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RESEARCH ARTICLE

A new dynamic distribution model for Antarctic krill reveals interactions with their environment, predators, and the commercial fishery in the south Scotia Sea region

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Abstract

The management strategy for the Antarctic krill (*Euphausia superba*) fishery is being revised. A key aim is to spatially and temporally allocate catches in a manner that minimizes impacts to both the krill stock and dependent predators. This process requires spatial information on the distribution and abundance of krill, yet gaps exist for an important fishing area surrounding the South Orkney Islands in the south Scotia Sea. To fill this need, we create a dynamic distribution model for krill in this region. We used data from a spatially and temporally consistent acoustic survey (2011–2020) and year-specific environmental covariates within a two-part hurdle model. The model successfully captured observed spatial and temporal patterns in krill density. The covariates found to be most important included distance from shelf break, distance from summer sea ice extent, and salinity. The northern and eastern shelf edges of the South Orkney Islands were areas of consistently high krill density and displayed strong spatial overlap between intense fishing activity and foraging chinstrap penguins. High mean krill density was also linked to oceanographic features located within the Weddell Sea. Our data suggest that years in which these features were closer to the South Orkney shelf were also years of positive Southern Annular Mode and higher observed krill densities. Our findings highlight existing fishery–predator–prey overlap in the region and support the hypothesis that Weddell Sea oceanography may play a role in transporting krill into this region. These results will feed into the next phase of krill fisheries management assessment.

The Scotia Sea is estimated to contain more than 50% of the global population of Antarctic krill (*Euphausia superba*; Atkinson et al. 2004). Here, krill dominate the flow of energy between primary producers and higher predators (Murphy et al. 2007). Particularly important are the waters surrounding the South Orkney Islands, which are a source of krill for dependent cetaceans, and for seabirds and pinnipeds that breed on the South Orkney Islands (Casaux et al. 2016; Dias et al. 2018) or further north at South Georgia (Atkinson et al. 2001). In large part, this is due to the South Orkney Island's position east of the Antarctic Peninsula and part of the rugged topography of the South Scotia Ridge (Fig. 1). Oceanographically, the archipelago lies within the Weddell-Scotia Confluence, which is bounded by two globally influential current systems—the southern boundary of the Antarctic Circumpolar Current to the north and the Weddell Sea Gyre to the south. The exchange of water across the Confluence impacts regional and Atlantic-scale circulation and thus pelagic ecosystem dynamics (Meredith et al. 2015).

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Data Availability Statement: Acoustic data used in this manuscript are stored at the Norwegian Marine Data Centre, held at the Institute of Marine Research. Access to them is welcomed for collaborative and comparative efforts; contact Bjørn A. Krafft. Environmental data are available online (sources listed in Supporting Information Table S1). Fisheries data were provided by the Commission for the Conservation of Antarctic Marine Living Resources Member States (data request number 698). Gridded spatial predictions of krill generated in this study and the source code for analyses and figures are available at https://doi.org/10.5285/4FD0A1BF-DA1A-4021-82EB-2FC513910E32.

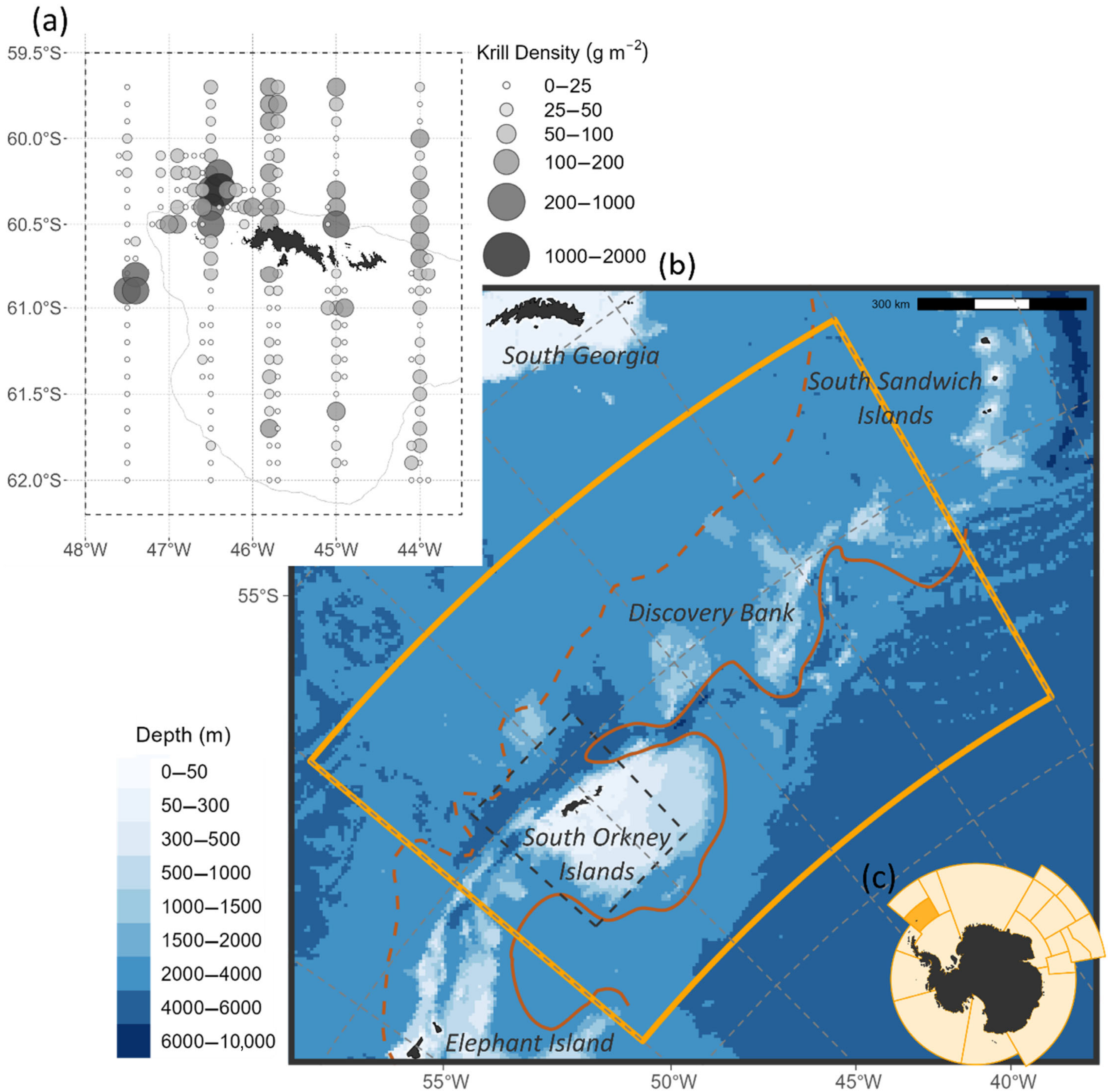

Fig. 1. (**a**) Map of krill density estimates, averaged across 10 years of the krill acoustic survey around the South Orkney Islands and (**b**) the wider study area of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Subarea 48.2, which is delimited by the orange box within the Southern Scotia Sea. Location of the Subarea 48.2 (dark orange) relative to other CCAMLR subareas (light orange) is shown in (**c**). Bathymetry scale across the region is shown in blue and the 500 m isobath is shown in light gray in panel (**a**). The Southern Boundary of the Antarctic Circumpolar Current and the Weddell Front are shown by dashed and solid lines, respectively, in panel (**b**).

Krill are also the target of the largest commercial fishery in the Southern Ocean (Nicol, Foster, and Kawaguchi 2012), which is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). The South Orkney Islands are located within Food and Agriculture Organisation Statistical Subarea 48.2 (Fig. 1), an area of

850,000 km^2 which, since 2019, has had the highest reported krill catch of any subarea where krill fishing takes place. Catch levels within the southwest Atlantic subareas are restricted by an interim annual catch limit of 620,000 t. To ensure precaution, this temporary limit was historically further subdivided between subareas, 45% of which was allocated to Subarea 48.2 (see box 3 within Trathan et al. 2024 for a full breakdown of krill catch limits in the region). Due to a lack of consensus within CCAMLR for maintaining the subdivision of the interim catch limit, the spatial allocation measure expired at the end of the 2023/2024 fishing season (SC-CAMLR 2024). Until further notice, the interim catch limit of 620,000 t may now be caught within any of the subareas.

The interim catch limit of 620,000 t will remain in place until CCAMLR has devised a means to spatially and temporally distribute a larger precautionary catch limit of 5.61 million t, so that concentrated harvesting does not negatively affect krill dependent predators (CCAMLR 2021a). Toward this goal, CCAMLR has endorsed a new management strategy which requires up-to-date spatial layers relating to krill abundance and predator foraging demand (Constable et al. 2023; Warwick-Evans et al. 2022a). Species distribution models are powerful tools that can provide such layers at the spatial and temporal scales necessary to inform such management decisions. These numerical methods have previously been used to relate krill abundance and biomass metrics to environmental correlates in the Western Antarctic Peninsula (Warwick-Evans et al. 2022b), South Georgia (Warwick-Evans et al. 2021), the South Sandwich Islands (Baines et al. 2022), and the wider Scotia Sea (Silk et al. 2016). Around the South Orkney Islands, models have previously been used to describe the distribution of foraging predators (Warwick-Evans et al. 2018), but the absence of an appropriate model for krill remains a significant gap which constrains the ability of managers to adequately regulate a growing krill fishery in Subarea 48.2. Addressing this gap is now urgent given the recent expiration of the management measure which ensured subdivision of the interim catch limit between subareas.

Efforts to fill this gap can now begin thanks to a decade of data from krill acoustic surveys conducted around the South Orkney Islands (Skaret et al. 2023). These acoustic data have begun to provide important insights into krill dynamics within the region. For example, flux and advection of krill have been found to be dominant features in the area, and krill have been shown to consistently occur at high densities within canyons at the northern shelf edge west of Coronation Island (Krafft et al. 2018; Krafft, Skaret, and Knutsen 2015). This hotspot aligns with known predator foraging areas (Warwick-Evans et al. 2018) and areas consistently targeted by the krill fishery since the 1980s (Santa Cruz, Krüger, and Cárdenas 2022). Extending the utility of long-term observations within a modeling framework provides an opportunity to acquire further understanding about the physical and biological drivers of krill distribution and abundance across space and time.

Further understanding of krill population dynamics is necessary because many factors contribute to its complexity. Krill recruitment is thought to be episodic (Reid et al. 1999) with krill biomass and density varying across ocean basin scales (Atkinson et al. 2009), within ocean basins (Krafft et al. 2021) and at finer scales (Warren and Demer 2010). Krill population dynamics also vary temporally, with many studies pointing to both intra- and interannual variability in krill biomass and density (Fielding et al. 2014; Reiss et al. 2008; Trathan et al. 2003). This temporal variability is likely driven by fluctuations in climate such as the Southern Annular Mode (SAM) and El Niño-Southern Oscillation forcing. These climatic fluctuations can lead to a cascade of physical and biological changes which alter advective pathways, sea ice extent, water column stability, and primary productivity, resulting in consequences for krill recruitment, abundance, distribution, and transport (Saba et al. 2014). Indeed, in simulations that combined a high-resolution ocean-sea ice model and an individual-based model of krill, Young et al. (2024) found that strong westerly winds associated with positive SAM phases influenced the strength of near-surface flows associated with the Weddell Front and the presence of sea ice, ultimately increasing the influx of krill onto the South Orkney shelf but reducing local retention. However, until now, the empirical relationship between South Orkney krill density and dynamic environmental variables accounting for multiple years and climatic conditions remains untested.

Here, we combine long-term krill-targeted acoustic survey data from the South Orkney Islands with a suite of environmental variables and develop a dynamic distribution model for Antarctic krill within Subarea 48.2. Having determined the most parsimonious model, outputs were used to assess how krill presence and density varied interannually given prevailing environmental conditions, and to quantify spatial overlap between hotspots of krill density, fishing activity, and predator foraging distributions.

Methods

Krill density

As part of the ongoing Norwegian scientific contribution to monitoring distribution, abundance, and population characteristics of Antarctic krill, an acoustic survey with associated trawl stations for biological sampling takes place annually in waters surrounding the South Orkney Islands (longitudinal stratum boundaries at 43.5°W and 48°W, and latitudinal boundaries at 59.7°S and 62°S; Fig. 1a). In the present study we use data from the first 10 years of this survey (2011–2020). All survey transects occurred between January and February each year, but in two of the years—2013 and 2015—sea ice prevented full completion of the survey (Krafft et al. 2018). The survey was designed according to the standards used in similar annual surveys undertaken in Subareas 48.1 and 48.3 (SC-CAMLR 2010) using the Norwegian commercial fishing vessels “Saga Sea” and “Juvel” (Aker Biomarine ASA, Oslo, Norway, and Rimfrost AS, Fosnavåg, Norway) as research platforms except in 2019 when RV "Kronprins Haakon" was used (*see* Skaret et al. 2023 for further details on design and acoustic sampling).

The acoustic data used in this study were collected using calibrated hull mounted Simrad echo sounders. Since different combinations of frequencies were available, we used the swarm-based approach for acoustic target identification of krill, which is recommended by CCAMLR when the 38, 120, and 200 kHz frequency combination is not available. Details on the Krafft et al.' (2021) processing procedure used to determine krill density are reported and evaluated by Skaret et al. (2023).

The retained nautical area scattering coefficient allocated to krill per nautical mile was converted to biomass density (g m^{-2}, hereafter referred to as density) using full stochastic distorted wave born approximation model runs to estimate backscattering cross-sectional areas (σ) for each krill length group of 1-mm increment present in the sample, according to the formula:

$$\sigma = 4\pi 10^{\mathrm{TS}/10}\ \left(\mathrm{m}^2\,\mathrm{per\,krill}\right),$$

where TS denotes the target strength value. The predicted target strengths were then used to calculate weighted conversion factors from nautical area scattering coefficient values to density:

$$\text{Conversion factor} = \left[\sum f_i \times W(\mathrm{TL}_i)\right] / \left[\sum f_i \times \sigma(\mathrm{TL}_i)\right],$$

where f is the frequency of occurrence of a specific length group (i), σ(TL) is the backscattering cross-sectional area at total length, and W(TL) is weight at total length, which was calculated following Hewitt et al. (2004):

$$W(g) = 2.236 \times 10^{-6} \times \mathrm{TL}^{3.314}$$

Environmental covariates

Twelve environmental covariates were identified as candidate explanatory variables for the species distribution model (Supporting Information Table S1). These included three static variables, that is, unchanging with survey year: water depth (bathymetry), bathymetric slope, and distance from shelf break defined as the 500-m isobath (where values on-shelf were positive, and those off-shelf were negative). The nine remaining variables were dynamic across survey years: distance from sea ice edge (defined as 15% ice concentration), seven sea surface variables (temperature, mixed layer thickness, sea surface height (SSH) above geoid, salinity, chlorophyll *a*, primary productivity, and geostrophic current velocity), and bottom temperature. Raster grids of all covariates were obtained from a combination of empirical observations and model re-analyses (*see* Supporting Information Table S1 for full details and data sources). These were processed and clipped to the study region (longitude: 50–30°W; latitude: 57–64°S) using the "*raster*" package (Hijmans 2015) in R v4.1.3 (R Core Team 2022).

For each of the dynamic covariates, two different temporal scales were extracted. These were: (1) a sample scale which averaged conditions during the sampling months (January–February) independently for each year; and (2) a decadal scale climatology which was the average of summer conditions (January–March) between 2011 and 2020. Each acoustic sample value was matched to the covariate raster data according to the latitude, longitude, and year of collection. Finally, the combined krill-covariate dataset was aggregated to the same spatial resolution as the environmental covariates (0.04 × 0.04 decimal degrees) by calculating the mean values within each grid cell for each year. This was done to avoid pseudo-replication given multiple acoustic samples within the same grid cell of environmental data, and to reduce any effect of spatial autocorrelation in model residuals.

Hurdle model approach

Krill density data were heavily skewed toward zero values (accounting for 48% of all data). As this violates the assumptions of many statistical approaches, whereby residuals should be normally distributed, we applied a two-part hurdle model or zero-altered model (Zuur et al. 2009), which allows for these types of distribution. This approach assumes that there is one process which determines the presence or absence of krill, and at locations where it is present, there is a second process which influences its density. By modeling these processes separately, the intention is that positive detections only occur once a threshold is crossed, or put another way, a hurdle is cleared. It is important to note that this approach does not allow a differentiation between false zeros (e.g., the krill were not detected due to survey design or observer error) and true zeros (e.g., the krill were not detected because the habitat is not suitable).

In the context of our data, the first model predicts the probability of the presence of krill. To do this, the krill density data were transformed into a binary zero/non-zero form ($n = 2709$) and modeled against the environmental covariates using a binomial generalized additive model (GAM; Wood 2017) with a logit link function. The second model investigates the relationship between non-zero data (i.e., presence-only data, $n = 1833$) and environmental covariates. This was carried out using a GAM with a Gaussian distribution and the default identity link function. Based on exploratory density plots, the presence-only data were log-transformed to follow a normal distribution. Finally, outputs from both parts were multiplied together. This allowed us to identify where krill were both likely to be present and occur at high densities.

Model fitting and selection

All GAMs were fitted using the R package "*mgcv*" (Wood 2019), with a restricted maximum likelihood optimization method to estimate splines, and penalized thin plate regression splines on all smooth terms (Eilers and Marx 1996). To reduce model overfitting the basis dimension (k) was limited to between 3 and 6 with the optimum number guided by edf values and associated p values reported in *mgcv*'s gam.check, and by visualizing the partial effects plots for each covariate with the raw data.

For both the binomial and Gaussian GAMs, model selection followed a forward stepwise selection approach with fivefold cross validation. Specifically, each covariate was modeled against the response variable independently and repeated five times, each time withholding a different random subset of data (fold) for evaluation. The model coefficients from each run were used to predict the outcome for the withheld fold and performance metrics of the prediction—root-mean-squared error and R^2—were extracted. The best-performing covariate (i.e., lowest root-mean-squared error and highest R^2 averaged over fivefolds) was retained within the model. This selection process was repeated allowing for all possible combinations of environmental covariates at their different temporal scales (sample and decadal). At each iteration, the retained set of covariates were assessed for collinearity using Pearson correlation coefficients and variance inflation factors, and for concurvity using the worst-case measure of overall concurvity for each smooth. If issues were identified (Pearson's $r > 0.7$, variance inflation factors > 3, concurvity > 0.8) the next highest-ranking covariate was selected. Forward selection continued until model performance metrics plateaued and/or issues of collinearity and concurvity could not be overcome. Predictions from the final Gaussian GAM were back-transformed to obtain outputs on the original density scale. Once the final set of covariates was selected, predictions for the probability of occurrence and estimated krill density were projected onto year-specific grids at the scale of Subarea 48.2. The mean and ± 1 standard deviation of predictions and their product (interpreted as the krill density weighted by the probability of occurrence) across all years were also visualized.

Finally, to assess the extent of extrapolation when projecting to the wider Subarea 48.2 region, we used multivariate environmental similarity surfaces (MESS) using the R package "*predicts*" (Hijmans 2023). These surfaces, one for each environmental covariate, measure the similarity between new environments and those used to build the model, with positive values indicating similar conditions (Elith, Kearney, and Phillips 2010). We transformed resulting MESS maps of each model covariate into a binary map (positive values $= 1$, negative values $= 0$) and then summed grid cells across all covariates. The result is a map of Subarea 48.2, showing the number of covariates within each grid cell that has conditions similar to the model training range.

Sea surface height and sea ice edge distance analysis

Partial effects plots from the GAM model output indicated that high krill densities were associated with a specific SSH value, -1.75 (hereafter referred to as "Weddell Sea SSH" due to its location within the Weddell Sea). Given that SSH values can be associated with oceanographic fronts (Venables et al. 2012), and that these may explain temporal variability in krill transport in and out of the region (Young et al. 2024), we assessed the interannual variability in the location of this SSH contour. We also tested whether its proximity to the South Orkney shelf was (1) influenced by SAM phases and (2) associated with an increase in observed krill density during surveys. Given the possible influence of sea ice presence on krill dynamics, we repeated these steps using contours of sea ice edge.

For years 2000–2020, the geolocation of the Weddell Sea SSH contour and the sea ice edge contour were extracted using the "contour" tool in ArcGIS v.10.6 (ESRI). Using the contiguous contour line for each year, the geodesic minimum distances between the contour and three different South Orkney shelf positions were calculated using the "near" tool in ArcGIS. Shelf positions included the entire 500-m isobath surrounding the South Orkney Islands, the northernmost point of the 500-m isobath, and the easternmost point of the 500-m isobath (*see* Fig. 1a). These positions were selected to capture the proximity of contours to the shelf in general, as well as their proximity to high mean krill density areas (north and eastern shelf edges).

Contour distances for each year were compared to annual and summer (January–March) mean Southern Hemisphere Annular Mode Index for the same years (https://legacy.bas.ac.uk/met/gjma/sam.html, accessed: April 24, 2023). Contour distances for survey years 2011–2020 were also compared to the sum of acoustic-derived krill densities observed in each survey year. Relationships were tested using a simple linear model and we report adjusted R^2 and significance values for the best fitting model for Weddell Sea SSH and sea ice edge analyses.

Quantifying overlap between krill, krill predators, and the krill fishery

We compared previously published model outputs on the distribution of chinstrap penguins (*Pygoscelis antarcticus*) breeding on the South Orkney Islands (Warwick-Evans et al. 2018) with our predictions of krill density distribution. Tracking data used for modeling penguin distributions were collected in years 2011–2016, within the years of the krill survey. Kernel density (KD) polygons of chinstrap penguin core range (95% of area used) and intensively used areas (upper 50%, 25%, and 10% of area used) were extracted for three breeding phases—incubation, brood, and crèche - which occur between December and February each year. For each breeding phase, the overlap of core range and intensively used foraging areas with areas of high and very high mean krill density was estimated. High and very high mean krill density areas are defined as the cells containing the upper 50% and upper 25% of cumulative krill density, respectively, using the combined hurdle model output averaged across all survey years.

Similarly, we created KD polygons for the core area (95% of area used) and intensively used areas (upper 50%, 25% and 10% of area used) of the krill fishery, using CCAMLR C1 krill catch and effort data obtained from the CCAMLR Secretariat. We used the sum of total krill catch from all commercial hauls that occurred within Subarea 48.2 during the months (January–February) and years (2011–2020) of the krill survey. Overlap of core and intense fishing areas with (1) areas of high and very high mean krill density and (2) penguin foraging areas, were then calculated.

Results

Acoustic krill densities

The acoustic surveys used to build our models demonstrated spatial and temporal variability in observed krill density, with the highest krill densities most frequently detected to the north and northwest of the South Orkney Islands (Fig. 1), and the highest densities in years 2012–2014 (*see* Supporting Information Fig. S1). Skaret et al. (2023) present an in-depth analysis of the acoustic data, reporting krill biomass values within the 60,000 km^2 survey area ranging between 1.4 and 7.8 million across the survey period, with no monotonic trends in krill biomass over time.

Hurdle model performance

Binomial GAM

After model selection, the optimal binomial GAM explained 13.1% of the deviance in presence–absence data, with a root-mean-squared error value of 0.43 and an adjusted R^2 of 0.15 (Table 1 for model summary, Supporting Information Table S2 for additional forward selection results, and Supporting Information Fig. S2 for diagnostic plots). The presence of krill was best predicted by a model that included salinity (temporal scale: sampling months, edf: 3.86, $p < 0.001$), distance from sea ice (sampling months, edf: 3.6, $p < 0.001$), sea surface temperature (sampling months, edf: 4.7, $p < 0.001$), primary productivity (decadal, edf: 2.9, $p < 0.005$), SSH (sampling months, edf: 2.9, $p < 0.001$), and mixed layer depth (decadal, edf: 1.4, $p < 0.001$). Partial effects plots indicated a declining probability of krill occurrence with increased mixed layer depth (Fig. 2). Intermediate values of salinity (33.5–34.0) and productivity (180–220 mg m^{-2} d^{-1}) were associated with higher presence probabilities. Both upper and lower values of temperature, SSH and distance from sea ice edge were predicted to have higher probabilities of presence relative to intermediate values, yet large confidence intervals at temperatures < 0°C and SSH > −1.6 m limit explanatory power at these bounds (Fig. 2).

Gaussian GAM

After model selection, the optimal Gaussian GAM explained 12.1% of the deviance in density of krill, with a root-mean-squared error value of 2.02 and an adjusted R^2 of 0.11 (Table 1 for model summary, Supporting Information Table S3 for additional forward selection results, and Supporting Information Fig. S3 for diagnostic plots). The density of krill was best predicted by a model that included, in order of importance to model fit, distance from sea ice (decadal, edf: 1.5, $p < 0.001$), SSH (sampling months, edf: 4.4, $p < 0.001$), distance from shelf edge (edf: 3.6, $p < 0.01$), salinity

Table 1. Summary of optimal binomial and Gaussian generalized additive models (GAMs) as selected by forward model selection process. The temporal scale of each covariate (whether averaged over sample collection or decadal time scales) and the metrics used to discern optimal model covariates are shown (averaged from fivefold cross-validation runs). Other performance metrics (akaike information criterion [AIC], adjusted R^2 and percentage deviance explained) and metrics from null models are given for comparison. Covariates in bold are those shared between the binomial and Gaussian GAMs. Full covariate names are provided in Table S1.

			Model performance metrics			Model prediction metrics	
Model	**Covariate**	**Temporal scale**	**AIC**	**Adj. R^2**	**% Deviance**	**R^2**	**Root-mean-squared error**
Binomial GAM	Null	-	2730	-	-	-	0.47
	so	Sample	2532	0.09	6.33	0.09	0.45
	+ **distice**	Sample	2521	0.10	8.00	0.10	0.44
	+ thetao	Sample	2472	0.12	10.32	0.11	0.44
	+ **pp**	Decadal	2445	0.13	10.96	0.13	0.44
	+ **zos**	Sample	2431	0.14	12.04	0.13	0.44
	+ mlotst	Decadal	2417	0.15	13.08	0.14	0.43
Gaussian GAM	Null	-	2730	-	-	-	2.14
	distice	Decadal	6302	0.06	5.31	0.06	2.07
	+ **zos**	Sample	6286	0.07	7.72	0.07	2.06
	+ distshelf	-	6261	0.09	9.46	0.09	2.04
	+ **so**	Sample	6254	0.10	10.66	0.09	2.04
	+ **pp**	Decadal	6246	0.11	11.40	0.10	2.03
	+ vel	Decadal	6235	0.11	12.08	0.11	2.02

Abbreviation: AIC, akaike information criterion.

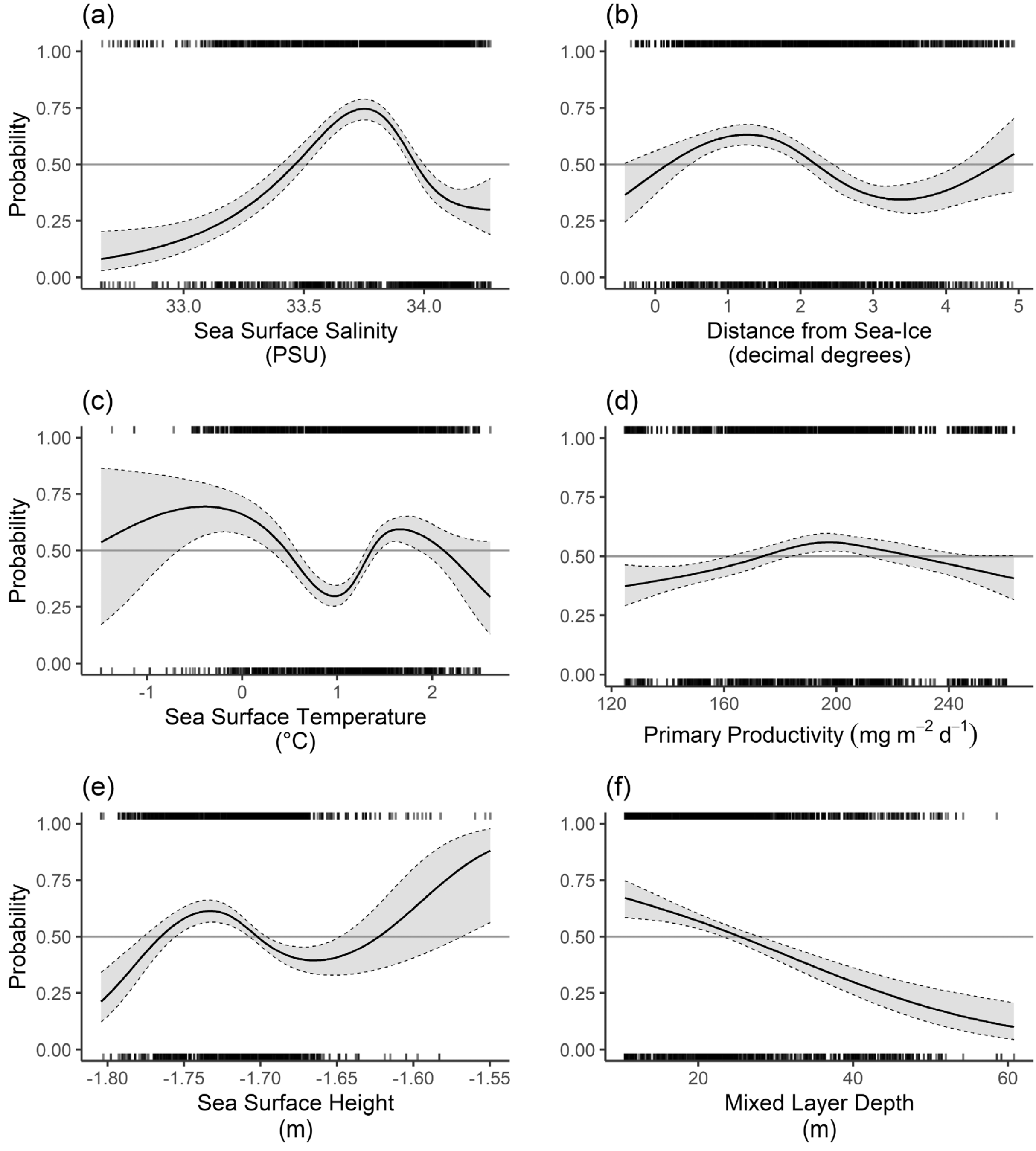

Fig. 2. Partial effects plots for each covariate outputted from final binomial GAM predicting probability of occurrence of krill. Solid lines show the mean and gray ribbons represent 95% confidence intervals. Confidence intervals are calculated to include the uncertainty around the overall mean. Values on the *y*-axis represent probability of occurrence. The distribution of observed data is denoted by the rug on the *x*-axis.

(sampling months, edf: 2.8, $p < 0.001$), primary productivity (decadal, edf: 2.2, $p < 0.01$), and geostrophic current velocity (decadal, edf: 1, $p < 0.005$). Partial effects plots from the GAM indicated an increase in log krill density with distance from sea ice edge and increasing velocity (Fig. 3). Higher log krill densities were associated with salinity values of ~ 33.75, SSH values of -1.75 and in the proximity of the shelf break but were lower for primary productivity values > 200 mg m^{-2} d^{-1} (Fig. 3).

Dynamic spatial predictions across models

Spatial predictions from the binomial GAM indicated a general pattern of higher probability of occurrence in the north than the south of Subarea 48.2 (Fig. 4a). Within the area

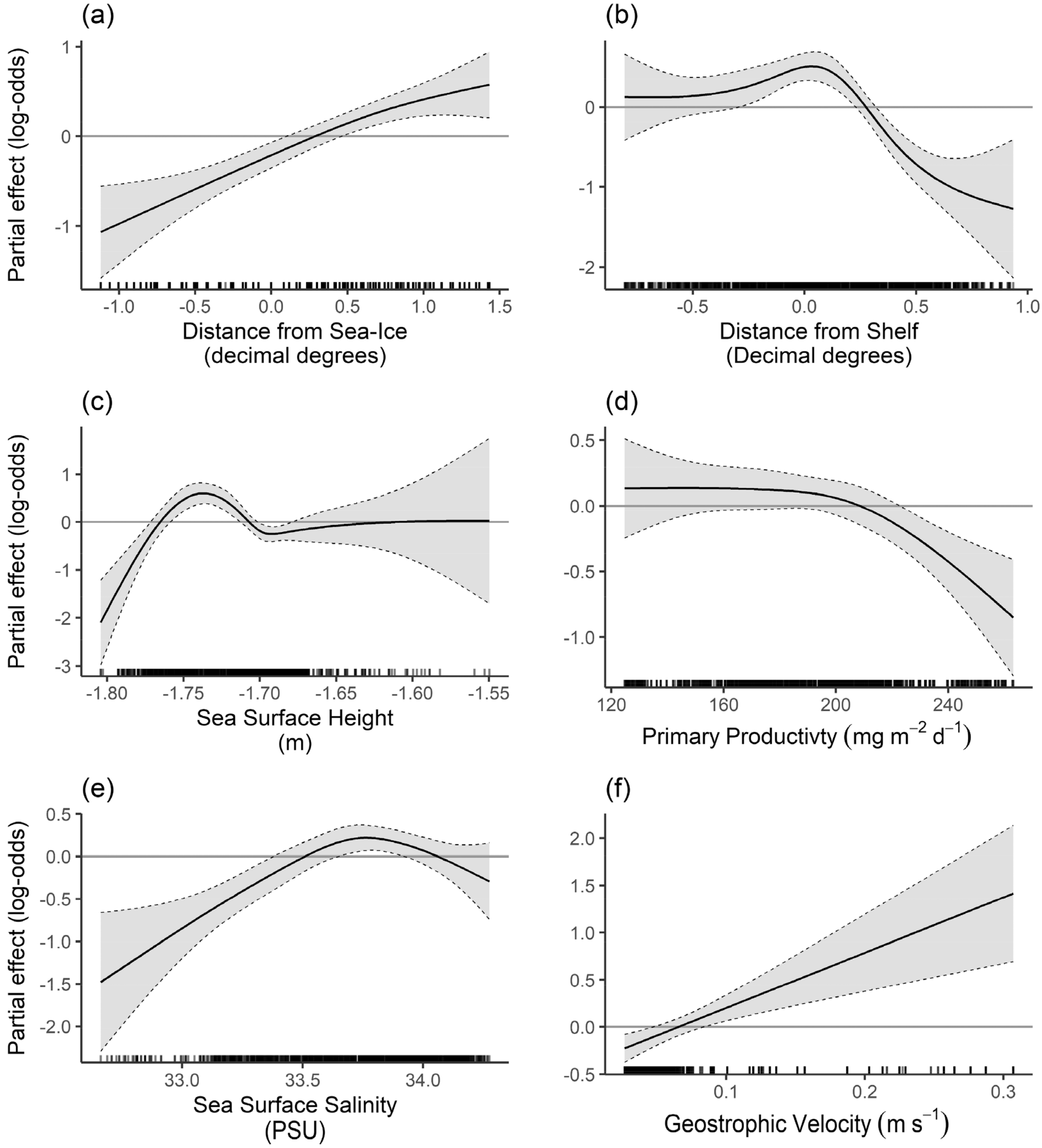

Fig. 3. Partial effects plots for each covariate outputted from final Gaussian generalized additive model predicting krill density (log-transformed, conditional of presence). Solid lines show the mean and gray ribbons represent 95% confidence intervals. Confidence intervals are calculated to include the uncertainty around the overall mean. Values on the *y*-axis represent the deviation from the mean predicted density on the scale of the covariate. The distribution of observed data is denoted by the rug on the *x*-axis.

covered by the acoustic surveys, high probabilities were estimated around the South Orkney shelf break and waters to the north of the archipelago (Fig. 4a). Spatial predictions of krill density from the Gaussian GAM indicated, on average, higher krill densities surrounding the shelf break, particularly at the north and eastern shelf edge, as well as in the shelf waters of the Discovery Bank to the east of the subarea (Fig. 4b). From the combined hurdle model output, we found that areas with both high occurrence and high density are confined to the north and northeastern shelf edge of the South Orkneys, and in the shelf waters of the Discovery Bank (Fig. 4c).

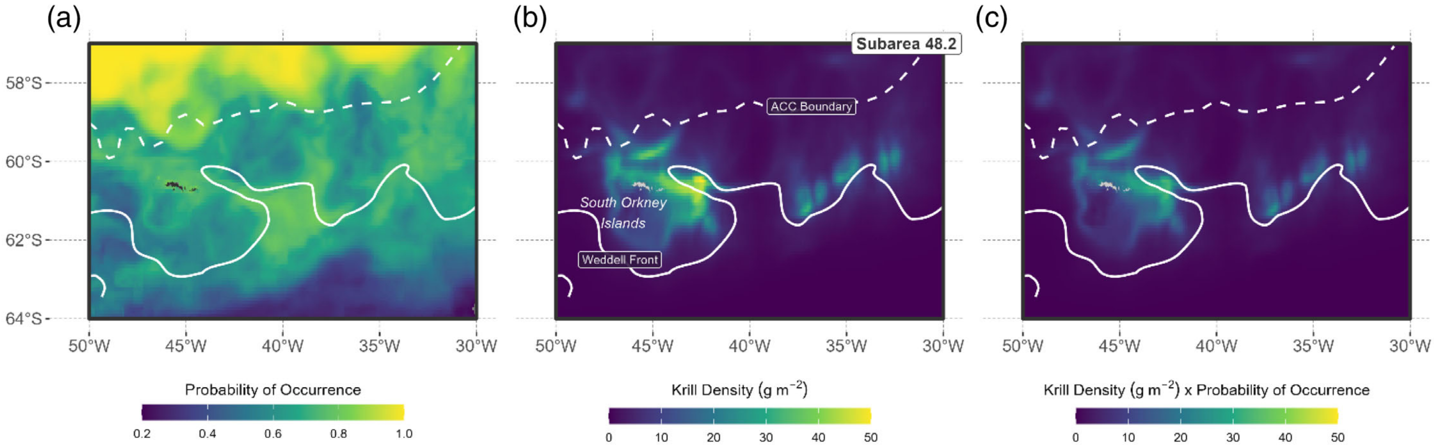

Fig. 4. Decadal averaged model predictions for Subarea 48.2 for (**a**) binomial generalized additive model (GAM), (**b**) Gaussian GAM, and (**c**) the product of the two GAMs showing the predicted krill density weighted by the probability of occurrence. The Southern Boundary of the Antarctic Circumpolar Current and the Weddell Front are shown by dashed and solid lines, respectively.

Model predictions showed high interannual variability in the probability of krill occurrence across the subarea, most especially in the South Orkney plateau (relatively low probability in years 2011, 2016, and 2018; Supporting Information Fig. S4) and in the south of the subarea (relatively high probability in years 2017–2019; Supporting Information Fig. S4). The northern shelf edge of the South Orkney Islands was found to be an area of consistently high krill density across years, with 2012–2014 predicted to have the highest densities, and 2015 predicted to have particularly low densities relative to other survey years (Supporting Information Fig. S5). Similar patterns of spatiotemporal variability were seen in the combined hurdle model output (Supporting Information Fig. S6).

The MESS analysis for the binomial GAM covariates indicated that the majority of Subarea 48.2 contains environmental conditions within the range used to build the GAM (Supporting Information Fig. S7a). Areas to the extreme north and south of the subarea have conditions most dissimilar to the training data and thus predictions in those areas should be interpreted carefully. The MESS analysis for Gaussian GAM covariates (Supporting Information Fig. S7b) and for combined hurdle model covariates (Supporting Information Fig. S7c) followed a similar pattern, with areas furthest off-shelf also falling outside the training conditions for some covariates.

Sea surface height and sea ice edge distance analysis

Contours of the Weddell Sea SSH and sea ice edge showed high interannual variability in their proximity to the South Orkney shelf during sampling months, being on average 60 ± 62 km and 108 ± 94 km from the shelf, respectively (Fig. 5a-b).

From 2000 to 2020, the sea ice edge was closer to the shelf in years when the SAM index was positive ($R^2_{adj} = 0.32$, $F_{1,8} = 10.6$, $p = 0.004$; Fig. 5c). Proximity of the Weddell Sea SSH contour showed a similar yet not statistically significant relationship with SAM index ($R^2_{adj} = 0.12$, $F_{1,8} = 3.60$, $p = 0.073$; Fig. 5d). Higher mean krill densities were observed when the Weddell Sea SSH contour was closer to the South Orkney shelf edge, although this trend was not statistically significant ($R^2_{adj} = 0.23$, $F_{1,8} = 3.71$, $p = 0.090$; Fig. 5f). Krill density showed no significant trend with distance of sea ice edge from the South Orkney shelf ($R^2_{adj} = 0.10$, $F_{1,8} = 2.02$, $p = 0.193$; Fig. 5e).

Quantifying spatial overlap between krill, krill predators, and the krill fishery

Areas of chinstrap penguin foraging had the highest spatial overlap with krill during the crèche breeding phase, when intensively used areas (10%, 25%, and 50% KDs) had at least 100% overlap with high mean krill density areas and 63% overlap with very high mean krill density areas (Table 2; Fig. 6a–c). These values dropped to 90% and 55% overlap, respectively, during brood phase, and to 74% and 26% overlap during incubation (Table 2). Throughout all breeding phases, the most intensively used foraging areas (10% KDs) overlapped 100% with high mean krill density areas and at least 71% with very high mean krill density areas (Table 2; Fig. 6a–c).

We found that all KDs of krill fishing activity had at least 90% spatial overlap with areas of high and very high mean krill density (Fig. 6d; Table 2). The areas of highest fishing catch (i.e., upper 10%, 25%, and 50% of cumulative catches) occupied a small area to the northward edge of the South Orkney Islands (Fig. 6d). These areas were located within the home range of chinstrap penguins regardless of breeding phase (Supporting Information Tables S4–S6) and almost entirely within the upper 25% and 50% of chinstrap foraging areas (77–100% overlap depending on breeding phase; Fig. 6e; Supporting Information Tables S4–S6).

Discussion

This study developed a dynamic distribution model for Antarctic krill within Subarea 48.2, a fundamental requirement for CCAMLR's revised management approach for the

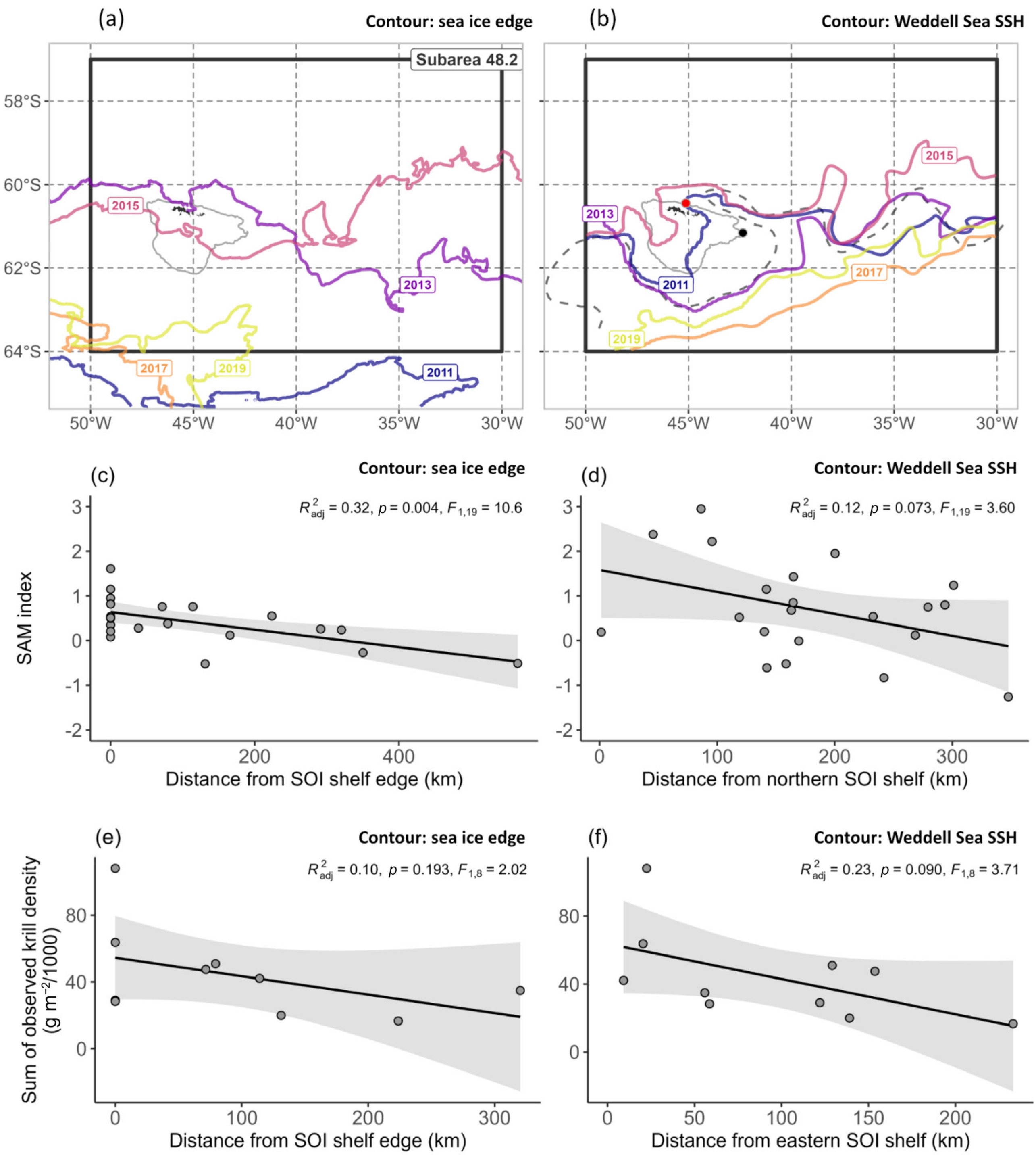

Fig. 5. Map showing the interannual variability in the position of sea ice edge (**a**) and Weddell Sea surface height (SSH) contour (**b**) for selected survey years in relation to the South Orkney Island shelf (SOI) edge (light gray line) within Subarea 48.2 (note some contours lie outside the subarea). In panel (**b**), dashed black line denotes typical Weddell Front position, red and black points denote northern and eastern shelf locations, respectively. Linear relationships between contour distance and Southern Annular Mode (SAM) index (**c**, **d**) and sum of observed krill density (**e**, **f**). For (**c**–**f**), solid black lines indicate line of best fit and ribbon denotes 95% confidence interval.

commercial fishery for krill. We discuss our findings in the context of understanding the interannual variability in krill distribution and abundance and, given the high overlap between krill, the commercial fishery and krill predators, we discuss how our results may contribute to krill management in the region.

Table 2. Percentage of spatial overlap between various kernel densities (KDs) of krill predator (chinstrap penguin) foraging or fishery activity, with areas of predicted high and very high mean krill density (i.e., areas of upper 50% and upper 25% of cumulative krill density estimates, respectively). The months from which data were used to create kernel densities are also given.

			Spatial overlap (%)	
Predator/fishery	Months of use	KD	High mean krill density area (upper 50%)	Very high mean krill density area (upper 25%)
Chinstrap incubation	December–January	10%	100.0	71.4
		25%	99.7	48.6
		50%	74.5	26.2
		Home range—95%	36.2	14.0
Chinstrap brood	January	10%	100.0	94.4
		25%	98.5	69.6
		50%	89.9	55.2
		Home range—95%	84.8	46.3
Chinstrap crèche	February	10%	100.0	84.8
		25%	100.0	71.8
		50%	100.0	63.8
		Home range—95%	86.6	46.2
Krill fishery	January–February	10%	100.0	100.0
		25%	100.0	100.0
		50%	100.0	99.8
		Full area—95%	99.2	89.7

Model performance

The explanatory power of the GAMs was low but lies within the lower range of similar krill modeling efforts in the Southern Ocean (Murase et al. 2013; Santora and Reiss 2011; Silk et al. 2016; Warwick-Evans et al. 2022b) noting that some of these studies utilized single years of data and were able to include spatial covariates which can increase model performance. Despite the high variance or noise in our models, the strong correlation between covariates and krill observations produced spatial predictions of krill density which largely followed expected patterns. High unexplained variance when modeling pelagic species such as krill could be due to the difficulty in predicting very high densities (i.e., dense krill swarms). This is perhaps not surprising given the fine-scale and complex dynamics involved in aggregating krill swarms which are likely responding to prey, predators, and local conditions which act on short (< 1 d) timescales (Klevjer, Tarling, and Fielding 2010). Thus, complex krill swarm dynamics are unlikely to be captured by climatic variables alone. Environmental conditions over broader timescales, including winter months, and from other regions, may also influence the dynamics of krill each year. Future efforts to understand the mechanisms behind krill dynamics will require investigating the relative influence of broad and fine-scale covariates, and should strive to incorporate behavior, biological interactions, and dispersal into model structures.

Spatial and temporal variability in krill presence

The results of the MESS analyses indicate that there is higher confidence in our binomial GAM extrapolation across the central region of Subarea 48.2 than in the areas to the far north and south. With this in mind, our predictions suggest that probability of krill presence is, on average, high in deeper waters adjacent to shelf regions such as north of the South Orkney Islands, south of Bruce Bank and east of Discovery Bank. The pattern of increased krill detection in coastal or shelf environments is consistent with observations and modeling results (e.g., Silk et al. 2016; Merkel et al. 2023). Sea ice conditions have previously been shown to correlate with krill recruitment (Siegel and Loeb 1995) and density (Atkinson et al. 2004) which may account for the increased probability of presence we find in years of high sea ice conditions. Our model is also in agreement with that of Merkel et al. (2023) who found that the probability of krill presence was greatest with shallow mixed layer depth and intermediate values of productivity. Importantly, our model also agrees with the spatial distribution of commercial catches used to develop CCAMLR's acoustic survey undertaken in 2000 (Trathan et al. 2001) when krill harvesting occurred in shallow waters across all the South Scotia Arc.

We find high interannual variability in the distribution of areas with high suitability of occurrence. Notably, the probability of krill presence in the South Orkney shelf waters was particularly low in 2016 relative to other survey years,

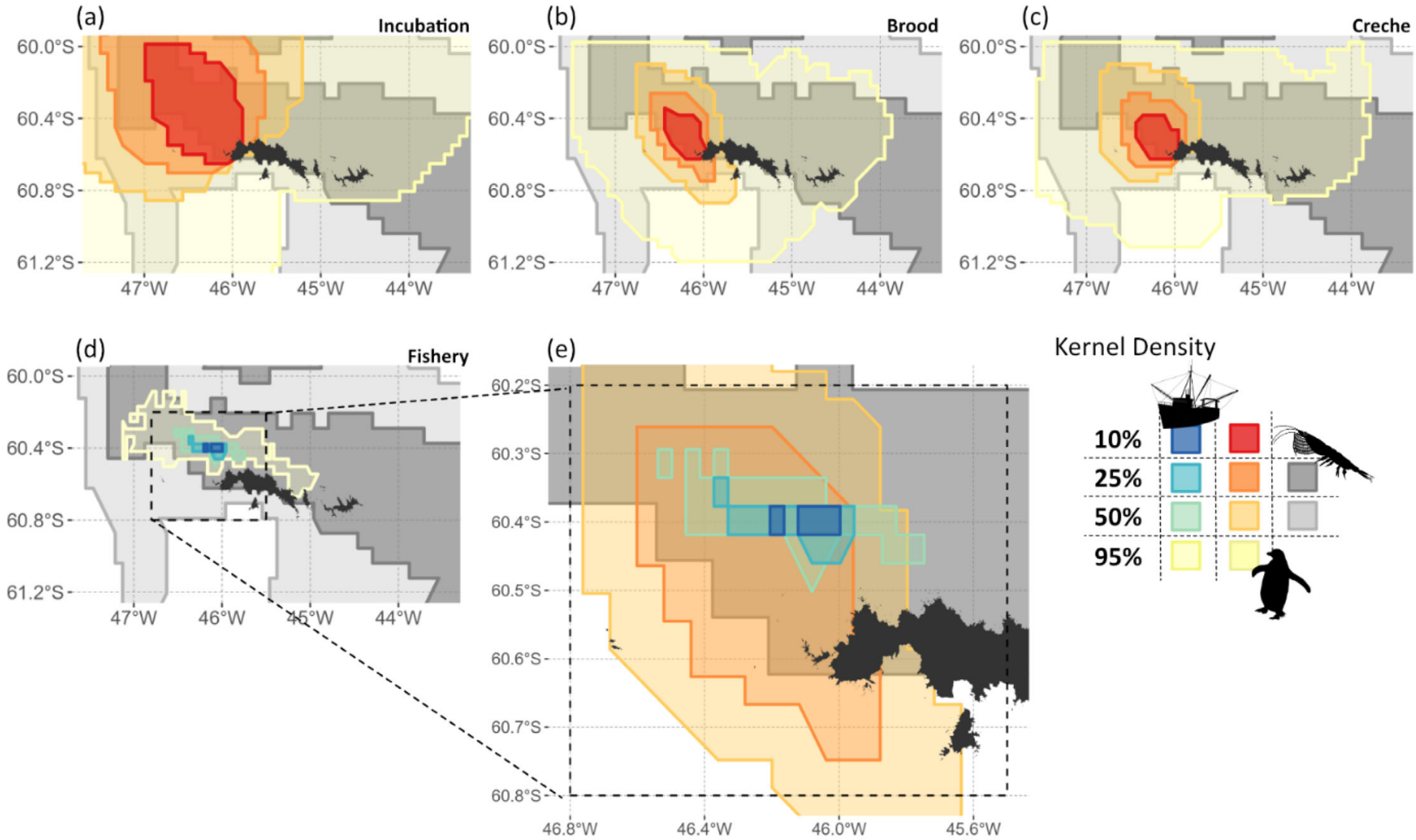

Fig. 6. The spatial overlap between kernel densities of mean krill (gray polygons), chinstrap penguin foraging (orange polygons; **a**–**c**), and krill fishing activity (blue polygons; **d**). Chinstrap foraging is divided into three breeding phases (**a**) incubation, (**b**) brood, and (**c**) crèche. Panel (**e**) shows the overlap between upper kernel densities of krill, krill fishing activity, and penguin foraging areas during brood phase. High and very high mean krill density areas are defined as the cells containing the upper 50% and upper 25% of cumulative krill density, respectively, using the mean combined hurdle model output. An expanded version of panel (**a**) showing the full area of chinstrap foraging is available in Supporting Information Fig. S8.

explained in our model by a deeper mixed layer and more saline surface waters compared to other years. A strong but short-lived El Niño event during 2016 altered the foraging distribution of chinstrap penguins from a typical on-shelf location to further off-shelf (Lowther et al. 2018). It was inferred from these tracking data that changes in local oceanographic conditions resulting from climate forcing, specifically increased windspeed and costal downwelling, altered the distribution of the krill prey field. Fisheries data also show a sharp decline in krill catch during 2015–2016 (CCAMLR 2021b) and the area occupied by the krill fishery was more extensive than average in 2016, presumably an indication of greater search effort.

Spatial and temporal variability in krill density

We found the shelf break to be an important area for krill. This association is well documented (Trathan et al. 2003), and may reflect a number of processes including advection, retention, and krill behavior (Young et al. 2014). The shelf break to the north of the South Orkney Islands was found to be particularly important. This area aligns with previous studies—the complex topography here including a steep slope reaching to abyssal depths and several canyons are thought to be important in retaining krill that are advected into the region (Krafft, Skaret, and Knutsen 2015). In recent years, the krill fishery has become aggregated in areas where krill are more predictable and abundant, including close to these canyons on the northern shelf area (Warwick-Evans et al. 2018). The shallow South Scotia Ridge to the east, including Discovery Bank, was also predicted to be an area of high krill density. This area has been used by the fishery in the past and was found to have some of the highest density estimates in the 2000 and 2019 synoptic surveys (Hewitt et al. 2004; Krafft et al. 2021). While the distribution of krill density remains consistent across years, some years are predicted to have greater or lower krill density than others, such as 2012 (high krill year) and 2015–2016 (low krill years). These patterns closely follow the annual krill biomasses estimated from the survey data (Skaret et al. 2023).

Sea surface height and sea ice edge distance analysis

The link between krill density and SSH, an indicator for the position of oceanographic fronts, was important in our model.

This aligns with previous studies that advective (and retentive) processes including fronts, eddies, and slope features are important in determining krill habitat (Santora et al. 2012). Specific SSH values were related to high krill density and contour plots show these values to be within the region of the Weddell Sea (Fig. 5a). The dominance of Weddell Sea oceanographic features in transporting krill to the South Orkney Islands and elsewhere in the Scotia Sea is highly plausible given the importance of Weddell Sea breeding grounds, observations of under ice transport of larval krill from this area (Meyer et al. 2017), and Lagrangian particle tracking simulations (Young et al. 2024).

The Weddell Sea SSH contour and the sea ice edge typically extended closer to the South Orkney shelf in years of positive SAM, a trend that has been reported for sea ice from remote sensing observations (Doddridge and Marshall 2017). This process is likely driven by increased strength of westerly and northly winds during a positive SAM phase, leading to an enhanced eastward component of near-surface currents in the northwest Weddell Sea and an acceleration of the Weddell Gyre (Young et al. 2024). Modeling of subsurface drifters has revealed that transport out of the northwest Weddell Sea is also influenced by SAM, with greater connectivity between the Weddell Sea and South Georgia in years of positive SAM, with implications for the transport of krill (Renner et al. 2012). Young et al. (2024) also relate results from their individual based model to SAM, finding greater flux of krill onto the South Orkney shelf in years of positive SAM due to associated changes in the position of the Weddell Front and sea ice. Our study, utilizing 10 years of empirical krill acoustic data, also suggests a trend (though not significant) of higher krill density in years when the Weddell Sea SSH contour is closer to the South Orkney shelf. This strengthens the hypothesis that krill abundance, distribution, and recruitment patterns within the study region are influenced by Weddell Sea oceanographic conditions and that they are sensitive to climate variability. Looking forward, our ability to associate temporal patterns in oceanographic features with krill abundance is dependent on the long-term time series of krill acoustic surveys, which for the South Orkney Islands is limited from 2011 until present. Given the importance of understanding the mechanisms underpinning interannual variability in krill, gaining further statistical power via continued annual acoustic surveys should be of high priority for future research in the area. As fishery demand for krill increases, enhanced monitoring is now of increasing importance (Trathan 2023).

Quantifying spatial overlap between krill, krill predators, and the krill fishery

At least 70% of chinstrap penguin's most intensely used areas (10% KD) were estimated to be within locations of very high mean krill density. Almost all of the commercial krill fishery catch within Subarea 48.2 in the last decade was found to lie both within our predicted areas of high and very high mean krill density, and within the identified foraging range of chinstrap penguins. This indicates that both predators and fishers rely on dense and predictable krill areas, a pattern common throughout the Antarctic Peninsula (Hinke et al. 2017). The overlap in krill, predator, and commercial fishery occurs at the known krill hotspot at the northward edge of the South Orkney shelf near to a series of submarine canyons, yet high krill densities were predicted to extend, in most years, to the east of the South Orkney shelf break where the fishery does not operate and where penguin tracking data are not available. The lack of resource utilization here may be due to increased distance from land, or the increased annual variability in krill density at these locations. However, summer telemetry data from Antarctic fur seals indicate favored distributions at the South Orkney plateau and at locations further north and northeast of South Orkneys (Lowther et al. 2020). Additional telemetry data of other krill dependent pelagic species, especially during months of fishing activity in the autumn and winter, would be valuable for further validating these results. For example, passive acoustic observations suggest that a suite of marine mammals use the krill hotspot area to the north of the islands (Åsvestad et al. 2024) and a compilation of records finds that fin whales are common throughout the South Orkney shelf between January and March (Viquerat et al. 2022).

Management implications

The estimated distribution and density of krill from the hurdle model presented in this work will be used to inform an ecological risk assessment (overlap analysis) as part of a new management strategy for the krill fishery (SC-CAMLR 2019; Warwick-Evans et al. 2022a). This ecological risk assessment (overlap analysis) of fishery–predator–prey interactions is becoming increasingly important to ensure the goals of ecosystem-based fisheries management are fulfilled (Trathan et al. 2022) because the spatial and temporal scales of these interactions should determine the spatial and temporal scales of management decisions such as fisheries catch allocations (Watters, Hinke, and Reiss 2020). While CCAMLR aims to integrate spatial protection with krill fisheries management, as of the 2024/2025 fishing season there is no measure in place to prevent increased spatial or temporal aggregation of catches. Given the steady rise in catch effort within Subarea 48.2, a higher proportion of the interim catch limit may be taken from this fishing hotspot until a revised management plan is adopted.

At the Antarctic Peninsula, and at South Georgia, where krill are also harvested, areas important to foraging krill dependent predators have been set aside as protected areas, either as voluntary measures or de jure measures (Godø and Trathan 2022; Trathan et al. 2014). Requirements for either seasonal or year-round protection should now also be evaluated close to the South Orkney Islands. Of relevance will be the designation of scientific research areas where the needs of fishers and natural predators are both scientifically evaluated (Godø and Trathan 2022).

Subarea 48.2 is an oceanographically complex and highly dynamic system, and the South Orkney Island acoustic survey covers a wide area with krill patchily and nonlinearly distributed. With a dense network of trawl stations, the design of the survey is well suited to provide a temporal snapshot of krill distribution and a representative picture of the demographic composition in the area (Krafft et al. 2018). With over a decade of annually repeated surveys, it is also now feasible to analyze patterns in local krill biomass and distribution (Skaret et al. 2023) and, as shown here, to determine which factors (physical and/or biological) contribute to the observed patterns during the sampling period. It is also important to be aware that regional snapshot surveys have limitations when working with a stock that is patchily distributed over many spatial scales and that is also highly dynamic over time. For example, the design does not provide representative estimates of biomass at all scales relevant for fishery management, and this must be considered when interpreting the results (Skaret et al. 2023). There is an ongoing Norwegian research effort to increase the relevance of the survey to other management objectives by (1) increasing the survey effort within the krill hotspot area, (2) combining nontransect data from both fishing vessels and autonomous platforms, and (3) developing statistical methods that robustly combine and analyze such data.

Conclusion

Developing the krill layer for Subarea 48.2 is the first step for the future development of CCAMLR's revised management procedure for this region. With spatial layers already available for penguins (Warwick-Evans et al. 2018), fur seals (Lowther et al. 2020), and baleen whales (Baines et al. 2021), CCAMLR now needs to develop appropriate layers for other krill-dependent predators, such as mesopelagic fish, and implement these within a risk assessment framework for the region. Other key steps will be to consider intra- and interannual variation in krill distribution and predator demands, and to ensure a continuous supply of ecological monitoring data to help evaluate whether the fishery is leading to negative ecosystem impacts. Developing a dynamic management framework that responds to changes in optimal environmental correlates of krill distribution, such as the Weddell Sea oceanographic features that this study and others have identified, may also be feasible in the longer term.

Author Contributions

Bjørn A. Krafft and Philip N. Trathan conceptualized the study and acquired funding; Georg Skaret and Bjørn A. Krafft contributed the data; Jennifer J. Freer analyzed the data with input from Victoria Warwick-Evans, Sophie Fielding, and Philip N. Trathan; Jennifer J. Freer wrote the manuscript with contributions from all co-authors.

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Conflicts of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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