted area of humpback whale habitat use occurs during the early summer period at the >33% threshold, where 41% of the total modelled area (overlapping with 25% of the total SGSSI MPA) corresponds to significant habitat use by humpback whales. The highest spatial overlap between the SGSSI MPA and likelihood of humpback whale occurrence was found in winter, with between 41 and 51% of the MPA overlapping with important whale habitat at the >50% and >33% thresholds, respectively (Table 4, column d).

In regard to individual management measures of the SGSSI MPA, two areas are of particular interest, as they are directly relevant to humpback

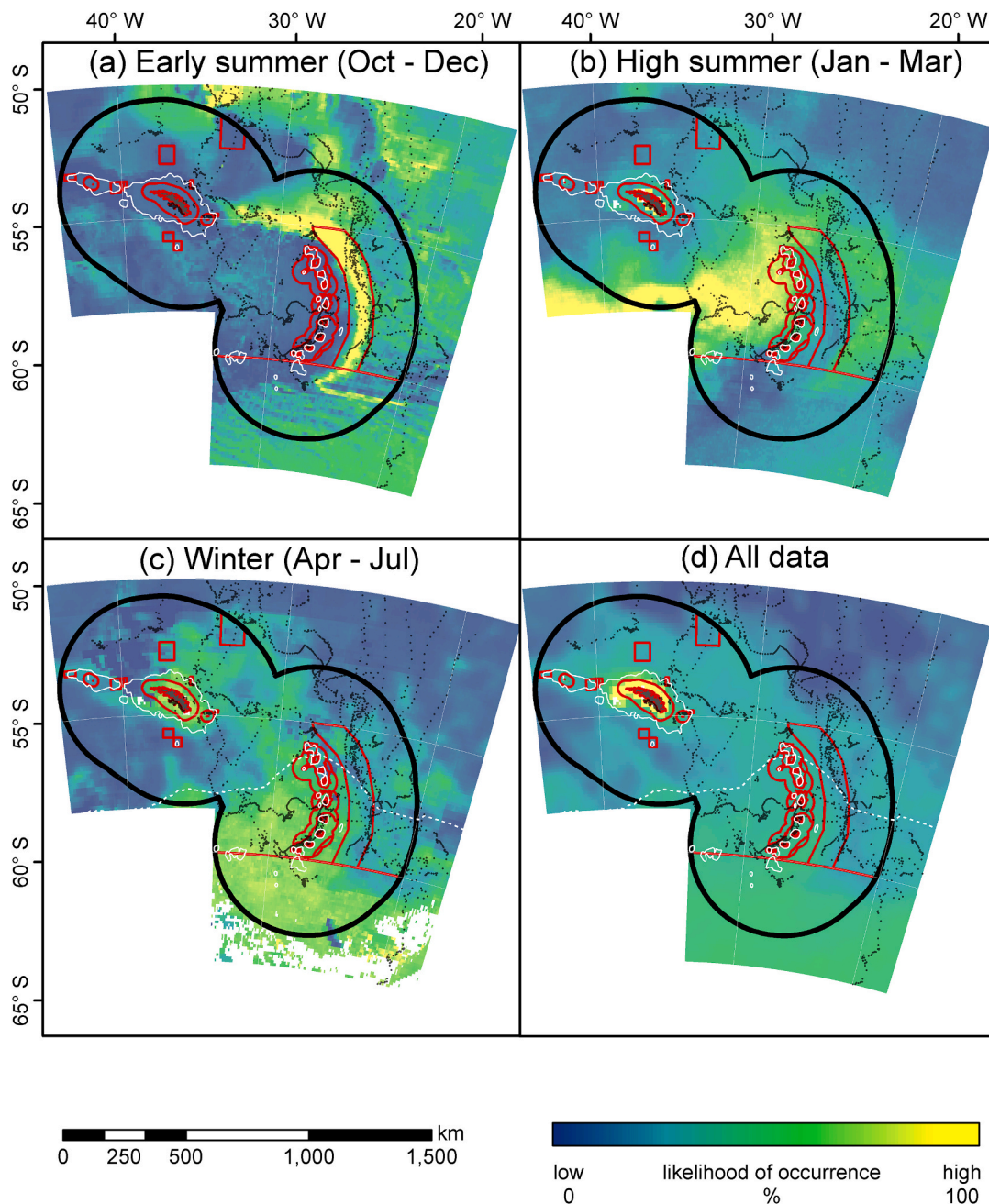


Fig. 4. Generalised Additive Model (GAM) projections of the likelihood of humpback whale habitat use over the South Georgia and South Sandwich Island region with standardised prediction ranges indicated (for ease of cross comparison). The solid white line indicates the 1000 m bathymetric contour; with the boundary of the SGSSI MPA denoted by the solid black line; the specific measures implemented under the MPA denoted by solid red lines; the white dashed line in panels c and d indicates the average maximum extent of the winter sea ice between 1981 and 2010; and the grey dots show the available tracking data.

whale use of the SGSSI system. The first of these areas is the no-take zone (NTZ) around Shag Rocks, which is the only management measure within the SGSSI MPA that specifically includes whales within its conservation objective (GSGSSI, 2019). However, our models found no overlap between predicted humpback whale habitat use and the Shag Rocks NTZ in any model period, with the exception of a small overlap with the winter model prediction. Our winter model showed that humpback whale presence was predicted to be >33%, but <50% over a 74 km² section of the Shag Rocks NTZ (2,337 km², GSGSSI (2019)), which equates to a 3.2% overlap between humpback whale predictions and the total area of this management measure.

The second management measure of interest is the year-round 18,520 km² NTZ around mainland South Georgia. Our models show

that predicted humpback whale overlap with this NTZ varies through the year; there is no overlap during the early summer period at any threshold levels and overlap increases from 1,521 km² (8.2%) in the high summer to 10,056 km² (54.3%) in the winter at >50% likelihood threshold, and from 1,951 km² (10.5%) to 10,056 km² (54.3%) at >33% likelihood threshold. In the all data model 7,824 km² (42.2%) of this NTZ is predicted to have a humpback occurrence probability of >33%.

4. Discussion

Humpback whales represent an important, yet relatively understudied consumer of krill in the Antarctic system (Reilly et al., 2004). Here we investigated the spatial distribution and overlap of humpback

Table 4

Overlaps between the humpback whale distributions and the SGSSI MPA at three likelihood of occurrence thresholds. Proportion of regularised tracking data located within the SGSSI MPA over the model periods shown as a percentage of the total data post covariate extraction and gap removal ($n = 1,913$). Dashes in this column indicate that the percentage values are the same irrespective of occurrence threshold. (a) Provides the total overlap between predicted humpback whale habitat thresholds within the modelled area, and for each modelled time period. (b) Provides the total area within the SGSSI MPA that spans predicted humpback whale habitat. (c) Provides the percentage of predicted humpback whale habitat falling within the SGSSI MPA (d) provides the percentage of humpback whale habitat within the total SGSSI MPA area ($1.27 \times 10^6 \text{ km}^2$). (e) Provides the percentage of humpback whale predicted habitat relative to the total model predicted area across all seasons and thresholds ($2.2 \times 10^6 \text{ km}^2$).

Likelihood of whale occurrence threshold	Model period	Percentage of regularised tracks within SGSSI MPA (%)	(a) Area within model extent (km^2)	(b) Overlap with the SGSSI MPA (km^2)	(c) Percentage of predicted habitat use area falling inside the SGSSI MPA (%)	(d) Percentage of total SGSSI MPA that includes areas of predicted habitat use (%)	(e) Percentage of predicted habitat use area relative to total modelled area (%)
		$n = 1,913$	2.2×10^6	1.27×10^6	57	–	–
>95%	Early summer (Oct–Dec)	68.6	1,186	–	–	–	0.1
	High summer (Jan–Mar)	69.7	1,665	1,665	100	0.1	0.1
	Winter (Apr–July)	96	2,271	–	–	–	0.1
	All data	72.7	1,592	–	–	–	0.1
>50%	Early summer (Oct–Dec)	<i>ibid</i>	240,206	120,959	50	10	11
	High summer (Jan–Mar)	<i>ibid</i>	51,907	38,022	73	3	2
	Winter (Apr–July)	<i>ibid</i>	538,503	515,704	96	41	24
	All data	<i>ibid</i>	7,544	–	–	–	0.3
>33%	Early summer (Oct–Dec)	<i>ibid</i>	895,020	313,778	35	25	41
	High summer (Jan–Mar)	<i>ibid</i>	286,674	237,338	83	19	13
	Winter (Apr–July)	<i>ibid</i>	856,552	651,265	76	51	39
	All data	<i>ibid</i>	16,471	16,471	100	1	1
	Average (%)	76.7					
	\pm sd (%)	13					

whales on their feeding grounds within the boundaries of the SGSSI MPA to assess whether existing spatial measures have been created in locations frequented by whales, and as such either offer a degree of protection currently or could be adapted to provide protection in the future.

These investigations are important to the IWC from a population dynamics perspective, and to CCAMLR, where the interest is geared towards investigating how cetaceans can be included in the ecosystem approach to krill management. Using tracking data from 16 whales, we modelled and predicted habitat use by humpback whales across seasons. Our models provide strong evidence that during the early summer, upon arrival south of 50°S , whales utilise the outer edge of the Scotia Arc. Here, they are concentrated over the South Sandwich Trench. Their distribution centre then shifts as the summer progresses, and the inner region of the arc and the shelf of South Georgia becomes the main region of focus. Our final seasonal model shows that during the winter humpback whales continue to use the shelf of mainland South Georgia, whilst also showing a south-easterly expansion throughout the study area moving back towards the South Sandwich Islands, the MPA's no-take zone south of 60°S and the reforming ice-edge. Below, we consider this in greater detail before making a number of recommendations for future research and possible adaptations to management measures that would better protect humpback whales within the SGSSI MPA during their feeding period. Importantly, we also recognise the limits of these data, and highlight the need for further information.

4.1. Model comparison – spatial and seasonal patterns

Our models show that humpback whale use of the SGSSI MPA is extensive and variable throughout the year. Our all-data model highlighted the importance of the South Georgia shelf as a habitat for

humpback whales, and also showed that whales range widely throughout the MPA. In terms of covariates from the all-data model, these show that humpback whales are influenced by positive sea surface heights and are attracted to areas associated with sea level anomalies, favouring areas that remain environmentally predictable, along with a strong positive relationship with iron concentration; a key correlate with enhanced primary productivity (Murphy et al., 2007b; Prend et al., 2019). This model encompasses data from all time periods, and as such predicts a wider and more smoothed likelihood of occurrence over the study area, with few discrete features that are easily differentiated from the background. The smoother patterns generated by this model could also be attributed to the number and type of covariates; these three covariates typically exhibit variation over larger spatial scales, rather than being associated with finer-scale spatial fluctuations, which are more common in variables such as depth or chlorophyll concentration.

Our early summer model shows that humpback whales are distributed to the east of the South Sandwich Islands and to the north of South Georgia along the Polar Front. During this period, the model suggests that humpback whale distribution was influenced by bathymetry, with whales favouring off-shelf, deeper water regions. The tagged whales show a particular affinity to waters $>2,000 \text{ m}$; this likely represents their post-migration arrival in the region, and their search for prey in off-shelf areas. Whales in this period also show an affinity towards dynamic waters with enhanced eddy velocities which are known to be linked with the aggregation of enhanced productivity in a region (Meredith et al., 2003). This period also shows that humpback whales display a preference for regions of negative sea level anomaly, which are potentially associated with upwellings of cooler water, and in turn, prey availability (Hill et al., 2006).

The post migration, early summer period shows that humpback

whales use vast areas of the SGSSI region, both inside and outside of the SGSSI MPA. Within the MPA, the area of the South Sandwich Trench appears to be important habitat, with this feature dominating in the early summer model. The South Sandwich Trench is unique in the Antarctic (Trathan et al., 2014), extending along the eastern edge of the SSI chain, and being formed by the subduction of the South American Plate under the Sandwich Plate (Rogers et al., 2015). This deep sea trench hosts unique hydrothermal habitats and chemosynthetic communities (Rogers and Linse, 2014), and is likely a source for upwelling currents (Vanhove et al., 2004), which promote productivity in the waters closer to the surface. This productivity likely makes the waters above this geomorphic feature an attractive focal point for whales wanting to target regions of higher prey abundance. However, the absence of this feature in the high summer, winter or all data model suggests that there could be a temporal component to this feature's importance, which needs further investigation.

For the high summer period, our model shows that humpback whale distribution is strongly influenced by dynamic biogeochemical covariates (i.e. salinity + sd, Fe & Si concentration, and temperature derived frontal features activity) rather than static covariates (i.e. depth or slope). The association with dynamic variables show that humpback whales are probably targeting regions of enhanced productivity, alluded to by the positive relationship with iron and silica concentration (Murphy et al., 2007b; Prend et al., 2019), where frontal features are mixing the water column. During this period whales appear to move into the Scotia Sea, to the west of the South Sandwich Islands as well as onto the shelf of mainland South Georgia. This movement may be in response to productivity associated with algal blooms that occur in the region each spring (Prend et al., 2019), and trophic transference of production through the food-web. Interestingly, our model suggests that during the high summer period, the predicted distribution of humpback whales contracts into the MPA, with much lower habitat use outside the MPA than earlier in the year. The shift in likelihood of humpback whale occurrence from east of the South Sandwich Islands into the centre of the Scotia Sea could indicate that whales are moving towards regions of higher productivity, from where the sea ice has recently retreated. This is comparable to humpback whale behaviour derived from satellite telemetry data in Eastern Antarctica (Reisinger et al., 2021; Riekkola et al., 2019).

The Northwest Georgia Rise (52.75 S 37.32°W) was identified by our models as being adjacent to a significant habitat for humpback whales during multiple modelled periods, notably as the season progressed. This region is understood to be associated with cyclonic water features, known as Taylor columns (Meredith et al., 2003). The rotation of these features in this region act to retain enhanced nutrient concentrations, and their associated biological productivity (Korb and Whitehouse, 2004; Korb et al., 2005), making this region an attractive post-migration feeding location for whales south of the Polar Front. This region has also been predicted to be an important foraging habitat for Antarctic fur seals (*Arctocephalus gazella*, Bamford et al., 2021), south of the Polar Front. Similar associations to bathymetric features have been recorded for Oceania humpback populations, whose southerly migration veers towards the Kerguelen Plateau; a region characterised by bathymetrically influenced ocean currents and the persistent, productive feeding grounds that arise in the plateau's vicinity (Bestley et al., 2019).

Our predictions during the winter suggest that humpback whales remaining south of 50°S late in the season disperse throughout the region. The variables that best predicted humpback distribution in this period can all be linked to enhanced productivity and dynamic features of the water column. Patterns show that humpback whale occurrence increases in regions which are persistently high in chlorophyll concentration; are associated with upwelling (negative wind stress curl); near to frontal features; and are not prone to sea surface height fluctuations. During this period, the South Georgia shelf is significant for these late-migratory, or non-migratory whales. Whale occupation of the continental shelf means that they are potentially in competition with the

licensed commercial krill fishery, which only operates at South Georgia during the winter. The krill fishery around South Georgia is primarily focussed over the northern shelf of the island (Bamford et al., 2021; Trathan et al., 1998, 2021). The extent to which this co-occurrence may translate into negative competitive or interference interactions is, however, uncertain due to the limited availability of winter-time data. Although our results suggest a spatial overlap on the northern shelf of South Georgia is likely, the scale of the overlap will be dependent upon the total number of whales delaying or abandoning migration and the number of fishing vessels operating in the MPA. We also note that due to data availability, our model here has a slight temporal discrepancy and includes tracking data that were collected prior to the krill fishery licensed period. However, it still provides preliminary indications as to the spatial distribution of humpback whales throughout the MPA over this time.

Our models show that between summer and winter humpback whale distribution expands back to the east towards South Sandwich Islands, consistent with the premise that if whales are present south of the Polar Front in this season, then they are feeding. This shift in distribution is consistent with the known association of krill with the sea-ice (Massom and Stammerjohn, 2010; Quetin and Ross, 2009), where whales would be targeting areas with a higher biomass of prey prior to either a late migration or overwintering in higher latitudes.

One further noteworthy observation is that except for localised areas of humpback whale occurrence during the winter months near to Shag Rocks, the waters surrounding the westerly extent of the archipelago were, in general, associated with a lower likelihood of occurrence, and thus limited overlap with the only management measure with a specified whale conservation objective. This is particularly interesting given recent sightings of mixed-species groups of whales (Jackson et al., 2020; Richardson et al., 2012), and the recording of super-groups of humpback whales feeding in the vicinity of Shag Rocks (Jackson et al., 2020; Martin et al., 2021). A likely explanation for this gap in the model prediction is that telemetry data were not available for this end of the island due to the relatively small sample sizes (Fig. S2), and that this, combined with the variable ecological conditions between the east and west of the archipelago (Atkinson et al., 2001; Korb and Whitehouse, 2004; Young et al., 2014), limit model extrapolation as the data were primarily from the east of the study area. Further data acquisition would provide additional insight into humpback habitat use patterns at the western end of South Georgia.

The inherent variability of the Scotia Arc ecosystem (Hill et al., 2012; Murphy et al., 1995, 2007a, 2007b, 2021) is reflected in our models both by the apparent variation in the predictions of each model period, and by differences in the suite of covariates included in the best performing models. This implies a complex relationship between humpback whales and their environment, and one that suggests that these animals respond to the state of their system that they face *in situ* rather than being influenced, and therefore predicted, by static environmental features that persist between years. Whilst this dynamic response to changeable environmental conditions seems a completely plausible explanation for the results presented herein, the possibility exists that this lack of predictor consistency between modelled periods is an artefact of one or more missing covariates that would more accurately parameterise the relationship between humpback whales and their environment. However, here we selected our covariates based on their ability to describe physical and biological oceanographic properties best suited to depict the habitat available to humpback whales. Our selection represents a suite of variables commonly used in such modelling efforts (e.g. Arthur et al., 2017; El-Gabbas et al., 2021; Hindell et al., 2020; Reisinger et al., 2021), and included several aimed at providing insight into location-specific micronutrient gradients (Holm-Hansen et al., 2004; Korb et al., 2005; Post et al., 2014), and as such we are confident in the parameterisation of the available habitat by the chosen covariates.

The SGSSI system displays strong spatial and temporal environmental fluctuations (Thorpe and Murphy, this issue) and our model

predictions also reflect this. In the modelled region, oceanic conditions (Young et al., 2014), as well as krill density (Saunders et al., 2007; Trathan et al., 2003) fluctuate throughout the year and are also influenced by multi-year climatological cycles (Forcada et al., 2008; Murphy et al., 2007b; Trathan et al., 2006). Undoubtedly, these large-scale climatic regimes play a role in the functioning of the South Georgia system, likely impacting localised conditions; the availability of krill in the system (Fielding et al., 2014); and, more recently, have been observed to influence humpback whale presence in the South Atlantic (Schall et al., 2021). However, in order to investigate such variability and its effect on whale habitat use, a much larger dataset is required than was available here to adequately capture, and explain these patterns. Further studies from multiple platforms, along with continued telemetry deployments, both on the feeding and breeding grounds, will be needed to substantiate this.

4.2. Overlap with the South Georgia and South Sandwich Island MPA

Based on our dataset, the ratio between data within the boundaries of the MPA and in the waters external to the SGSSI MPA was in excess of 3:1 (Table 4). At a simplistic level, this shows that the waters of the MPA are preferentially targeted by humpback whales post-migration compared to waters outside of the MPA. When further broken down into the three respective temporal model periods, the degree of overlap with the MPA shows an increase as the season progresses from the early summer through to the winter period. On further examination, the overlap between likely humpback whale occurrence and the MPA were highest at the >33% occurrence threshold. Only the high summer model showed an overlap at the >95% threshold within the SGSSI MPA (Table 4, column b). The absence of an overlap at higher thresholds is unsurprising given the common home-range of humpback whales, and their ability to exist over vast regions. This means that the models were more likely to predict lower instances of occurrences, but over greater areas, rather than a few high-likelihood regions. Our models show that there appears to be an initial increase in habitat occupation in the early summer, which then decreases during the high summer, as whales operate more widely over the region with lower occurrence likelihoods in each $0.1^\circ \times 0.1^\circ$ grid cell. The overlap then rises again in the winter period.

Within the SGSSI MPA, the krill fishery is closed during the summer months (GSGSSI, 2019), and as such the MPA offers protection to humpback whales throughout its extent. During this period, 313,778 km² of whale habitat overlaps with directly named management areas (i.e. those listed in Fig. 2). However, whale habitat overlap increases as the season progresses towards winter, when krill fishing is permitted, meaning that those whales that may remain in the region could be exposed to concurrent use of the system with the krill fishery. The number of whales remaining in the region in winter is unknown, although it is likely to be a small proportion of the total population. The functional impact of this co-occurrence, i.e. resource competition, ship strike, or incidental mortality in fishing gear therefore remains to be demonstrated; no incidental mortalities have been reported to date in SGSSI waters.

Within the SGSSI MPA, very few taxa are directly listed as beneficiaries of individual management measures. This is because the MPA was designed to conserve with mutual benefit rather than by targeting issues or taxa in isolation. However, one instance where whales are referred to, alongside other species is within the NTZ around Shag Rocks. Here our models show that humpback whales use 3.2% of the Shag Rocks NTZ, with this use occurring only during the winter period. Given recent observations of high numbers of whales in the vicinity of this feature (Jackson et al., 2020; Martin et al., 2021), such low overlap could be attributed to the spatial bias in the modelled tracking data, with this emphasising the need for continued data collection to the west of South Georgia to better parametrise future models. We also show that humpback whales use large areas of the South Georgia NTZ through the

season, with use increasing as the season progresses; the maximum spatial use of this South Georgia NTZ peaks at 54.3% in the winter months. However, due to annual humpback whale migration, the total number of whales present within the MPA during the winter months is likely far lower than the numbers present during the summer, since the majority of whales are present (and periodically surveyed) on Brazilian wintering grounds during this time (e.g. Bortolotto et al., 2016).

The extent to which winter presence may change in the future remains unknown (for example, with population growth there may be more whales present that periodically choose to feed rather than migrate), and migration timings need to be better understood. Given the small dataset used in this study, we anticipate that overlaps may change when more data (i.e. an increased sample of tagged whales) are modelled. Currently the focus of the MPA is on shelf waters. Our models suggest that there is merit for pelagic protection, which would expand the original focus on the coastal NTZ into offshore regions. To do so, a krill fisheries research zone over the shelf edge (Trathan et al., 2021) would be able to provide information to enhance the ability to locate static measures so that they have sufficient plasticity in their design to be able to account for a mobile prey resource. Expanding protection further offshore could enhance protection to the feeding grounds for whales and to those centrally-placed predators that make extended foraging trips into deeper waters.

4.3. Model performance and caveats

Our models show AUC scores that fall within the range commonly perceived as acceptable, although in some instances these scores were on the lower end of this spectrum (Mandrekar, 2010). Whilst confident in the reliability of our models, a plausible explanation for the slightly lower AUC scores for the high summer and the all data model relates to the size of the dataset available. A small heterogeneous dataset, comprised from multiple individuals and demographics means that the model has to capture potentially divergent relationships with covariates (i.e. males, females, adults and juveniles likely exhibit differing behavioural strategies); this could lead to lower assessment scores. Future applications with adequate data, should use models to investigate intra and inter-animal variations in movement patterns to provide information on location specific behaviour (Bedriñana-Romano et al., 2021; Jonsen et al., 2019; Riekkola et al., 2019), rather than only spatial occurrence, as applied here. As a whole, the overall size of our dataset was impacted by tag longevity, whereby tags stopped transmitting shortly after arrival on the feeding grounds, and before they had begun their northerly migration. This is consistent with previous works, where average tag duration is similarly limited (Zerbini et al., 2006, 2011, 2015, 2016). As a result, the opportunity to gather further whale foraging data were lost.

The effect of sample size is a key constraint for cetacean research; here we used well-established habitat modelling techniques, which have sufficient resilience to cope with this limitation. However, we note that the small sample here increases the uncertainty around the presented results. The reduced whale dataset in winter was primarily due to the lower level of research effort on the feeding grounds compared to breeding grounds, and the effect of tag longevity limiting the availability of winter data. Additionally, late into the season the majority of whales have begun their northerly migration, and as such this naturally limits the availability of winter data. Since the majority of tags in this study were deployed on the winter breeding grounds (over 6 months prior), only one whale (ID: 81123) had sufficient tag longevity to transmit behaviour indicative of a northerly migration – this individual crossed over the 50°S threshold on the May 23rd, 2019. Here we present evidence that, at least three whales were present into the winter months, which complements previous winter observations of humpbacks in the Southern Ocean (Clark and Clapham, 2004; Moore et al., 1999) and suggests that whale presence south of 50°S during the winter is now something that requires further consideration. This reinforces the need

for further telemetry deployments on the summer feeding grounds, as well as dedicated autumn and winter surveys to characterise winter density and habitat use patterns in more detail.

With the current dataset, there was not the opportunity to examine inter-whale or inter-year variation, as models of these type (Wood, 2006) are often computationally demanding and difficult to apply to smaller datasets (Raymond et al., 2015). With this, there also arises the issue that some whales with long tag deployments are represented disproportionately in these models; only further data collection in the high latitudes can correct for this. Furthermore, our models may have been limited by our use of climatologies for some environmental covariates, which was dictated by atmospheric interference of satellite data acquisition and satellite mission duration, meaning that covariate data were not always available at a specific location or for the time-span of our modelled data. However, sources of remotely sensed data are becoming available with increased frequency (Grün, 2008; Toth and Józków, 2016), and as such coverage are likely to improve in the future. We also note that our analyses used data that were predominately from the east of the SGSSI archipelago, as such model predictions and overlaps calculated may be biased towards the biophysical characteristics of this portion of the study area.

4.4. Areas of future consideration

Encouragingly, humpback whales are now frequently sighted at South Georgia (Jackson et al., 2020; Kennedy et al., 2020), which suggests that this system is now increasingly important to the recovering population in the western South Atlantic. However, model-based predictions suggest that climate change may imperil the recovery of this population in the coming decades (Tulloch et al., 2019). Therefore, there is a crucial need to develop an understanding of how humpback whales use the system, before extrapolating predictions under different scenarios (e.g. Hindell et al., 2020) to best inform effective habitat and resource management. Our spatial predictions are similar to those made by previous studies (Bombosch et al., 2014; El-Gabbas et al., 2021; Hindell et al., 2020; Reisinger et al., 2021), all which utilised different techniques or data, which adds to the broader evidence base for humpback whale habitat use patterns across the region, and the resultant need for further conservation of this species. Accurately describing the distribution of krill-dependent predators within the SGSSI MPA is a crucial component of understanding and assessing whether management measures are sufficient. Here our models show that through the season humpback whales use the SGSSI MPA differently, and that the existing measures provide protection over sizable portions of whale habitat.

Continued data collection towards the west of the island would be beneficial for validating these predictions and assessing the efficacy of such conservation actions. A further recommendation, but one that extends beyond the remit of GSGSSI would be to consider conducting investigative surveys in the region due north of the SGSSI MPA at approximately 50°S 34°W. This region appears to be a migratory hotspot of humpback whale activity prior to their arrival in the SGSSI MPA, and has been shown to be an area of interest for multiple avian and pinniped species (Handley et al., 2020). We suggest that this region would benefit from additional investigation to establish the environmental drivers behind its significance, and to what extent this region is important to multiple species.

We suggest that there should be a continued effort towards multi-species management within the MPA. This policy would approach shared issues and agendas holistically, rather than in isolation, and will likely enhance the efficacy of the SGSSI MPA in the future. Our results show the inherent variability of how humpback whales use the SGSSI MPA, which underpins the need to consider the SGSSI system at seasonal scales, rather than applying management of a uniform nature. This is particularly important when it comes to delineating regions of significance, as these vary seasonally, are linked to a mobile resource (i.e.

prey), and species are constrained in differing ways during their respective life-cycles. Conducting multi-species risk assessments for periods throughout the annual cycle, and over multiple years, would help to enhance the process of developing and affording protection to vulnerable krill-dependent species within the MPA, whilst also facilitating the ongoing operation of a sustainably managed krill fishery.

To underpin conservation efforts, and to continue to support existing measures, data deficiencies need to be addressed, particularly through the autumn and winter, with the aim of avoiding data collection hot-spots around areas and times associated with ease of access. Here we report a spatial discrepancy in data availability between the eastern and western regions of the SGSSI MPA; a discrepancy that currently means that models predicted into data-poor regions have greater uncertainties. Obtaining data from different sources or platforms will enhance our ability to investigate how whales use this region, and would complement the high resolution locational data provided by satellite telemetry. Modern tracking devices, if deployed correctly, have the capability to transmit data for several months (Zerbini et al., 2018), a period which could provide a paradigm shift in the volume of high latitude data available to researchers if they could be deployed at South Georgia during the summer feeding season. However, the duration that telemetry devices transmit are inherently limited by the precision of the deployment location on the animal, and to a lesser extent in recent years, battery life. Alternative platforms, such as at-sea line-transect surveys could be used as a valuable complimentary method from which to obtain additional data, especially in seasons where data collection is traditionally difficult. One value of diversifying sources of data collection would be that each data-type could be used to validate and inform the predictions or the implementation of the other. For instance, using available tagging data to inform at-sea survey locations (i.e. Kennedy et al., 2020), or conversely, using at-sea data to validate the outputs of predictive models. Data deficiency is particularly pronounced at high latitudes for whale populations in the western South Atlantic. However, techniques and methods are now available that offer the ability to address existing deficiencies, which if applied offer a real chance of succeeding in achieving a sustainable ecosystem approach to management.

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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The scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of NOAA or the U.S. Department of Commerce. All authors declare that no competing interests exist.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr2.2022.105074>.

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