Ecological interactions between Antarctic krill (*Euphausia superba*) and baleen whales in the South Sandwich Islands region – Exploring predator-prey biomass ratios

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A B S T R A C T

Following the cessation of whaling, the southwest Atlantic humpback whale (*Megaptera novaeangliae*) population is thought to be close to pre-exploitation size, reversing 20th century changes in abundance. Using a model-based approach applied to concurrently collected data on baleen whale abundance and Antarctic krill (*Euphausia superba*) biomass in the South Sandwich Islands (SSI) region, we explore ecological interactions between these taxa. Krill biomass and baleen whale density were highest to the north and northeast of the SSI, where the Antarctic Circumpolar Current (ACC) is deflected around the island chain. Humpback whale density was elevated at locations of krill biomass density >150 gm^{-2}. Krill consumption by baleen whales was estimated at 19–29% of the available krill standing stock. We used historic whaling data to confirm the plausibility of these consumption rates and found evidence of rapid weight gain in humpback whales, such that blubber depleted during the breeding season could be restored in a much shorter period than previously assumed. Little is known about krill replenishment rates in the flow of the ACC, or about niche separation between recovering baleen whale populations; both factors may affect species carrying capacities and further monitoring will be required to inform the management of human activities in the region.

1. Introduction

Southern Ocean ecosystems suffered extreme, direct anthropogenic impacts throughout the 20th century era of modern industrial whaling (Ballance et al., 2006; Bonner, 1980), which were in addition to impacts experienced during the earlier sealing period (Payne, 1977) and the later fin-fish exploitation period (Kock, 1993). Between 1904 and 1965 some 175,250 whales were processed at South Georgia whaling stations and in the whole of the Southern Ocean some 1,432,862 whales were taken between 1904 and 1978, when hunting of the larger species ceased (Allison, 2016; Rocha et al., 2014). Following the cessation of commercial whaling in the 1980s, the recovery of southwest Atlantic baleen whale populations (Baines et al., 2021; Bortolotto et al., 2016; Calderan et al., 2020; Zerbini et al., 2019) demonstrates the potential for ecosystem recovery, given appropriate management action to prevent

further anthropogenic damage. Nevertheless, such recovery now presents new challenges to our understanding of the ecology of the region, as major changes in whale abundance occur once again.

The southwest Atlantic population of humpback whales (*Megaptera novaeangliae*) was reduced to the brink of extinction (Zerbini et al., 2019), before whalers moved on to take large catches of other species, including blue (*Balaenoptera musculus*), fin (*B. physalus*) and sei (*B. borealis*) whales. Southern right whales (*Eubalaena australis*) were already very rare following heavy exploitation in the early 19th century (IWC, 2001). Recent surveys indicate that the humpback whale population breeding in the coastal waters of Brazil and feeding in the northern Scotia Sea has now recovered to a level of abundance similar to that of the 19th century, prior to exploitation by industrial whaling (Baines et al., 2021; Bortolotto et al., 2016; Zerbini et al., 2019). Other baleen whale species also show encouraging signs of recovery, including

fin (Viquerat and Herr, 2017) and southern right whales (Best et al., 2001; Crespo et al., 2019; Groch et al., 2005), and increased sighting rates of Antarctic blue whales have been reported from the South Georgia area (Branch et al., 2004; Calderan et al., 2020).

The recovery of the southwest Atlantic humpback whale population has been realised over a period of some 40 to 50 years, which is comparable to, or only slightly shorter than the period of industrial exploitation of this species in the region. Thus, in terms of rates of ecosystem change, notably in predator – prey dynamics, the two periods of exploitation and recovery are similar in scale. We might therefore expect recent increases in whale abundance to reverberate throughout Antarctic food webs in which Antarctic krill (*Euphausia superba*) (hereafter krill) is the principal prey species for a wide range of other taxa, including baleen whales; this is because increased predation on krill by humpback whales may potentially impact the availability of krill to other species (Trathan et al., 2012; Trathan and Hill, 2016). Whales also recycle nutrients, excreting bioavailable iron in surface waters, which plays an important role in fertilising primary productivity (Ratnarajah, et al., 2014) and in particular diatoms, the staple food of krill (Schmidt and Atkinson, 2016). For example, Nicol et al. (2010) calculated that the Antarctic krill population contains ~24% of the total iron in the surface waters in the Southern Ocean and that pre-exploitation populations of whales and krill must have stored and recycled more iron in surface waters, enhancing overall ocean productivity through a positive feedback loop.

In the current era, climate change is another factor likely to impact krill ecology. In the Scotia Sea, patterns of krill abundance have been reported to be variable (Murphy et al., 2007; Trathan et al., 2021) and there is evidence of considerable interannual fluctuation in krill abundance that appears to be related to El Niño – Southern Oscillation cycles modulated by the Southern Annular Mode (Fielding et al., 2014; Loeb

and Santora 2015; Reiss et al., 2008; Steinberg et al., 2015). There is some evidence that krill may have been declining in abundance in the Scotia Sea as a consequence of climate warming, in concert with other factors (Atkinson et al., 2004, 2019). However abundance patterns are very noisy and difficult to interpret, and researchers are divided over whether there is evidence of a long-term decline (e.g. Cox et al., 2018; Krafft et al., 2021). Nevertheless, modelled scenarios of continued warming into the future suggest a high likelihood that declines in krill abundance will occur (Hill et al., 2013; Poloczanska et al., 2016; Richardson, 2008) with consequent impacts on recovering whale populations (Tulloch et al., 2019). Documented changes in whale abundance and likely changes in krill distribution potentially arising from climate change, highlight the need to better understand ecological relationships between baleen whales and krill, especially in the South Atlantic where the majority of Antarctic krill biomass exists (Atkinson et al., 2004). Recent work by Savoca et al. (2021) suggests krill consumption by whales is much higher than previously assumed, further highlighting the need to understand these interactions.

Humpback whales are the most abundant baleen whale species encountered in the northern Scotia Arc (Baines et al., 2021). While they are broadly distributed across the area, satellite tracking of individuals shows that on migration many animals enter this feeding ground to the north of the South Sandwich Islands (SSI), in the eastern Scotia Sea (Horton et al., 2020; Zerbini et al., 2011b), although tracking in the past decade suggests a broadening of this migratory movement to include areas to South Georgia and west (Bedriñana-Romano et al., 2022). The SSI archipelago is an arc of volcanic islands located some 700 km southeast of South Georgia, to the east of which is a deep trench, with ocean depths >8,000 m (Fig. 1). This active volcanic region forms the eastern boundary of the Scotia Sea. The Antarctic Circumpolar Current (ACC) that flows eastwards through the Scotia Sea is deflected
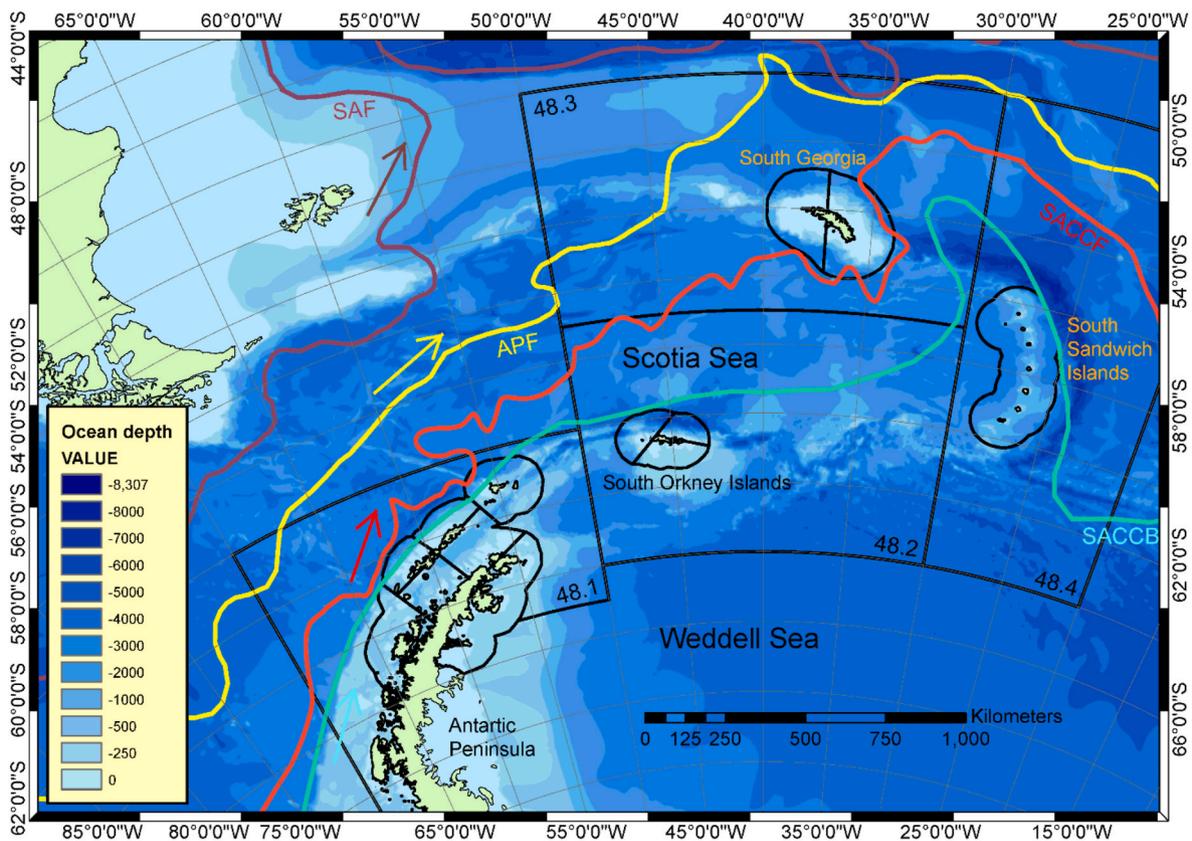

Fig. 1. The Scotia Sea showing the fronts in the Antarctic Circumpolar Current (ACC); Brown: Sub-Antarctic Front; Yellow: Antarctic Polar Front; Red: Southern ACC Front; Blue: Southern ACC Boundary. Also shown are the boundaries of FAO Subareas 48.1 to 48.4 and the boundaries of the CCAMLR Small Scale Management Units (SSMU; Hewitt et al., 2004; Trathan et al., 2008).

northwards by the island chain, and then turns southeast to flow down the eastern side of the islands, having reached its most northerly extent to the northwest of the SSI (Orsi et al., 1995). The islands therefore lie south of the ACC within waters influenced by the wind-driven cyclonic Weddell Gyre and close to ACC frontal systems. The SSI lie within the seasonal sea ice zone, the extent and phenology of which shows considerable interannual variability (Fetterer et al., 2017; Massom and Stammerjohn, 2010; Murphy et al., 2014) and is influenced by climate change, with consequent effects on the ecology of a wide range of taxa (Constable et al., 2014). The SSI have been little studied and cetacean and krill surveys have been rare, though a limited amount of historical data exists (e.g. Hewitt et al., 2004; Reilly et al., 2004).

Within the Scotia Sea, krill distribution and abundance has previously been studied by direct sampling with scientific nets (e.g. Atkinson et al., 2004) and by active acoustic methods (Fielding et al., 2014; Hewitt et al., 2004; Reiss et al., 2008). The acoustic approach typically uses line transects and has the advantage that line transect data for whales can also be collected concurrently. Line transect data provide the opportunity for modelling the abundance of both whales and krill. Robust methods for spatially explicit modelling of whale abundance that use environmental covariates to predict into un-surveyed areas are well established (Hedley et al., 1999; Hedley and Buckland, 2004; Miller et al., 2013). However, the behaviour of krill is complex and variable (Tarling and Fielding, 2016) resulting in diverse and unpredictable 3-dimensional distribution patterns. In different locations or times, the plasticity of krill aggregation may result in swarms of sizes ranging from a few metres to kilometres across, and they may disperse both horizontally and vertically. Consequently, the statistical distribution of data collected by acoustic line transect methods is likely to be spatially heterogeneous, presenting challenges to the selection of appropriate statistical methods for the estimation of abundance and distribution. Spatial heterogeneity and autocorrelation can both introduce bias in significance tests and sub-optimal predictions in regression models (Anselin and Griffith, 1988; Zhang et al., 2009). The survey design (parallel line transects) may also be sub-optimal for the application of regression models (Foster et al., 2020; Thomas et al., 2007), and a parametric method (Jolly and Hampton, 1990) has typically been applied to acoustic surveys for krill (e.g. Fielding et al., 2014; Krafft et al., 2021; Reiss et al., 2008).

Here, we investigate the environmental habitat drivers of both krill and baleen whale distribution in the SSI region, with particular emphasis on humpback whales, and investigate interactions between these two taxa, including the estimation of krill biomass consumed by whales. We use data from a wide-scale survey carried out in 2019 that included the SSI region, in which krill were acoustically sampled (Krafft et al., 2021) and baleen whales were visually surveyed using a line transect protocol (Baines et al., 2021). We propose a spatially explicit method for analysis of krill biomass density derived from line transect acoustic data, based on a Maxent (Phillips et al., 2006) relative abundance model to which presence only data are input, which is then calibrated using krill absolute abundance data collected along transect lines. Our approach for krill overcomes the challenges arising from the non-parametric distribution of krill biomass density. Using krill and baleen whale data concurrently recorded in the SSI region, we then explore aspects of their ecology and predator – prey relationships. Finally, we review historic whaling data from the Antarctic region to characterise the pattern of krill consumption by whales across the feeding season, in an attempt to reconcile high daily consumption rates (e.g. Savoca et al., 2021) with overall annual prey biomass estimated by energetic demand (e.g. Baines et al., 2021).

2. Methods

2.1. Data source and study area

The data analysed here were collected during the DY098 cruise on the *RRS Discovery* in January and February 2019 at South Georgia and the South Sandwich Islands, part of a large-scale synoptic krill survey primarily designed to estimate krill biomass for the southwest Atlantic (Krafft et al., 2021). Arising from the multi-vessel survey, humpback and baleen whale abundance, together with bioenergetic-based estimates of krill consumption by whales have previously been reported (Baines et al., 2021) together with krill biomass in the Scotia Sea (Krafft et al., 2021). Here we focus on humpback and baleen whale abundance and krill biomass estimates in Food and Agriculture Organisation (FAO) Subarea 48.4 (Fig. 1) an area spanning the SSI, with sub-strata corresponding to a proposed Small Scale Management Unit (SSMU) (Hewitt et al., 2004) defined for the SSI (Trathan et al., 2008) and a 50 km buffer zone around the SSI archipelago declared by the Government of South Georgia and the South Sandwich Islands (Trathan et al., 2014; see also www.gov.gs/32110-2/).

2.2. Krill biomass density data

2.2.1. Derivation of krill biomass density from acoustic data

Krill biomass density data used here were derived from an acoustic survey of Subarea 48.4 (Fielding et al., 2019). Calibrated (following standard acoustic procedures after Demer et al., 2015) acoustic backscatter (S_v, dB re 1 m^{-1}) data at 120 kHz recorded on a Simrad EK60 echosounder were collected along transects (Fig. 2) in daylight. Detail of the acoustic survey, calibration, echosounder settings and processing is given in Krafft et al. (2021). In summary, krill swarms were detected using a swarm identification algorithm (Barange, 1994) on calibrated and cleaned data (spikes, interference and background noise removed). Data shallower than 20m and deeper than 250m or below the seabed when shallower were excluded. Acoustic data identified as krill were integrated into 1 nautical mile sections by 250 m deep cells and expressed as Nautical Area Scattering Coefficient (NASC, m^2 nmi^{-2}). The NASC was converted to krill biomass density (*rho*) in units of gm^{-2} using an acoustic scattering model (Stochastic Distorted Wave-born Approximation, McGehee et al., 1998) parameterised using net samples (Krafft et al., 2021). The dataset used consisted of 1,216 samples of NASC and *rho* respectively, each with associated position (WGS84 longitude and latitude), date and time.

2.2.2. Preliminary investigation of the statistical distribution of krill biomass density data

Moran (1950) and Geary (1954) tests were applied to assess positive spatial autocorrelation in the krill biomass density data. However, given the swarming behaviour of krill, there was a possibility of negative autocorrelation, in which high local values correlate with low proximal values and *vice versa*, due to depletion of surrounding areas that may result from aggregating krill. Negative spatial autocorrelation is a neglected concept (Griffith, 2019) that may nevertheless impact on spatial statistical procedures (Griffith and Arbia, 2010). In order to address this potential issue, a neighbourhood-mean method was developed to investigate the relationship between georeferenced *rho* values and the mean of surrounding values. The data were rasterised in a grid of resolution 0.05° which gave a latitudinal resolution of approximately 5.5 km and, as the transect lines ran N – S, this approximated to the distance between adjacent rasterised data points. The raster was then parsed with a weighted matrix of set size, such that the focal cell in the centre was given zero weight and the mean value of surrounding cells within the matrix calculated, ignoring cells without data. Smoothed plots were then generated with spot values on the x-axis and neighbourhood means on the y-axis, using the *R* package *ggplot2*.

2.2.3. Krill biomass density distribution modelling

Environmental covariates commonly used in the development of habitat models were compiled (Table 1) and a Pearson correlation matrix generated to identify correlated covariates. Initial attempts to fit single-stage Generalised Additive Models with *rho* as the response
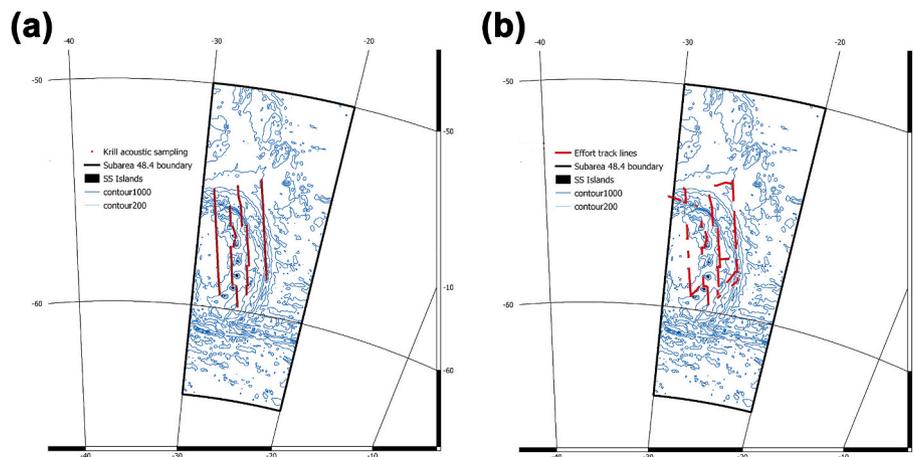
Fig. 2. Location of acoustic sample points in FAO sub-area 48.4 (above) and visual survey effort (below) in relation to bathymetry. 1000m isobaths depicted in dark blue, 200m isobaths where depth <1000m in pale blue.

Table 1
Covariates compiled for modelling krill biomass.

Name	Spatial resolution of source data	Temporal resolution	Units	Notes
Depth	<1 km	NA	M	From GEBCO
Slope	<1 km	NA	Degrees	Derived from GEBCO using an R function.
distBreak	1 km	NA	Km	Distance to 1000m bathymetric contour
CHL	4 km	Monthly	mg/m^3	Interpolated to fill gaps in coverage
Salinity	0.083°	Daily	g/kg	
SST	0.083°	Daily	°C	°K - 273
sstFronts	0.083°	Daily	°C/100 km	Calculated from SST with R package *grec*
eastward	0.083°	Daily	m/s	Eastward component of current velocity
northward	0.083°	Daily	m/s	Northward component of current velocity
Velocity	0.083°	Daily	m/s	Current velocity from east- & north-ward
npp	0.083°	Daily	mg/d/m^2	Net primary production[a]
mesoNekton	0.083°	Daily	g/m^2	Upper mesopelagic micro-nekton[b]
zooc	0.083°	Daily	g/m^2	Zooplankton[c]
iceMaxDist	0.083°	NA	M	Distance to ice at maximum extent in 2018

[a] Net Primary Production computed from chlorophyll, Sea Surface Temperature and Photosynthetically Active Radiation observations (chlorophyll from CMEMS multiyear product, SST from NOAA NCEI AVHRR-only Reynolds, PAR from INTERIM) and relaxed by model outputs at high latitudes (CMEMS biogeochemistry multiyear product). Expressed as carbon in sea water.
[b] Mass content of upper mesopelagic micronekton expressed as wet weight in sea water.
[c] Mass content of zooplankton expressed as carbon in sea water.

variable, and a two-stage or hurdle approach (Cragg, 1971; Potts and Elith, 2006), in which the probability of presence was estimated in a binomial first stage, and the spatial distribution of abundance estimated in a second stage, both yielded unrealistic results with confidence intervals approaching infinity.

An alternative approach was pursued using a point process model as a first step to predict relative abundance. Maxent is a Java application that uses presence data together with environmental covariates to estimate species distribution models (SDM) (Phillips et al., 2006) and, as it only uses presence records, it is immune to zero-inflation and challenges arising from the non-parametric distribution of quantitative data. Maxent has primarily been applied to informally collected data, such as that from platforms of opportunity or citizen science schemes, but it is equally applicable to data collected in designed surveys, especially, as in this case, when the distribution of data presents difficulties in obtaining a satisfactory fit with conventional regression methods. The main problem affecting Maxent is sampling bias (Fithian and Hastie, 2013; Kramer-Schadt et al., 2013; Newbold, 2010; Renner et al., 2015), however, in the case of a designed transect survey, sampling bias can be precisely accounted for, making this a potentially useful approach for the estimation of areal krill biomass from acoustic transect data.

Previous studies have demonstrated that Maxent is equivalent to an inhomogeneous Poisson process (Aarts et al., 2012; Fithian and Hastie, 2013) and that the *raw* output format from Maxent represents relative abundance (Phillips et al., 2017). Estimation of absolute abundance requires independent measures of local abundance, and Maxent models have been shown to correlate with such independently measured data (VanDerWal et al., 2009; Weber et al., 2017). Here we applied a generalised linear model (GLM) to correlate the Maxent *raw* output with *rho* values.

As the krill biomass density data *rho* is a continuous variable, rather than a count, the criterion for presence needed to be defined before input of presence location data to Maxent, as low *rho* values (e.g. <1 gm^{-2}) suggest krill may not be present in any m^2 with such a value, and that a threshold *rho* level should be set as the criterion for presence. A test was carried out to compare model performance for a series of unitary steps for *rho* from 0 to 5 gm^{-2} from which a threshold of *rho* = 4 gm^{-2} was selected, at which value the area under the curve (AUC) metric (Fielding and Bell, 1997) was maximised.

A bias raster was constructed at the same resolution as the covariate rasters (0.05° latitude and longitude) as a normalised sum of the count of sampling points in each grid cell. Where covariates were correlated, those making the least contribution to model fit in initial trial runs were removed, together with any covariates making no contribution. The final model was run with 100 replicate cross-fold validation and Maxent set to *raw* output, to generate a rasterised estimate of relative abundance with associated standard deviation (SD).

A quasipoisson GLM was then applied to model *rho* values recorded along transects with the corresponding Maxent *raw* output values as the predictor variable. This GLM was then used to predict *rho* values across

the full study area from the Maxent output and, by multiplying the area of each cell in the raster by the *rho* value predicted for that cell, an abundance estimate was obtained and 95% CIs were calculated from the SD. To calculate overall 95% CIs, the lower 95% interval from Maxent was used to generate the lower 95% interval from the GLM and likewise for the upper 95% interval, so that variation from Maxent was propagated through to the GLM variation estimates.

2.3. Whale density data

2.3.1. Abundance estimation

Sightings data were collected following a line transect protocol (see supplementary data for details) and analysed in a two-stage process. First we estimated detection functions from perpendicular distances and then we applied generalised additive models (GAM) to predict whale density as a function of environmental covariates, using detection functions to generate offsets for the effective area searched (for full details see Baines et al., 2021). Density surface models with associated variance were generated using *R* package *dsm* (Miller et al., 2013) for FAO Subarea 48.4, the CCAMLR SSI SSMU and GSGSSI 50 km buffer zone using raster grids with resolution of 0.05° latitude and longitude. Abundance estimates for humpback whales and all baleen whales were then calculated by summing the product of predicted density and cell area across rasters.

2.3.2. Estimation of krill consumption by baleen whales

We followed Baines et al. (2021) to determine energetic demand for the baleen whale abundance data from the DY098 survey, scaling consumption estimates according to abundance estimates for the FAO SSI Subarea 48.4, the SSI SSMU and the SSI 50 km buffer zone. To test the plausibility of these estimates we compared them with historical whaling data giving the date and weight of 781 adult humpback whales taken in Antarctic whaling grounds near the Balleny Islands (southwest Pacific, 66°55′0″S, 163°45′0″E) between 1949 and 1953 (Ash 1953, 1957). The data available were mean daily weights from 17 days between December 28 and February 19, so it was not possible to estimate variability within the weights of each day's catch. Weights were calculated from cooker fillings and therefore exclude blood and the contents of stomach and intestines. Mean daily weights were converted to metric units and a GAM applied to model weight as the response variable, using the number of elapsed days from December 28 as the predictor variable. The resulting model was used to predict weight gain over time, from which daily consumption rates of krill were calculated, using values for the energetic content of blubber as 32,000 kJ kg^{-1} (Vikingsson, 1990) and of krill 4.64 kJ g^{-1} (Clarke, 1984), assuming a metabolic efficiency in digestion and blubber deposition of 80% (Kenney et al., 1997; Lockyer, 1981).

2.3.3. Ecological relationship between krill and humpback whales

The DY098 survey collected whale sightings and krill biomass density data concurrently. However, application of GAMs to predict whale abundance using krill biomass density data as a covariate was not possible, as the krill data were confined to the transect lines and were not universally available. Three approaches were therefore taken to investigate the correlation of abundance and distribution between krill and humpback whales, one using observed values along transect lines, the others by comparing rasters of predicted abundance.

In the first method, we used the krill data to investigate the relationship between krill and humpback whale abundance along transect lines and test the hypothesis that there was a positive correlation between the spatial distribution of the two species.

Whale observation effort data were split into segments, using changes in observer team or sea state as break points (mean segment length = 14.4 km) and a detection function was then fitted to the perpendicular distances of humpback whale sightings. The effective strip width (ESW) for each effort segment was then estimated, taking into account the covariates applying to each respective segment. The density of whales in each segment was then estimated as the count of whales within the truncation distance, divided by the area effectively searched:

$$\sum_{d=0}^{t} c * \frac{1}{2 * l * ESW}$$

Where *t* is the truncation distance, *c* the count of whales, *l* is transect length.

A set of krill biomass density indices was calculated for each effort segment as the sum and mean of *rho* values, and as maximum and mean areal values calculated by multiplying sum and mean *rho* values by the area effectively searched for whales. A data frame was then assembled including all whale effort segments for which there was concurrent krill biomass density data (n = 92), using data collected in both FAO Subareas 48.3 (Figs. 1) and 48.4 to maximise sample size. GAMs were applied with humpback whale density as the response variable and a krill biomass density index as the predictor variable.

In the second method, rasters of predicted abundance of humpback whales and biomass density of krill (see below) were first normalised by dividing the value of each cell by the sum of the values of all cells. Pearson correlation coefficients between the two rasters were calculated, using a focal neighbourhood function to compare clusters of adjacent raster cells between two rasters of the same extent and resolution (R function *corLocal*). This allowed the selection of progressively larger cluster sizes to generate rasters of correlation coefficients, together with rasters of significance with *p*-tests.

A third visual comparison of the spatial distribution of density was made by aggregating the raster data to produce raster plots of predicted humpback whale and krill biomass densities at a resolution of 1° latitude and longitude.

3. Results

3.1. Distribution of effort

Navigational concerns in the poorly charted waters of the SSI region resulted in relatively few data being collected over the shelf; 97% of acoustic data points were from depths >1000m and 85% were from depths >2000m (Fig. 2, left). Survey effort was not evenly distributed throughout the FAO Subarea 48.4 study area, being confined to an area proximal to the islands and the SSI trench (Fig. 2, right).

3.2. Krill biomass density

3.2.1. Distribution and spatial autocorrelation

Krill biomass density data were markedly zero-inflated, with 48% zero values, and were characterised by extreme skew and kurtosis. The *fitDist* function in *R* package GAMLSS (RigbyStasinopoulos, 2005) indicated that the data followed a PARETO 2 or LOMAX distribution. Both Moran (1950) and Geary (1954) tests indicated that the krill biomass density data were not positively autocorrelated (Moran I statistic = 0.05, *p* = 0.15; Geary C statistic = 0.91, *p* = 0.04). However, plots of single raster cell density values against neighbourhood mean values indicated negative spatial autocorrelation in which locations with density values in the region 0–100 gm^{-2} were surrounded by higher average values, the steepness of the curve indicating rapidly increasing negative autocorrelation until a threshold was reached at around 150 gm^{-2}, where the slope abruptly changed, and cells with higher density values tended to have lower-value neighbouring cells (see supplementary file for details).

3.2.2. Relative krill biomass density model

We used the AUC metric (Fielding and Bell, 1997) to evaluate Maxent models, where values of 0.5 indicate the model performs no better than random whereas values of 1.0 indicate a perfect fit. The

mean test AUC for the replicate runs was 0.879, with a standard deviation of 0.062. Distance to the shelf break was the most significant covariate, followed in importance by distance to ice at its maximum extent (Table 2). Response curves for individual covariates are shown in Fig. 3.

3.2.3. Absolute abundance estimation

We used a Generalised Linear Model (GLM) to relate the Maxent output with the corresponding *rho* values; finding a highly significant relationship ($p < 0.001$) (Fig. 4). Areal krill biomass estimates from the application of the GLM to the Maxent output are included in Table 3 and the predicted distribution plotted in Fig. 5, showing the highest concentration of krill biomass density to the north and northeast of the islands.

3.3. Baleen whale abundance and distribution

Abundance estimates for the entire study area, the SSI SSMU and the SSI 50 km buffer zone are included in Table 3. Model outputs are plotted in Fig. 6, showing predicted concentrations of both humpback and all baleen whales to the north and northeast of the islands. See the supplementary data file for further detail.

3.4. Ecological relationship between krill and humpback whales

3.4.1. Spatial correlation between krill biomass and humpback whale density

The best fitting detection function for humpback whale sightings data was obtained with truncation at 2 km, observer team and sea state as covariates, using a hazard rate model with no adjustment terms. Based on our first method to determine an ecological relationship between krill and humpback whales, a quasipoisson GAM with humpback whale density as the response variable and the mean *rho* index of krill biomass density as the sole predictor explained 12.9% of deviance and the mean *rho* predictor had low significance ($p = 0.2$). However, including other explanatory variables improved the explanatory power of models; including SST fronts, distance to shelf break and current velocity as covariates increased the significance of krill biomass density as a predictor of humpback whale density. The plotted smooth function of mean krill *rho* values (Fig. 7) suggested no clear relationship between humpback whale and krill biomass density at low mean *rho* values, but showed a positive relationship with whale density as *rho* values increased beyond 150 gm^{-2}.

Comparison of fine-scale rasters (resolution 0.05°) of predicted humpback whale abundance and krill biomass density found only a weak correlation, which reduced with increasing focal neighbourhood scale and, when plotted, the distribution of Pearson coefficient values appeared random (see supplementary data). However, when predicted humpback whale abundance and krill biomass density were plotted at a resolution of 1°, the highest values for each raster were found in the same cell, for which the Pearson correlation coefficient was 0.89 and 60% of cells had a coefficient >0.5 (see supplementary data).

3.4.2. Krill consumption by baleen whales

Estimates of krill consumption by baleen whales ranged from 19% to 29% of estimated krill biomass (Table 3). When weights of humpback whales were modelled with the number of days after December 28 as the predicting variable, a highly significant ($p < 0.001$) relationship was found, with 81% of deviance explained by the GAM. Some variation was to be expected because no distinction was made in the raw data between males, females and pregnant animals. When predicted over a 60 day period (Fig. 8), body weight increased rapidly over a period of approximately 3 weeks before levelling off. Krill consumption rates required to achieve this weight gain (Fig. 9) show a corresponding decline over the same period. Note that this represents the excess consumption over levels necessary to maintain daily activity.

3.4.3. Predator – prey ratios

Point estimates of baleen whale and krill areal biomass between the 2000 and 2019 surveys are compared in Table 4. Note that baleen whale estimates in 2019 were confined to FAO Subareas 48.3 and 48.4, where those for 2000 covered a wider area encompassing the Scotia Sea. While whale biomass increased five-fold between the two surveys, krill biomass remained similar, resulting in a commensurate change in predator – prey ratio.

4. Discussion

4.1. Krill biomass density distribution and areal krill biomass

Modelling the spatial distribution of krill biomass density using GAMs proved challenging, due to the statistical distribution of the data. We overcame this by using Maxent to model relative biomass density based solely on presence data and then converting relative to absolute biomass density using a GLM to model the relationship between the Maxent output and the krill biomass density data. It is plausible that the statistical distribution of krill biomass density is highly variable between different times and locations, such that regression models may be appropriate in some cases, but not in others (e.g. Silk et al., 2016).

Modelled krill biomass density distribution can be informative for management, especially where ecological co-variates are found to be significant. Such models can inform about the areal distribution of biomass as well as ecological drivers of biomass density. From a management perspective it may therefore be valuable to develop approaches to krill biomass estimation that improve on the parametric approach suggested by Jolly and Hampton (1990), by incorporating spatially explicit models with robust estimates of variance. The Maxent/GLM method used here has the potential to provide such a general solution, and a wider study comparing our approach with other modelled approaches such as GAM, and with Jolly and Hampton (1990), would now be useful for evaluating the general applicability of the Maxent/GLM approach.

The areal krill biomass estimate presented here for the whole of Subarea 48.4 (7,326,404 t, 95% CI 4,470,795 - 10,674,991) does not differ markedly from the estimate reported by Krafft et al. (2021) for the Eastern Scotia Sea (7,677,000 t, variance component 1,555,000) using the Jolly and Hampton (1990) approach. Although the variance estimation metrics differ between these two estimates, it is apparent that estimated variance was greater in our results than in those of Krafft et al. (2021). However, in heterogenous data that are (negatively) spatially autocorrelated it is recognised that confidence intervals can be biased (Anselin and Griffith, 1988; Zhang et al., 2009), resulting in values that are lower than data justify, so the higher variance values presented here may in fact be more realistic.

Previous large scale studies have generally failed to find strong, consistent relationships between krill biomass density and individual environmental variables (Silk et al., 2016). Our finding that distance to the SSI shelf break was the single most significant covariate driving krill distribution was consistent with a fine-scale study at South Georgia
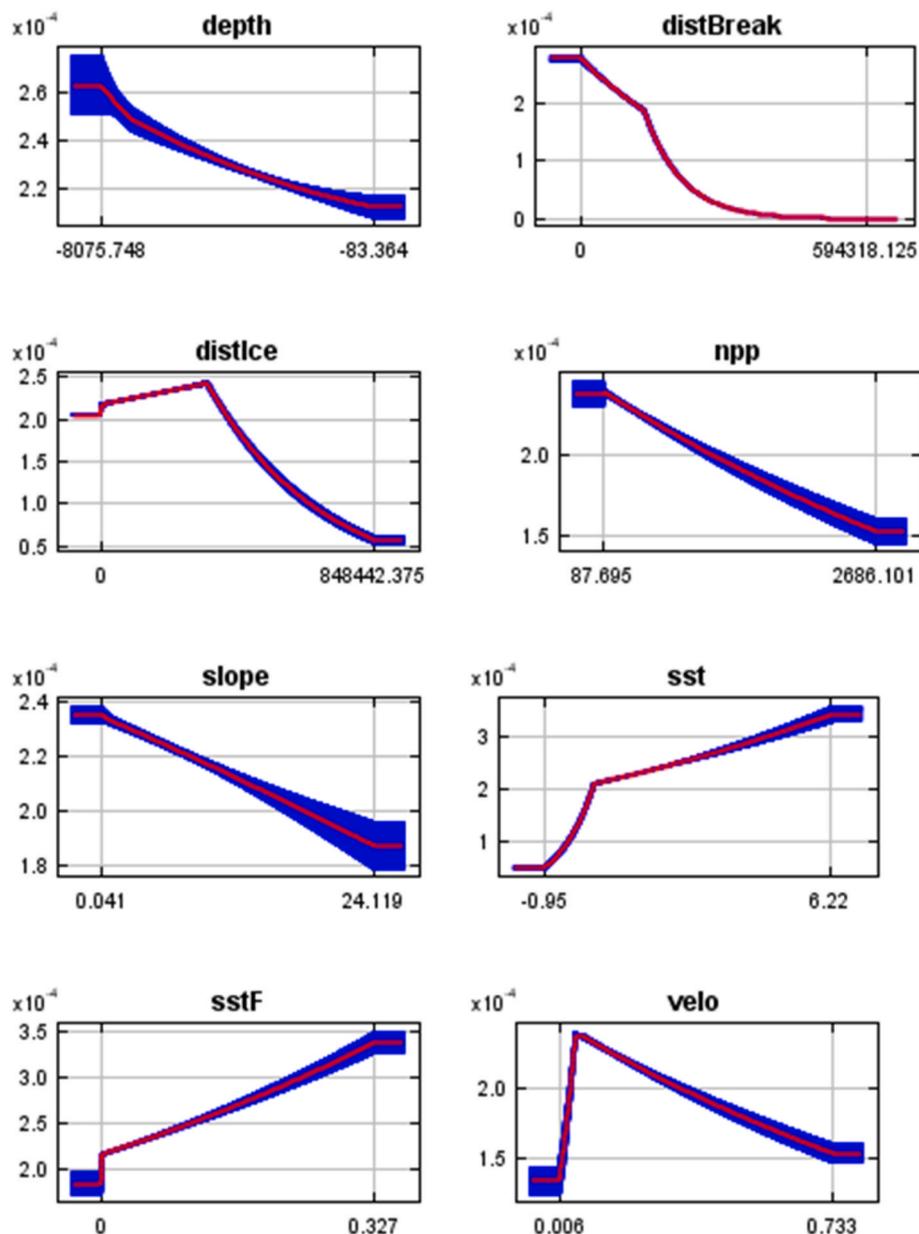
Table 2
Relative contributions of covariates in the Maxent model. See Table 1 for variable definitions.

Variable	Percent contribution	Permutation importance
distBreak	86.1	72.6
distIce	6.8	9.9
depth	2.4	1.6
Sst	2	9.9
sstF	1	2
slope	0.9	0
velo	0.5	3.4
npp	0.3	0.7

Fig. 3. Response curves of variables in the Maxent model (mean of 100 runs in red, ± 1 SD in blue). See Table 1 for variable definitions.

where Trathan et al. (2003) found the highest densities of krill in the shelf-break zone. An association between topographic breaks, *Euphausiid* concentrations and feeding baleen whales has also been noted in many regions (Baines and Reichelt, 2014; Croll et al., 2005; Moors--Murphy, 2014; Schoenherr, 1991; Simard and Lavoie, 1999), thought likely to be caused by current-driven advection through shelf-edge gulleys or canyons and consequent enrichment and concentration of prey.

While the estimated areal krill biomass for the wider Scotia Sea was similar between the CCAMLR 2000 survey (Fielding et al., 2011) and the 2019 survey, there were major differences in the spatial pattern and distribution, with the estimated krill density in 2019 for the Eastern Scotia Sea (Subarea 48.4) being 13.9 times greater than in 2000 (Krafft et al., 2021). Model-based estimates of humpback whales in the Scotia Sea also increased by an order of magnitude from the 2000 survey (Hedley et al., 2001) to 2019 (Baines et al., 2021). The great whales recycle large volumes of nutrients, especially in feeding habitats, excreting nutrients that fertilise oceanic habitats (Lavery et al., 2014; Nicol et al., 2010; Roman et al., 2014) and it is plausible that increased

abundance of humpback whales has contributed to the increased biomass of krill in the SSI region. However, while the humpback whale data presented here are consistent with a continuous trend of recovery observed in breeding habitats (Zerbini et al., 2019), the krill data represent two snapshot estimates some 19 years apart, for a species known to display significant inter-annual variability (Fielding et al., 2014; Loeb and Santora 2015; Reiss et al., 2008; Steinberg et al., 2015). Further monitoring of krill biomass and nutrient cycling in the region would be needed to better understand interannual variation in krill biomass.

The aggregating behaviour of krill results in a patchy distribution, with marked variation in swarm shape, size and biomass (Tarling et al., 2009). We found a threshold for krill biomass density at approximately 150 gm^{-2} associated with increased humpback whale density. A number of studies have classified krill swarm types on the basis of parameters such as size, shape and density (reviewed by Tarling and Fielding, 2016), with spatially large swarms not having a lower density of krill compared with small, tight swarms (Tarling et al., 2009). We speculate here that this density threshold may be a useful reference with which to
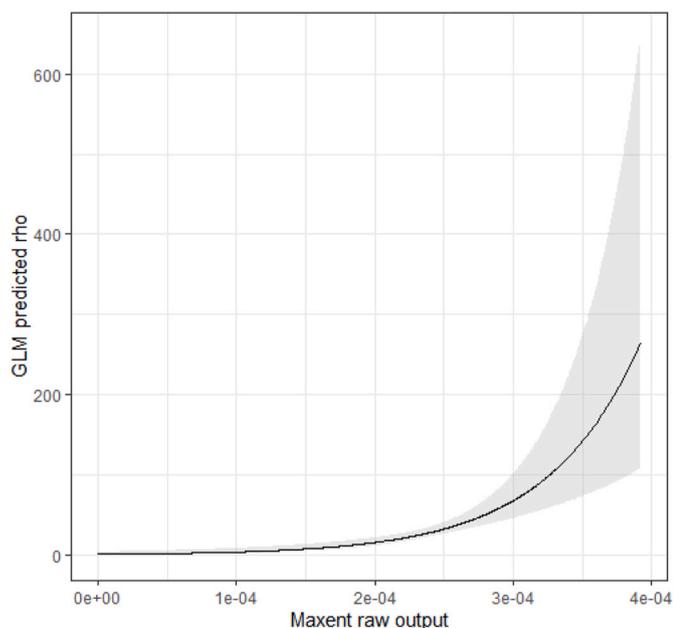
Fig. 4. Relationship between the Maxent raw output and *rho* values predicted by the GLM with 95% CI shaded.

distinguish densely swarming krill that is attractive to baleen whales (Piatt and Methven, 1992; Goldbogen et al., 2019), and could also be indicative of swarm size. Aggregating behaviour to form swarms has probably evolved as a response to predation (Olson et al., 2016) and is likely to be most effective in relation to smaller predators such as penguins and pinnipeds that capture single or small numbers of krill at a time. Penguins and fur seals are land-based during the breeding season and therefore forage in habitats within a limited radius of their breeding colonies (e.g. Warwick-Evans et al., 2018). In contrast, baleen whales are bulk feeders, and while some have evolved foraging behaviour that allows skimming, others are lunge feeders that preferentially exploit large, dense swarms of krill (Werth, 2000). Humpback whales are lunge feeders, so it is not surprising that our results show their colocation with high krill biomass density. If predation pressure is a key driver of krill behaviour then it might be expected that krill in coastal or shelf waters, where land-based predators are more common, exhibit different aggregation states compared to krill in the open ocean where the main risk of predation is from whales.

4.2. Baleen whale abundance and distribution

Fitting models to multi-species groups, in this case to all baleen whales, raises issues associated with potential differences between species in their response to environmental covariates. Ideally, it would be useful to include species as a covariate, but this was not possible given the relatively high proportion of sightings not identified to species level.

Table 3
Abundance estimates for humpback and all baleen whales, estimated krill biomass and estimated biomass of krill consumed by all baleen whales at different spatial scales in SSI waters. The percentage of krill consumed is based on the point estimate of krill biomass.

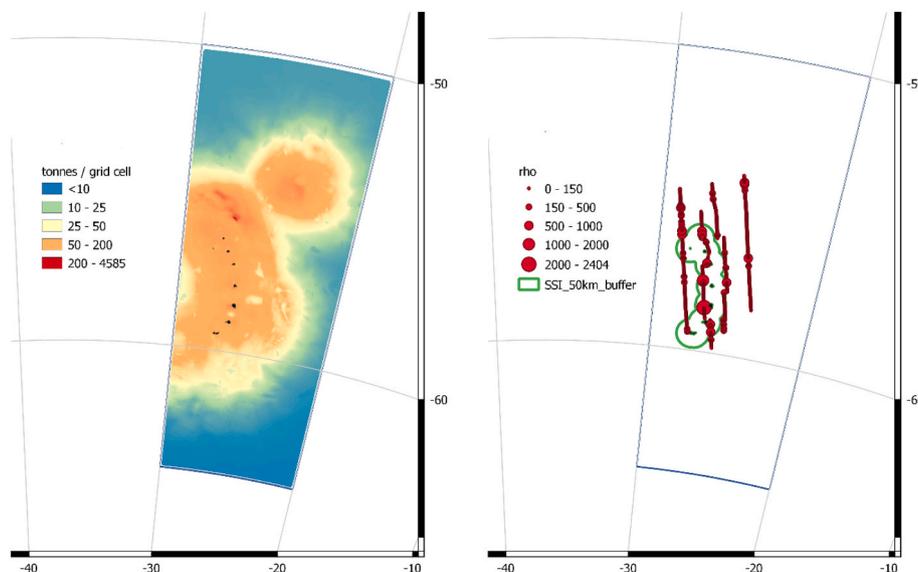| Stratum	Subarea 48.4	CCAMLR SSI SSMU	GSGSSI SSI 50 km buffer
Area (km^2)	944,953	129,754	82,987
Humpback whales	11,656	3,121	1,490
(95% CI)	(5,865–23,164)	(1,970–3,935)	(895–1,966)
Baleen whales	12,919	2,481	1,224
(95% CI)	(7,796–21,409)	(1,566–3,128)	(735–1,615)
Krill (tons)	7,326,404	2,261,137	1,338,179
(95% CI)	(4,470,795 - 10,674,991)	(1,523,091–2,669,443)	(936,489–1,541,972)
Krill consumed (tons)	1,415,005–2,122,508	271,742–407,612	134,064–201,095
Percent krill consumed	19% – 29%	12% - 18%	10% - 15%

Fig. 5. The distribution and abundance of krill biomass (t per gridcell, where mean cell area = 16.75 km^2) predicted by the Maxent/GLM method (left); *rho* values (gm^{-2}) from acoustic data along transect lines (right).
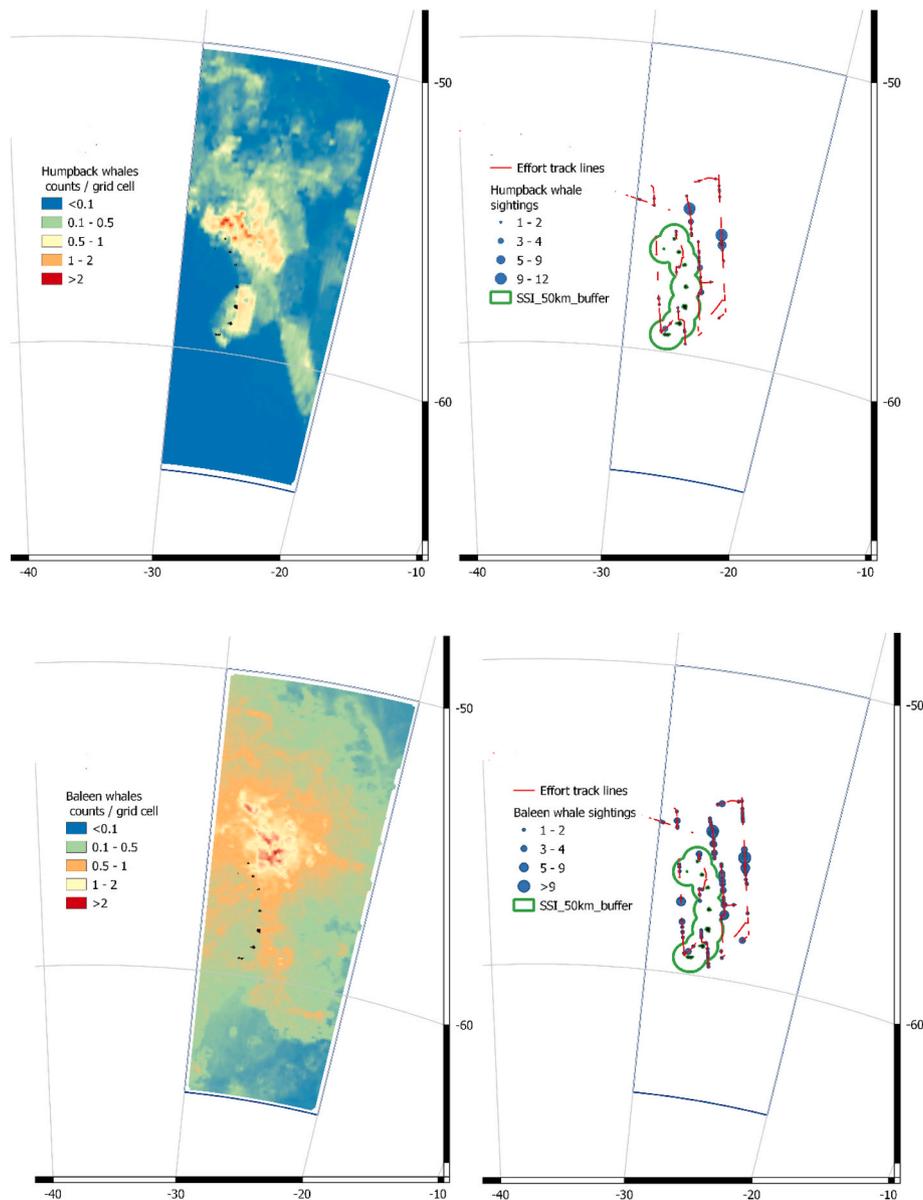
Fig. 6. GAM predictions of the spatial distribution of abundance of humpback whales per grid cell (mean cell area = 16.75 km^2) (upper left) and all baleen whales per grid cell (lower left) with corresponding sightings along track lines (right).

Fewer covariates were retained in the baleen whale model and therefore the fine-scale detail in the humpback and baleen whale models differed, although the overall patterns were similar. These differences were most evident when smaller areas were considered, for example the CCAMLR SSI SSMU and GSGSSI 50 km buffer zone where estimates of humpback whales exceeded that for all baleen whales. However, given the 95% CI of baleen whale abundance, this apparent anomaly was not statistically significant.

It may be expected that the main driver of predator distribution is the distribution of prey. This is self-evident at a scale of 1° latitude and longitude, though only a weak correlation between humpback whale and krill abundance was found at finer scales or along transect lines when krill biomass density was the sole predictor in models. A similar scale-dependent relationship between whale abundance and krill density has been reported from South Georgia (Reid et al., 2000), in a study that also found whales were absent from inshore areas (<300m), despite supporting relatively high krill densities. Including additional environmental covariates improved model fit, in this case proximity to SST fronts and the shelf break were both significant covariates and current

velocity further improved model performance. This may indicate that humpback whales seek environmental conditions suitable for finding prey and that their distribution may be predicted equally well using environmental variables as proxies for prey distribution, as has been shown to be the case for bottlenose dolphins (*Tursiops truncatus*) (Torres et al., 2008). The most significant environmental factors driving humpback and baleen whale distribution in our models were chlorophyll-a concentration and proximity to sea surface temperature fronts, which is consistent with other studies of humpback whales in feeding habitats (Meynecke et al., 2021).

The data used in this study were collected over a two-week period, so they represent a snapshot of summer abundance and distribution at that time. Whales are highly mobile species and the swarming behaviour of krill results in highly variable patterns of prey distribution. The fine detail of distribution patterns presented here is therefore less important than the general picture, which is of relatively high levels of whale abundance on the east side of the South Sandwich Islands, with a notable concentration to the north and northeast of the islands. Predicted krill biomass density distribution was also highest to the north of the islands,
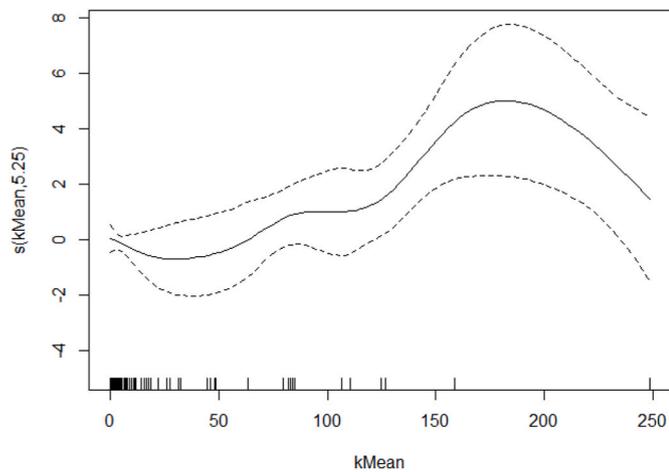
Fig. 7. GAM smooth term for krill mean *rho* (gm^{-2}) with 95% confidence limits (dashed lines) from a GAM incorporating SST fronts, distance to shelf break and current velocity as additional covariates and humpback whale density as the response variable.
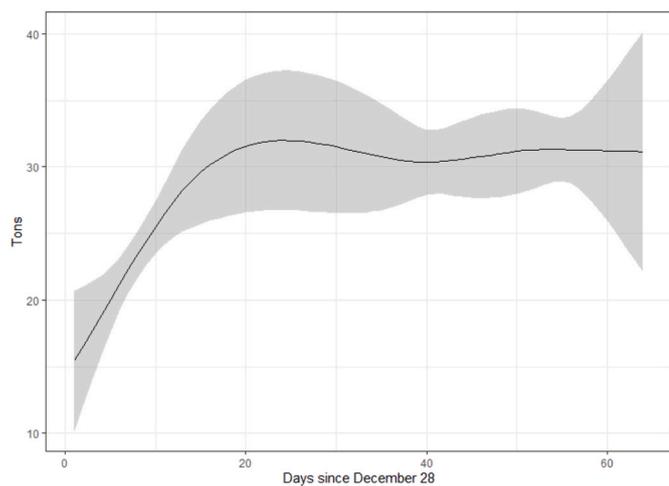

Fig. 8. Humpback whale weight increase over time predicted by GAM with 95% CI shaded.
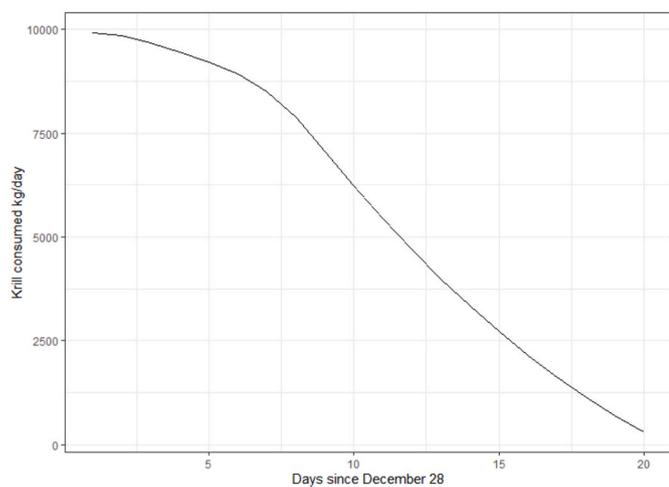

Fig. 9. Daily krill consumption required to achieve model-predicted weight gain by an individual humpback whale per day since December 28.

Table 4

Estimates of baleen whale and krill biomass for 2000 and 2019 with predator – prey ratios for these taxa. Sources of data: [1] Hedley et al. (2001); [2] Fielding et al. (2011); [3] Baines et al. (2021); [4] Krafft et al. (2021).

Year & Stratum	Baleen whale biomass (t)	Krill Biomass (t)	Predator-prey ratio
2000 Scotia Sea	266,460[1]	34,928,000[2]	1 : 131
2019 Scotia Sea	1,314,720[3]	31,585,000[4]	1 : 24
2019 SSI	387,570[3]	7,326,404[4]	1 : 19

coincident with the area of highest predicted whale density. The location of this focus of activity corresponds with results of satellite tracking studies (Zerbini et al., 2011b) that found whales tagged in Brazil moving to feeding grounds to the north of the SSI, where they were tracked for up to 102 days (see also Bamford et al., 2022).

At smaller scales, topographic features such as headlands and islands obstruct and therefore accelerate current flow, thereby concentrating and funnelling prey to the advantage of predators. This effect has been observed over a wide range of spatial scales and taxa, with predators typically gathering to exploit prey in the wake of such features (e.g. Allen et al., 2001; Chenoweth et al., 2011; Cox et al., 2018; Harrison et al., 2020; Holm and Burger, 2002; Pierpoint, 2008; Wolanski and Hamner, 1988). A key property of these habitats in terms of attractiveness to predators is the spatio-temporal predictability of prey availability.

The term Island Mass Effect (IME) was first coined by Doty and Oguri (1956) in order to describe enhanced primary production in the vicinity of islands. For example, IME has been associated with a number of physical and oceanographic processes, including interaction between current flows and subsea topography, upwellings, micronutrient (iron) availability, and freshwater run-offs (Elliott et al., 2012). Stabilisation of the surface layer by meltwater is thought to contribute to the IME around the SSI (Perissinotto and LaubscherMcQuaid, 1992). High productivity around South Georgia has been linked to an enhanced supply of iron (Atkinson et al., 2001) and Blain et al. (2001) found surface waters in the wake of the Kerguelen archipelago rich in both chlorophyll-a and dissolved iron. Harrison et al. (2020) found increased density and biomass of krill near the Balleny Islands compared to adjacent open water, associated with high sightings rates of humpback whales, and attributed this to the IME. In addition to enhanced productivity through IME, the SSI archipelago forces the ACC to deviate around the north of the islands, funnelling advected krill to the north and northeast where our models predicted the highest concentrations of both krill and baleen whales.

4.3. Krill consumption by baleen whales

There are essentially two approaches to the estimation of krill consumption by baleen whales: estimation of daily ingestion rates (e.g. Reilly et al., 2004; Savoca et al., 2021) and estimation of annual energy demand (e.g. Baines et al., 2021). Both approaches make assumptions, or rely on extrapolations from other systems or taxa; in the case of ingestion rates these include the number of days of active feeding and variation in feeding rates arising from prey availability and the nutritive condition of whales. The energy demand approach requires an assumption regarding the proportion of the whale's annual energy needs that are consumed and stored in their high latitude feeding grounds and estimation of field metabolic rates.

We favoured an energetic demand approach (see Baines et al., 2021 for our justification) to provide an envelope of estimated krill consumption. This approach does not allow calculation of confidence intervals, so we used historical whaling catch data to assess our consumption estimates. Few data are available for weights of humpback whales (Lockyer, 1976), as weighing large whales is non-trivial and the

operational challenges of weighing a live whale are insurmountable. Catch statistics from 20th century whaling (Allison and Smith, 2004) tend only to give linear morphological measurements. However, Lockyer (1981) analysed data on weight gain in whales from seasonal catch weights and concluded that most humpback whales arrived in South Georgia before the end of December with a body weight of around 15 t, and gained weight rapidly, before weight increase declined in February, with an overall weight gain of 15 t. As such, our expectation was that total prey consumed would be energetically equivalent to 15 t of accumulated blubber generated with a digestion efficiency of 80%, plus additional energy required for feeding. Assuming the energy density of blubber to be 39,300 kJkg^{-1} (Schmidt-Nielsen, 1997; quoted in Braithwaite et al., 2015) and the energetic value of krill to be 4.64 kJg^{-1} (Schaafsma et al., 2018), this would require consumption of 158,810 kg of krill to form 15 t of blubber, plus additional consumption to fuel the energetic costs of feeding. This is consistent with the consumption rates for humpback whales feeding in the Scotia Arc based on Baines et al. (2021) of 167 – 215 t, although given the relatively high energetic costs of lunge-feeding (Goldbogen et al., 2017) the upper limits of consumption estimates in Baines et al. (2021) are likely to be realistic.

Our GAM, based on humpback whale weight data from Ash (1953), predicted consumption rates comparable to those proposed by Savoca et al. (2021), but for much shorter periods of time than those indicated by Savoca et al. (2021). It has been widely assumed that, as southwest Atlantic humpback whales are thought to spend around 120 days in what is generally referred to as their high latitude feeding grounds, this is the length of time they feed, and therefore daily consumption rates have been multiplied by such numbers of days to measure total consumption (e.g. Reilly et al., 2004; Savoca et al., 2021). However, viewed differently, if humpback whales are primarily a species of prey-rich Southern Ocean habitats that migrate to oligotrophic, calm, warm, coastal waters to calve and breed, then we might expect a brief period of intensive feeding on return from their warm-water breeding habitats in order to restore depleted blubber, followed by feeding at a reduced rate sufficient to meet daily energetic requirements and support foetal development. Blubber plays an important role in thermoregulation (Favilla et al., 2021) and it would be advantageous for whales to accumulate insulation as quickly as possible on returning to cold-water habitats.

A number of theories have been proposed to explain the migratory reproductive strategy of humpback whales, including predator avoidance, and the need for calm waters in which to give birth and nurse neonates and warm water to reduce thermoregulatory stress on calves (Clapham, 2018). The penalty for this behaviour is seasonal starvation and consequent loss of nutritive condition. Such a penalty would be compensated for if there were sufficiently high densities of available krill. As such, high ingestion rates (Savoca et al., 2021) are required so that condition can be restored quickly and our analysis of historic whaling data suggests this can be achieved in three or four weeks.

Variation between demographic groups within the population is likely to affect individual feeding rates, as e.g. lactating females, growing sub-adult animals and adult males will differ in their energetic demand. Our estimate of the duration of intensive feeding is therefore likely to be highly variable and indeed, it may be possible that whales engage in a final period of more intensive feeding immediately prior to their migration. This highlights the need for future work focusing on fine-scale behaviours of foraging whales to assess the number of foraging days per year, and changes in whale foraging effort over the feeding season.

The rapid recovery of the southwest Atlantic humpback whale population raises questions concerning how and at what level the population size may be limited. Recent studies (Bortolotto et al., 2021; Zerbini et al., 2011a, 2019) have assumed that the population was at carrying capacity prior to exploitation by industrial whaling, and that population growth will be constrained by a carrying capacity of similar magnitude. However, the historical carrying capacity, and indeed the current

carrying capacity, is likely to be limited by the biomass of available krill, and the biomass of other consumers competing for the same resource. Such resource competition will plausibly lead to habitat differentiation and niche partitioning as, in such long-lived large mammals with low reproductive rates, populations tend to be limited by resources. Various ecological consequences may then may result, as density-dependent changes occur when the population nears carrying capacity (Fowler, 1981). For example, a study of North Atlantic fin whales found blubber thickness declined at times of low prey availability and pregnancy rates declined at low blubber thickness, demonstrating a density-dependent response of pregnancy to prey limitation, mediated through body condition (Williams et al., 2013). Here, we confirm a preference by humpback whales for areas with dense krill swarms, as reported by other authors (e.g. Burrows et al., 2016) and a threshold prey density for foraging behaviour (Piatt and Methven, 1992) has been suggested. The distinction between prey biomass and density is important as the energetic efficiency of lunge feeding is proportional to krill density (Goldbogen et al., 2017, 2019) and we may therefore expect the fecundity of southwest Atlantic humpback whales to be dependent on the availability of krill swarms of sufficient density and abundance, as it is for southern right whales (Seyboth et al., 2021).

In the pre-whaling era, humpback whales competed for prey with large populations of other baleen whale species that were subsequently heavily depleted by whaling. Antarctic blue whales were formerly abundant in the Southern Ocean (Branch et al., 2007) and while there are indications of recovery in the Scotia Arc (Calderan et al., 2020), sightings surveys reveal that blue whales remain relatively scarce (e.g. 2% of baleen whales identified by Baines et al., 2021). If the carrying capacity of humpback whales before the whaling era was determined largely by the availability of krill at a time when there were significantly larger populations of other krill-feeding whales than currently exist, we might predict a higher carrying capacity now and dynamic interaction between species competing for the same prey resource, such that an increased carrying capacity for humpback whales may reduce that of competitors such as blue whales. However, as the abundance of larger fin and blue whales increases, niche partitioning between sympatric krill predators (Friedlaender et al., 2021; Santora et al., 2010) may become more evident. The synchronous nature of humpback whale migration emphasises the importance of krill biomass density in the SSI region during January and February (Horton et al., 2020). Ash (1953) noted that the rapid rate of weight increase during this time of year in humpback whales was not seen in blue and fin whales, from which he inferred a lack of synchronicity in the migratory behaviour of those species. However, niche partitioning (Clapham and Brownell, 1996; Friedlaender et al., 2009; and Friedlaender et al., 2021) may be a more likely response to interspecific competition in baleen whales than adjustment of migratory timing.

At the SSI, the proportion of the standing stock of krill estimated to be consumed by baleen whales depends upon the scale of assessment. For FAO Subarea 48.4, consumption by baleen whales was estimated at 19 - 29% of the available krill biomass, for the CCAMLR SSI SSMU 12 - 18%, and for the GSGSSI 50 km buffer 10 - 15%. Thus, with increasing scale of estimation, the proportion consumed increases. Almost certainly, this reflects the scale of habitat use by baleen whales. At the smaller scale, i.e. at the scale of the GSGSSI 50 km buffer, Clucas et al. (2022) estimate that the dominant avian krill consumer on the SSI, the chinstrap penguin *Pygoscelis antarctica*, consumes approximately 258, 000 t of krill over the chick-rearing period, not accounting for the requirements of non-breeding adults or chicks. Therefore, minimum estimates suggest that close to the island, consumption may be equivalent to 31.8% of krill standing stock. This figure does not account for other krill consumers, such as gentoo penguins *P. papua*, Adélie penguins *P. adeliae*, or macaroni penguins *Eudyptes chrysolophus*, each of which is known to have large breeding populations on the SSI (Lynch et al., 2016). With potentially large consumption ratios, the temporal-spatial dynamics of the SSI region become important (Clucas et al., 2022) and remain

uncertain, as the replenishment rates of krill in the flow of the ACC are unknown. How replenishment rates interact with baleen whale feeding rates, especially intensive feeding early in the season, is key to understanding how krill availability propagates into predator biomass.

The dynamic balance between krill availability and predator demand raises a number of important issues. Firstly, the relevant scale needed for ecosystem assessment, and secondly, whether existing assessments reflect ecosystem operation in a meaningful manner. For large baleen whales, assessment of large geographic areas of habitat will be needed to properly document ecosystem function and change. Without appropriate monitoring at scales relevant to predators, removal of krill by humans should be extremely closely managed, if allowed at all. Areas and seasons in which whales (or penguins) feed intensively should be highly protected. Our findings suggest the need for strong protections for whales within the first month they arrive to the Antarctic, including the period from November to February.

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.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2022.103867.

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