





Changing circumpolar distributions and isoscapes of Antarctic krill: Indo-Pacific habitat refuges counter long-term degradation of the Atlantic sector

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Abstract

The Southern Ocean provides strong contrasts in rates and directions of change in temperature and sea ice between its sectors, but it is unknown how these affect plankton species that are distributed right around Antarctica. Here, we quantify the changing circumpolar distributions of Antarctic krill, based on the CHINARE 2013/14 circum-Antarctic expedition, plus independent analyses of compiled abundance data (KRILLBASE: 1926–2016). In the 1920s–1930s, average krill densities in the Atlantic-Bellingshausen sector were eight times those in the other sectors. More recently, however, the concentration factor has dropped to only about twofold. This reflects a rebalancing broadly commensurate with climatic forcing: krill densities declined in the Atlantic-Bellingshausen sector which has warmed and lost sea ice, densities may have increased in the Ross-Pacific sector which showed the opposite climatic trend, while densities showed no significant changes in the more stable Lazarev-Indian sectors. Such changes would impact circumpolar food webs, so to better define these we examined circumpolar trends of isotopic values in krill and other zooplankton based on the CHINARE cruise and a literature meta-analysis. Krill $\delta^{15}\text{N}$ values ranged significantly between sectors from 2.21‰ (Indian) to 3.59‰ (Ross-Pacific), about half a trophic level lower than another key euphausiid, *Thysanoessa macrura*. These isoscapes form a baseline for interpreting the reliance of predators on euphausiids, within the varying food webs around the continent. Overall, we suggest that the Indo-Pacific sector has acted as a refuge for the circumpolar krill stock while conditions for them deteriorated rapidly in the Atlantic sector.

The rapid rates of warming and sea ice loss in polar environments, coupled to the fact that the resident ectotherms are stenothermal, sensitive even to small increases in temperature, has generated much concern over how polar food webs will respond in future (Murphy et al. 2016). Various experimental

and modeling studies have been conducted, but a critical element for gauging projections is knowledge of how biota have responded to the rapid changes that have already occurred (Flores et al. 2012). The inaccessibility of polar environments, however, has led to the absence of long (> 30 yrs) time series that span the full geographical ranges of species.

Euphausia superba (hereafter “krill”) provide one exception to the general paucity of long-term, large scale plankton data at the poles. The fact that this is a key species in Southern Ocean food webs, is important in elemental cycling (Schmidt et al. 2016), supports an array of predators and is commercially exploited, have all contributed to the intensive sampling of this species for over a century (Mackintosh 1973; Atkinson

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et al. 2014; Siegel and Watkins 2016). Based on circumpolar data mainly assembled in the *Discovery era* of the 1920s and 1930s, the current paradigm is that the Atlantic sector (0–90°W) supports nearly three-quarters of the global krill stock (Atkinson et al. 2008). Within this sector, the Antarctic Peninsula waters form a juxtaposition of key spawning grounds (Perry et al. 2019), locally intense fishing effort (Watters et al. 2020) and exceptionally fast warming (Meredith and King 2005). This has led to much recent research effort within the SW Atlantic sector, but relative neglect of how this key species is faring over the rest of its circumpolar range.

This research focus on the SW Atlantic has led to intense recent debate over whether krill and other zooplankters have been sensitive or resilient to the rapid warming of this sector. Evidence for resilience is suggested by reports of relatively stable krill populations (Fielding et al. 2014; Cox et al. 2018; Kinzey et al. 2018) and lack of range shifts in mesozooplankton (Tarling et al. 2018). On the other hand, evidence for sensitivity to change is provided by other studies, which suggest southward contraction in the range of krill, decreases in their abundance and recruitment (Atkinson et al. 2004, 2019; Hill et al. 2019), decreasing availability of krill to predators (Huang et al. 2011; McMahon et al. 2019) and increasing salp and copepod densities (Pakhomov et al. 2002; Ward et al. 2018). A further complication is that sequential overharvesting of seals, whales and fish last century has perturbed the balance of the food web, so the changes in krill and zooplankton may include readjustments to changing top down control as well as to climate (Ainley et al. 2015; Murphy et al. 2016).

The above examples of change within the food web pertain mainly to the SW Atlantic sector, but the krill and zooplankton have much wider distributions, within complete circumpolar rings offering suitable habitat (Foxton 1956; Andrews 1966; Mackintosh 1973). Since the *Discovery era* of the 1920s and 1930s, climatic change has differed in strength and direction strongly between these sectors (Jones et al. 2016). Warming and ice loss have been most intense west of the Antarctic Peninsula (Meredith and King 2005; Stammerjohn et al. 2012; Henley et al. 2019), and these effects are generally considered adverse to krill (Flores et al. 2012; Schmidt et al. 2018). By contrast, the Ross Sea area has experienced significant cooling and gains in sea ice in the post-1979 satellite era (Jones et al. 2016).

These contrasting rates of change across the different sectors of the Southern Ocean could be viewed as a “natural experiment” in how circumpolar populations respond, across the full extent of their range. Our central study hypothesis is that rapid degradation of suitable conditions in the Atlantic sector has reduced krill density within this sector, but the less adverse (or even positive) effects elsewhere provide circumpolar habitat refuges. Because the paradigm of a highly asymmetric krill distribution is based heavily on data obtained during the 1920s and 1930s (Mackintosh 1973; Atkinson et al. 2008),

our hypothesis would be supported if krill circumpolar distribution has readjusted to become more even nowadays than it was 90 yrs ago. In addressing the important, ongoing debate over whether krill have declined in response to warming and ice loss in the Atlantic sector, the other, more stable sectors then become “controls” in this natural experiment.

The CHINARE 2013/14 survey (Fig. 1) provides an opportunity to address our hypothesis. This survey circumnavigated Antarctica, sampling in all sectors during a single austral season (2013/2014), providing coverage of krill and other zooplankton that is possibly unique in the modern scientific literature. In a separate approach to our hypothesis, we have used KRILLBASE, a circumpolar compilation of all available net sampling data for krill spanning 1926–2016 (Atkinson et al. 2017). This provides longer-term context for the snapshot provided by the survey. Wider context is also provided by comparing the circumpolar distribution of krill from CHINARE 2013/14 with those of other major zooplankton groups.

The need for an integrated, circumpolar approach to understand climate change responses is widely recognized by Southern Ocean ecosystem research programs including ICED (Integrating Climate and Ecosystem Dynamics) and MEASO (Marine Ecosystem Assessment for the Southern Ocean) (e.g., Murphy et al. 2016; Brasier et al. 2019). These programs have begun to assess the circumpolar-scale status and understanding of food web components (Constable et al. 2016; Brasier et al. 2019) with isotopic data on trophic level being recognized a core requirement (Bengtson Nash et al. 2018; McMahon et al. 2019). We contribute to this objective by providing $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ “isoscapes” from the CHINARE 2013/14 survey, (sensu Braut et al. 2018) augmented by all available krill isotope data compiled from the literature. By presenting here an updated, circumpolar comparison of both the density and trophic baseline values of krill and other zooplankton, we aim to improve the understanding of food web structure under climate change, a central need for management and conservation around Antarctica (Hindell et al. 2020).

Materials and methods

CHINARE 2013/2014 cruise: Sample collection

The 30th Chinese National Antarctic Research Expedition (CHINARE) in the austral summer of 2013/2014 aboard RV “*Xuelong*” was a circumpolar cruise (Fig. 1). It began a clockwise circum-Antarctic navigation at 107.57°E on 27 November 2013, finishing on 5 March 2014. Krill and zooplankton samples were collected at 103 stations (78 d time and 25 night time stations; see Supplementary Fig. S1), using a modified Gulf high speed plankton sampler (HSPS, mouth area: 38.5 cm², mesh size: 330 μm ; Wiebe and Benfield 2003) to conduct horizontal surface layer hauls. Zooplankton samples were typically collected at four times per day (mainly at 0:00,

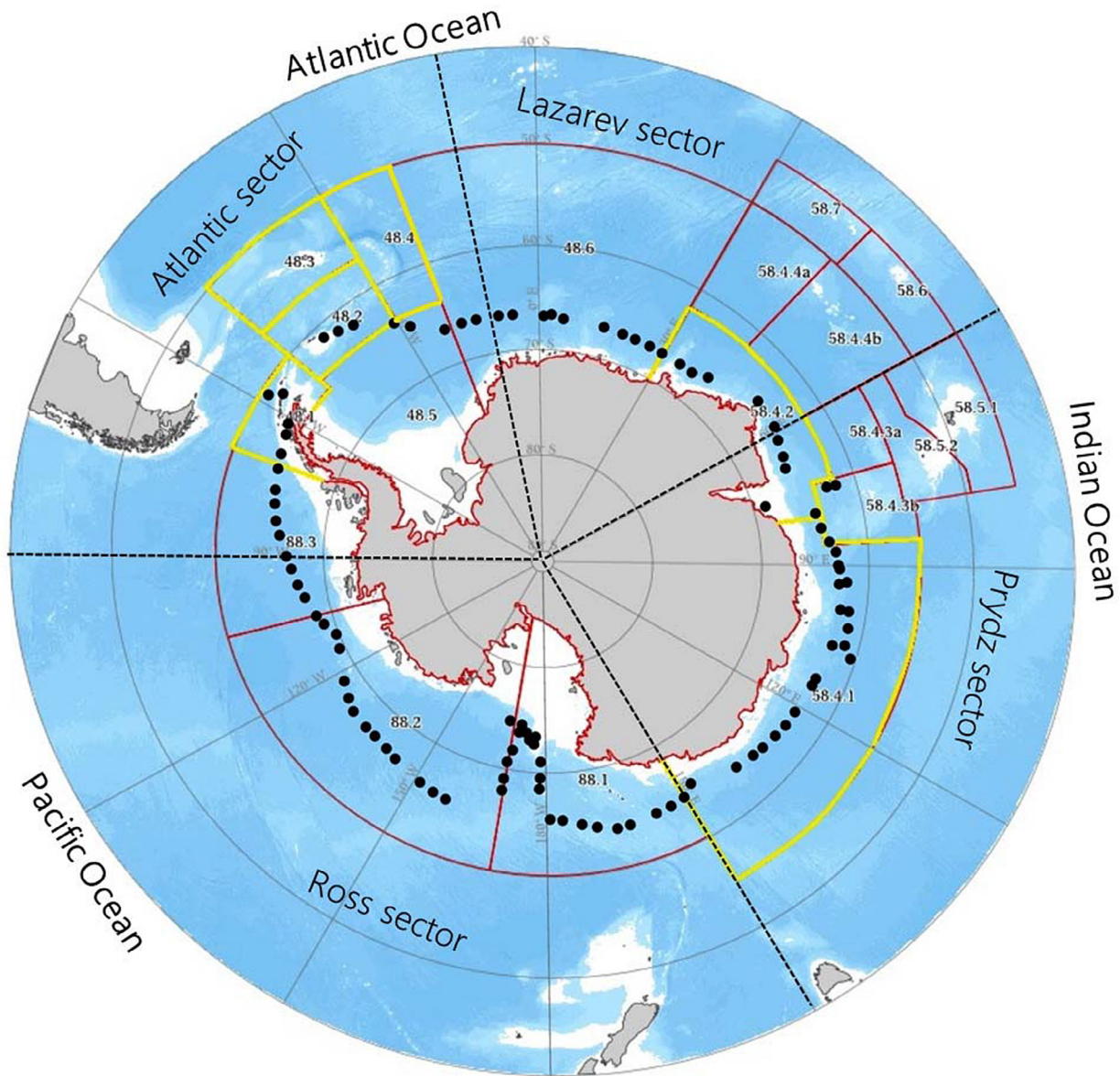


Fig. 1. Sampling stations (black dots) in CHINARE 2013/2014 cruise and the CCAMLR (Commission for the Conservation of Antarctic marine living resources) area. CCAMLR subareas 48.1, 48.2, 48.3, 48.4, 58.4.1, and 58.4.2 have krill catch limits and are marked in yellow. The current study divides the Southern Ocean into the following four sectors: Atlantic: 90°W–10°W; Lazarev: 10°W–60°E; Prydz: 60°E–150°E, and Ross: 150°E–90°W. The starting point of the clockwise circumnavigation is shown with a triangle.

6:00, 12:00 and 18:00, local time) subject to suitable ice-free conditions. At a typical ship speed of 14–16 knots, the winch wire was paid out at a speed of about 0.7 m s^{-1} to lengths of 400 m. Typically the HSPS reached about 30 m depth. After 20 min of trawling, the HSPS was hauled in at a speed of about 0.3 m s^{-1} . After the sampling gear was recovered, zooplankton samples were transferred from the cod end into a bucket with surface seawater. The approximate volume filtered for each sample was estimated based on the vessel's speed, sampling time and the mouth area of the sampling gear.

Before the formalin-preservation of the bulk of the catch, individuals of the dominant zooplankton taxa (including the two major krill species *E. superba* and *Thysanoessa macrura*, large copepods, amphipods, and pteropods) were picked out, rinsed with filtered seawater and immediately frozen at -80°C for stable isotopic analysis in the laboratory (Supplementary Table S1). Also, 3–5 liter of surface water from 20 stations were filtered onto GF/F filters and frozen at -80°C to determine stable isotopes of particulate organic matter (POM). In the Atlantic sector, krill and zooplankton samples used for isotopic

analysis were supplemented with those from 15 stations around the South Shetland Islands collected in the top 200 m of the water column using a Norpac net (0.5 m² net mouth, mesh 330 µm). In this study, most krill sampled were adult (Supplementary Table S1). After the removal of a subsample for isotopic analysis, the remainder of the catch was preserved in a 4% formalin and filtered sea water mixture.

Laboratory identification of zooplankton taxa

In the laboratory, large macrozooplankton (total length > 3 mm) were counted in the entire sample using a dissecting microscope (Nikon SMZ 745 T), while the other samples were divided using a Folsom plankton splitter and a subsample of 1/2–1/16 (depending on the numerical density of each sample) were counted. In the current study, we focused on the zooplankton which includes *E. superba*, *T. macrura*, late copepodite stages (CIII–CV) and adults of the large copepods *Calanoides acutus*, *Calanus propinquus*, *Metridia gerlachei*, *Rhincalanus gigas*, plus pteropods, and amphipods. Other species, such as ice krill *Euphausia crystallorophias* were much rarer in the samples and not included in the current analysis. Circumpolar maps with contoured densities were produced in Ocean Data View (Schlitzer 2018).

Isotopic analysis

This analysis focuses on *E. superba* and *T. macrura* as the two most abundant euphausiids in the Southern Ocean, with data presented for the other zooplankton to provide context for the krill results. A total of 291 specimens of *E. superba* from 50 stations and 162 specimens of *T. macrura* from 35 stations were used for δ¹³C and δ¹⁵N analysis. In the laboratory, each frozen krill was placed on ice and two sections were immediately removed for stable isotope analysis. These were the cephalothorax and abdomen (comprising the second and third abdominal segments).

The GF/F filters, cephalothorax and abdomen sections of krill, and other zooplankton samples were freeze dried for 48 h. The filters were packed into tin capsules, while the krill and zooplankton were ground in an agate mortar. About 1 mg of each sample was weighed and placed into tin cups for stable isotope detection using a Thermo Delta IV Isotope Ratio Mass Spectrometer. δ¹³C and δ¹⁵N stable isotopic values were expressed following the equation:

$$\delta^{13}\text{C or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

The standard reference material is Pee Dee belemnite (PDB) for δ¹³C and atmospheric N₂ for δ¹⁵N. An internal standard was run for every 10 samples. Measurement precision was 0.1‰ for δ¹³C values and 0.2‰ for δ¹⁵N values.

In this study, lipids were not extracted and none of the filters or zooplankton samples was acidified before the isotopic analysis. Thus, the δ¹³C and δ¹⁵N values shown in this study are original data without correction.

Meta-analysis of stable isotopes

To improve resolution of the circumpolar isoscape of *E. superba*, we performed a meta-analysis of postlarvae isotope values from the available literature and from databases (Supplementary Table S2). These provided 24 source studies reporting δ¹³C and δ¹⁵N values of krill, spanning 1987 to 2019. Supplementary Table S2 provides further information on each study such as sampling time, region, isotopic values and source reference.

Statistical analysis of differences between sectors and between eras

To examine whether there is any regional variation in the density, frequency of occurrence and isotope values of major zooplankton groups, the circumpolar data were divided into four sectors (Fig. 1): 90°W–10°W (Atlantic-Bellingshausen sector, hereafter “Atlantic sector”), 10°W–60°E (Lazarev-Cosmonaut sector, hereafter “Lazarev sector”), 60°E–150°E (Prydz-Kerguelen sector, hereafter “Prydz sector”), and 150°E–90°W (Ross-Pacific sector, hereafter “Ross sector”). These sector divisions were selected, first, to demarcate broadly a series of putative “stocks” or distinct subpopulations of krill identified from the *Discovery* era by Mackintosh (1973). Second they separated the main aggregations of krill sampling stations in our KRILLBASE database (see below). Within each sector, arithmetic mean isotope values or zooplankton density values from all component stations are presented. For the zooplankton data we also present frequency of occurrence, i.e., the fraction of hauls within the sector where the taxon was encountered. One-way ANOVA was used to examine the regional variation and post hoc analysis was used to test the inter-regional difference if normal distribution (Kolmogorov–Smirnov test or Shapiro–Wilk test) was given. Before the post hoc tests, homogeneity of variances were tested using Levene’s test. Depending on the results of the homogeneity test, Fisher’s LSD (least significant difference) test (homogeneous) and Tamhane’s T2 test (not homogeneous) were used in post hoc comparisons. We performed a nonparametric Kruskal–Wallis test when the data were not normally distributed and a Tukey type multiple pairwise comparisons test was used to examine the inter-regional difference.

KRILLBASE: Analysis of changes in circumpolar krill distribution

The CHINARE cruise, while circumpolar, was a single season only, and was not synoptic. We thus used additional, independent datasets to improve the generality of our circumpolar perspective. For the isotope data this was supplied by a meta-analysis whereas for the zooplankton data this was provided by a database of historical krill data (KRILLBASE; Atkinson et al. 2017). Because KRILLBASE spans 1926 to 2016, it also allowed us to examine whether krill circumpolar distribution has changed over the last 90 yrs.

All the data in KRILLBASE are derived from nontargeted oblique or vertical hauls in prefixed positions (Atkinson et al. 2017). For consistency with previous circumpolar krill work (Atkinson et al. 2008), we used data spanning October to April and with the top sampling depth no deeper than 20 m and bottom sampling depth no shallower than 50 m. To improve sample coverage in the Ross sector, we supplemented KRILLBASE with data from 36 stations in the Ross Sea during January to February, 2000, that were kindly provided by Sala et al. (2002). The KRILLBASE data were derived from a variety of net types, sampling depths, times of day and times of year of sampling, each of which can decrease the comparability of krill densities (no. m⁻²) between stations. The high concentration of sampling in restricted parts of the SW Atlantic sector using different methods allowed us to quantify these sources of variability and adjust for them in a model, which standardized all density estimates to a common sampling method (Atkinson et al. 2017). This model converts observed densities to those expected from a relatively efficient, single sampling method, namely a night-time RMT8 haul from 0 to 200 m on 1 January. The KRILLBASE data, including the added Ross Sea data, comprised a total of 11,779 net haul records of Antarctic krill.

The KRILLBASE database comprises data from 1926–1939, 1951 (*Discovery* era) and thereafter coverage in most years from 1976–2016. To examine whether differences between sectors changed over time we followed several approaches, one being that of Atkinson et al. (2019) of dividing the data into distinct multidecadal eras, namely the austral summer seasons spanning 1926–1951, 1976–1995, and 1996–2016.

The KRILLBASE data are compiled from multiple surveys, so the sampling locations and sampling frequency vary over time. To allow for this we used a series of analysis methods, analysis scales and combinations of data to examine circumpolar distribution of krill and whether this has changed over time. We compared sector-based mean krill densities (as described above for the CHINARE cruise), both for the April–October period and the December–February (midsummer) periods of each era. In our second approach to looking at time trends, we used a series of Mann–Kendall tests (Desmit et al. 2020) to assess the direction and significance of time trends in krill density in each sector. These nonparametric tests are suited to data such as KRILLBASE, because they are not sensitive to the treatment of gaps in time series, nor are they sensitive to the exact type of data transformation; valuable for highly skewed distributions such as those of krill.

We first standardized the number of data points in each sector by arranging each sector's data in date order and then dividing them into 20 time segments with the same number of sampling stations in each. The dependent variable in the test was the mean density across all the stations in each time segment. This means that the Mann–Kendall test is equally sensitive across sectors and the influence of krill's patchy distribution is standardized across the set of mean densities for

each sector. With the Mann–Kendall test, each data point is compared to each of the values preceding it, giving a total of $n(n - 1)/2$ pairs of data. If the later data point in each pairwise comparison is higher than the earlier data point the comparison is given a score of 1, and if it is lower it is given a score of -1 , with no difference given a score of 0. These scores are then summed to calculate Kendall's S statistic (S) (i.e., the number of increases minus the number of decreases). Next, the variance of S is calculated according to Millard (2013) and used to standardize S into a "Z-score." The Z-score test statistic has an approximate normal distribution, and is used to assign a significance level to the presence of a trend. High positive Z-scores or high negative Z-scores indicate clear increasing and decreasing monotonic trends, respectively, with statistically significant trends suggesting the null hypothesis (no monotonic trend) can be rejected.

The above analyses were based on broad sectors, and the resultant trends may be influenced by temporal change in the distribution of sampling within each of the sectors. To address this, we repeated the Mann–Kendall analysis, but at a finer spatial scale. We thus divided the circumpolar KRILLBASE coverage into 36 finer-scale units each spanning 10° longitude. For each of these, average density of krill in each season was used in the Mann–Kendall test. Thirteen longitude sections based on data from 1926–2016 and 7 based on data from 1976–2016 meet the requirement of the Mann–Kendall test that the data set must contain at least 10 values for the normal approximation method to produce valid results.

T-tests, ANOVA and Kruskal–Wallis analysis were conducted using SPSS 25.0 software and the Mann–Kendall test was conducted using Minitab.

Results

Circumpolar distribution of *E. superba* in 2013/2014: CHINARE Data

Based on the CHINARE survey in 2013/2014 the average density of *E. superba* was highest in the Atlantic sector and lowest in the Prydz sector (Fig. 2), although there were no significant differences between these sectors ($p > 0.05$, Kruskal–Wallis test). Average krill density in the Atlantic sector was 210% of the average across all other sectors. Frequency of occurrence was similar in all sectors except the Prydz sector where it was rather lower (Fig. 2).

To set a context for the circumpolar distribution of *E. superba*, we have also presented that of another highly abundant euphausiid *T. macrura* (Fig. 2), as well as other dominant zooplankton (Supplementary Fig. S2). Both mean density and frequency of occurrence of *T. macrura* were highest in the Prydz and Ross sectors, although no significant differences were found based on a Kruskal–Wallis test. Likewise, none of the other large zooplankton species showed strong concentrations in the Atlantic sector (Supplementary Fig. S2). No significant regional differences in their density and frequency of

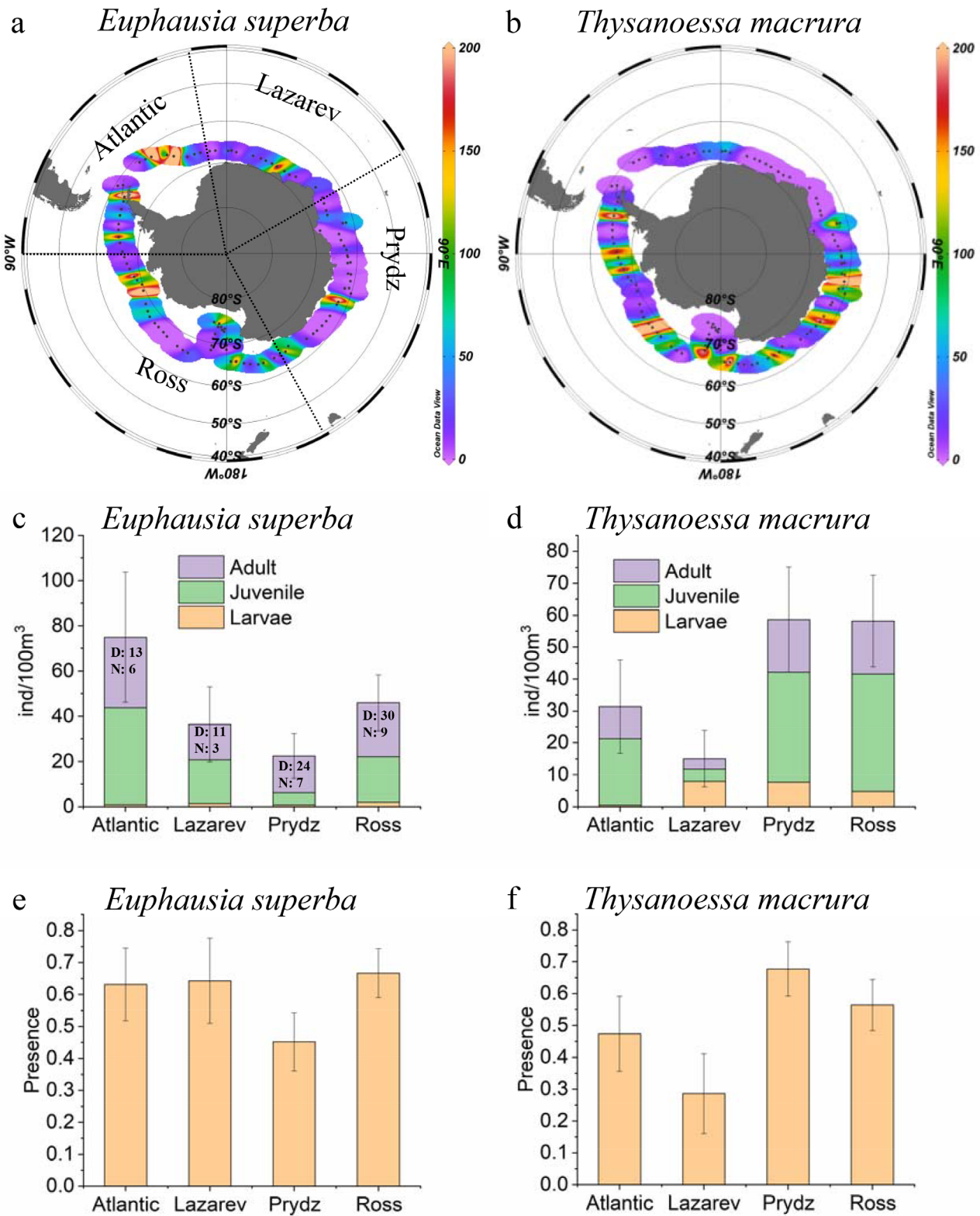


Fig. 2. CHINARE 2013/2014 cruise: Distribution of *E. superba* and *T. macrura*. **(a, b)** Circumpolar density (ind. 100 m⁻³), **(c, d)** mean density in each sector, and **(e, f)** frequency of occurrence in each sector (i.e., fraction of hauls containing krill). Number of stations sampled in day time (D) and night time (N) in each sector are indicated in panel c. error bars represent the standard error of krill abundance and frequency of occurrence in each sector.

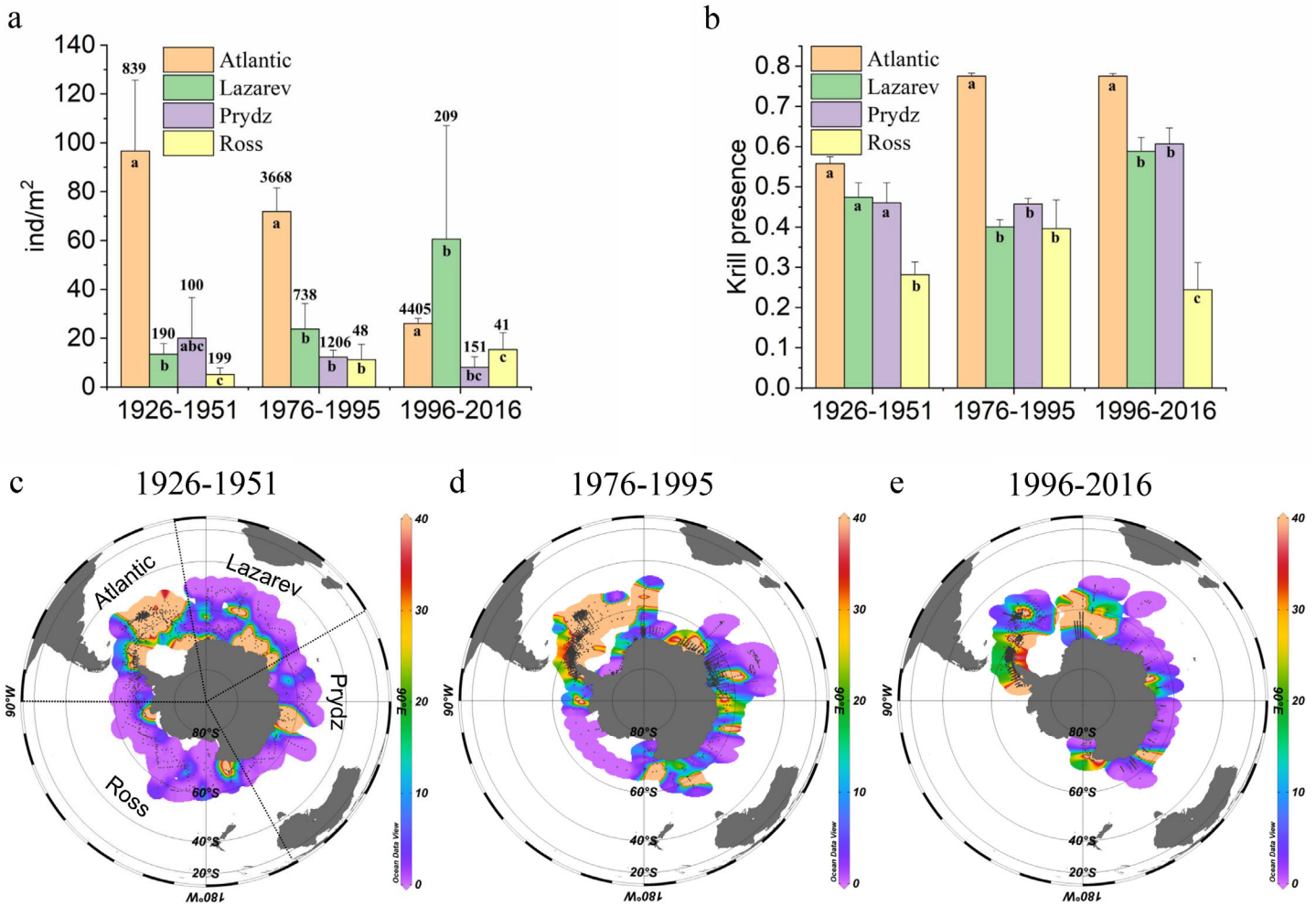


Fig. 3. KRILLBASE: Temporal changes in circumpolar distribution of *E. superba*. (a) Abundance and (b) frequency of occurrence of krill in three eras of each sector. A different letter indicates significant difference, while at least one same letter indicates insignificant difference, e.g., $a > b > c$, $a = ab$, $b = ab$. Number of nets in each sector and era is indicated on the top of each error bar. (c–e) Circumpolar distribution and densities of krill in era 1926–1951 (c), 1976–1996 (d) and 1996–2016 (e) based on data retrieved from KRILLBASE (October–April, 1926–2016). Error bars represent the standard error of krill abundance and frequency of occurrence in each sector.

occurrence were found from the Kruskal–Wallis test, despite the high density of large copepods, pteropods and amphipods found in the Ross, Atlantic and Prydz sectors respectively (Supplementary Fig. S2).

Changes in circumpolar distribution of *E. superba*: KRILLBASE Data

In the KRILLBASE dataset, the Atlantic sector was the most intensively sampled region, while data in the Ross sector were rare, especially in the modern era (Fig. 3a,b). As shown in previous research (Atkinson et al. 2004, 2019), the density of *E. superba* in the Atlantic sector decreased from the *Discovery* era to the modern eras (Fig. 3). Based on the data from KRILLBASE, the Atlantic sector showed the highest average krill density in the first two of the three eras (Kruskal–Wallis multiple pairwise comparisons test, Fig. 3). Frequency of

occurrence of krill was highest in the Atlantic sector (Fig. 3) in all three eras. While these results comprise the whole October–April period, they were similar to those based on summer-only (December to February) data (Supplementary Fig. S3).

In the *Discovery* era, mean KRILLBASE krill density for Atlantic sector was 8.5 times that across all other sectors, but this factor fell to 4.4 during the 1975–1996 era and 0.72 during the 1996–2016 era (Fig. 3). This latter value was strongly influenced by one exceptionally high value in the Lazarev sector (9692 ind. m⁻²; 26 April 2004). When this record was omitted, the factor rose to 2.2, the same value as that derived from the CHINARE cruise.

To provide alternative perspectives on the changing krill densities across sectors, we analyzed KRILLBASE in two other ways that respectively provide finer temporal and spatial

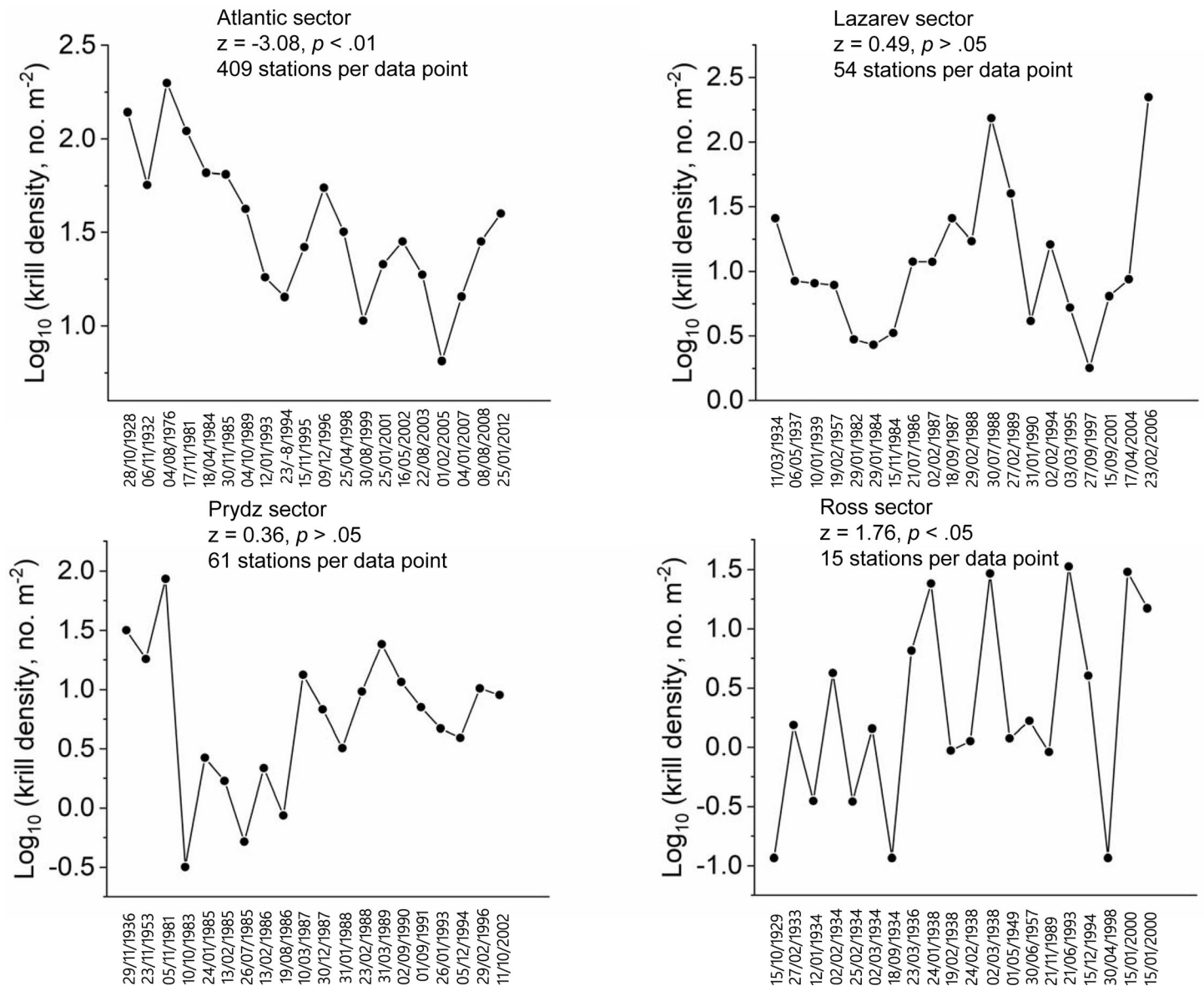


Fig. 4. KRILLBASE: Long-term changes in krill density in each sector. For each sector, the sample size has been standardized by dividing into 20 portions each with the same number of stations (see the KRILLBASE: Analysis of changes in circumpolar krill distribution section). The dates under each sample point thus refer to the mid date of each sampling time portion. Z-score (negative for a decline trend and positive for an increasing trend) and its significance are also shown in each sector.

resolution. First, Mann-Kendall time-trend analysis (Fig. 4) confirmed the negative trend reported previously in krill density in the Atlantic sector and the lack of any significant trend in Lazarev and Indian sectors. The Z-scores in all non-Atlantic sectors were positive (suggesting an increase) and this increase was statistically significant in the Ross sector. However, the low number of records makes any firm conclusion of a long-term increase in krill density outside the Atlantic sector difficult.

Using our second alternative analysis method, we divided Antarctica into a finer longitude resolution (Supplementary Fig. S4). This revealed a similar basic pattern, namely decreases

specific to the Atlantic sector and increases elsewhere. The longitudes 80°W–70°W, 10°W–0°, 0°–10°E, and 60°E,70°E showed significant upward trends in krill density, while downward trends were detected in the Atlantic sector 40°W–30°W and 30°W–20°W (Supplementary Fig. S4).

Isoscapes of *E. superba* and *T. macrura*

In contrast to the highly variable $\delta^{15}\text{N}$ values (*E. superba*: 0.21–6.45‰; *T. macrura*: 3.14–8.32‰), the $\delta^{13}\text{C}$ values were more consistent (*E. superba*: –31.16‰ to –23.90‰; *T. macrura*: –32.72‰ to –25.88‰) (Fig. 5; Supplementary Fig. S5).

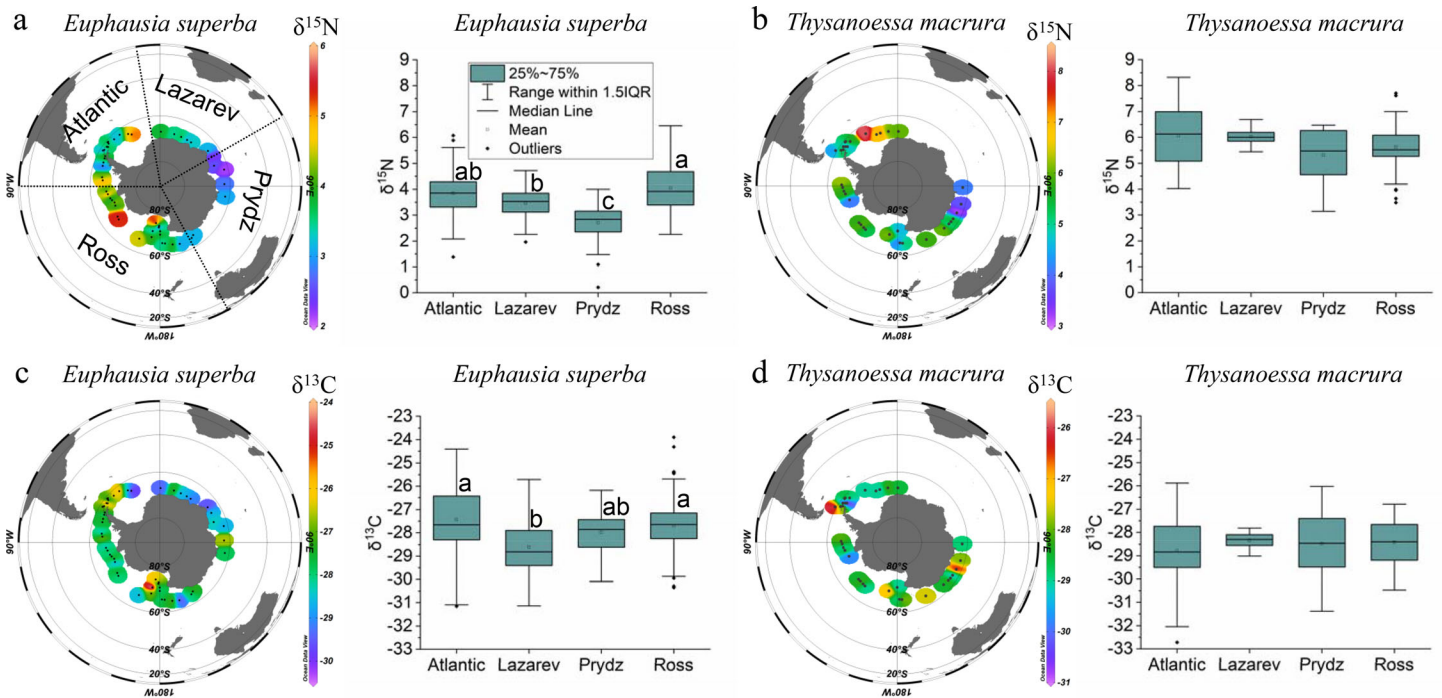


Fig. 5. CHINARE 2013/2014 cruise: Stable isotopes from abdomen of *E. superba* (a, c) and *T. macrura* (b, d). Significance in regional difference is indicated by letter on the top of the column. The sectors are respectively Atlantic sector: 90°W–10°W, Lazarev sector: 10°W–60°E, Prydz sector: 60°E–150°E, and Ross sector: 150°E–90°W.

Stable isotope values (both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) from the abdomens of *E. superba* and *T. macrura* were significantly higher than those from the cephalothoraxes ($p < 0.01$, *t*-test, Supplementary Fig. S6). A previous study found that sex-specific differences in stable isotopes of krill were reflected in the digestive gland region (part of the cephalothorax) but not in the abdominal section (Schmidt et al. 2004). Because krill sexes were not distinguished before our isotopic analysis, we focused on the values from the abdomen when assessing regional differences. The abdominal $\delta^{15}\text{N}$ values of *E. superba* showed significant regional differences (Fig. 5), with higher values in the Ross and Atlantic sectors but low values in the Prydz sector ($p < 0.05$, Kruskal–Wallis pairwise test). The abdominal $\delta^{13}\text{C}$ values in *E. superba* were higher in the Ross and Atlantic sectors but lower in the Lazarev sector ($p < 0.05$, Kruskal–Wallis pairwise test). Similar regional differences in stable isotopes were also found in the cephalothorax section of *E. superba* (Supplementary Fig. S5). In contrast to *E. superba*, the isotopic values of *T. macrura* tended not to differ significantly among various sectors (Fig. 5; Supplementary Fig. S5).

In the 12 stations where both *E. superba* and *T. macrura* were collected, their abdominal $\delta^{15}\text{N}$ values were significantly correlated ($p < 0.05$). While $\delta^{15}\text{N}$ values of *T. macrura* were higher than those from *E. superba* (*t*-test, $p < 0.05$, Fig. 6), the increase in values for the more omnivorous *T. macrura* between stations was more rapid than the corresponding increase for *E. superba*.

Comparison of *E. superba* stable isotope data with those from the literature

The $\delta^{15}\text{N}$ values of *E. superba* from the literature (Supplementary Table S2) showed similar regional patterns to those found in our study (low average value in the Prydz sector and high in the Atlantic and Ross sector), ANOVA did not reveal any significant regional difference (Fig. 7). The $\delta^{13}\text{C}$ values in this study were about 2 units lower than those from the literature data (Supplementary Fig. S7). The possible reason is that samples in the current study were not delipidated prior to the isotope detection and the $\delta^{13}\text{C}$ values were raw values without any lipid-correction.

Discussion

The circumpolar distribution of *E. superba* has become more even

The prevailing paradigm is that *E. superba* are very unevenly distributed in the Southern Ocean, with 70% of the total stock concentrated between longitudes 0° and 90°W (Atkinson et al. 2008; Siegel and Watkins 2016). This is a very unusual pattern, since other studies, as well as our current CHINARE data, suggest fairly even circumpolar distributions of most zooplankton, either of individual species (Andrews 1966) or total biomass (Foxtton 1956). There have been several suggestions for why *E. superba* are concentrated in this sector. For instance, some localized productive regions within it are considered as hotspots for enhanced growth,

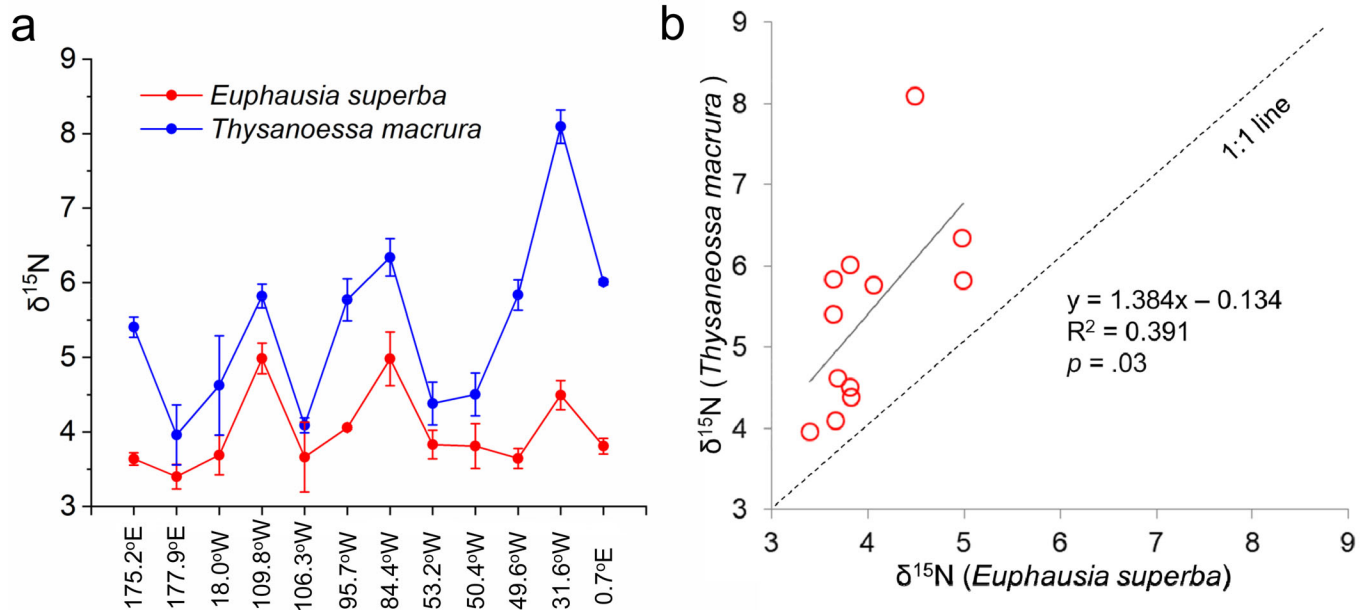


Fig. 6. CHINARE 2013/2014 cruise: $\delta^{15}\text{N}$ of *E. superba* and *T. macrura* at the same station. **(a)** Average and SE of $\delta^{15}\text{N}$ values of *E. superba* and *T. macrura* in the 12 stations where both krill species were collected for stable isotope analysis, **(b)** relationships in $\delta^{15}\text{N}$ value from abdomen section of both krill species.

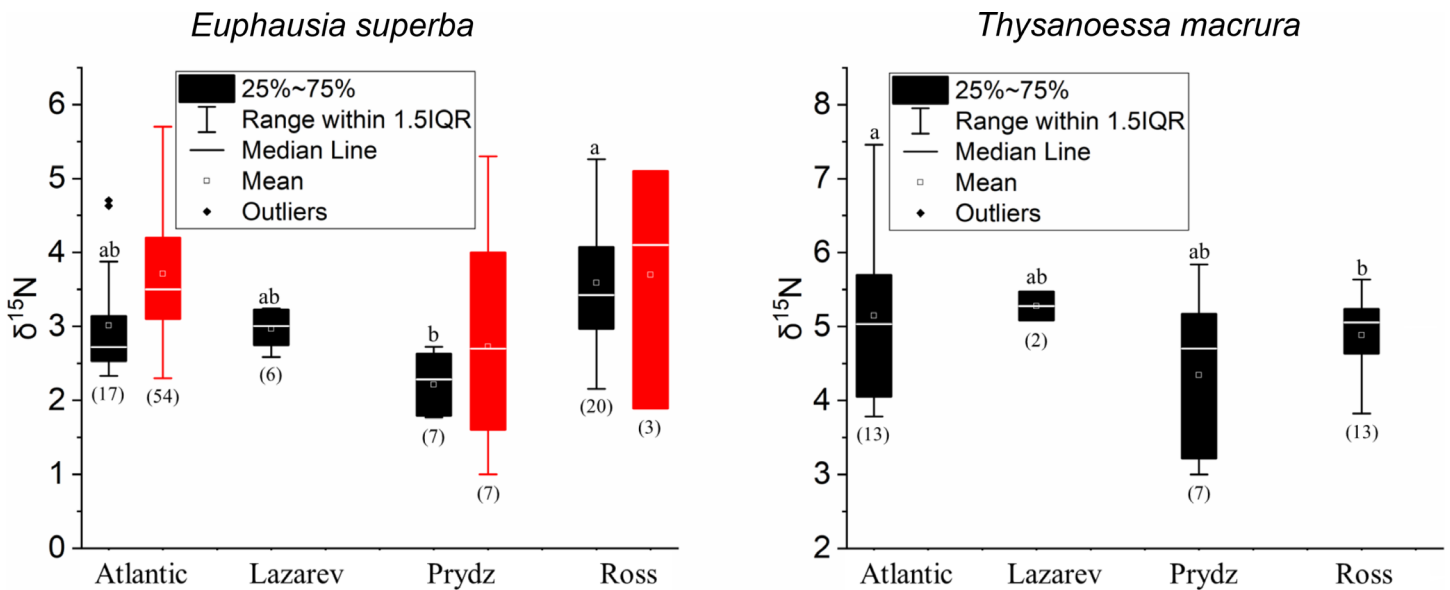


Fig. 7. Comparison of krill $\delta^{15}\text{N}$ values from CHINARE 2013/2014 with a meta-analysis of *E. superba* from the literature. Regional differences are marked with a letter on the top of bar in each column (black: data from this study; red: data from literature). Average isotope values between the cephalothorax and abdomen section of each krill (Supplementary Table S1) were used in this plot to make a better comparison with the literature (Supplementary Table S2), most of which used the whole krill in stable isotope analysis. Number of stations is shown in brackets at the bottom of each column.

spawning, nursery and early stage development of krill (Hofmann and Husrevoglu 2003; Murphy et al. 2017; Perry et al. 2019).

However, evidence is accumulating that habitats within the Atlantic sector have become less optimal for krill over the last

century. Sea ice coverage is thought to be one factor as it provides suitable shelter, food and pelagic preconditioning effects throughout the season (Meyer et al. 2017; Schmidt et al. 2018). Long-term warming, sea ice decline and climatically-induced reduction in recruitment have been linked to declines in the

SW Atlantic krill stock (Loeb et al. 1997; Atkinson et al. 2004) and its contraction southward toward the Antarctic continent (Atkinson et al. 2019). Shifts in the dominance of krill compared to other zooplankton taxa such as salps are suggested to be having major consequences for krill-dependent predators and food webs of the Atlantic sector (Huang et al. 2011; Trivelpiece et al. 2011; McMahon et al. 2019). By contrast, however, other studies suggest relative stability of the krill stock (Fielding et al. 2014; Cox et al. 2018; Kinzey et al. 2018). The uncertainty and debate around this issue impedes both scientific understanding of the ecosystem and management of the krill fishery in a changing climate (Hill et al. 2019).

Our study approached this issue by expanding the analysis beyond the Atlantic sector to examine relative krill trajectories across all sectors, under both more stable and improving conditions for krill. In contrast to the profound changes reported in our study and elsewhere in the Atlantic sector, no clear temporal trends in krill stocks have been established in other sectors within the last 50 yrs (Flores et al. 2012). In common with the Atlantic sector, the distribution of Prydz sector krill also appears to be related to sea ice, both spatially (Nicol et al. 2000) and temporally (Braithwaite et al. 2015). With more stable sea ice cover, no significant evidence of declines in krill stocks in these sectors was found (Atkinson et al. 2004). The positive Z-scores, although not significant (Fig. 4), also indicated stability or even increases in krill densities in these sectors. In the Ross sector, ice cover has been increasing in the Ross Sea but decreasing in the Amundsen Sea (Comiso et al. 2011; Stammerjohn et al. 2012). The environmental changes in the Ross Sea could benefit diatoms and change krill availability in future, although krill are not considered able to invade much of the continental shelf owing to the requirement for larval development at great depth (Smith et al. 2014). The Amundsen Sea has been identified as a potential new habitat, which could support successful krill spawning and recruitment in future due to delayed sea ice formation, lower ice concentration and stronger phytoplankton blooms (Piñones and Fedorov 2016). Our Mann–Kendall tests (Fig. 4) do indeed show significant krill increases in the Ross sector, as may perhaps be expected since it has cooled and gained sea ice. An important caveat, however, is that krill data coverage is very sparse in this sector, so we cannot draw any firm conclusions on this.

Notwithstanding these uncertainties, the CHINARE 2013/2014 data and KRILLBASE independently support our hypothesis that krill are more evenly distributed around Antarctica nowadays than they were 80 yrs ago. The calculation that nearly three-quarters of the global krill stock is located in one quarter of the longitudinal extent of the Southern Ocean (0–90°W; Atkinson et al. 2008) was based heavily on data from the *Discovery* era. Sadly, net sampling in the last 25 yrs is no longer extensive enough to update this calculation robustly, but we know that the percentage will be much lower. Based on mean krill densities, the krill concentration factor in

the Atlantic sector compared to the other sectors was 8.5 in the *Discovery* era, but only 2.2 in the last 25 yrs, based on both CHINARE and KRILLBASE data. In this modern era (1996–2016), the ratio of average krill densities among the Atlantic: Lazarev: Prydz: Ross sectors from KRILLBASE is 1: 2.33: 0.31: 0.59 (Fig. 3). If a single extreme value from the Lazarev sector (9692 ind. m⁻²; see Results) is omitted, the ratio becomes 1 : 0.56 : 0.31 : 0.59 which is very similar to that from the CHINARE 2013/2014 survey (1 : 0.49 : 0.30 : 0.61). Acoustic biomass surveys also support the idea that the concentration of krill density in Atlantic sector habitats is relatively modest in the modern era. Acoustic data based on CCAMLR's Atlantic sector surveys in 2000 and 2019 (Scientific Committee for the Conservation of Antarctic Marine Living, SC-CAMLR 2019), the Baseline Research on Oceanography, Krill and the Environment (BROKE) survey in 1996 and the BROKE-West survey in 2006 show a ratio of 1 : 0.86 : 0.40 : NA, based on table 2 in Siegel and Watkins (2016) and table 7 in Jarvis et al. (2010). Krill are difficult to sample quantitatively, either with nets or acoustics, so this broad agreement between CHINARE, KRILLBASE and acoustics over the lack of a strong concentration in the Atlantic sector in the modern era is important. The similarity of the results from three independent data sources using diverse sampling methods suggest that the progressive “evening-up” of circumpolar krill distribution in the last 90 yrs is unlikely to be an artifact of sampling issues.

The differing trends in Fig. 3 between the mean density and the frequency of occurrence are symptomatic of the fact that the majority of the KRILLBASE records that we analyzed register the presence of krill but the density of krill in these records spans four orders of magnitude (Atkinson et al. 2017). A large fraction of the krill stock is concentrated in dense swarms (Tarling et al. 2009; Fielding et al. 2014) and, with sufficient sampling, mean density captures the influence of these high density swarms. Frequency of occurrence data, on the other hand, does not distinguish between low and high densities.

With rapid regional environmental changes occurring around Antarctica, modeling studies have been used to provide insights into how habitat suitability for krill is changing (Hill et al. 2013; Piñones and Fedorov 2016; Veytia et al. 2020). Geographical variation in the seasonal growth of Antarctic krill, which is dominated by the concentration, composition and duration of phytoplankton blooms, may be a major factor determining their circumpolar distribution (Murphy et al. 2017). Based on models using surface temperature and chlorophyll, the Antarctic Peninsula, Scotia Sea, Kerguelen Plateau, and edges of the continent were considered as regions of enhanced krill growth (Murphy et al. 2017). The same growth model suggested that, under future climate scenarios, the eastern Weddell and western Ross Seas would improve as habitats supporting krill growth (Veytia et al. 2020). Another temperature-based model suggested that limited regions such

as the western Weddell Sea, isolated areas of the Prydz and Lazarev sectors and the Amundsen Sea/Bellingshausen Sea will support successful spawning habitats for krill by the year 2100 (Piñones and Fedorov 2016). Taken together, these models suggest that other regions besides the Atlantic sector could become krill hotspots in future.

Defining circumpolar isoscapes for *E. superba* and *T. macrura*

In addition to numerical densities, the isotopic baselines of krill and other zooplankton are also important in defining the trophic relationships among the higher trophic-level species (Stowasser et al. 2012; Pakhomov et al. 2019). Understanding the degree of regional variability in these baselines is thus important to interpret spatial and temporal variation in the diets of the suite of higher trophic levels that are wholly or partially reliant on zooplankton (Bengtson Nash et al. 2018; McMahan et al. 2019). Such zooplankton “isoscapes” were recently produced for the West Antarctic (Brault et al. 2018), and our study is perhaps the first to compare the isoscapes of key zooplankton species such as *E. superba* and *T. macrura* at a circumpolar scale.

For $\delta^{15}\text{N}$, this variation reflects two key factors, the first being natural variation in the $\delta^{15}\text{N}$ values of Particulate Organic Matter (POM) at the base of the food web. For instance, more complete NO_3^- utilization in productive regions was suggested to lead to high $\delta^{15}\text{N}$ values for zooplankton in the productive Ross- and Amundsen Seas (Pinkerton et al. 2013; Brault et al. 2018), which parallels our results. Both the CHINARE data and the meta-analysis found similar trends in $\delta^{15}\text{N}$ values for *E. superba* between the sectors of the Southern Ocean, with lower values in the Prydz sector compared to the other sectors (Fig. 7). Isotopic POM baselines are known to be highly variable in space and time, and because the slower growth rates of the grazers partially integrate this variability, they form a more stable baseline against which to interpret predator diets (Schmidt et al. 2003; Stowasser et al. 2012; Pakhomov et al. 2019).

A second key factor causing variation in $\delta^{15}\text{N}$ values of zooplankton is their trophic level relative to the POM. Thus, *E. superba* showed lower $\delta^{15}\text{N}$ values than *T. macrura*, suggesting a more herbivorous diet. Furthermore, based on the 12 stations where both *E. superba* and *T. macrura* were measured, the $\delta^{15}\text{N}$ of *E. superba* varied only slightly, while that of *T. macrura* varied by about 1 trophic level (Fig. 6b). This suggests that *T. macrura* may switch more actively from herbivory to carnivory compared with *E. superba*. *E. superba* is mainly considered to occupy a lower trophic level than other Southern Ocean krill species (Stowasser et al. 2012; Jia et al. 2016; Kohlbach et al. 2019). While they do ingest small copepods, this seems to be mainly through incidental filtration along with their main phytoplankton food, rather than switching to carnivory (Schmidt et al. 2014). In contrast, both fatty acid biomarkers and morphology (strong thoracic leg

and setae in the dactylus) suggested that *T. macrura* are less dependent on diatoms but could feed carnivorously on dominant copepods (Phleger et al. 2002; Farber-Lorda and Mayzaud 2010). Overall, these results indicate that *E. superba* is mainly dependent on phytoplankton while *T. macrura* is more prone to switch to carnivory. This variability underlines the importance of assessing zooplankton as a food web baseline for higher trophic levels over large scales.

Concluding remarks

The currents encircling Antarctica, with continuous rings of suitable habitat, provide distributions of zooplankton that are circumpolar. This globally unique circulation contrasts with that in the warming Arctic, where currents from the Atlantic and Pacific provide pulsed intrusions of warmer waters and their resident biota into high latitudes (Dalpadado et al. 2014). In this sense, the relative simplicity of the Southern Ocean system, with strong contrasts in climate change observed between sectors, allows a “natural experiment” approach to test how varying rates and directions of change affect species across their whole global range.

While the Southern Ocean might be amenable to this circumpolar approach, it has its own complications. First, it is difficult to separate the effects of climatic- and bottom-up forcing from those of changing top-down controls due to past over-exploitation of vertebrate predators (Ainley et al. 2015; Trathan and Hill 2016). Second, the observational data for krill outside of the Atlantic sector are too sparse to reveal the detail of trends, e.g., whether there have been abrupt shifts in geographical range or abundance. Notwithstanding these issues, we see basic contrasts in krill trajectory between sectors that align with the directions of change in temperature and ice cover. This provides support for the strong role of climatic forcing on krill, while not negating the importance of parallel top-down controls.

Antarctic krill support the largest fishery by tonnage in the Southern Ocean (Nicol and Foster 2016). Even though present catches of Antarctic krill are nearly 400,000 tons per year and increasing, it has been highlighted as one of only a handful of underexploited fisheries worldwide, with catches nowadays taken almost exclusively in limited regions of the Southwest Atlantic sector (Nicol and Foster 2016). It is in the interest of all stakeholders that any exploitation of key species such as krill is well managed to minimize impacts, both on the targeted stock and its dependent food web. The current focus of management is within the Atlantic sector, which is not surprising; the fishery is currently based here and the rapid warming and potential sensitivity of krill to a worsening climate in this sector has generated much debate (Cavanagh et al. 2016; Hill et al. 2016; Brooks et al. 2018).

However, underpinning this focus on the Atlantic sector are widely held views that it is the epicenter of their global distribution, perhaps even a key source area for the circumpolar

stock, thus deserving special conservation status (Atkinson et al. 2008). Our results challenge this notion, showing that the importance of the Atlantic sector for krill has diminished over the last 80 yrs, and that other sectors may have acted as refuges from the rapid decline in habitat suitability within the Atlantic sector. This larger-scale, longer-term view suggests that the species has some resilience to the rapid changes that have degraded part of its habitat.

With these variable rates of climatic change around Antarctica, there is an increasing emphasis on the need to take circumpolar-scale perspectives for effective management and conservation in the Southern Ocean (Constable et al. 2016; Hindell et al. 2020). Large scale analyses are hampered, however, by a relatively poor understanding of how krill-based food webs vary between sectors and different areas of ecological significance. Detailed food web reconstructions have only been completed for a handful of systems in the Southern Ocean, and these show major differences in reliance on *E. superba* (e.g., Hill et al. 2012; Pinkerton and Bradford-Grieve 2014; Dahood et al. 2019). Furthermore, some predator species may migrate or integrate across systems (Bengtson Nash et al. 2018; Hindell et al. 2020), requiring a circumpolar-scale baseline of their potential food sources. With initiatives underway to generate a circumpolar network of observation, protection and management within the Southern Ocean (Grorud-Colvert et al. 2014; Constable et al. 2016), our reappraisal of the distributions and trophic levels of krill and other key species provide some of the circumpolar-scale context that is needed.

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Conflict of interest

None declared.

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