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KRILLBASE: a circumpolar database of Antarctic krill and salp numerical densities, 1926-2016

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Abstract

Antarctic krill (*Euphausia superba*) and salps are major macroplankton contributors to Southern Ocean food webs and krill are also fished commercially. Managing this fishery sustainably, against a backdrop of rapid regional climate change, requires information on distribution and time trends. Many data on the abundance of both taxa have been obtained from net sampling surveys since 1926, but much of this is stored in national archives, sometimes only in notebooks. In order to make these important data accessible we have collated available abundance data (numerical density, no. m^{-2}) of postlarval *E. superba* and salps (combined aggregate and solitary stages and species) into a central database, KRILLBASE, together with environmental information, standardisation and metadata. The aim is to provide a temporal-spatial data resource to support a variety of research such as biogeochemistry, autecology, higher predator foraging and food web modelling in addition to fisheries management and conservation. Previous versions of KRILLBASE have led to a series of papers since 2004 which illustrate some of the potential uses of this database. With increasing numbers of requests for these data we here provide an updated version of KRILLBASE that contains data from 15,194 net hauls, including 12,758 with krill abundance data and 9,726 with salp abundance data. These data were collected by 10 nations and span 56 seasons in two epochs (1926-1939 and 1976-2016). Here, we illustrate the seasonal, inter-annual, regional and depth coverage of sampling, and provide both circumpolar- and regional-scale distribution maps. Krill abundance data have been standardised to accommodate variation in sampling methods, and we have presented these as well as the raw data. Information is provided on how to screen, interpret and use KRILLBASE to reduce artefacts in interpretation, with contact points for the main data providers.

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Keywords: *Euphausia superba*, *Salpa thompsoni,* krill, salps, Antarctica, Southern Ocean, KRILLBASE, database.

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INTRODUCTION

The crustacean euphausiid species *Euphausia superba* (hereafter "krill") and the tunicate family salpidae (hereafter "salps") are key large zooplankton taxa of the Southern Ocean. Both taxa are important in biogeochemical cycling and nutrient export (Pakhomov et al., 2002; Phillips et al., 2009; Gleiber et al., 2012; Schmidt et al., 2016). They have broadly similar size, but have fundamentally different life cycles, habitat preferences, and nutritional composition and thus have contrasting roles in the food web. Krill is a major food item for a suite of vertebrate and invertebrate predator species (Murphy et al., 2007; Trathan and Hill, 2016). Salps appear in the diets of various invertebrates, fish and birds but do not seem to be as important as krill to most of the air-breathing predator group (Pakhomov et al., 2002). Also, compared to krill, salps seem to prefer warmer, deeper water habitats with moderate food concentrations and less sea ice (Pakhomov et al., 2002; Loeb and Santora, 2012).

Over the past 100 years the Southern Ocean has experienced regional warming (Gille, 2002; Meredith and King, 2005; Whitehouse et al., 2008) and regionally-variable changes in sea ice cover (de la Mare, 1997; Murphy et al., 2014; Stammerjohn et al., 2012). Whether there has been a consequent reorganisation of plankton distributions is a topic of much interest and debate (Pakhomov et al., 2002; Atkinson et al., 2004; Ward et al., 2012; Loeb et al., 2015). Climate model ensembles predict that current positive trends in atmospheric Southern Annular Mode (SAM) anomalies will continue this century (Gillett and Fyfe, 2013). Since the population dynamics of key euphausiid and salp species relate to these climatic drivers (Saba et al., 2014; Ross et al., 2014; Steinberg et al., 2015; Loeb and Santora, 2015), we need to understand the spatial and temporal dynamics of both krill and salps.

In addition to their ecological role, krill are also the dominant fished species in the Southern Ocean in terms of catch weight, with a potential sustainable yield equivalent to 11% of current global fishery landings (Grant et al., 2012). The Antarctic krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) which is committed to precautionary, ecosystem-based management. This means that CCAMLR is responsible for managing the impacts of the fishery on the health, resilience and integrity of the wider ecosystem. However, there is little information about many relevant aspects of krill ecology and population dynamics (Siegel and Watkins 2016), including stock identity (Jarman and Deagle, 2016), and predator-prey relationships (Trathan and Hill, 2016). Reducing these uncertainties might be necessary for CCAMLR to achieve its conservation objectives (Constable, 2011).

Fishery managers and stakeholder groups aim to improve management using feedback approaches and spatial and temporal protection, but more information is needed to achieve this (Hill and Cannon, 2012). Thus, understanding krill distribution and dynamics is also important for the development of sustainable fishery management and conservation policy (e.g., identifying suitable Marine Protected Areas and assessing the dynamics of fished stocks). Consequently, a cross-sector group representing the fishing industry, scientists and conservation NGOs has recently called for improvements in the availability of information to improve understanding of the state of the krill-based ecosystem and management of the fishery (Hill et al., 2014).

Spatial-temporal information on krill and salps can come from scientific surveys using acoustics or nets, predator studies or data from the fishery. Each has its strengths and weaknesses and these are expanded on elsewhere (Atkinson et al. 2012b). For net sampling surveys, data are available from a variety of expeditions since the 1920s. These individual surveys provide important snapshots of the ecosystem but in isolation they cannot provide a broader context. Annual monitoring programmes collecting net and acoustics data over standardized survey grids were initiated in the late 1980's and early 1990's (Reiss et al., 2008; Fielding et al., 2014; Steinberg et al., 2015; Kinzey et al., 2015; Krafft et al., 2016). However, despite the technology used, these multi-year time series surveys only cover a tiny fraction of the Southern Ocean area. A larger-scale and longer-term perspective is thus useful to provide context for the standardised monitoring datasets.

The KRILLBASE project was started at the end of the 1990s to bring together the data necessary for this broader context. It was initiated by Angus Atkinson, Evgeny

Pakhomov and Volker Siegel and is one of many examples of international collaboration in Antarctic research. Over the last 15 years we have documented and collated over 200 datasets, some of which are 90 years old and previously only available on paper log-sheets, distributed across library archives. KRILLBASE thus pre-dates many other data rescue and compilation initiatives. Only by combining data in this way can we provide coverage on a scale commensurate with that of large marine ecosystems or with management and conservation areas (Fig. 1). The most recent update to KRILLBASE was completed in 2016, and making these data more accessible improves the capacity of a broader community to investigate the dynamics and distribution of ecologically important krill and salps, and to enhance the responsible management of krill fisheries and the conservation of Southern Ocean ecosystems.

The objectives of publishing the revised KRILLBASE are a) to provide a link to key data and metadata for those wishing access to the krill and salp data sets, b) to illustrate the scope and coverage, with examples of potential uses of these data, c) to explain in detail its structure, with caveats and guidelines on how the data can be used, and (d) to provide a single, citable reference for these combined data sets.

2. DATA AND METHODS

2.1 KRILLBASE overview: summary

The data introduced here were compiled as part of a long term project to rescue and compile data on a range of krill and salp variables, derived from net sampling surveys. This paper introduces the most recent version of the krill and salp abundance data. More specifically, the main fields indicate numerical density (i.e. the number of individual postlarval krill or salps under $1 m^2$ of sea surface area), which we refer to as abundance for brevity. The version of the data that we present here (doi: http://doi.org/brg8, which can be accessed via https://www.bas.ac.uk/project/krillbase) amalgamates existing time series and other surveys of numerical density of postlarval krill, *Euphausia superba,* and salps. These data span 1926-1939 (plus 1951) and 1976-2016, albeit with variable spatial and temporal coverage. It

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is important to emphasise that this is a multi-national composite database not a synoptic snapshot or a true time series, so care is needed when using and interpreting these data due to the different sampling methods used. Table 1 provides a summary of its composite structure. In this paper phrases referring to KRILLBASE column headings are in bold italics (e.g. *BOTTOM_SAMPLING_DEPTH_M*) whereas searchable terms within the data (e.g. *stratified haul*) are italicised.

The basic dataset is in a single table with an accompanying table of column descriptions available either in their entirety as two downloadable CSV files, or as a resource that can be queried online. Both of these versions can be accessed via the doi: http://doi.org/brg8. Metadata are available via a) this paper, which forms a reference that needs to be cited for the data source and b) detailed descriptions of data sources for each row of the data. These data are held at the Polar Data Centre at British Antarctic Survey to allow traceability, continuity of access and future updating.

2.2 Relationships to other databases

A previous version of KRILLBASE was published in this journal as part of a global dataset of macroplankton biomass on a grid (Moriarty et al. 2013). The present version augments this with 50% more data. If necessary the abundance values can be converted to an approximation of biomass (mg.C.m^{-3}) using, for example, the procedure of Moriarty et al. (2013) who first calculated the number of individuals per m^{3} by dividing density by sampling depth (*BOTTOM_SAMPLING_DEPTH_M - TOP_SAMPLING_DEPTH_M*), and then applied fixed conversion factors of 63 and 24 mg.C.ind^{-1} for krill and salps respectively. Previous subsets of the KRILLBASE data are also stored as presence/absence data at Pangaea https://pangaea.de/ and at CCAMLR. Two of the datasets used in KRILLBASE are available from their respective data websites (http://pal.lternet.edu/ and https://swfsc.noaa.gov/aerd/), Although these do not include the standardised krill abundances available in KRILLBASE, we refer the user to these two websites to obtain the most up to date source data from the Palmer-LTER and US-AMLR time series data. A separate data holding external to

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KRILLBASE, for example including winter krill data from US SO-GLOBEC, is at BCO-DMO http://www.bco-dmo.org/. KRILLBASE and other data collections and time series are linked into a global network entitled IGMETS (International Group of Marine Time Series, http://igmets.net/), a metabase that provides a catalogue of marine biological time series.

2.3 Structure of KRILLBASE

It is important to differentiate "records" (i.e., rows of the data in KRILLBASE) from "net hauls" and from "sampling stations". The most common situation is for each record to represent a single net haul at a single station. There is one indexing column (labelled "STATION" and 28 further columns (i.e. fields) describing searchable and filterable date, time, position, sampling and environmental information as well as krill and salp abundance. The detailed description of each of these columns is provided in Table 2, while more detail on the nets used for sampling is in Table 3).

While most of the 14,543 records pertain to a single haul made at a station, there are actually four types of record. These are differentiated in the "RECORD_TYPE" column. The most common record, where a single net haul was taken at the station, is simply labelled "*haul*". The second category is labelled "*stratified haul*", (2,243 records), and these hauls form part of a depth-resolved stratified series made at a station (e.g., 0-50, 50-100, 100-200). The third category is "*stratified pooled haul*" (567 records) and these pool the abovementioned *stratified haul*s into a single combined 'virtual haul', in this example from 0-200m. The fourth category (48 records), are labelled "*survey mean*". In these the record provides the arithmetic mean abundance from multiple stations within a survey. While less than optimal, this aggregated information was the only data recoverable from the relevant surveys, which provided data from a valuable 1290 stations during the 1980s.

The krill data are presented as both the observed abundance (*NUMBER_OF_KRILL_UNDER_1M2,* no.m^{-2}) and the abundance standardised relative to a benchmark (*STANDARDISED_KRILL_UNDER_1M2,* no.m^{-2}), which is explained in Section 2.7. The salp data are presented as observed abundance for all species combined, where

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an individual can be either a solitary oozoid or an individual within an aggregate chain (*NUMBER_OF_SALPS_UNDER_1M2,* no.m^{-2}).

Overall there are 15,191 hauls in the database, from 13,542 stations. Of these hauls, 7,295 have abundance information on both krill and salps. Others have absent data for either salps or krill, and these are flagged as "Not a Number" (*NaN*). This distinguishes it clearly from zero, which indicates that either no krill or no salps were caught. Absent data should therefore not be confused with zeros.

In *stratified pooled haul* records the *NUMBER_OF_KRILL_UNDER_1M2* and *NUMBER_OF_SALPS_UNDER_1M2* values are the sums of the component *stratified hauls*, but are not given (*NaN*) if data were missing from one or more of the *stratified hauls*. Location information is generally taken from the deepest component *stratified haul*. Time information is taken from the shallowest component *stratified haul* as krill densities are most sensitive to light levels in the surface layers.

2.4 Data processing and error checking

Stations were plotted one survey at a time to identify errors in station positions, stations plotting on land, or with latitude and longitudes transposed or with the wrong sign. Implausibly large distances between consecutive sampling points were identified and corrected. Suspiciously low densities were identified, based on known or estimated volumes filtered by the various nets and the assumption that no fewer than one krill could have been caught. This test identified and led to the correction of a major error made on one portion of the data when converting numbers of krill per 1000 m^3 to numbers of krill per m^{-2}. Tests of date, time and position coincidence led to the removal of several portions of data that had been entered twice with different station numbers.

The veracity of high krill abundances are hard to check, since densities in swarms have been estimated in the thousands per m^3 of water. The highest density values for krill and salps were 9384 and 5886 inds. m^{-3}, respectively. These form a natural tail to the frequency distribution of catch densities (Fig. 2) and are not isolated outliers. They are also

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well within expected values (Hamner and Hamner, 2000). The highly patchy spatial distribution of each taxon results in right-skewed frequency distributions, with modes at zero, i.e. no krill caught (Fig.2). This distribution type is an important consideration in analyses.

Water depths for each net sample were obtained by superimposing the stations on a GEBCO_2014 Grid, version 20150318, www.gebco.net bathymetry using Arc GIS 10.4.1 and extracting the minimum, mean and maximum water depth within 10km of each station. The bathymetric information derived from this provides an additional check of the veracity of position information. We identified 32 records in which the *BOTTOM_SAMPLING_DEPTH_M* was implausibly deeper than the maximum depth in the vicinity of the haul. For 10 of these, the longitude or latitude was reported as an integer. Integer coordinates and shallow bathymetry may indicate inaccuracies in position information. Users should be aware that inaccuracies in latitude can also affect the assessment of *DAY_NIGHT* information used in the calculation of standardised krill abundances. A couple of reported krill catches were from warmer waters north of the Antarctic Polar Front, giving grounds for suspicion, for example of identification. We kept these records since expatriated individuals are a possibility and we did not want to pre-judge the data provided. Data caveat issues are indicated and described in the fields DATE_ ACCURACY and CAVEATS respectively.

2.5 Variation in sampling coverage and method

Fig. 1 shows that KRILLBASE sampling is highly uneven, focussing on areas of fishing or historical interest to nations focussing on the Atlantic sector (USA, GERMANY, UK, Poland, South Africa, Spain) or Indian sectors (Soviet Union, Japan, Australia). While Fig 1 plots the stations with either krill or salp data or both, Supplementary Fig. 1 plots only those stations with krill data. Data compilation was mainly focused on the Antarctic zone; 765 records are north of the Antarctic Polar Front. "Discovery" sampling (i.e., those data obtained as part of the Discovery Investigations) in the 1920's and 1930's started nearer South Georgia and

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became increasingly circumpolar but, despite this, major gaps in sample coverage exist in important areas such as the Ross Sea, Weddell Sea and in large parts of the Pacific sector.

The composite nature of KRILLBASE means that the sampling methods vary. Fig. 3 illustrates this with a circumpolar comparison of the seasonal timing of sampling (Fig 3a), bottom depth of sampling (Fig 3b) and mouth area of the net (Fig. 3c). Time of year of sampling has a potentially strong influence on the abundance of zooplankton, due to life cycle- and behavioural traits such as seasonal vertical migration (Foxton, 1966; Atkinson et al., 2012a; Cleary et al. 2016). While samples were obtained during most months of the year, 89% of the hauls were conducted in the period December to March (Fig 4), with no longitudinal bias in timing (Fig 3a). However, in sparsely sampled areas, particularly north of the Antarctic Polar Front, sample timing varied greatly, underlining the caution needed in interpreting these samples. The original objectives for using KRILLBASE did not require winter samples but some winter data are available from several key surveys e.g http://www.bco-dmo.org/ and could be included in subsequent updates of KRILLBASE.

Most hauls in KRILLBASE were made between the surface and 100-200 m depth, but vertical coverage varied greatly between the component surveys, as indicated by the chequered colours of Fig 3b. Some screening is necessary to remove stations where an unrepresentative portion of the depth distribution was covered. Fig. 5 summarises the vertical distribution of krill and salps where stratified series of net hauls were undertaken (269 krill stations and 563 salp stations). This shows the highest densities of krill in the top 200 m, with declining densities below this. KRILLBASE is suitable for exploring the horizontal distribution of krill in the important epipelagic zone, but is unsuitable to map horizontal distribution below 200m. These deeper and near- seabed zones are being increasingly recognised as important habitats for krill (Gutt and Siegel, 1994; Clarke and Tyler, 2008; Schmidt et al., 2011; Cleary et al., 2016).

Salps have a deeper distribution than krill (Fig. 3) as a result of greater diel and seasonal vertical migrations (Foxton, 1966; Tsuda and Nemoto, 2001; Loeb and Santora

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2012). Care is therefore needed to avoid negative bias due to shallow net sampling. A standardisation method similar to that applied to krill may reduce these inconsistencies and provide a better picture of the spatial distribution of salps.

2.6 Inter-annual coverage

Fig 6 divides the Southern Ocean into broad sectors to illustrate the inter-annual coverage of sampling. The coverage for salps broadly follows that for krill, with good coverage in the Atlantic sector from 1926-1938 and after 1976. In the Indian Ocean sector some data exist from the late 1930's when "Discovery" sampling became circumpolar, reasonable coverage occurred from 1981 to the mid-1990s, but few data have been collected there since. While coverage in the Pacific sector is too sporadic to document time trends, data for the other two sectors are sufficient to examine sectorial patterns of inter-annual and decadal scale variability of both krill and salps.

The *survey mean* data are included in Fig 6, and they provide important information for the period before coordinated monitoring programmes. These data can be included in regional scale analyses (e.g. time-series analyses), but since the data pertain only to the whole survey and not the component stations, care is needed when interpreting the data at finer scales than the 3° latitude by 9° longitude grids illustrated.

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2.7 Standardisation: methods

The compiled data represent a range of sampling methods with different net types, sampling depths, times of day and times of year (Fig. 3). Such differences in sampling strategy could potentially bias the outcome of analyses. For example, differences in net mouth size will lead to variable avoidance and the mesh size will affect retention. Differences in net geometry, towing speed and trajectory will further affect catches, as will light levels and swarm packing density (Hamner and Hamner, 2000; Everson and Bone, 1986; Krag et al., 2014). For example, catchability decreases as light levels increase meaning that there can be a latitudinal effect because summer days are much longer at high latitudes (Fig. 7).

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These issues were recognised by Marr (1962) and Mackintosh (1973) who adjusted the densities accordingly when producing circumpolar distribution maps.

To minimise the influence of sampling differences, our database includes both the raw numerical abundances of krill and values standardised to a single sampling method. We calculated the standardised krill abundances using the process and conversion factors described in the supplementary appendix of Atkinson et al. (2008). The standardised abundance (*STANDARDISED_KRILL_UNDER_1M2*) is an estimate of the krill abundance that would have been observed if the haul had conformed with a sampling method consisting of a night-time haul on 1st January, fishing to a depth of 200 m with a mouth area of 8 m^2. This strategy achieves near-maximum krill catch that is possible with scientific nets.

Standardisation was implemented by multiplying the raw abundances (*NUMBER_OF_KRILL_UNDER_1M2, N*) by conditional conversion factors as follows:

$$N' = N \frac{0.11B}{1+105B} .2.255X. \frac{2.5208}{K_{pred}}$$

where *N'* is the standardised krill abundance, *B* is the bottom sampling depth, *X* is a scalar to adjust the day-to-night conversion factor (2.255) and K_{pred} is the expected krill abundance based on a general linear model in which mouth area and time of year are the independent variables (see Table 4 and Atkinson et al. 2008 for further details). *X*=1 when the net was hauled in daylight and *X*=1/2.255 when it was hauled at night. We also calculated standardised krill densities for nets where there was insufficient information to determine whether hauling occurred in daylight or at night. In these cases the value of *X* is the probability that the net was hauled in daylight (i.e. day length in hours/24).

The revision of KRILLBASE included reassessment of the DAY_NIGHT field (indicating whether the net was hauled in the daylight or at night; see Table 5). Where valid sampling time information was available (consisting of a GMT NET_TIME or a local NET_TIME and sufficient information to adjust to GMT), we used the *Twilight* Excel workbook available from http://www.ecy.wa.gov/programs/eap/models.html to determine whether the haul was conducted in daylight (defined by a solar elevation >–0.833°). Where

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no valid sampling time information was available, but there was an indication of day or night in the original data, we used this information. Where it was not possible to make this assessment because of insufficient information, we used the *Twilight* Excel workbook to calculate day length for the sampling date and location, which was then used to adjust the standardised krill density as described above. As this type of standardised krill abundance (indicated by a value of 3 in the DAY_ NIGHT_METHOD field) uses a different time of day adjustment from other standardised krill abundances it is good practice to assess its influence on results.

2.8 Standardisation: Caveats on the use of standardised krill densities

KRILLBASE includes standardised krill abundance information for every haul, stratified pooled haul and survey mean except those with TOP_SAMPLING_DEPTH_M deeper than 50m (because hauls which exclude the surface layers are not comparable with those that include these layers). These standardised densities will be most reliable when the information underlying the standardisation is accurate and within the range of values used to derive the conversion factors. The database provides information on the accuracy of date information (DATE_ACCURACY) and the type of time information (DAY_ NIGHT_METHOD) available in each record. The effects of averaging dates and times for *survey mean* data should also be considered.

Although the ideal method for depth standardisation is to make all hauls equivalent to a haul sampling from 0 m to 200 m depth, the standardisation described in Atkinson et al. (2008) and used here, is a partial solution which standardises bottom sampling depth to 200 m when the actual value is less than 200 m. It does not exclude krill caught deeper than 200 m, where krill densities are generally lower (Schmidt et al., 2011), nor does it adjust for nets that did not sample to the surface (TOP_SAMPLING_DEPTH greater than 0m). Users are advised to screen the data to ensure that top sampling depths are consistent with their requirements, noting that there are 691 *hauls* in the current version of KRILLBASE have top sampling depths deeper than 5m and Atkinson et al (2008) excluded such hauls before calculating the conversion factors.

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Date information affects the standardisation through the adjustments for time of year and time of day. Atkinson et al. (2008) derived the conversion factors from a dataset where the latest sampling date was 26th April. Recent KRILLBASE updates include hauls taken as late as 30th August, but we have not provided standardised krill densities for sampling dates after 30th April because the standardisation is extremely sensitive to dates after this point (e.g. the time-of-year adjustment for 30th August increases krill density by a factor of 3834, compared to a factor of 10 for 26th April, and a factor of 1.16 for 31st January). This strong effect of time of year of sampling on abundance likely reflects both mortality and seasonal vertical migration of krill out of the surface layer late in the season (Cleary et al. 2016)

Inaccuracies in the date will also affect the time-of-year adjustment applied in standardisation. In the single record where the date is given only to the year, the assigned date was 1st January, meaning that there is no time-of-year adjustment and standardised density is conservative. When the date is given for month as well as year, the assigned full date is the middle of the month, meaning that true dates further away from 1st January will be treated more conservatively as a consequence and true dates closer to 1st January will be treated less conservatively. The effect of any date inaccuracies increases with time from 1st January. The *DATA_CAVEATS* field in the database clearly indicates for each row which, if any, of the above caveats applies.

3. RESULTS AND DISCUSSION

3.1 Effects of heterogeneous data sources and standardisation: Spatial effects

Fig 8 compares the circumpolar distribution of krill and salps, allowing a comparison between the standardised and un-standardised krill values. While hauls with zero krill remained as such, median standardised krill abundance of positive hauls was 2.2 times greater than that of un-standardised values. The overall circumpolar pattern of relative abundance is similar whether based on raw or standardised abundances but the detail in some areas does differ. This is likely due to longer summer days at higher latitudes

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(requiring upwards adjustment of most catches to night values) or the localised use of poor sampling combinations (e.g. smaller nets and/or early or late season sampling).

The patchy distributions of krill and salps and spatial differences in sampling density influence the spatial patterns shown in the maps. A few red cells suggest extremely high krill or salp abundance, but some of these cells only encompass a few stations. Conversely, cells suggesting absence frequently have too few stations for a reliable picture. Users need to allow for variable sampling coverage, and while our standardisation attempts to reduce net sampling inconsistencies, it does not adjust for variable precision.

3.2 Effects of heterogeneous data sources and standardisation: Temporal effects

The South Georgia area exemplifies the krill-based ecosystem and this has been sampled for many years (Murphy et al. 2007). We have therefore selected a subset of KRILLBASE in this area to show how sampling method can vary from year to year and how this could affect time trends (Fig. 9). This area has been sampled with a wide variety of methods since the 1920s, and the mean krill abundance varies greatly from year to year due to recruitment variability (Fig. 9a; see also Murphy et al., 2007; Fielding et al., 2014). While the standardised annual mean krill abundances are typically greater than the un-standardised values, the offset varies substantially. This is for a number of reasons, including variable mouth areas and sampling depths of the net (Fig 9b) and variable time of year and time of day of sampling (Fig 9c). For example, net mouth area is generally larger (albeit more variable) in the modern post 1970s era, concomitant with an increase in bottom sampling depth of the nets. Likewise, during the modern era, the proportions of hauls in mid-summer and at night have increased.

The above factors are included in the standardisation process, but other issues may be important when deciding how to screen data and interpret time trends from a heterogeneous data set such as KRILLBASE. One factor is the density of sampling coverage within any given year. We have not plotted years when there are very few stations sampled (<10 stations) because a patchy swarming species like krill is likely to be missed altogether by such limited sampling. However, the number of stations sampled varies greatly from year to year (Fig. 6) so we have scaled the size of the symbols according to numbers of stations to illustrate the variable confidence in the annual means.

A second important feature may be the geographical coverage of sampling (Fig 9d). Even within a defined area such as South Georgia, the emphasis of sampling campaigns may change. For example 1926- and 1927 were local krill surveys aimed for management of the whaling industry then based at South Georgia, but throughout the 1930s "Discovery" sampling became increasingly circumpolar. The 1980s were characterised by large-scale surveys, for instance coordinated by the international Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS) programme, while monitoring in the 1990s and 2000s was more shelf-orientated.

4. CONCLUSONS AND RECOMMENDATIONS

4.1 Uses and limitations of KRILLBASE

The first version of KRILLBASE was used by Atkinson et al. (2004) to quantify the circumpolar distribution of krill and salps, examine regional trends in their densities and determine inter-annual relationships between krill density and winter sea ice cover. Inter-annual changes in mean krill abundance were subsequently related to temperature by Whitehouse et al. (2008), to whale dynamics by Braithwaite et al. (2015) and to the dynamics of other so-called wasp-waist species by Atkinson et al. (2014). The fact that krill and salp abundances vary so much between years is an advantage for this inter-annual scale of analysis, because the signal is stronger than the noise.

The spatial component of KRILLBASE has been used more widely. Circumpolar distributions have been used as a context and validation for various models and analyses including biogeochemical carbon cycling (Moriarty, 2009), krill and climate change (Flores et al., 2012; Hill et al., 2013; Piñones and Federov, 2016), population connectivity (Thorpe et al., 2007; Siegel and Watkins, 2016), predator foraging (Pangerc, 2010) and vertical and

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horizontal krill habitat analyses (Atkinson et al., 2008; Schmidt et al. 2011). These studies have tended to focus on large scales, but smaller scale analyses of well-sampled areas (as shown in Fig. 10) are amenable to KRILLBASE, for example to interpret predator foraging areas. The caveat here is that these maps are not synoptic, but instead are more akin to probability maps of where krill or salps occur and a context for more synoptic snapshots from surveys (Siegel et al., 2004; Kawaguchi et al. 2004).

In parallel to expansion of the abundance component of KRILLBASE, we are generating a large database on krill length frequency, sex, and maturity stage from scientific and fisheries data, a work still in progress. Combining the length frequency and abundance components provides insights into biomass and production at large scales, allowing a degree of scaling-up of acoustics-derived biomass surveys (Atkinson et al., 2009). The sex/length frequency component has since been used, for example, to relate circumpolar trends in body length to feeding conditions (Schmidt et al., 2014), and to examine sex-related changes in seasonal growth and shrinkage (Tarling et al., 2016).

In comparison to krill, fewer studies have used the salp component of KRILLBASE. Lee et al., (2010) examined inter-annual variability in krill and salps simultaneously, emphasising the opposite nature of the trends observed in the two taxa. Given the fact that about half of the current KRILLBASE net hauls have both krill and salps recorded, a simultaneous evaluation of the two taxa would be valuable. In any of these analyses, however, we emphasise that great care is needed when interpreting time trends, in order to prevent aliasing of real patterns with differences in sampling methods. This applies equally to salps and to krill, for example, the seasonal and diel vertical migrations of salps mean they are prone to under-sampling by shallow nets (Fig 4).

An additional caveat concerns the issues of net sampling efficiency for mobile species such as krill. RMT8 catches during nighttime were set as our benchmark for standardisation because they were the most efficient means of capturing krill, but even these catches were likely to have underestimated absolute abundance. This is due to both net avoidance and escapement of the smallest juveniles through the meshes. Nevertheless, the

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overall circumpolar biomass of krill based on averaged KRILLBASE data is 379 million tonnes, so it is unlikely that this sampling method is yielding order of magnitude underestimates (Atkinson et al., 2009). KRILLBASE may provide insights on the relative distribution and temporal variation in krill density, but modern acoustic methods calibrated with nets are the accepted method for determining krill biomass (Fielding et al., 2014). Integrating the assessments from these two fundamentally different types of sampling represents the most robust practise to achieve large-scale and long-term estimates of krill biomass.

4.2 Using KRILLBASE

The comprehensive data descriptions in this paper allow potential users to understand the breadth of the database and the main caveats that need to be considered to ensure that interpretations are realistic and valid. Two of the components of KRILLBASE, the Palmer Antarctica Long-Term Ecological Research (Palmer LTER) and Antarctic Marine Living Resources (AMLR) projects are live, ongoing monitoring programmes. Please consult appropriate websites http://pal.lternet.edu/ and https://swfsc.noaa.gov/aerd/, respectively, for the most up to date versions of these two time series. For the Palmer LTER time series, we have presented only the standardised versions of the krill data, and not the raw krill or salp data. These are instead available direct from http://pal.lternet.edu/. For the KRILLBASE dataset described in this paper, please use the doi http://doi.org/brg8 to obtain data and consult the relevant data sources (Table 1) regarding queries. This data paper in addition to the data doi should be cited as the metadata and the source of the data, to allow traceability in the use of this database. This will hopefully provide leverage for obtaining future funding to continue rescuing and update valuable historical datasets from the Southern Ocean. As a final word we urge users to take a few minutes to consult the metadata, in particular Table 2, since almost every use of KRILLBASE will require first screening off some of the records.

Author contributions

AA, SH, EP and VS are the instigators of KRILLBASE, this project to produce the data paper, and are listed in alphabetical order. The remaining authors are contributors to the database and the current paper, also listed in alphabetical order. Original concept and initial database: AA, VS, EP. Additional datasets: VL, CR, DS, LQ, RR, PW, SK, GH, SC, JN, RA, BK, Data checking, manipulation, spatial analysis, standardisation and editing, AA, SH, RS, HP, LG, PF, MJ, KS, VS, EP. Final maps: LG. Final data-basing HP, Drafting manuscript SH, AA. Input to manuscript: all.

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Table 1. Sources of data for KRILLBASE, according to nation and major sampling program. Sources are listed in descending order of number of hauls provided. More information on the actual data sources (including the references used where data were transcribed from publications) is provided in the SOURCE field of the database. Coverage is not necessarily evenly spread within the longitudinal boundaries, which are presented in nearest integer degrees. For Haul type H: normal haul, SH: Stratified haul that has been pooled into an equivalent "stratified pooled haul", SM: survey mean haul, where density estimates are only available as a mean from multiple stations comprising a survey (see section 2.3).

National data source	Number of net hauls			Haul type	Sampling years	Range of longitude covered	Months covered	Net types	Median bottom sampling depth (m)	Source of data
	Total	krill data	salp data							
US AMLR program	3864	3164	1440	H,SM	1990-2011	63°W – 44°W	Jan-Mar	Isaacs-Kidd Midwater Trawl	170	Sent by Loeb, Hewitt, Reiss, data via US AMLR Reports
Discovery (UK) data	3156	1637	2723	H, SH	1926-1939, 1951	Circumpolar	Jan-March, Nov-Dec	N70V, N100b, N200B		Archived data from original net sampling logsheets checked against a euphausiid Discovery era database by Atkinson
German GAMLR data	2352	2352	1694	H,SH, SM	1976, 1978 1980-1986, 1988-1990, 1994, 1995, 1997, 2001, 2004	122°W to 14°E	Jan-June, Oct-Dec	Mainly RMT8, also 0.6 m Bongos and Isaacs-Kidd Midwater Trawl	185	Sent by Siegel, plus a small amount of data transcribed from publications
Soviet data	1579	1557	1577	H, SH	1983-1990, 1992	Circumpolar	Jan-April, Dec	Bongo, Isaacs-Kidd trawl, Melnikov's net, Modified Juday net	100	Sent by Pakhomov
US Palmer LTER Program	1247	1247	0	H	1993-2016	78°W to 64°W	Jan-Feb	2x2m fixed frame with 700 µm mesh.	120	From Palmer LTER data holdings http://pal.lternet.edu/ accessed July 2016
British Antarctic Survey data	923	923	810	H[1]	1982,1985,1996-1999 2001-2005, 2007-2009	66°W to 26°W	Jan-April, Oct-Dec	RMT1, RMT 8, 0.62 cm Bongo, LHPR with 38 cm nosecone	205	Sent by Ward, also data accessed from BAS Polar Data Centre and including SIBEX data holdings

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Other US National Programs	593	550	219	H SM	1981, 1983, 1984, 1986, 1994	62°W to 36°W	Jan-March Nov-Dec	0.6 m Bongo, Plummet net, Tucker trawl	200	Data mainly transcribed from various publications, with AMERIEZ cruise data sent by Daly
Australian data	508	508	316	H SH	1981,1983-1987, 1991-1993, 1996, 1999, 2001, 2006	30°E to 150°E	Jan-March Aug, Oct-Dec	Square 0.5 m net, 0.5 m and 1 m Bongos, ORI net, RMT 8	200	Data sent by Hosie and Kawaguchi, Some data transcribed from Anare Research Notes and from publications.
South African data	413	343	413	H	1980, 1981, 1983, 1994-1998, 2001, 2003	86°W to 179°E	Jan-May Oct, Dec	Bongo, Mocness, RMT8	300	Sent by Pakhomov
Japanese data	163	81	163	H SH	1984, 1988-1996	63°W to 158°E	Jan-March Dec	Norpac net, Square 0.5 m net, ORI net, Large Isaacs-Kidd Trawl, Kaiyo Maru trawl	150	JARE data from Chiba, SIBEX data from Nishikawa, also transcribed from publications
Polish data	159	159	159	H SH	1981, 1984	66°W to 43°W	Jan-March Dec	0.5 and 0.6 m Bongos	175	Transcribed from publications
CCAMLR data (internationa l)	117	117	117	H	2000	69°W to 23°W	Jan-Feb	RMT8	200	International data from CCAMLR Synoptic survey data obtained via CCAMLR
Spanish data	99	99	99	H	1996	66°W to 59°W	Dec-Jan	Modified WP2 net	200	FRUELA Cruise data sent by Anadon
Norwegian data	21	21	0	H	2008	37°W to 15°E	Jan-March	Macroplankton trawl	750	AKES data sent by Krafft

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Table 2. Detailed description of the columns in KRILLBASE

COLUMN HEADING	DESCRIPTION
STATION	Unique identifier for each record (row). The first three letters identify the source of the data (starting letters of the name of the individual, national program, or country which provided the data). The next 4 numbers identify the season of sampling (e.g. 1926 spans Oct 1925 to Sept 1926). The next 3 letters provide additional sample information, often referring either to the net type used or the name of the sampling survey. Additional characters at the end list the station numbers etc. These are, as far as possible, the same as used in the original sources, with British Antarctic Survey and Palmer LTER cruise station numbers being replaced by cruise-unique "event numbers". Records are typically resolved to station but see RECORD_TYPE for more information on resolution.
RECORD_TYPE	This is an important field that will need screening before any use of the database. Records labelled "*haul*" are the usual situation meaning that the record refers to a single net haul. "*Survey mean*" represents a record where the krill or salp density represents an arithmetic mean of a group of stations whose central position and sampling point are thus provided in the database with less accuracy then the other records. *Survey means* are given only when it was not possible to obtain station-specific data. "*Stratified haul"* represents a haul, usually within the top 200 m, which forms part of a stratified series (e.g. 0-50m, 50-100m, 100-200m). "*Stratified pooled haul*" represents a record that integrates these respective *stratified hauls*, whereby the krill or salp densities from the component nets have been summed (in this example into an equivalent 0-200m haul). Thus to avoid double counting any use of the data should sift out either *stratified hauls* or *stratified pooled hauls*.
NUMBER_OF_STATIONS	For *Survey mean* data (see RECORD_TYPE) this refers to the number of stations that have been averaged to provide the krill or salp density values.
NUMBER_OF_NETS	This refers to the number of sequentially fished nets included in the estimate (e.g. the value would be 3 for a *stratified pooled haul* consisting of a stratified series sampling 0-50m, 50-100m and 100-200m, and it would be 32 for a *survey mean* which averages 32 hauls). A LHPR haul counts as one net despite multiple gauzes being cut. This value is also 1 for a paired Bongo haul (2 nets fished concurrently).
LATITUDE	South is negative. Units are decimal degrees
LONGITUDE	West is negative. Units are decimal degrees
SEASON	This is the austral "summer" season of sampling. For example the 1926 season spans all data from 1 Oct 1925 through to 30 Sept 1926.
DAYS_FROM_1ST_OCT	This is the day of sampling during the austral season. Therefore 1 Oct is DAYS_FROM_1ST_OCT =1. The value for dates after 28 February vary depending on whether they occur during a leap year.
DATE	The date of sampling, based on the dates provided to us (see "DATE ACCURACY" column).

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DATE_ACCURACY	"*D*" means the exact day of sampling is known. "*M*" means that we have been provided only with the month in which samples were taken, so the record's DATE value is entered as the middle of the month. "*Y*" means only the year of sampling is known, so the date is recorded as 1st January (this affects one record only)
NET_TIME	This is the time of the haul: Either the start, midpoint or end times of hauls were used, as provided to us. Absent data means no net time information was available, or it was not entered into the database because the station was already classified as either day or night (Discovery data net times are recorded in their published "Station Lists" but not entered in KRILLBASE). Net times for *Stratified pooled hauls* represent that of the shallowest net of the series.
GMT_OR_LOCAL	Information on whether the time in the previous column is GMT (labelled "*GMT*"). Data which were provided as local times with a stated offset to GMT have been converted to GMT. Data which were provided as local times with no offset have not been converted and are labelled "*local*". Absent data means there was no net time information
DAY_NIGHT	This field indicates whether the net was hauled in daylight (labelled "*day*") or night time (labelled "night") and was used in the calculation of standardised krill densities. See DAY_NIGHT_METHOD for information on the source of these data.
DAY_NIGHT_METHOD	Method used to determine whether the net was hauled in daylight or at night time, which depends on the time information available: 1 - DAY_NIGHT is based on calculated solar elevation determined using NET_TIME, 2 - DAY_NIGHT is as recorded in the ship's log , 3 - no DAY_NIGHT information was available, and standardised krill densities were adjusted for the probability that the haul was conducted in daylight.
NET_TYPE	This is a brief name for the sampling net used. See Table 3 for more detailed descriptions of each net
MOUTH_AREA_OF_NET_M2	This is a nominal mouth area of the net calculated from the net dimensions. It is typically the simple linear area of the mouth, but for RMT8 and 1 it is assigned as value of 8 and 1 respectively. Bongo nets are assigned as an area of both openings combined and LHPR is given as maximum net diameter – both of these are used to crudely compensate for the lack of towing bridles and wire/release gear directly in front of the net, as compared to the standard ring nets often of similar net dimensions.
TOP_SAMPLING_DEPTH_M	Shallowest sampling depth (m)
BOTTOM_SAMPLING_DEPTH_M	Deepest sampling depth (m). Note that whilst most hauls were oblique, double oblique or vertical, a small minority were nearly horizontal, as shown by similar top and bottom depths. These would need to be screened out of nearly all analyses as they provide little information on numerical densities (no. m^{-2}).
VOLUME_FILTERED_M3	Volume of water (m^3) filtered by the net. This value is provided only when the value is provided with the density data.
N_OR_S_POLAR_FRONT	Position (North or South) relative to the Antarctic Polar Front as published by Orsi *et al*. (1995).
WATER_DEPTH_MEAN_WITHIN_10KM	Mean water depth within a 10 km radius. In South Polar Stereographic projection, the stations were superimposed on the Gebco 2014 Grid bathymetry (http://www.gebco.net) and all pixels within a 10 km radius of the station were extracted. After removing data above sea level, the remaining pixel value for water depth was averaged.
WATER_DEPTH_RANGE_WITHIN_10KM	Depth range within a 10 km radius. In the procedure above, having removed pixels above sea level, the range in water depth was calculated as the difference between the shallowest and the deepest pixel. This will provide an index of even-ness of bathymetry (e.g. proximity to seamounts, canyons, continental slope).
CLIMATOLOGICAL_TEMPERATURE	Long term average February sea surface temperature for the sampling locale. This is not the actual sea temperature at the time of sampling but a climatological mean sea-surface value for February, averaged over the years 1979 to 2014, based on data downloaded July 2016 from http://apps.ecmwf.int/datasets/data/interim-full-moda/levtype=sfc/ . Data were provided on a 0.75° by 0.75° grid and we extracted mean values using the same 10 km buffer method used for the bathymetry. These values may indicate a relative thermal regime as a basis for station characterisation
SD_OF_SURVEY_MEAN_KRILL	The standard deviation of the krill densities extracted from the publications where the *survey mean* value of krill density is

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	provided (see column RECORD_TYPE)
NUMBER_OF_KRILL_UNDER_1M2	Numerical density, N, of numbers of postlarval krill under 1 m^2 (or, where based on a length frequency distribution as in the Discovery Investigations, it is krill >19mm in length). Where the numbers of krill n were provided per m^3 filtered, the density of krill was calculated based on top sampling depth t and bottom sampling depth b in metres as $N = n *(b-t)$
STANDARDISED_KRILL_UNDER_1M2	Standardised numerical density of postlarval krill. To reduce possible artefacts arising from differences in sampling method in KRILLBASE, this column presents krill density according to a single sampling method. This method is a 0-200 m night-time RMT8 haul on 1 January, following the standardisation method in Atkinson et al. (2008). See main text for more details.
CAVEATS	Any issues which might require particular caution when using the data (e.g. potential inaccuracies in estimated date or day/night or sampling depths outside of the normal range) are listed here. Default is blank.
NUMBER_OF_SALPS_UNDER_1M2	The numerical density of salps, calculated as for krill. All individuals are counted, irrespective of which salp species or whether they are the solitaries of components of aggregate chains. Standardised salp densities have not been calculated.
SOURCE	Information about the source of the data, including a citable reference where available.

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Table 3. Nets used in KRILLBASE. The nets are listed in alphabetical order.

Name given in KRILLBASE	Nominal Mouth area	Number of hauls	Description of net
0.5 m Bongo	0.39	23	0.5 m diameter Bongo from ABDEX cruises (nominal mouth area is that of both nets)
0.6 m Bongo	0.57	1040	0.6 m diameter Bongo net (nominal mouth area is of both nets)
0.62 m Bongo	0.6	452	BAS Bongo: 62 cm diameter (nominal mouth area is of both nets), 0.1 and 0.2 mm mesh
0.71 m Bongo	0.79	261	0.71 cm Bongo net (Nominal mouth area is of both nets)
1 m ringnet	0.79	111	Modern 1m diameter ring net
2 m fixed frame net	4	1247	2m square sided, fixed frame net, 700 micron main mesh, 500 micron cod end (Palmer LTER grid)
IKS net	1	48	IKS 1mm mesh net, 1 m^2, 1 mm mesh
Isaac Kidd	3.08	4217	Isaac Kidd midwater trawl, 4.5 mm mesh
Juday net	0.11	15	0.37 m diameter Juday net, 0.15 mm mesh
Kaiyu Maru trawl	8	50	Kaiyo Maru Mid-water Trawl (KYMT: 9 and 7 m2 mouth area), 3.4 mm mesh (Nishikawa et al. 1995)
Large Isaac Kidd	6	300	Large Isaac-Kidd trawl including 10' one used for Japanese SIBEX and the 6m^2 (4.5 mm mesh) one for Russian/Ukrainian sampling
Large Melnikov net	0.5	17	0.5m^2 Melnikov trawl, 0.63 mm mesh
LHPR	0.45	28	Longhurst Hardy Plankton Recorder with 38 cm diameter nosecone used by BAS (0.2 mm mesh)
MOCNESS	1	6	MOCNESS net
Modified Juday net	0.5	694	Modified Juday net, 0.5m^2mouth area, 0.178 mm mesh
N100B	0.79	1835	Discovery's N100B net (1m diam. ring net)
N200B	3.14	18	N200B net used briefly in 1926 (2 m diameter ring net: soon abandoned as hard to handle)
N70V net	0.39	1396	Discovery's closing N70V net, also Polish N70V net
Norpac net	0.16	44	0.45m diameter NORPAC net of JARE expeditions (330 micron net with flowmeter)
ORI net	2.01	35	Japanese ORI net, 1.6 m diameter mouth, 2mm mesh
Plummet net	1	26	1 m^2 plummet net used on AMERIEZ (US) cruises in 1980s
RMT1	1	94	RMT 1 net, 0.33 mm mesh
RMT8	8	2753	RMT 8 net, 5 mm mesh

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Macroplankton trawl	38	21	"Macroplankton trawl" of research vessel G.O. Sars (AKES data), 3 mm mesh size measured from knot to knot/ 7 mm stretched mesh. The trawl has the same mesh in all panels from mouth to cod end. Towing speed was 2.5-3 knots. Data and trawl gear is described in Krafft et al. (2010).
Small Melnikov net	0.22	178	0.22 m^2 Melnikov trawl, 0.63 mm mesh
ORI-VMPS	0.25	85	Square net, 0.5 m across from Australian ANARE and Japanese (Nishikawa) sampling
Tucker trawl	9	98	Tucker trawl, 4mm main mesh to a 1mm cod end, towed at 2 knots. Described in Lancraft et al. (1989)
WP2	0.26	99	WP2 net from Spanish FRUELA cruises

Table 4 Summary of standardisation process.

Standardise for	**Standard haul characteristics**	**Conversion factor**	**Definitions**	**Conversion factor applied when:**
Sampling depth	0 to 200m	0.11B/(1 + 0.105B)	B= BOTTOM_SAMPLING_DEPTH_M	BOTTOM_SAMPLING_DEPTH_M <200
Time of day	Night-time	2.255		DAY _NIGHT = 0 (day time)
		2.255X	X = NEW_DAYLENGTH (specified as a proportion)	DAY _NIGHT = *blank* (no information)
Net mouth area and time of year of sampling	Net mouth area = 8m^2 Time of year = January 1st	$L_{pred}^{opt} / K_{pred}$	$K_{pred}=P * K_{non\text{-}zero}$ P=exp(L)/[1+exp(L)] $Log_{10}(K_{non\text{-}zero})= 0.474 – 0.1912Log_{10}M + 0.00416J – 0.00002898J^2$ $L= -0.6478+2.335*Log_{10}M+0.0204J-0.0001086J^2$ M = MOUTH_AREA_OF_NET_M3 J = JULIAN_DAY_FROM_OCT $L_{pred}^{opt}=P_{opt} * K_{non\text{-}zero}^{opt}$ P_{opt}=0.92 $K_{non\text{-}zero}^{opt}$=2.74	MOUTH_AREA_OF_NET_M3 <>8 or DAYS_FROM_1st _OCT <>93

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Table 5 Derivation of *Day or night* information.

Information available	**Information used to standardise time of day**
Valid *Net time* (GMT, or Local with specified offset)	Calculate solar elevation and use to determine *Day or night*
No valid *Net time* but valid day or night information from ship's log (values 0 or 1)	Use ship's log information to indicate *Day or night*
No valid *Net time* or ship's log information (e.g. when a Local time is specified but no offset is given, and the ship's log does not specify day or night or indicates twilight)	Calculate *Day-length* and use to adjust conversion factor

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FIGURE CAPTIONS

Figure 1 Distribution of sampling stations in KRILLBASE, showing generally elevated sampling effort in and around designated areas of protection and management. These stations may have krill or salp data or both; Supplementary Fig. 1 provides the distribution of just the krill sampling stations.

Figure 2 Frequency distribution of krill and salp abundances in the database. The data were filtered to remove *stratified hauls* before plotting the frequency of remaining hauls in relation to logarithmic bins. Data are presented for **a** krill raw (unstandardised) abundance, **b** krill standardised abundance and **c** salp (unstandardised) abundance.

Figure 3 Circumpolar variation in sampling method. This plot is based on all data in KRILLBASE, whether for krill or salps or both. **a** Time of year of sampling (mean day from 1 October), **b** Bottom depth of sampling. The dataset plotted includes the stratified pooled hauls and thus excludes their component stratified hauls (see section 2.3) **c** Mean mouth area of the net, based on the nominal values presented for each net type in Table 3. Antarctic Polar Front position is from Orsi et al. (1995).

Figure 4 Relative frequency of stations sampled within each month of the year.

Figure 5 Vertical distribution of krill and salps based on 793 stratified krill hauls and 2130 stratified salp hauls. Given the non-standard depth horizons between the various surveys sampling in this manner, the data were first subdivided into a nominal 7 categories of mean sampling depths, namely 0—50m, 50-100m, 100-150 m, 150-200 m, 200-300 m, 300-500 m and >500 m. Mean krill or salp densities are presented in each of these mean depth groups, plotted against mean sampling depth within each depth band.

Figure 6 Inter-annual sampling coverage. Number of stations sampled south of the Antarctic Polar Front in each austral season (October to following September). These are presented for **a** the Atlantic sector (nominally defined as 90^{o}W to 10^{o}E), **b** the Indian sector (10^{o}E to 120^{o}E) and **c** the Pacific sector (120^{o}E to 90^{o}W).

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Figure 7 Change in day-length with time of year at various latitudes, indicating the effect of date inaccuracies on time of day adjustments made during standardisation of krill abundance.

Figure 8 Circumpolar distribution maps of krill based on **a** un-standardised krill densities (no. m^{-2}), **b** standardised krill densities and **c** un-standardised salp densities, showing the stations sampled for these. All maps are South Polar Stereographic projection with grid size of 3^{o} latitude by 9^{o} longitude. Positions of krill stations are in Supplementary Fig. 1. The legend values and colour codings of cells refer to the arithmetic mean krill densities recorded within the cell.

Fig. 9 Inter-annual variability in sampling. Year-to-year variation in net sampling, and its effect on the difference between standardised and unstandardized krill density. Austral season is plotted on the x-axis of all panels with a vertical line demarcating the Discovery sampling era from the post-1975 sampling era. **a** inter-annual variation in arithmetic mean krill densities in the greater South Georgia area (30^{o}-40^{o}W, 50^{o}-60^{o}S, based on hauls from October to April with a top sampling depth < 20m and bottom sampling depth >50 m following Atkinson et al. 2008). While we have not plotted data with fewer than 10 hauls in any year, the symbols are in three sizes to illustrate the variability in sampling effort: smallest: 10-20, medium: 20-50 and largest >50 hauls per season. **b** Inter-annual variability in mean mouth area of the net and mean bottom sampling depth of the net from the hauls in panel a. **c** Inter-annual variability in Julian day of sampling (days from 1 October) and the percentage of nigh-time hauls. **d** Percentage of hauls over continental shelves of the sampling area, defined as water depth < 1000 m.

Fig. 10 Basin-scale krill (panels **a** and **b**) and salp distribution (panels **c** and **d**) within two well studied sectors of the Southern Ocean, plotted on a finer, 1^{o} latiutude by 2^{o} longitude grid to highlight habitat differences between the two taxa.

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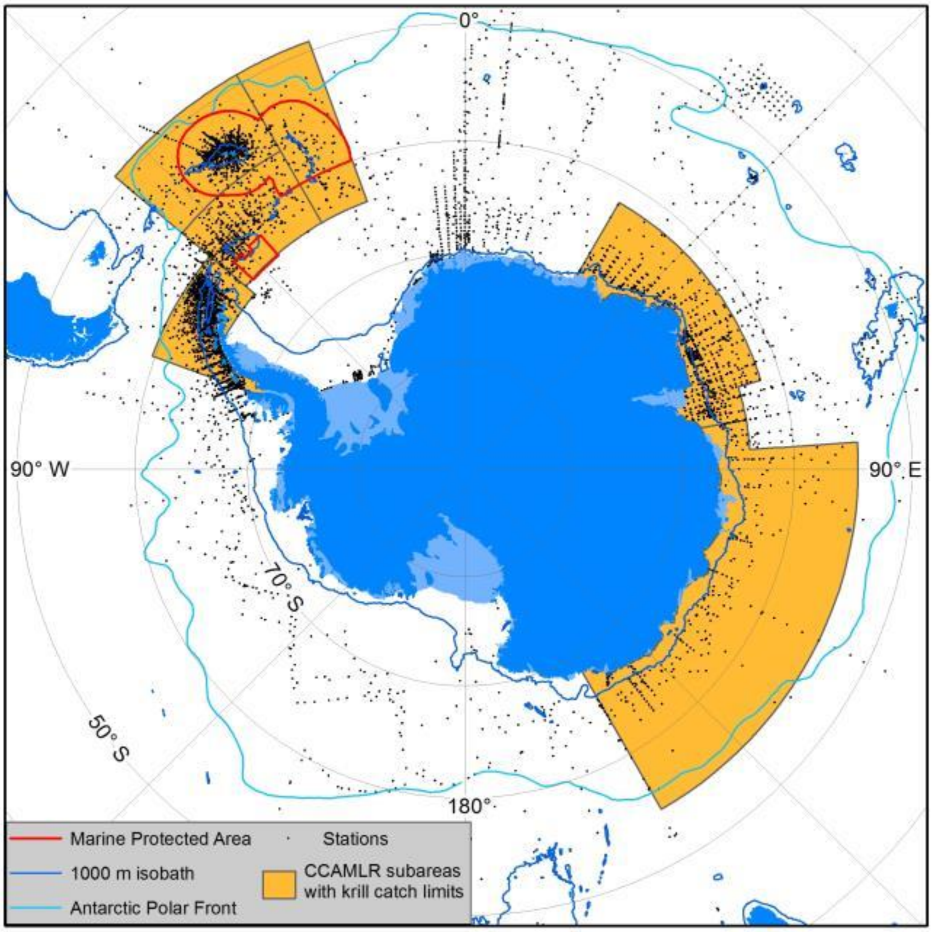

Fig. 1

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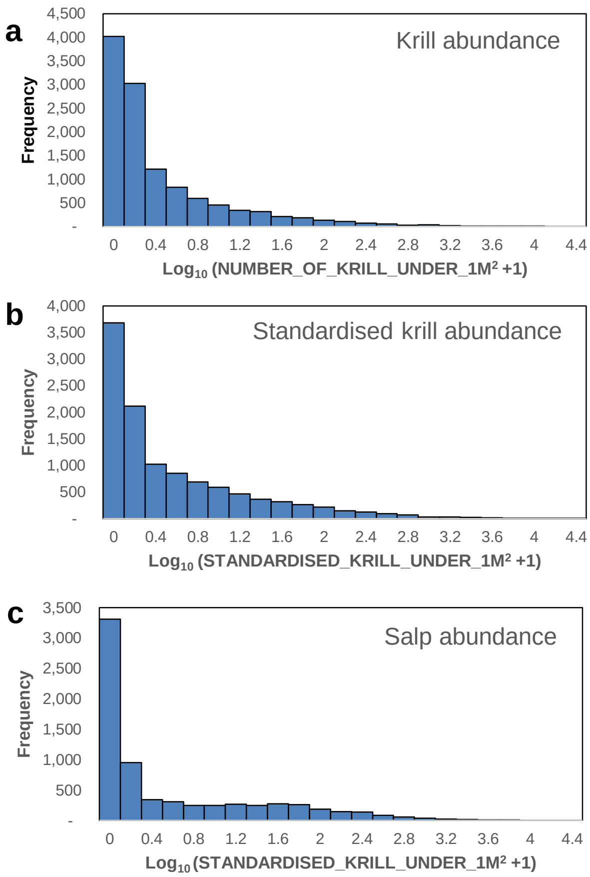

Fig. 2

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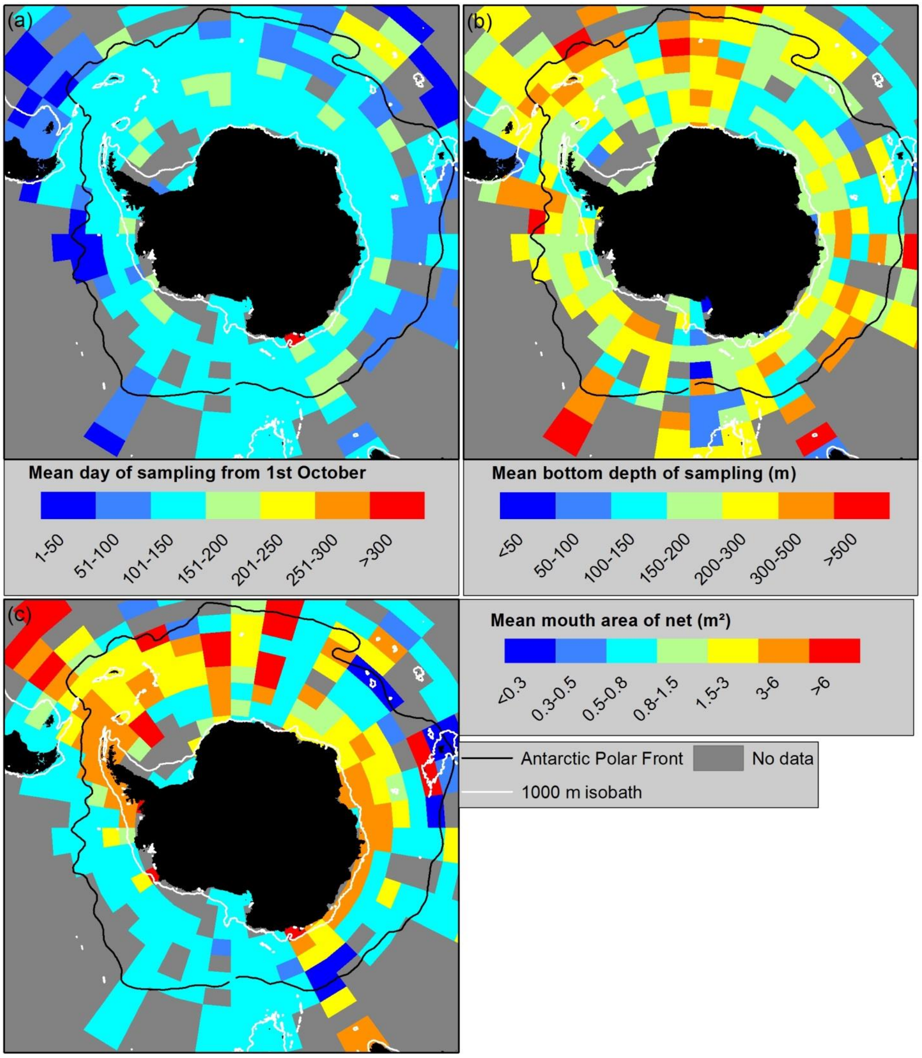

Fig. 3

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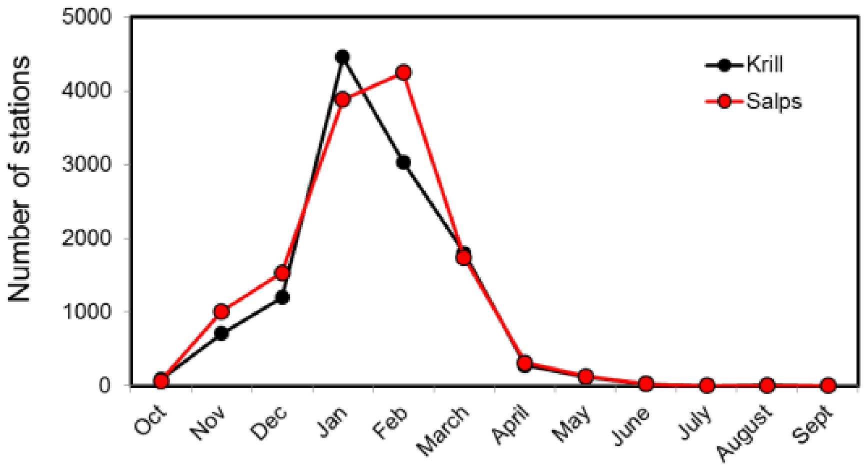

Fig. 4

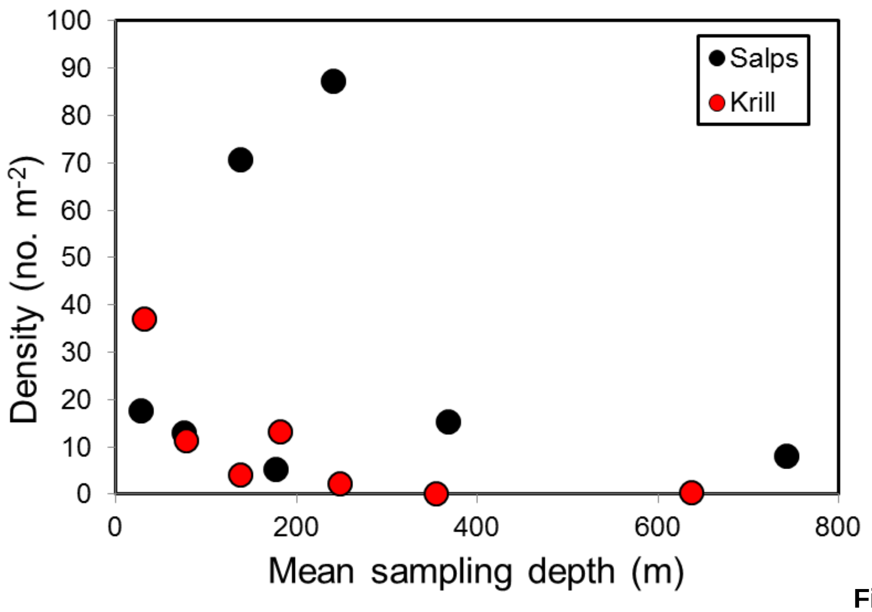

Fig. 5

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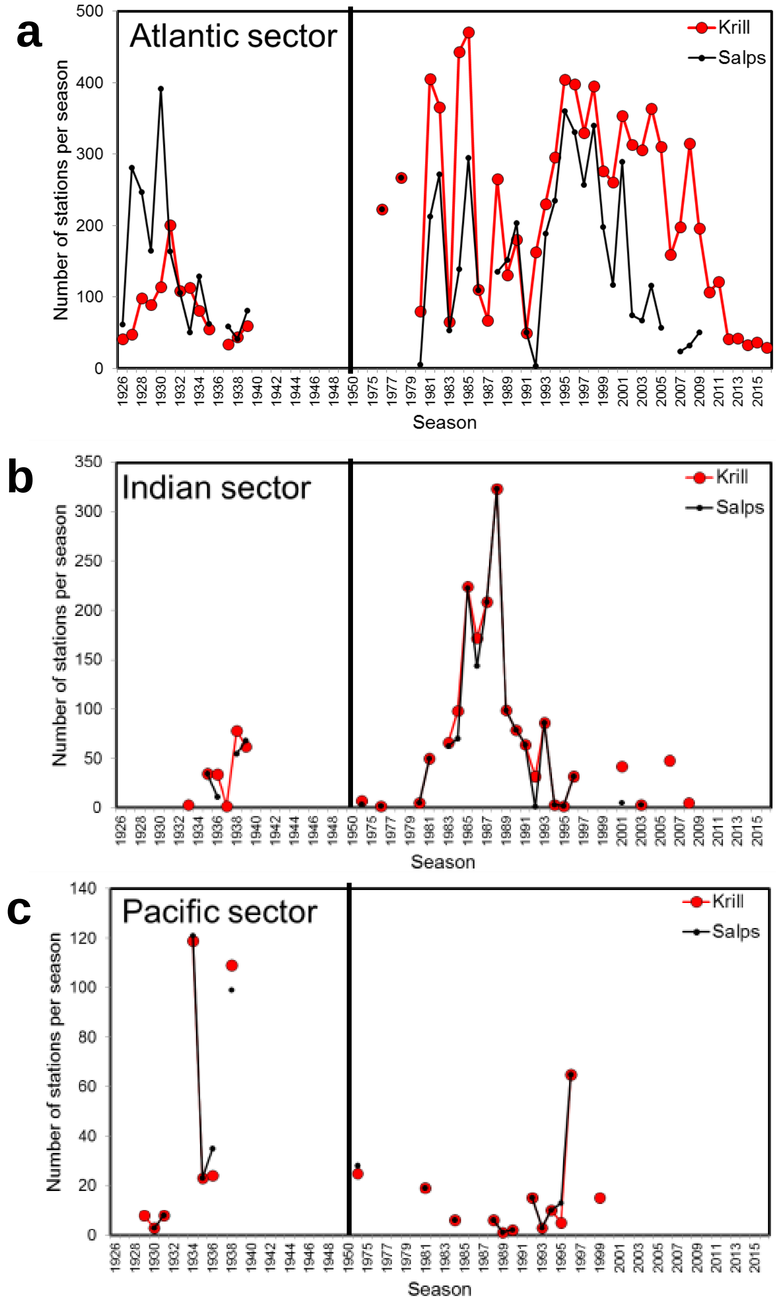

Fig. 6

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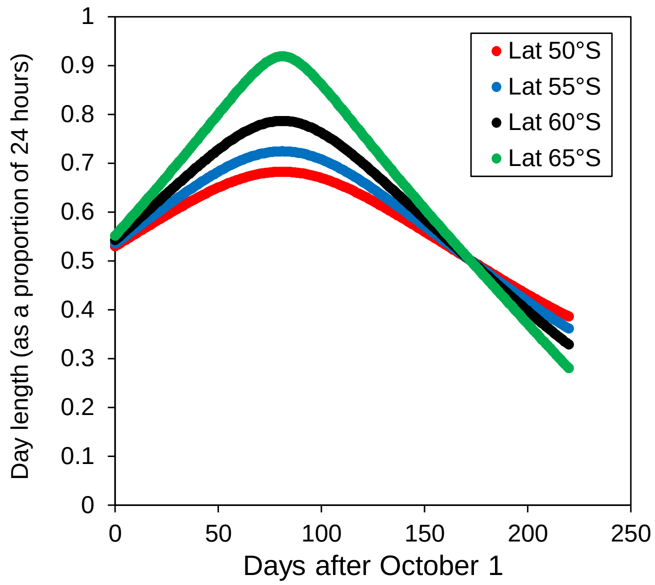

Fig. 7

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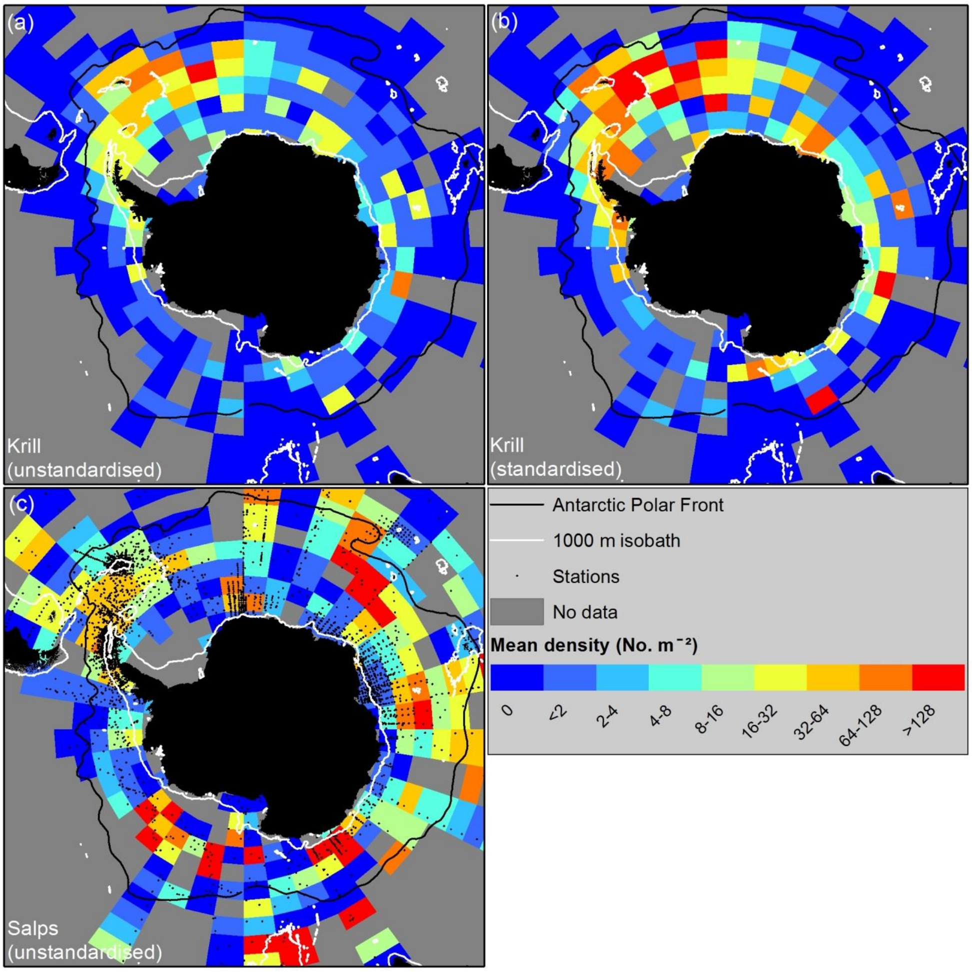

Fig 8

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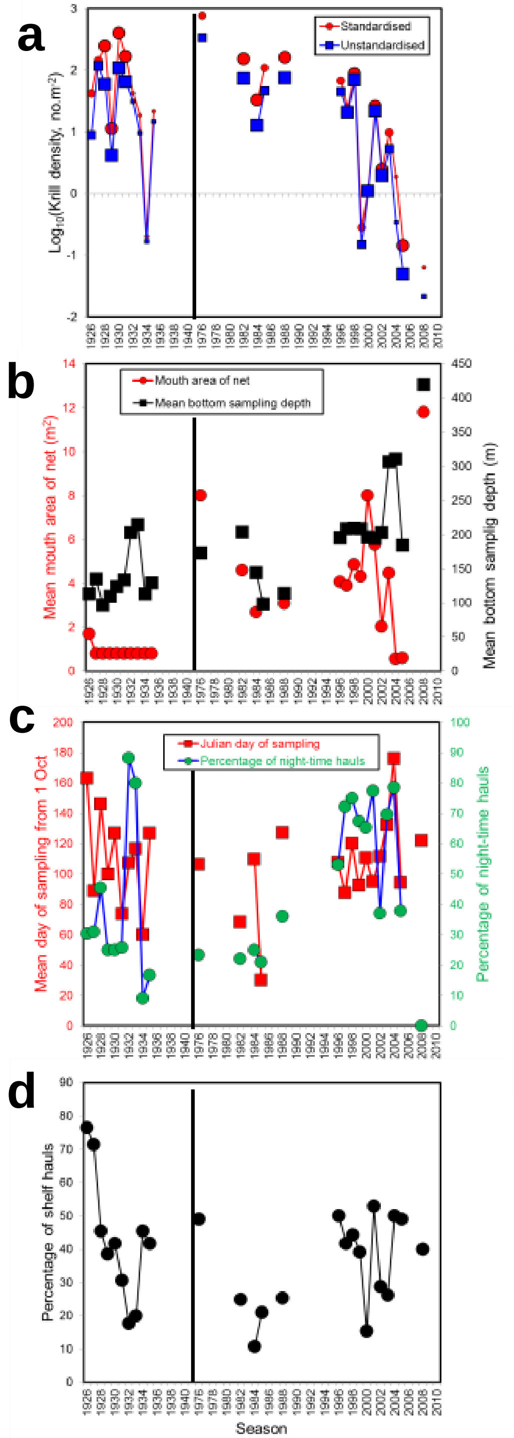

Fig. 9

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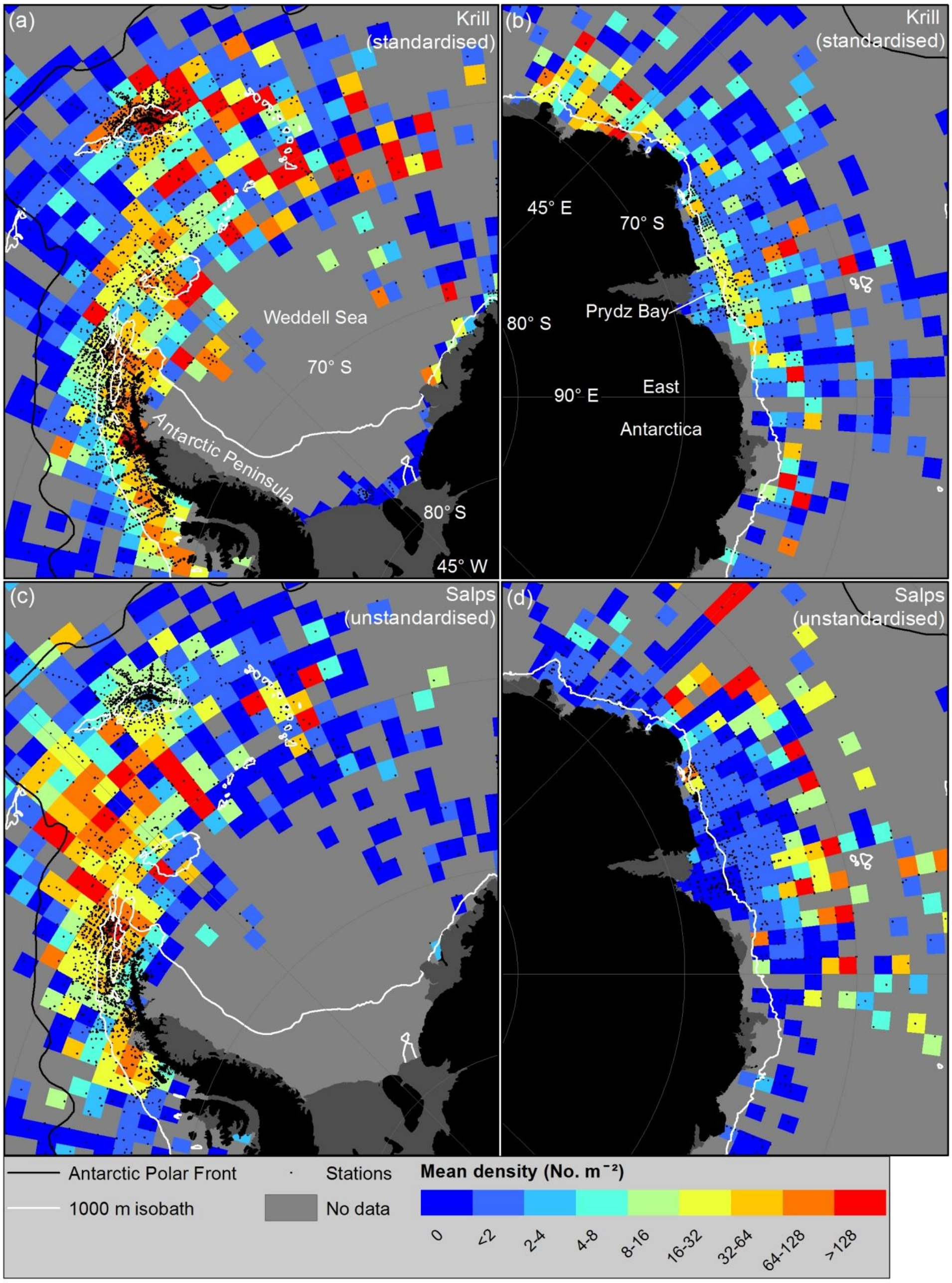

Fig. 10