Spatial distributions of Southern Ocean mesozooplankton communities have been resilient to long-term surface warming

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ABSTRACT

The biogeographic response of oceanic planktonic communities to climatic change has a large influence on the future stability of marine food webs and the functioning of global biogeochemical cycles. Temperature plays a pivotal role in determining the distribution of these communities and ocean warming has the potential to cause major distributional shifts, particularly in polar regions where the thermal envelope is narrow. We considered the impact of long-term ocean warming on the spatial distribution of Southern Ocean mesozooplankton communities through examining plankton abundance in relation to sea surface temperature between two distinct periods, separated by around 60 years. Analyses
considered 16 dominant mesozooplankton taxa (in terms of biomass and abundance) in the southwest Atlantic sector of the Southern Ocean, from net samples and \textit{in situ} temperature records collected during the \textit{Discovery Investigations} (1926-1938) and contemporary campaigns (1996-2013). Sea surface temperature was found to have increased significantly by 0.74°C between the two eras. The corresponding sea surface temperature at which community abundance peaked was also significantly higher in contemporary times, by 0.98°C. Spatial projections indicated that the geographical location of community peak abundance had remained the same between the two eras despite the poleward advance of sea surface isotherms. If the community had remained within the same thermal envelope as in the 1920s-1930s, community peak abundance would be 500 km further south in the contemporary era. Studies in the northern hemisphere have found that dominant taxa, such as calanoid copepods, have conserved their thermal niches and tracked surface isotherms polewards. The fact that this has not occurred in the Southern Ocean suggests that other selective pressures, particularly food availability and the properties of underlying water masses, place greater constraints on spatial distributions in this region. It further demonstrates that this community is thermally resilient to present levels of sea surface warming.

\section*{INTRODUCTION}

Biogeographic changes in the distributions of populations and communities are a widely reported outcome of recent rapid climatic shifts (Parmesan and Yohe 2003). The single most important physical variable affecting marine systems is temperature, as manifested in the close alignment between the distribution patterns of marine ectotherms and latitudinal and vertical thermal gradients (Somero 2010). These patterns are no doubt influenced by the strong relationship between temperature and physiological performance.
However, other ecological aspects such as species interactions, trophic efficiency and community composition are also strongly related to temperature gradients (Richardson 2008). The rate and extent of ocean warming is therefore of critical importance to the viability of future marine populations (Richardson 2008).

Recent biogeographic shifts in marine zooplankton have most commonly been associated with the warming of the sea surface (Beaugrand et al. 2002, Hinder et al. 2014). In the northeast Atlantic, Beaugrand et al. (2002) reported that members of warm water assemblages of crustacean mesozooplankton (the southern shelf-edge assemblage and the pseudo oceanic assemblage) moved more than 1100 km polewards over the past 50 years (approximately 200 km per decade) although Chust et al. (2013) determined these translocations to have been considerably lower (8 to 16 km per decade for *Calanus finmarchicus*). Similarly, Lindley and Daykin (2005) determined *Centropages chierchiae* and *Temora stylifera* to have both moved north from the vicinity of the Iberian Peninsula in the 1970s and 1980s to the English Channel in the 1990s (6° of latitude, amounting to around 300 km per decade). In both of these instances, the reported distributional shifts took place over periods where sea surface temperature warmed by 1°C although the shifts may also be partially influenced by stronger northward currents on the European shelf edge.

The Southern Ocean has undergone some of the world’s most rapid regional ocean warming, with a summertime increase at the sea surface of more than 1°C recorded west of the Antarctic Peninsula between 1951—1998 (Meredith and King 2005) and an increase in the upper 100 m of ~0.9°C in January at South Georgia between 1925—2006 (Whitehouse et al. 2008). This long-term shift in sea surface temperature must be placed within the context of seasonal temperature variation, which is just a few degrees in the surface layers (Venables et al. 2012). Individuals in contemporary times may therefore be experiencing average water temperatures towards the upper limits of historical seasonal temperature fluctuations.
Furthermore, the potential for a biogeographic shift polewards in the Southern Ocean is limited because of the Antarctic continental landmass, strong circumpolar currents and extensive sea-ice. The resilience of Southern Ocean marine taxa to ocean warming must therefore contend with both a geographic narrowing of their temperature envelope, and a seasonal temperature experience that is comparatively small in relation to species found in more temperate regions. If such temperature changes cannot be tolerated, a contraction of their range and replacement with more temperate species will result, with ecological consequences both to the secondary productivity of the system and its foodwebs.

Nevertheless, sea surface temperature is not the only constraint on biogeographic patterns in mesozooplankton. Much of the Southern Ocean is characterised as being a high nutrient low chlorophyll environment since iron deprivation frequently limits levels of primary productivity (Boyd 2002, Korb and Whitehouse 2004). Large phytoplankton blooms persist where iron is naturally enriched through sea-ice melt and continental run off or entrainment from sediments (Pollard et al. 2009) and their location can be a major influence on zooplankton productivity and abundance (Atkinson et al. 1996). Furthermore, some biomass dominant polar zooplankton species, such as the large calanoid copepods, have multiyear lifecycles and spend much of the year in deeper water masses, some in a state of diapause, occupying the surface layers only during the productive season (Atkinson 1998, Tarling et al. 2004). Conditions in the surface layers may therefore not be the ultimate influence on the distributions of some of these species in the context of their lifecycles.

Here we consider how Southern Ocean mesozooplankton populations have responded to a period of substantial ocean warming that has continued since the early part of the twentieth century. We compare the distributions of a number of key taxa between two periods, the first sampled by the *Discovery Investigations* between 1926 and 1938 and, the second, by contemporary campaigns between 1996 and 2013. The analyses were performed
on net samples and *in situ* sea surface temperatures collected during the summertime period within the southwest Atlantic sector of the Southern Ocean. Both datasets encompassed more than a decade of sampling (13 and 18 years respectively) in order to synthesise across intradecadal climatic cycles and minimise the influence of interannual variability on comparative analyses (Murphy et al. 2007, Loeb and Santora 2015, Steinberg et al. 2015). Our analyses establish relationships between the distributions of key taxa and prevailing sea surface temperature to determine how individual species, and the mesozooplankton community as a whole, have responded to the intervening period of ocean warming. Although our findings must be placed within the unique set of circumstances that are faced by open ocean communities in the Southern Ocean, they also provide a wider case study of the potential resilience of such communities to climatic change.

**MATERIALS AND METHODS**

**Mesozooplankton species composition and abundance** We analysed net samples from 155 stations south of the Polar Front in the southwest Atlantic sector of the Southern Ocean, collected as part of the *Discovery Investigations* (1926-1938, Fig. 1a). The samples were obtained via a series of N70V plankton nets deployed vertically between 250 m and the surface (see Kemp et al. 1929). Mesh sizes in this net decrease in stages from 5 mm in the upper part, to 440 µm and then 195 µm in the mid and lower parts respectively (measurements are metric equivalents of the original imperial units). A further 451 samples were analysed from nets taken in the same ocean sector in contemporary times (1996-2013, Fig. 1c). The contemporary samples were obtained from deployments of either RMT1 nets (330 µm mesh) fished obliquely from 200-0 m or Bongo nets (200 µm) fished vertically from either 200-0 m or 400-0 m. During sample analysis, larger organisms were either enumerated
from complete samples, or the whole sample placed in a Folsom plankton splitter and fractionated into replicate aliquots until countable numbers (~200 individuals) were estimated to be present. For smaller, more numerous organisms, the sample was further fractionated until countable replicates (~500-800 organisms) were obtained. Abundances of taxa were standardised according to the split fraction, and the amount of water each net filtered was estimated based on mouth area and distance towed, to derive individual species concentrations (ind. m$^{-3}$).

**Sea surface temperature** Sea surface temperature was measured at the zooplankton sampling sites and additional locations using water bottle samples during the *Discovery Investigations* (Kemp et al. 1929) and with high resolution conductivity temperature depth (CTD) instruments during the contemporary cruises (Whitehouse et al. 2008) (Fig. 1).

To determine the change in sea surface temperature between the 1920s-1930s and present day, data from all available stations from the *Discovery Investigations* and contemporary cruises between the months of October and April and located south of the Polar Front in water depths >500 m were analysed for the region 65—49°S, 80—20°W (Fig. 1). Stations were identified as being south of the Polar Front from their vertical temperature profile (Gordon et al. 1977). Duplicate temperature measurements, defined as measurements taken within 1 day and 5 km of another sample, were excluded. The surface temperature datasets were compared with the World Ocean Atlas (WOA) 2013 v2 monthly mean 1° surface climatology for 2005—2012 (Locarnini et al. 2013). For each dataset, nearest neighbour interpolation was used to extract the WOA temperature at each station from the corresponding mean monthly objectively analysed field at 0 m depth. WOA grid cells with zero contributing data points were excluded (Meredith and King 2005). The resulting differences between the station data points and the WOA temperature fields were averaged at 1° spatial resolution to remove geographic bias from the station coverage. The median offset
from the WOA data for the gridded data from the *Discovery Investigations* and contemporary
data was -0.78°C and -0.04°C, respectively (N = 106 for Discovery, N = 91 for
contemporary).

We used these offsets to produce mean October—April sea surface temperature fields for the
*Discovery Investigations* and contemporary eras. WOA monthly mean 2005—2012
climatological temperature fields at 0 m for October to April were averaged and the
corresponding offset applied uniformly. In this case, all grid cell values were retained to
provide a spatially complete coverage for the study region.

**Numerical methods** Mesozooplankton data analyses focussed on the crustacean fraction
which made up approximately 90% of all organisms within net samples. Analyses considered
16 taxa from this fraction chosen because they were major contributors to either the
abundance or the biomass of the samples (biomass was determined through multiplying
abundance by typical dry weight and was calculated only for the purpose of identifying
species that were less abundant but still major contributors through their large individual
size). Analyses were restricted to net samples taken between October and April. The datasets
were normalised such that each taxon made an equal contribution to the metric of community
response (*CRel*, see below) and that the influence of less abundant species was the same as
more abundant ones. This ensured that the response metric was not dominated by a small
number of highly abundant taxa.

The first stage in this process was to derive relative abundance for each taxon, as follows:

\[
Rel_{x,y} = \frac{Abs_{x,y}}{\sum_{y=1}^{n} Abs_x}
\]  

(1)
where Rel is relative abundance, Abs, absolute abundance (ind. m\(^{-3}\)), x, taxon, y, the sample station and n, the total number of sampling stations. For the contemporary sample set, it was necessary to determine Rel separately for three different types of net deployment (RMT1 200-0 m, Bongo 200-0 m and Bongo 400-0 m). The resulting three matrices were subsequently concatenated into a single matrix before further analysis. Community relative abundance (CRel) was calculated as:

\[
\text{CRel} = \sum_{x=1}^{x=16} \text{Rel}_y
\]

Cumulative probability curves were generated for (i) cumulative station rank as a function of sea surface temperature and (ii) cumulative Rel or CRel as a function of sea surface temperature. Medians and percentiles of Rel were calculated, from which the corresponding temperatures were determined to ascertain the relationship of each taxon to temperature. For CRel, the residual difference between (i) and (ii), the community relative abundance anomaly (CRel\(_A\)), was calculated to derive a metric of abundance that normalises for the distribution of sample stations between sea surface temperatures. CRel\(_A\) trajectories were fitted by a Gaussian distribution function (\(G(T°C)\)) where the inflection point, \(X_0\), denotes the sea surface temperature at which peak relative abundance occurs. The respective \(G(T°C)\) functions were plotted spatially, using the sea surface temperature fields described above, to identify regions of peak CRel\(_A\). A bootstrapping analysis was performed to determine the level of difference in \(X_0\) between the Discovery Investigations and contemporary datasets, following Hilborn and Mangel (1997). CRel\(_A\) was resampled through selecting 148 datapoints with replacement from either the Discovery Investigations or contemporary datasets 30 times. \(G(T°C)\) and the value of \(X_0\) was derived for each resampled dataset. The significance level of the difference in
between *Discovery Investigations* and contemporary datasets was tested by a two tailed t-test, having first passed tests for Normality (Shapiro-Wilk) and Equal Variance. It was not possible to fit a Gaussian distribution to the temperature distributions of a number of individual taxa since they were not normally distributed, so the median temperature of occurrence (termed \( M_0 \)) was derived for all individual taxa for comparative purposes (Table 1).

**Influence of extreme values** A potential confounding influence on the statistical comparisons made between eras is that a small number of extreme values in one or other dataset is responsible for the observed significant differences. This would mean the differences between eras may be the result of including or excluding anomalous instances in one or other dataset rather than reflecting a change in the mean situation. We approached this issue through considering three of the main sources of variability within the datasets, namely (i) interannual variability, (ii) differences between taxa, (iii) the degree of spatial overlap between eras. Our null hypothesis was that exclusion of extreme values within these sources of variability reduces the difference between the respective \( X_0 \) values to the point that they are no longer significantly different. Rejection of this hypothesis means that analyses are not overly influenced by extreme values and that all data could be included when testing for the difference in \( X_0 \) between eras. The datasets were prepared as detailed above but, prior to the generation of the cumulative probability curves, certain net samples or taxa were excluded according to the respective test. Exclusions for: (i) interannual variability, were the years with either the highest or lowest mean sea surface temperatures; (ii) differences between taxa, those taxa with the highest or lowest \( X_0 \) values; and (iii) the degree of spatial overlap, those areas that had extremely high or low sea surface temperatures. Further details are given in *Supplementary Information*. Once the particular subset of data had been excluded, community relative abundance (\( CRelA \)) trajectories were generated and the \( X_0 \) value
determined. This was compared to the original value of the opposing era and tested statistically to determine if the difference in $X_0$ between eras remained significant.

**Comparison of relative abundance ranks between eras** To establish whether community structure had altered between eras, rankings in relative abundance of individual taxa were compared. For contemporary samples, only the Bongo nets that fished from 200-0 m were used for the comparison, given that they were the closest in sampling method to the N70V nets. Differences in the sampling efficiencies of the nets were accommodated through conversion factors derived from corresponding *in situ* net trials (Ward et al. 2012). Briefly, when both nets were fished to a depth of 200 m, the Bongo net captured ~3 times more copepods overall than the N70V and ~4 times more if the <0.5 mm body length size class alone was considered. Above a body length of 1 mm, the difference in favour of the Bongo net was broadly invariant, averaging 1.7 across all other classes. Therefore in the case of copepod life stages in the <0.5 mm and 0.5–0.99 mm size classes, which numerically dominated the plankton, we determined the Bongo: N70V ratio for each individual taxon and applied this factor to the N70V data. For size groups >1 mm, the average factor of 1.7 was applied. Where stage structure of a species was not distinguished we have summed abundances of all stages and used an average factor. In the present study, the N70V nets routinely divided the 250-0 m water column into 3 depth strata (250-100 m, 100-50 m and 50-0 m) and so, for each station, the contents of each net were summed and averaged over the entire 250 m. As the Bongo nets only fished from 200-0 m, we multiplied the N70V catch data by 250/200 to provide a conservative m$^{-3}$ abundance estimate to compensate for the difference in depth.

**RESULTS**
In an examination of the summer (October to April) sea surface temperature in our two sampling periods, we determined a significant degree of warming with a median increase of 0.74°C from the *Discovery Investigations* (1920s—1930s) to contemporary times (Mann-Whitney, $T = 11545$, $n = 91, 106$, $P < 0.001$, Fig. 2). The median value of $X_0$ (i.e. the sea surface temperature at which community relative abundance peaked) was 1.27°C (SD 0.29°C) during the 1920-1930s and 2.26°C (SD 0.22°C) during contemporary times (Fig. 2). Bootstrap analyses determined these peaks to be significantly different ($t$-test, $t = -14.989$, 58 df, $P < 0.001$) with $X_0$ being 0.98°C warmer in contemporary times compared to the 1920-1930s. We found the significant difference in $X_0$ between eras was not altered by (1) the influence of extreme years, (2) peripheral spatial regions and (3) taxa with affinities to comparatively high or low temperatures (Table 2, see also Supplementary Information 1). Therefore, all data were included in the final analysis. Compared to a warming in $X_0$ between eras of 0.98°C when analysing the entire dataset, the three exclusion tests found the smallest degree of such warming in $X_0$ to be 0.64°C and the largest, 1.24°C. Across all three exclusion tests there was a consistent trend towards warming in $X_0$ to within ±0.3°C of the mean level. The level of warming in $X_0$ was most sensitive to the inclusion or exclusion of peripheral spatial regions. The taxa chosen to represent the mesozooplankton community was found to have less of an influence on $X_0$, which reflects that the difference between eras was not overly dependent on the analysis including or excluding any one taxon. Nevertheless, each taxon showed a different distributional relationship to sea surface temperature (Fig. 3). In the contemporary era, species such as *Metridia gerlachei* and *Calanus propinquus* had values for $M_0$ (the median temperature of occurrence) close to 2°C while those of *Calanus simillimus* and *Subeucalanus longiceps* were around 4°C. This
reflects differing biogeographic affinities of these species, with the former pair being considered as true Antarctic inhabitants, rarely found north of the Polar Front, while the latter pair span both Antarctic and sub-Antarctic water masses. Despite these different temperature distributions, we found a high degree of uniformity in the response to ocean warming, with the \( M_0 \) values of 15 out of the 16 taxa being higher in contemporary times than in the 1920s-1930s, with the difference being between 0.4 and 1.6°C (Fig. 3). The ranking of taxa according to \( M_0 \) values did alter between the eras (Table 1) with species such as *Pareuchaeta antarctica* and *Clausocalanus breviceps* showing below average increases between the 1920s-1930s and contemporary times, moving them towards colder rankings and others, such as *Calanoides acutus*, above average increases, making their rankings warmer. We did not observe species replacement or a major shift in rank of the dominant zooplankton taxa in terms of relative abundance between the two sampling periods (Table 1). Those taxa that did increase in rank abundance between eras, such as *Calanus simillimus* and *Metridia lucens*, were more associated with warmer waters while taxa which decreased in rank abundance by a similar order, such as *Microcalanus pygmaeus* and *Metridia gerlachei*, had colder temperature distributions. Nevertheless, the median place shift in abundance rank order between eras was 1, signifying only a marginal biogeographic change in community composition.

Geographic projections of \( CRel_A \) show that community peak abundance occurred in much the same locations in both eras (Fig. 4), which was around 60°S to 62°S in the Drake Passage, then broadening and moving northwards across the Scotia Sea to envelope South Georgia, before narrowing into a band between 52°S and 55°S east of South Georgia. Comparatively, the distribution of peak abundance was slightly wider in 1920s-1930s (Fig. 4a) than in contemporary times (Fig. 4b), which reflects the broader temperature relationship function \( G(T\degree C) \) in the former era (See Supplementary Information 2). In Fig. 4d, we assume that the
mesozooplankton community maintains its relationship to surface temperature as observed in the 1920s-1930s and project this relationship onto the surface temperature conditions of the contemporary era. This predicts that peak community abundance would occur further south by approximately 500 km, occurring below 62°S in Drake Passage and remaining south of South Georgia and below 55°S further east. This projection severely underpredicts mesozooplankton community abundance levels in the northern half of the survey region and overpredicts it to the south, compared to contemporary observations (Fig. 4e).

DISCUSSION

We found that, in the intervening period between the Discovery Investigations (1926-1938) and contemporary times (1996-2013), the relationship between mesozooplankton community abundance and sea surface temperature changed, with the temperature of peak community abundance ($X_0$) being 0.98°C warmer in contemporary times compared to the 1920s-1930s. In spatial terms, this changed thermal relationship was manifested in peak community abundance remaining in approximately the same location between the two eras despite a poleward shift in surface isotherms. The observed warming did not alter community composition, with the species assemblage and the relative abundance of key species within the community remaining principally unchanged with the exception of two warmer water species that became marginally more abundant in contemporary times. Individually, as well as combined, key mesozooplankton in the Southern Ocean now peak in abundance at surface temperatures towards the outer limits of the 1920s-1930s thermal envelope.

When we assumed that the mesozooplankton community maintained the same relationship with temperature as seen in the 1920s-1930s, peak abundance in contemporary times was predicted to be up to 500 km further south. This was a severe overprediction of contemporary
abundance observations in that region, in contrast with abundances further north, which were underpredicted. The assumption that communities remain within their thermal envelope, or within the limits of other key environmental variables, and shift their distribution accordingly is one that is widely made in attempts to predict the impacts of future climate change (Guisan and Thuiller, 2005, Helouet and Beaugrand 2007) and is supported by a wide body of empirical evidence (Parmesan and Yohe 2003). In a consideration of multidecadal range changes in the *Calanus finmarchicus* and *C. helgolandicus* populations of the North Atlantic and adjacent subarctic regions for example, Hinder et al. (2014) found that the abundance versus sea surface temperature relationships of both species remained relatively fixed over time. In the Southern Ocean, Mackey et al. (2012) assumed a fixed relationship between macrozooplankton species distribution and sea surface temperature and predicted a general poleward movement as a result of a 1°C rise. Our findings show that a fixed relationship between species distribution and sea surface temperature cannot be assumed in the case of the Southern Ocean mesozooplankton community.

The changed relationship between Southern Ocean mesozooplankton and sea surface temperature between the 1920s and 1930s and contemporary times is likely to reflect the particular set of circumstances faced by zooplankton communities in this polar region. Unlike the northern hemisphere, where there is geographic scope to move polewards to comparatively high latitudes, the potential for poleward displacement in the Southern Hemisphere is limited because of the Antarctic continental landmass, strong circumpolar currents and extensive sea ice. Specifically, within the Atlantic sector, surface waters of the Antarctic Circumpolar Current flow in a northeastward direction and are bounded to the south by the cyclonic Weddell Gyre, where sea ice persists until late in the Antarctic summer. Large-scale poleward range shifts are therefore not presently possible for Southern Ocean populations.
Furthermore, factors other than temperature may dominate distribution and abundance in this region, particularly the availability of phytoplankton. Park et al. (2010) have shown that regular and predictable phytoplankton blooms occur in only a small proportion of the southwest Atlantic sector of the Southern Ocean, but primary production is generally high throughout much of the region that we identified to contain peak abundances in mesozooplankton. Primary production in this region generally occurs from November onwards, facilitated variously by the supply of limiting nutrients to the upper mixed layer via deep mixing, topographic upwelling or water column stabilisation particularly in the region of the retreating ice-edge (Park et al. 2010). This would facilitate zooplankton recruitment and underpin the distribution patterns we observe through the summer months. We cannot quantitatively assess whether chlorophyll distribution and periodicity has changed appreciably in the 60 years between sampling eras but it is unlikely given that mixing and topographical supply of limiting nutrients are so important within the region. In particular, there is strong evidence that iron availability controls the distribution and biomass of phytoplankton in the southwest Atlantic sector, since high Chl-a concentrations are mainly associated with temperature and density profiles that indicate mixing between Antarctic Circumpolar Current waters and iron enriched waters originating from coastal regions or from upwelling of deeper waters associated with bathymetric features (Holm-Hansen et al. 2004). By contrast, the distribution of primary productivity in the Arctic is tightly coupled to the extent and timing of sea-ice, which affects the availability of light and nutrients (Tremblay et al. 2006) meaning that zones of high productivity are much less likely to be geographically fixed. Consequently, ocean warming and sea-ice retreat will have a large impact on the distribution of high productivity zones in the Arctic (Popova et al. 2012).

Another major factor that influences the distribution of many polar mesozooplankton species is their lifecycle patterns, particularly for those that spend parts of their life in deeper water.
masses. Over seasonal cycles, many mesozooplankton taxa change vertical distribution, moving between overlying water masses (Atkinson 1990). During spring and summer, the majority of Southern Ocean mesozooplankton have a modal depth that is centred in Antarctic Surface Water (AASW, between 0 and 100 m). However, by autumn, taxa such as *Calanoides acutus*, *Calanus simillimus*, *Rhincalanus gigas* and *Eucalanus longiceps* descend to the Winter Water layer between 100 m and 250 m and, by winter, they have largely descended beyond 250 m where they occupy Circumpolar Deep Water (CDW). Although there has been reported warming of the CDW over recent decades (Gille, 2008; Schmidtko et al, 2014), it is an order of magnitude lower than that of the AASW. From a physiological perspective therefore, the temperature experienced by mesozooplankton species inhabiting the CDW during winter has essentially remained unchanged over the last century. Wintertime occupancy of the thermally invariant CDW may allow seasonally migrating species to complete their lifecycles successfully despite the physiological challenge of occupying the increasingly warm AASW during summer. For some deep diapausing species, such as *Calanoides acutus*, the overwintering phase of the lifecycle may be even more influential, with the species spending up to 8 months a year in the CDW at depths of around 1000 m to 1500 m (Andrews 1966). Spending only a limited period within the surface layers may explain how this species was able to tolerate one of the largest degrees of warming in $M_0$ (the median sea surface temperature of occurrence) between the two eras.

Even for those mesozooplankton taxa that largely remain in the surface layers year round, such as *Oithona spp.*, *Clausocalanus laticeps* and *Ctenocalanus vanus*, there is marked seasonality in temperatures that are likely to condition their physiology. A flexibility and responsiveness to changing environmental conditions allows species to optimise their performance over annual cycles. For instance, in the Arctic, Freese et al. (2016) found distinct seasonal oscillations in digestive enzyme activity in the copepod *Calanus glacialis*.
with much lower activity levels during winter, while Lischka et al. (2008) found differing seasonal patterns in digestive enzyme between two further Arctic copepod species, *Pseudocalanus minutus* and *Oithona similis*, with a spring activity peak in the former and a lower level of seasonal oscillation in the latter. The differing patterns of activity in each species reflects the diversity in their respective life-cycle strategies, both in terms of timing of reproduction and peak energy demand and their optimal diets. A community level response to ocean warming will typically be comprised of such a mixture of responses at the species level.

In the southwest Atlantic sector of the Southern Ocean, seasonal oscillations in sea surface temperatures between summer and winter range between 3 and 5°C (Venables et al. 2012). This is considerably less than the 10°C seasonal change experienced by subpolar and temperate pelagic species. Nevertheless, even a 3°C seasonal oscillation means that higher temperatures in contemporary Southern Ocean sea surface environments were at least within the experience of the populations that existed in the 1920 and 1930s, if at the outer limits. This Southern Ocean region is also notable for the high numbers of mesoscale eddies and large meanders of oceanographic fronts, particularly the Polar Front and the Southern Antarctic Circumpolar Current Front, which result in short term oscillations in sea surface temperatures of several degrees across much of the survey area of the present study (Moore et al. 1999, Boehme et al. 2008, Barré et al. 2011, Venables et al. 2012). Only species that are resilient to such variability in sea surface temperature will succeed within these Southern Ocean environments, which may further precondition them to longer-term thermal changes.

Our finding that the spatial distributions of Southern Ocean mesozooplankton communities have not advanced polewards despite surface layer warming in the Atlantic sector over at least the past six decades has meant that the lower trophic levels of this system have remained relatively stable in the face of at least one facet of environmental change. This is key not only
to our understanding of the resilience of marine food webs to climatic change but also to
decision making regarding the location and timing of fisheries while accounting for the wider
ecosystem impacts (Watters et al. 2013, Constable et al. 2014). At present, most projections
of ecosystem response do not factor in the capacity of the resident communities to be resilient
to change and retain locations and distributional ranges (Angilletta 2009). Efforts to
parameterise potential resilience in a mechanistic way must be increasingly undertaken if we
are to predict the future distributional ranges of species and communities in a robust manner.

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**Figure captions**

**Figure 1.** Distribution of sample stations. Distribution of zooplankton abundance estimates and sea surface temperature measurements used to determine warming in the Atlantic sector of the Southern Ocean.  

- **a,** Discovery Investigations (October to April 1926—1938) zooplankton abundance.  
- **b,** Discovery Investigations sea surface temperature.  
- **c,** Contemporary cruises (October to April 1996—2013) zooplankton abundance.  
- **d,** Contemporary cruises sea surface temperature.  

Ocean depths < 500 m shaded grey. Only stations south of the Polar Front, as determined from the vertical temperature profile at each station, were used. Inset shows study region and 7-year mean (1987-1993) position of the Polar Front (Moore et al. 1999).

**Figure 2.** Comparison of sea surface temperature offset (black) and the temperature of peak mesozooplankton community abundance ($X_0$, red) between October and April in the Southern Ocean Atlantic sector (65°S—49°S, 80°W—20°W) during the Discovery Investigations (October to April 1926—1938) and contemporary times (October to April 1996—2013). The horizontal line within each box denotes, respectively, the median value of temperature offset and the median $X_0$, upper and lower box limits, the 25th and 75th percentiles, whiskers, 5th and 95th percentiles, and dots, maximum and minimum. Sea surface temperature offset values represent the difference between sample station values and the World Ocean Atlas (WOA) 2013 v2 monthly mean 1° surface climatology over 2005—2012. Differences were averaged for every grid cell containing at least 1 sampling station.

**Figure 3.** Sea surface temperature ranges of individual mesozooplankton taxa between eras.  

Sea surface temperature ranges of 16 dominant taxa (in terms of abundance and biomass) in the Southern Ocean Atlantic sector (65°S—49°S, 80°W—20°W) during the
*Discovery Investigations (October to April 1926—1938) and contemporary times (October to April 1996—2013).* The horizontal line in each box represents the median temperature of occurrence (M0). Upper and lower box limits denote the 25th and 75th percentiles, whiskers, 5th and 95th percentiles, and dots, maximum and minimum. The names of taxa have been abbreviated, as detailed in Table 1.

**Figure 4.** Projected distributions of observed and predicted mesozooplankton community abundance between eras. Zooplankton community relative abundance anomaly (CRelA) as \( f(\text{sea surface temperature}) \) in the Southern Ocean Atlantic sector during the *Discovery Investigations (October to April 1926—1938)* and contemporary times (October to April 1996—2013).

- **a**, CRelA for *Discovery Investigations*.
- **b**, CRelA for contemporary times.
- **c**, Difference between CRelA for contemporary times and *Discovery Investigations*.
- **d**, Expected present day CRelA assuming the zooplankton community maintained a fixed relationship with sea surface temperature since the *Discovery Investigations* era to contemporary times.
- **e**, Expected difference in CRelA from *Discovery Investigations era to contemporary times* had the relationship to sea surface temperature remain fixed (d – a). Mean sea surface isotherms (°C) for October-April for the *Discovery Investigations* (a) and contemporary times (b, d) are plotted.
<table>
<thead>
<tr>
<th>Taxon</th>
<th>Discovery Investigations</th>
<th>Contemporary era</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$M_0$ (°C)</td>
<td>Rank</td>
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<tr>
<td>Microcalanus pygmaeus</td>
<td>0.43</td>
<td>1</td>
</tr>
<tr>
<td>Metridia gerlachei (M. ger)</td>
<td>0.89</td>
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</tr>
<tr>
<td>Calanoides acutus (C.acu)</td>
<td>1.08</td>
<td>3</td>
</tr>
<tr>
<td>Oncaea spp. (Oncae)</td>
<td>1.08</td>
<td>4</td>
</tr>
<tr>
<td>Pareuchaeta antarctica (P. ant)</td>
<td>1.14</td>
<td>5</td>
</tr>
<tr>
<td>Racovitzanus (Racov)</td>
<td>1.21</td>
<td>6</td>
</tr>
<tr>
<td>Calanus propinquus (C.pro)</td>
<td>1.26</td>
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</tr>
<tr>
<td>Ctenocalanus vanus (Cteno)</td>
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<tr>
<td>Scolecithricella minor (S.min)</td>
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<tr>
<td>Metridia lucens (M.luc)</td>
<td>1.85</td>
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<tr>
<td>Oithona spp. (Oitho)</td>
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<tr>
<td>Clausocalanus laticeps (C.lat)</td>
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<tr>
<td>Rhincalanus gigas (R.gig)</td>
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<tr>
<td>Clausocalanus breviceps (C.brev)</td>
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<tr>
<td>Calanus simillimus (C.sim)</td>
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</tr>
<tr>
<td>Subeucalanus longiceps (S.lon)</td>
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<td>C. acu</td>
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<tr>
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**Table 1.** Median rank order of 16 dominant taxa of net-caught mesozooplankton in the Atlantic sector of the Southern Ocean during the Discovery Investigations (October to April 1926—1938) and contemporary era (October to April 1996—2013) with respect to median temperature ($M_0$) (left) and relative abundance rank (right). In descending order, rankings are from lowest to highest temperatures and from
highest to lowest relative abundance. Note that Contemporary relative abundance ranks were based only on Bongo 200-0m samples. All taxa are arthropods belonging to the sub-class Copepoda
Table 2. Tests to determine the effect of the exclusion of certain subsets of data on $X_0$, namely years or spatial regions that were either extremely warm or cold, or those species whose distributional ranges were the warmest or the coldest (Calanus simillimus and Microcalanus spp. respectively). Mean $X_0$ represents the mean (±1 SD) surface temperature at which peak community relative abundance occurs. The mean difference to the opposing dataset was calculated as the modulus difference in $X_0$ values between the dataset from which a subset had been excluded and the original dataset of the opposing era. All differences were found to be statistically significant at $P<0.05$. 

<table>
<thead>
<tr>
<th>Excluded data</th>
<th>1920s-1930s</th>
<th>Mean $X_0$ (°C)</th>
<th>Mean difference to contemporary era (°C)</th>
<th>Contemporary</th>
<th>Mean difference to Discovery Investigations era (°C)</th>
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<tr>
<td>None</td>
<td>1.27 (0.29)</td>
<td>0.98</td>
<td>2.26 (0.22)</td>
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<tr>
<td>High temperature year</td>
<td>1.05 (0.30)</td>
<td>1.21</td>
<td>2.38 (0.17)</td>
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<tr>
<td>Low temperature year</td>
<td>1.50 (0.36)</td>
<td>0.76</td>
<td>2.38 (0.19)</td>
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<td>Warmest sectors</td>
<td>0.97 (0.29)</td>
<td>1.29</td>
<td>2.25 (0.20)</td>
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<tr>
<td>Coldest sectors</td>
<td>1.62 (0.49)</td>
<td>0.64</td>
<td>2.40 (0.33)</td>
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<tr>
<td><em>Microcalanus</em> spp.</td>
<td>1.25 (0.26)</td>
<td>1.00</td>
<td>2.31 (0.21)</td>
<td>1.04</td>
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<tr>
<td><em>Calanus simillimus</em></td>
<td>1.02 (0.38)</td>
<td>1.24</td>
<td>2.28 (0.33)</td>
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