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Seasonal and spatial patterns of adult Antarctic krill at the Antarctic Peninsula: insights from a 41 year data analysis

F. A. Perry[1,*], S. F. Sailley[2], A. Atkinson[2], D. J. Mayor[1,3], C. H. Lucas[4], G. A. Tarling[5]

[1]Department of Biosciences, University of Exeter, Exeter EX4 4PS, UK
[2]Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, UK
[3]National Oceanography Centre Southampton, European Way, Southampton SO14 3ZH, UK
[4]University of Southampton, National Oceanography Centre Southampton, Southampton SO14 3ZH, UK
[5]British Antarctic Survey, Natural Environmental Research Council, High Cross, Cambridge CB3 0ET, UK

ABSTRACT: Locating the spawning grounds of Antarctic krill *Euphausia superba* is key to understanding their population dynamics and managing the commercial krill fishery. In the shelf waters of the Antarctic Peninsula where krill and their fishery are concentrated, a recent relaxation of fishing quotas has meant that locally successful spawning grounds could become increasingly targeted. This study revisits the existing paradigm that in summer, larger adult krill migrate away from these shelf-based fishing grounds, out towards oceanic waters to spawn off the shelf break (>1000 m). Our findings support a seasonal on-shelf division of adult krill, with smaller krill closer inshore. However, contrary to current understanding, our results suggest that 85% of the largest and most fecund >50 mm krill remain on-shelf during the summer spawning season. All adults (>30 mm) were strongly concentrated over the shelf throughout the whole spring—summer—autumn transition, with no evidence for any summer redistribution off-shelf. The Western Antarctic Peninsula (WAP) has strong on-shelf—off-shelf gradients in chlorophyll *a* and sea surface temperature, and based on generalised additive models, our study suggests that the high food requirement of adult krill, coupled with an oligotrophic off-shelf environment, contributes to the distribution of krill observed at the Antarctic Peninsula. The concentration of large, nutritious krill over the shelf throughout the season may be advantageous to land-based predators but raises concern for the management of fisheries that are becoming increasingly concentrated within the key adult krill habitat along the northern shelf of the WAP.

KEY WORDS: Antarctic krill · *Euphausia superba* · Seasonal · Off-shelf · Distribution · Commission for the Conservation of Antarctic Marine Living Resources · CCAMLR

1. INTRODUCTION

The southwest Atlantic sector of the Southern Ocean is significant for Antarctic krill *Euphausia superba* (hereafter 'krill'), as this area contains key krill spawning grounds, the highest reported densities of the species and the entire commercial krill fishery (Grant et al. 2013, Perry et al. 2019). Within this sector, krill densities vary at a range of scales. Spatially, there is habitat partitioning of krill life stages, with localised hotspots of spawning and reproduction in the Southern Scotia Arc (Perry et al. 2019). Considerable variation in densities has been noted between seasons (Siegel 1988, Lascara et al. 1999, Siegel et al. 2002, Cleary et al. 2016, Reiss et al. 2017) and years (Siegel et al. 2002, Quetin & Ross 2003, Fielding et al. 2014, Ross et al. 2014, Steinberg et al. 2015, Conroy et al. 2020). However, the spatial distributions of

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*Corresponding author: f.perry@exeter.ac.uk

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these varying densities have been less well characterised, precluding any mechanistic understanding of the processes involved (Meyer et al. 2020).

Seasonal differences in krill distributions are attributed to both horizontal and vertical migration patterns (Siegel 1988, Sprong & Schalk 1992, Lascara et al. 1999, Atkinson et al. 2008, Krafft et al. 2012). At the Western Antarctic Peninsula (WAP), 2 major, and possibly inter-linked, horizontal krill migrations have been proposed. The first is a seasonal northward expansion of krill in summer and southward contraction towards inner shelf waters in winter (Kanda et al. 1982, Atkinson et al. 2008, Cleary et al. 2016, Reiss et al. 2017). The second is a migration of older krill from shelf waters to deeper-off-shelf waters to spawn in summer, with a migration back to the shelf in autumn (Siegel 1988, 2005, Trathan et al. 1993, Lascara et al. 1999, Siegel et al. 2002, 2013). Importantly, the largest adults are thought to migrate farthest off-shelf and thus over the deepest water (>1000 m depth). This summer movement of adult krill is thought to be a crucial component of the life cycle, as it would allow spawned eggs to undertake their developmental descent to ~850 m without encountering the benthos before they hatch (Quetin & Ross 1984, Hofmann et al. 1992, Hofmann & Hüsrevoğlu 2003, Nicol 2006, Meyer et al. 2020). Although this migration has become the commonly agreed paradigm for the WAP, there is uncertainty regarding aspects of this theory which have been highlighted in recent studies (Conroy et al. 2020, Meyer et al. 2020). This topic has seen renewed interest recently, with the fisheries management organisation Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) overseeing the development of a krill stock hypothesis, a conceptual view of the redistribution of the movement of krill across habitats throughout the whole life cycle (Meyer et al. 2023).

An off-shelf summer spawning migration of adults (Siegel 1988, Siegel et al. 2013) would reduce the availability of energy-rich prey for large populations of land-based predators and their young along the WAP (Ruck et al. 2014, Trathan & Hill 2016). For krill there is a potential risk–benefit trade-off in the habitat they occupy (Atkinson et al. 2008) with greatly reduced food availability in the oligotrophic off-shelf WAP waters counterbalanced by lower predation pressure. Energy demands for spawning are high (Clarke et al. 1988, Quetin et al. 1994), so krill need high quantities of suitable food to sustain reproduction (Yoshida et al. 2011). Adult krill undergo profound changes in their metabolic demands as they grow, given the comparatively high weight exponent (>0.9) in respiration rate (Tarling 2020). Consequently, different length categories of adult krill may have different relationships with key environmental variables, such as food availability. This may be especially true in the case of adult females that must also provide for the accumulation of large egg masses, underscoring the need to understand the dynamics of post-larval krill according to size or stage (Marr 1962, Perry et al. 2019).

The notion that adult krill migrate off-shelf to spawn in midsummer (typically around January) before returning in autumn to shelf waters to join the younger population originated from the study of Siegel (1988). Since then, the idea of a major redistribution of progressively larger adult krill from the shelf, across the shelf break, to oceanic waters and back again in autumn has been repeated in multiple reviews and syntheses, including Nicol (2006), Atkinson et al. (2008), and Meyer et al. (2020). To date, however, the off-shelf summer spawning migration theory has not been revisited using the multi-decadal composite databases now available. Using average krill densities created from 41 yr of krill abundance and length frequency data, as well as sea surface temperature (SST), chlorophyll *a* (chl *a*), distance from the shelf (1000 m) and bathymetry data, seasonal adult krill distributions along the WAP and their relationship to these environmental variables were investigated. In so doing, we tested the hypothesis that the largest krill move off-shelf into waters >1000 m deep during the austral summer.

2. METHODS

2.1. Spatiotemporal domain of analysis

Our selected study domain was CCAMLR Subarea 48.1, located within the Atlantic sector of the Southern Ocean and includes the WAP (Fig. 1). This area was selected because it contains a major spawning area for krill (Perry et al. 2019), a strong focus of fishing activity (Grant et al. 2013), and is where the current paradigm of an off-shelf summer spawning migration theory originated (Siegel 1988, 2005, Lascara et al. 1999, Siegel et al. 2002, 2013, Meyer et al. 2020). The region has also produced the greatest amount of scientific net catch data.

To examine the off-shelf summer spawning hypothesis, data from 2 large composite databases on krill, namely KRILLBASE-abundance (Atkinson et al. 2017) and KRILLBASE-length frequency (Atkinson et al. 2020), were combined. Data spanning 41 yr (1976–2016) were selected (for seasonal data coverage, see Table A1 in the Appendix). The off-shelf summer

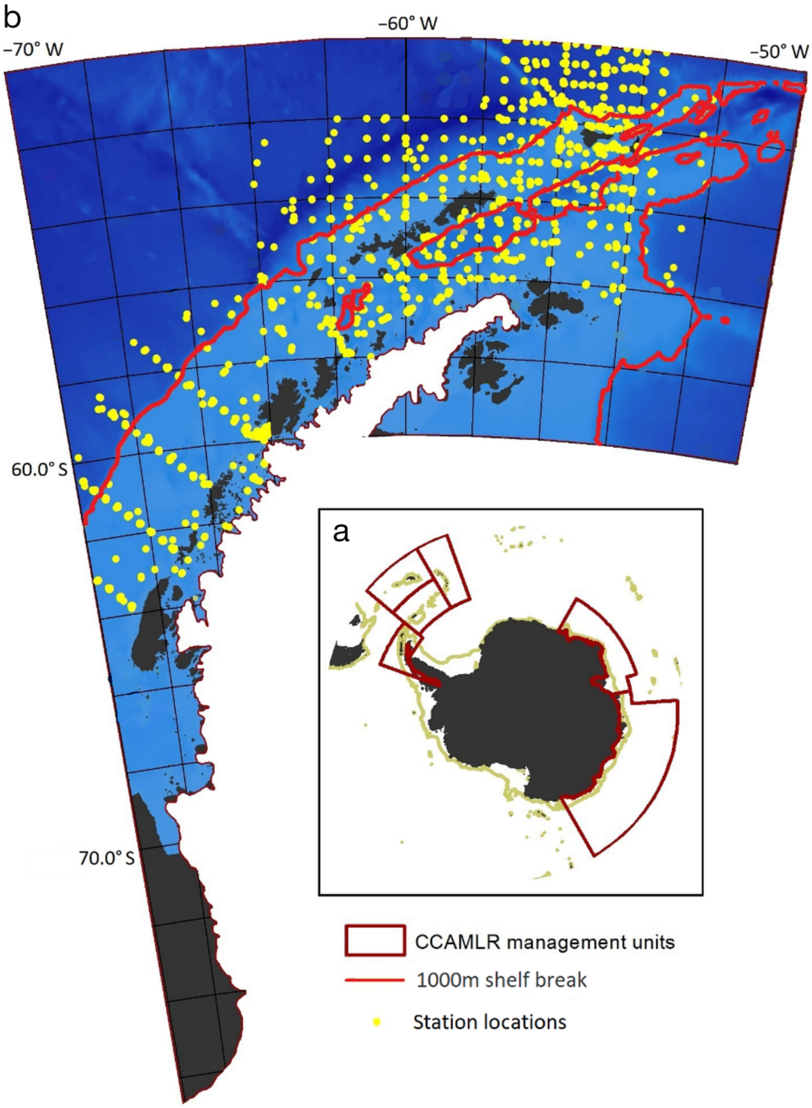

Fig. 1. Study area: Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Subarea 48.1 and its position in relation to other CCAMLR management units. (a) CCAMLR management units (outlined in red) within the Southern Ocean. (b) Subarea 48.1 within the southwest Atlantic sector of the Southern Ocean. The 1° latitude × 2° longitude grid cells used for some of our analyses are shown in black. The 1000 m isobath is shown in red. Yellow circles identify the locations of KRILLBASE-abundance station points used as the key sampling units within this study

spawning migration hypothesis describes differential movement of krill in relation to maturity stage (i.e. juvenile, immature and adult; see Meyer et al. 2020). KRILLBASE-length frequency has some data categorised as such, but the vast majority are simply length measurements of individual krill. For this reason, length (subdivided within categories 30–39, 40–49 and 50–69 mm) was used as a reasonable proxy for dominant maturity stage over this range (Siegel & Watkins 2016). Further, fecundity also scales positively with krill length (Tarling et al. 2016), and the large majority of >50 mm krill in our largest length class are adult females (Kawaguchi et al. 2006).

For fisheries management Subarea 48.1, data were selected for each of our 3 krill length classes and 3 seasonal periods: (1) October to December, (2) January and (3) February to April, excluding the austral winter period (May to September) owing to the paucity of data. This process required an approach to combine information from the 2 different krill databases, namely KRILLBASE-abundance (Atkinson et al. 2017) and KRILLBASE-length frequency (Atkinson et al. 2020). The composite nature of these krill databases means the data they contain are not evenly distributed in space or time. As a result, several methods of data selection were applied. Only krill data from the 'modern era' 1976–2016 were used for the present study, with data from the older 'Discovery era' excluded. This modern era covers 41 yr of data and represents the most comprehensive period of uninterrupted krill net catch data that overlap with satellite-derived environmental data. Subarea 48.1 is a highly dynamic region that has undergone rapid climate change, including significant ocean warming (Meredith & King 2005). However, since the late 1990s, Subarea 48.1 has experienced a warming hiatus, when the recorded change in mean atmospheric temperature was <0.05°C (Turner et al. 2016).

Krill density data were related to 4 environmental variables which fell into 2 categories: static and dynamic, of which the former were bathymetry and distance from the shelf and the latter were SST and surface chl *a* concentration (Table 1). Because of the lack of concurrently measured variables, climatologies for SST and chl *a* were necessary, which generally moderate regional levels of variability.

2.1.1. Abundance database

KRILLBASE-abundance is an open access database that contains net-catch derived juvenile and adult krill and salp densities (doi:10.5285/8b00a915-94e3-4a04-a903-dd4956346439) (Atkinson et al. 2017). The database contains only data from pre-fixed stations (hauls targeted on krill swarms were not included). However,

Table 1. Environmental variables included in our generalised additive models

Classification	Variable name	Units	Spatial resolution	Temporal resolution	Source
Static					
Bathymetry	Depth	m	10 km^2	-	GEBCO 1-min grid
Distance from shelf break	Shelf distance	km	m	-	GEBCO 1-min grid
Latitude	Lat	Decimal degrees	1 km	-	KRILLBASE-abundance
Longitude	Long	Decimal degrees	1 km	-	KRILLBASE-abundance
Dynamic					
Chlorophyll *a*	Chl *a*	mg m^{-3}	60 km^2	Monthly	SeaWiFS
Sea surface temperature	SST	°C	10 km^2	Read method	KRILLBASE-abundance

KRILLBASE-abundance compiles data from >200 independent surveys using different sampling techniques with varying sampling efficiencies. This necessitated all krill densities (number per m^2) to be standardised to a common sampling method to reduce the effect of this imbalance. Further details of the standardisation methods are available in Atkinson et al. (2017).

From the KRILLBASE-abundance database, all standardised krill density data from stations within Subarea 48.1 were extracted. In common with previous data extractions from this database and to remove tows which poorly represented krill distribution, the data were further filtered to ensure that the upper sampling depth was at least 20 m below the surface and the bottom sampling depth was at least 50 m below the surface, as described by Atkinson et al. (2008). This left 6644 stations.

2.1.2. Length frequency database

The KRILLBASE-length frequency database contains length measurements for 612 888 individual krill collected from scientific net hauls throughout the Southern Ocean (doi:10.5285/dfbcbbf9-8673-4fef-913f-64ea7942d97a) (Atkinson et al. 2020). Sex and maturity stage data are also available for a portion of the database. In contrast to the KRILLBASE-abundance database, horizontal hauls and non-random hauls (i.e. targeted hauls where nets were deployed in response to acoustically detected krill) were included in this study as they contained substantial amounts of data on targeted krill schools. We filtered the KRILLBASE-length frequency database using the same spatiotemporal criteria as for the KRILLBASE-abundance database. In addition, records sampled with a >6 mm mesh were excluded due to the possibility of net mesh selection and under-representation of smaller krill. This removed both commercial trawl data and some of the scientific trawls. Data from some scientific nets (i.e. net samples collected during scientific cruises) were further excluded where mesh size was not stipulated, including nets described as trawls. This left 134 953 krill, measured from 2422 stations.

From these filtered length frequency data, ratios of different length categories of adult krill were constructed (defined here as ⩾30 mm following Saba et al. 2014) for each 1° latitude × 2° longitude grid cell within our study area; Fig. 1). Subsequently, these length frequency records were subdivided into 3 further categories: 30–39 mm (small), 40–49 mm (medium) and 50–69 mm (large). Only grid cells containing abundance and length frequency for all 3 seasonal periods were used for analysis; this gave us 29 cells. In total 275 653 krill lengths were extracted from the length frequency database which were added to 4827 stations from KRILLBASE-abundance. No minimum number of stations per grid cell was set. A full breakdown of data distribution for both KRILLBASE databases is given in Table A1.

2.1.3. Creating densities of adult krill length categories

For our generalised additive model (GAM) analyses, the key sampling unit was each KRILLBASE-abundance station, and the final screening provided 5211 of these stations within Subarea 48.1. Using ArcGIS version 10.2.2, our 1° × 2° grid was overlaid onto our baseline map in the WGS 1984 stereographic coordinate system. By joining the KRILLBASE-length frequency stations to the grid, the mean fraction of different size classes of adult krill within each grid cell was obtained. The abundance of each size fraction was thus obtained for each individual station as a product of its value for total post-larval abundance (from KRILLBASE-abundance) and the relevant grid mean value for the fraction of the size class (from KRILLBASE-length frequency). Calculations were only made if values from both KRILLBASE databases existed for a respective grid cell.

2.2. Environmental variables

Although there are several environmental variables that can affect adult krill distributions, this study focuses on 4 principal variables: SST, chl *a*, bathymetry and distance from shelf, identified as being influential by several previous studies (Hofmann & Hüsrevoğlu 2003, Atkinson et al. 2008, Piñones & Fedorov 2016, Silk et al. 2016) (Table 1). The key sampling unit used for each of the environmental variables was KRILLBASE-abundance station location (Fig. 1).

2.2.1. SST climatology

SST values were extracted from the KRILLBASE-abundance data set (Atkinson et al. 2017). These SST values were not taken at the time of sampling but were based on long-term averages of climatological mean sea surface values for the month of February in the years 1979–2014 (Atkinson et al. 2017), generating the SST values by extracting a mean value using a 10 km radius point around a station location. Further information on how the SST data were treated is available in Atkinson et al. (2017). SST climatology values are shown in Fig. 2b.

2.2.2. Chl *a* climatology

Chl *a* data were extracted from the European Space Agency's Ocean Colour—Climate Change Initiative (OC-CCI v5) data portal, where satellite-derived ocean colour data are available from 1997 through to the present day. Of the available data, this study used 19 years of data (September 1997 to December 2016). Further information on the structure of this database is available in Sathyendranath et al. (2019). Each respective 1° × 2° grid cell was required to contain at least 30% data coverage for each month for a mean chl *a* value to be valid. This severely limited the number of grid cells with monthly chl *a* averages due to the cloudy nature of the Southern Ocean. Consequently, a monthly climatology of chl *a* values was created, i.e. a monthly average was created across all

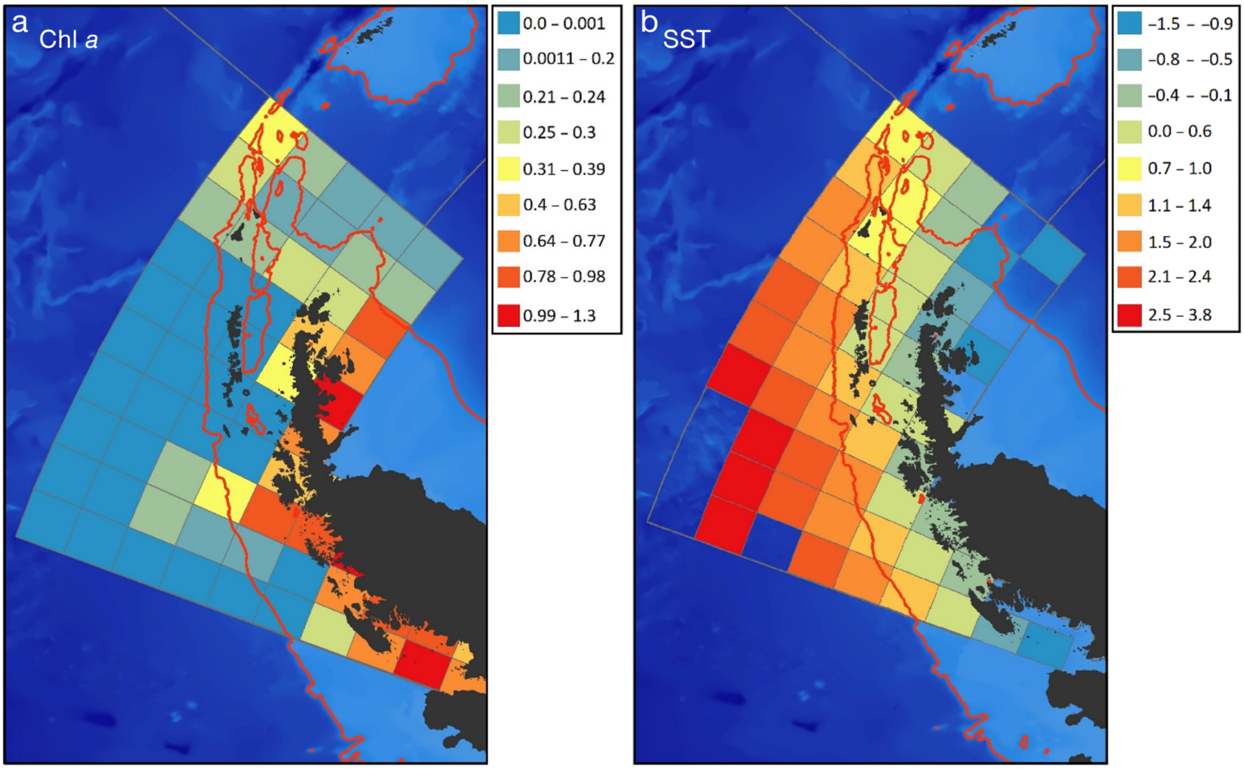

Fig. 2. February climatologies of (a) chlorophyll *a* (chl *a*) (mg m^{-3}) and (b) sea surface temperature (SST) (°C). Chl *a* climatologies created from 19 years of Ocean Colour — Climate Change Initiative data from the European Space Agency. Monthly means from each year of data were generated using a minimum of 30% data coverage from each month for the 1° latitude by 2° longitude grid cell to be included in the climatology. Mean SST, based on long-term averages of mean SST values in the month of February between 1979 and 2014. Further information on SST data treatment available in Atkinson et al. (2017). Data are displayed for February, when sea ice is at its lowest extent, thus creating the fewest issues with averaging data. The 1000 m isobath is shown in red

19 years of data for each of the 1° × 2° grid cells in our study area (Fig. 2a). This gave us chl *a* values for 3127 out of 5211 data points within our study area.

2.2.3. Bathymetry

The bathymetry values generated previously by Atkinson et al. (2017) for the KRILLBASE-abundance stations using the 2014 GEBCO bathymetry were used in this study (https://www.gebco.net/news/gebco-2014-grid). Atkinson et al. (2017) applied a 10 km radius around each station location and averaged each of the GEBCO bathymetry values from within this radius. Any data points on land were removed before averaging the values.

2.2.4. Distance from shelf

GEBCO 2014 grid bathymetry (www.gebco.net) was also used to determine the distance of each station from the shelf break, defined as the 1000 m isobath for the purpose of this study, following Hofmann & Hüsrevoğlu (2003). ArcGIS version 10.2.2 was used to calculate the minimum distance between each KRILLBASE-abundance station and the 1000 m isobath. To maintain consistency of approach, stations that fell within the region of the Bransfield strait that has a depth of >1000 m were also classified as off-shelf. Values were negative if the station was on-shelf (<1000 m) and positive if it was off-shelf (>1000 m).

2.3. Data analysis

Before determining functional relationships between krill distribution and environmental variables, checks for collinearity were conducted. Significant collinearity was found between latitude and longitude and between latitude and SST. For this reason, both latitude and longitude were removed from our analysis.

2.3.1. GAMs

Outliers were identified using Cleveland dot plots; collinearity using multi-panel scatterplots, Pearson correlation coefficients and variance inflation factors (Zuur et al. 2010). The resulting data exclusions left 2203 stations, divided into 376, 980 and 847 stations in October–December, January, and February–April, respectively. Our environmental variables exhibited non-linear trends and were therefore analysed using GAMs. Krill density data were not transformed prior to analysis. The optimal GAM structure for each krill length category was forward-selected using Akaike's information criterion (AIC) (Akaike 1974). Using AIC values rather than p-values meant that the chance of inflation of false positive results and model overfitting was reduced. Model validation was applied to our optimal GAMs to verify our underlying assumptions. Having tested several GAM families, a negative binomial GAM was best for our database due to slight over dispersion of our data. All calculations were done in R version 4.4.0 (R Core Team 2024) using the package 'mgcv' (Wood 2006).

2.3.2. One-way ANOVA

Using the metadata associated with the 2203 KRILLBASE-abundance stations, the seasonal period during which the sample had been collected was identified (i.e. October to December, January and February to April). Abundance stations from any 1° × 2° grid cell that contained data from at all 3 seasonal periods were then selected. All filtered abundance station data were associated with 1 of 9 bands of longitude, 2° wide, and were categorised as either on-shelf or off-shelf. Consequently, mean densities for each 1° × 2° grid cell from the sorted abundance station data were created. This resulted in us comparing 371 mean krill densities on-shelf and 339 data points off-shelf. Within each band of longitude, the mean densities of krill on/off-shelf for each seasonal period were compared. A Shapiro-Wilk test was conducted to test for normal distribution of data ($p = 0.576$), and no transformation of data was carried out.

To test for any significant difference between various combinations of percentage of adult krill size fractions found off-shelf and season, a 1-way ANOVA was used. This was followed by a Tukey multiple comparison of means to determine if any pairs of combinations were also significantly different. The level of accepted statistical significance ($\alpha = 0.05$) was reduced in cases where multiple testing occurred using the Bonferroni correction (0.05/number of tests).

3. RESULTS

3.1. Seasonal location of adult krill population

Our seasonal density distribution maps of adult krill highlight the importance of the tip of the Antarctic Peninsula (east of the South Shetland Islands) for consistently supporting high krill densities (Fig. 3).

Inspection of Fig. 3 shows no evidence for the hypothesised off-shelf summer spawning migration. This is examined more numerically in Fig. 4, which shows that the mean percentage of the adult krill off-shelf was lowest in January and higher in the seasonal periods either side of this month (Fig. 4). However, the mean percentage values of krill densities found off-shelf between seasons (October to December, January and February to April) were not significantly different for any length category of krill (30–39 mm: ANOVA, $F_{2,23}$ = 0.647, p = 0.533; 40–49 mm: ANOVA, $F_{2,23}$ = 0.537, p = 0.592; Fig. 4). The 50–69 mm krill had a p-value that was close to significant without a Bonferroni correction for multiple comparisons (50–69 mm: ANOVA, $F_{2,23}$ = 3.005, p = 0.069), specifically between the January and February to April seasonal periods when a larger percentage of these animals appear to be found off-shelf later in the season. This analysis was repeated by subdividing krill density data into other spatial and temporal categories (i.e. by decade, by latitude) but none of these variants was statistically significant ($F \leqslant 0.05$, $p \geqslant 0.05$ in all cases). This supports our original finding that there is a lack of seasonal change in spatial distribution.

Further investigation into the relationship between different length categories of adult krill densities and our static environmental variables (bathymetry and distance from shelf) revealed certain trends. For instance, there was a tendency for the 2 smaller length categories of krill to be found in shallower waters, particularly in October to December (Fig. 5a). There is also evidence to suggest a temporal increase in the highest densities of small, medium and large krill in deeper waters during January, and to some extent February to April (Fig. 5a).

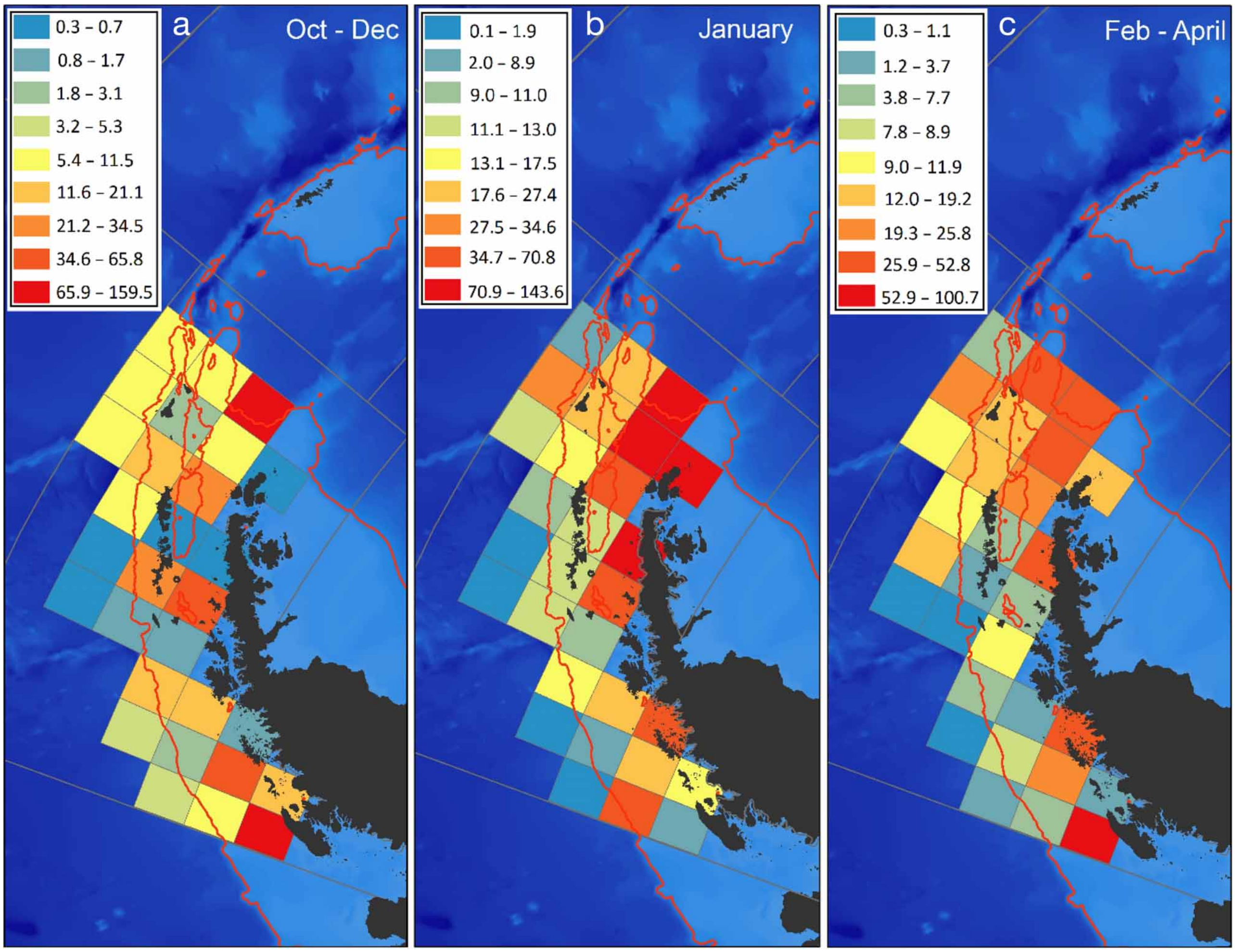

Fig. 3. Mean adult krill distributions in CCAMLR Subarea 48.1 for 3 seasonal periods: (a) October–December, (b) January and (c) February–April. Mean densities (no. m^{-2}) for all adult krill (≥30 mm). The red line shows the location of the 1000 m isobath, and the grey boxes show the limits of the CCAMLR fisheries management units. Note the different scales between panels. Grid cells are 1° latitude by 2° longitude

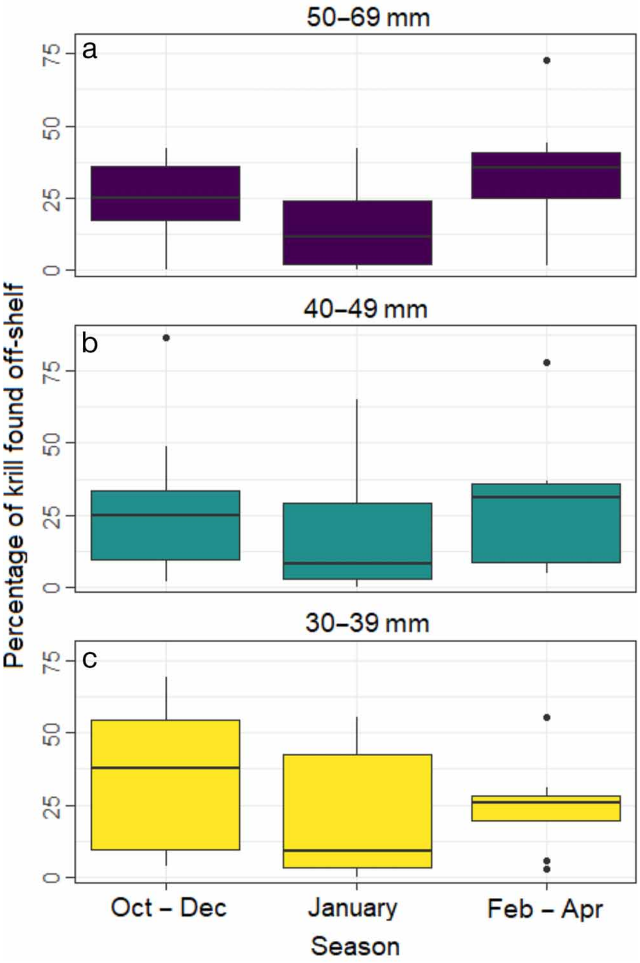

Fig. 4. Seasonal mean percentages of 3 length categories of post-larval krill [(a) 50–69 mm, (b) 40–49 mm, (c) 30–39 mm] off-shelf (>1000 m) in CCAMLR Subarea 48.1. The horizontal black bar shows the median percentage of krill found off-shelf. The upper and lower extents of the coloured boxes show the 25th and 75th percentiles, and the thin vertical black lines are the minimum and maximum values for each category. Black dots show outlying data points

Nevertheless, in January, all 3 length categories showed peaks and troughs in density with increasing water depth. In relation to the shelf, adult krill were found with the greatest certainty ⩽25 km inside the shelf break. Although krill densities often appeared greatest ~75 km inshore of the shelf break, this was most notable in the 50–69 mm size class across all 3 seasons (Fig. 5b), but was also clear in the 40–49 mm size class in October to December and January, and the 30–39 mm size class in January. As indicated by the bathymetric analysis, smaller krill also tended to be inshore, particularly during the periods October to December and January. Confidence intervals widen towards the spatial limits of the dataset, making trends difficult to identify beyond ±150 km from the shelf edge and into bathymetric depths greater than 2500 m.

3.2. Adult krill relationship with environmental variables

Chl *a* and SST climatology data for February are visualised in Fig. 2, showing clear on-shelf–off-shelf gradients for both dynamic variables. SST is cooler on-shelf and in the Weddell Sea, whereas the more northerly off-shelf waters are consistently warmer. Chl *a* concentrations tend to be greater on-shelf and are greatest in nearshore regions.

The percentage deviance explained by the 4 environmental variables was 5, 9 and 17% for 30–39, 40–49 and 50–69 mm krill respectively. The deviance explained was therefore low for all 3 krill length categories but increased with krill length. SST, shelf distance and chl *a* described most of the variation in the density of small, medium and large krill, respectively (Fig. 6). Chl *a* abundance is the only environmental variable that increases in importance as krill length increases. In the 50–69 mm length category, chl *a* exhibits a clear inverse relationship with krill density (Fig. 6). The models and the smoothing coefficients for each length category of krill are provided in Table 2.

4. DISCUSSION

Our results show evidence for an on-shelf length separation of krill size classes, with smaller krill found farther in-shore, especially from October up to the peak spawning time in January. However, no evidence was found for a large-scale movement of the largest adult krill (50–69 mm) off-shelf during the summer. These large krill appear to be the most environmentally constrained of the 3 length categories of adult krill, for whom the colder, food-rich, on-shelf environment is most advantageous.

4.1. Evidence for a size fractionated off-shelf summer spawning migration

The concept of a size-fractionated off-shelf summer spawning migration of adult krill at the WAP originated from Siegel (1988), who used data from 6 surveys carried out between October and June between 1977 and 1986 to describe a pattern of spatial succession of krill life stages along the WAP. Data collection occurred during a period of variable and exceptionally high krill recruitment, specifically 1980/81 and 1985/86 (Siegel & Loeb 1995). In summer, juveniles were found on the inner shelf and the largest adults

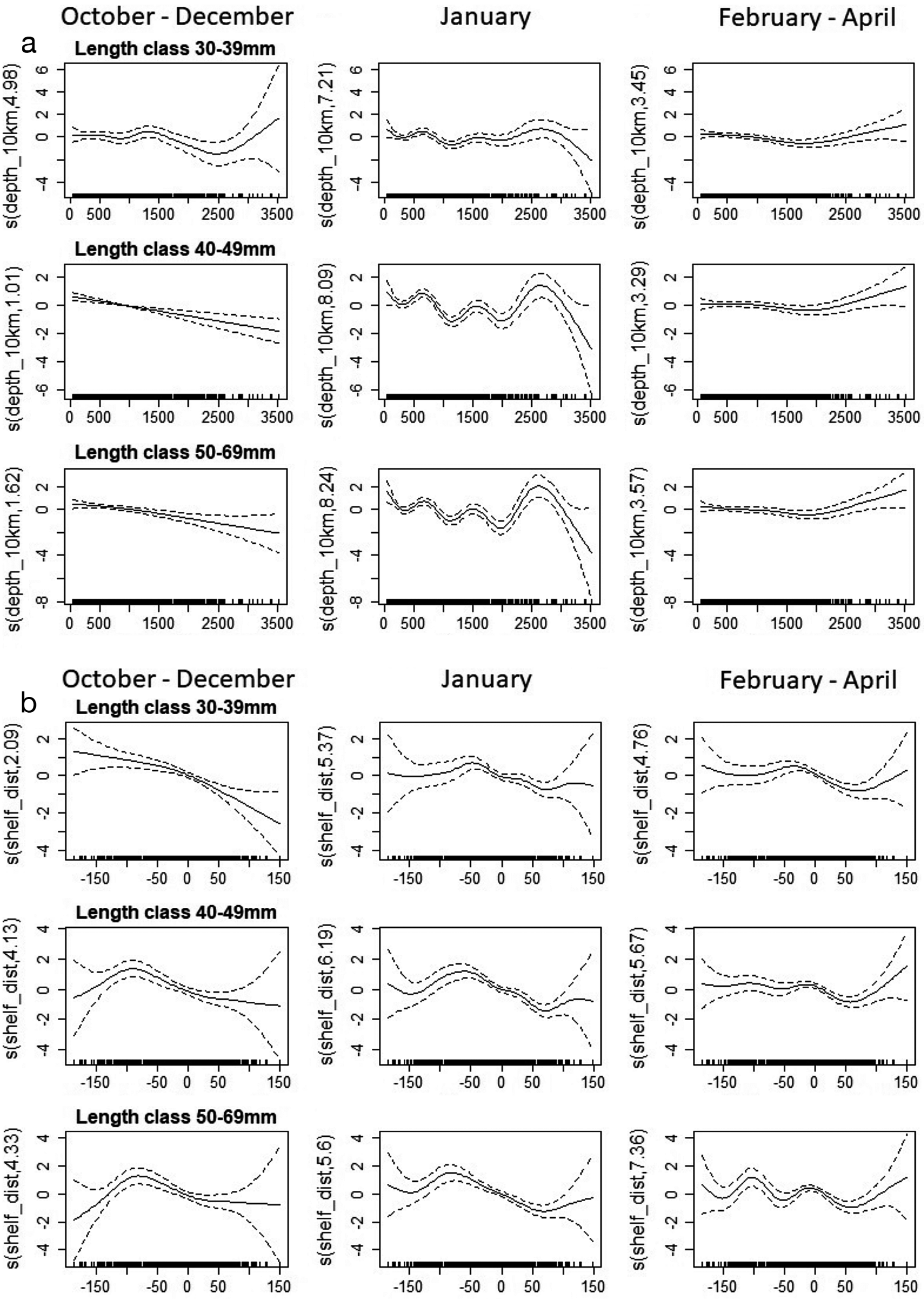

Fig. 5. Seasonal relationships between densities of adult krill in 3 size classes (30–39, 40–49 and 50–69 mm) and (a) bathymetry (m) and (b) distance from the 1000 m depth contour (km) using generalised additive models. On the x-axis, 0 represents the 1000 m depth contour; negative and positive numbers indicate the kilometer distance inside and outside this contour (i.e. above and below this depth, respectively). The degrees of freedom foreach smoother are given in brackets on the y-axis. The dashed lines indicate the 95% confidence interval. The black bars at the bottom of each plot shows data density

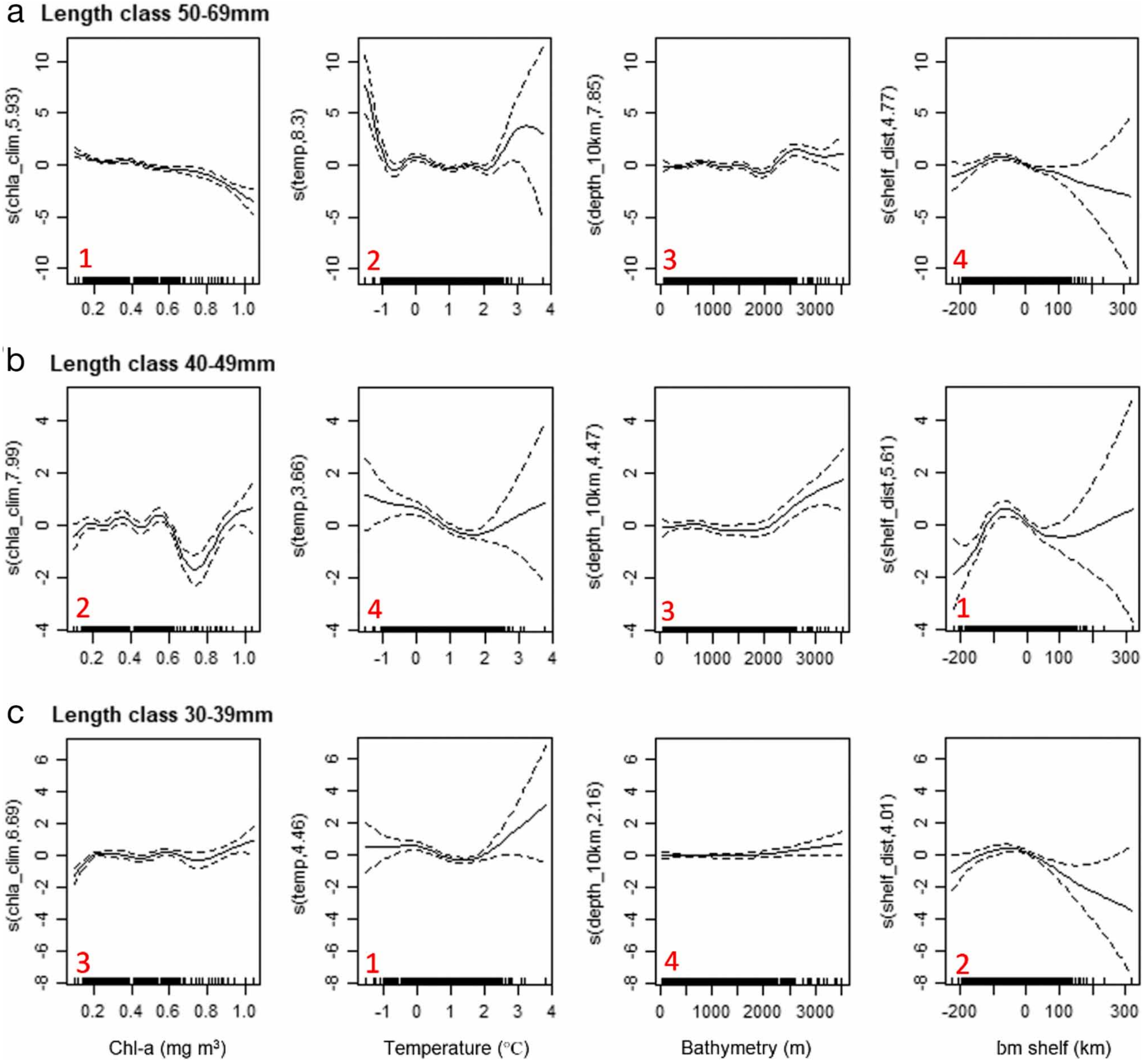

Fig. 6. Generalised additive models of the relationships between 3 length categories of post-larval krill [(a) 50–69 mm, (b) 40–49 mm, (c) 30–39 mm] and environmental variables (chlorophyll *a* concentration, sea surface temperature, depth, and distance from shelf, which refers to the distance from the 1000 m depth contour [km]) in CCAMLR Subarea 48.1. All of the environmental variables are displayed in columns to allow comparison between the krill length categories. The degrees of freedom for each smoother are given in brackets on the *y*-axis. Note that the scales on the *y*-axes vary between the size classes. The dashed lines indicate the 95% confidence intervals. Red numbers indicate the ranking of a variable in its contribution to deviance explained. The black bars at the bottom of each plot shows data density

were found in off-shelf oceanic waters, a trend that reversed after the spawning season. Siegel (1988) reported densities of krill being far greater in off-shelf waters during the summer season compared to autumn, a feature of the krill population that has also been described by Reiss et al. ((2017). An interaction between krill migratory behaviour and current regimes was suggested as the cause for the staggered distribution of krill life stages (Siegel 1988). This idea that a horizontal migration of krill may contribute to seasonal variations in krill biomass at the WAP were furthered by Lascara et al. (1999), who reported an across-shelf pattern of length frequency distribution of krill in all seasons except winter at the WAP. They described a trend for large adults (45–60 mm) to predominate off-shelf, and that larger (>40 mm) krill were often found farther off-shore than smaller individuals during the summer period. The thorough mul-

Table 2. Generalised additive model equations for all 3 length categories of adult krill. Each of the environmental variables (sea surface temperature [SST], distance to shelf, chlorophyll *a* and depth) used within the model is given with the smoothing coefficient (*s*) applied

Length category (mm)	Model
30–39	$\rho = s(SST,\ 4.46) + s(\text{shelf dist.},\ 4.01) + s(\text{chl}\ a,\ 6.69) + s(\text{depth},\ 2.16)$
40–49	$\rho = s(\text{shelf dist.},\ 5.61) + s(\text{chl}\ a,\ 7.99) + s(\text{depth},\ 4.47) + s(\text{SST},\ 3.66)$
50–69	$\rho = s(\text{chl}\ a,\ 5.93) + s(\text{temp},\ 8.3) + s(\text{depth},\ 7.85) + s(\text{shelf dist.},\ 4.77)$

tiyear databases used in both studies and the clear separation between length categories of krill, in addition to several other studies (Trathan et al. 1993, Siegel et al. 2002, 2013, Siegel 2005), have helped to establish the seasonal spawning migration of adults at the WAP as a key paradigm in krill research (Meyer et al. 2020).

Surprisingly, our results contrast with some of the findings regarding seasonal horizontal krill migrations. Importantly, the composite nature of both the KRILLBASE databases means that our analyses include the original krill density data from the studies by both Siegel (1988) and Lascara et al. (1999), and length frequency data from Siegel (1988), alongside a wealth of other data from this region. Our analyses clearly do not show any evidence of an off-shelf migration. The mean percentage of adult krill found off-shelf did not differ significantly between seasons. Indeed, mean percentages of adult krill off-shelf were lowest in January, which is the peak month of spawning (Spiridonov 1995). Given that the off-shelf spawning migration of larger adult krill is considered such a crucial component of the natural history of the WAP (Siegel 1988, 2005, Trathan et al. 1993, Lascara et al. 1999, Meyer et al. 2020), our lack of evidence supporting this theory was unexpected.

Our findings of spawning krill remaining on the shelf also seemingly contrast with those multiple studies (e.g. Marr 1962, Perry et al. 2019) which show that the calyptope larvae have a strongly oceanic distribution in summer. The requirement for eggs to be spawned over deep water (~850 m) to allow them to complete their developmental descent–ascent cycle (Ikeda 1984, Hofmann et al. 1992) without encountering the benthos is the driving concept behind the summer off-shelf spawning migration (Nicol 2006). However, during much of the spawning season at the WAP, the additional depth needed for embryos to hatch before encountering the benthos is <100 m (Hofmann & Hüsrevoğlu 2003) and sinking rates may be reduced through local upwelling features (Thorpe et al. 2019). Additionally, egg densities (no. m^{-2}) at the WAP are more uniformly distributed on or near the shelf boundary than off-shelf (Perry et al. 2019). Crucially, the highest densities of nauplii and metanauplii are also in these on-shelf waters (Perry et al. 2019), as are mature female krill (Conroy et al. 2020). The on-shelf locations of these life stages further support the idea that off-shelf migration of 50–69 mm adults during summer may not be key to successful adult spawning at the WAP. The possibility that the small minority of adult krill found off-shelf at the WAP contribute significantly to recruitment cannot be ruled out. Importantly however, our study shows that this is not achieved through a summer off-shelf spawning migration.

A further point to consider is that this study used averaged data over 41 yr, so any consistent seasonal trends should be highlighted in our results. However, if off-shelf migrations only occurred in some years, our analyses would not resolve such inter-annual variability. Therefore, the possibility that off-shelf migration does take place in some years, with a high degree of inter-annual variability, still exists. The size of our study area may also obscure krill migrations that occur at smaller regional scales, especially those that interact with local current regimes and bathymetric features. Previous studies have suggested a southward contraction of the krill population in autumn (Kanda et al. 1982, Atkinson et al. 2008), and that the krill population spends the winter in more southerly locations. This summer expansion of adult krill is a distinctly different concept to the off-shelf spawning migration defined by Siegel (1988) and Lascara et al. (1999). Evidence of a north–south seasonal migration of krill has been found in other regions of the Southern Ocean, including the Weddell Sea and the Pacific sector of the Southern Ocean off Enderby Land (Kanda et al. 1982, Sprong & Schalk 1992). This life history strategy keeps adult krill separate from developing larvae at a time of low food availability, which may provide a selective advantage. Further understanding of this seasonal expansion and contraction of the krill population requires greater quantities of krill density data, specifically between May and September.

Notwithstanding these summer–winter uncertainties, the possibilities that krill spawning migrations (1) may be small, (2) do not cross the shelf break and

(3) occur only in some years, or (4) that the few krill residing off-shelf contribute greatly to successful recruitment, our data clearly do not support a wholesale off-shelf summer spawning migration figured schematically in Nicol (2006), Atkinson et al. (2008) and Meyer et al. (2020).

4.2. Environmental drivers of krill distribution

Our GAMs reveal that SST, chl *a*, bathymetry and distance from shelf explain only a part of the variance seen in the distribution of 30–39, 40–49 and 50–69 mm adult krill, and consequently are not reliable predictors of krill density. Clear relationships between single environmental factors and krill are difficult to find, and vary considerably between regions and individual studies (Weber & El-Sayed 1985, Siegel 2005, Nicol 2006, Silk et al. 2016). The low explanatory power of environmental variables found in previous studies is likely attributable to the intense swarming behaviour of krill, a factor which makes their distribution inherently difficult to understand and predict. Prior studies at the Antarctic Peninsula demonstrate that krill are associated with on-shelf waters (Siegel 2005, Atkinson et al. 2008) and with moderate chl *a* concentrations (Silk et al. 2016). A domed relationship between krill and chl *a* has also been reported from other regions of the Southern Ocean (Atkinson et al. 2008, Whitehouse et al. 2009). The deviance explained by the results of our GAMs is highest for the largest length category of krill (50–69 mm; 17%) and lowest for the smallest length category (30–39 mm; 5%).

Two noticeable trends did appear from our GAM analysis (Fig. 6). Firstly, adult krill of all length categories are most abundant on-shelf in Subarea 48.1, a trend that has previously been described using both fisheries data (Murphy et al. 1997, Trathan et al. 1998) and scientific haul data (Siegel 2005, Atkinson et al. 2008, Silk et al. 2016, Conroy et al. 2020). More specifically, all length categories were found in the highest densities ~75 km inside the shelf break. High densities of krill inside the shelf break may be due to the deep canyons that bisect the shelf-break at the Antarctic Peninsula through which circumpolar deep water currents transport krill onto the shelf (Ashjian et al. 2004, Lawson et al. 2004). Physical and biological properties of submarine canyons can also create episodically higher biological activity, as they act as conduits for horizontally transported nutrients from off-shore upwelling zones (Kavanaugh et al. 2015, Hudson et al. 2019).

Secondly, we found that the relationship with chl *a* differs between different length categories. The highest densities of the largest length category of krill appear to be associated with low chl *a* concentrations (Figs. 2 & 6). Our chl *a* climatologies also displayed a strong on–off-shelf gradient (Fig. 2), a trend that concurs with prior chl *a* measurements at the WAP, where values can be 4 times greater in-shore than off-shore (Smith et al. 1998, Garibotti et al. 2003). In general, the Southern Ocean is a high nutrient, low chl *a* region (Holm-Hansen et al. 1977), and is considered to be limited by iron availability (Takeda 1998, Garibotti et al. 2003). The low and unpredictable nature of food availability in the open Scotia Sea has been found to leave adult krill with an energy deficit (Fach et al. 2002, 2006). In contrast, the inshore waters at the tip of the Antarctic Peninsula is one of the most biologically productive regions in the Southern Ocean, where the krill-based ecosystem supports numerous apex predators (Fraser & Trivelpiece 1996, Arrigo et al. 1998, Marrari et al. 2008). Adult krill require a food-rich environment prior to and during the spawning period, as both the quantity and quality of food available to female krill affect the viability of their embryos (Yoshida et al. 2011). A study by Whitehouse et al. (2009) in the waters around South Georgia also found that, in areas of high krill density, krill can drive down their food supply. The negative relationship between the abundance of large krill and chl *a* potentially suggests that this size class exerts top-down control on their food owing to their increased metabolic demands. Our results estimate that a 50–69 mm krill could graze a maximum of 74% of available phytoplankton per day, compared to 15% by 40–49 mm krill, and just 5% by 30–39 mm krill (see Text A1). The high energy demands of maturation and reproduction (Clarke & Morris 1983) in addition to the relationship between body size and their pelagic lifestyle (Kils 1981) are likely to explain these results.

5. IMPLICATIONS

At the scale of our analysis, no evidence was found to support the established paradigm of a regularly repeating summer off-shelf migration of adult krill. Our results suggest that high densities of adult krill within Subarea 48.1 are most predictably found on-shelf throughout much of the season, including the largest adult krill that are the most fecund and likely to contribute to the spawning stock. If the descent–ascent model of early development is necessary for successful recruitment, the population in Subarea 48.1 may be reliant on the relatively small proportion adult krill found off-shelf during the spawning season, irrespective of whether these krill successfully spawn on- or off-shelf. Uncertainty regarding the depth requirement to complete this ascent–descent cycle indicates that better understanding of this area of the krill life cycle is vital before we can grasp the sensitivity of both the on-shelf and off-shelf environment particularly to projected climatic changes.

The on-shelf location of large, lipid-dense krill during the summer reproductive period means that they could be within the foraging range of shelf-based predators. This may be especially beneficial, as many krill predators are size-selective foragers that preferentially target larger krill (Osman et al. 2004, Miller & Trivelpiece 2008). The recent increase in both the spatial and temporal concentration of fisheries catches (Santa Cruz et al. 2018) has coincided with a greater occurrence of poor krill predator performance (Watters et al. 2020). This has led to questioning of the suitability of the current fisheries management as the spatio-temporal scales of current krill catch limits are coarser than those of predator–prey interactions (Watters et al. 2020).

The current krill fishery management has also been questioned over its impact to the krill stock itself, as well as its predators. The fishery uses relatively coarse nets which therefore target spawning age krill relative to juveniles, and the shelf waters of Subarea 48.1 are also being increasingly targeted (Meyer et al. 2020). Added to this, a recent (2024) inability to renew the spatial segregation of catch limits within CCAMLR means that fishing pressure within Subarea 48.1 may become even more concentrated. In this context, our findings that most of the spawning-size krill do not migrate off-shelf but remain over this locally heavily fished shelf are relevant to the need for smaller-scale management.

In a parallel management initiative, a marine protected area has been proposed at the WAP and Southern Scotia Arc to protect the krill-centric food web (CCAMLR 2017). Increasing the resilience of the krill population, and the ecosystems they support, by creating no-take zones in specific regions pivotal to the krill life cycle will help by mitigating the detrimental effects of climate change on krill stocks (Dahood et al. 2020). Concurrently, CCAMLR are supporting the development of a krill stock hypothesis to improve understanding of the spatio-temporal connections throughout the krill life cycle in order to improve management (Meyer et al. 2023). Our study and others that consider the seasonal distributions of krill, and the impact of migratory behaviours, provide a step towards effectively managing krill habitats.

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Appendix

To calculate the mean maximum percentage of carbon content of krill consumed per day, the maximum 1° latitude by 2° longitude cell value for each length category of adult krill was taken. This was then used to calculate the daily carbon ration of these krill length categories (using relationships in Lenz 1974, Morris et al. 1988), assuming a conservative daily carbon ration of 17% (Schmidt & Atkinson 2016). Across Subarea 48.1, the maximum chl a value is 1.038 mg m^{-3} which is the equivalent of 51.9 mg C m^{-3} (using a C:chl a ratio of 50; Whitehouse et al. 2009). This equals 3.9 g C m^{-2} over a typical 75 m surface mixed layer (Korb & Whitehouse 2004).

Table A1. Data extracted from both KRILLBASE datasets for this study are shown here with reference to the season and the1° latitude × 2° longitude grid cell grid number

Grid cell number	Length frequency (total no. krill)				Abundance (no. of stations)			
	Oct–Dec	Jan	Feb–Apr	Total	Oct–Dec	Jan	Feb–Apr	Total
4196	346	519	6211	7076	29	30	36	95
4197	61	420	890	1371	20	29	40	89
4376	75	316	4	395	42	27	48	117
4377	92	1084	1674	2850	31	17	46	94
4378	7	33	22	62	5	8	22	35
4556	155	148	34	337	20	12	21	53
4577	5	678	10	693	32	14	39	85
4558	2094	1222	2142	5458	76	45	78	199
4737	6	126	18	150	17	14	25	56
4738	241	906	927	2074	7	9	8	24
4739	3127	1859	170	5156	7	15	15	37
4740	3954	4087	5119	13160	17	76	35	128
4741	2217	740	3340	6297	6	36	22	64
4743	20	296	2652	2968	5	8	4	17
4919	339	153	301	793	11	32	24	67
4920	2905	833	9026	12764	23	79	60	162
4921	2039	1401	2310	5750	20	122	72	214
4922	5914	1053	5534	12501	28	158	114	300
4923	3133	1631	5212	9976	9	61	30	100
4924	316	372	2961	3649	2	10	8	20
5099	1	34	10	45	5	23	10	38
5100	399	539	589	1527	15	95	41	151
5101	958	1355	767	3080	22	101	82	205
5102	10939	12298	11570	34807	48	247	174	469
5103	9786	9269	18691	37746	69	310	168	547
5104	4458	2671	3816	10945	22	82	70	174
5282	5714	8264	5740	19718	60	197	184	441
5283	18160	14608	33565	66333	68	296	262	626
5284	3359	1228	3385	7972	34	112	74	220
Total	80820	68143	126690	275653	750	2265	1812	4827

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