

a note of the completeness of preservation (isolated bone, group of bones, complete skull, complete skeleton) for each.

In the past, Western authors have tended to rename Russian svitas as 'formations', and horizons as 'horizons', but this masks their true meanings. In Russia, horizons are the main regional stratigraphic units, identified primarily from their palaeontological characteristics, and they do not pertain to lithostratigraphic units. Svitas are largely lithostratigraphic units, given a locality name that is close to their characteristic exposure. The definition of a svita incorporates a mix of field lithological observations and biostratigraphic assumptions.

Analysis

The records were converted into range charts (Fig. 1), including Lazarus taxa²², from which total numbers (*N*) and numbers of originations (*O*) and extinctions (*E*) per time bin were calculated. Percentage origination and extinction metrics (*O/N*, *E/N*) were calculated for each time bin (Fig. 2). There are many other possible measures of extinction and origination rates, most calculated with respect to time; such measures would be inappropriate here because the durations of the svitas are poorly constrained. Boundary-crossing measures of extinction and origination rates were not used because the sample sizes are small, and 10 of the 38 families are restricted to one time bin and would have to be discarded. Generic rates are not presented because many genera are singletons (restricted to one time bin) and most are in need of taxonomic revision. Binomial error bars³⁰ are calculated for the percentage metrics.

The possible influence of sampling was assessed from the raw data (Fig. 3), and by the application of three sampling standardizations. In the first standardization, units that had yielded fewer than 50 specimens were ignored (namely the Osinovskaya, Belebey, Bolshekinelskaya, Gostevskaya and Bukobay svitas); sample sizes then ranged from 49 to 147 specimens. In the second sampling standardization, the two oldest units were ignored, and the others with small sample sizes were combined with adjacent units (Bolshekinelskaya + Amanakskaya, Gostevskaya + Petropavlovskaya, Donguz + Bukobay), yielding a range of sample sizes from 50 to 147 specimens. In the third sampling standardization, rarefaction analysis was applied to the units that had yielded larger samples of specimens (Kopanskaya, Kzylsaiskaya, Staritskaya) to assess what their apparent diversity would have been had the sample size been 50, within the range 49–63 specimens, as for the other moderately well sampled units.

The data sets and analyses are available as Supplementary Data, and may be downloaded at <http://palaeo.gly.bris.ac.uk/Data/RussiaPTR.xls>.

Dating

The timescale indicated in Fig. 1 is based on refs 10, 23, 24 and 25. The date for the Permian–Triassic boundary, 251 Myr, from ref. 10, has been debated²⁶, but is widely accepted and will be the accepted date in the new Cambridge geologic timescale^{27,28}. Other aspects of the scales may seem less familiar, in that the Kazanian and Tatarian are much longer than is often assumed, 16 Myr instead of 4–5 Myr, and the Middle Triassic is dated as older than normally accepted. Should the old dates prove to be correct, and the newer ones incorrect, the conclusions here are not affected because we do not make claims about the longer-term timing of events, nor do we present rates of origination or extinction calculated against time.

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Correspondence and requests for materials should be addressed to M.J.B. (mike.benton@bris.ac.uk).

Long-term decline in krill stock and increase in salps within the Southern Ocean

Angus Atkinson¹, Volker Siegel², Evgeny Pakhomov^{3,4} & Peter Rothery⁵

¹British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

²Sea Fisheries Institute, Palmaille 9, 22767 Hamburg, Germany

³Department of Earth and Ocean Sciences, University of British Columbia, 6339 Stores Rd, Vancouver, British Columbia, V6T 1Z4, Canada

⁴Department of Zoology, Faculty of Science and Technology, University of Fort Hare, Private Bag X1314, Alice 5700, South Africa

⁵NERC Centre for Ecology and Hydrology, CEH Monks Wood, Abbots Ripton, Huntingdon PE28 2LS, UK

Antarctic krill (*Euphausia superba*) and salps (mainly *Salpa thompsoni*) are major grazers in the Southern Ocean^{1–4}, and krill support commercial fisheries⁵. Their density distributions^{1,3,4,6} have been described in the period 1926–51, while recent localized studies^{7–10} suggest short-term changes. To examine spatial and temporal changes over larger scales, we have combined all available scientific net sampling data from 1926 to 2003. This database shows that the productive southwest Atlantic sector contains >50% of Southern Ocean krill stocks, but here their density has declined since the 1970s. Spatially, within their habitat, summer krill density correlates positively with chlorophyll concentrations. Temporally, within the southwest Atlantic, summer krill densities correlate positively with sea-ice extent the

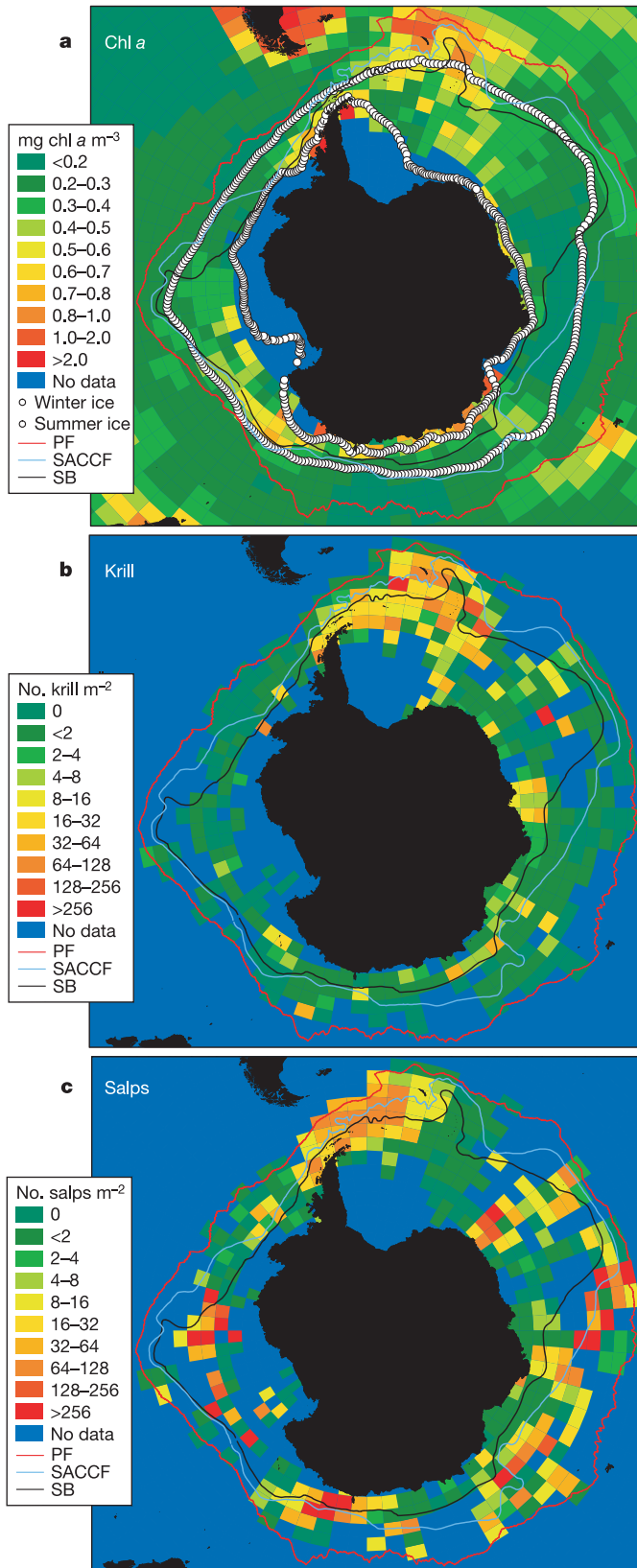


Figure 1 Krill, salps and their food. **a**, Mean (November–April) chlorophyll *a* (chl *a*) concentration, 1997–2003. **b**, Mean krill density (6,675 stations, 1926–2003). **c**, Mean salp density (5,030 stations, 1926–2003). $\log_{10}(\text{no. krill m}^{-2}) = 1.2 \log_{10}(\text{mg chl } a \text{ m}^{-3}) + 0.83$ ($R^2 = 0.051$, $P = 0.017$, $n = 110$ grid cells). Historical mean positions are shown for the PF²⁹, Southern ACC Front (SACCF)³⁰, SB³⁰ and northern 15% sea-ice concentrations in February and September (1979–2004 means).

previous winter. Summer food and the extent of winter sea ice are thus key factors in the high krill densities observed in the southwest Atlantic Ocean. Krill need the summer phytoplankton blooms of this sector, where winters of extensive sea ice mean plentiful winter food from ice algae, promoting larval recruitment^{7–11} and replenishing the stock. Salps, by contrast, occupy the extensive lower-productivity regions of the Southern Ocean and tolerate warmer water than krill^{2–4,12}. As krill densities decreased last century, salps appear to have increased in the southern part of their range. These changes have had profound effects within the Southern Ocean food web^{10,13}.

Our database comprises 11,978 net hauls from 9 countries, spanning the summers of 1926–39 and 1976–2003. This database shows a concentration of krill in the productive southwest (SW) Atlantic sector (Fig. 1a, b). On the basis of catches with equivalent nets (Supplementary Information), 58–71% of krill are located here.

Potential krill habitat lies between the Polar Front (PF) to the north and the ice-covered Antarctic shelves to the south^{1,7,14}, but krill do not occupy all of this range. There are various explanations for regional variations in krill density, invoking the seasonal ice

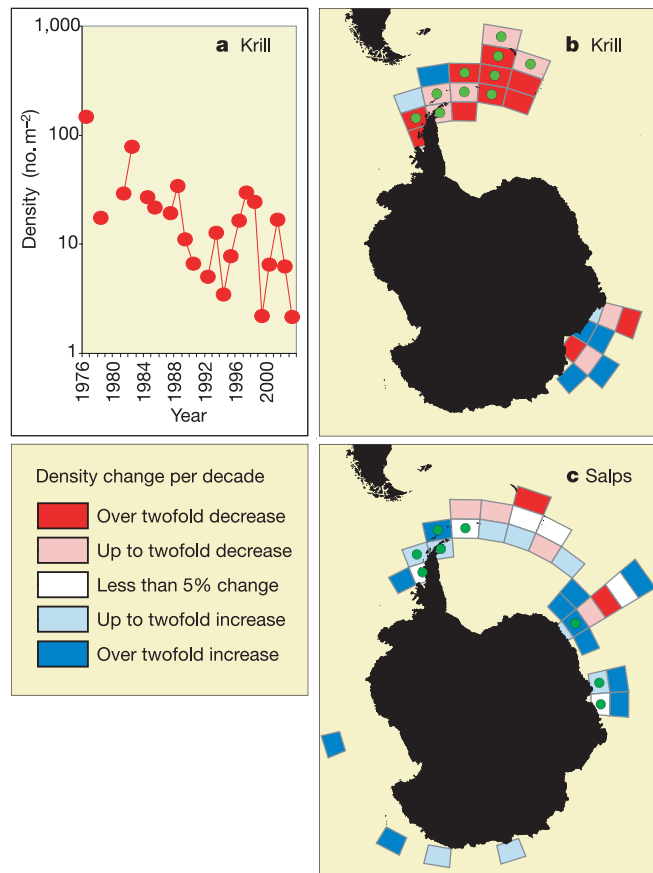


Figure 2 Temporal change of krill and salps. **a**, Krill density in the SW Atlantic sector (4,948 stations in years with >50 stations). Temporal trends include **b**, post-1976 krill data from scientific trawls; **c**, 1926–2003 circumpolar salp data south of the SB. Regressions of $\log_{10}(\text{mean no. m}^{-2})$ on year were calculated for cells with ≥ 3 yr of data, weighted by number of stations in that year. One-sample *t*-tests supported a post-1976 decrease in krill density in the SW Atlantic (scientific trawls: $t = -3.4$, $P = 0.004$, 16 cells, smaller nets: $t = -2.5$, $P = 0.04$, 8 cells). Salp densities increased south of the SB after 1926 ($t = 3.1$, $P = 0.004$, 32 cells) Green spots denote cells usable in the spatio-temporal model.

Table 1 Significant temporal trends krill and salp density

Taxon	Subset of data analysed			Estimated % increase (+) or decrease (-) per decade (s.e.m)		P value
	Era	Net type	Region			
Salps	Post 1926 (34 yr)	All	Circumpolar (8 grid cells)	+66 (23)	+ 87 (20)	0.007 < 0.001
Krill	Post 1976 (21 yr)	Scientific trawls	SW Atlantic (10 grid cells)	-38 (24)	- 38 (15)	0.12 0.023
Krill	Post 1976 (14 yr)	All other nets	SW Atlantic (8 grid cells)	-75 (21)	- 81 (16)	0.004 < 0.001

A spatio-temporal model for \log_{10} (no. krill or salps m^{-2}) with linear trend, grid cell effects, and including random year effects (upright font) or ignoring random year effects (italic font). See Methods.

zone^{12,15} (SIZ), the Southern Boundary (SB) of the Antarctic Circumpolar Current¹⁶ (ACC) or the province to its south¹². But none of these relationships hold at the circumpolar scale¹⁷. For example, krill densities are high near South Georgia, north of both the SB and the SIZ (Fig. 1). However, all of these models link krill density to the abundance of food, which is likely to be the primary factor determining abundance. Together, sea ice, oceanography and nutrients promote primary production near shelves, fronts and ice edges¹⁸, and krill occupy this full range of habitats. Within the distributional range of krill, their mean density correlates positively with the concentration of chlorophyll *a* (chl *a*; Fig. 1).

Salps tend to occupy warmer water than krill^{2-4,12}, and prefer oceanic regions with lower food concentrations^{2,3}. Thus the lower productivity across most of the ACC means that the habitat of salps is much larger than that of krill, with no concentration into one sector (Fig. 1c). The hotspot of krill in the SW Atlantic—a feature very unlike that of zooplankton⁶—suggests an ability to maintain their 5–7-yr life cycle here, withstanding entrainment into the great current systems encircling Antarctica.

We studied temporal trends in krill and salp density using a grid, which incorporates inter-annual variability in density (Fig. 2a) into a time-series regression within each of its cells. These are used in one-sample *t*-tests (for example, Fig. 2b, c) and a spatio-temporal model (Table 1). Salp densities increased south of the SB over the whole time series. For krill in the SW Atlantic sector, densities have declined significantly since 1976.

Monitoring surveys⁷⁻¹⁰ show shorter-term changes in krill and salp density. However, these are too localized to tell whether they reflect changes in overall population size¹⁷. The trends reported here are longer-term and over larger scales, supported by independent surveys with scientific trawls (that is, Rectangular midwater

trawls and Isaac Kidd midwater trawls) and with smaller nets (Supplementary Information).

Controls on grazer populations include top-down (predation) and bottom-up (resource-based) factors¹⁷. We have examined temporal links between krill density and a key physical parameter—winter sea ice⁷⁻¹¹. To find the appropriate scale for analysis, we compared krill densities between the eastern (30°–50° W) and western (50°–70° W) sub-areas of the SW Atlantic. Over the 19 available summers, krill density in the east and west are positively related ($R^2 = 0.47$, $P < 0.001$). Whether this reflects advection^{19,20} or common controls on krill populations¹⁷, it suggests a basin-scale synchrony in the inter-annual signal.

We therefore compared net data from the whole SW Atlantic to indices of sea ice. Here, summer krill density correlates to both the duration (Fig. 3a) and the extent (Fig. 3b) of sea ice the previous winter in the same area. Salps showed no such relationships, despite a negative one being postulated previously off the Antarctic Peninsula⁸. With shorter life cycles than krill and explosive population growth rates, salps can respond to environmental variation over shorter timescales²⁻⁴.

The population size of krill has been linked both to predation controls^{11,13,17,20,21} and to food resources within winter sea ice⁷⁻¹¹. Our results are, to our knowledge, the first to show a direct, large-scale link between annual krill density and sea-ice cover. This is not a localized, short-term effect—it relates to >50% of their stock and the data span 1926–2003. Given the problems of net sampling⁵, the existence of a relationship with sea ice suggests that this factor plays a dominant role, not just in krill recruitment⁷⁻¹¹, but also in their population size.

Various mechanisms have been proposed to explain how sea ice benefits krill^{7-11,22}. Sea-ice algae are a critical food resource, boosting early adult spawning in spring or survival of the larvae the following winter. Sea ice could also shield krill from predation. However, the only link with summer krill density that we found was with ice cover the preceding winter—ice cover from the winter before that had no significant effect. A 6-month lag points to larval over-wintering as a key process affected by ice—larvae need to survive their first winter to recruit the following summer, and thus replenish the adult population. At the Antarctic Peninsula, only a few years of strong recruitment per decade are needed to maintain the local krill population⁷⁻¹¹.

These positive temporal relationships between krill density and sea-ice extent (Fig. 3) do not equate to positive spatial relationships (Fig. 1a, b). High krill densities can be found at South Georgia outside the SIZ, whereas low densities coincide with an extensive SIZ, for example, in the SW Indian sector. Hence sufficient winter ice in the major spawning and nursery areas (the Antarctic Peninsula and Southern Scotia Arc^{1,7,11,23}) affects krill density across a whole ocean basin, including areas north of the SIZ. Krill larvae do not merely need to survive the winter—they need to double in length¹¹. Sufficient food year-round may thus be the feature of the SW Atlantic that maintains its high krill stocks.

The western Antarctic Peninsula is one of the world's fastest warming areas, and (atypically for the Southern Ocean) winter sea-ice duration in this sector is shortening²⁴. Key spawning and nursery

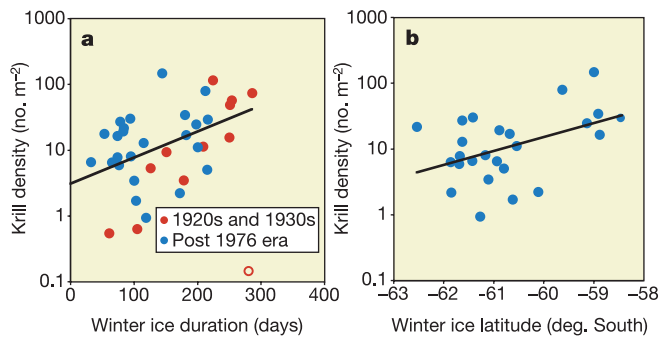


Figure 3 Krill–ice relationships. Annual mean density of krill across the SW Atlantic versus **a**, sea-ice duration²⁷ (that is, days of fast ice observed at the South Orkneys the previous winter), and **b**, the mean September latitude of 15% ice cover along a transect¹⁰ across the western Scotia Sea. Regression identified one outlier season (1934, open circle) with exceptionally long ice duration and only 24 net stations, so for the remaining years $\log_{10}(\text{no. krill } m^{-2}) = 0.49 + 0.0040$ (sea-ice duration, days) $R^2 = 0.21$, $P = 0.006$, $n = 35$. $\log_{10}(\text{no. krill } m^{-2}) = 14 + 0.21$ (sea ice latitude, degrees) $R^2 = 0.21$, $P = 0.02$, $n = 25$.

areas of krill are thus located in a region that is sensitive to environmental change. Deep ocean temperatures have increased²⁵, and a circumpolar, pre 1970s decrease in sea ice²⁶ has been indicated at several locations^{27,28}. The regional decrease in a high-latitude species with high food requirements (krill) coincides with an increase in a lower-latitude group with lower food requirements (salps). However, as the mechanisms underlying these changes are uncertain, future predictions must be cautious.

These changes among key species have profound implications for the Southern Ocean food web. Penguins, albatrosses, seals and whales have wide foraging ranges but are prone to krill shortage^{3,10,13,21}. Thus the wide extent of our indicated change in krill density—not just its magnitude—is important. The basin-scale decline in krill may underlie the post 1980s shift in demography of krill predators, seen across the SW Atlantic^{10,13}. Earlier last century, over-exploitation of whales preceded a rapid increase in smaller krill predators such as fur seals in the SW Atlantic^{20,21}. Added to this shift in the predator balance, a return of the whales to pre-exploitation levels now faces the further problem of lower krill density. □

Methods

Satellite data

Average values of SeaWiFS Level-3 standard mapped images of chl *a* concentration were calculated in Arc GIS 8.2 for grid cells with data for November–April (Fig. 1a). Sea-ice images, calculated from DMSP-SSM/I passive microwave data by NOAA/NCEP, were pre-processed as the northern extent of 15% ice concentration to remove spurious values before calculating mean monthly positions.

The krill and salp database

The full database (Supplementary Table 2) comprises data from the UK, Germany, USA, the Ukraine, South Africa, Japan, Australia, Poland and Spain. All are non-targeted oblique or vertical hauls from pre-fixed positions. The data were either from samples sorted by the authors, available within our institutes, sent by our collaborators, or transcribed from the literature. Krill densities (no. m⁻²) include only postlarvae, or just the krill >19 mm long from the *Discovery* (1926–51) era. Salp densities are the total solitary plus aggregate individuals of *S. thompsoni* and the rarer *Ihlea racovitzai*, pooled to avoid identification problems. Historical *Discovery* data (1926–51) were cross-checked from three archived sources: the net sampling logs, the original tables used to construct the published figures¹⁴, and an electronic krill database. The *Discovery Report Station Lists*¹⁴ were used to calculate densities.

Extraction and analysis of data

From the full database, we extracted November–April data south of the PF where at least the topmost 75 m (krill) or 100 m (salps) was sampled. Sampling was mainly much deeper (Supplementary Table 3) and 90% was in December–March. Regression of krill density on chl *a* concentration (Fig. 1) used mean grid cell values, and was restricted to post-1976 scientific trawl data in cells where krill were caught.

We tested spatio-temporal trends among: stations south of the PF, PF to SB, south of the SB, the post 1926 era, the post 1976 era, the SW Atlantic sector only and circumpolar. We report only trends significant in two tests—first, a one-sample *t*-test of whether the regression slopes of cells (Fig. 2) differ from zero, supporting a widespread shift in abundance. Second, to further test for a temporal trend we used a spatio-temporal model: $y_{kt} = g_k + bt + B_t + E_{kt}$, where y_{kt} is the log₁₀ transformed mean density (+*c*) in grid square *k* and season *t*, g_k is a fixed effect for grid square *k*, *b* is the slope, the average change per season on a log₁₀ scale, B_t is a random effect for season *t* and E_{kt} is a random square by season effect. The constant *c* (added to allow for log transformation of zero densities) was half the minimum density. The variance of the cell-season effect was assumed to be inversely proportional to the number of net hauls (n_{kt}) for each cell-season combination. Cells with sufficient data for inclusion in the mixed model (Fig. 2) were defined as those with at least 5 seasons and 50 stations. The model was fitted by residual maximum likelihood, with the *t*-test for trend based on $n - 2$ degrees of freedom, where *n* is the number of seasons. A general linear model ignoring the random year effect (that is, the values shown in italics in Table 1), gave similar estimated slopes but smaller standard errors—an effect of pseudo-replication from treating the observations as statistically independent.

Potential sampling artefacts

The asymmetrical circumpolar distribution of krill density persisted last century and is supported independently by differing sampling gear (Supplementary Fig. 4) Our spatio-temporal analyses encompass broad-scale spatial differences in sampling location, but Supplementary Fig. 5 shows that at finer scales, sampling has focused increasingly onto productive shelf/shelf break areas favoured by krill^{14,17} but not by salps^{2,3}. The trends are thus not artefacts of sampling emphasis. Likewise, any systematic changes in sampling method (Supplementary Table 3) observed would tend to increase krill density in recent years rather than decrease it. Station positions were pre-fixed, so generally sampled on arrival—that is, at random times of the day or night, thus not biasing our grid-based

analyses. The sea-ice relationships were supported by multiple subsets of krill data and sea-ice indices (Supplementary Table 4).

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Correspondence and requests for materials should be addressed to A.A. (aat@bas.ac.uk).