RESEARCH ARTICLE

Stepping stones towards Antarctica: Switch to southern spawning grounds explains an abrupt range shift in krill

Angus Atkinson[1] | Simeon L. Hill[2] | Christian S. Reiss[3] | Evgeny A. Pakhomov[4,5] | Gregory Beaugrand[6] | Geraint A. Tarling[2] | Guang Yang[7] | Deborah K. Steinberg[8] | Katrin Schmidt[9] | Martin Edwards[1] | Emilce Rombolá[10,11] | Frances A. Perry[12]

[1]Plymouth Marine Laboratory, Plymouth, UK

[2]British Antarctic Survey, Cambridge, UK

[3]South West Fisheries Science Centre, NOAA Fisheries, La Jolla, California, USA

[4]Department of Earth, Ocean and Atmospheric Sciences and Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada

[5]Hakai Institute, Heriot Bay, British Columbia, Canada

[6]Laboratoire d'Océanologie et de Géosciences, UMR 8187 LOG, Centre National de la Recherche Scientifique, Station Marine de Wimereux, Université de Lille, Université du Littoral Côte d'Opale, Wimereux, France

[7]Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, Qingdao, China

[8]Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, Virginia, USA

[9]School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, UK

[10]Instituto Antártico Argentino, Dirección Nacional del Antártico, Buenos Aires, Argentina

[11]Consejo Nacional de Investigaciones Cientifcas y Técnicas, Buenos Aires, Argentina

[12]Marine Biological Association, Plymouth, UK

Correspondence
Angus Atkinson, Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL13DH, UK.
Email aat@pml.ac.uk

Abstract

Poleward range shifts are a global-scale response to warming, but these vary greatly among taxa and are hard to predict for individual species, localized regions or over shorter (years to decadal) timescales. Moving poleward might be easier in the Arctic than in the Southern Ocean, where evidence for range shifts is sparse and contradictory. Here, we compiled a database of larval Antarctic krill, *Euphausia superba* and, together with an adult database, it showed how their range shift is out of step with the pace of warming. During a 70-year period of rapid warming (1920s–1990s), distribution centres of both larvae and adults in the SW Atlantic sector remained fixed, despite warming by 0.5–1.0°C and losing sea ice. This was followed by a hiatus in surface warming and ice loss, yet during this period the distributions of krill life stages shifted greatly, by ~1000 km, to the south-west. Understanding the mechanism of such step changes is essential, since they herald system reorganizations that are hard to predict with current modelling approaches. We propose that the abrupt shift was driven by climatic controls acting on localized recruitment hotspots, superimposed on thermal

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niche conservatism. During the warming hiatus, the Southern Annular Mode index continued to become increasingly positive and, likely through reduced feeding success for larvae, this led to a precipitous decline in recruitment from the main reproduction hotspot along the southern Scotia Arc. This cut replenishment to the northern portion of the krill stock, as evidenced by declining density and swarm frequency. Concomitantly, a new, southern reproduction area developed after the 1990s, reinforcing the range shift despite the lack of surface warming. New spawning hotspots may provide the stepping stones needed for range shifts into polar regions, so planning of climate-ready marine protected areas should include these key areas of future habitat.

1 | INTRODUCTION

Temperature is a major driver of marine species distribution at global scales (Beaugrand et al., 2019; Burrows et al., 2011, 2019; Pinsky et al., 2013) and, accordingly, one of the 'universal' responses to climatic warming is a poleward shift in distribution (Chen et al., 2011; Parmesan & Yohe, 2003). This accords with the general principle of thermal niche conservatism, a central concept of species distribution models, which project distributions under future climatic states based on the assumption that the relationship of a species to its environment (including temperature) remains unchanged (Brun et al., 2016). The urgent need to gauge species- and ecosystem-level responses to a warmer world has led to a rapid increase in such projections. These are valuable, for example, in providing broad-brush, large-scale approximations of end-of-century distributions (Cheung et al., 2009).

Despite their clear value at large scales, the utility of such projections at smaller scales has been questioned on several counts. They can be limited in projecting the distributions of individual species, particularly over the shorter timescales (years to a few decades) required by resource managers (Brun et al., 2016; Fernandes et al., 2020). Further, the underpinning assumptions for the concept of niche conservatism (Crisp et al., 2009) are also under scrutiny, given the potential for genetic adaptation, phenotypic variability, life stage-specific responses and other compensation mechanisms (Dam, 2013; Pinsky et al., 2020). Indeed, range shifts among individual species are highly variable and can be much faster, slower, unresponsive or even opposite in direction to the general poleward shifts of isotherms in a warming environment (Chen et al., 2011; Chivers et al., 2017; Fuchs et al., 2020; Tarling et al., 2018). Beaugrand and Kirby (2018) have proposed a theoretical framework to understand the reasons behind this apparent lack of congruence, in terms of interacting processes at multiple levels of spatial and biological organization.

Polar ectotherms are temperature sensitive and yet their habitats are warming faster than the global average rate, so we urgently need to understand and project range shifts to gauge their future roles in ecosystem functioning, food provision and biogeochemical cycling. With some notable exceptions in parts of the Arctic and subarctic (Dalpadado et al., 2020; Edwards et al., 2021; Ershova et al., 2021; Fossheim et al., 2015), polar data sets rarely have sufficient temporal and spatial coverage to understand how rapid polar warming has translated into range shifts (Wassmann, 2011). Poor understanding of the mechanisms behind past change challenges our confidence in the future projections (Pinsky et al., 2020).

Within the Southern Ocean, Antarctic krill (*Euphausia superba*) play a central role in the food web, and the spatio-temporal dynamics of this single species impact both higher and lower trophic levels (Reiss et al., 2020; Schmidt et al., 2016). For this reason, studies are increasingly projecting krill distribution (Mackey et al., 2012; Piñones & Fedorov, 2016) or growth potential (Hill et al., 2013; Murphy et al., 2017; Veytia et al., 2020) based on the untested assumption that the relationship of krill with its environment remains fixed. Fortunately, this assumption is testable, since extensive abundance data have been collected over the last century. For this study, we built a long-term, large-scale database for krill larvae to complement an existing one on adults (Atkinson et al., 2017). The overall range of these adult stages has previously been shown to have contracted southwards over the last century (Atkinson et al., 2019). By adding the new larval data set, we show here that the range contraction is actually a step change, which is decoupled from the pace of climate warming. The larval and adult databases allow us to hypothesize a mechanism, based on spawning dynamics, to explain such abrupt shifts.

2 | METHODS

2.1 | Source krill data

The data set on post-larval krill (i.e. all juvenile and adult krill, hereafter termed collectively as 'adults') was obtained from KRILLBASE-abundance, which is described in Atkinson et al. (2017). This is a multinational compilation of all available data on adult abundance (no.

m^{-2}) of *E. superba*, based on net samples. It spans the period 1926–2016 and, while circumpolar in scope, has most data in the Atlantic sector. For this study, we also generated a large, parallel database for larval *E. superba* abundance for the Atlantic sector only (KRILLBASE-larvae). An earlier version of this composite database was analysed by Perry et al. (2019) but we have since added several thousand extra net hauls. This larval database, like the one on adults, is a compilation of individual survey data transcribed by one of us (AA) from catch notebooks, appendices of publications or sent directly by the data originators. The original data supplied were presented as numbers of larvae per m^3 or numbers per m^2, based on a volume filtered estimated typically by multiplying the mouth area of the net by the distance towed. In common with the adult database, we have converted all densities to numbers per m^2. With 9497 records, KRILLBASE-larvae builds on an original database of around 1000 records for the Atlantic sector, compiled by Siegel and Watkins (2016). Table S1 lists the main sources of data that we used for KRILLBASE-larvae.

None of the data in the adult or larval abundance databases are based on sampling targeted on krill aggregations. Both databases include a variety of sampling nets, depths and times of year. Because of the ability of adult krill to escape nets, we base our analyses here on adult densities that have been numerically standardized to a single, relatively efficient net sampling method (a night-time RMT8 net fishing from 0 to 200 m on 1 January). The standardization methods used are detailed in Atkinson et al. (2017). The larval data have not been standardized due to their smaller size, and thus reduced ability to evade nets. However, we checked that the main trends observed were followed independently by both component larval stages, namely calyptopes and furcilia, which differ greatly in size and vertical distribution and thus in their catchability by nets. The sampling coverage for each life stage is shown in Table 1.

For most of the analyses, we divided the sampling period into three eras of approximately 20 years each, with the exact era boundaries selected to be consistent with analyses in Atkinson et al. (2019). Thus, era 1 was 1926–1939 (The 'Discovery era'), era 2 was 1976–1995 and era 3 was 1996–2016. Table 1 shows the station coverage from larval and adult databases for each era, after the data screening described in the next section.

2.2 | Krill data screening

From the complete larval and adult krill databases, we first performed screening procedures to exclude outlying hauls which provided poor or unbalanced representations of krill density or distribution (Table 1). For the adults, these were based on previous screenings according to sampling depth of nets and time of year of sampling so as to remain consistent with the methods used in Atkinson et al. (2008, 2019). The same screening was applied to larvae, except the additional months of October and November were removed due to the rarity of larvae at that time of year. The full larval database includes density (no. m^{-2}) data on eggs, nauplii plus metanauplii, and each of the three calyptope and six furcilia stages. To maximize sample size, we pool all calyptope and furcilia into one single category entitled 'larvae'. The exceptions are Figures S1 and S4, which compare trends in calyptopes and furcilia separately to investigate any biases related to net mouth area and mesh selection.

2.3 | Environmental data

Most records of the two krill databases did not have parallel environmental data, so we needed to add them separately. GEBCO bathymetry data were added to each data record as described in Atkinson et al. (2017). To provide an estimate of sea surface temperature at the time of sampling, we used the Extended Reconstructed Sea Surface Temperature (ERSST) data set (Huang et al., 2018; https://www.ncdc.noaa.gov/data-access/marineocean-data/extended-reconstructed-sea-surface-temperature-ersst-v5). The data set is derived from a reanalysis based on the most recently available International Comprehensive Ocean-Atmosphere Data Set (ICOADS). Improved statistical methods have been applied to produce a stable monthly reconstruction, on a 2° × 2° spatial grid, based on sparse data (Smith et al., 2008). An annual average was calculated for each geographical cell (between 52 and 74°S and 80 and 20°W) and each year (1854–2018). These values were extracted in Matlab and then each larval or adult station was interpolated onto this grid to extract an annual mean sea surface

TABLE 1 Screening of the full larval and adult krill KRILLBASE databases for our analysis. Further spatial screening applied to some of the subsequent analyses. Sampling eras are described in Section 2.1, with numbers of sampling stations after screening presented for each era

Attribute	KRILLBASE-larvae	KRILLBASE-adults
Stages included	Calyptopes and furcilia	Post-larvae (Juveniles and adults)
Time span of coverage	1926–2014	1926–2016
Filter for month of coverage	December to April inclusive	October to April inclusive
Filter for top sampling depth	20 m or shallower	20 m or shallower
Filter for bottom sampling depth	50 m or deeper	50 m or deeper
No. stations 1926–1939 (era 1)	772	772
No. stations 1976–1995 (era 2)	969	3297
No. stations 1996–2016 (era 3)	3339	4405
Total stations	5080	8474

temperature relevant to its year of sampling. We chose to extract annual averages for this analysis, rather than those months specific to sampling to maximize the ERSST data input for this high-latitude region. To further account for incomplete spatio-temporal coverage of temperature data, the 2° × 2° grid cells were analysed here based on their average annual values over the whole ~20-year period encompassing each era.

Sea ice is important for the krill life cycle and its winter coverage provides an index of long-term environmental change independent from that of the ERSST data set. The most reliable sea ice index in this sector that spans a century is the South Orkney Fast Ice Series (SOFI) which is the recorded and interpolated timing of fast ice formation and breakout at Signy Island, South Orkneys (an island group on the Southern Scotia Arc at approx. 60°40′S, 45°00′W). This annual time series, starting in 1903, is described in more detail in Murphy et al. (2014). SOFI pertains to just one part of the SW Atlantic sector, and while it does not represent conditions further SW down the Antarctic Peninsula, it provides a parallel indication of long-term environmental change in the major spawning ground of krill along the southern Scotia Arc.

Based on prior work, the Southern Annular Mode (SAM) was the climatic mode with the clearest link to krill population processes across the whole sector (Atkinson et al., 2019), so we focussed on SAM as a correlate of population dynamics acting alongside direct temperature effects on the krill distribution. SAM is measured as a pressure difference between reference points (Marshall, 2003) and more positive anomalies reflect a southerly translation of the low-pressure belts encircling Antarctica and a general increase in wind strength in the latitudes at which the krill population is centred in the SW Atlantic. For the SAM, annual values used in Figure 1 were obtained from http://www.nerc-bas.ac.uk/icd/gjma/sam.html (accessed 11 November 2020). These annual means were based on the method described in Marshall (2003).

2.4 | Multiple approaches to range shift analysis

Since our databases do not provide an evenly weighted spatial and temporal coverage, we approached the range shift analysis of larval and adult krill in six different ways, which contrast greatly in the way they combine and analyse the data. These were: first, simple gridding and visualization of the data, based both on three sampling eras (Figure 2) and individual sampling years (Figure S1); second, calculation of changes in latitude and longitude of the leading, central and trailing portions of the distribution during the three eras (Figure 3); third, by doing similar analyses but dividing into latitudinal bands not grid cells and using five eras rather than three (Figure S5); fourth, by calculating commensurate changes in thermal habitat of the krill stages (Figure 4); fifth, by comparing time trends of krill life stages in northern and southern subregions of the sector, again dividing the data according to sampling eras, individual year or larval stage (Figure 5; Figure S4); and sixth, by dividing again into northern and

southern subregions but using a non-parametric test on equalized sample sizes and a different metric of krill abundance. These six methods are detailed below.

2.4.1 | Method 1: Plotting krill distribution in each era and year

Using Arc GIS version 10.2.2 in South Polar Stereographic Projection, we provide in Figure 2 a simple visualization of mean gridded distributions during the three above-mentioned sampling eras. The grid size used (2° latitude by 5° longitude) was selected as a compromise between data coverage and resolution. Data were plotted as the arithmetic mean density of all stations in each era that lay within each grid cell in each era. At this same grid resolution, the distributions of individual larval stages in individual years are provided by Figure S1.
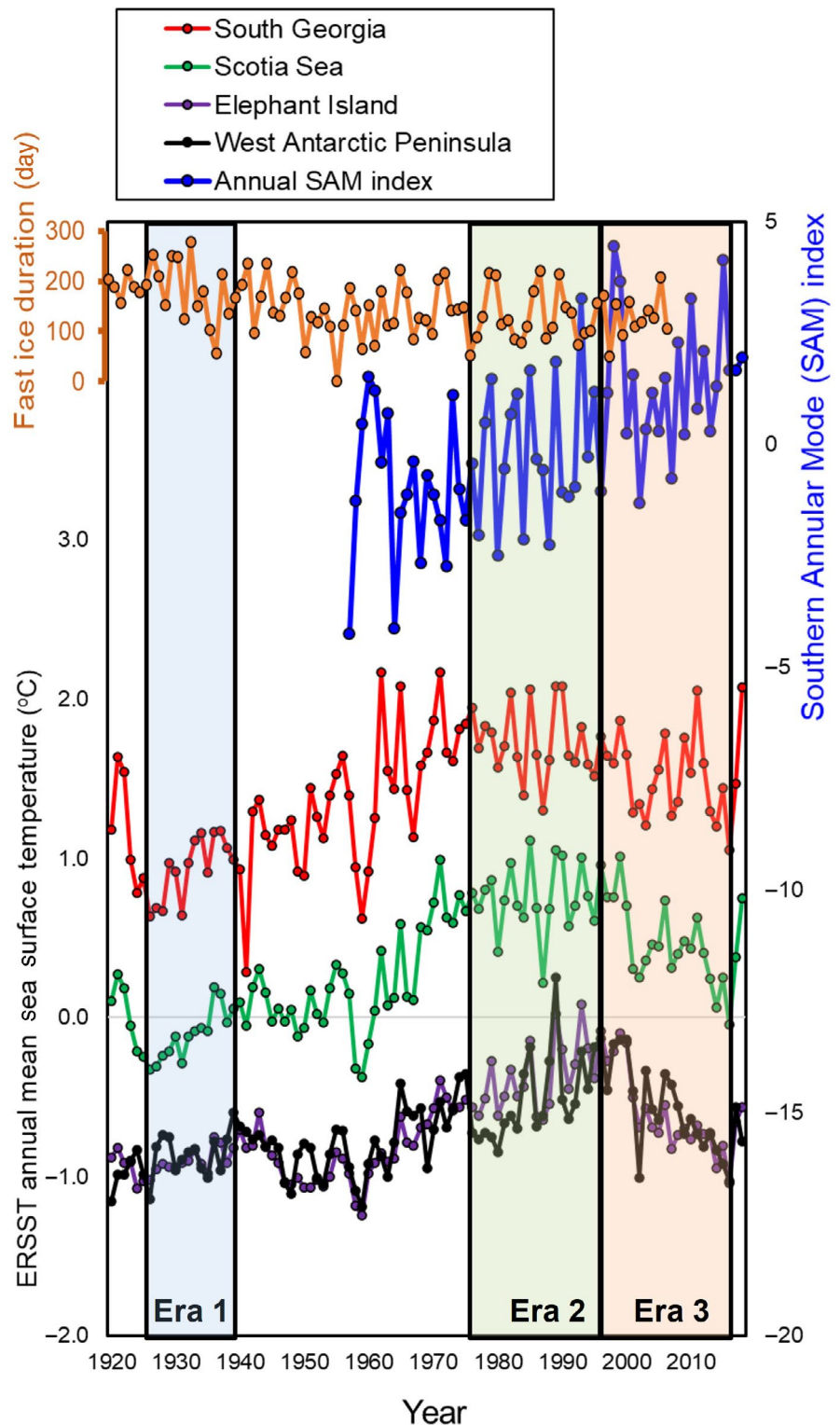
2.4.2 | Method 2: Geographical range shift quantifications based on the three eras

To provide a numerical analysis of range shifts, we analysed both their latitudinal and longitudinal components (Figure 3) and then summarized these in terms of kilometre per decade using the 'measurement' tool in GIS. To measure latitudinal and longitudinal range shifts in a robust way, we needed to identify the group of grid cells that were sampled in every one of the three eras (Figure S2). For the larvae, this comprised nine latitudinal bands (of 2° latitude) spanning 50–68°S and 11 bands (of 5° longitude) spanning 20–75°W. For the adults, this generated nine latitudinal bands spanning 50–68°S and 12 longitudinal bands spanning 20–80° W. Hence, the larval comparable area consisted of 37 cells while the adult grid comprised 43 comparable cells.

To examine the 'centre of gravity' range shift in terms of latitude, we first averaged, for each era, the available means for the respective grid cells within each of the nine latitudinal bands. This had the effect of stratifying the data coverage (such that each of our comparable grid cells was given the same weight). This method was chosen for all our range shift analysis here, to account for uneven sampling distribution, with some cells sampled much better than others. We then calculated the centre of gravity as the sum of the product of band mean density and mean latitude of the band, divided by the sum of the densities in each band. Similar calculations of the centre of gravity were performed for the longitudinal bands.

To calculate range shifts in terms of cumulative percentiles (Figure 3), we took the mean densities in each latitudinal band, as described above, and calculated the cumulative sum of the densities, from north to south. The 'northern range edge' was defined here as the interpolated latitude of the 10% cumulative density values, the northern quartile as 25%, range centre as 50%, southern quartile as 75% and the 'southern range edge' as 90%. These 10% and 90%

FIGURE 1 Contrasting trends in SW Atlantic sector temperature, SAM index and sea ice. ERSST annual mean sea surface temperature (1920–2018) in selected 2° latitude by 2° longitude grid cells spanning the SW Atlantic sector. Grid cells were South Georgia (cell centred at 54°S, 36°W), Scotia Sea (58°S, 42°W), Elephant Island (62°S, 56°W) and West Antarctic Peninsula (66°S, 70°W). Annual SAM indices are plotted for the period of available data on the right-hand axis. Sea ice cover represents the duration of winter fast ice in the South Orkneys Fast Ice time series; values plotted here spanning 1920–2008 are as described in Murphy et al. (2014). Superimposed are the time spans of the three sampling eras of krill larvae and adults over which we compared distributions. Era 1 (*Discovery* era) spans 1926–1939, era 2 spans 1976–1995 and era 3 spans 1996–2016. ERSST, Extended Reconstructed Sea Surface Temperature; SAM, Southern Annular Mode
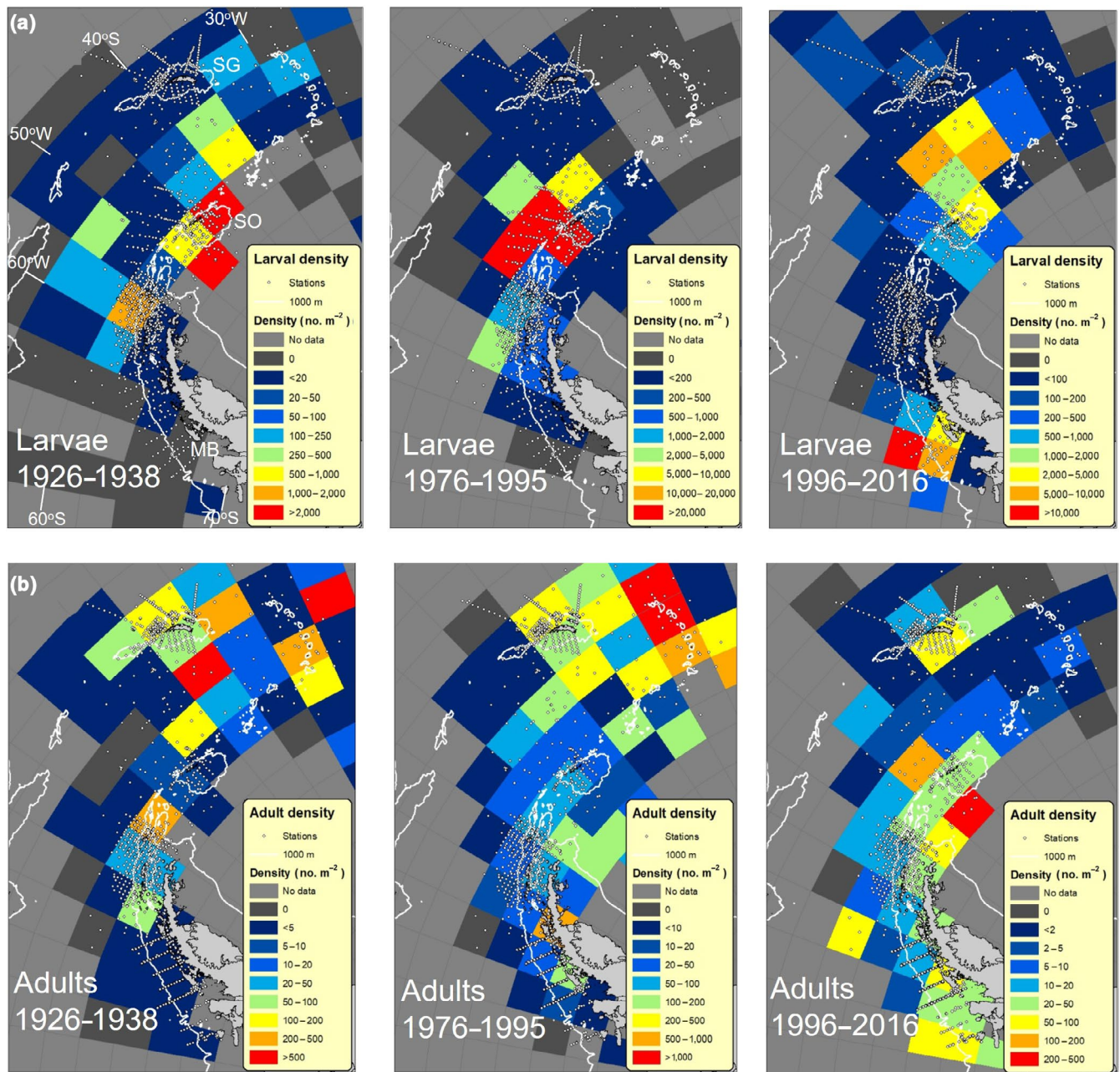

quantiles are not extreme range edges which are very hard to define accurately for plankton due to sampling limitations. Interpolation for latitude was linear, based on the two adjacent cumulative sum densities and their respective latitudes. Similar calculations of cumulative quantiles of longitude were performed, running from east to west, such that the eastern range edge was defined as the 10% quantile.

2.4.3 | Method 3: Improved definition of the timing of the range shifts

Division of the 1926–2016 period into only three eras, each of about 20 years, loses some of the definition of timing of the range shift. To address this, we divided the period also into five eras, each of about 10 years each. To maintain adequate sample size in
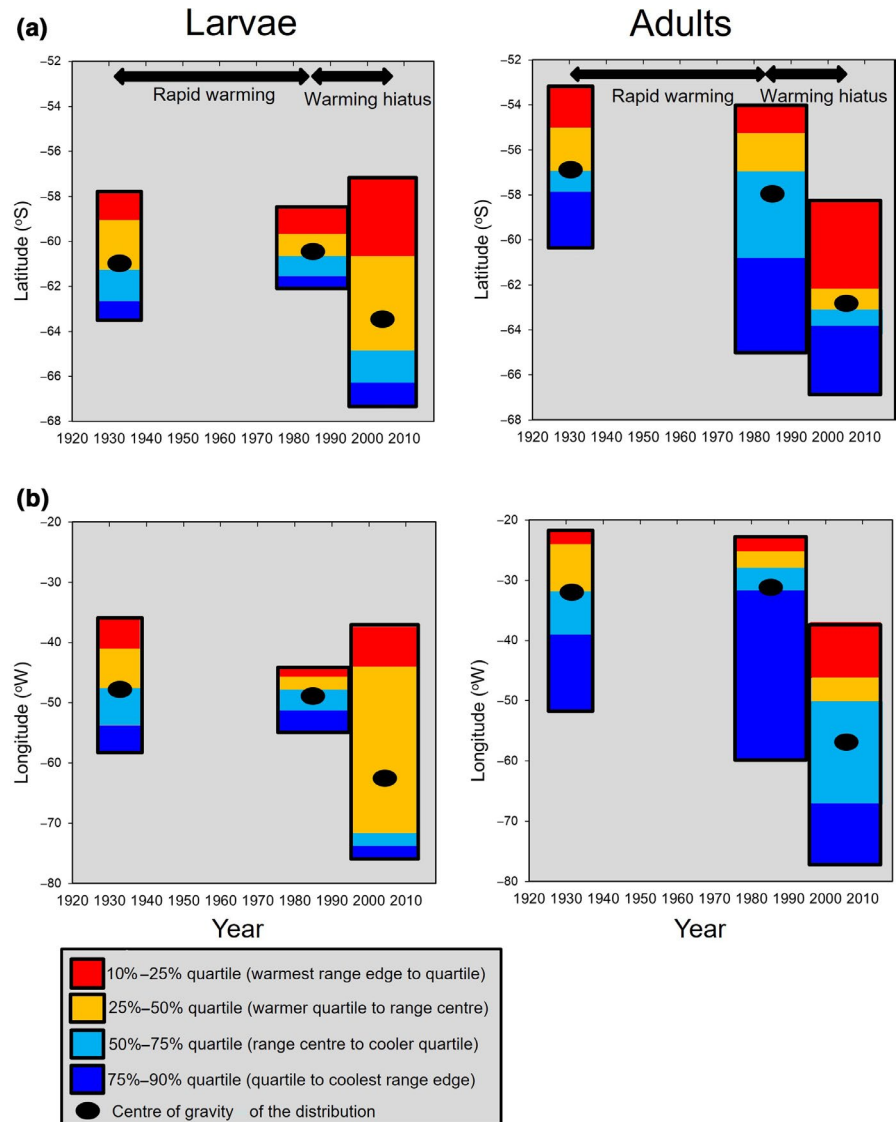
FIGURE 2 Changing distributions of (a) larvae and (b) adult krill over the last 90 years. Note the different scales, which were selected based on natural breaks to provide an even colour scale to indicate the main distribution centres (bright colours). This obscures major changes in overall density between eras which are better depicted in Figure 5. Dots represent stations sampled in each era. Latitudes and longitudes are depicted on top left-hand map, with abbreviations MB, Marguerite Bay; SG, South Georgia; SO, South Orkney Islands

an increased number of eras, we used a simpler method whereby the data were divided into latitudinal bands rather than into grid cells. This had the advantage of reducing the weighting of sparsely sampled grid cells, some of which had high krill densities (Figure 2). We thus divided into four latitudinal bands each of 5° and spanning 50–70°S, calculating the mean density per band. Population centre of gravities were calculated as the sum of the products of mean density per band and latitude of the middle of the band, divided by the sum of the mean densities per band. These results are presented in Figure S4.

2.4.4 | Method 4: Shifts in thermal habitat of krill stages

In common with the analyses of geographical range shift in the three eras, the source data were the set of grid cells common to each era (Figure S2), with each cell providing both the mean SST for the krill records and mean krill density, averaged over each respective era. To calculate thermal habitat in each era, the comparable grid cells were ranked according to their mean SST in each era in turn, then following the method of Edwards et al. (2021), the SST grid cell values were

FIGURE 3 An abrupt southward and westward shift in krill distribution since the 1970s. (a) Latitudinal shifts and (b) longitudinal shifts. From north to south (panel a), and from east to west (panel b), the cumulative quantiles describe the range edges (10% and 90%), quartiles (25% and 75%) and range centre (50%). These, as well as the centre of gravity of the population are calculated as described in Methods. Width of bars corresponds to the duration of sampling averaged within each era. During the warming period between the 1920s and mid-1990s, distributions were fairly stable, with strong shifts only during the surface warming hiatus spanning the second and third eras
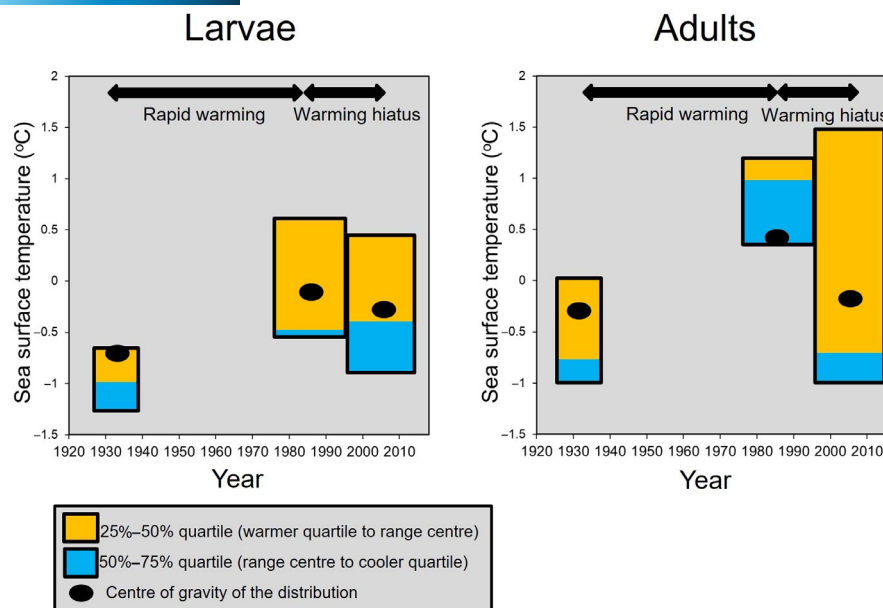

weighed by multiplying by the mean krill densities for the respective cell and sampling era. Weighted centre of gravity of temperature for an era was then calculated as the sum of the product of mean temperature for the cell and its mean krill density, divided by the sum of mean krill density across all cells (Figure 4). Cumulative percentiles were calculated as before, by calculating cumulative sums of the product of temperature and mean density for the cells ranked in order of increasing mean temperature and then calculating the median temperature of cold and warm quartiles, based on interpolation of the position of the 25%, 50% and 75% quantile values relative to adjacent values.

2.4.5 | Method 5: Population trajectories in northern and southern parts of the SW Atlantic sector

The era-based analyses of changes in the distribution of krill described above reflect changes in distribution pattern between eras,

based on data averaged over periods of several decades. Thus, the density scales of Figure 2 change between eras in order to portray shifts in the distribution centres denoted by the red hotspots of highest density. However, the major range shift observed over the last 40 years is accompanied by major changes in density of both larvae and adults. To examine the causes of this, Figure 5c–f and Figure S5 show the larval and adult abundance data at two contrasting scales. At one extreme, we calculated a time series of annual mean densities, based on the austral summer season. Thus, for example, the year 1981 for krill larvae spans 1 December 1980 to 30 April 1981. At the resolution of annual mean data, the sample size, particularly for the larvae, was highly unbalanced with only a few stations sampled in some years. This led to some stations having mean abundance of zero, so data were plotted and regressed here as $Log_{10}(x + n)$, where n is half of the minimum annual mean recorded for the time series. For this reason, we also used the opposite extreme for pooling the data, namely by presenting a simple arithmetic mean density of krill in each sampling era, irrespective of the year of sampling. These data were not normally distributed so we compared

FIGURE 4 Larval and adult krill have not maintained a fixed thermal niche during periods of warming and cooling. Change in annual mean sea surface temperature inhabited by larval and adult krill over the three eras. As for Figure 3, we only included grid cells sampled in each era. Grid cells were ordered in increasing temperature and cumulative percentiles and centre of gravity were calculated as per Figure 3, weighting according to krill density in each cell. Because of sparse data coverage at the thermal extremes, coupled to the coarse resolution of Extended Reconstructed Sea Surface Temperature, we were not able to provide a reliable picture of outer thermal limits (i.e. 10% and 90% thermal quantiles)

them between eras with a Mann–Whitney test. For these analyses, adult data are extracted from the whole area due to the wide distribution, while larval data were obtained only from their main distribution area (i.e. 56–68°S, 20–70°W) to reduce variable weighting by stations outside the main larval nursery areas.

2.4.6 | Method 6: A non-parametric test of trends in swarm frequency and density in northern and southern parts of the SW Atlantic sector

Krill occur in dense swarms and this highly skewed distribution poses challenges to the analysis of trends additional to the uneven time and space coverage of available data. The previous methods rely on trends in arithmetic mean krill density from groups of stations, some of these (e.g. Figure 5d,f) having been logged before analysis. To provide an independent method, we also examined time trends in the frequency of encountering swarms (Figure S6). This required equalizing the sample size, achieved by ordering stations in each of the two subregions by sampling day and then dividing each into 20 portions with the same number of stations in each (Yang et al., 2020). Based on all station data from the whole sector over the whole time period, we defined swarm densities as those within the top 10% of those observed (thresholds 44 adults m^{-2} and 121 larvae m^{-2}) and computed a time trend for the percentage of hauls with krill at swarm densities within each of the 20 sampling periods. Mann-Kendall trend tests have the advantages of being non-parametric, measuring directions of trends (thus not sensitive to the exact transformation of data) as well as being robust to gaps in time series. For

these reasons, they have proved useful for analysing plankton trends (Bedford et al., 2020; Desmit et al., 2020; Pinkerton et al., 2020). Mann-Kendall tests were then applied both to trends in mean abundance and swarm percentage, with models including autocorrelation described in Supporting Information.
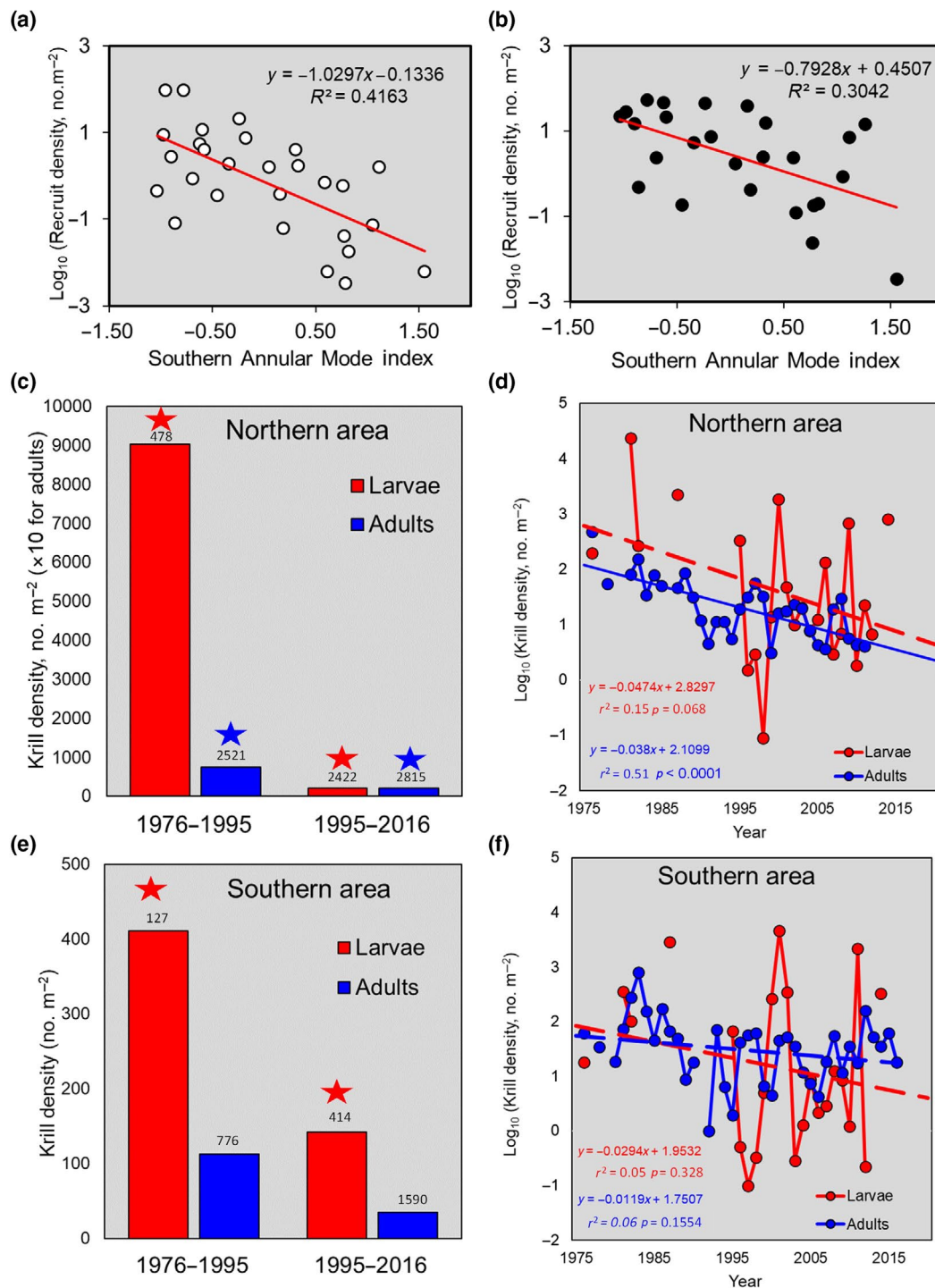
3 | RESULTS

3.1 | Environmental changes

Within the 90-year period, there has been a warming of the surface waters of the SW Atlantic sector at a much higher rate than either the global ocean average or the Southern Ocean average (Meredith & King, 2005; Whitehouse et al., 2008). Based on the ERSST annual mean values (Figure 1) for a series of 2° latitude by 2° longitude grid cells spanning the SW Atlantic, surface temperatures increased between the 1920s and the 1990s by approximately 0.5–1.0°C, depending on region. There was then a hiatus in surface warming between the 1990s and 2010s, with the exact timing and extent also region dependent. This hiatus was marked by two decades of surface cooling, followed by a rapid resumption of the upward trend in warming in the last few years. Importantly, this meant that, in the southern part of the SW Atlantic sector (i.e. Scotia Sea, Elephant Island and West Antarctic Peninsula), the period 1996–2016 was, on average, cooler than 1976–1995 (Figure 1).

The trends in sea ice concentration over the last century at the South Orkneys showed a broadly similar pattern to those of sea surface temperature (Figure 1). There was a reduction in winter

FIGURE 5 Climatic controls on recruitment along the South Scotia Arc may have caused the recent abrupt range shift. The SAM index is not available for the first sampling era, so this figure pertains to the 1976–2016 period (Eras 2 and 3). (a) Significant relationship between recruit density and the SAM index (mean monthly SAM of March–September in the year before the recruit density measurements). This panel pertains to oceanic stations (water depth >1000 m) along the Southern Scotia Arc, 60–62.5°S. This band had the strongest climate-recruit density relationships seen. (b) Same relationship as for panel a, but for the shelf stations within the 60–62.5°S latitudinal band. This key band for recruitment is illustrated in Figure S3, in relation to larval distribution. (c) Mean density of larvae and adults in the SW Atlantic sector each year in the northern part of the sector (i.e. north of 62.5°S). Stars represent significant differences between eras (Mann–Whitney test; red stars for larvae, blue stars for adults), while numbers over bars represent numbers of stations from each era pooled in these tests. (d) Time trends for krill larvae and adults in this northern area, with each data point representing mean krill density during an austral summer. Dashed lines signify trend lines that are non-significant ($p < .05$) while solid lines represent significant regressions. (e, f) Plots as for panels c and d, only for the area south of 62.5°S. Inclusion of a model that accounted for autocorrelation did not materially alter the slopes or their significance values (Figure S7; Tables S2 and S3). SAM, Southern Annular Mode

fast ice duration in the middle of last century, followed by relatively stable conditions (albeit with inter-annual and subdecadal periodicity) over the last 30 years which correspond to the warming hiatus. Figure S4d shows trends in average duration of open water per decade, calculated as 365 minus the fast ice duration to ease comparison with temperature trends and including recent unpublished British Antarctic Survey data. This shows likewise a broadly similar trend last century in sea ice and water temperature. The relatively stable sea ice conditions in this sector over the last few decades is also reported for the Antarctic Peninsula (Henley et al., 2019).

In contrast to the recent hiatus in warming and loss of sea ice in the SW Atlantic sector, SAM indices (only available since 1957) have shown an ongoing general increase in positive SAM anomalies since the 1950s (Figure 1).

3.2 | Range shifts of larval and adult krill

Figure 2 depicts the distributions of larval and adult krill in each of the three eras. The range shift, in a generally SW direction, is evident across the measurement period for both larvae and adults. However, a fragmented distribution of larvae develops in era 3, not only with the retention of the main larval nursery area in the southern Scotia Sea, but the development of a separate larval hotspot off Marguerite Bay on the Western Antarctic Peninsula (WAP). While larval data coverage is not so good as that of adults, data from individual years and the individual component larval stages (Figure S1) support the average case depicted in Figure 2a. Thus, during the 1900s, highest larval densities were always within the region from the tip of the Antarctic Peninsula to the Scotia Sea. It is only after the year 2000 that highest calyptope and furcilia larval densities have been found at the WAP, for instance in 2001, 2002 and 2011 (Siegel et al., 2013). In parallel with this SW range shift of larvae, Figure 2b suggests an increase in relative importance of the WAP in supporting adults in this sector over time.

These shifts are quantified by calculations of the latitudinal and longitudinal translation of range edges and centres throughout the last 90 years (Figure 3), based only on grid cells sampled in all three eras (Figure S2). During the rapid warming between the first and second eras, the ranges of both larvae and adults were fairly static, the only exception being the leading (south-westward) range edge of adults, which moved south and westwards down the WAP. By contrast, in the warming hiatus between eras 2 and 3, the ranges of both larvae and adults moved dramatically. For the larvae, the northern range edge was rather static, whereas the leading (southward) edge moved greatly to the SW, pulling the centre of gravity of the population also in that direction. The adults, by contrast, showed a SW translocation of both trailing and leading range edges over the last 40 years. Based on an overall movement of the centre of gravity of the populations over the last 90 years, larvae moved 832 km and adults moved 1400 km in a SW direction. However, due to the bimodal population distributions and differential movements of the leading and trailing range edges, the actual distances shifted vary according to the metric chosen (Figure 3).

To obtain more detail on the timing of range shifts, we divided the time period into five eras (each of around a decade) rather than the three periods as used above. This analysis (Figure S4) showed fairly unchanging latitudinal distributions of larvae and adults until the mid-1990s, and it was only in the last two of the decades that the centre of gravity of their distributions moved substantially to the south. This finer time resolution clearly shows the out-of-step relationship between the main environmental warming and ice loss (before the 1980s) and the krill range shift (after the 1980s). Importantly, this shift of the centre of gravity of the population did not simply reflect a decline in krill densities in the far north, since densities of larvae increased substantially in the southernmost latitudes (Figure S4a).

3.3 | Shifts in the thermal range occupied by krill

A common method of assessing range shifts is to compare them to the pace of isotherm movement over the corresponding period (Chivers et al., 2017). However, since isotherms run broadly SW–NE in this region, parallel to the range shifts themselves (rather than running across them) and also broadening in extent from west to east (Hofmann & Murphy, 2004), this metric was not used in the present study. Instead, each station was allocated a sea surface temperature value based on a gridded ERSST v5 product (see Sections 2.3 and 2.4.3), allowing an analysis of how the thermal habitat of krill has changed over the study period (Figure 4). During the rapid warming of the whole sector between the first and second eras, the spatial distributions of both larvae and adults were fairly static (Figure 3), which means that they were inhabiting increasingly warm water. Figure 4 shows that this increase is typically 0.5–1.0°C; similar to the temperature increase in specific locations (Figure 1). The changes in thermal regime during the cooling period between eras 2 and 3 are more varied, but frequently show the larvae inhabiting increasingly cool waters. This variation reflects a combination of a cooling of waters over this time and variable degrees of range shift (into cooler regions) between leading and trailing edges. Therefore, despite some radical changes in thermal regime and krill distribution over the last century, the net result is that the centre of larval distribution nowadays is in water about 0.5°C warmer than it was 90 years ago, while that of adults is in water of broadly similar temperature.

3.4 | Causes of the abrupt distributional shift during the warming hiatus

The abrupt poleward shift over the last 40 years is surprising, since it spanned the hiatus in warming and was marked by a period of surface cooling (Figure 1). Fortunately, the near-continuous time series of krill data over this period, coupled with the availability of climatic indices, allows us to examine the mechanisms behind this surprising response (Figure 5). To examine how the SAM acts on portions of the population, thereby modulating the range shift, we divided the SW Atlantic

sector into a series of bands, each of 2.5° latitude, following Atkinson et al. (2019). By far the strongest SAM–recruit density relationship was found in the band from 60.0 to 62.5°S (Figure S3), that is along the Southern Scotia Arc, previously identified as a key nursery area (Perry et al., 2019). Here, years with strong positive SAM indices tended to precede years of poor recruitment, an effect that was seen in both the oceanic (Figure 5a) and the shelf (Figure 5b) regions of this zone.

The facts that there are two population centres of larvae in the modern era (Figure 2) and that SAM effects on recruitment were only seen in the northernmost area provide a natural division of the sector into northern and southern portions (Figure S3). The relative population trajectories between the northern and southern portions of the range of krill are central to interpretations of range shifts. In the north, a decline in larvae is suggested, whether data are averaged according to sampling era (Figure 5c), individual years (Figure 5d) or the component larval stage (Figure S4). These substantial declines in northern larvae are in line with the declines in adults, shown both here and previously (Atkinson et al., 2019; Hill et al., 2019). By contrast, in the southern area along the WAP, changes in both larval and adult densities are not so marked, as would be expected if the distribution of both life stages had contracted towards the south. The seasonality, size, mobility, vertical distributions and thus catchability of calyptopes, furcilia and adults differ greatly (Siegel & Watkins, 2016), so their parallel trends are hard to explain simply in terms of any temporal changes in sampling method.

These insights on differing trends in the northern and southern portions of the larval and adult krill range are provided by relative changes in arithmetic mean density. Figure S5 also examines parallel trends in the frequency of swarms in each area. The non-parametric Mann-Kendall test on equalized sample sizes shows consistently more negative z-scores in the northern part of the range than the south, indicating steeper decline trends. These declines were seen for both swarm frequency and for mean density, supporting previous findings that changes in mean krill density may actually be related to changing numbers of swarms in any given area (Brierley & Cox, 2015).

Taken together, the evidence suggests that in this northern portion of the SW Atlantic, there has been a sharp downward trend in density of all three major krill life stages, namely calyptopes, furcilia and adults, since the 1970s. These trends are reflected also in declining frequency of swarms or dense aggregations and likely result from declining recruitment from the major spawning and nursery areas adjacent to the Southern Scotia Arc. This in turn reflects the SAM index becoming increasingly positive during this period, diminishing the importance of this northern spawning and nursery area, concomitantly with the increase in importance of a southern spawning area.

4 | DISCUSSION

Our six main approaches to analysing the distributions of calyptope, furcilia and adult stages of krill all show that, during the last 90 years, their distributions have shifted substantially (~1000 km) within the SW Atlantic sector. While a range contraction of adults has been reported

previously in this sector (Atkinson et al., 2019), our new larval database now shows how this shift occurred. Understanding the mechanism is important for several reasons. First, the sheer speed of the recent shift is alarming. Assuming that it started from the 1990s (Figure S4c), it is a jump of ~500 km per decade—far faster than most observed and projected values (Pinsky et al., 2020). Second, and despite much speculation on Southern Ocean range shifts, their existence is not a general phenomenon and so demands a mechanistic explanation. A suite of copepod species, broadly similar in size and swimming ability to krill larvae, showed no evidence for a range shift last century; they maintained their distributions within the SW Atlantic while their environment warmed (Tarling et al., 2018). By contrast, the macroplanktonic salps expanded their leading range edge southwards in a similar way to krill (Atkinson et al., 2004; Pakhomov et al., 2002).

These contrasting examples for and against plankton range shifts in the Southern Ocean differ from the increasing evidence for northward range shifts in the Arctic (Campana et al., 2020; Ershova et al., 2021; Fossheim et al., 2015; Møller & Nielsen, 2019). Is a range shift into the high-latitude Southern Ocean impeded by the particular challenges of bathymetry and hydrography? While the Arctic Ocean is a deep basin supplied by localized northward inflows from the Atlantic and Pacific Oceans (Wassmann, 2011), the other pole comprises a central landmass encircled by a continuous, powerful Antarctic Circumpolar Current (ACC). Establishment in a warming Arctic Ocean relies on the reproduction of already advected populations, while occupation of the high-latitude Southern Ocean requires not only successful reproduction but also an additional transport mechanism across or against the currents. Indeed, the SW range shift of krill is actually in the reverse direction to the prevailing ACC flow and its northward surface Ekman component (Hofmann et al., 1998; Hofmann & Murphy, 2004).

For this reason, we need to examine whether we are really observing a range shift related to warming, or instead population expansions and contractions that seem to have the effect of moving the range. For instance, the 'basin model', as applied to small pelagic fish, suggests that in periods of strong recruitment and high total abundance, the range expands, while density within the range centre increases (Barange et al., 2009). This type of basin model may indeed apply to krill; for instance, adults extended almost to the Polar Front after exceptional recruitment years 1981 and 1996, and the rapid retreat of the northern range edge of adults since the 1980s coincided with a major decline in their density and swarm frequency (Figures S4 and S6). However, the southern (leading) edges of both larvae and adult distributions have also moved south over the last century, and larvae have increased greatly in the far south (Figure S3). This strongly suggests that we are observing a temperature-induced range shift, in addition to a range contraction as abundance has declined. In the future, this southern area may become the main successful spawning area of krill in this sector since a series of habitat models, both of larvae (Thorpe et al., 2019) and adults (Hill et al., 2013; Piñones & Fedorov, 2016; Veytia et al., 2020), project increasingly favourable conditions for krill towards the south.

Our ability to observe both multiple life stages of krill and their recruitment over time and space sheds light on the mechanisms behind range shifts. The movements do not comply in a simple manner with thermal niche theory: between the 1920s and the 1990s, the central and northern edges of adults and larvae remain in place while their environment warmed. This parallels the observations of Scotia Sea copepods over a similar time span (Tarling et al., 2018), but runs counter to many projection models of species distributions, such as Mackey et al. (2012), which assume that species track thermally optimum isotherms poleward. With a non-continuous time series between eras 1 and 2, we can only speculate why this is the case. One explanation relates to the depth distribution of krill. In common with most other long time-series analyses and projections, we were forced by data availability to use surface values for our temperature index. However, krill distribution extends to depth (Marr, 1962; Schmidt et al., 2011; Tarling & Thorpe, 2017), in waters insulated from the rapid changes at the surface (Meredith & King, 2005; Whitehouse et al., 2008) and this may provide a more geographically stable thermal environment for krill.

This similarity in distributions between eras 1 and 2 amid a warming surface environment contrasts with the major (~1000 km) jump to the SW during the 25-year warming hiatus from the 1990s. Could this rapid shift also be interpreted in terms of differential warming of surface and deep waters? The hiatus in surface warming (Turner et al., 2016) and more stable sea ice conditions (Henley et al., 2019) appear to be marked by a general cooling of the topmost ~50 m layer only; this being suggested to be related to strengthening winds and associated sea ice transport (Haumann et al., 2020). Below this near-surface layer, at the 55–65°S latitudes important for krill, there has been a continuation of the longer term warming since the 1980s, albeit with little change below 200 m (Haumann et al., 2020). There is certainly no evidence for a major acceleration in subsurface warming in recent decades that would account for such an abrupt shift in krill distribution. Neither would such an explanation fit with the fact that during the previous decades of warming of surface and subsurface waters (Gille, 2002; Whitehouse et al., 2008), the krill distribution was fairly static.

To explain this abrupt, non-linear range shift of krill, we instead suggest a putative model (Figure 6) in which two separate mechanisms interact. First is the underlying change in thermal regime, and this warming allows the extension of the adult range down the WAP last century. The second effect is indirect: from climatically driven changes in the food environment that affect krill recruitment. Winter sea ice was initially shown to be an important predictor of recruitment (Atkinson et al., 2004; Loeb et al., 1997; Siegel & Loeb, 1995), but work since has shown that recruitment is better predicted statistically by climatic indices which relate not only to winter sea ice, but which also modulate food supply for larvae in the ice-free season (Loeb & Santora, 2015; Saba et al., 2014). Thus, at the whole-sector scale of our study, the SAM has a dominant role in driving recruitment (Atkinson et al., 2019). Here (Figure 5a,b) we pinpoint its effect as being specifically in the main reproductive and nursery grounds which are along the Southern Scotia Arc (Perry et al., 2019).

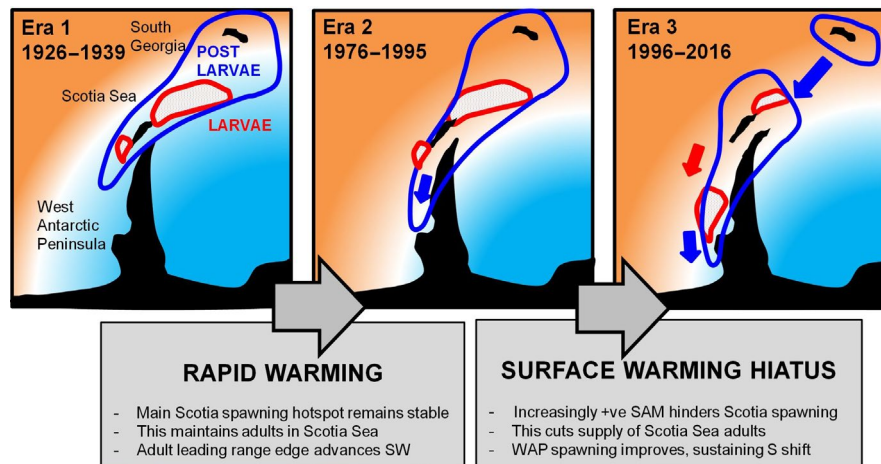How does SAM affect krill recruitment? The increasingly positive SAM is thought to relate to warmer, windier and more unsettled weather at the northern Antarctic Peninsula; unfavourable conditions for larval fitness (Loeb et al., 1997; Quetin et al., 2007; Saba et al., 2014). We suggest that this combination of conditions has reduced krill replenishment to the main northern (Scotia Sea) part of the range (Figure 6). This is evidenced by the sharp declines in larvae and adult density (Figure 5c,d), swarm frequency (Figure S4) and recruitment indices (Atkinson et al., 2019). SAM also has an effect on recruitment in the WAP populations, but here its influence is not nearly so strong, with El Niño Southern Oscillation (ENSO) also having a major effect (Saba et al., 2014). Consequently, we suggest that reproductive success has been more stable in the southern part of the range. There is a subdecadal periodicity in adult density but little directional change evident since the early 1990s (Steinberg et al., 2015; see also Figure 5e,f; Figure S6) and increasing larval densities at the leading range edge (Figure S4a). Together, this has contributed to a shift of the overall range to the south (Figure 6).

Observations of phytoplankton distributions along the WAP (Montes-Hugo et al., 2009) support the concept that changing food as well as temperature contributed to the rapid range shift of krill. Over the period 1978–2006, these authors found a significant decrease in summer chlorophyll *a* concentration north of 63°S with an increase to its south. This time span broadly encompasses our observation of the abrupt range shift, and the northern area showing the decline in chlorophyll *a* corresponds broadly to our northern area which has experienced the rapid decline in krill densities. The mechanisms behind these changes are likely to be complex (Reiss et al., 2020), include changes in food quality as well as quantity (Schofield et al., 2017) and act on separate spawning locations along the Antarctic Peninsula (Conroy et al., 2020). This situation is similar to that in the rapidly warming Arctic, where poleward range shifts have been interpreted as a combination of direct temperature effects and superimposed effects from food web interactions (Dalpadado et al., 2020; Ershova et al., 2021).

Whatever the mechanisms, our results emphasize the decoupling between the range shifts of krill and the pace of climatic warming. At the largest scale, krill have broadly maintained their thermal niche because, in the last few decades, their adults are centred in a similar thermal regime as they were 90 years ago, with this regime now found at higher latitudes. However, they have not smoothly tracked these thermal changes, withstanding about 1°C of warming in situ before undergoing an enormous shift during the warming hiatus now to occupy a new spawning ground. This has major implications for future projections, since processes are strongly non-linear, with the possibility of further abrupt shifts unrelated to temperature but more strongly related to climatic controls in localized recruitment hotspots.

Differential range shifts among species, particularly if they involve key species, can reconfigure food web interactions (Wallingford et al., 2020). Krill are important biogeochemically (Schmidt et al., 2016), supporting an iconic food web of penguins, seals, fish, flying seabirds and whales (Constable et al., 2014) and an expanding fishery (Meyer et al., 2020). Some of these dependent predators, for example gentoo penguins, have themselves expanded their ranges southwards (Korczak-Abshire et al., 2021). Given the pace of previous warming, there is widespread concern over future

FIGURE 6 Hypothesized mechanism for the stepwise range shift. The schematic depicts the warm (red) to cool (blue) temperature gradient across the SW Atlantic sector in the warming era and the subsequent warming hiatus, with main population centres of larvae (red) and adults (blue), based on Figure 2. The hypothesized mechanism for this shift is based on the adults moving their southern range edge south during the warming period, supporting spawning off Marguerite Bay (WAP, Western Antarctic Peninsula), which then fuels increasing adult stocks in this southern area. Meanwhile deteriorating conditions for recruitment in the former Scotia Sea spawning stronghold, due to an increasingly positive Southern Annular Mode (Figure 5), cuts the recruitment of adults to the northern part of the range. We suggest that this differential recruitment process drives the main range shift which is seen, surprisingly, during the surface warming hiatus

trends, particularly over the possibility of step changes or other non-linear responses to climatic change. Range shifts of krill can lead to substantial increases or decreases in availability to krill-dependent predators, already suggested through reductions in the contribution of krill to the diet of a krill specialist, the gentoo penguin (McMahon et al., 2019) and reduced fur seal pup birth weights (Forcada & Hoffman, 2014). The great speed of the recent larval and adult poleward shift, at a time when parts of the region were actually cooling, is a warning of more surprises in store.

Designing 'climate-ready' areas for protection that help key, vulnerable or exploited species such as krill needs to account for future climate moving their distribution (Queirós et al., 2016; Visalli et al., 2020). To project the future, species distribution models are particularly valuable at larger scales, including over 50-year time frames and global scales. At these scales, for example, they help gauge vulnerable biomes and potential hotspots of change (e.g. Jones & Cheung, 2015). Likewise, mapping of climate change velocities may help conservation planning in many areas of the world ocean where biological data are sparse (Brito-Morales et al., 2018; Burrows et al., 2011). All of these approaches carry limitations, especially for certain taxa (Brun et al., 2016), for short projection periods or for limited geographical areas (Cheung et al., 2016; Fernandes et al., 2020). In this context, a ~1000 km jump in krill distribution, in two decades and under stable surface temperature, provides a sobering reminder about projection at management-relevant timescales. Krill provide a case study of the mechanisms by which such surprises can occur, for which a dogged maintenance of time series has proved essential. Understanding the drivers of step changes is critical (Beaugrand, 2012; Beaugrand et al., 2019; Conversi et al., 2015), since they can herald system reorganizations that impact on food web structure, biogeochemical function and fisheries management. Equally important is the protection of habitats, such as the new southern krill reproduction area, that sustain populations as distributions change.

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Most data supporting this paper are published in Atkinson et al. (2017; ESSD) and the remaining data will be available from the BAS Polar Data Centre on publication.

ORCID

Angus Atkinson https://orcid.org/0000-0002-5931-4325

Simeon L. Hill https://orcid.org/0000-0003-1441-8769

Evgeny A. Pakhomov https://orcid.org/0000-0002-6145-2129

Gregory Beaugrand https://orcid.org/0000-0002-0712-5223

Geraint A. Tarling https://orcid.org/0000-0002-3753-5899

Guang Yang https://orcid.org/0000-0002-9410-0189

Deborah K. Steinberg https://orcid.org/0000-0001-9884-4655

Katrin Schmidt https://orcid.org/0000-0002-6488-623X

Martin Edwards https://orcid.org/0000-0002-5716-4714

Emilce Rombolá https://orcid.org/0000-0003-1863-1911

Frances A. Perry https://orcid.org/0000-0003-1560-1506

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