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1	Zooplankton community structure and dominant copepod population structure on the
2	southern Kerguelen Plateau during summer 2016
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# 17 Abstract

18 The influence of environmental factors on the horizontal community structure of 19 zooplankton over the southern Kerguelen Plateau was investigated during summer in 2016. Zooplankton abundance ranged from 1,490 to 363,484 ind. 1000 m<sup>-3</sup>, with highest numbers 20 21 observed in the eastern and central areas. Based on cluster analysis the zooplankton were 22 divided into six groups (A-F), and these were only distinguished based on water masses and 23 frontal systems. Groups A to C had abundant zooplankton and were consistent with areas of 24 high chlorophyll *a* concentration. Group D represented low abundance near the southern 25 Antarctic Circumpolar Current front, while group E was clustered south of the Southern 26 Boundary and group F comprised two stations to the east of the Fawn Trough. Generalised linear model (GLM) highlighted both fronts and chlorophyll a concentration as drivers of 27 28 overall zooplankton distribution. However, the population structures of key species were 29 more likely a result of species-specific life cycles rather than water masses and frontal 30 systems.

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Keywords: Calanoides acutus, Calanus propinquus, Metridia gerlachei, Metridia lucens,
 *Rhincalanus gigas*, Fawn Trough, Princess Elizabeth Trough, BANZARE Bank
 34

35 1. Introduction

36 The Kerguelen Plateau, and areas to the south, represents one of the most important regions for primary production in the Indian sector of the Southern Ocean (Arrigo et al., 37 38 2008), with high stocks of toothfish and krill found in the north and south, respectively 39 (Duhamel et al., 2014; Nicol, 2006). However, the southern Kerguelen Plateau has never been 40 investigated as a single region to determine the distribution and abundances of key species, 41 their habitat characteristics, and the transition between the northern fish-based food web 42 (Pruvost et al., 2005) and the southern krill-based food web (Nicol et al., 2012). Zooplankton 43 play a key role in both food webs, as conduits for transferring energy from primary producers 44 to higher trophic levels. To date, the zooplankton in the southern Kerguelen region have not 45 been well described.

46 In the Southern Ocean, seawater temperature and variability in sea-ice extent are 47 increasing (Bracegirdle et al., 2008; Turner et al., 2014), although the magnitude and 48 direction of these changes differ among regions around Antarctica (Constable et al., 2014). 49 Zooplankton communities are influenced by the different frontal zones in the Southern Ocean 50 (Errhif et al., 1997; Hunt and Hosie, 2005; Ward et al., 2012; Tachibana et al., 2017), and 51 shifts in the fronts are expected to induce changes in zooplankton distributions (Constable et 52 al., 2014). For example, a modelled 1 °C temperature rise produced a pole-ward shift for all 53 zooplankton taxa (Atkinson et al., 2012). Food web structures are not well understood for the 54 East Antarctic, compared to, for example, the Scotia Sea (Murphy et al., 2007), the Antarctic 55 Peninsula (Ducklow et al., 2006) and the Ross Sea (Smith et al., 2007). Long-term programs 56 such as the Southern Ocean CPR survey (McLeod et al., 2010) have provided information on 57 the patterns of abundance and distribution of zooplankton for much of East Antarctica; however, they do not cover the southern Kerguelen Plateau, the focus of the current study. 58 59 The Kerguelen Plateau is an area of significant ecological value, with high krill biomass

60 to the south (Pauly et al., 2000), and seabirds, seals and whales, using the plateau for migration 61 and feeding (Patterson et al., 2016). The Kerguelen Axis (KAxis) voyage was designed as a synoptic survey, with multiple transects between 57.6 °S and 65.5 °S and 73.3°E and 93.6 °E 62 (Fig 1). The transects encompassed an oceanographically complex region (Park et al., 2009), 63 64 including the ice-edge, the Southern Boundary (SB) of the ACC and the Southern ACC Front (SAACF). The KAXIS research project aimed to identify and spatially distinguish krill-based 65 and copepod-fish-based food webs and was designed to examine distribution of the food web 66 67 components from bacteria to mid-trophic levels (fish and squid). This part of the program 68 aimed to describe the horizontal distribution of zooplankton over the Southern Kerguelen 69 Plateau. The population structures of dominant large (> 2 mm) copepods are also presented. Finally, to evaluate the effects of environmental factors on zooplankton distribution, and to 70 71 determine whether distinct communities were associated with large-scale oceanographic 72 features we applied generalized linear modelling (GLM) and multivariate statistics. This approach has the potential to provide powerful insights into the influence of environmental 73 74 factors on zooplankton distributions in the Southern Ocean, particularly environmentally 75 variable regions such as the Kerguelen Plateau (Park et al., 2009).

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- 77

# 78 2. Materials and Methods

#### 79 2.1. Field sampling

80 Thirty-seven sites were sampled over the southern Kerguelen Plateau, including the

- 81 BANZARE Bank and the Princess Elizabeth Trough, from 23 January to 19 February 2016,
- 82 onboard the RSV Aurora Australis (Fig. 1, Supplementary 1). At each site zooplankton were
- 83 sampled using an RMT1+8 net, which was deployed by standard double oblique tows from
- 84 the surface to 200 m. The RMT1 net had a mesh size of 315  $\mu$ m and mouth area of 1 m<sup>2</sup>. The

towing speed of the RMT1+8 net ranged between 0.8 and 1.5 m s<sup>-1</sup> knots (mean = 1.1 m s<sup>-1</sup>).
A flow meter was positioned in the mouth of the RMT8 net to calculate the volume of water
filtered; these values were divided by a factor of 9.42 to calculate the volume of water filtered
by the RMT1, as per Ikeda et al. (1986). The RMT was fitted with hard cod ends to ensure
that the organisms collected were in good condition. Upon retrieval, samples were
immediately preserved in 4% buffered formaldehyde solution.

A SeaBird SBE911 plus CTD mounted on a SeaBird rosette sampler was deployed at
each station to the full depth of the water column (see Bestley et al., 2018 for details).

93 Profiles of salinity, temperature and fluorescence were recorded at each station.

94

# 95 2.2 Samples and data analysis

96 In the laboratory, zooplankton samples were split with a Motoda box splitter so that a

97 minimum of 550 individuals was enumerated per sample. Zooplankton were identified to

98 species level where possible and counted under a stereomicroscope (Leica M165C). Large-

99 sized copepods (adults >2 mm; i.e. Calanoides acutus, Calanus propinquus, Calanus

100 simillimus, Metridia gerlachei, Metrida lucens and Rhincalanus gigas) were identified to

101 copepodite stage. To identify the zooplankton, we referred to Razouls (1994) for copepods,

102 Kirkwood (1982) for euphausiids and Boltovskoy (1999) for other species. Abundance is

103 reported as the number of individuals  $1000 \text{ m}^{-3}$ .

104 The mean copepodid stage (*MCS*) of the six large copepods was calculated for each station
105 where they occurred using the following equation:

106 
$$MCS = \frac{\sum_{i=1}^{6} i \times Ai}{\sum_{i=1}^{6} Ai}$$
(1)

107 where *i* is the copepodite stage (1-6 indicates copepodid stage 1– copepodid stage 6), and *Ai* 108 is the abundance (ind. 1000 m<sup>-3</sup>) of the *i*th copepodid stage (Marin, 1987). 109 Multivariate analyses, designed to explore relationships between zooplankton and their environment, were performed with PRIMER v7 (PRIMER-e). Abundance of each taxon was 110 111 fourth-root transformed prior to cluster analysis to reduce the effect of abundant species 112 (Quinn and Keough, 2002). A similarity matrix based on stations was constructed using the 113 Bray-Curtis index, which is useful for biological data when there are many zeros (Quinn and 114 Keough, 2002). For grouping the samples (Q-mode analysis), the similarity indices were 115 coupled with hierarchical agglomerative clustering using a complete linkage method: 116 Unweighted Pair Group Method using Arithmetic mean (UPGMA; Field et al., 1982). 117 Accompanying this analysis, similarity profile analysis (SIMPROF) was added to determine 118 if groupings of the stations were statistically significant (at 5% significance level). Similarity 119 percentages (SIMPER) analysis was applied to determine which species contributed to the 120 top 50% of total abundance for each group. Non-metric multi-dimensional scaling (NMDS) 121 with multiple regression analysis was undertaken to explore relationships between the 122 sampling sites and environmental data. 123 Regional differences in mean abundance among groups were tested by one-way 124 ANOVA and the Tukey-Kramer post-hoc test was applied to distinguish which groups were 125 statistically different. Additionally, a Mann-Whitney U-test was performed on abundance 126 between the clustering groups (A-C vs D-F) using R (version 3.4.0; R Core Team, 2017). 127 To find potential indicator species in the groups that resulted from the cluster 128 analysis, the program Indicator Value (IndVal) was applied (Dufrêne and Legendre, 1997). 129 IndVal was calculated as:

130

$$IndVal_{ij} = A_{ij} * B_{ij} * 100$$
<sup>(2)</sup>

131 Where A<sub>ij</sub>=Nindividuals<sub>ij</sub>/Nindividuals<sub>i</sub>, and B<sub>ij</sub>=Nsite<sub>ij</sub>/Nsites<sub>j</sub>.

132  $A_{ij}$  is a measure of site specificity, where Nindividuals<sub>ij</sub> is the mean number of individuals in 133 species *i* across sites of group *j*, and Nindividuals<sub>i</sub> is the sum of the mean numbers of individuals of species *i* over all groups.  $B_{ij}$  is a measure of group fidelity, where Nsite<sub>ij</sub> is the number of sites in group *j* where species *i* is present, while Nsite<sub>j</sub> is the total number of sites in that group (Dufrêne and Legendre, 1997).

137 To evaluate the effects of environmental drivers on zooplankton community 138 structure, we applied generalised linear models (GLMs, R version 3.4.0; R Core Team, 2017). 139 To run the GLMs for each taxon we used a negative binominal distribution based on count 140 data, with filtered volume applied as an offset. MCS of the copepods were tested based on the 141 Gaussian distribution. We tested for overdispersion by calculating the dispersion parameter 142 (Pearson's chi-square statistic / degrees of freedom in residual deviance) and found that 143 values were close to 1 (0.89 - 1.34), indicating the models captured most of the variation. 144 Only radiolarians had a dispersion parameter (1.89) that justified their removal from further 145 GLM. The following factors were included in the GLM: depth (of the water column); 146 chlorophyll a concentration (chl.a) as a measure of food availability; density averaged over 147 the top 10 dbar, where low values can indicate recent sea ice melt; salinity<sub>200</sub>, which has a 148 direct effect on zooplankton physiology; MLD (mixed layer depth) as shallower depths can 149 enhance primary production leading to more food for zooplankton; Temp<sub>200</sub>, average 150 temperature over the top 200 m as zooplankton metabolism is coupled tightly to temperature; 151 time since melt, with the ice edge a region of high productivity and enhanced food supply; 152 SST (sea surface temperature); and PAR (photosynthetically active radiation), as time when 153 zooplankton are sampled can influence their position in the water column. Further details for 154 defining each of these environmental variables are shown in Table 1. To remove 155 multicollinearity among the environmental parameters we calculated variance inflation 156 factors (VIF) for each parameter. If the VIF was higher than 3, it was removed from the explanatory parameters (O'Brien, 2007). To derive the final model, full models with all 157 158 environmental variables were first constructed. Then, model selection was applied by

159 "stepAIC" in the "MASS" package to choose the final models. Comparison between null and

160 final models by ANOVA confirmed the goodness of fit of the model. If the p value <0.05,

161 then the final model was deemed to be better than the null model.

# 162 **3. Results**

163 *3.1. Spatial changes in hydrographic condition* 

The surface mixed layer (SML) varied among stations, with the deepest at KX34 (68 m) and 164 165 the shallowest at KX18-20 (13 m; Fig 2a). Across the sampling region, the mean temperature 166 of the upper 20 m of the water column (defined as SST) ranged from -1.68 to 3.75 °C; the 167 north-east area was warmest, while the southern area was cooler (Fig. 2b). The mean 168 temperature averaged over the top 200 m of the water column (Fig. 2c) had a smaller range (-169 1.65 to 1.76 °C) compared with the top 20 m, while Mean salinity in the top 200 m ranged 170 from 34 to 34.48, with the north-east area being slightly fresher (Fig. 2d). Mean density in the upper SML ranged from 26.309 to 27.144 kg m<sup>-3</sup>, indicting recent ice melt (Fig. 2e). Finally, 171 Integrated chlorophyll a ranged from 19.7 to 132.8 mg m<sup>-2</sup>, with stations KX04-KX09, KX39 172 and KX47 having concentrations higher than 100 mg m<sup>-2</sup> (Fig. 2f). 173

# 174 *3.2* Spatial changes in the zooplankton community

175 Total zooplankton abundance ranged from 1,490 to 363,484 ind. 1000 m<sup>-3</sup>, with the lowest

abundance at KX43, and the largest at KX15 (Fig. 3a). Higher abundances were observed in

177 the eastern and central areas. The zooplankton community was divided into 6 groups (A–F)

- 178 at 75.7 and 78.7% similarity by Q-mode cluster analysis with SIMPROF, based on
- 179 zooplankton abundances at each site (Fig. 4a). Based on one-way ANOVA and a Tukey-
- 180 Kramer post-hoc test, the abundances of groups A and C were significantly higher than those
- 181 of the remaining four groups (B, D-F; p < 0.0001). Additionally, the mean abundance of

182 groups A-C was about 10 times higher than that of groups D-F ( $67,230\pm79,473$  vs  $6,193\pm$ 183 4035 ind. 1000 m<sup>-3</sup>; Mann-Whitney U-test, p < 0.01). Copepods were the dominant taxon in all 184 six groups (59-76%), while foraminifera were the next most abundant group (4-31%; Fig. 185 4b). NMDS showed clear separation among the groups, with low stress (0.11). Five 186 environmental factors, namely latitude, longitude, temperature, salinity and fluorescence, had 187 correlations of  $R^2 > 0.3$  with the groups based on associations among stations. The 188 distribution of the groups across the sampling region broadly corresponded to water mass 189 distribution (Fig. 5). Groups A, B and C were observed in the central and eastern areas, north 190 of the subpolar zone and along the Kerguelen Plateau. Group D occurred in the central 191 region, mainly in the northern part of the transect. Group E was observed from the Antarctic 192 Slope Current to the Southern Boundary front, while Group F was located in the Fawn 193 Trough Current. 194 Based on the SIMPER analysis the copepods Calanoides acutus, Calanus

195 propinquus, Calanus simillimus, Ctenocalanus spp., Metridia gerlachei, Metridia lucens,

196 Oithona spp., Oncaea spp. and Rhincalanus gigas, the chaetognath Eukrohnia hamata, the

197 euphausiid *Thysanoessa macrura*, radiolarians and foraminiferans were all important

198 contributors to at least one group (Table 2). Foraminifera was the dominant taxon in four

199 groups (A-D), while *C. acutus* was the second dominant species in groups A-C. *Oithona* spp.

200 was the second dominant taxon in group D, and M. gerlachei was dominant in group E;

201 *Ctenocalanus* spp. and *C. simillimus* were the dominant species in group F.

# 202 *3.3. Spatial distribution of large-sized copepods*

*Calanoides acutus* occurred at all stations along the transect, predominantly around the
 central region, with *MCS* values falling between CIII and CIV in the northwest and around

205 CV towards the southeast (Fig. 6). Calanus propinquus also occurred at all stations, with

206 younger copepodid stages more prelavent than for the C. acutus population  $(3.05\pm0.54 \text{ vs})$ 207  $3.54 \pm 0.72$ , Mann-Whitney U-test, p<0.01). Calanus simillimus was observed at only nine 208 stations, most of them north of the Southern Boundary and mainly to the east of plateau; MCS 209 was > 4. Metridia gerlachei occurred at all stations and was abundant on the eastern-most 210 transect and close to the continent; its average MCS was ~ 4. Metridia lucens had a more 211 northerly distribution than M. gerlachei, and its MCS ranged between 3.2 and 5. Rhincalanus 212 gigas occurred at all stations, though in lower numbers than C. acutus and C. propinguus  $(728 \pm 832 \text{ vs } 6,262 \pm 12,834 \text{ and } 2,989 \pm 4,737 \text{ ind. } 1000 \text{ m}^{-3}, \text{ respectively})$ . The mean MCS 213 214 of R. gigas ( $4.5\pm0.67$ ) was higher than those of C. acutus and C. propinguus.

# 215 *3.4* Environmental drivers of the zooplankton community

216 Summaries of the results from the GLM are shown in Tables 3 and 4. For total zooplankton at 217 each site higher abundances were generally associated with warmer temperatures, higher 218 chlorophyll a, shallower depths and decreased light intensity (night). When split into the 219 main taxonomic groups, the effects of environmental drivers were similar to those shown for 220 total zooplankton abundance. For euphausiacea, higher abundance was observed at stations 221 where the mixed layer depths were shallow. The GLMs showed that abundances of five of the 222 large-size (> 2 mm) copepods (modelled separately), responded in a similar fashion to the 223 total copepod group, although *M. gerlachei* showed higher abundances with cooler 224 temperatures in the top 200 m of the water column. Calanoides acutus and M. lucens had 225 increased abundance at stations where sea ice had persisted for longer. 226 For the mean copepodid stages of the large-sized copepods, the effects of

227 environmental drivers varied with species. Calanoides acutus showed two positive (density

- and time since melt) and three negative relations (Temp<sub>200</sub>, MLD, and chl.*a*), while *C*.
- 229 propinquus exhibited one positive (Density) and two negative relationships (Salinity<sub>200</sub> and

SST). *Metridia gerlachei* had a weak positive relationship with Temp<sub>200</sub> and *M. lucens* had
one positive (SST) and one negative (Depth). Younger stages in *R. gigas* occurred at stations
were the MLD was shallower.

# 233 4. Discussion

234 Effects of water masses and frontal systems on zooplankton community 4.1. 235 Studies of zooplankton on the southern Kerguelen Plateau are limited. Swadling et al. (2010) 236 investigated the zooplankton community based on RMT1 samples to the region west 237 (BROKE-West; 30-80°E) of the current study (71.2-93.6°E) during summer in 2006. In that 238 survey, foraminifera, small copepods and appendicularians dominated the zooplankton 239 community, while euphausiids (Euphausia crystallorophias) and the copepod Metridia 240 gerlachei were highlighted as indicator species (Swadling et al., 2010). In the present study 241 appendicularians were three orders of magnitude lower than observed in the BROKE-West 242 study, while foraminiferans and radiolarians were much more abundant. Appendicularians 243 have a short generation time (e.g., eight days at 15 °C), which increases in colder 244 temperatures (Deibel and Lowen, 2012). In polar regions, they can develop quickly and time 245 their reproduction to the ice-edge phytoplankton bloom (Acuña et al., 1999); after 246 reproduction their abundance decreases rapidly following end of the phytoplankton bloom. 247 One hypothesis is that the lower numbers of appendicularians observed in the present study 248 reflect some of the sites being sampled after the end of the phytoplankton bloom. 249 High numbers of foraminifera are found in the sea ice of the Southern Ocean, and 250 they release into the water column with sea-ice melt (Ojima et al., 2017). This fact suggests 251 foraminifera might be abundant where sea ice cover persisted for the longest time and cells

were released during the ice melt. Given that days after melt were generally lower than thoserecorded in Swadling et al. (2010) it might explain why the abundances recorded in the

present study were up to 20 times higher than reported for BROKE-West. In spite of this we did not see a significant relationship between the ice-melt indices (i.e., Density and Time since melt) and abundance of foraminiferans. This might be explained by the fact that foraminifera are known to be influenced by many environmental factors, including snow depth and chl. *a* in the water column (Wallis et al., 2016). In our study, foraminifera were abundant in areas with high primary production, indicating that feeding preferences of foraminiferans might be an important driver.

261 The zooplankton communities found across the Southern Kerguelen Plateau in 262 summer 2016 were split into two groups via multivariate analyses (groups A–C vs groups 263 D-F) based on abundance. The distribution of the high-abundance group (i.e., groups A-C) 264 was consistent with the distribution of high chl. a, highlighting possible foodweb interactions 265 where the zooplankton were tracking the higher concentrations of phytoplankton. The GLM 266 showed that total abundance of zooplankton was positively influenced by water-mass indices 267 (i.e., Temp<sub>200</sub>), lower light intensity (i.e., PAR) and increased phytoplankton biomasss (i.e., 268 chl.a). The negative effect of light intensity on abundance suggested most species performed 269 diel vertical migration during summer, whereby they were distributed deeper in the water 270 column during the day (Takahashi et al., 2017). According to Swadling et al. (2010), the 271 zooplankton community between 30 °E and 80 °E was correlated with chlorophyll a 272 concentration, proximity to the Antarctic Slope Current and length of time without an ice 273 cover. Thus, the zooplankton community across the western side of the Indian sector appears 274 to be governed by the interplay of frontal systems, their vertical migration and bottom-up 275 factors affecting productivity around the Kerguelen Plateau during summer.

Zooplankton assemblages are closely related to the different frontal zones in the
Southern Ocean (Hunt and Hosie, 2005, 2006a, b; Hosie et al., 2014; Tachibana et al., 2017).
Around the Kerguelen Plateau, several currents and frontal zones are observed (Park et al.,

279 2009; Bestley et al., 2018). The Antarctic Circumpolar Current (ACC) is disrupted by the 280 plateau, which forces the core of the ACC to pass along its northern escarpment (e.g., Park et 281 al., 1993). Following that, the southern Antarctic Circumpolar Current front (sAACf) and the 282 Southern Boundary (SB) extend northward on the eastern edge of the Kerguelen Plateau. The 283 Fawn Trough Current flows southeasterly at the north-east of the Kerguelen Plateau (Roquet 284 et al., 2009). However, zonal homogeneity is broken by features such as gyres (Kaiser et al., 285 2009). These features of complicated oceanographic conditions potentially relate to 286 zooplankton distribution. In this study the Southern Boundary clearly divided the 287 zooplankton assemblages in the south-east region, while the central region was more 288 homogeneous. This implies that a stable frontal system was present in the south-east region, 289 while an unstable system induced gyres in the central region (Bestley et al., 2018).

# 290 4.2. Environmental drivers of zooplankton abundance and population structure of large291 sized copepods

Population structure reflects growth and reproductive capacity and assists in our understanding of life cycles and the condition of a population (e.g., Atkinson, 1989). Mean copepodid stage (*MCS*) of copepods is a useful index for evaluating their population structure, with the value decreasing with input of new generations by reproduction and increasing with ontogenetic development within the population.

297 *Calanoides acutus* and *C. propinquus* are distributed widely in the Southern Ocean, from

the Polar Front to the Antarctic coast; however, they are usually more abundant north of the

299 SB-ACC and decrease towards the continent (e.g., Atkinson, 1996; Hosie et al., 2000;

300 Tanimura et al., 2008). In the present study, these two species were mainly found north of the

301 Southern Boundary, and their population structures were similar in terms of abundance and

302 MCS. Wallis et al. (2016) reported a positive influence on C. propinquus abundance from

303 chl.a in water and sea ice, snow depth, latitude and year. In the present study, C. propinguus 304 showed positive relationships with average temperature in the top 200 m and chlorophyll 305 concentration, and negative relationships with average salinity, surface temperatures, water 306 column depth and PAR. This species migrates into the surface layer in spring and reproduces, 307 before descending into the deep layer for diapause during autumn (Schnack-Schiel et al., 308 1991, Atkinson, 1996). While the environmental drivers of abundances of C. acutus and C. 309 propinguus were similar, the sea-ice melt indices (Density and Time since melt) showed 310 negative relationships only with C. acutus abundances and positive relationships with their 311 MCS. Thus, higher abundance of the younger stages was associated with lower surface 312 density, suggesting a shorter time since sea-ice melt. Calanoides acutus reproduces from 313 November to March in the Weddell Sea (Hagen and Schnack-Schiel, 1996), and the 314 appearance of the cohort likely coincides with the high chlorophyll a concentration in the 315 summer period (Atkinson, 1998). Calanus simillimus occurred in the north-east regions, 316 particularly near the Fawn Trough Current. This species might have been transported south 317 from more northerly warmer waters, because it is known to be distributed in subantarctic 318 waters and northern parts of the ACC (Atkinson, 1998).

319 The two species of Metridia had different distributions: M. gerlachei was dominant 320 in the south, while *M. lucens* had higher abundances in the north, a common pattern in the 321 Southern Ocean (e.g., Atkinson, 1989). The GLM results indicated that abundance of M. 322 gerlachei showed similar responses to those of C. propinguus, except for the effects of 323 temperature: higher temperatures in the lower mixed layer resulted in higher abundance of C. 324 propinguus and lower abundance of M. gerlachei. Light intensity did not have a strong 325 influence on Metridia species compared to the other copepods. This was interesting because this genus is known to undertake diel vertical migration rather than seasonal vertical 326 migration (Atkinson and Peck, 1988; Huntley and Escritor, 1992; Schnack-Schiel and Hagen, 327

328 1995). The MCS for the two Metridia species were high and might not relate directly to 329 chlorophyll distribution because these species have a long reproductive period (i.e., there is 330 no clear reproductive-peak season) and distribute rather patchily without any apparent link to 331 the distribution of chlorophyll (Atkinson, 1989, 1998). For Rhincalanus gigas, late copepodid 332 stages were dominant, although their nauplii were observed in almost all samples (data not 333 shown). The reproduction of this species is reported to occur mainly during summer 334 (Atkinson, 1998), though with regional differences; e.g. reproduction continues into late 335 autumn around the Antarctic Peninsula (Martin and Schnack-Schiel, 1993). Rhincalanus 336 gigas was reproducing during the January and February in the Indian sector. From the GLM, 337 the relationships of R. gigas with environmental drivers was similar to the other copepods, 338 although chlorophyll *a* concentration was not a strong influence on this species.

339 Recently, research investigating environmental drivers of zooplankton abundance in 340 the Southern Ocean via statistical modelling (e.g., GLM, generalised additive models) has 341 increased (e.g., Wallis et al. 2016; Kelly et al. this issue), but studies using aspects of 342 population structure (e.g., MCS) as a response variable in GLM are limited. In this study, the 343 discussion of population structure was augmented by comparing the environmental drivers of 344 developmental stages of copepods using GLM. Thus, GLM is a powerful analytical tool 345 capable of distinguishing structure within copepod populations even within complex 346 oceanographic regions such as the south Kerguelen Plateau. Also, GLM helped determine 347 those conditions that are most suited to each taxonomic assemblage. This information is 348 useful for identifying productive regions and understanding the response of zooplankton to 349 environmental change. In future, detailed information (e.g., population structure) for the main 350 zooplankton species should be monitored and used in assessing the influence of climate 351 change on key zooplankton species.

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#### 365 **References**

- 366 Acuña, J.L., Deibel, D., Bochdansky, A.B., Hatfield, E., 1999. In situ ingestion rates of
- 367 appendicularian tunicates in the northeast water Polynya (NE Greenland). Mar. Ecol.

368 Prog. Ser. 186, 149–160.

- Arrigo, K.R., Van Dijken, G.L., Bushinsky, S., 2008. Primary production in the Southern
  Ocean, 1997–2006. J. Geophys. Res. 113, C08004.
- Atkinson, A., 1989. Distribution of six major copepod species around South Georgia in early
  summer. Polar Biol. 9, 353–363.
- 373 Atkinson, A., 1996. Subantarctic copepods in an oceanic, low chlorophyll environment:
- ciliate predation, food selectivity and impact on prey populations. Mar. Ecol. Prog. Ser.
  130, 85–96.
- Atkinson, A., 1998. Life cycle strategies of epipelagic copepods in the Southern Ocean. J.
  Mar. Syst. 15, 289–311.
- Atkinson, A., Peck, J.M., 1988. A summer-winter comparison of zooplankton in the oceanic
  area around South Georgia. Polar Biol. 8, 463–473.
- 380 Atkinson, A., Ward, P., Hunt, B.P.V., Pakhomov, E.A., Hosie, G.W. 2012. An overview of
- 381 Southern Ocean zooplankton data: abundance, biomass, feeding and functional
- 382 relationships. CCAMLR Science 19, 171–218.
- Bestley, S., van Wijk, E., Rosenberg, M., Eriksen, R., Corney, S., Tattersall, K., Rintoul, S.,
- 384 2018. Ocean circulation and frontal structure near the southern Kerguelen Plateau: The
- 385 physical context for the Kerguelen Axis ecosystem study. Deep-Sea Res. II,
- 386 https://doi.org/10.1016/j.dsr1012.2018.1007.1013.
- Boltovskoy, D., (Ed.) 1999. South Atlantic Zooplankton volumes 1 & 2, Backhuys, Leiden.
- 388 Bracegirdle, T.J., Connolley, W.M., Turner, J., 2008. Antarctic climate change over the
- 389 twenty-first century. J. Geophys. Res. 113, D03103.

390	Cavalieri, D.J., Parkinson, C.L., Gloersen, P., Zwally, H.J., 1996. updated yearly. Sea Ice
391	Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave
392	Data, Version 1. [January - February 1997 - 2015]. NASA National Snow and Ice Data
393	Center Distributed Active Archive Center. Boulder, Colorado USA.
394	Constable, A.J., Melbourne-Thomas, J., Corney, S.P., Arrigo, K.R., Barbraud, C., Barnes, D.
395	K., Bindoff, N.L., et al. 2014. Climate change and Southern Ocean ecosystems I: how
396	changes in physical habitats directly affect marine biota. Glob. Change Biol. 20,
397	3004–3025.
398	de Boyer Montégut, C., Madec, G., Fischer, A.S., Lazar, A., Iudicone, D., 2004. Mixed layer
399	depth over the global ocean: An examination of profile data and a profile-based
400	climatology. J. Geophys. Res. 109, C12003.
401	Deibel, D., Lowen, B., 2012. A review of the life cycles and life-history adaptations of
402	pelagic tunicates to environmental conditions. ICES J. Mar. Sci. 69, 358-369.
403	Ducklow, H.W., Fraser, W., Karl, D.M., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn,
404	S.E., Vernet, M., Daniels, R.M., 2006. Water-column processes in the West Antarctic
405	Peninsula and the Ross Sea: interannual variations and foodweb structure. Deep-Sea
406	Res. Part II, 53, 834-852.
407	Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a
408	flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.
409	Duhamel, G., Hulley, PA., Causse, R., Koubbi, P., Vacchi, M., Pruvost, P., Vigetta, S.,
410	Irisson. JO., Mormède, S., Belchier, M., Dettai, A., Detrich, H.W., Gutt, J., Jones,
411	C.D., Kock, KH., Lopez, Abellan, L.J., Van de Putte, A.P., 2014. Chapter 7.
412	Biogeographic Patterns of Fish, in: De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond,
413	B., Udekem d'Acoz C. d', Van de Putte, A.P., Danis, B., David, B., Grant, S., Gutt, J.,
414	Held, C., Hosie, G., Huettmann, F., Post, A., Ropert-Coudert, Y. (Eds.), Biogeographic
	18

- 415 Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge,
  416 pp. 328–362.
- 417 Errhif, A., Razouls, C., Mayzaud, P., 1997. Composition and community structure of pelagic

418 copepods in the Indian sector of the Antarctic Ocean during the end of the austral
419 summer. Polar Biol. 17, 418–430.

Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analyzing
multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8, 37–52.

422 Hagen, W., Schnack-Schiel, S.B., 1996. Seasonal lipid dynamics in dominant Antarctic

423 copepods: Energy for overwintering or reproduction? Deep-Sea Res. I 43, 139–158.

424 Hosie, G.W., Schultz, M.B., Kitchener, J.A., Cochran, T.G., Richards, K., 2000.

- 425 Macrozooplankton community structure off East Antarctica (80–150°E) during the
  426 Austral summer of 1995/1996. Deep-Sea Res. II 47, 2437–2463.
- 427 Hosie, G., Mormède, S., Kitchener, J., Takahashi, K., Raymond, B., 2014. 10.3. Near-surface
- 428 zooplankton communities, in: De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond, B.,

429 Udekem d'Acoz C. d', Van de Putte, A.P., Danis, B., David, B., Grant, S., Gutt, J.,

- 430 Held, C., Hosie, G., Huettmann, F., Post, A., Ropert-Coudert, Y. (Eds.), Biogeographic
- 431 Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge,

432 pp 422–430.

433 Hunt, B., Hosie, G. 2005. Zonal structure of zooplankton communities in the Southern Ocean

434 South of Australia: results from a 2150 km continuous plankton recorder transect.

- 435 Deep-Sea Res. I 52, 1241–1271.
- Hunt, B., Hosie, G., 2006a. The seasonal succession of zooplankton in the Southern Ocean
  south of Australia, part I: the seasonal ice zone. Deep Sea Res. I, 53, 1182–1202.
- 438 Hunt, B., Hosie, G., 2006b. The seasonal succession of zooplankton in the Southern Ocean
- 439 south of Australia, part II: the sub-antarctic to Polar Frontal Zones. Deep Sea Res. I 53,

440 1203–1223.

- Huntley, M.E., Escritor, F., 1992. Ecology of *Metridia gerlachei* Giesbrecht in the western
  Bransfield Strait, Antarctica. Deep-Sea Res. 39, 1027–1055.
- 443 Ikeda, T., Hosie, G., Stolp, M., 1986. SIBEXII cruise krill/zooplankton data. ANARE
  444 Research Notes 32, 1–70.
- 445 Kaiser, S., Barnes, D.K.A., Sands, C.J., Brandt, A., 2009. Biodiversity of an unknown
- Antarctic Sea: assessing isopod richness and abundance in the first benthic survey of
  the Amundsen continental shelf. Mar. Biodiv. 39, 27. https://doi.org/10.1007/s12526-
- 448
   009-0004-9.
- 449 Kelly, P., Corney, S.P., Melbourne-Thomas, J., Kawaguchi, S., Bestley, S., Fraser, A.,
- 450 Swadling, K.M., this issue, Salpa thompsoni in the Indian Sector of the Southern
- 451 Ocean: environmental drivers and life history parameters. Deep-Sea Res. II.
- 452 Kirkwood, J.M., 1982. A guide to the Euphausiacea of the Southern Ocean (No. 1-5).
- 453 Information Services Section, Antarctic Division, Dept. of Science and Technology.
- 454 Marin, V., 1987. The oceanographic structure of eastern Scotia Sea-IV. Distribution of
- 455 copepod species in relation to hydrography in 1981. Deep-Sea Res. 34, 105–121.
- 456 Martin, V.H., Schnack-Schiel, S.B., 1993. The occurrence of *Rhincalanus gigas*, *Calanoides*
- 457 *acutus*, and *Calanus propinquus* (Copepoda: Calanoida) in late May in the area of the
  458 Antarctic Peninsula. Polar Biol. 13, 35–40.
- 459 Maslanik, J., Stroeve, J., 1999. updated daily. Near-Real-Time DMSP SSMIS Daily Polar
- 460 Gridded Sea Ice Concentrations, Version 1. [January February 2016]. Boulder,
- 461 Colorado USA. NASA National Snow and Ice Data Center Distributed Active Archive
- 462 Center. Boulder, Colorado USA.
- 463 McLeod, D.J., Hosie, G.W., Kitchener, J.A., Takahashi, K.T., Hunt, B.P.V. 2010. Zooplankton
- 464 atlas of the Southern Ocean: the SCAR SO-CPR survey (1991–2008). Polar Sci. 4, 353-

465 385.

- 466 Murphy, E.J., Watkins, J.L., Trathan, P.N., Reid, K., Meredith, M.P., Thorpe, S.E., Johnston,
- 467 N.M., Clarke, A., Tarling, G.A., Collins, M.A., Forcada, J., Shreeve, R.S., Atkinson, A.,
- 468 Korb, R., Whitehouse, M.J., Ward, P., Rodhouse, P.G., Enderlein, P., Hirst, A.G.,
- 469 Martin, A.R., Hill, S.L., Staniland, I.J., Pond, D.W., Briggs, D.R., Cunningham, N.J.,
- 470 and Fleming, A.H., 2007. Spatial and temporal operation of the Scotia Sea ecosystem: a
- 471 review of large-scale links in a krill centred food web. Phil. Trans. Royal Soc. London
- 472 Series B, 362, 113-148.
- 473 Nicol, S., 2006. Krill, currents, and sea ice: *Euphausia superba* and its changing
- 474 environment. BioScience 56, 111–120.
- Nicol, S., Foster, J., Kawaguchi, S., 2012. The fishery for Antarctic krill recent
  developments. Fish Fish. 13, 30–40.
- 477 O'Brien, R.M., 2007. A caution regarding rules of thumb for variance inflation factors. Qual.
  478 Quant. 41, 673–690.
- 479 Ojima, M., Takahashi, K.T., Iida, T., Moteki, M., Miyazaki, N., Tanimura, A., Odate, T.,
- 480 2017. Variability of the fauna within drifting sea ice floes in the seasonal ice zone of the
- 481 Southern Ocean during the austral summer. Polar Sci. 12, 19–24.
- 482 Park, Y.-H., Gambéroni, L., Charriaud, E., 1993. Frontal structure, water masses and
- 483 circulation in the Crozet Basin. J. Geophys. Res. 98, 12361–12385,
- 484 doi:10.1029/93JC00938.
- 485 Park, Y.-H., Vivier, F., Roquet, F., Kestenare, E., 2009. Direct observations of the ACC
- 486 transport across the Kerguelen Plateau. Geophys. Res. Lett. 36, L18603,
- 487 doi:10.1029/2009GL039617.
- 488 Patterson, T.A., Sharples, R.J., Raymond, B., Welsford, D.C., Andrews-Goff, V., Lea, M.A,
- 489 Goldsworthy, S.D., Gales, N.J., Hindell, M. 2016. Foraging distribution overlap and

- 490 marine reserve usage amongst sub-Antarctic predators inferred from a multi-species
  491 satellite tagging experiment. Ecol. Indic. 70, 531-544.
- 492 Pauly, T., Nicol, S., Higginbottom, I., Hosie, G., Kitchener, J. 2000. Distribution and
- 493 abundance of Antarctic krill (*Euphausia superba*) off East Antarctica (80–150 E) during
- 494 the Austral summer of 1995/1996. Deep-Sea Res. II 47, 2465-2488.
- 495 Pruvost, P., Duhamel, G., Palomares, M.L.D., 2005. An ecosystem model of the Kerguelen
- 496 Islands' EEZ. in: Palomares, M.L.D., Pruvost, P., Pitcher, T.J., Pauly, D. (Eds.),
- 497 Modeling Antarctic marine ecosystems. Fisheries Centre Research Reports 13 (7).
- 498 Fisheries Centre, University of British Columbia, Vancouver, Canada, pp 40–64.
- 499 Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists.
- 500 Cambridge University Press, Cambridge.
- R Core Team, 2017. R: A language and environment for statistical computing. R Foundation
  for Statistical Computing, Vienna, Austria.
- 503 Razouls, C., 1994. Manuel d'identification des principals espèces de copépods pélagiques
- 504antarctiques et subantarctiques. Annales de L'Institut Océanographique 70, 1–204.
- 505 Roquet, F., Park, Y.-H., Guinet, C., Bailleul, F., Charrassin, J.-B., 2009. Observations of the
- Fawn Trough Current over the Kerguelen Plateau from instrumented elephant seals. J.
  Mar. Syst. 78, 377–393.
- Schnack-Schiel, S.B., Hagen, W., 1995. Life-cycle strategies of *Calanoides acutus*, *Calanus propinquus*, and *Metridia gerlachei* Copepoda: Calanoida in the eastern Weddell Sea,
- 510 Antarctica. ICES J. Mar. Sci. 52, 541–548.
- 511 Schnack-Schiel, S.B., Hagen, W., Mizdalski, E., 1991. Seasonal comparison of *Calanoides*
- 512 *acutus* and *Calanus propinguus* (Copepoda: Calanoida) in the southeastern Weddell
- 513 Sea, Antarctica. Mar. Ecol. Prog. Ser. 70, 17–27.
- 514 Smith, W.O. Jr, Ainley, D.G., Cattaneo-Vietti, R. 2007. Trophic interactions within the Ross

515	Sea continental shelf ecosystem. Phil. Trans. Royal Soc. London Series B, 362, 95-111.
516	Swadling, K.M., Kawaguchi, S., Hosie, G.W., 2010. Antarctic mesozooplankton community
517	structure during BROKE-West (30°E-80°E), January-February 2006. Deep-Sea Res. II
518	57, 887–904.
519	Tachibana, A., Watanabe, Y., Moteki, M., Hosie, G.W., Ishimaru, T., 2017. Community
520	structure of copepods in the oceanic and neritic waters off Adélie and George V Land,
521	East Antarctica, during the austral summer of 2008. Polar Sci. 12, 34-45.
522	Takahashi, K.T., Hosie, G.W., Odate, T., 2017. Intra-annual seasonal variability of surface
523	zooplankton distribution patterns along a 110°E transect of the Southern Ocean in the
524	austral summer of 2011/12. Polar Sci. 12, 46–58.
525	Tanimura, A., Kawaguchi, S., Oka, N., Nishikawa, J., Toczko, S., Takahashi, K.T., Terazaki,
526	M., Odate, T., Fukuchi, M., Hosie, G., 2008. Abundance and grazing impacts of krill,
527	salps and copepods along the 140°E meridian in the Southern Ocean during summer.
528	Antarct. Sci. 20, 365-379.
529	Turner, J.A., Barrand, N.E., Bracegirdle, T.J., Convey, P., Hodgson, D.A., Jarvis, M., Jenkins,
530	A., Marshall, G., Meredith, M.P., Roscoe, H., Shanklin, J., 2014. Antarctic climate
531	change and the environment: an update. Polar Rec. 50, 237-259.
532	Wallis, J.R., Swadling, K.M., Everett, J.D., Suthers, I.M., Jones, H.J., Buchanan, P.J.,
533	Crawford, C.M., James, L.C., Johnson, R., Meiners, K.M., Virtue, P., Westwood, K.,
534	Kawaguchi, S., 2016. Zooplankton abundance and biomass size spectra in the East
535	Antarctic sea-ice zone during the winter-spring transition. Deep-Sea Res. II 131,
536	170–181.
537	Ward, P., Atkinson, A., Venables, H.J. Tarling, G.A., Whitehouse, M.J., Fielding, S., Collins,
538	M.A., Korb, R., Black, A., Stowasser, G., Schmidt, K., Thorpe, S.E., Enderlein, P.,
539	2012. Food web structure and bioregions in the Scotia Sea: a seasonal synthesis. Deep-

- 540 Sea Res. II 59, 253–266.
- 541 Weatherall, P., Marks, K.M., Jakobsson, M., Schmitt, T., Tani, S., Arndt, J.E., Rovere, M.,
- 542 Chayes, D., Ferrini, V., Wigley, R., 2015. A new digital bathymetric model of the
- 543 worlds oceans. Earth Space Sci. 2, 331–345.
- Westwood, K., Pearce, I., 2018. Chlorophyll K-Axis Voyage V3 2015/16 Australian Antarctic
  Data Centre, doi:10.4225/15/5a94c701b98a8.
- 546 Wright, S.W., van den Enden, R.L., Pearce, I., Davidson, A.T., Scott, F.J., Westwood, K.J.,
- 547 2010. Phytoplankton community structure and stocks in the Southern Ocean (30–80°E)
- 548 determined by CHEMTAX analysis of HPLC pigment signatures. Deep-Sea Res. II 57,
- 549 758–778.
- 550

# 551 Figure captions

Fig. 1. Sampling stations along the Kerguelen Axis in the Southern Ocean during January andFebruary 2016.

554 Fig. 2. Hydrographic conditions along the Kerguelen Axis. (a) depth of surface mixed layer

- 555 (SML); (b) mean temperature in upper layer of SML averaged over the upper 20 dbar;
- 556 (c) average temperature over the top 200 m; (d) average salinity over the top 200 m; (e)
- density averaged over the top 10 dbar: (f) chlorophyll *a* concentration averaged over thetop 150 dbar.

Fig. 3. Spatial distribution of total zooplankton abundance along the Kerguelen Axis duringJanuary and February 2016.

561 Fig. 4. (a) Results of Q-mode clustering based on abundance of zooplankton community. Red

562 lines mean station groupings are not significant, as tested by SIMPROF. Labels show

563 sampling stations. (b) Abundance and species composition of groups based on the

564 cluster analysis at two similarity levels (from (a)). Error bars indicate standard

565 deviation around total abundance of each group. (c) Non-metric multi-dimensional

scaling (NMDS) plot with multiple regression analysis showing six groups based on the

567 cluster analysis. Vectors show significant environmental factors.

568 Fig. 5. Station groupings along the Kerguelen Axis, as determined from cluster analysis and

569 NMDS. Positions of frontal systems based on Bestley et al., 2018. ACC: Antarctic

570 Circumpolar Current; ASF: Antarctic Slope Front; FTC: Fawn Trough Current; SB:

571 Southern Boundary; SACCF: Southern Antarctic Circumpolar Current Front.

572 Fig. 6. Spatial distribution of dominant copepods along the Kerguelen Axis. Circle size and

573 colour denotes the abundance and mean copepodite stage of each species.

574

- 575 Table 1. Physical and biological variables included as predictors in the generalised linear
- 576 models (GLMs). Oceanographic variables (temperature, salinity and density) were all derived

577	from in situ CTD	measurements undertaken	at each RMT sampling site.
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Variable	Explanation and source
Depth	Bathymetric depth (m) at sampling stations (Weatherall et
	al., 2015). Values are log10 transformed.
Chl.a	Integrated estimate of water column chlorophyll-a (mg m <sup>-2</sup>
	Westwood and Pearce, 2018) obtained using High
	Performance Liquid Chromatography following Wright et
	al. (2010), based on six CTD sampling depths within the
	upper 150 dbar.
Density	Mean potential density (kg m <sup>-3</sup> ) calculated relative to the
	surface (averaged over the upper 10 dbar). Low values (e.g
	<26.8 kg m <sup>-3</sup> ) are indicative of recent ice influence/melt.
Salinity <sub>200</sub>	Mean salinity over the depth between the surface and 200
	m (the net sampling depth).
MLD	Mixed layer depth (m) estimates based on a change in
	density criterion of $\Delta\sigma\theta$ =0.05 kg m <sup>-3</sup> relative to 10 dbar,
	following de Boyer Montégut et al. (2004).
Temp <sub>200</sub>	Mean temperature over the depth between the surface and
	200 m (the net sampling depth).
Time since melt	The time since ice melted (days) calculated from daily
	passive microwave estimates of sea ice concentration (%)
	obtained from the National Snow and Ice Data Center
	SMMR-SSM/I polar product available for the Southern
	Hemisphere gridded at 25 km resolution (Cavalieri et al.,
	1996, updated yearly; Maslanik and Stroeve, 1999, updated
	daily).
SST	Mean near-surface water temperature (°C, averaged over
	the upper 20 dbar).
PAR	Ship-based measurement of PAR (photosynthetically activ
	radiation, Watts m <sup>-2</sup> ) averaged from the port and starboard
	underway data during the RMT sampling periods.

581	Table 2. Mean abundance	(1000 m <sup>-3</sup>	) for all species/taxon.	<b>Bold</b> indicates IndVal of greater
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- 582 than 25% for that group. \* represents top 50% of species in each group according to SIMPER
- analysis. Number in () represents N: number of sampling stations.

Spacios/taxon	Groups							
Species/taxon	A (4)	B (14)	C (2)	D (8)	E (7)	F (2)		
Aetideopsis antarctica	0	1	0	0	1	0		
Aetideopsis australis	0	0	9	0	0	0		
Appendicularia	158	25	62	25	15	30		
Calanoides acutus	18223*	5836*	34173*	607*	479	282*		
Calanus nauplii	1383	109	444	164	7	0		
Calanus propinquus	6868*	3279*	14628*	485*	468*	401*		
Calanus simillimus	36	3	1267	0	0	442*		
Calanus spp. C1	13345*	2895*	16408	468*	268	134*		
<i>Candacia</i> sp.	34	0	9	0	0	1		
Clausocalanus brevipes	383	205	639	37	38	13		
Clausocalanus laticeps	62	26	9	5	0	35		
Clio pyramidata forma sulcata	223	59	18	28	1	0		
Clione limacina antarctica	0	18	0	1	4	0		
Ctenocalanus spp.	6847*	2165*	6872*	285*	760*	458*		
Cyllopus magellanicus	13	5	0	0	1	0		
Euchirella rostromagna	79	24	9	5	5	1		
Eukrohnia bathypelagica	0	5	148	1	0	0		
Eukrohnia hamata	2690*	1809*	6289*	355*	461*	186		
Euphausia superba	0	32	62	1	21	0		
Euphausia triacantha	0	0	89	0	0	0		
Foraminifera	28765*	9032*	60372	1072*	1255	124		
Gaedius tenuispinus	13	7	0	2	4	0		
Haloptilus longicirrus	194	41	0	2	6	2		
Heterorhabdus austrinus	353	129	35	10	27	0		
Hyperiella macronyx	88	9	296	6	0	42		
<i>Hyperiella</i> sp.1(larva)	0	19	148	4	38	0		
Isopoda	0	6	0	0	4	0		
Limacina helicina	135	97	157	56	2	5		
Limacina retroversa australis	0	0	18	1	0	47		

Medusa	34	52	157	1	37	0
Metridia gerlachei	2523	1031	183	92	1088*	12
Metridia lucens	2831	627	9925*	181	100	204*
Microcalanus pygmaeus	237	121	0	2	3	0
Oithona spp.	10186*	1589*	7458*	645*	276*	123*
Oncaea spp.	3311*	1524*	6621	251*	308	81
Ostracoda	809	223	1073	54	139	3
Paraeuchaeta antarctica	634	166	517	17	168	6
Paraeuchaeta barbata	0	0	9	0	0	0
Pleuromamma robusta	57	7	248	9	5	0
Polychaeta	1549	406	2070	131	63	1
Primno macropa	72	92	44	5	43	1
Pseudochirella mawsoni	13	3	0	0	2	0
Racovitzanus antarcticus	554	147	1931	31	67	0
Radiolaria	1582	931*	5293*	150	404*	209*
Rhincalanus gigas	1714	828	2406*	104	378*	94
<i>Rhincalanus gigas</i> nauplii	2961*	776	9352	72	18	33
Sagitta gazellae	0	2	0	0	1	0
Sagitta marri	80	139	349	14	40	12
Sagitta maxima	0	13	452	0	5	3
Salp	310	82	263	11	53	0
Scaphocalanus farrani	156	35	18	4	3	0
Scaphocalanus vervoorti	265	28	0	0	29	0
Scina borealis	0	1	0	0	0	0
Scolecithricella minor	642	187	946	30	113	22
Scolecithricella ovata	37	4	0	0	0	0
Stephos longipes	41	12	0	1	0	1
Themisto gaudichaudii	96	10	18	4	20	26
Thysanoessa macrura	1642	945	4927	103	600*	60
Undinella brevipes	13	0	0	0	0	0
Urchin larva	0	26	444	0	2	0
Vibilia antarctica	25	2	0	0	1	0
Vibilia armata	0	0	0	2	0	5
Total abundance	112264	35844	196864	5531	7832	3101

Table 3. Result of GLM and "stepAIC" analysis for zooplankton abundance and mean copepodid stage along the Kerguelen Axis transect. If a variable is included in the model for a taxon it is shown as positive (up arrow) when higher abundances are associated with higher values of the variable and negative (down arrow) when higher abundances are associated with lower values of the variable. Int.: intercept, remaining variables as per Table 1. If a variable is included in the model for a taxon it is shown with an arrow -: p \*: p < 0.05; \*\*: p < 0.01; \*\*\*: p < 0.001. MCS – mean copepodite stage.

	Intercept	Density	Salinity <sub>200</sub>	SST	Temp <sub>200</sub>	MLD	Depth	Chl.a	PAR	Time since melt	<i>p</i> value (ANOVA, null vs final)
Total zooplankton	*** ↑		*** ↓	***↓	*** ↑		*** ↓	*** ↑	**↓		***
Amphipoda								* ↑			0.0605
Chaetognatha	*** ↑	*** ↓			** ↑		** ↓	*** ↑	** ↓		**
Copepoda	*** ↑		*** ↓	***↓	*** ↑		** ↓	*** ↑	** ↓		***
Euphausiacea	* ↑					*↓	* ↓		- ↓		*
Foraminifera	*** ↑		*** ↓	***↓	*** ↑		*** ↓	*** ↑	**↓		***
Copepods											
C. acutus	*** ↑	* ↓	** ↓		*** ↑		*** ↓	*** ↑	*** ↓	* ↓	***
C. propinquus	*** ↑		*** ↓	**↓	*** ↑		*** ↓	*** ↑	*** ↓		***
M. gerlachei	** ↑		** ↓		*** ↓		- ↓	*** ↑	* ↓		***
M. lucens	** ↑		** ↓		*** ↑		** ↓	** ↑		* ↓	***

R. gigas	** ↑	* ↓			- ↑		*↓	* ↑	** ↓		*
Mean copepodite stage											
MCS_C. acutus	** ↓	*** ↑			** ↓	** ↓		*** ↓		* ↑	***
MCS_C. propinquus	* ↑	*** ↑	*** ↓	***↓		- ↓	- ↓				***
MCS_M. gerlachei					- ↑						0.3302
MCS_M. lucens	*** ↑			** ↑			**↓				***
MCS_R. gigas	** ↑					**↓	- ↓		- ↑		**

591 Table 4. Summary of the important environmental dependencies evident in the models.

Model	Features
Total zooplankton	Generally, higher abundances were associated with
abundance	warmer temperatures, higher chlorophyll-a
	concentration and shallower depth, which was consistent
	with high abundances observed over the southern
	Kerguelen plateau (Fig. 3a). Lower abundances were
	associated with increased daylight.
Taxon abundances	Relationships mainly consistent with those reported for
	total zooplankton abundance. Additionally, chaetognaths
	were associated with surface low-Density. Higher
	abundances of euphausiids were associated with
	shallower mixed layer depths.
Large copepods	Relationships mainly consistent with those reported for
	total zooplankton abundance. However, M. gerlachei
	showed an opposite relation with temperature below the
	MLD. C. acutus and M. lucens were more abundant
	when there was a shorter time since sea-ice melt.
Copepod stages	The relationships varied with species.

Station	Lat (S)	Long (E)	Date	Time
				(UTC)
KX04	63.473	93.551	23/01/16	09:56
KX05	62.998	93.590	23/01/16	17:24
KX07	61.718	93.327	24/01/16	07:44
KX08	61.134	93.595	24/01/16	18:43
KX09	61.976	92.536	25/01/16	07:16
KX12	62.470	87.158	27/01/16	07:44
KX13	62.482	85.887	27/01/16	20:07
KX14	62.530	83.905	28/01/16	07:21
KX15	62.529	81.949	28/01/16	23:57
KX16	63.292	82.042	29/01/16	20:20
KX17	63.930	83.065	30/01/16	11:08
KX18	64.345	83.633	31/01/16	09:48
KX19	64.410	84.769	01/02/16	05:30
KX20	65.172	85.330	01/02/16	22:32
KX22	65.042	91.494	02/02/16	21:50
KX23	64.318	89.843	03/02/16	14:12
KX24	63.607	88.232	04/02/16	01:14
KX25	63.133	87.259	04/02/16	15:43
KX26	62.502	86.128	04/02/16	22:16
KX27	61.936	85.035	05/02/16	11:23
KX28	61.222	83.863	06/02/16	00:31
KX29	60.363	82.496	06/02/16	13:27
KX30	59.344	81.073	07/02/16	09:14
KX31	58.648	80.160	07/02/16	21:33
KX32	58.223	81.912	08/02/16	10:19
KX33	57.930	83.353	08/02/16	21:47
KX34	57.608	84.608	09/02/16	10:05
KX35	57.839	85.290	09/02/16	19:01
KX37	59.101	84.411	10/02/16	16:21
KX38	60.027	86.750	11/02/16	10:34
KX39	60.052	85.833	11/02/16	23:54

Supplementary 1. Information about the sampling stations along the Kerguelen Axis inthe Southern Ocean during January and February 2016.

KX40	60.319	83.580	12/02/16	13:41	
KX42	60.910	79.882	13/01/16	15:03	
KX43	61.317	77.592	14/02/16	08:26	
KX44	61.846	74.115	15/02/16	01:28	
KX45	62.704	73.314	15/02/16	10:46	
KX47	64.866	71.177	16/02/16	07:51	





Fig. 2. (Matsuno et al.)



Fig. 3. (Matsuno et al.)







Fig. 4. (Matsuno et al.)





Fig. 6. (Matsuno et al.)