

Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming

Angus Atkinson^{1,11*}, Simeon L. Hill^{2,11*}, Evgeny A. Pakhomov^{3,4,5}, Volker Siegel⁶, Christian S. Reiss⁷, Valerie J. Loeb⁸, Deborah K. Steinberg⁹, Katrin Schmidt¹⁰, Geraint A. Tarling², Laura Gerrish² and Sévrine F. Sailley¹

High-latitude ecosystems are among the fastest warming on the planet¹. Polar species may be sensitive to warming and ice loss, but data are scarce and evidence is conflicting^{2–4}. Here, we show that, within their main population centre in the southwest Atlantic sector, the distribution of *Euphausia superba* (hereafter, 'krill') has contracted southward over the past 90 years. Near their northern limit, numerical densities have declined sharply and the population has become more concentrated towards the Antarctic shelves. A concomitant increase in mean body length reflects reduced recruitment of juvenile krill. We found evidence for environmental controls on recruitment, including a reduced density of juveniles following positive anomalies of the Southern Annular Mode. Such anomalies are associated with warm, windy and cloudy weather and reduced sea ice, all of which may hinder egg production and the survival of larval krill⁵. However, the total post-larval density has declined less steeply than the density of recruits, suggesting that survival rates of older krill have increased. The changing distribution is already perturbing the krill-centred food web⁶ and may affect biogeochemical cycling^{7,8}. Rapid climate change, with associated nonlinear adjustments in the roles of keystone species, poses challenges for the management of valuable polar ecosystems³.

The pelagic food webs at both poles comprise iconic species, have important biogeochemical functions¹ and are commercially exploited, prompting concern over how they will respond to future climate change^{2,3}. At the foundation of these food webs are large, lipid-rich zooplankton species (for example, euphausiids, copepods and amphipods), which may be particularly sensitive to warming, given their narrow temperature tolerance and ice-associated life cycles^{1–3,9}. Poleward shifts in species' distributions are a major response to climatic warming¹⁰. These shifts have been observed at both poles, but they are highly variable between species, since other compensation mechanisms are possible^{3,4,10}. Projections are particularly uncertain at the poles because of the scarcity of long-term, large-scale data on past changes^{2,4}.

With its central role in the food web, Antarctic krill is one of the few polar species with spatially extensive sampling that spans the past 90 years¹¹. The Southwest Atlantic sector (20–80°W), which holds >50% of the circumpolar krill stock¹², has also warmed rapidly

over this time¹³. This provides a rare opportunity to understand how a cold water stenotherm responds to rapid environmental change. Within the multinational KRILLBASE project (see Methods), we compiled all available krill net catch data spanning 1926–2016 into two large databases: one containing their numerical density (numbers of post-larval krill m⁻²; hereafter, density) and the other including length frequency, sex and maturity-stage data.

During the 1920s and 1930s, the highest krill densities were centred in the northern part of the southwest Atlantic sector (Fig. 1a). Since then, this distribution has contracted southward and became centred more strongly over Antarctic continental shelves. Most of this contraction seems to have occurred since the 1970s, before which high densities were maintained in the South Georgia area. The overall southward contraction across 90 years was ~440 km, manifested as a major decrease in mean density in the north and a modest decrease in the south (Fig. 1a).

The data available for the Southwest Atlantic sector since the mid-1970s, including near-continuous krill time series and multiple indices of environmental variability, are amenable to further analysis using mixed models (Table 1) to detect systematic change over time. In addition to standardization for net type, sampling depth, time of day and time of year, our analysis accounted for the effects of uneven data coverage and known covariates of krill abundance, including latitude and bathymetry¹². It also ameliorated the effects of variance inhomogeneity and temporal autocorrelation, and used detrending to avoid spurious correlation (see Methods). The data analysed in each model included up to 12 spatiotemporal averages per austral summer season (referred to as 'year' in the figures). Figs. 1b, 2 and 3 illustrate these statistically robust results with simpler models fitted to annual averages. The mixed models show a strongly negative time trend in krill density north of 60°S and a weaker trend further south (Table 1; see Fig. 1b). Indeed, density trends at the highest latitudes sampled (south of 65°S) were neutral or positive (Fig. 2a). The overall trend was apparent in independent subsets of the data based on net size (Supplementary Table 1), and the stronger negative trends north of 60°S are seen in encounter probability data (Supplementary Fig. 3).

There was also a long-term, spatially coherent trend in the mean krill length dataset (Figs. 2b and 3a). Individuals in the current krill population are on average 6 mm longer than those in the 1970s,

¹Plymouth Marine Laboratory, Plymouth, UK. ²British Antarctic Survey, Cambridge, UK. ³Department of Earth, Ocean and Atmospheric Sciences, University of British Columbia, Vancouver, British Columbia, Canada. ⁴Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada. ⁵Hakai Institute, Heriot Bay, British Columbia, Canada. ⁶Thuenen Institute of Sea Fisheries, Bremerhaven, Germany. ⁷Antarctic Ecosystem Research Division, South West Fisheries Science Centre, NOAA Fisheries, La Jolla, CA, USA. ⁸Moss Landing Marine Laboratories, Moss Landing, CA, USA. ⁹Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, VA, USA. ¹⁰School of Geography, Earth and Environmental Sciences, University of Plymouth, Plymouth, UK. ¹¹These authors contributed equally: Angus Atkinson, Simeon L. Hill.

*e-mail: aat@pml.ac.uk; sih@bas.ac.uk

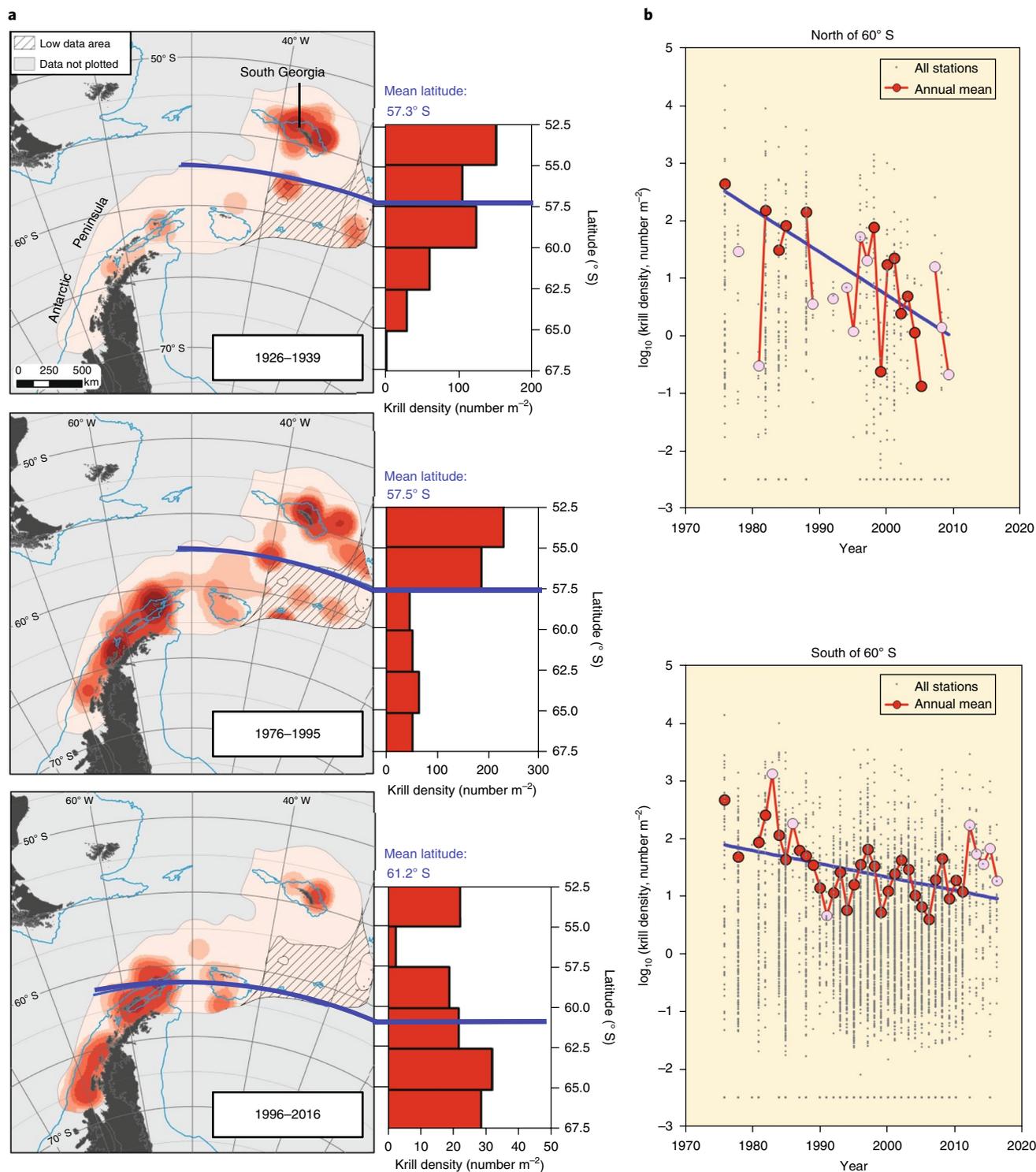


Fig. 1 | Southward contraction of krill distribution within the Southwest Atlantic sector. **a**, Kernel analysis visualizing hotspots of post-larval krill density in the Southwest Atlantic sector during the 1920s and 1930s (top) and the first (middle) and second (bottom) halves of the modern era, based on the area sampled heavily across all three periods (see Methods and Supplementary Fig. 4). Blue isobaths denote the 1,000 m boundary between shelf and oceanic habitats. Within each map, the analysis identifies relative hotspot areas of high density, indicated by the intensity of the red shading. The histograms denote the mean standardized post-larval krill density in 6 comparable 2.5° latitude bands with >50 stations sampled in each era (see Methods). Note the changes in scale between each of the three eras. Thick blue lines across maps and histograms indicate the centre of krill density (that is, the density-weighted mean latitude; see Methods). **b**, Trends in log₁₀-transformed mean standardized post-larval krill density north (top) and south (bottom) of 60° S. Small points represent the densities in underlying records. Large dots represent the annual means of these data, weighted by the number of stations per record. Pink dots represent seasons with <50 stations (an average of 27 compared with an overall average of 123 stations per season). Solid blue trend lines were fitted to the annual means using simple linear regression ($P < 0.001$; <0.01 adjusted coefficient of determination, $R^2 = 0.52$ for north and 0.22 for south). Linear mixed model 1 in Table 1 and Supplementary Table 1 provides statistical support for these trends and the significantly greater decline in the north. Fig. 2 provides finer latitudinal resolution; for instance, showing an increase in density in the far south.

Table 1 | Significant relationships among krill density, mean length, SAM and year

Model	Fixed-effects model	m_1 (P)	m_2 (P)	m_3 (P)	c	n	R^2_m	R^2_c (AIC)
1	DENSITY = ($m_1 \times \text{YEAR}$) + ($m_2 \times \text{LAT}$) + ($m_3 \times \text{YEAR} \times \text{LAT}$) + c	-0.065 (<0.001)	-87.437 (<0.01)	0.044 (<0.001)	131	290	0.08	0.15 (773)
2	LENGTH = $m_1 \times \text{YEAR}$ + c	0.173 (<0.001)			-305	146	0.04	0.33 (931)
3	RECRUIT DENSITY = $m_1 \times \text{YEAR}$ + c	-0.069 (<0.001)			137	124	0.08	0.10 (426)
4	D.DENSITY = $m_1 \times \text{D.LENGTH}$ + c	-0.044 (<0.001)			0.138	124	0.01	0.01 (283)
5	D.DENSITY = ($m_1 \times \text{D.SAM}$) + ($m_2 \times \text{SHELF}$) + c	-0.229 (<0.001)	0.577 (<0.05)		-0.186	290	0.01	0.02 (768)
6	D.LENGTH = $m_1 \times \text{D.SAM}$ + c	2.197 (<0.01)			0.093	146	0.03	0.38 (918)
7	D.RECRUIT DENSITY = $m_1 \times \text{D.SAM}$ + c	-0.352 (<0.05)			-0.024	115	0.01	0.03 (417)

Linear mixed model results indicating: significant time trends in \log_{10} -transformed standardized post-larval krill density (number m^{-2} ; model 1), mean length (mm; model 2) and \log_{10} -transformed recruit density (number m^{-2} ; model 3); covariance in length and density (model 4); and relationships between the SAM index and standardized krill density (model 5), mean length (model 6) and recruit density (model 7). The fixed effects are expressed in terms of the coefficients m_1 , m_2 , m_3 and c . n is the number of observations (these are plotted in Fig. 2). All models include random spatial unit effects. Models 2 and 6 also include random year effects. R^2_m is the marginal pseudo-coefficient of determination, R^2_c indicating variance explained by the fixed effects, and R^2_c is the conditional pseudo- R^2 indicating variance explained by both fixed and random effects. Variables prefixed 'D' were detrended. LAT values 0 and 1 represent latitudes north and south of 60° S, respectively, and SHELF values 0 and 1 represent shelf ($\leq 1,000$ m depth) and oceanic waters, respectively. AIC, Akaike information criterion.

equating to a roughly 75% increase in their mean body mass. This is opposite in direction to the more common finding of reduced body size of species in response to warming¹⁴, and instead reflects changes in the demographic structure of the krill population. Given the counteracting effects of decreasing numbers and increasing individual mass, the substantial (70%) decrease in numerical density over 20 years spanning the 1976–1996 and 1996–2016 eras equates to a smaller (59%) decline in biomass density. In addition to the opposing long-term trends, length also varied with density on an interannual scale, such that low-density years were characterized by a higher-than-average mean length (Fig. 3b and Table 1).

Previous studies have identified various potential environmental drivers of krill population dynamics^{5,11,15–18}. The clearest environmental covariate of krill density that we found was the Southern Annular Mode (SAM) (Fig. 3c), which is also related to mean length and recruit density (Fig. 3d and Table 1). The SAM is an index of hemisphere-scale atmospheric circulation that might influence krill population dynamics by affecting the recruitment of small (≤ 30 mm) krill to the population each year^{3,5}. Summers of strong recruitment tend to follow periods with negative SAM anomalies. Sequential years of poor recruitment are periodically boosted by a year or two of good recruitment where many small krill swell the numbers but depress the average size^{5,15,16}. This explains the negative relationship between krill density and mean length (Table 1) illustrated in Fig. 3b.

Over the past 40 years, recruitment has declined sharply (Fig. 2c, Supplementary Fig. 1a and Table 1) and indeed significantly more abruptly than the decline in the total krill density (Supplementary Fig. 1b). This coincides with an ongoing trend towards increasingly positive SAM anomalies (Fig. 3c), which indicate the southward influence of storm tracks across the Southwest Atlantic sector, low pressure, warmer, cloudier and windier conditions, and reduced sea ice^{5,18–20}. Such conditions negatively affect adult feeding, impacting early spawning in spring, early larvae in summer and later larval stages that may need early-forming, complex and well-illuminated marginal sea ice to promote survival¹⁷. The exact mechanisms are likely to vary with latitude. For example, increasing summer temperatures present a physiological challenge for this stenothermal species at its northern limit⁹, where a strong link between climate, temperature anomalies and krill recruit biomass has also been identified¹⁸. Further south, near the tip of the Antarctic Peninsula, the biomass and quality of phytoplankton food have also declined²¹. In contrast, at the southern part of the Western Antarctic Peninsula, the loss of permanent sea ice and increases in phytoplankton biomass²⁰ are associated with a more stable or even increasing krill density^{5,16} (Fig. 2a).

Suggestions that krill density has declined within the southwest Atlantic sector^{11,15} have major ramifications for fisheries management and are the subject of some debate^{3,16,22}. Indeed, a recent paper²³, which reports an analysis of a subset of our data, argues that previous evidence of a decline¹¹ “is a consequence of not considering interactions between krill density and unbalanced sampling in time and space in the data, and not accounting for the different net-types used”. We agree with these authors²³ that analyses of this complex database require care. Our study considered each of the issues they identify, which suggests that the contrast between their²³ conclusions and ours reflects other differences in approach. First, we excluded negatively biased records resulting from sampling in winter or solely in deeper strata, while they did not. Second, we followed established practice^{5,11,15,18,24} in using spatially resolved annual mean densities as a basic unit and logging these as appropriate. Conversely, they²³ log-transformed at the level of individual records, down-weighting the influence of the high swarm densities that are a critical feature of krill distribution¹². This substantially underestimates the mean and variance in krill density (their²³ Figs. 1 and 3) compared with previous studies¹². Third, while we used statistical hypothesis testing to assess the probability that the detected decline is a false trend (type I error, indicated by our P values), they did not quantify the probability of failing to find a real trend (type II error). Overall, we consider that our findings provide a more robust picture of the spatial pattern of krill density time trends within the Southwest Atlantic sector.

Notwithstanding differences in the way that krill density data may be screened and analysed, the length frequency database provides independent evidence that krill dynamics have changed fundamentally. The coherent interrelationships among krill density, mean length and SAM also provide a plausible driving mechanism. The spatial coherence in these changes supports the concept of a large and connected marine ecosystem linked by advection^{18,25}. Reduced birth weights of fur seals at South Georgia⁶ suggest major changes in the krill-based food web in the northern part of krill's range. Likewise, in the far south, observations of more stable krill densities and recruitment^{5,16} align with our conclusion that the distribution of krill is contracting southward.

Polar food webs are structured by both top-down and bottom-up effects, but their relative roles are debated^{1,2,22}. Several strands of evidence point to climatic change as a major driver of krill dynamics in this sector. First, in the Indian sector of the Southern Ocean, where sea ice and temperature have been more stable over the past 50 years¹⁹, there was no evidence for the basin-scale decline in krill stocks that is observed in the rapidly warming Southwest Atlantic sector¹¹. Second, within the Southwest Atlantic sector, the gradation from a steep decline in density at lower latitudes towards more

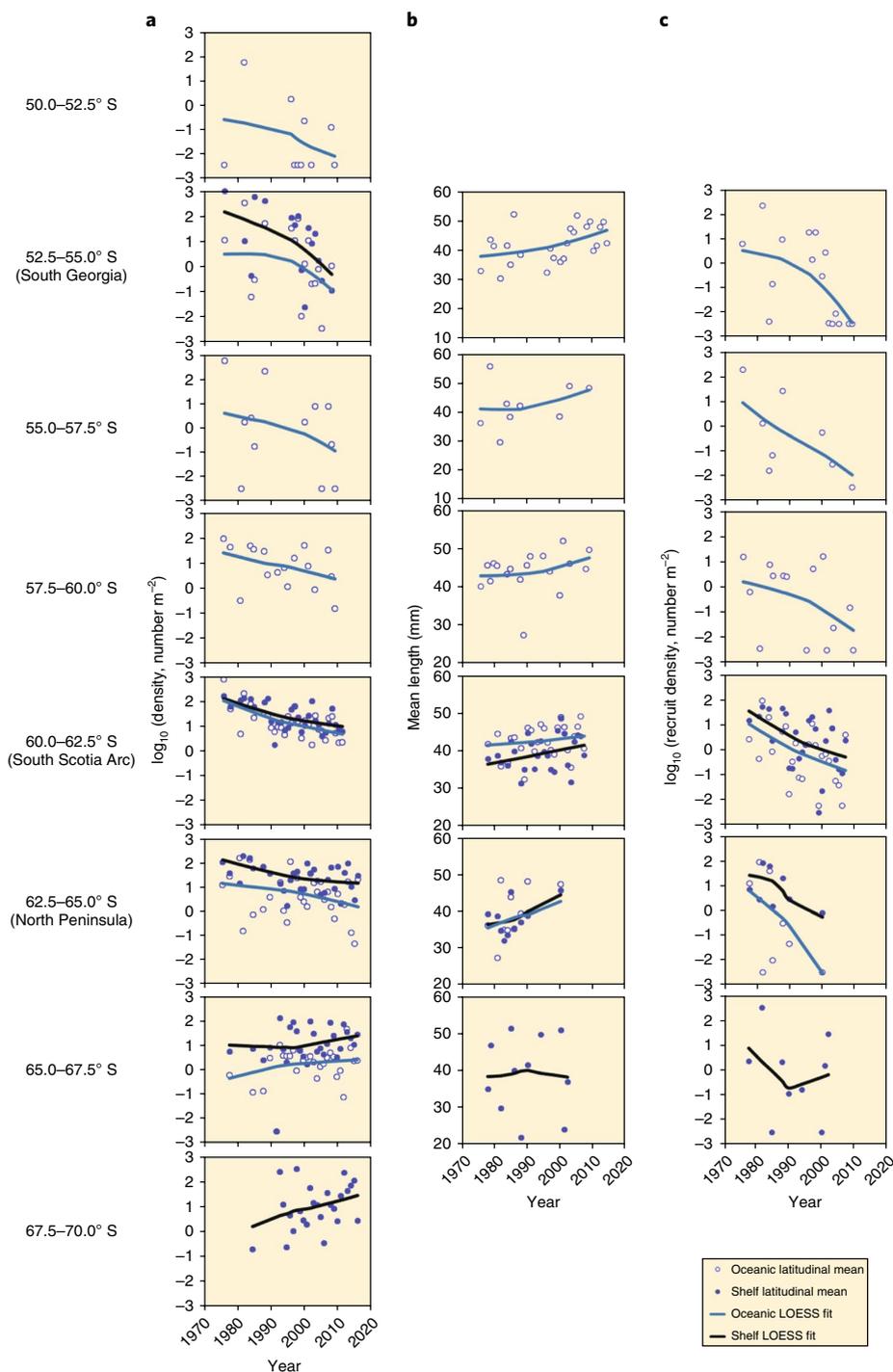


Fig. 2 | A latitudinal gradation of change in krill dynamics over the past 40 years. The points are the spatiotemporal means included in the linear mixed model analysis in Table 1. These are grouped by latitude (2.5° band) and bathymetry (shelf ($\leq 1,000$ m water depth) versus oceanic waters). LOESS curves indicate trends within each spatial unit. The particularly well-sampled bands at South Georgia and near the tip of the Antarctic Peninsula (Supplementary Fig. 4) are labelled for reference. **a**, Density of total post-larvae (that is, new recruits plus older krill) from 7,625 stations. Evidence for a range contraction is the sharp decline in density at the northern range fringes, with progressive stabilization and then reversal of the trends towards the south. **b**, Data from 4,308 length frequency sampling stations showing spatially consistent increases in mean length. **c**, Recruit density has declined very abruptly over the past 40 years in all areas except possibly the far south. This is reflected both in the increase in mean length and the decline in density of total post-larvae. These trends appear to be broadly congruent across both shelf and oceanic habitats.

stable densities in the south concurs with observed and projected poleward distribution shifts under warming^{2,3,10}. These changes cannot be explained by any known changes in the suite of krill predators. The relationships between detrended SAM and krill population

variables are both significant and coherent, but other drivers and time-lags, which are unresolvable at our scale of analysis, will also influence krill dynamics throughout the sequence from spawning, through larval stages, to the >5 -year post-larval life.

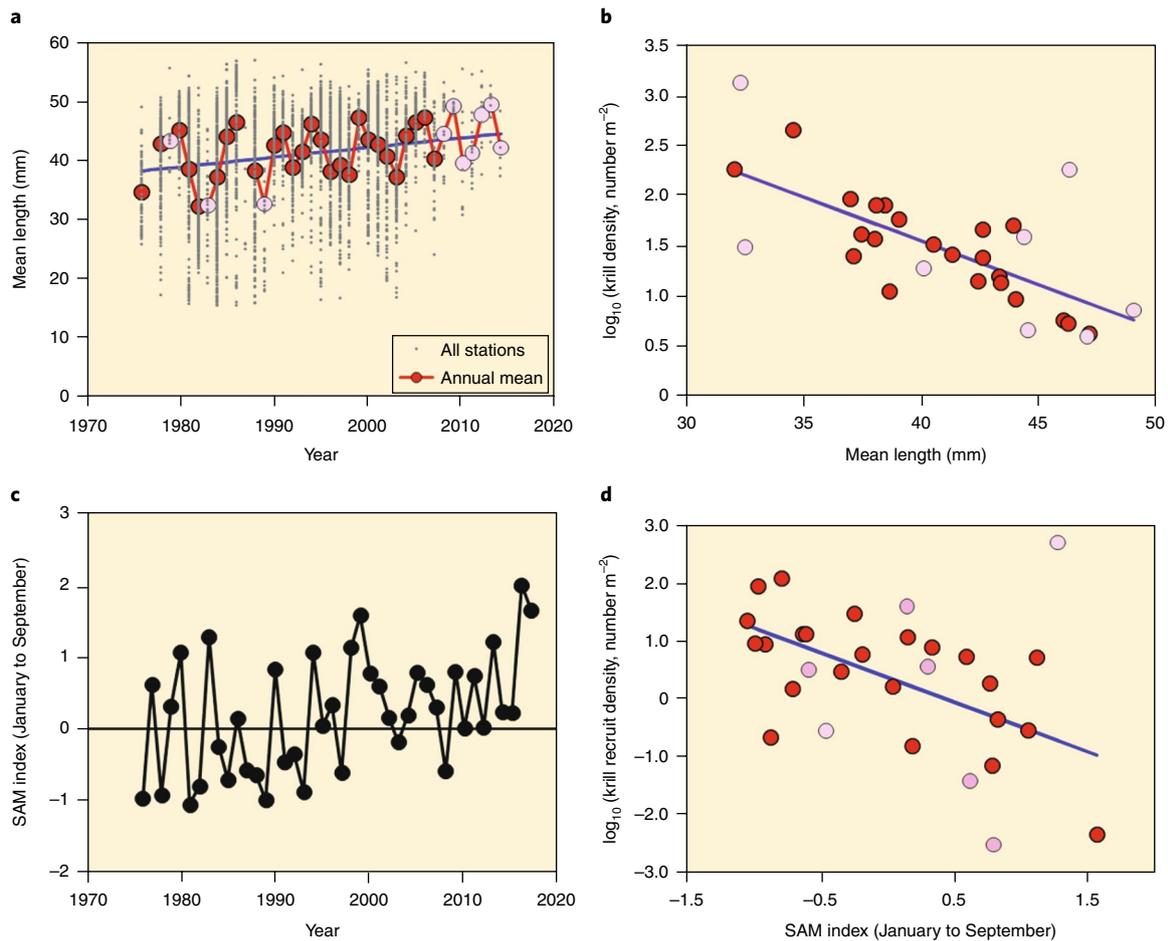


Fig. 3 | Climatic forcing provides one mechanism for an increase in mean krill length and declines in recruitment and density. The linear mixed model results in Table 1, which include detrending where appropriate, provide statistical support for the simple linear regression relationships illustrated here. **a**, Increase in the mean length of krill (regression $P < 0.05$; adjusted coefficient of determination, $R^2 = 0.09$; see mixed model 2 in Table 1). Small points represent the mean lengths in underlying records. Pink dots represent seasons with < 50 stations (an average of 18 compared with an overall average of 116 stations per season). **b**, Relationship between the mean standardized post-larval krill density and mean length (regression $P < 0.001$; adjusted $R^2 = 0.47$; for detrended data, see mixed model 4 in Table 1). **c**, Interannual variation in the January to September SAM anomaly during the modern era. Data are plotted with a one-year lag (that is, the January to September 2015 anomaly is plotted as 2016). **d**, Relationship between the \log_{10} -transformed mean standardized recruit density (density of individuals ≤ 30 mm long) and the SAM anomaly in the January to September period preceding the krill sampling season (regression $P < 0.001$; adjusted $R^2 = 0.30$). Mixed models 5–7 in Table 1 provide relationships between krill and SAM. Pink dots represent seasons with < 50 stations for either length or density.

While the weight of evidence above suggests a predominantly bottom-up control on krill that has caused a contraction in its distribution, the relative strength of top-down and bottom-up factors will probably be scale dependent. At small scales, predation can drive risk–reward trade-offs such as schooling behaviour and vertical migrations²⁶. Over the much longer timespan of changing predator populations, the extent and sources of top-down control will vary^{1–3}. Indeed, total density has not declined so rapidly as recruit density (Supplementary Fig. 1). One possible explanation is a counteracting increase in the survival of older krill, due to long-term changes in predation, intraspecific competition²⁴ or other density-dependent factors¹⁸.

The changes in krill density, mean size and range have a series of profound implications (Supplementary Fig. 2). First, because of the Earth's geometry, the distribution is contracting into a diminishing area, and further retreat is blocked by the continent itself. As total abundance is a product of numerical density and area, reductions in numerical density will translate to greater reductions in total abundance². Population genetics studies suggest fluctuations in krill population size over longer timescales²⁷, perhaps reflecting expansions

and contractions from habitat refugia during glacial and interglacial epochs²⁸. The highest krill densities tend to occur in shelf habitats¹², so the greater area of shelf in the south would result in an increasingly shelf-orientated population during warm periods. In a warmer world, a more fragmented, shelf-based distribution may restrict access to the deep water needed for spawning and limit dispersal and basin-scale connection within the Antarctic Circumpolar Current^{22,29}. The primary production in alternative, high-latitude spawning areas might increase in the future, but projections suggest that these areas will become more spatially restricted²⁹, have a shorter growing season and, over the longer term, become adversely affected by ocean acidification effects on egg hatch success³⁰.

Such changes in krill dynamics would have major ramifications for food web linkages and biogeochemical cycling (Supplementary Fig. 2). When high densities of krill extend across the Southwest Atlantic sector, they support a suite of predators^{3,18}. The faecal pellets cascading from krill schools provide pulses of carbon that can dominate particle export⁷. Their feeding and digestion also mobilize iron from diatoms and lithogenic sediment, in turn helping to

fertilize phytoplankton blooms^{8,26}. In a reorganized food web with a contracted distribution of larger krill over high-latitude shelves, these functions will change. For example, the increased krill size might alter predator–prey interactions and allow greater swimming speeds, with the potential to migrate to cooler feeding grounds near the seabed²⁶. This has major implications for nutrient cycles^{1,8}, and could link krill to a different suite of predators²⁶.

Given the implications for food security and biodiversity, there is intense interest in projecting future stock sizes of krill and other high-biomass species such as anchovies or sardines^{3,18,25}. Current management of the krill fishery sets conservative catch limits but does not yet account for trends in stock size or distribution²². Models point to an ongoing increase in positive SAM anomalies for the next 50 years²⁰, coupled with warming and reduced ice cover. This would suggest a further contraction in krill distribution, associated with a suite of mainly adverse effects (Supplementary Fig. 2). However, climate–population relationships are inherently nonlinear and can change abruptly as food webs shift into new states². For example, abrupt latitudinal changes in bathymetry may constrain readjustments of distribution in polar regions, and Supplementary Fig. 1 suggests a possible increase in survival, partially compensating for the sharp decline in recruitment. Species vary greatly in the extent to which their distributions change¹⁰, these responses being modulated by genetic adaptation or via adjustments to phenology or behaviour³⁴. Various projections for krill have been made^{9,16,18,29,30}, but given the likelihood of nonlinearities¹⁸, these remain uncertain. Long-term data therefore remain the lifeblood of our understanding of climate change responses and are key to the informed management of polar ecosystems.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41558-018-0370-z>.

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Author contributions

A.A. and S.L.H. provided the initial concept and analysis. A.A., V.S. and E.A.P. conceived and constructed the KRILLBASE databases. A.A., E.A.P., V.S., C.S.R., V.J.L., D.K.S. and G.A.T. supplied data to KRILLBASE. L.G. performed the mapping. S.L.H. performed the statistical analyses. All authors provided input of ideas to the study and manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Methods

KRILLBASE-abundance database. We have created a database, entitled 'KRILLBASE-abundance'³¹, to rescue and collate all available data from untargeted net catches across the Southern Ocean. It was compiled through 'data rescue' from old notebooks, the authors' datasets, published reports and submissions by other data contributors. The full database comprises 15,194 net hauls spanning the 1926–2016 period and has data on the numerical density (number m⁻²) of post-larval *Euphausia superba*—hereafter, described simply as 'density'. This dataset (Supplementary Fig. 4) is derived from sampling stations at predetermined or randomly selected positions and excludes hauls targeted on krill swarms. It includes ~50% more data than previously published versions of the database^{11,32}. The full database is circumpolar and comprises data from 10 nations spanning 56 sampling seasons (see the Data availability statement).

KRILLBASE-length frequency database. We have compiled a separate database, entitled 'KRILLBASE-length frequency', which includes length, sex and maturity-stage data for *E. superba*. Unlike the abundance counterpart, this contains data from hauls targeted on krill schools as well as those from random or predetermined locations. This database is also circumpolar, comprising over 11,000 sampling stations over 47 seasons within the period 1926–2014 (Supplementary Fig. 5). With over 1 million individual krill length measurements from both scientific and commercial nets, the length frequency database is much larger than, and compiled independently of, the abundance database³³. The full dataset comprises data from 10 nations, either available in the authors' home institutes, sent directly by other contributors or transcribed from publications and reports (see the Data availability statement).

Transformation and screening of data. Both the density and length frequency databases required some screening for the current analyses. The Southwest Atlantic sector of interest was defined as 20–80°W and between the Antarctic Polar Front and 75°S. We divided hauls according to the 'austral summer' season (for example, the 1985 season encompassed all stations sampled between 1 October 1984 and 30 April 1985), thereby screening out winter data. Most sampling in both screened datasets was in the summer months, with 76% of hauls in the period December to February. For consistency with other work³², the density data were further screened according to the net sampling depths, removing all hauls where the upper sampling depth was >20 m or the lower sampling depth was <50 m. The median upper and lower depths were 0 and 170 m, respectively, in the screened density dataset. The length frequency dataset was screened by removing all krill <15 mm long, since these include larvae. Nets with large meshes provide biased estimates of the size distribution; therefore, we excluded data from all commercial or semicommercial trawls and scientific nets with meshes >6 mm (for example, RMT25s).

We have included both targeted and non-targeted hauls for analysis of length frequency distribution, following the recommendation³⁰ that the priority is to sample a sufficient number of krill to be representative of the wider population, which can require combining targeted and non-targeted hauls where necessary. However, to test whether this may have caused a bias in the time trends, we divided the hauls into those that provided a representative sample of the whole top 100 m layer and the remainder (including targeted hauls). An increase in mean krill length was seen independently in both subsets of data, supporting Figs. 2 and 3. Therefore, we pooled the two data sources for subsequent analyses.

The krill density estimates were based on a wide range of sampling net types, depth ranges and times of year, all of which can potentially bias spatiotemporal trends. We therefore applied conversion factors to each haul to standardize to a single, relatively efficient net sampling method. The chosen efficient sampling combination was a night-time haul with an 8 m² net from 0–200 m on 1 January. The statistical method of adjusting the krill density values to this sampling method, including model coefficients and sensitivity analysis, are described in previous papers^{31,32}.

It is important to note that this standardization model only used nets sampled concurrently within the modern era; we could not use the 1-m-diameter nets with release gear used during the 1920s and 1930s for the standardization as there were no other net types fished concurrently. Therefore, the absolute values of standardized krill density presented for the 1920s and 1930s (top panels of Fig. 1a) must be considered as approximate. Nevertheless, and particularly for the modern era, we believe that this data standardization provides a more consistent view of spatiotemporal changes in krill density than the raw density data. Therefore, for all analyses in the main text, we used standardized densities. Unstandardized data, as well as subsets of the data by sampling method, were analysed to assess the sensitivity of our results to the sampling method and standardization. These analyses indicate that the results are broadly coherent across the different methods (see Supplementary Table 1).

Environmental data. The KRILLBASE-abundance database includes data on depth at each sampling station, based on a mean value for a 10-km-radius buffer around each station from the General Bathymetric Chart of the Oceans bathymetry³¹. These values provide a basis for characterizing whether the station was over the shelf (<1,000 m) or in oceanic waters (>1,000 m). We tested krill indices against a variety of physical variables (see the Methods section 'Preliminary analysis of

relationships with environmental variables'). These included the SAM anomalies obtained from the British Antarctic Survey, Natural Environment Research Council³⁵ (NERC; <http://www.nerc-bas.ac.uk/icd/gjma/sam.html>). Multivariate El Niño/Southern Oscillation (ENSO) (Multivariate ENSO Index (MEI)) values were obtained from the Earth System Research Laboratory—part of the Physical Sciences Division at the National Oceanic and Atmospheric Administration³⁶ (<https://www.esrl.noaa.gov/psd/data/correlation/mei.data>).

For sea ice, median values of ice cover were obtained from two passive microwave radiometer datasets: the Microwave Scanning Radiometer-Earth Observation System (AMSR-E)³⁷ aboard the National Aeronautics and Space Administration's Aqua satellite and the Defense Meteorological Satellite Program Special Sensor Microwave/Imager (<http://nsidc.org/data/nsidc-0051.html>). From these, the northern latitudes of 15% concentration were obtained. In addition, we tested indices of fast ice timing of formation, breakout and duration from the South Orkney Islands time series³⁸.

KRILLBASE data coverage and spatiotemporal pooling. Because KRILLBASE is a data rescue and compilation project, data from the abundance and length frequency databases were not distributed homogeneously in time and space. To counteract this, we used a suite of methods and sampling units to examine key relationships. Spatially, these include division of the Southwest Atlantic sector (20–80°W) data into 2.5° latitudinal bands, and into shelf versus oceanic portions. This resulted in 12 spatial units defined by 2.5° latitudinal band and bathymetry (shelf versus oceanic waters). Following ref.¹¹, we excluded spatial units with fewer than 50 stations or 5 sampling seasons from the spatial visualizations in Fig. 1a and Supplementary Fig. 5. Temporally, we used the austral 'year' (that is, from October of the previous year to April in the given year) as the basic unit of sampling, based on the great variability in krill density and mean length observed between successive years due to interannual variation in recruitment^{15,18,24,39–41}. Our analyses (for example, Figs. 1b and 2 and Supplementary Figs. 3 and 5b) provide time trends and relationships that were broadly coherent across the Southwest Atlantic sector. For this reason, our illustration of key relationships in Fig. 3 is at this whole-sector scale, supported by the mixed models that include the finer subdivisions described above.

Visualization of the contraction in distribution. To provide a visualization of the changes in distribution revealed statistically by mixed model 1 (Table 1), we divided the sampling into three periods based on sequential years of sampling (namely, the 1920s and 1930s, and a modern era, 1976–2016, further divided into two roughly equal time spans). Sample coverage in each period is provided in Supplementary Fig. 4. We further restricted the analysis to an area sampled adequately in all three eras. This was defined by a polygon (red line in Supplementary Fig. 4) including a subregion that was sampled consistently but in lower density (hatched area in Supplementary Fig. 4). To visualize changes in the hotspots of krill density (Fig. 1a), we used the kernel density tool in ArcGIS to grid the density sample points from each sampling era. Kernel density estimation is a non-parametric smoothing interpolation that calculates the density of points in a specified distance around each feature. We used this approach because it is not prone to edge effects and, across the domain of each map, could objectively identify hotspot areas of elevated density.

Calculation of population central latitude in each era. We calculated the population central latitude in each era based on the stratification into six 2.5° latitudinal bands (described in the section 'KRILLBASE data coverage and spatiotemporal pooling' above, and illustrated in Fig. 1a). Population central latitude is the sum of the products of stratum mean density and stratum mid-latitude, divided by the sum of stratum mean densities. While the substantial southward contraction of range within the modern era (Fig. 1a) is supported independently by both shelf and oceanic krill sampling stations, we should stress that this analysis, plus the spatial depictions in Fig. 1a, are for illustrative purposes only. Statistical evidence for a range contraction is provided by the spatiotemporal analysis in mixed model 1 in Table 1 (see also the section 'Preliminary analysis of trends' below).

Calculation of recruit density. Recruit density is defined here as the mean density of post-larval krill ≤30 mm in length⁴⁰. This is an estimation of the density of post-larval krill that are likely to be about 1 year old within the October to April timeframe of each year's observations⁴⁰. The density of new recruits in each season was thus calculated as a product of proportional recruitment (the fraction of the krill measured that were 15–30 mm in length) and mean standardized post-larval krill density.

Preliminary analysis of relationships with environmental variables. In a series of preliminary analyses, we examined interannual variability in a series of response variables; namely, total post-larval krill density, recruit density and mean length at a range of spatial and temporal scales. The candidate explanatory variables included winter sea-ice cover (indexed by ice formation, duration and breakout times from the South Orkneys fast ice dataset³⁸) plus the satellite-derived monthly northerly extent of 15% ice averaged within a series of 10° longitude

bands. Climatic indices included SAM and MEI monthly data with variable lags and integration periods. The best-fit Gaussian generalized linear model (weighted by the number of krill-sampling stations per year) had SAM as the explanatory variable (that is, the average of monthly SAM anomalies for the period January to September preceding the October to April season of the krill observations). At the large scale of our study, the best sea-ice relationship explained much less of the variance than SAM, perhaps reflecting more localized specific conditions of ice-krill relationships^{16,40,41}. ENSO has also been identified as a driver of krill dynamics near the Antarctic Peninsula^{39–41}. We found that ENSO (indexed by the MEI) related significantly to krill with very short and long lag times, but these disappeared when added to models alongside SAM, which was thus by far the clearest predictor at the whole Southwest Atlantic scale.

Preliminary analysis of trends. We used locally estimated scatterplot smoothing (LOESS) regression, implemented using the loess function in the R package stats⁴² (span = 1, degree = 1) to visualize time trends in response variables. These were across-station averages of standardized post-larval density, length and recruit density, grouped by season and spatial unit. The spatial units were defined by latitude (2.5° bands) and bathymetry (shelf versus oceanic waters >1,000 m deep) (Fig. 2). Post-larval density and recruit density were increased by a constant (half of the minimum post-larval density across all spatiotemporal units) and log₁₀-transformed before analysis.

Encounter probability (the proportion of samples in which the subject species is present) is a common metric of species distribution. This metric (Supplementary Fig. 3) corroborated our findings on numerical density (Fig. 2)—namely, a strong decline in the north, trending towards a more stable situation towards the south, suggestive of a contraction in the distribution. However, we chose density as the focus of our main analysis, given the highly heterogeneous distribution of krill.

Linear mixed models. The datasets used in this analysis were compiled from multiple surveys with a variety of designs, locations and sampling methods. Standardization^{31,32} allows comparison of data from individual stations, but analysis of temporal patterns in such data must also ameliorate the effects of pseudoreplication and inhomogeneity of variance. Further issues include potential temporal autocorrelation and the risk of spurious correlation due to time trends in multiple variables. Our exploration of changes in krill population characteristics and their relationships with environmental variables in the modern era (1976–2016) addresses each of these issues. We used R⁴³ for all statistical analyses.

To ameliorate the effects of pseudoreplication, our analysis was conducted using linear mixed models that considered the spatial unit, year and the interaction between them as random effects. We used the lme function in the R package nlme⁴² to fit models using restricted maximum likelihood.

We investigated the fixed effects of latitude by including a candidate variable, LAT, indicating whether the sample was north or south of 60°S. This gave a reasonable balance of data between north and south, but it was not possible to explore bathymetric contrasts in length and recruit density north of 60°S (Fig. 2). The main candidate explanatory variable was year for models 1–3 in Table 1, detrended mean length for model 4 and detrended SAM (average of monthly anomalies for the period January to September preceding the krill sampling season) for models 5–7. We considered the most complete form of each model, including fixed effects for the main candidate variable plus latitude and bathymetric bin where feasible, interactions between them, and random effects.

We arrived at the final models presented in Table 1 using model selection to identify fixed and random effect variables from the set of candidates listed above, including interactions. Model selection also identified appropriate representations of variance as a function of the reciprocal of the number of stations (from candidate fixed, power and exponential functions), to ameliorate the effects of inhomogeneity of variance. It also identified an appropriate correlation structure (from candidate autoregressive order 1 and autoregressive moving-average functions) to ameliorate the effects of temporal autocorrelation where relevant. All model selection was based on the Akaike information criterion, and the identification of fixed effects also considered differences between models based on likelihood ratios. The selected variance function was a power function for all models except model 2, which used a linear function.

To avoid spurious correlations when both the response and main candidate explanatory variable included a time trend, we detrended both variables using the relevant time-trend model. The detrended variable was the original value minus the fitted value based on fixed effects.

We used visual checks to verify that response data were approximately normally distributed and that model fits were convincing. We verified that the autocorrelation statistics in the selected models were not significantly different from zero. We also used the Levene test (R package car⁴⁴) to verify that each model was not significantly affected by heteroscedasticity. Finally, we used the r.squaredGLMM function in the R package MuMIn⁴⁵ to estimate the variance explained by the fixed and random effects in each model. In high-variability datasets such as ours, the variance explained by linear models featuring one or two explanatory variables is typically low, particularly when variables are detrended. The main statistic for detecting relationships is the *P* value, which indicates whether the linear model slope is significantly different from zero.

To assess the difference in time trends between recruit density and total post-larval density (Supplementary Fig. 1), we restricted the dataset to years and spatial units for which both types of density estimate were available. We constructed a linear mixed model with density as the response variable, year as the main explanatory variable and an additional explanatory variable indicating the type of density estimate (recruit or total post-larval). A significant interaction between explanatory variables indicates a significant difference in the slope.

We explored the sensitivity of the time trend in krill density to data selection and processing by fitting model 1 to alternative versions of the dataset (Supplementary Table 1). Specifically, we used: (1) unstandardized krill density data; (2) data only from nets with nominal mouth areas >3 m²; and (3) data only from nets with nominal mouth areas ≤3 m². All models identified the negative time trend, but the models fitted to smaller datasets filtered by net size did not identify a latitudinal difference in trend. As krill aggregate in dense swarms with few krill between, the probability of the mean density being zero increases at low sample sizes. Consequently, when means based on <15 stations are included, there is a weak relationship between the number of stations and mean density. To confirm that the variance function ameliorates this effect, we also fitted all models with density or recruit density as a response variable to restricted datasets that excluded averages based on <15 stations. In all cases, the main fixed effects remained significant.

Calculated decline in density and biomass during the modern sampling era. The average separation between sampling in the first and second halves (1976–1995 and 1996–2016) of the modern era is 20.5 years. Therefore, we used the time trends in Table 1 to determine respective average changes in density and length over 20.5 years. We used the unweighted mean of the north and south slopes for density, so the estimated change is analogous to that expected for a transect with equal length on either side of latitude 60°S. Mean lengths were converted to individual dry mass using Scotia Sea-specific length–mass regressions⁴⁶, and biomass density was calculated as the product of individual dry mass and numerical density. These revealed the 70% decline in density and 59% decline in biomass density quoted in the text.

Data availability

We have made the KRILLBASE-abundance database publicly available from the Polar Data Centre at the British Antarctic Survey (<http://doi.org/brg8>), with supporting metadata³¹, which should be consulted for further details. Likewise, KRILLBASE-length frequency data are also available on request to the Polar Data Centre, with supporting metadata.

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