

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

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13

14 **ABSTRACT**

15 The biogeographic response of oceanic planktonic communities to climatic change has a
16 large influence on the future stability of marine food webs and the functioning of global
17 biogeochemical cycles. Temperature plays a pivotal role in determining the distribution of
18 these communities and ocean warming has the potential to cause major distributional shifts,
19 particularly in polar regions where the thermal envelope is narrow. We considered the
20 impact of long-term ocean warming on the spatial distribution of Southern Ocean
21 mesozooplankton communities through examining plankton abundance in relation to sea
22 surface temperature between two distinct periods, separated by around 60 years. Analyses

23 considered 16 dominant mesozooplankton taxa (in terms of biomass and abundance) in the
24 southwest Atlantic sector of the Southern Ocean, from net samples and *in situ* temperature
25 records collected during the *Discovery Investigations* (1926-1938) and contemporary
26 campaigns (1996-2013). Sea surface temperature was found to have increased significantly
27 by 0.74°C between the two eras. The corresponding sea surface temperature at which
28 community abundance peaked was also significantly higher in contemporary times, by
29 0.98°C. Spatial projections indicated that the geographical location of community peak
30 abundance had remained the same between the two eras despite the poleward advance of sea
31 surface isotherms. If the community had remained within the same thermal envelope as in the
32 1920s-1930s, community peak abundance would be 500 km further south in the
33 contemporary era. Studies in the northern hemisphere have found that dominant taxa, such as
34 calanoid copepods, have conserved their thermal niches and tracked surface isotherms
35 polewards. The fact that this has not occurred in the Southern Ocean suggests that other
36 selective pressures, particularly food availability and the properties of underlying water
37 masses, place greater constraints on spatial distributions in this region. It further demonstrates
38 that this community is thermally resilient to present levels of sea surface warming.

39

40 INTRODUCTION

41 Biogeographic changes in the distributions of populations and communities are a
42 widely reported outcome of recent rapid climatic shifts (Parmesan and Yohe 2003). The
43 single most important physical variable affecting marine systems is temperature, as
44 manifested in the close alignment between the distribution patterns of marine ectotherms and
45 latitudinal and vertical thermal gradients (Somero 2010). These patterns are no doubt
46 influenced by the strong relationship between temperature and physiological performance

47 (Pörtner 2002). However, other ecological aspects such as species interactions, trophic
48 efficiency and community composition are also strongly related to temperature gradients
49 (Richardson 2008). The rate and extent of ocean warming is therefore of critical importance
50 to the viability of future marine populations (Richardson 2008).

51 Recent biogeographic shifts in marine zooplankton have most commonly been
52 associated with the warming of the sea surface (Beaugrand et al. 2002, Hinder et al. 2014). In
53 the northeast Atlantic, Beaugrand et al. (2002) reported that members of warm water
54 assemblages of crustacean mesozooplankton (the southern shelf-edge assemblage and the
55 pseudo oceanic assemblage) moved more than 1100 km polewards over the past 50 years
56 (approximately 200 km per decade) although Chust et al. (2013) determined these
57 translocations to have been considerably lower (8 to 16 km per decade for *Calanus*
58 *finmarchicus*). Similarly, Lindley and Daykin (2005) determined *Centropages chierchiae* and
59 *Temora stylifera* to have both moved north from the vicinity of the Iberian Peninsula in the
60 1970s and 1980s to the English Channel in the 1990s (6° of latitude, amounting to around
61 300 km per decade). In both of these instances, the reported distributional shifts took place
62 over periods where sea surface temperature warmed by 1°C although the shifts may also be
63 partially influenced by stronger northward currents on the European shelf edge.

64 The Southern Ocean has undergone some of the world's most rapid regional ocean
65 warming, with a summertime increase at the sea surface of more than 1°C recorded west of
66 the Antarctic Peninsula between 1951—1998 (Meredith and King 2005) and an increase in
67 the upper 100 m of ~0.9°C in January at South Georgia between 1925—2006 (Whitehouse et
68 al. 2008). This long-term shift in sea surface temperature must be placed within the context of
69 seasonal temperature variation, which is just a few degrees in the surface layers (Venables et
70 al. 2012). Individuals in contemporary times may therefore be experiencing average water
71 temperatures towards the upper limits of historical seasonal temperature fluctuations.

72 Furthermore, the potential for a biogeographic shift polewards in the Southern Ocean is
73 limited because of the Antarctic continental landmass, strong circumpolar currents and
74 extensive sea-ice. The resilience of Southern Ocean marine taxa to ocean warming must
75 therefore contend with both a geographic narrowing of their temperature envelope, and a
76 seasonal temperature experience that is comparatively small in relation to species found in
77 more temperate regions. If such temperature changes cannot be tolerated, a contraction of
78 their range and replacement with more temperate species will result, with ecological
79 consequences both to the secondary productivity of the system and its foodwebs.

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

92 Here we consider how Southern Ocean mesozooplankton populations have responded
93 to a period of substantial ocean warming that has continued since the early part of the
94 twentieth century. We compare the distributions of a number of key taxa between two
95 periods, the first sampled by the *Discovery Investigations* between 1926 and 1938 and, the
96 second, by contemporary campaigns between 1996 and 2013. The analyses were performed

97 on net samples and *in situ* sea surface temperatures collected during the summertime period
98 within the southwest Atlantic sector of the Southern Ocean. Both datasets encompassed more
99 than a decade of sampling (13 and 18 years respectively) in order to synthesise across
100 intradecadal climatic cycles and minimise the influence of interannual variability on
101 comparative analyses (Murphy et al. 2007, Loeb and Santora 2015, Steinberg et al. 2015).
102 Our analyses establish relationships between the distributions of key taxa and prevailing sea
103 surface temperature to determine how individual species, and the mesozooplankton
104 community as a whole, have responded to the intervening period of ocean warming.
105 Although our findings must be placed within the unique set of circumstances that are faced
106 by open ocean communities in the Southern Ocean, they also provide a wider case study of
107 the potential resilience of such communities to climatic change.

108

109 MATERIALS AND METHODS

110 **Mesozooplankton species composition and abundance** We analysed net samples from 155
111 stations south of the Polar Front in the southwest Atlantic sector of the Southern Ocean,
112 collected as part of the *Discovery Investigations* (1926-1938, [Fig. 1a](#)). The samples were
113 obtained via a series of N70V plankton nets deployed vertically between 250 m and the
114 surface (see Kemp et al. 1929). Mesh sizes in this net decrease in stages from 5 mm in the
115 upper part, to 440 µm and then 195 µm in the mid and lower parts respectively
116 (measurements are metric equivalents of the original imperial units). A further 451 samples
117 were analysed from nets taken in the same ocean sector in contemporary times (1996-2013,
118 [Fig. 1c](#)). The contemporary samples were obtained from deployments of either RMT1 nets
119 (330 µm mesh) fished obliquely from 200-0 m or Bongo nets (200 µm) fished vertically from
120 either 200-0 m or 400-0 m. During sample analysis, larger organisms were either enumerated

121 from complete samples, or the whole sample placed in a Folsom plankton splitter and
122 fractionated into replicate aliquots until countable numbers (~200 individuals) were estimated
123 to be present. For smaller, more numerous organisms, the sample was further fractionated
124 until countable replicates (~500-800 organisms) were obtained. Abundances of taxa were
125 standardised according to the split fraction, and the amount of water each net filtered was
126 estimated based on mouth area and distance towed, to derive individual species
127 concentrations (ind. m⁻³).

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

132 To determine the change in sea surface temperature between the 1920s-1930s and present
133 day, data from all available stations from the *Discovery Investigations* and contemporary
134 cruises between the months of October and April and located south of the Polar Front in
135 water depths >500 m were analysed for the region 65—49°S, 80—20°W ([Fig. 1](#)). Stations
136 were identified as being south of the Polar Front from their vertical temperature profile
137 (Gordon et al. 1977). Duplicate temperature measurements, defined as measurements taken
138 within 1 day and 5 km of another sample, were excluded. The surface temperature datasets
139 were compared with the World Ocean Atlas (WOA) 2013 v2 monthly mean 1° surface
140 climatology for 2005—2012 (Locarnini et al. 2013). For each dataset, nearest neighbour
141 interpolation was used to extract the WOA temperature at each station from the
142 corresponding mean monthly objectively analysed field at 0 m depth. WOA grid cells with
143 zero contributing data points were excluded (Meredith and King 2005). The resulting
144 differences between the station data points and the WOA temperature fields were averaged at
145 1° spatial resolution to remove geographic bias from the station coverage. The median offset

146 from the WOA data for the gridded data from the *Discovery Investigations* and contemporary
147 data was -0.78°C and -0.04°C, respectively (N = 106 for Discovery, N = 91 for
148 contemporary).

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

154 **Numerical methods** Mesozooplankton data analyses focussed on the crustacean fraction
155 which made up approximately 90% of all organisms within net samples. Analyses considered
156 16 taxa from this fraction chosen because they were major contributors to either the
157 abundance or the biomass of the samples (biomass was determined through multiplying
158 abundance by typical dry weight and was calculated only for the purpose of identifying
159 species that were less abundant but still major contributors through their large individual
160 size). Analyses were restricted to net samples taken between October and April. The datasets
161 were normalised such that each taxon made an equal contribution to the metric of community
162 response (*CRel*, see below) and that the influence of less abundant species was the same as
163 more abundant ones. This ensured that the response metric was not dominated by a small
164 number of highly abundant taxa.

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

166

$$167 \quad Rel_{x,y} = \frac{Abs_{x,y}}{\sum_{y=1}^{y=n} Abs_x} \quad (1)$$

168

169 where Rel is relative abundance, Abs , absolute abundance (ind. m^{-3}), x , taxon, y , the sample
170 station and n , the total number of sampling stations. For the contemporary sample set, it was
171 necessary to determine Rel separately for three different types of net deployment (RMT1
172 200-0 m, Bongo 200-0 m and Bongo 400-0 m). The resulting three matrices were
173 subsequently concatenated into a single matrix before further analysis. Community relative
174 abundance ($CRel$) was calculated as:

175

176
$$CRel = \sum_{x=1}^{x=16} Rel_y \quad (2)$$

177

178 Cumulative probability curves were generated for (i) cumulative station rank as a function of
179 sea surface temperature and (ii) cumulative Rel or $CRel$ as a function of sea surface
180 temperature. Medians and percentiles of Rel were calculated, from which the corresponding
181 temperatures were determined to ascertain the relationship of each taxon to temperature. For
182 $CRel$, the residual difference between (i) and (ii), the community relative abundance anomaly
183 ($CRel_A$), was calculated to derive a metric of abundance that normalises for the distribution of
184 sample stations between sea surface temperatures. $CRel_A$ trajectories were fitted by a
185 Gaussian distribution function ($G_{(T^{\circ}C)}$) where the inflection point, X_0 , denotes the sea surface
186 temperature at which peak relative abundance occurs. The respective $G_{(T^{\circ}C)}$ functions were
187 plotted spatially, using the sea surface temperature fields described above, to identify regions
188 of peak $CRel_A$. A bootstrapping analysis was performed to determine the level of difference
189 in X_0 between the *Discovery Investigations* and contemporary datasets, following Hilborn and
190 Mangel (1997). $CRel_A$ was resampled through selecting 148 datapoints with replacement
191 from either the *Discovery Investigations* or contemporary datasets 30 times. $G_{(T^{\circ}C)}$ and the
192 value of X_0 was derived for each resampled dataset. The significance level of the difference in

193 X_o between *Discovery Investigations* and contemporary datasets was tested by a two tailed t-
194 test, having first passed tests for Normality (Shapiro-Wilk) and Equal Variance. It was not
195 possible to fit a Gaussian distribution to the temperature distributions of a number of
196 individual taxa since they were not normally distributed, so the median temperature of
197 occurrence (termed M_o) was derived for all individual taxa for comparative purposes (Table
198 1).

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

218 determined. This was compared to the original value of the opposing era and tested
219 statistically to determine if the difference in X_0 between eras remained significant.

220 **Comparison of relative abundance ranks between eras** To establish whether community
221 structure had altered between eras, rankings in relative abundance of individual taxa were
222 compared. For contemporary samples, only the Bongo nets that fished from 200-0 m were
223 used for the comparison, given that they were the closest in sampling method to the N70V
224 nets. Differences in the sampling efficiencies of the nets were accommodated through
225 conversion factors derived from corresponding *in situ* net trials (Ward et al. 2012). Briefly,
226 when both nets were fished to a depth of 200 m, the Bongo net captured ~3 times more
227 copepods overall than the N70V and ~4 times more if the <0.5 mm body length size class
228 alone was considered. Above a body length of 1 mm, the difference in favour of the Bongo
229 net was broadly invariant, averaging 1.7 across all other classes. Therefore in the case of
230 copepod life stages in the <0.5 mm and 0.5–0.99 mm size classes, which numerically
231 dominated the plankton, we determined the Bongo: N70V ratio for each individual taxon and
232 applied this factor to the N70V data. For size groups >1 mm, the average factor of 1.7 was
233 applied. Where stage structure of a species was not distinguished we have summed
234 abundances of all stages and used an average factor. In the present study, the N70V nets
235 routinely divided the 250-0 m water column into 3 depth strata (250-100 m, 100-50 m and
236 50-0 m) and so, for each station, the contents of each net were summed and averaged over the
237 entire 250 m. As the Bongo nets only fished from 200-0 m, we multiplied the N70V catch
238 data by 250/200 to provide a conservative m^{-3} abundance estimate to compensate for the
239 difference in depth.

240

241 **RESULTS**

242 In an examination of the summer (October to April) sea surface temperature in our two
243 sampling periods, we determined a significant degree of warming with a median increase of
244 0.74°C from the *Discovery Investigations* (1920s—1930s) to contemporary times (Mann-
245 Whitney, $T = 11545$, $n = 91, 106$, $P < 0.001$, Fig. 2)

246 The median value of X_0 (i.e. the sea surface temperature at which community relative
247 abundance peaked) was 1.27°C (SD 0.29°C) during the 1920-1930s and 2.26°C (SD 0.22°C)
248 during contemporary times (Fig. 2). Bootstrap analyses determined these peaks to be
249 significantly different (t-test, $t = -14.989$, 58 df, $P < 0.001$) with X_0 being 0.98°C warmer in
250 contemporary times compared to the 1920-1930s.

251 We found the significant difference in X_0 between eras was not altered by (1) the influence of
252 extreme years, (2) peripheral spatial regions and (3) taxa with affinities to comparatively high
253 or low temperatures (Table 2, see also Supplementary Information 1). Therefore, all data
254 were included in the final analysis. Compared to a warming in X_0 between eras of 0.98°C
255 when analysing the entire dataset, the three exclusion tests found the smallest degree of such
256 warming in X_0 to be 0.64°C and the largest, 1.24°C. Across all three exclusion tests there was
257 a consistent trend towards warming in X_0 to within $\pm 0.3^\circ\text{C}$ of the mean level. The level of
258 warming in X_0 was most sensitive to the inclusion or exclusion of peripheral spatial regions.
259 The taxa chosen to represent the mesozooplankton community was found to have less of an
260 influence on X_0 , which reflects that the difference between eras was not overly dependent on
261 the analysis including or excluding any one taxon.

262 Nevertheless, each taxon showed a different distributional relationship to sea surface
263 temperature (Fig. 3). In the contemporary era, species such as *Metridia gerlachei* and
264 *Calanus propinquus* had values for M_0 (the median temperature of occurrence) close to 2°C
265 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_o 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_o 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 ($G_{(T^{\circ}C)}$) 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).

298

299 **DISCUSSION**

300 We found that, in the intervening period between the *Discovery Investigations* (1926-1938) 301 and contemporary times (1996-2013), the relationship between mesozooplankton community 302 abundance and sea surface temperature changed, with the temperature of peak community 303 abundance (X_0) being 0.98°C warmer in contemporary times compared to the 1920s-1930s. 304 In spatial terms, this changed thermal relationship was manifested in peak community 305 abundance remaining in approximately the same location between the two eras despite a 306 poleward shift in surface isotherms. The observed warming did not alter community 307 composition, with the species assemblage and the relative abundance of key species within 308 the community remaining principally unchanged with the exception of two warmer water 309 species that became marginally more abundant in contemporary times. Individually, as well 310 as combined, key mesozooplankton in the Southern Ocean now peak in abundance at surface 311 temperatures towards the outer limits of the 1920s-1930s thermal envelope.

312 When we assumed that the mesozooplankton community maintained the same relationship 313 with temperature as seen in the 1920s-1930s, peak abundance in contemporary times was 314 predicted to be up to 500 km further south. This was a severe overprediction of contemporary

315 abundance observations in that region, in contrast with abundances further north, which were
316 underpredicted. The assumption that communities remain within their thermal envelope, or
317 within the limits of other key environmental variables, and shift their distribution accordingly
318 is one that is widely made in attempts to predict the impacts of future climate change (Guisan
319 and Thuiller, 2005, Helouet and Beaugrand 2007) and is supported by a wide body of
320 empirical evidence (Parmesan and Yohe 2003). In a consideration of multidecadal range
321 changes in the *Calanus finmarchicus* and *C. helgolandicus* populations of the North Atlantic
322 and adjacent subarctic regions for example, Hinder et al. (2014) found that the abundance
323 versus sea surface temperature relationships of both species remained relatively fixed over
324 time. In the Southern Ocean, Mackey et al. (2012) assumed a fixed relationship between
325 macrozooplankton species distribution and sea surface temperature and predicted a general
326 poleward movement as a result of a 1°C rise. Our findings show that a fixed relationship
327 between species distribution and sea surface temperature cannot be assumed in the case of the
328 Southern Ocean mesozooplankton community.

329 The changed relationship between Southern Ocean mesozooplankton and sea surface
330 temperature between the 1920s and 1930s and contemporary times is likely to reflect the
331 particular set of circumstances faced by zooplankton communities in this polar region. Unlike
332 the northern hemisphere, where there is geographic scope to move polewards to
333 comparatively high latitudes, the potential for poleward displacement in the Southern
334 Hemisphere is limited because of the Antarctic continental landmass, strong circumpolar
335 currents and extensive sea ice. Specifically, within the Atlantic sector, surface waters of the
336 Antarctic Circumpolar Current flow in a northeastward direction and are bounded to the
337 south by the cyclonic Weddell Gyre, where sea ice persists until late in the Antarctic summer.
338 Large-scale poleward range shifts are therefore not presently possible for Southern Ocean
339 populations.

340 Furthermore, factors other than temperature may dominate distribution and abundance in this
341 region, particularly the availability of phytoplankton. Park et al. (2010) have shown that
342 regular and predictable phytoplankton blooms occur in only a small proportion of the
343 southwest Atlantic sector of the Southern Ocean, but primary production is generally high
344 throughout much of the region that we identified to contain peak abundances in
345 mesozooplankton. Primary production in this region generally occurs from November
346 onwards, facilitated variously by the supply of limiting nutrients to the upper mixed layer via
347 deep mixing, topographic upwelling or water column stabilisation particularly in the region
348 of the retreating ice-edge (Park et al. 2010). This would facilitate zooplankton recruitment
349 and underpin the distribution patterns we observe through the summer months. We cannot
350 quantitatively assess whether chlorophyll distribution and periodicity has changed
351 appreciably in the 60 years between sampling eras but it is unlikely given that mixing and
352 topographical supply of limiting nutrients are so important within the region. In particular,
353 there is strong evidence that iron availability controls the distribution and biomass of
354 phytoplankton in the southwest Atlantic sector, since high Chl-a concentrations are mainly
355 associated with temperature and density profiles that indicate mixing between Antarctic
356 Circumpolar Current waters and iron enriched waters originating from coastal regions or
357 from upwelling of deeper waters associated with bathymetric features (Holm-Hansen et al.
358 2004). By contrast, the distribution of primary productivity in the Arctic is tightly coupled to
359 the extent and timing of sea-ice, which affects the availability of light and nutrients
360 (Tremblay et al. 2006) meaning that zones of high productivity are much less likely to be
361 geographically fixed. Consequently, ocean warming and sea-ice retreat will have a large
362 impact on the distribution of high productivity zones in the Arctic (Popova et al. 2012).

363 Another major factor that influences the distribution of many polar mesozooplankton species
364 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 *Mo* (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*

390 with much lower activity levels during winter, while Lischka et al. (2008) found differing
391 seasonal patterns in digestive enzyme between two further Arctic copepod species,
392 *Pseudocalanus minutus* and *Oithona similis*, with a spring activity peak in the former and a
393 lower level of seasonal oscillation in the latter. The differing patterns of activity in each
394 species reflects the diversity in their respective life-cycle strategies, both in terms of timing of
395 reproduction and peak energy demand and their optimal diets. A community level response to
396 ocean warming will typically be comprised of such a mixture of responses at the species
397 level.

398 In the southwest Atlantic sector of the Southern Ocean, seasonal oscillations in sea surface
399 temperatures between summer and winter range between 3 and 5°C (Venables et al. 2012).
400 This is considerably less than the 10°C seasonal change experienced by subpolar and
401 temperate pelagic species. Nevertheless, even a 3°C seasonal oscillation means that higher
402 temperatures in contemporary Southern Ocean sea surface environments were at least within
403 the experience of the populations that existed in the 1920 and 1930s, if at the outer limits.
404 This Southern Ocean region is also notable for the high numbers of mesoscale eddies and
405 large meanders of oceanographic fronts, particularly the Polar Front and the Southern
406 Antarctic Circumpolar Current Front, which result in short term oscillations in sea surface
407 temperatures of several degrees across much of the survey area of the present study (Moore et
408 al. 1999, Boehme et al. 2008, Barré et al. 2011, Venables et al. 2012). Only species that are
409 resilient to such variability in sea surface temperature will succeed within these Southern
410 Ocean environments, which may further precondition them to longer-term thermal changes.
411 Our finding that the spatial distributions of Southern Ocean mesozooplankton communities
412 have not advanced polewards despite surface layer warming in the Atlantic sector over at
413 least the past six decades has meant that the lower trophic levels of this system have remained
414 relatively stable in the face of at least one facet of environmental change. This is key not only

415 to our understanding of the resilience of marine food webs to climatic change but also to
416 decision making regarding the location and timing of fisheries while accounting for the wider
417 ecosystem impacts (Watters et al. 2013, Constable et al. 2014). At present, most projections
418 of ecosystem response do not factor in the capacity of the resident communities to be resilient
419 to change and retain locations and distributional ranges (Angilletta 2009). Efforts to
420 parameterise potential resilience in a mechanistic way must be increasingly undertaken if we
421 are to predict the future distributional ranges of species and communities in a robust manner.

422

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429

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572 **Figure captions**

573

574 **Figure 1.** Distribution of sample stations. Distribution of zooplankton abundance estimates
575 and sea surface temperature measurements used to determine warming in the Atlantic
576 sector of the Southern Ocean. *a*, Discovery Investigations (October to April 1926—
577 1938) zooplankton abundance. *b*, Discovery Investigations sea surface temperature.
578 *c*, Contemporary cruises (October to April 1996—2013) zooplankton abundance. *d*,
579 Contemporary cruises sea surface temperature. Ocean depths < 500 m shaded
580 grey. Only stations south of the Polar Front, as determined from the vertical
581 temperature profile at each station, were used. Inset shows study region and 7-year
582 mean (1987-1993) position of the Polar Front (Moore et al. 1999).

583 **Figure 2.** Comparison of sea surface temperature offset (black) and the temperature of peak
584 mesozooplankton community abundance (X_0 , red) between October and April in the
585 Southern Ocean Atlantic sector ($65\text{--}49^\circ\text{S}$, $80\text{--}20^\circ\text{W}$) during the Discovery
586 Investigations (October to April 1926—1938) and contemporary times (October to
587 April 1996—2013). The horizontal line within each box denotes, respectively, the
588 median value of temperature offset and the median X_0 , upper and lower box limits, the
589 25th and 75th percentiles, whiskers, 5th and 95th percentiles, and dots, maximum and
590 minimum. Sea surface temperature offset values represent the difference between
591 sample station values and the World Ocean Atlas (WOA) 2013 v2 monthly mean 1°
592 surface climatology over 2005—2012. Differences were averaged for every grid cell
593 containing at least 1 sampling station.

594 **Figure 3.** Sea surface temperature ranges of individual mesozooplankton taxa between eras.
595 Sea surface temperature ranges of 16 dominant taxa (in terms of abundance and
596 biomass) in the Southern Ocean Atlantic sector ($65\text{--}49^\circ\text{S}$, $80\text{--}20^\circ\text{W}$) during the

597 *Discovery Investigations (October to April 1926–1938) and contemporary times*
598 *(October to April 1996–2013). The horizontal line in each box represents the median*
599 *temperature of occurrence (Mo). Upper and lower box limits denote the 25th and 75th*
600 *percentiles, whiskers, 5th and 95th percentiles, and dots, maximum and minimum. The*
601 *names of taxa have been abbreviated, as detailed in Table 1.*

602 **Figure 4.** *Projected distributions of observed and predicted mesozooplankton community*
603 *abundance between eras. Zooplankton community relative abundance anomaly*
604 *(CRel_A) as f(sea surface temperature) in the Southern Ocean Atlantic sector during*
605 *the Discovery Investigations (October to April 1926–1938) and contemporary times*
606 *(October to April 1996–2013). a, CRel_A for Discovery Investigations. b, CRel_A for*
607 *contemporary times. c, Difference between CRel_A for contemporary times and*
608 *Discovery Investigations. d, Expected present day CRel_A assuming the zooplankton*
609 *community maintained a fixed relationship with sea surface temperature since the*
610 *Discovery Investigations. e, Expected difference in CRel_A from Discovery*
611 *Investigations era to contemporary times had the relationship to sea surface*
612 *temperature remain fixed (d – a). Mean sea surface isotherms (°C) for October–April*
613 *for the Discovery Investigations (a) and contemporary times (b, d) are plotted.*

Taxon	Temperature rank			
	<i>Discovery Investigations</i>		Contemporary era	
	M_0 (°C)	Rank	M_0 (°C)	Rank
<i>Microcalanus pygmaeus</i> (Micro)	0.43	1	2.00	2
<i>Metridia gerlachei</i> (M. ger)	0.89	2	2.04	3
<i>Calanoides acutus</i> (C.acu)	1.08	3	2.51	7
<i>Oncaea</i> spp. (Oncae)	1.08	4	2.50	6
<i>Pareuchaeta antarctica</i> (P. ant)	1.14	5	2.00	1
<i>Racovitzanus</i> (Racov)	1.21	6	2.27	4
<i>Calanus propinquus</i> (C.pro)	1.26	7	2.36	5
<i>Ctenocalanus vanus</i> (Cteno)	1.47	8	2.89	10
<i>Scolecithricella minor</i> (S.min)	1.70	9	2.59	8
<i>Metridia lucens</i> (M.luc)	1.85	10	3.45	13
<i>Oithona</i> spp. (Oitho)	1.88	11	2.68	9
<i>Clausocalanus laticeps</i> (C.lat)	1.90	12	3.48	14
<i>Rhincalanus gigas</i> (R.gig)	2.37	13	3.29	12
<i>Clausocalanus breviceps</i> (C.brev)	3.24	14	3.08	11
<i>Calanus simillimus</i> (C.sim)	3.44	15	4.30	16
<i>Subeucalanus longiceps</i> (S.lon)	3.86	16	4.27	15

Taxon	Relative abundance rank	
	<i>Discovery Investigations</i>	
	Rank	Contemporary era
Oitho	1	1
Cteno	2	2
Oncae	3	3
C. acu	4	5
Micro	5	8
C.pro	6	8
C.sim	7	3
R.gig	8	7
M.ger	9	12
S.min	10	9
P.ant	11	11
M.luc	12	9
C.lat	13	12
Racov	14	15
C.brev	15	14
S.lon	16	15

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

Excluded data	1920s-1930s		Contemporary	
	Mean X_0 (°C)	Mean difference to contemporary era (°C)	Mean X_0 (°C)	Mean difference to <i>Discovery Investigations</i> era (°C)
None	1.27 (0.29)	0.98	2.26 (0.22)	0.98
High temperature year	1.05 (0.30)	1.21	2.38 (0.17)	1.11
Low temperature year	1.50 (0.36)	0.76	2.38 (0.19)	1.11
Warmest sectors	0.97 (0.29)	1.29	2.25 (0.20)	0.98
Coldest sectors	1.62 (0.49)	0.64	2.40 (0.33)	1.13
<i>Microcalanus</i> spp.	1.25 (0.26)	1.00	2.31 (0.21)	1.04
<i>Calanus simillimus</i>	1.02 (0.38)	1.24	2.28 (0.33)	1.00

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 $P < 0.05$.







