**Winter and summer biogeography of macrozooplankton community structure in the northern Antarctic Peninsula ecosystem**

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**Highlights**

- Macrozooplankton community in the northern Antarctic Peninsula was examined over five consecutive winter seasons and compared with historic summer sampling.
- Multivariate analyses showed that the number of identifiable groups varied between seasons. Winter macrozooplankton community structure was more spatially and temporally consistent compared to summer regardless of sea ice conditions.
- Water masses (defined by salinity) and biological conditions (defined by average Chl $a$) were important in structuring the macrozooplankton communities in both seasons. Upper mixed layer depth and time of day in winter and average temperature, average phaeopigments to 100 m and year in summer were also highly significant in explaining cluster distribution and variability.
- Observations from the past two decades indicate wide variation in the seasonality of species abundance; however, we have not observed vast distributional shifts or intrusions of sub-Antarctic macrozooplankton into this area, nor changes in the stability of macrozooplankton community composition.

**Abstract**

Climate forcing is impacting polar marine ecosystems through increased variability of winter sea-ice dynamics, which likely influences the distribution, abundance and structure of zooplankton assemblages, and thereby trophodynamics of marine food webs. Due to the challenges of working in polar marine ecosystems, most knowledge on polar zooplankton community structure is derived from summer surveys. Here we examine the spatial distribution, abundance and community structure of macrozooplankton in relation to sea-ice and ocean-climate dynamics within the Antarctic Peninsula marine ecosystem over five consecutive winters. We compare the patterns revealed during winter with historical data collected in the same region during austral summer. Hydrographic and macrozooplankton data were collected from >100 standard stations off the northern Antarctic Peninsula during summer (2003-2011) and winter (2012-2016). Using multivariate methods, the environmental drivers and geographic structuring of the macrozooplankton community during winter and summer were investigated.

Eight taxa made up 90% of total macrozooplankton abundance in winter including *Metridia* species, post-larval and larval *Euphausia superba*, post-larval *Thysanoessa macrura*, *Limacina helicina*, Chaetognatha, Ostracoda and Radiozoa.  Eight slightly different taxa including *Calanoides acutus*, *Salpa thompsoni*, *T. macrura* (post-larvae and larvae), *Metridia* spp., *E. superba* larvae, Chaetognatha, and *Rhincalanus* spp. made up 87% of the total abundance in summer. Macrozooplankton clustered into five groups in winter and seven groups in summer. Winter macrozooplankton structure was more spatially consistent among years compared to summer regardless of sea-ice conditions. Salinity, chlorophyll *a* biomass, upper mixed layer depth and time of day were most strongly correlated with the multivariate ordination in winter whereas salinity, phaeopigment biomass and year had the highest correlations for summer, indicating the importance of similar physical features in both seasons. However, the importance of time scales differed among seasons.

Although environmental determinants of summer and winter macrozooplankton community structure indicate that community structure and occurrence were strongly tied to regional variability of salinity and primary productivity gradients, macrozooplankton community structure is likely much more complex than only a few hydrographic variables can explain.

59 Cluster boundaries are likely driven by dynamic locations of currents, fronts and localized eddies

60 in any given season or year.

## 1.0 Introduction

63

64    Climate change is impacting polar marine ecosystems through increased variability of winter

65    sea-ice dynamics (e.g., declines in sea-ice extent and concentration), which likely influences the

66    distribution, abundance and structure of zooplankton assemblages, and thereby trophodynamics

67    of marine food webs (Constable et al., 2014; Murphy et al., 2016; Meredith and Brandon, 2017;

68    Mintenbeck, 2018). Due to the challenges of working in polar marine ecosystems, most

69    knowledge of polar zooplankton community structure is derived from summer surveys and

70    usually reflects high profile taxa (e.g., amphipods, euphausiids) that are ecologically important as

71    food for other trophic levels, carbon cycling and fisheries (Reid et al., 2005; Johnson et al., 2011;

72    Simonsen et al., 2016). Baseline observations of zooplankton during winter, particularly at

73    regional scales over consecutive years, are needed to better understand how zooplankton

74    biodiversity patterns and communities are likely influenced by sea-ice and ocean conditions, and

75    to understand the sensitivity of these communities and their dependent species to climate

76    variability.

77    In the Antarctic, short-term studies of winter macrozooplankton communities indicate

78    community composition is likely structured by broad-scale environmental relationships and

79    sensitivity to sea-ice conditions (Atkinson and Peck, 1988; Siegel and Piatkowski, 1990;

80    Lancraft et al., 1991; Hopkins et al., 1993; Nordhausen, 1994; Ashjian, 2004; Hunt et al., 2011).

81    It has been hypothesized that reduced winter phytoplankton growth and changes in the

82    occurrence and distribution of some winter macrozooplankton species may imply that winter

83    ecosystem dynamics could be more representative of and structured by top-down predation

84    pathways (Hunt et al., 2011). During winter, several macrozooplankton species (e.g., *Euphausia*

85    *frigida*, *Thysanoessa macrura*, *Paraeuchaeta antarctica*, *Themisto gaudichaudii*) breed or spawn

86    so that production of larvae or young are timed to precede or coincide with the spring bloom

87    following sea-ice melt (Torres et al., 1994; Mayzaud et al., 2011). Further, assessment of winter

88    macrozooplankton community structure may have implications for understanding ecosystem

89    productivity cycles and informing ecosystem management involving managed species (Eisner et

90    al., 2014; Meyer et al., 2020). Considering the strong seasonal variability of polar environments,

91    biogeographic assessments of macrozooplankton community composition should include

92    seasonal comparisons to determine if species composition patterns shift or are spatially and

93  temporally consistent. Therefore, a multi-year assessment of winter and summer

94  macrozooplankton community structure is critical for improving our understanding of polar

95  macrozooplankton biogeography and will benefit future empirical and modeling studies of polar

96  ecosystem dynamics.

97  Throughout the Antarctic Peninsula marine ecosystem, increasing air and sea temperatures and

98  declining sea-ice extent and concentration during winter are impacting the pelagic environment

99  (Stammerjohn et al., 2008; Meredith et al., 2017). Summertime assessments of

100  macrozooplankton have laid the foundation for understanding connections between ocean-

101  climate conditions, such as El Niño–Southern Oscillation (ENSO), on the recruitment variability

102  of Antarctic krill (*Euphausia superba)* (Loeb et al., 2009b; Lee et al., 2010; Loeb and Santora,

103  2015), the numerical dominance of either euphausiids or gelatinous salps (Loeb et al., 1997;

104  Loeb and Santora, 2012), as well as the spatial organization of macrozooplankton species

105  composition (Siegel and Piatkowski, 1990; Steinberg et al., 2015). Specifically, distribution of

106  summer macrozooplankton assemblages reflects differences in bathymetry and source water

107  inputs from the Weddell, Scotia and Bellingshausen Seas, and through coastal currents within

108  Bransfield Strait (Fig. 1; (Jazdzewski et al., 1982; Rakusa-Suszcewski, 1983; Witek et al., 1985;

109  Piatkowski, 1989; Siegel and Piatkowski, 1990; Loeb et al., 2010; Loeb and Santora, 2013; Loeb

110  and Santora, 2015)). Climate-driven change in sea-ice conditions is also hypothesized to have

111  impacted Antarctic krill populations, reducing recruitment strength and causing population

112  declines and an apparent poleward distribution shift or contraction of this species (Ross et al.,

113  2014; Atkinson et al., 2019). Given the critical importance of sea-ice and winter environmental

114  conditions to Antarctic krill populations around the Antarctic Peninsula, it seems likely that these

115  conditions during winter may also impact the entire macrozooplankton community in this

116  ecosystem. Such impacts would likely have effects throughout the marine food web because

117  macrozooplankton are a critical energy pathway for fish, seabird and marine mammal species

118  (Hunt et al., 1992; Nicol et al., 2008; Ballerini et al., 2014; Saunders et al., 2019); no species can

119  be understood in isolation.

120  Herein, we examine the spatial distribution, abundance and community structure of

121  macrozooplankton in relation to sea-ice and ocean-climate dynamics within the Antarctic

122  Peninsula marine ecosystem over five consecutive winters. We use the term community structure

123 because the macrozooplankton species assessed in this study interact through host associations

124 (e.g., salps and amphipods), competition (filter feeding grazers) and predator-prey dynamics

125 (e.g., chaetognaths and copepods) (Øresland, 1990; Pakhomov et al., 1999; Phleger et al., 2000).

126 A previous synthesis of this survey documented that it coincided with drastic differences in

127 winter sea-ice extent and concentration patterns, as well as the onset of a strong El Niño
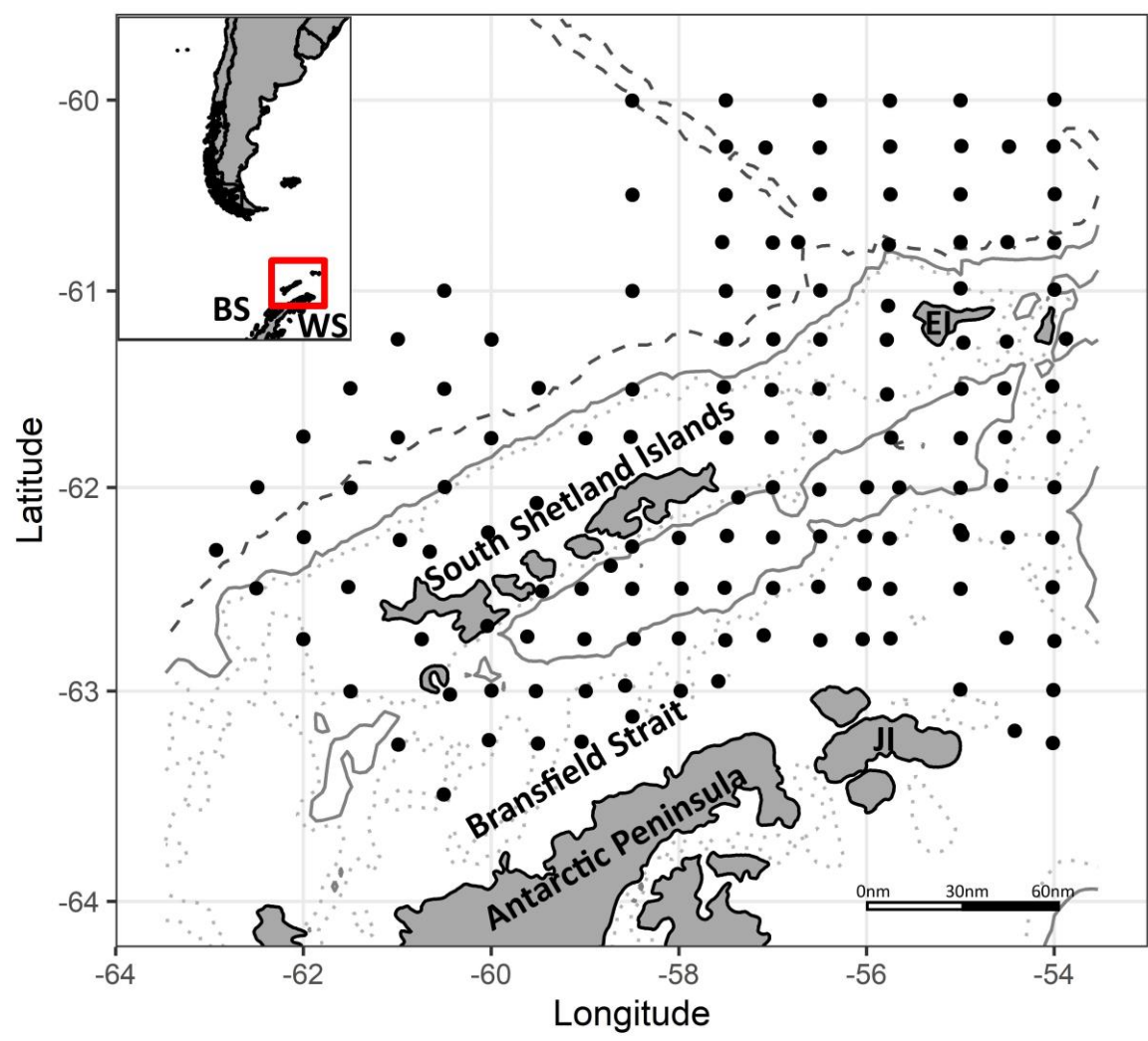
128

129 **Fig. 1** Schematic of general station locations (black circles). Study region, highlighted by red box, in relation to South America
130 and Antarctic peninsula (inset). Not all stations were sampled in every year; Fig. 3 and 5 detail spatial locations among years and
131 Supplemental Table 1 describes timing and sample size for each survey. Bathymetry indicated with light grey – 500 m (dotted),
132 1000 m (solid) and 2500 m (dashed). Scale bar distance calculated at 62°S. BS – Bellinghausen Sea; WS – Weddell Sea; EI –
133 Elephant Island; JI – Joinville Island.

134

135 (Reiss et al., 2017). We expand our synthesis to investigate the environmental drivers and

136 geographic structuring of the macrozooplankton community during winter and summer, and to

137 determine whether community structure is more or less seasonally consistent (i.e., stable and less

138 variable) in terms of geographic complexity and species assignment to cluster groups. Given the

139 increased productivity due to mesoscale ocean conditions during summer combined with

140 population dynamics of macrozooplankton, we predict that summer community structure should

141 be considerably more variable compared to winter. Therefore, as part of a natural experiment

142 involving contrasting sea-ice and environmental conditions, we describe the winter

143 biogeographic patterns of macrozooplankton community structure and assess the stability of

144 relationships relative to hydrography and bathymetry, and compare these patterns with summer.

145 We tested the hypothesis that macrozooplankton community structure during winter is stable,

146 despite the high interannual variability of sea-ice and ocean-climate conditions. Specifically,

147 using a combination of multivariate statistics and distribution mapping, we: (a) determine the

148 spatial patterns of macrozooplankton community structure and assess their spatial and temporal

149 variability; (b) determine areas of high macrozooplankton biodiversity; and (c) assess the degree

150 to which geographic changes in salinity, temperature and upper mixed layer depth impact

151 community structure. Further, to provide greater context on the seasonal variability of

152 macrozooplankton community structure, we compare our results from winter surveys with

153 synoptic long-term summer surveys to highlight potential differences in the consistency of

154 macrozooplankton community structure.

155 **2.0 Methods**

156 *2.1 Study area*

157 The northern Antarctic Peninsula large marine ecosystem comprises several offshore islands

158 defined by the South Shetland Islands to the north, Smith and Anvers Islands to the south and

159 Joinville Island to the east (Fig. 1). Between the islands and the Antarctic Peninsula, water

160 derived from the Bellingshausen Sea flows into Bransfield Strait, which opens to the northeast

161 into the Weddell Sea. Inshore connections to the western Antarctic Peninsula occur through

162 Gerlache Strait. The southern Antarctic Circumpolar Current front and its southern boundary are

163 definitive hydrographic features that influence the distribution and abundance and species

164 assemblages of macrozooplankton, seabirds and marine mammals (Loeb et al., 2010; Santora et

165   al., 2010; Santora et al., 2017). Further, the rugged coastal bathymetry and mixing of coastal and

166   higher latitude water sources generate meso- and sub-mesoscale variability, influencing

167   ecosystem structure and spatial organization (Hofmann et al., 1996; Wilson et al., 1999; Amos,

168   2001; Klinck et al., 2004; Santora et al., 2012; Santora et al., 2017; Moffat and Meredith, 2018).

169   Thus, the region is oceanographically complex, and a variety of water masses, currents and

170   fronts with distinctly different properties are modified by local conditions, creating a dynamic

171   pelagic environment around the northern Antarctic Peninsula (Amos, 2001; Zhou et al., 2006;

172   Loeb et al., 2010; Sangrà et al., 2011).

173   Ecosystem studies including hydrography, phytoplankton, macrozooplankton, Antarctic krill and

174   krill predators around the northern Antarctic Peninsula were conducted during austral summers

175   (January-February) of 2003-2011 on the Research Vessel (RV) *Yuzhmorgeologiya* and RV

176   *Moana Wave* and during austral winters (August-September) of 2012-2016 aboard the RV Ice

177   Breaker (RVIB) *Nathaniel B. Palmer*. Survey stations were selected based on ship time

178   availability (especially in 2012) and sea-ice conditions at the location from the U.S. Antarctic

179   Marine Living Resources (AMLR) Program's standard grid described more fully in Loeb et al.

180   (2010). The summer survey area was consistently free of sea-ice. However, due in part to the

181   2002 breakup of the Larsen B ice shelf (Rignot et al., 2004), the high incidence of icebergs in

182   2003 and 2004 precluded sampling in the southern- and eastern-most portions of Bransfield

183   Strait. Large tabular icebergs in the vicinity of Joinville Island also limited station sampling in

184   the Weddell Sea in most years (J. Santora; Pers Obs.). In general, stations were approximately

185   15-20 nm apart and the survey area ranged from 60° to 63.5° south and 54° to 63° west

186   surrounding the South Shetland Islands and including Bransfield Strait (Fig. 1).

187   *2.2 Data*

188   All methods apply to both summer and winter surveys with the exception of section 2.2.1. Not

189   all stations were sampled in every year; Supplemental Table 1 describes survey dates and sample

190   sizes. Summer sampling primarily occurred in January and winter sampling occurred in August

191   (Supplemental Table 1). Hauls with tow depths >200 m or occurring outside the standard AMLR

192   grid (Fig. 1) were excluded. The 2010 summer survey was removed due to a depth meter

193 malfunction and the 2008 survey was removed due to unsolved database management issues (C.

194 Reiss, Pers. Obs.).

195 *2.2.1 Winter sea-ice conditions*

196 To characterize winter sea-ice variability within the study area, monthly percent sea-ice

197 concentration maps, derived from satellite observations (www.nsidc.org), were examined for the

198 two months prior to winter surveys, during and up to one month after survey completion. We

199 calculated sea-ice areal extent ($km^2$) for the 15% and 50% sea-ice concentrations and then

200 calculated the ratio of the area of 50% to 15% sea-ice concentration, and used this ratio as an

201 index of ice consolidation.

202 During each net deployment, sea-ice concentration (categorical percent cover) and ice type were

203 classified based on definitions in Worby (1999) and visually estimated within a 100 m

204 hemisphere on the starboard side of the vessel when the net started its ascent at each sampling

205 station. In 2012, ice was classified as present or absent as stations in the ice were mostly 95% or

206 greater ice covered, and there was no extensive marginal ice zone.

207 *2.2.2 Hydrographic and chlorophyll measurements*

208 At each station, water column data were collected with a Sea-Bird Inc. SBE-9/11+ Conductivity,

209 temperature and depth (CTD) profilers (calibrated post-cruise) with a carousel water sampler

210 equipped with 11 ten-liter Niskin sampling bottles. In general, CTD casts were made to 750 m

211 depth or 5 m above the sea bottom when shallower than 750 m. Water samples were collected at

212 11 standard depths (750, 200, 100, 75, 50, 40, 30, 20, 15, 10 and 5 m). The chlorophyll-a (Chl *a*)

213 concentration (mg m$^{-3}$) at each standard depth over the upper 200 m of the water column was

214 determined by measurement of Chl *a* fluorescence after extraction in methanol. Sample volumes

215 of 100 mL (250 ml in winter) were filtered through glass fiber filters (Whatmann GFF, 25mm).

216 Chl *a* was extracted from the filters in 10 mL of absolute methanol, at 4°C for at least 12 hours.

217 The samples were then shaken, centrifuged, and the clear supernatant poured into cuvettes for

218 measurement of Chl *a* fluorescence before and after the addition of two drops of 1.0 N HC1

219 (Holm-Hansen et al., 1965; Holm-Hansen and Riemann, 1978). Fluorescence was measured

220 using either a Turner Designs 10A (1990-1996), TD-700 (1997-2009), or a TD-Trilogy (2010-

221 2016) fluorometer calibrated using a solution of pure Chl *a* (Sigma Chemicals, Inc.), the

222 concentration having been determined spectrophotometrically (Jeffrey and Humphrey, 1975).

223 Stability of the fluorometer was verified daily by use of various reference standards.

224 Because net tows were oblique tows and integrate their catch over the depth of the tow, we

225 integrated the bottle data for Chl *a* and phaeopigment concentrations to 100 m depth at each

226 station (Reiss et al., 2009) to obtain integrated biomass (mg m$^{-2}$). The upper mixed layer (UML)

227 depth was calculated as the depth (m) where the potential density ($\sigma_t$) differed by 0.05 kg m$^{-3}$

228 from the average of the potential density over the 5 m to 10 m depth (Mitchell and Holm-

229 Hansen, 1991). Salinity, temperature, and density differences were also averaged over the upper

230 mixed layer (UML) depth of each station. We classified the water zone present at each station

231 following Amos (2001); these zones represent Antarctic Circumpolar Current (ACC) water

232 (Zone I); modified ACC water (Zone II), Shelf water (Zone III), Bransfield Strait water (Zone

233 IV), and Weddell Sea outflow (Zone V). An additional water zone (VI) comprises shallow

234 waters with vertically mixed water columns that are very close to the coast. Hydrographic data

235 from stations classified as Zone VI were not used in any analyses (Hewes et al., 2008; Loeb et

236 al., 2010). In winter, because of increased mixed layer depths a greater proportion of stations

237 could be classified as water zone VI.

238 *2.2.3 Macrozooplankton sampling and processing*

239 Macrozooplankton samples were collected at each station using a 1.8 m Isaacs-Kidd Midwater

240 Trawl (IKMT) fitted with a 505 μm mesh net and fished obliquely to 170 m, or within 10 m of

241 the bottom in shallow depths. Real-time tow depths were derived from a pressure sensor

242 mounted on the trawl bridle connected via coaxial cable to a Precision Digital Universal Process

243 Meter onboard the ship. Water volume filtered was measured using a calibrated General

244 Oceanics flow meter (model 2030R) mounted on the net frame (overall average: 3923.6 ± 28.3

245 m$^3$; Supplementary Table 1). The IKMT was deployed at approximately 40 m min$^{-1}$ and

246 retrieved at 20 m min$^{-1}$ while targeting tow speeds of ~2 knots. Time-of-day (day, night) was

247 assigned to each macrozooplankton haul using the R spatial packages *maptools* and *sp* (Pebesma

248 and Bivand, 2005; Bivand et al., 2013; Bivand and Lewin-Koh, 2018). Civil twilight was used to

249 split day and night to ensure that the majority of diel vertical migration was complete. Summer

250    tows occurred predominately during the day (85%) whereas winter tows were more evenly

251    distributed (46% day: 54% night) among time-of-day levels.

252    Net hauls were processed at sea immediately following each tow. Processing included sorting

253    fresh samples and enumerating macrozooplankton taxa to the lowest taxonomic level given

254    program priorities, experience of personnel, quality of identification keys, and time constraints

255    between stations. Every attempt was made to maximize the proportion of the sample examined

256    and subsampling was employed as appropriate. Due to variable personnel among years, species

257    or species group counts were aggregated to a level where the resolution of identification was

258    consistent among years (K. Dietrich Pers. Obs.), resulting in 78 potential taxa (Supplemental

259    Table 2). Taxonomic resolution varied widely among phyla consistent with other zooplankton

260    community studies (Hosie and Cochran, 1994; Chiba et al., 2001; Keister and Peterson, 2003;

261    Ward et al., 2004; Eisner et al., 2014; Hunt et al., 2014; David et al., 2016) and the same

262    resolution was used for the winter and summer analysis components. Species of Euphausiidae

263    were split into larval (including calyptopis and furcilia) and post-larval (including juvenile and

264    adult) stages and considered as separate taxa for analyses purposes due to different feeding

265    strategies and distributions consistent with other studies (Siegel and Piatkowski, 1990; Ward et

266    al., 2004). *E. superba* larvae were staged in more detail although all calyptopis (CI-III) and

267    furcilia (FI-VI) stages were combined for analysis. In general *E. superba* larvae were primarily

268    calyptopis stage in summer and furcilia stage in winter samples. A detailed protocol for

269    processing, subsampling and species identification is available from the U.S. AMLR program.

270    Samples were preserved in 4% buffered formalin and stored by the AMLR Program.

271    *2.3 Statistical analysis*

272    Prior to analysis, all net hauls and species criteria were screened for data quality.

273    Macrozooplankton abundance was standardized to number of individuals per volume of water

274    filtered (ind 1000 m$^{-3}$). Abundance was log-transformed ($\log_{10}(x+1)$) to minimize the influence

275    of highly abundant taxa in subsequent multivariate analysis. To minimize the influence of rare

276    taxa, taxa were excluded if they did not occur in at least 5% of the net hauls (Singh et al., 2011;

277    Poos and Jackson, 2012). We examined macrozooplankton and biophysical correlation matrices

278    to assess the strength and frequency of correlations during summer and winter surveys.

279 We conducted several complementary multivariate analyses to quantify and compare the spatial

280 organization of macrozooplankton assemblages during winter and summer. A Bray-Curtis

281 dissimilarity matrix based on abundance was calculated for multivariate analyses. Separate

282 hierarchical agglomerative cluster analyses of taxa abundance were performed with the R

283 package *cluster* (Maechler et al., 2015) to assess species assemblage patterns for summer and

284 winter surveys (Everitt and Hothorn, 2011). Ward's minimum variance was selected as the

285 linkage method due to having the highest agglomerative coefficient (Singh et al., 2011). We used

286 indicator species analysis to investigate seasonal variability of macrozooplankton taxa and

287 stability of macrozooplankton assemblage patterns. Indicator values were calculated for each

288 taxa cluster combination based on formulas in Dufrene and Legendre (1997) and implemented in

289 the R package *labdsv* (Roberts, 2016). A high indicator value for a given taxa signifies high

290 frequency of occurrence and high abundance relative to other clusters. An arbitrary cutoff of

291 indicator values greater than 25% was selected to simplify the number of taxa presented. We

292 followed the cluster analyses with non-metric multidimensional scaling (NMDS) using the Bray-

293 Curtis dissimilarity matrix within the R package *vegan* (Oksanen et al., 2018) and three axes

294 were retained for assessment of taxa assemblage structure. NMDS reduces multivariate data into

295 a smaller set of dimensions to examine the structure of species assemblages and to assess

296 environmental relationships (Borcard et al., 2011; Oksanen, 2015). The direction and magnitude

297 of greatest change in NMDS ordination space for each biophysical and temporal variable (Table

298 1) were calculated using least squares regression (e.g., *envfit* function in *vegan*). Each

299 biophysical variable was used as a response variable and the three NMDS coordinates of the

300 samples were used as covariates. The resulting regression coefficients provide vector coordinates

301 in multidimensional space, representing the direction of maximal change. The $r^2$ statistic

302 provides an indication of the strength statistic provides an indication of the strength of the

303 correlation between the

| Variable | Definition; unit | Summer | Winter |
|---|---|---|---|
| Upper mixed layer (UML) depth | Depth at which the density differed by 0.05 kg m$^{-3}$ from the average density of the upper 10 m of the water column ((Mitchell and Holm-Hansen, 1991); meters | x | x |
| Temperature | Average UML temperature; °C | x | x |

| Variable | Description | Summer | Winter |
| --- | --- | --- | --- |
| Salinity | Average UML salinity; PSU | x | x |
| Water zone | 5-level factor based on definitions in Amos (2001) | x | |
| Chl $a$ | Average integrated Chl $a$ to 100m from bottles; mg m$^{-2}$ | x | x |
| Phaeopigment | Average integrated Phae to 100m from bottles; mg m$^{-2}$ | x | x |
| Time of day | 2-level factor (split at civil twilight)<br>Day – sun ≤ 6° below horizon<br>Night – sun > 6° below horizon | x | x |
| Year | Factor based on survey year | x | x |
| Ice cover | Factor with four levels<br>None – open water<br>10-75%[1]<br>76-100%[1]<br>Ice[2] | | x |
| Ice present? | Yes / No | | x |

304   [1]2013-2016
305   [2]2012 only

306 **Table 1** Biophysical and temporal variables included in NMDS regression analysis for summer and winter data sets.

307 configuration of samples in ordination space and each variable (assuming a linear relationship;

308 Bergsveinson et al. (2019)). Correlations were assessed statistically using a randomization test

309 with 10,000 permutations. All analyses were implemented in R version 3.5.1 (R Core Team,

310 2018).

311 To explore biodiversity patterns of macrozooplankton, we calculated species-accumulation

312 curves, and several biodiversity metrics, including Shannon-Weaver diversity index, species

313 richness and Pielou's evenness, per sampling location (Oksanen, 2019). All taxa included in the

314 Bray-Curtis dissimilarity matrix were used to calculate biodiversity metrics. Additionally, cluster

315 and annual descriptive statistics (mean ± standard error) were calculated for biophysical data,

316 abundance of macrozooplankton taxa and diversity indices. Normality was tested using the

317 Shapiro-Wilk test and homogeneity of variance was assessed with Levene's test. Cluster or

318 annual means were compared for key taxa and biophysical data using the Welch's one-way test

319 when a variable violated the normality assumption or a nonparametric Kruskal-Wallis test when

320 both normality and homogeneity of variance assumptions were violated (Zar, 1999). Post-hoc

321 tests included pairwise t-tests with no assumption of equal variances or Wilcoxon rank sum tests

322 following Welch's one-way and Kruskal-Wallis tests, respectively. A Bonferroni correction was

323 used for all post-hoc multiple comparisons among clusters or years. Seasonal comparisons of

324 macrozooplankton abundances were made using the Wilcoxon rank sum test.

325 **3.0 Results**

326 *3.1 Winter ecosystem dynamics*

327 *3.1.1 Winter sea-ice conditions*

328 At the scale of the study region, monthly satellite observations of winter sea-ice concentration

329 indicated 2012 and 2013 had much thicker, consolidated ice throughout Bransfield Strait (Fig.

330 2A), which restricted some of our sampling in the southern and eastern portions of the study area

331 (Fig. 3). However, during 2014, 2015 and 2016, although high ice concentrations were observed,

332 the sea-ice type consisted of mostly thin pancake ice floes, thereby allowing greater survey

333 coverage. Sea-ice concentration extent preceding the survey also indicated greater heterogeneity

334 in sea-ice conditions during June, July and August of 2014-16 compared to 2012-13 (Fig. 2B-C).

335 Furthermore, the sea-ice extent ratio indicated that sea-ice variability was greater during July and

336 August compared to previous months. At the scale of macrozooplankton sampling, sea-ice

337 concentration within the 100 m observation zone varied among years; 2012 and 2014 had 18 and

338 17 stations, respectively, with no ice observed, whereas 2013, 2015 and 2016 had 76-100% ice

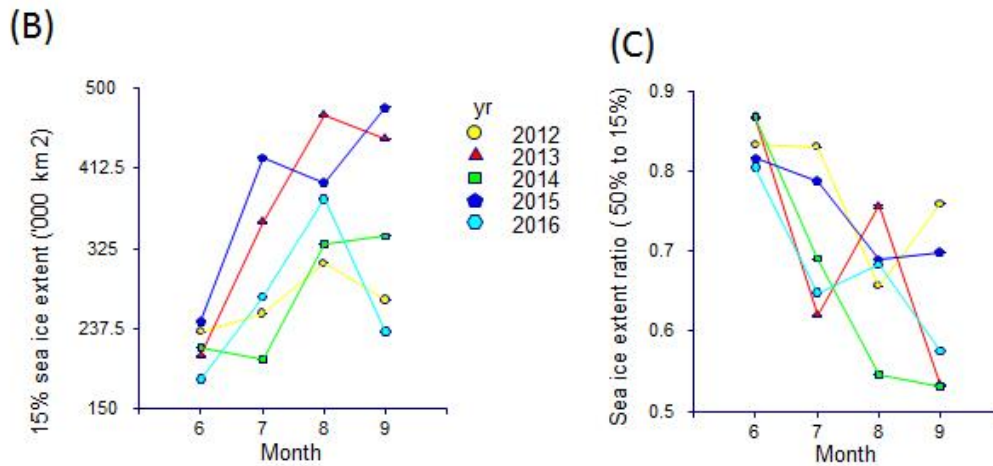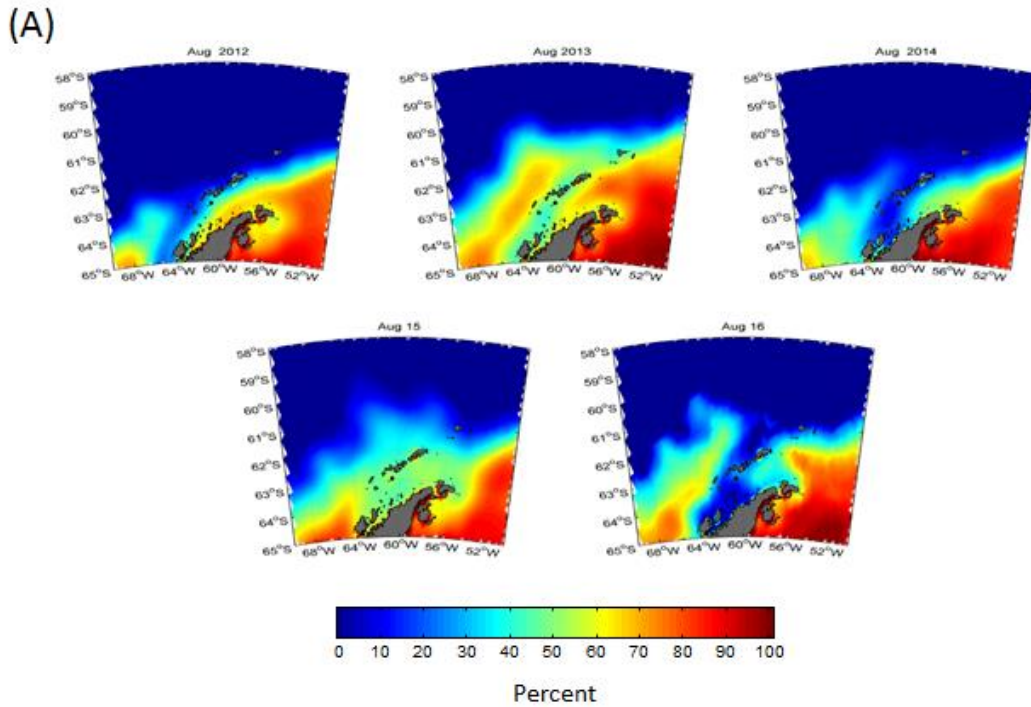339 cover at nearly all net-deployment stations.

**Fig. 2** Monthly sea-ice concentration maps for August in each of five winters (2012-2016; A). Monthly sea-ice extent (15% concentration) from June through September (B). Ratio of 50% sea-ice extent to 15% sea-ice area (consolidation index) for June through September 2012-2016 (C).

*3.1.2 Hydrographic and productivity conditions*

Winter average UML depth was 93.9 m. UML depth varied among years (Kruskal-Wallis $X^2 =$ 37.59, $p < 0.001$) and the annual average ranged from a minimum of 71.4 m in 2014 to a maximum of 118.0 m in 2015. The deepest UML depths consistently occurred throughout the southeast portion of the survey area, with especially deep values during 2012, 2015 and 2016 within Bransfield Strait. The average winter UML temperature was -1.74 °C; the annual average

15

350 ranged between -1.77 and -1.67 °C and did not vary significantly among years (Kruskal-Wallis

351 $X^2 = 5.76$, $p = 0.22$). In general, higher UML temperatures were observed north and west of

352 Elephant Island. Average winter UML salinity was 34.13; the annual average was variable

353 (Welch's $F = 27.51$, $p < 0.001$; range 34.00-34.24) with the highest average salinity in 2015 and

354 the lowest in 2013. Salinity was typically highest in the southeast section of the survey area

355 owing to the influx of high latitude Weddell Sea water into the southeastern portion of Bransfield

356 Strait. We were not able to consistently classify winter stations into water zones due to UML

357 depths which were outside the parameters of the classification code, especially in 2015 and 2016,

358 where 81% and 100% of the sampling stations, respectively, were not assigned a water zone.

359 Average winter 100 m integrated Chl $a$ was 12.31 mg m$^{-2}$; the annual average biomass varied

360 from 7.28 mg m$^{-2}$ in 2012 to 15.28 mg m$^{-2}$ in 2013 (Kruskal-Wallis $X^2 = 60.58$, $p < 0.001$).

361 Stations with consistently higher Chl $a$ biomass were located north of Elephant Island whereas

362 lower biomass occurred within Bransfield Strait. Average winter 100 m integrated phaeopigment

363 biomass was 3.35 mg m$^{-2}$ and varied from 2.17 mg m$^{-2}$ (2014) to 5.07 mg m$^{-2}$ (2016; Kruskal-

364 Wallis $X^2 = 68.14$, $p < 0.001$). Stations with the highest phaeopigment biomass were in the

365 northern portion within the oceanic waters of the Antarctic Circumpolar Current (ACC), with the

366 most extreme differences between the offshore waters north of the South Shetland Islands and

367 southern stations in Bransfield Strait in 2015 and 2016.

368 *3.1.3 Macrozooplankton abundance, distribution and assemblages*

369 Sixty-one taxa (Supplemental Table 2) were retained to examine the winter spatial organization

370 of macrozooplankton assemblages. Across all winter surveys, eight taxa made up 90% of total

371 macrozooplankton abundance including *Metridia* spp., post-larval and larval (primarily furcilia

372 stage) *Euphausia superba*, post-larval *Thysanoessa macrura*, *Limacina helicina*, Chaetognatha,

373 Ostracoda and Radiozoa. Each year, these eight taxa represented 89-94% of total

374 macrozooplankton abundance, indicating the preponderance of these taxa was consistent across

375 winter surveys.

376 Cluster analysis of winter sampling stations resulted in five clusters of macrozooplankton taxa,

377 representing strong spatial organization of the marine ecosystem (Fig. 3). Clusters with similar

378 UML depth, Chl $a$ and average salinity were labeled with the same cluster number and

16

379 differentiated with small letters (e.g., 2a, 2b). Indicator species analysis resulted in 53 taxa with

380 significant indicator values ($p < 0.05$), although only 38 taxa were above the 25% threshold.

381 Cluster 1 indicator taxa included the tunicate *Salpa thompsoni* and the gastropod *Clione*

382 *limacina*, although abundances of each were very low relative to other taxa (8.8 ± 1.6 and 3.9 ±

383 0.5 1000 m$^{-3}$, respectively; Table 2; Supplemental Table 3). Indicator taxa in cluster 2a were

384 more diverse, resulting in a mixture of euphausiids, copepods, amphipods, pteropods, and larval

385 fish species/groups. The highest indicator values in cluster 2a included Radiozoa (66% / 164.1 ±

386 35.1 1000 m$^{-3}$), the post-larval and larval euphausiid *E. frigida* (62% / 39.1 ± 3.8 1000 m$^{-3}$ and

387 76% / 151.8 ± 23.0 1000 m$^{-3}$, respectively) and the post-larval euphausiid *Euphausia triacantha*

388 (61% / 9.35 ± 1.2 1000 m$^{-3}$). Cluster 2b was dominated by post-larval *T. macrura* (37% / 193.3 ±

389 31.9 1000 m$^{-3}$), which was the lone indicator taxa. Cluster 3a was also very diverse;

390 chaetognaths, *Calanoides acutus* and siphonophores had the highest indicator values and

391 relatively high abundances (61% / 288.2 ± 32.6, 60% / 101.1 ± 36.9 and 71% / 63.4 ± 5.8 1000

392 m$^{-3}$, respectively). Cluster 3b indicator taxa included the two largest euphausiids (*E. superba* PL

393 and *Euphausia crystallorophias* PL; 91% / 2,288.2 ± 846.7 and 33% / 11.9 ± 6.8 1000 m$^{-3}$,

394 respectively).


395 Biophysical properties varied among clusters (UML depth Kruskal-Wallis $X^2 = 51.4$, $p < 0.001$;

396 integrated Chl *a* to 100 m Kruskal-Wallis $X^2 = 151.3$, $p < 0.001$; salinity Welch's $F = 213.18$, $p <$

397 0.001). The spatial distribution of macrozooplankton cluster 1 indicates a coastal association and

398 occurred both north and south of the South Shetland Islands in shallower depths on the

399 continental shelf (Fig. 3B). The biophysical properties of macrozooplankton cluster 1 were

400 associated with intermediate UML depths (122.3 ± 6.6 m;), integrated Chl *a* to 100 m (10.8 ± 0.6

401 mg m$^{-2}$; cluster 1:all other clusters, $p < 0.001$) and salinity (34.2 ± 0.01; cluster 1:all other

402 clusters, $p < 0.001$) compared with all other clusters. Cluster 1 was the most ubiquitous cluster,

403 occurring in 29%-52% of stations in any given year (Fig. 3). Spatial distribution of

404 macrozooplankton clusters 2a and 2b were located primarily within deep water off the

405 continental shelf north and west of the South Shetland Islands. Those clusters had similar,

406 shallow mean UML depths (79.5 ± 3.0 m and 85.7 ± 7.1 m, respectively; 2a:2b, p > 0.05), higher

407 integrated Chl *a* to 100 m (16.6 ± 0.5 mg m$^{-2}$ and 14.2 ± 0.7 mg m$^{-2}$, respectively; 2a:2b, p >

408 0.05), and lowest salinity (34.0 ± 0.01 and 33.9 ± 0.02, respectively; 2a:2b, p > 0.05). Cluster 2a

409 occurred in all years with annual proportions of stations ranging from 18% (2012) to 48%

410    (2013). Cluster 2b was rare in 2015 and 2016 (2 and 5% of stations, respectively) and had higher

411    representation in 2012-2014 (14%-27%).

412    A)
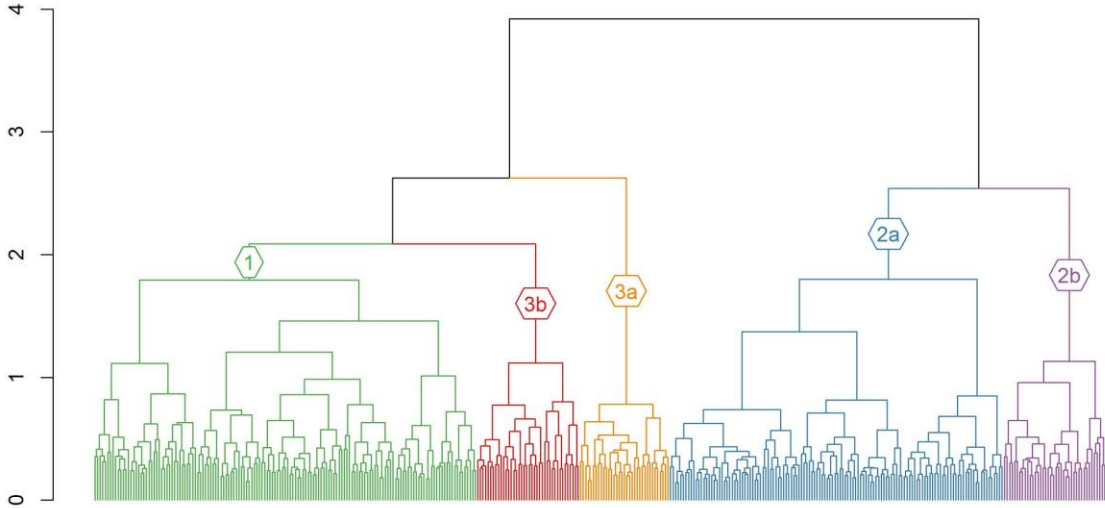


413

414    B)
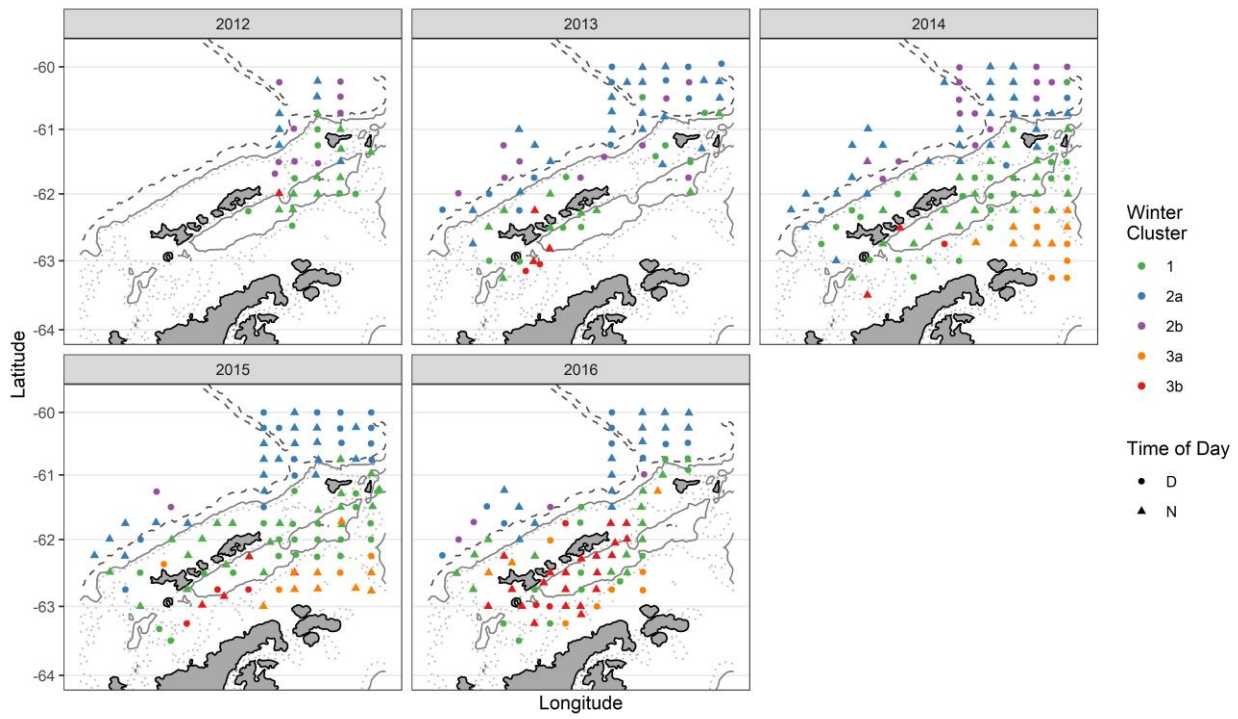


415
416    **Fig. 3** Winter cluster dendrogram (A) and station locations coded by cluster and year (B). Bathymetry indicated with light grey –
417    500 m (dotted), 1000 m (solid) and 2500 m (dashed). Clusters with similar numeric labels reflect association with similar
418    hydrographic and biophysical conditions (e.g., 2a-b). Not all stations were sampled in every year; Fig. 3 and 5 detail spatial
419    locations among years and Supplemental Table 1 describes timing and sample sizes for each survey.

**Table 2** Taxa with indicator values higher than 25% (p<0.05) for each winter cluster (Indicator values in parentheses). Supplemental Table 3 includes mean cluster abundance for each taxa. PL=post-larvae, L=larvae

| Clusters: 1 | 2a | 2b | 3a | 3b |
|---|---|---|---|---|
| *Salpa thompsoni* (34%) | *E.frigida* L (76%) | *Thysanoessa macrura* PL (37%) | Siphonophorae (71%) | *E.superba* PL (91%) |
| *Clione limac*ina (29%) | Radiozoa (66%) | | Chaetognatha (61%) | *E.crystallorophias* PL (33%) |
| | *E.frigida* PL (62%) | | *Calanoides acutus* (60%) | *Rhynchonereella bongraini* (29%) |
| | *E.triacantha* PL (61%) | | Sipuncula (52%) | |
| | Myctophidae L (55%) | | *Metridia* spp. (50%) | |
| | *Limacina helicina* (49%) | | Nototheniidae L (47%) | |
| | *Calanus propinquus* (48%) | | Polychaeta, Other (38%) | |
| | *Pleuromama* spp.(43%) | | Ostracoda (36%) | |
| | *Primno macropa* (42%) | | *Vanadis antarctica* (33%) | |
| | *Rhincalanus* spp.(41%) | | Isopoda (33%) | |
| | *Vibilia antarctica* (36%) | | *Paraeuchaeta* spp.(31%) | |
| | *Spongiobranchaea australis* (34%) | | *Pseudorchomene* spp. (31%) | |
| | Pisces, Other L (31%) | | *Hyperiella* spp.(29%) | |
| | *Pegantha martagon* (30%) | | *Tomopteris* spp.(28%) | |
| | *Themisto gaudichaudii* (30%) | | *Pelagobia* spp.(27%) | |
| | | | *Clio pyramidata* (27%) | |
| | | | *Pleuragramma antarctica* L (26%) | |

20

The spatial distribution of macrozooplankton clusters 3a and 3b occurred primarily within the eastern and western portions of Bransfield Strait, respectively (Fig. 3B). These clusters had similar and, compared to other clusters, deeper mean UML depths (163.7 ± 25.5 m and 177.7 ± 17.5 m, respectively; 3a:3b, $p > 0.05$), low integrated Chl $a$ to 100 m (6.0 ± 0.5 mg m$^{-2}$ and 6.3 ± 0.4 mg m$^{-2}$, respectively; 3a:3b, $p > 0.05$), and higher salinity (34.5 ± 0.01 and 34.3 ± 0.02, respectively; 3a:3b, $p < 0.001$). Macrozooplankton cluster 3a did not occur in 2012 or 2013, which may be attributed to limited sampling in the southeastern Bransfield Strait, near Joinville Island in those years. Macrozooplankton cluster 3b consisted of a higher proportion (28%) of sampling locations in 2016, with only 3%-8% of locations assigned to cluster 3b in other years.

Three dimensions were retained in the NMDS analysis (stress = 0.14) and the station groupings identified by the cluster analysis grouped well in the NMDS ordination (Fig. 4). Eight variables were retained in the regression analysis of the ordination (Table 3); however, average salinity, UML depth, average Chl $a$ integrated to 100 m and time of day were most strongly correlated with the NMDS direction cosines ($r^2 > 0.10$; Fig. 4 and Supplemental Fig. 1).
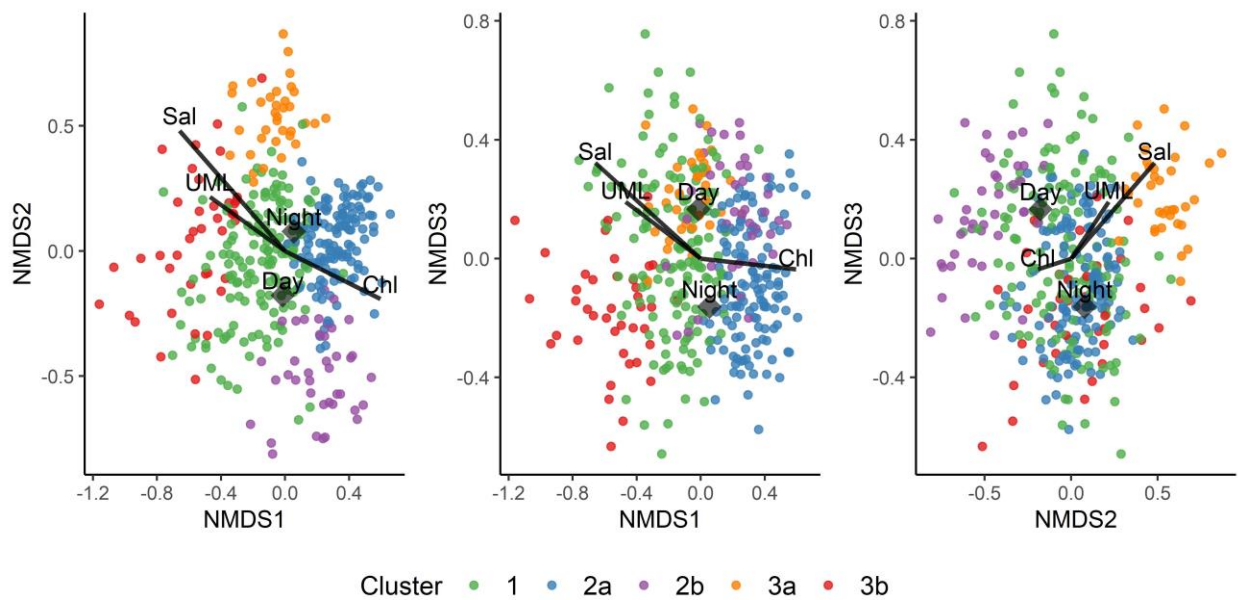


**Fig. 4** Winter clusters of abundance plotted on NMDS ordination (stress = 0.14) of all dimension combinations. Environmental vectors and factor centroids plotted (dark grey) were limited to regression r$^2 > 0.10$ (see Table 3 for full list of significant variables). Vector length is proportional to the correlation strength and the angle of the line represents the direction of forcing relative to the station distribution. UML – upper mixed layer depth; Sal – average UML salinity; Chl - average integrated Chl $a$ to 100 m.

445    **Table 3** Results of NMDS regression analysis for winter.

| Variables | Direction cosines | | | $r^2$ | $p$ |
|---|---|---|---|---|---|
| | $x_1$ | $x_2$ | $x_3$ | | |
| Salinity (UML) | -0.751 | 0.549 | 0.367 | 0.703 | <0.001 |
| Temp (UML) | 0.992 | -0.053 | 0.118 | 0.028 | 0.025 |
| Depth (UML) | -0.853 | 0.392 | 0.346 | 0.278 | <0.001 |
| Chl $a$ – Integrated 100m | 0.950 | -0.306 | -0.057 | 0.358 | <0.001 |
| Phae – Integrated 100m | 0.854 | 0.273 | -0.443 | 0.093 | <0.001 |
| Time of Day | | | | 0.160 | <0.001 |
| Day | -0.014 | -0.170 | 0.159 | | |
| Night | 0.052 | 0.074 | -0.155 | | |
| Year | | | | 0.094 | <0.001 |
| 2012 | -0.096 | -0.182 | -0.269 | | |
| 2013 | 0.147 | -0.045 | 0.046 | | |
| 2014 | 0.053 | -0.143 | -0.062 | | |
| 2015 | 0.010 | 0.097 | 0.050 | | |
| 2016 | -0.091 | 0.006 | 0.040 | | |
| Ice | | | | 0.051 | <0.001 |
| 10-75% | 0.036 | -0.108 | 0.026 | | |
| 100% | 0.025 | -0.020 | 0.016 | | |
| Ice | -0.260 | -0.150 | -0.326 | | |
| None | 0.149 | -0.155 | -0.108 | | |

446

447   *3.1.4 Diversity patterns of macrozooplankton assemblages*

448   Biodiversity patterns among winter macrozooplankton clusters varied substantially. Shannon-

449   Weaver diversity and Pielou's evenness varied among clusters (Kruskal-Wallis $X^2$ = 80.8, $p$ <

450   0.001 and $X^2$ = 76.3, $p$ < 0.001, respectively). Macrozooplankton clusters 1, 2a and 2b had the

451   highest mean Shannon-Weaver diversity indices (1.6 ± 0.0, 1.5 ± 0.0 and 1.4 ± 0.1, respectively;

452   1-2a, $p$ = 0.739; 2a-2b, $p$ = 0.859; 1-2b, p = 0.035) as well as the highest Pielou's evenness (all

453   0.5 ± 0.0; 1-2a, $p$ = 0.181; 2a-2b, $p$ = 1.0; 1-2b, $p$ = 0.272). Species richness also varied among

454   clusters (Welch's $F$ = 20.7, $p$ < 0.001). Clusters 2a and 3a had the highest richness (24.9 ± 0.4

455   and 25.5 ± 0.8, respectively; 2a-3a, $p$ = 1.0) and groups 2b and 3b the lowest (19.8 ± 0.6 and 18.2

456   ± 1.1, respectively; 2b-3b, $p$ = 1.0).

457   *3.2 Summer ecosystem dynamics*

458   *3.2.1 Hydrographic and productivity conditions*

459   Average summer UML depth was 45.5 ± 1.3 m. Annual means varied (Kruskal-Wallis $X^2$=

460   80.39, $p$ < 0.001) and ranged from 33.6 ± 2.4 m in 2006 to 57.1 ± 3.2 m in 2007. UML depths

461   were shallower in offshore waters in the ACC north of the South Shetland Islands compared to

462   Bransfield Strait. Average summer UML temperature was 1.53 ± 0.03 °C. Annual mean

463   temperatures varied (Kruskal-Wallis $X^2$= 143.24, $p$ < 0.001) and ranged from 1.14 ± 0.06 °C in

464   2004 to 2.51 ± 0.12 °C in 2006. Spatial gradients of UML temperature and salinity corresponded

465   to previously reported patterns in oceanic and coastal waters within the study area (Hofmann et

466   al., 1996; Amos, 2001; Loeb et al., 2010). Lowest temperatures were consistently found in

467   southern coastal waters of Bransfield Strait and at stations near the Weddell Sea. Highest

468   temperatures occurred offshore to the north of the South Shetland Islands. Average summer

469   UML salinity was 34.04 ± 0.01. Annual mean salinity varied (Kruskal-Wallis $X^2$ = 73.32, $p$ <

470   0.001) and ranged 33.95 ± 0.01 in 2004 to 34.15 ± 0.01 in 2009. Lowest salinities were

471   consistently found offshore to the north of the South Shetland Islands, whereas highest salinities

472   occurred within Bransfield Strait in all years.

473   Average summer 100 m integrated Chl *a* was 56.5 ± 1.7 mg m$^{-2}$. Annual mean Chl *a* biomass

474   varied (Kruskal-Wallis $X^2$ = 120.64, $p$ < 0.001) and ranged from 33.5 ± 1.9 mg m$^{-2}$ in 2003 to

475    $95.3 \pm 6.5$ mg m$^{-2}$ in2006. Areas of low Chl *a* biomass were consistent in offshore waters north

476    of the South Shetland Islands. However, coinciding with increased temperature, integrated Chl *a*

477    biomass to 100 m were highest in 2006 (2006: all years, $p < 0.05$), with moderate to high levels

478    in 2007 and 2009. Average summer 100 m integrated phaeopigment was $11.8 \pm 0.4$ mg m$^{-2}$.

479    Annual means varied (Kruskal-Wallis $X^2 = 293.45$, $p < 0.001$) and ranged from $5.1 \pm 0.4$ mg m$^{-2}$

480    in 2011 to $26.2 \pm 1.4$ mg m$^{-2}$ in 2006. Phaeopigment biomass was very low in 2004 and 2011 and

481    in general, lower biomasses were found north of the South Shetland Islands. Unusually high

482    phaeopigment biomasses were observed in 2006 with moderate levels in 2007 (2006 and 2007:

483    all years, $p < 0.05$).

484    *3.2.2 Macrozooplankton abundance, distribution and assemblages*

485    Fifty-nine taxa (Supplemental Table 1) were retained to examine the summer spatial organization

486    of macrozooplankton assemblages. During the summer surveys, eight taxa including *C. acutus*,

487    *S. thompsoni*, *T. macrura* (post-larvae and larvae), *Metridia* spp., *E. superba* larvae (calyptopis

488    stage), Chaetognatha, and *Rhincalanus* spp. made up 87% of the total abundance. However,

489    within each year the combined abundance of these taxa ranged from 67% to 93%, indicating

490    greater variability of dominant taxa compared to the winter composition.

491    Cluster analysis of summer sampling stations resulted in seven clusters of macrozooplankton

492    taxa (Fig. 5). Indicator species analysis resulted in 49 taxa with significant indicator values ($p <$

493    0.05), with 25 taxa above the 25% threshold (Table 4; Supplemental Table 2). Cluster 1 included

494    three indicator taxa: *S. thompsoni* (64%) and two amphipods, *Vibilia antarctica* (38%) and

495    *Cyllopus magellanicus* (31%). Indicator taxa were absent from cluster 2. Cluster 3 indicator taxa

496    comprised a broad mixture of copepods, amphipods and gastropods. Cluster 3 also included two

497    smaller euphausiid larvae, *T. macrura* and *E. frigida* (93% / $3,303.8 \pm 714.5$ and 32% / $59.4 \pm$

498    $16.0$ 1000 m$^{-3}$, respectively) and chaetognaths (65% / $544.2 \pm 81.6$ 1000 m$^{-3}$). Cluster 4 indicator

499    taxa consisted of *E .superba* larvae (calyptopis stage; 53% / $1030.0 \pm 383.2$ 1000 m$^{-3}$)*,* post-

500    larval *E. frigida* (36% / $27.3 \pm 4.1$ 1000 m$^{-3}$), *Metridia* spp. (51% / $1,426.2 \pm 300.0$ 1000 m$^{-3}$)

501    and a larval fish (*Notolepis* spp.; 39% / $0.88 \pm 0.26$ 1000 m$^{-3}$). Cluster 5 indicator taxa included

502    sipunculids and isopods (40% / $6.9 \pm 2.0$ and 30% / $2.7 \pm 0.5$ 1000 m$^{-3}$, respectively). Clusters 6

503 and 7 each had a single indicator taxa including the amphipods *Themisto gaudichaudii* (26% /

504 $13.8 \pm 2.5$ 1000 m$^{-3}$) and *C. lucasii* (26% / $1.3 \pm 0.3$ 1000 m$^{-3}$), respectively.

505 The temporal occurrence and spatial distribution of the seven summer macrozooplankton clusters

506 displayed substantial variability (Fig. 5B). Spatial distribution of cluster 1 indicated a strong

507 presence in oceanic waters north and offshore of the South Shetland Islands in 2004, 2005, 2007

508 and 2009. Cluster 1 was most prevalent in 2011 (56% of all stations), occurring throughout the

509 study area in many coastal stations. However, cluster 1 did not occur in 2003 or 2006. Cluster 2

510 occurred predominantly within Bransfield Strait and around Elephant Island in 2003, 2005, 2007,

511 2009 and 2011 and north of the South Shetland Islands in 2004. Cluster 3 occurred

512 predominately offshore in 2006 and 2011 and did not occur in 2003, 2004 or 2005. Cluster 4 was

513 most prevalent in 2006 and 2007, occurring mostly north of the South Shetland Islands. Cluster 5

514 occurred within coastal waters on the continental shelf north and south of the South Shetland

515 Islands in 2003, 2006 and 2007, and further south in the Bransfield Strait in 2005, 2009 and

516 2011. Cluster 5 was present in highest annual proportions in 2006 and 2007 (43% and 53%,

517 respectively). Cluster 6 displayed an oceanic distribution pattern in 2003 and 2007 and occurred

518 on the shelf or at the shelf break in 2005 and 2009.

**Table 4** Taxa with indicator values higher than 25% (p<0.05) for each summer cluster (indicator values in parentheses). Supplemental Table 4 includes mean cluster abundances for each taxa. PL=post-larvae, L=larvae, C=calyptopis

| 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|
| *Salpa thompsoni* (64%) *Vibilia antarctica* (38%) *Cyllopus magellanicus* (31%) | | *Thysanoessa macrura* L (93%) *Calanoides acutus* (85%) Radiozoa (77%) Chaetognatha (65%) *Limacina helicina* (63%) *Rhincalanus* spp. (62%) *Tomopteris* spp. (53%) *Calanus propinquus* (45%) *Clione limacina* (40%) *Paraeuchaeta* spp. (36%) *Spongiobranchaea australis* (33%) *Primno macropa* (33%) *E. frigida* L (32%) *Haloptilus* spp. (30%) | *E. superba* L(C) (53%) *Metridia* spp. (51%) *E.frigida* PL (36%) *Notolepis* spp. L (39%) | Sipuncula (40%) Isopoda (30%) | *Themisto gaudichaudii* (26%) | *Cyllopus lucasii* (26%) |

26

523   A)



524
525   B)
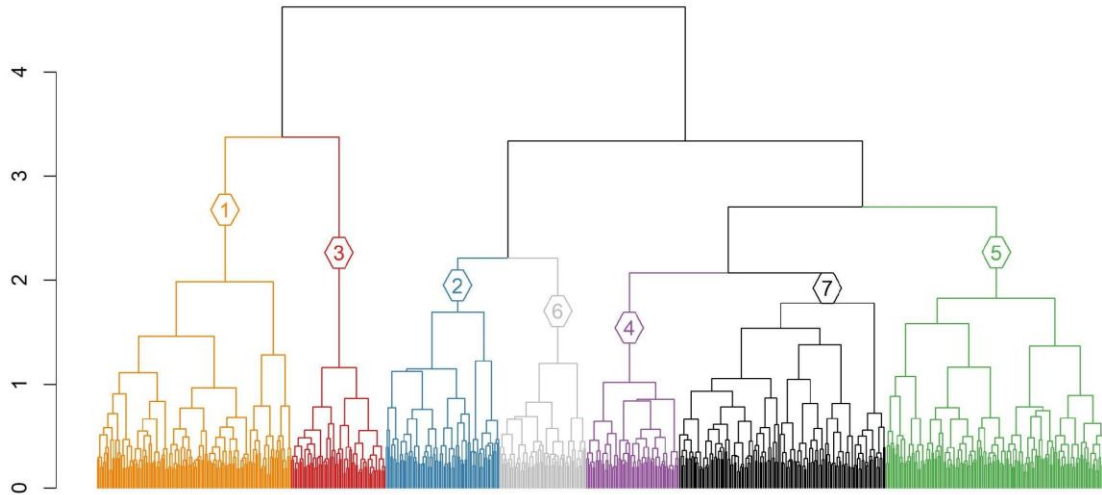


526
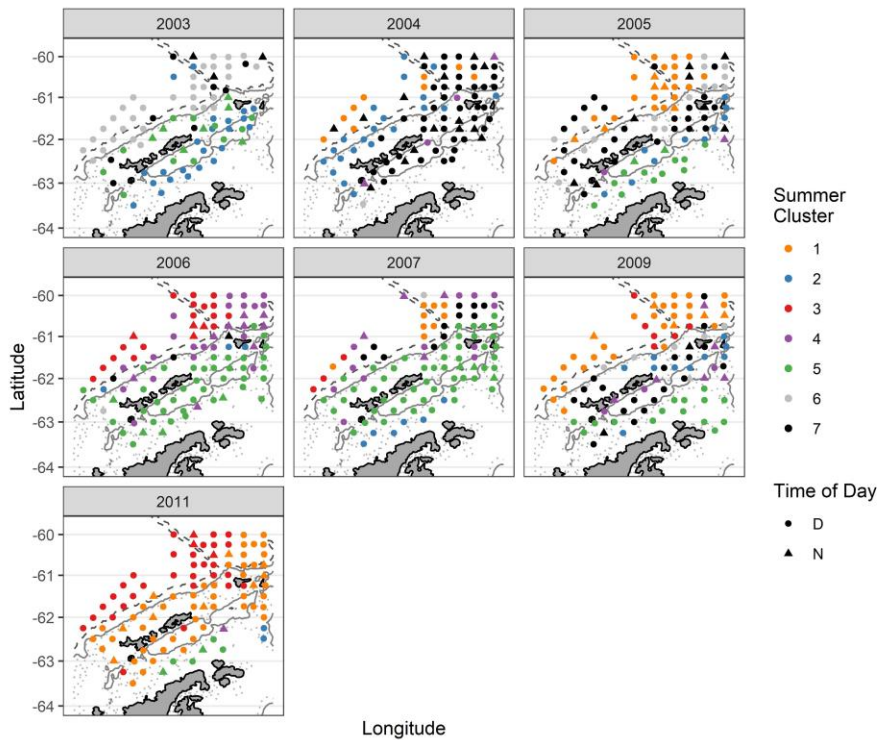527   **Fig. 5** Summer cluster dendrogram (A) and station locations coded by cluster and year (B). Bathymetry indicated with light grey
528   – 500 m (dotted), 1000 m (solid) and 2500 m (dashed). Not all stations were sampled in every year; Fig. 3 and 5 detail spatial
529   locations among years and Supplemental Table 1 describes timing and sample sizes for each survey.
530

27

531   Cluster 7 occurred in a mixture of oceanic and coastal waters in 2003 and 2005, was distributed

532   along the coast north of the South Shetland Islands and within Bransfield Strait in 2009, and was

533   more widespread in 2004, occurring throughout the study area (62% of sampling locations).

534   Although water zone was determined for most (80%) of the summer stations, there was no clear

535   relationship between cluster and classified water zone. Mean UML depth varied among clusters

536   (Kruskal-Wallis $X^2$ = 21.16, $p$ = 0.002), although many clusters overlapped due to similar

537   regional associations. Integrated Chl $a$ to 100 m also varied among clusters (Kruskal-Wallis $X^2$ =

538   192.6, $p$ < 0.001).  Clusters 1, 3 and 6 occurred in areas with low mean integrated Chl $a$ to 100 m

539   (38.0 ± 2.8, 28.0 ± 2.5 and 35.9 ± 3.4 mg m$^{-2}$, respectively; clusters 1:3:6, all $p$ = 1.0), whereas

540   clusters 4 and 5 coincided with the highest observed Chl $a$ (87.8 ± 5.5 and 82.3 ± 4.5 mg m$^{-2}$,

541   respectively; cluster 4:5, $p$ = 1.0). Due to regional variability and differences in oceanic and

542   coastal ocean conditions, temperature and salinity also differed among clusters (Kruskal-Wallis

543   $X^2$ = 231.7, $p$ < 0.001 and $X^2$ = 132.7, $p$ < 0.001, respectively). Specifically, clusters 3 and 4 were

544   found in areas with the highest mean UML temperatures (2.5 ± 0.1 and 2.1 ± 0.1 °C,

545   respectively, although cluster 4 was not different from clusters 1 or 6 (1.6 ± 0.04 and 1.8 ±

546   0.1 ℃, respectively; cluster 4:1 and 4:6, $p$ > 0.05)). Clusters 2, 5 and 7 had the lowest mean

547   UML temperatures (1.1 ± 0.1, 1.1 ± 0.1 and 1.3 ± 0.1 °C, respectively). Cluster 3 had the lowest

548   mean salinity (33.8 ± 0.01) and clusters 2 and 5 occurred within regions of the highest salinity

549   (34.1 ± 0.02 and 34.2 ± 0.01, respectively).

550   Three dimensions were retained in the NMDS analysis (stress = 0.17) and the station groupings

551   identified by the cluster analysis grouped well in the NMDS ordination (Fig. 6). Seven variables

552   were retained in the regression analysis of the ordination (Table 5); however, average salinity,

553   average temperature, average Chl $a$, phaeopigment to 100 m and year were most strongly

554   correlated ($r^2$ > 0.10) with the NMDS direction cosines (Fig. 6 and Supplemental Fig. 2).

555
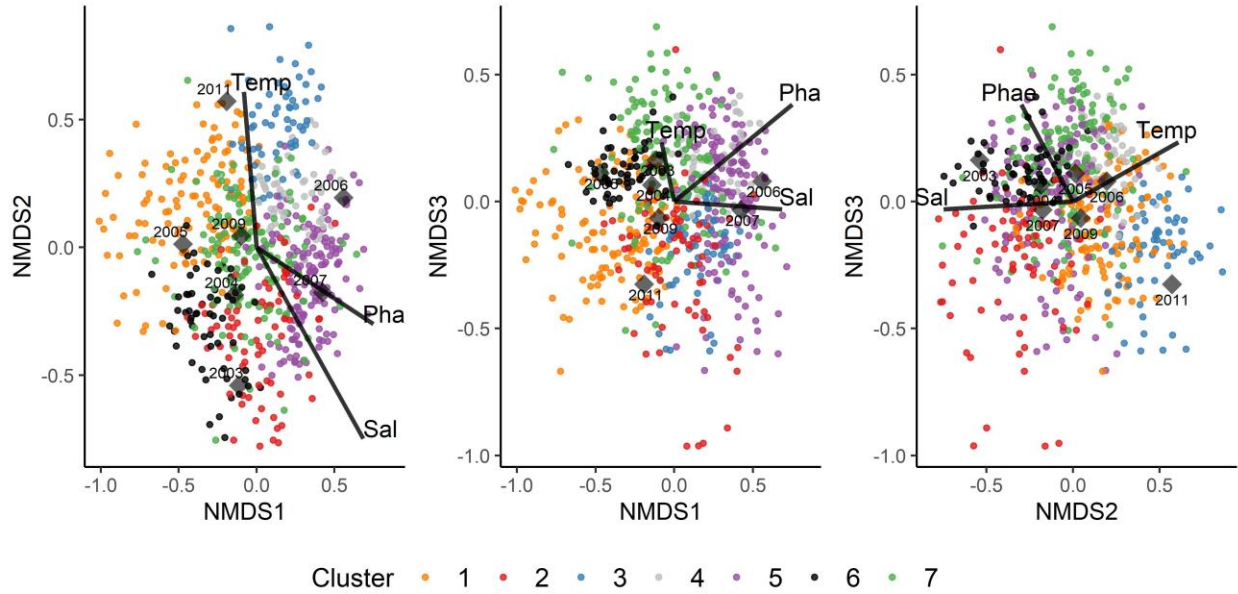
**Fig. 6** Summer clusters of abundance plotted on NMDS ordination (stress = 0.17) of all dimension combinations. Environmental vectors and factor centroids (dark grey) were limited to regression $r^2 > 0.10$ (see Table 5 for full list of significant variables). Chl *a* excluded from plot due to overlap with phaeopigment. Vector length is proportional to the correlation strength and the angle of the line represents the direction of forcing relative to the station distribution. Sal – average UML salinity; Phae - average integrated phaeopigment to 100 m; Temp – average UML temperature.

563  **Table 5** Results of NMDS regression analysis for summer.
564

| Variables | Direction cosines | | | $r^2$ | $p$ |
|---|---|---|---|---|---|
| | $x_1$ | $x_2$ | $x_3$ | | |
| Salinity (UML) | 0.657 | -0.753 | -0.039 | 0.291 | <0.001 |
| Temp (UML) | -0.081 | 0.932 | 0.355 | 0.126 | <0.001 |
| Depth (UML) | 0.006 | -0.188 | -0.982 | 0.015 | 0.020 |
| Chl $a$ – Integrated 100m | 0.777 | -0.411 | 0.478 | 0.171 | <0.001 |
| Phaeopigment – Integrated 100m | 0.844 | -0.328 | 0.423 | 0.225 | <0.001 |
| Time of day | | | | 0.062 | <0.001 |
| Day | -0.007 | -0.037 | -0.042 | | |
| Night | 0.011 | 0.194 | 0.235 | | |
| Year | | | | 0.253 | <0.001 |
| 2003 | -0.060 | -0.284 | 0.086 | | |
| 2004 | -0.075 | -0.098 | 0.035 | | |
| 2005 | -0.249 | 0.007 | 0.059 | | |
| 2006 | 0.294 | 0.103 | 0.043 | | |
| 2007 | 0.223 | -0.093 | -0.017 | | |
| 2009 | -0.060 | 0.027 | -0.034 | | |
| 2011 | -0.116 | 0.302 | -0.181 | | |

565

566  *3.2.3 Diversity patterns of macrozooplankton assemblages*

567  Biodiversity patterns among summer macrozooplankton clusters varied (Kruskal-Wallis $X^2 =$

568  130.6, $p < 0.001$, $X^2 = 175.6$, $p < 0.001$, and $X^2 = 116.5$, p < 0.001, for Shannon-Weaver

569  diversity, richness and Pielou's evenness, respectively). Diversity and evenness were similar

570  among clusters 2 through 7 ($p > 0.05$ for all pairwise combinations); only cluster 1 was different

571  and less for both measures. Although richness varied among clusters, there was no clear

572  combination of similar clusters (e.g., many overlapping cluster combinations of 2 or 3 clusters).

573  There was also no clear spatial pattern in any of the diversity indices.

574  *3.3 Seasonal macrozooplankton comparisons*

575 Abundance was variable between summer and winter for most taxa (Table 6; Supplemental

576 Table 5). Here we summarize aspects of each of the reported high abundance taxa according to

577 their major taxonomic groupings.

578 Euphausiids

579 Average winter abundance of *E. superba* post-larvae was higher in winter compared to summer

580 (Table 6, Supplemental Table 5) although no difference was found when analysis was restricted

581 to night tows. *E. superba* post-larvae was an indicator taxon for winter cluster 3b, where higher

582 abundances were concentrated in Bransfield Strait (Fig. 3B). Our assessment indicates that *E.*

583 *superba* larvae were highly abundant in both summer and winter. *E. superba* larvae (calyptopis

584 stage) was an indicator taxa of summer cluster 4 and had relatively high abundance in summer

585 cluster 3 as well (Supplemental Table 4). *E. superba* larvae (furcilia stage) were highly abundant

586 in all winter clusters except cluster 2b, hence did not appear as a winter indicator taxon

587 (Supplemental Table 3).

588 *T. macrura* post-larvae were highly abundant in both summer and winter surveys, although

589 slightly higher in summer (Table 6, Supplemental Table 5). Depending on year, the summer

590 macrozooplankton cluster 5 had the highest abundance of *T. macrura* post-larvae and occurred

591 either on the continental shelf around the South Shetland Islands or within Bransfield Strait (Fig.

592 5, Supplemental Table 4). *T. macrura* post-larvae were an indicator taxon for winter

593 macrozooplankton cluster 2b, with relatively high abundances in both "offshore" clusters (2a and

594 2b; Fig. 3, Supplemental Table 3). *T. macrura* post-larvae appear to make a slight shift south in

595 summer. Relatively few *T. macrura* larvae were encountered in the winter. However, *T. macrura*

596 larvae in summer were the third most abundant taxa and were also a summer indicator taxon for

597 macrozooplankton cluster 3, which was located offshore north of the South Shetland Islands.*E.*

598 *frigida* post-larvae and larvae had higher abundances in winter although when restricted to night

599 tows post-larvae did not differ between seasons (Table 6). *E. crystallorophias* (post-larvae)

600 abundance also did not differ between seasons.

601 Copepods

31

602 *Metridia* spp. were highly abundant in both summer and winter, although winter abundance was

603 three times higher (Supplemental Table 5). *Metridia* spp. was an indicator taxon in both seasons

604 (winter cluster 3a and summer cluster 4). The abundance of the copepod *Paraeucheata* spp. was

605 higher in summer, while *C. propinquus* was the same between seasons. Other highly abundant

606 copepods in summer included *C. acutus* and *Rhincalanus* spp., which are strong seasonal

607 migrators to greater depths (Yamanaka, 1976; Atkinson and Peck, 1988; Schnack-Schiel et al.,

608 1991; Hopkins et al., 1993; Atkinson and Sinclair, 2000). Both taxa were also indicator taxa in

609 the summer cluster 3 and *Rhincalanus* spp. was an indicator taxon in winter cluster 2a; these

610 clusters consistently occurred in oceanic waters north of the South Shetland Islands (Figs. 5B

611 and 3B, respectively).

### Gastropods

613 Regardless of season, *L. helicina* was the most abundant gastropod in the survey area

614 (Supplemental Table 5). The abundances of gastropods *C. limacina* and *L. helicina* were greater

615 in winter and *Spongiobranchaea australis* and *Clio pyramidata* did not differ between seasons

616 (Table 6).

### Tunicata

618 Summer abundance of *S. thompsoni* was 50 times higher than winter abundance (Supplemental

619 Table 5). However, frequency of occurrence of *S. thompsoni* was only 8% higher in summer

620 (81% vs. 73%; annual summer range 47%-99% vs. winter range 49%-90%). *S. thompsoni* had

621 highest winter abundances and frequency of occurrence within macrozooplankton clusters 1, 2a

622 and 3b, and highest summer abundances and frequency of occurrence in clusters 1, 3 and 7

623 (Supplemental Tables 3 and 4). These clusters were distributed throughout the shelf around the

624 South Shetland Islands and/or north of the shelf in deep water; winter cluster 2b, which was also

625 off shelf, was the exception and did not have high salp abundance.

### Other

627 In general, the Hyperiidean amphipods had higher summer abundances except for *Scina* spp.,

628 whereas the Amphilochidean amphipods had higher winter abundances. Chaetognatha, a

629 predatory macrozooplankton phylum, were widely distributed throughout the study region and

32

630 their abundance was similar in winter and summer (Table 6; Supplemental Table 5). We found

631 that abundance of Ostracoda in winter was approximately an order of magnitude higher

632 compared to summer (Supplemental Fig. 3H). Although Radiozoa were highly abundant in both

633 seasons, we did not make any formal comparison because our sampling gear was not optimal for

634 sampling this phylum.

635 **Table 6** Summary of seasonal comparisons by taxa (significantly different/greater $p<0.05$). PL=post-larvae, L=larvae, F=furcilia,
636 C=calyptopis

| Group | Summer > Winter | Winter > Summer | No difference |
|---|---|---|---|
| **Amphipoda** | | | |
| | *Cyllopus lucasii* | *Eusirus* spp. * | |
| | *C. magellanicus* | *Psceudorchomene* spp. | *Psceudorchomene* spp.⁂ |
| | *Cyllopus* spp. | *Scina* spp. | *Scina* spp. ⁂ |
| | *Hyperiella* spp. | | |
| | *Primno macropa* | | |
| | *Themisto gaudichaudii* | | |
| | *Vibilia antarctica* | | |
| **Copepoda** | | | |
| | *Calanoides acutus* | *Metridia* spp.* | *Calanus propinquus* |
| | *Paraeucheata* spp. | *Pleuromama* spp. | *Pleuromama* spp. ⁂ |
| | *Rhincalanus* spp. | | |
| **Euphausiids** | | | |
| | *T. macrura* PL * & L | *E. frigida* PL & L * | *E.crystallorophias* PL |
| | E.*superba* L(C) | *E. superba* PL & L(F) | *E. frigida* PL ⁂ |
| | | *E. triacantha* PL | *E. superba* PL ⁂ |
| | | | *E. triacantha* PL⁂ |
| **Gastropoda** | | | |
| | | *Clione limacina* | *Spongiobranchaea australis* |
| | | *Limacina helicina* | *Clio pyramidata* |
| **Pisces** | | | |
| | *Notolepis* spp. | Bathydraconidae | Bathylagidae |
| | Nototheniidae | Myctophidae Ad & L | Harpagiferidae |
| | | Other L | *Pleuragramma antarctica* L |
| | | Channichthyidae | |
| | | Fish Eggs | |
| **Polychaeta** | | | |
| | *Tomopteris* spp. | *Pelagobia longicirrata* | |
| | | *Rhynchonereella bongraini* | |
| | | *Vanadis antarctica* | |
| **Gelatinous** | | | |
| | Ctenophora | Hydromedusae | |
| |  *Beroe* spp. |  *Pegantha martagon* | |
| |  Mertensiidae | | |
| | Tunicata | Siphonophorae | |
| |  *Ihlea racovitzai* | | |
| |  *Salpa thompsoni* | | |
| **Other macrozooplankton** | | | |

| Group | Summer > Winter | Winter > Summer | No difference |
|---|---|---|---|
| | | Isopoda | Chaetognatha |
| | | Ostracoda * | |

637    *winter significantly different and greater using full and night subset of the data; ‡ night only sets

**4.0 Discussion**

639    Macrozooplankton research around the northern Antarctic Peninsula has focused primarily on

640    summer sampling (Jazdzewski et al., 1982; Piatkowski, 1989; Nordhausen, 1991; Lee et al.,

641    2004; Loeb et al., 2005; Loeb et al., 2009b; Loeb and Santora, 2015) with sporadic spring, fall

642    and winter cruises (Siegel and Piatkowski, 1990; Ross, 1996; Cleary et al., 2016). Yet there is

643    increased interest in understanding the impacts of winter physical and biological processes on

644    spring and summer ecosystem dynamics (Siegel and Loeb, 1995; Hunt et al., 2011; Rozema et

645    al., 2017). Similar to other Southern Ocean macrozooplankton studies, our results from multi-

646    year sampling in winter and summer showed abundance was dominated by a few taxa. However,

647    dominant taxa differed among seasons and clusters (this study; (Siegel and Piatkowski, 1990;

648    Hunt et al., 2011)), months and years (Loeb and Armstrong., 2005; Loeb et al., 2005), years

649    (Hosie and Cochran, 1994) and regions and years (Steinberg et al., 2015).

*4.1 Spatial variability of macrozooplankton community structure*

651    The spatial distribution of winter macrozooplankton clusters was consistent across the study

652    region among years, whereas summer macrozooplankton clusters were more variable in space

653    and time (next section). The spatially recurrent patterns of winter macrozooplankton clusters

654    compared to summer cluster patterns clearly suggest higher stability in terms of the

655    biogeographic structure of macrozooplankton communities. For example, winter clusters 2a and

656    2b (containing several euphausiids, Hyperiidean amphipods and larger copepod species)

657    primarily occurred off the continental shelf (waters > 1000 m) north of the South Shetland

658    Islands, while winter clusters 3a and 3b (containing the two larger euphausiids, chaetognaths,

659    several polychaetes and *Metridia* spp.) occurred mainly in the Bransfield Strait. Winter cluster 1

660    (comprised of *S. thompsoni* and *C. limacina*) was mostly limited to shallower, continental shelf

661    waters straddling north and south of the South Shetland Islands regardless of year (Fig. 3). In

662    contrast, although summer cluster 3 (containing euphausiid larvae, Hyperiidean amphipods,

663    chaetognaths and larger copepods) was consistently distributed off the shelf north of the South

664 Shetland Islands, the remaining summer clusters varied widely in their spatial locations from

665 year to year (Fig. 5). In summer, only 3-5 cluster groupings occurred in any given year and the

666 high abundance of single taxa appear to drive the occurrence of clusters in some years (e.g., *E.*

667 *superba* larvae in 2006; *S. thompsoni* in 2011).

668 Previous studies have found high spatial and interannual variability in summer

669 macrozooplankton abundance and distribution throughout the Antarctic Peninsula region (Siegel

670 and Piatkowski, 1990; Loeb et al., 2005; Loeb et al., 2009b; Steinberg et al., 2015). Siegel and

671 Piatkowski (1990) assessed seasonal macrozooplankton community patterns derived from four

672 cruises across summer, winter and spring from sampling locations within our study area, as well

673 as parts of the western Antarctic Peninsula. They resolved three winter clusters from sampling

674 depths less than 200 m that were defined as "oceanic", "neritic" and "transitional." Their clusters

675 overlap with clusters we defined off the continental shelf north of the South Shetland Islands,

676 clusters at the southern edge of Bransfield Strait and shallower on-shelf waters straddling the

677 South Shetland Islands, respectively. During their summer survey, Siegel and Piatkowski (1990)

678 resolved three macrozooplankton clusters which would be similar to our results if one focused on

679 a single summer of our study (e.g., 2011) but in aggregate, the spatial distribution of our clusters

680 exhibited more variability in presence and location. Ward et al. (2004) analyzed summer survey

681 data from the Antarctic Peninsula to South Georgia and found evidence of six macrozooplankton

682 community clusters. Where the Ward et al. (2004) survey overlapped with ours in the northern

683 Antarctic Peninsula, three clusters were described: 1) north of the southern Antarctic

684 Circumpolar Current front (sACCf), 2) between the sACCf and the southern boundary of the

685 ACC and 3) the Weddell Sea water zone. It is likely that some of the interannual spatial

686 variability within our macrozooplankton clusters may be linked to the dynamic locations of the

687 sACCf and the southern boundary (Sprintall, 2003; Loeb et al., 2009a). Therefore, due to the

688 apparent variability found in our survey and past surveys, future biogeographic assessment of

689 summer macrozooplankton community structure requires integration of multiple surveys to

690 better understand dynamics underlying the macrozooplankton community composition and

691 structure.

692 There are several challenges when comparing macrozooplankton community structure studies

693 including 1) differences in net type/mesh size (Atkinson et al., 2012), time-of-day and depths

36

694 sampled, which impact selectivity of species caught; 2) differences in the level of taxonomic

695 identification (i.e., resolution; Genera, Family) ; 3) decisions to include/exclude certain taxa; and

696 4) statistical decisions regarding data standardization and selection of dissimilarity matrix type,

697 which may impact analysis outcomes and comparisons among studies. However, our

698 standardized multi-year survey assessment involving consistent sampling stations and statistical

699 procedures represents a robust biogeographic assessment of macrozooplankton community

700 composition, by which results from previous and future surveys can be informed. Moreover, the

701 broad consistency between findings in our studies and those conducted by other researchers

702 suggests that the main drivers of community organization have been identified adequately to

703 make cross-study comparisons.

704 Overall, macrozooplankton community clusters and indicator species analysis confirmed that

705 spatial patterns of macrozooplankton were related to hydrographic conditions of the Antarctic

706 Peninsula marine ecosystem. We also found that some indicator taxa were consistent from

707 summer to winter and that cluster patterns were related to oceanic (low salinity/high

708 temperature) or higher latitude (high salinity/low temperature) conditions. For example, within

709 summer cluster 3 and winter cluster 2a, which were distributed off the shelf north of the South

710 Shetland Islands, each had 7 indicator taxa in common (Radiozoa, *L. helicina*, *Rhincalanus* spp.,

711 C. *propinquus*, *Primno macropa*, *S. australis* and *E. frigida* larvae). During years when summer

712 macrozooplankton clusters 1 and 6 were present north of the South Shetland Islands, the

713 amphipods *V. antarctica* and *T. gaudichaudii* were indicator taxa in both summer and winter

714 (cluster 2a). Using species abundance correlations to define indicator taxa, Siegel and Piatkowski

715 (1990) found several "oceanic" indicator taxa in common with our results, including *S. australis,*

716 *P. macropa, C. limacina* in summer and *E. triacantha*, *E. frigida* post-larvae, and *T.*

717 *gaudichaudii* in winter. Notable differences were found for *T. macrura* post-larvae, which we

718 found to be more "oceanic" in both summer and winter, whereas Siegel and Piatkowski (1990)

719 classified *T. macrura* as a "neritic" indicator taxa during their single winter cruise. Although not

720 a formal community analysis, Jazdzewski et al. (1982) also found higher abundances of several

721 copepods, *Rhincalanus* spp., C. *propinquus*, and *C. acutus*, in summer in what they describe as

722 the Antarctic Zone beyond the continental shelf north of the South Shetland Islands. In our study,

723 sipunculids and isopods were consistent indicator taxa in both summer (cluster 5) and winter

724 (cluster 3a) and were related to presence of high salinity (> 34.3)/ low temperature (average -

37

725 1.79 °C) water in the southwest Bransfield Strait, although their abundances were low

726 (Supplemental Tables 3 and 4). Also in our study, in the northern and eastern regions of

727 Bransfield Strait, post-larvae of the two larger euphausiids, *E. superba* and *E. crystallorophias*,

728 were indicator taxa in winter and similarly identified by Siegel and Piatkowski (1990) as

729 "neritic" indicator taxa in winter. Other taxa appear to be more flexible in their habitat

730 associations (e.g., *Metridia* spp. and Chaetognatha), but it is important to note that there may be

731 species-specific associations or depth distributions that could confound the identification of

732 indicator taxa (David, 1959; Atkinson and Sinclair, 2000).

733 We found no strong patterns in diversity or species richness with respect to macrozooplankton

734 clusters that indicate the presence of spatial or temporal hotspots (i.e., areas of recurrent high

735 diversity). However, oceanic and coastal stations within winter clusters 1, 2a and 2b had higher

736 diversity compared to clusters located within Bransfield Strait (e.g., 3a and 3b). Oceanic (cluster

737 2a) and cold, high salinity water (cluster 3a) had higher species richness than other oceanic and

738 Bransfield Strait clusters (2b and 3b, respectively). Siegel and Piatkowski (1990) found an

739 opposite pattern, with highest diversity and evenness occurring within their neritic

740 macrozooplankton cluster identified during their single winter (May/June) survey. Further,

741 Siegel et al. (1990) also found higher diversity in their summer oceanic cluster, which is similar

742 to our summer cluster 1 locations in 2004, 2005, 2007 and 2009. However, summer cluster 1

743 occurred on the shelf in 2011. It is important to note that the diversity indices of these two

744 studies are not fully comparable due to net selectivity differences.

745 *4.2 Seasonal variability of macrozooplankton community structure*

746 As expected, due to variability in source waters, environmental conditions and species

747 population dynamics, we found that many taxa displayed marked changes in abundance during

748 and between summer and winter surveys (Table 6; Supplemental Fig. 1). Although some of our

749 results contrast with results from other studies, the species abundance patterns we identified are

750 important for understanding temporal variability of macrozooplankton community structure.

751 The current study extends on a previous assessment of winter *E. superba* distribution and

752 occurrence (Reiss et al., 2017) and continues to support the hypothesized seasonal shift of *E.*

753 *superba* into Bransfield Strait in the winter (Siegel, 1988; Siegel, 1989), although perhaps the

754 shift is stronger for smaller size classes and larvae. Siegel et al. (2013) performed a cluster

755 analysis on the distribution of post-larval *E. superba* age classes in summer along the entire

756 western Antarctic Peninsula and found that smaller, juvenile post-larvae tended to be more

757 concentrated inshore with larger, older classes clustering offshore. In summer, we found a

758 broader but more variable distribution pattern compared to that described by Makarov et al.

759 (1990), who characterized larval distribution as occurring closer to shore in  continental shelf and

760 slope habitats. Siegel et al. (2013), Perry et al. (2019) and Conroy et al. (2020) all noted high

761 larval abundance offshore of the entire western Antarctic Peninsula area in summer although the

762 similarity to our results may be partially due to some overlap of data analyzed.

763 For *T. macrura* larvae Makarov et al. (1990) found a pattern similar to ours with consistently

764 high abundance located off-shelf within the oceanic zone in summer, whereas they found more

765 variability in abundance on the continental shelf. However, differences in mesh size and

766 sampling depth likely influence these disparities.

767 Winter abundance of *Metridia* spp. was three times higher than summer; winter was also higher

768 when the analysis was restricted to night tows. It is possible that species-specific differences in

769 the epipelagic zone may be driving abundances in different seasons (Atkinson and Peck, 1988;

770 Schnack-Schiel and Hagen, 1994; Atkinson and Sinclair, 2000). A quirk of summer cluster 4 was

771 a disproportionate percent of night tows (38% of all cluster 4 stations) compared to other

772 summer clusters which had many fewer night tows (0-21%); this may partially explain why

773 *Metridia* spp. was an indicator species for this cluster since some *Metridia* spp. are known diel

774 migrators (Lopez and Huntley, 1995).

775 Average abundance of *L. helicina* was more than two times greater in winter compared to

776 summer (Supplemental Fig. 3D), contrary to the findings of most other studies. Hunt et al.

777 (2011) found a decrease in *L. helicina* abundance during winter surveys in the Lazarev Sea. Hunt

778 et al. (2008) report higher spring and summer densities of *L. helicina* for the Antarctic Peninsula,

779 East Antarctica and South Georgia, but none of these areas were sampled fully in winter.

780 Possible differences in seasonal trends of *L. helicina* may in part be due to different net and mesh

781 sizes used in different surveys. We also found a slight shift of *L. helicina* to the north in winter,

782 although this could also be due to higher Chl *a* at lower latitudes, a function of different 'age'

783 classes encountered among seasons, or a combination of both. Furthermore, Loeb and Santora

784 (2013) examined the long-term variability of summer abundance and distribution of *L. helicina*

785 and determined that temporal fluctuation of this species may relate to the ESNO variability and

786 shifts in the position of sACCf.

787 Chaetognaths were also a frequent contributor to the summer mesopelagic cluster reported by

788 Siegel and Piatkowski (1990). It is possible that seasonal differences in abundance of individual

789 Chaetognatha species in the epipelagic zone may confound our seasonal results. For example,

790 Atkinson and Peck (1988) reported higher chaetognath abundance in the upper water strata in

791 summer compared to winter around South Georgia and classified them as strong seasonal

792 migrators. In the surface areas of the Lazarev Sea, Flores et al. (2011) described seasonal

793 differences between *Sagitta gazellae* (significantly more abundant in summer) and *Eukrohnia*

794 *hamata* (more abundant in autumn and winter).

795 Błachowiak-Samołyk and Żmijewska (1997) describe an opposite trend in Ostracoda abundance

796 compared to our findings and report a lower Ostracoda abundance in winter compared to summer

797 within Croaker Passage and in general, determined that the most abundant Ostracod species

798 exhibited seasonal vertical migrations and a few exhibited diel vertical migrations. As with

799 Chaetognatha, there may be species-specific seasonal differences that confound the interpretation

800 of seasonal fluctuations of Ostracoda.

801 Our results for *S. thompsoni* are similar to Siegel and Piatkowski (1990), who found high

802 abundance and frequency of occurrence of salps in oceanic and transitional macrozooplankton

803 clusters during March and May/June surveys, respectively. *S. thompsoni* also exhibited high

804 interannual variability in both seasons with lower abundance in winter which was expected given

805 this species migrates deeper in winter (Foxton, 1966; Atkinson and Peck, 1988; Loeb and

806 Santora). Previous analysis also linked summer abundance to large scale climate indices, such as

807 the seasonal Southern Oscillation Index (Loeb and Santora, 2012).

808 *4.3 Relationships to hydrographic and physical variables*

809 Biogeographic patterns of macrozooplankton communities are indicators of hydrographic

810 conditions and source water variability (Siegel and Piatkowski, 1990; Loeb et al., 2009a).

811 Environmental determinants of summer and winter macrozooplankton community structure

812    indicate that community structure and occurrence were strongly tied to regional variability of

813    salinity and primary productivity gradients (Tables 3 and 5; Figures 4 and 6; Supplemental

814    Figures 1 and 2) and is similar to other broad-scale macrozooplankton studies in the Southern

815    Ocean. For instance, Hopkins et al. (1993) found relationships between macrozooplankton

816    community structure and temperature, salinity and bottom depth in winter around the South

817    Orkney Islands and Hunt et al. (2011) reported significant correlations with winter chlorophyll

818    biomass in the Lazarev Sea.

819    Winter macrozooplankton community structure is relatively stable from year to year in terms of

820    presence and geographic location of clusters (Fig. 3B) regardless of high variation in UML depth

821    and sea ice. The absence of cluster 3a in 2012 and 2013 is likely due to our lack of sampling in

822    the northeast Bransfield Strait. In 2015 and 2016, when sea ice was thinner and east and south

823    winds were stronger, there were extreme increases in UML depth, especially in the northeast

824    Bransfield Strait (Reiss, In Prep). Venables et al. (2013) also found that winters with little sea ice

825    cover had increased mixed layer depths, with a subsequent decrease in phytoplankton production

826    in the following summers in Ryder Bay south of our study area.

827    On the other hand, summer macrozooplankton community structure exhibited more interannual

828    variability in the presence and geographic location of clusters (Fig. 5B) and relatively stable

829    salinity and UML depths. Mitchell and Holm-Hansen (1991) found an inverse relationship

830    between Chl $a$ and UML depth in summer in an area that partially overlapped our study area.

831    However, in our study summer Chl $a$ was not correlated with UML depth. Cluster groupings

832    representing macrozooplankton communities are likely much more complex than only a few

833    hydrographic variables can explain, especially in summer. Cluster boundaries are likely driven

834    by dynamic locations of currents, fronts and localized eddies in any given year and the latter may

835    account for lone stations that are isolated from similar cluster groupings.

836    *4.4 Conclusions*

837    Our synthesis regarding multi-year sampling of winter and summer macrozooplankton species

838    abundance, community composition and biodiversity patterns, provides a robust assessment of

839    the spatial and environmental variability impacting macrozooplankton ecology within the

840    northern Antarctic Peninsula. Although coastal and pelagic species compositions reflected

841 known habitat associations and population dynamics of some species (e.g., *E. superba, S.*
842 *thompsoni*) including cycles or episodic patterns of occurrence, the species assemblage patterns
843 were considerably stable during winter compared to summer. Predicting future climate impacts
844 remains a challenge, especially at regional scales within the Antarctic, but this synthesis
845 established species assemblage patterns that could be examined to better anticipate how the
846 macrozooplankton community may change collectively, rather than focusing primarily on
847 individual species assessments. Therefore, species associations and interactions are important for
848 interpreting climate change impacts on macrozooplankton (i.e., no macrozooplankton species
849 lives in isolation). While some species in polar subregions have shown resilience to recent
850 climate changes (e.g., Tarling et al. (2018); Thibodeau et al. (2019)), further declines in sea-ice
851 extent and duration, increases in water temperature and acidification, and intrusions of higher
852 salinity water into some regions of the system could alter the macrozooplankton community in
853 unforeseen ways. Observations from the past two decades indicate wide variation in the
854 seasonality of species abundance; however, unlike the Arctic, we have not observed vast
855 distributional shifts or intrusions of sub-Antarctic macrozooplankton into this area, nor changes
856 in the stability of macrozooplankton community composition.

857 The Southern Ocean currently provides substantial ecosystem services to our planet including
858 fisheries, nutrient cycling and climate regulation (Grant et al., 2013). Further, Antarctic
859 macrozooplankton community composition plays a vital and integral role in regulating the food
860 web that fisheries rely upon. Thus, there is a need for long-term monitoring across a range of
861 time and space scales to establish potential impacts of climate change that may be outside the
862 boundaries of natural variation (Newman et al., 2019). Trends and variability of
863 macrozooplankton species composition are difficult to infer with sporadic sampling in a
864 mismatch of seasons and years, so our synthesis can inform models that assess climate impacts
865 on particular macrozooplankton community components. Further development of ecosystem
866 sampling transects and essential variables in the Southern Ocean Observing System proposed by
867 Constable et al. (2016) and recommendations for improved ecosystem-based management of the
868 krill fishery (Meyer et al., 2020) would begin to address the need to monitor changes to Southern
869 Ocean ecosystems. We urge that monitoring of essential variables should include components
870 regarding Antarctic macrozooplankton species composition and their associated environmental
871 conditions to better anticipate climate related changes in biodiversity and ecosystem function.

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1205

**Supplemental Table 1** Sample size, dates of sample collection and average volume filtered among year, season and vessel.

| Vessel | Year | Season | Start Date | End Date | Sample Size | Volume filtered (± se; m$^3$) |
|---|---|---|---|---|---|---|
| *Yuzhmorgeologiya* | 2003 | Summer | 1/14/2003 | 1/27/2003 | 84 | 4,172.6 (46.2) |
| | 2004 | Summer | 1/16/2004 | 1/31/2004 | 91 | 3,833.0 (43.4) |
| | 2005 | Summer | 1/17/2005 | 1/31/2005 | 99 | 3,440.8 (58.8) |
| | 2006 | Summer | 1/16/2006 | 2/1/2006 | 99 | 3,527.2 (44.9) |
| | 2007 | Summer | 1/11/2007 | 1/27/2007 | 98 | 3,689.5 (46.0) |
| | 2009 | Summer | 1/13/2009 | 1/29/2009 | 99 | 5,014.7 (76.0) |
| *Moana Wave* | 2011 | Summer | 1/17/2011 | 2/4/2011 | 96 | 4,034.7 (78.9) |
| *Nathaniel B Palmer* | 2012 | Winter | 8/7/2012 | 8/14/2012 | 33 | 3,419.9 (145.7) |
| | 2013 | Winter | 8/15/2013 | 9/5/2013 | 66 | 3,798.1 (133.8) |
| | 2014 | Winter | 8/24/2014 | 9/14/2014 | 108 | 3,760.9 (111.2) |
| | 2015 | Winter | 8/7/2015 | 8/27/2015 | 100 | 3,692.5 (92.4) |
| | 2016 | Winter | 8/7/2016 | 8/27/2016 | 87 | 4,434.0 (140.3) |

1

Line numbers in left margin: 1, 2, 3, 4, 5, 6, 7... with 1210, 1211, 1212 near top.

**Supplemental Table 2** List of taxa, consistently identified over the full survey period (2003-2016). Taxa based on World Register of Marine Species (*https://www.marinespecies.org*). "x" in Summer or Winter column indicates the taxa met the 5% occurrence threshold for inclusion in the multivariate analyses.

| Taxa Count | Taxa | Summer | Winter |
|---|---|---|---|
| | Amphipoda Latreille, 1816 | | |
| | Hyperiidea H. Milne Edwards, 1830 | | |
| 1 | *Cyllopus lucasi* Spence Bate, 1862 | x | x |
| 2 | *Cyllopus magelanicus* Dana, 1853 | x | x |
| 3 | *Cyllopus* spp. Dana, 1852 | x | |
| 4 | *Cyphocaris richardi* Chevreux, 1905 | | |
| 5 | *Hyperia* Latreille, 1823 spp. | | |
| 6 | *Hyperiella* Bovallius, 1887 spp. | x | x |
| 7 | *Hyperoche medusarum* (Kröyer, 1838) | | |
| 8 | *Primno macropa* Guérin-Méneville, 1836 | x | x |
| 9 | *Scina* Prestandrea, 1833 spp. | | x |
| 10 | *Themisto gaudichaudii* Guérin, 1825 | x | x |
| 11 | *Vibilia antarctica* Stebbing, 1888 | x | x |
| | Amphilochidea Boeck, 1871 | | |
| 12 | *Eusirus Krøyer, 1845* spp. | x | x |
| 13 | *Oedicteroides calmani* Walker, 1906 | | |
| 14 | *Pseudorchomene* Schellenberg, 1926 spp. | x | x |
| 15 | Other / Unidentified | x | x |
| 16 | Cephalopoda Cuvier, 1795 | | |
| 17 | Chaetognatha | x | x |
| 18 | Cirripedia Burmeister, 1834 | x | x |
| | Copepoda Milne Edwards, 1840 | | |
| 19 | *Calanus propinquus* Brady, 1883 | x | x |
| 20 | *Calanoides acutus* (Giesbrecht, 1902) | x | x |
| 21 | *Haloptilus* Giesbrecht, 1898 *spp.* | x | x |
| 22 | *Heterorhabdus* Giesbrecht, 1898 spp. | x | x |
| 23 | *Metridia* Boeck, 1865 spp. | x | x |
| 24 | *Paraeucheata* Scott A., 1909 spp. | x | x |
| 25 | *Pleuromamma robusta* (Dahl F., 1893) | x | x |
| 26 | *Rhincalanus* Dana, 1852 spp. | x | x |
| 27 | Other / Unidentified | x | x |
| | Ctenophora Eschscholtz, 1829 | | |
| 28 | *Beroe* Muller, 1776 spp. | x | x |
| 29 | Mertensiidae L. Agassiz, 1860 | x | x |
| 30 | Other / Unidentified | x | x |

2

| Taxa Count | Taxa | Summer | Winter |
|---|---|---|---|
| 31 | Cumacea Krøyer, 1846 | | |
| | Decapoda Latreille, 1802 | | |
| 32 | *Acanthephyra pelagica* (Risso, 1816) | x | |
| 33 | Other / Unidentified | x | |
| | Euphausiidae Dana, 1852 | | |
| 34 | *Euphausia superba* Dana, 1850 | x | x |
| 35 | *E. superba* Larvae (Calyptopis stage) | x | |
| 36 | *E. superba* Larvae (Furcilia stage) | | x |
| 37 | *E. crystallorophias* Holt & Tattersall, 1906 | x | x |
| 38 | *E. frigida* Hansen, 1911 | x | x |
| 39 | *E. frigida* Larvae | x | x |
| 40 | *E. triacantha* Holt & Tattersall, 1906 | x | x |
| 41 | *Thysanoessa macrura* G.O. Sars, 1883 | x | x |
| 42 | *T. macrura* Larvae | x | x |
| | Gastropoda Cuvier, 1795 | | |
| 43 | *Clio pyramidata* Linnaeus, 1767 | x | x |
| 44 | *Clione limacina* (Phipps, 1774) | x | x |
| 45 | *Limacina helicina* (Phipps, 1774) | x | x |
| 46 | *Spongiobranchaea australis* d'Orbigny, 1836 | x | x |
| 47 | Other / Unidentified | x | x |
| | Hydrozoa Owen, 1843 | | |
| 48 | *Calycopsis borchgrevinki* (Browne, 1910) | | x |
| 49 | *Pegantha martagon* Haeckel, 1879 | x | x |
| 50 | Other / Unidentified | x | x |
| 51 | Isopoda Latreille, 1817 | x | x |
| 52 | Mysidae Haworth, 1825 | | |
| 53 | Ostracoda Latreille, 1802 | x | x |
| | Pisces | | |
| 54 | Eggs | | x |
| | Larvae | | |
| 55 | Artedidraconidae Andriashev, 1967 | | |
| 56 | Bathydraconidae Regan, 1913 | | x |
| 57 | Bathylagidae Gill, 1884 | | |

| Taxa Count | Taxa | Summer | Winter |
|---|---|---|---|
| 58 | Channichthyidae Gill, 1861 | | x |
| 59 | Myctophidae Gill, 1893 | x | x |
| 60 | Nototheniidae Günther, 1861 | x | x |
| 61 | *Notolepis* Dollo, 1908 spp. | x | x |
| 62 | *Harpagifer* Richardson, 1844 spp. | | |
| 63 | *Pleuragramma antarctica* Boulenger, 1902 | x | x |
| 64 | Other / Unidentified | x | x |
| | Adult | | |
| 65 | Myctophidae Gill, 1893 | x | x |
| 66 | *Pleuragramma antarctica* Boulenger, 1902 | | |
| | | | |
| | Polychaeta Grube, 1850 | | |
| 67 | *Pelagobia longicirrata* Greeff, 1879 | x | x |
| 68 | *Rhynchonereella bongraini* (Gravier, 1911) | x | x |
| 69 | *Tomopteris* Eschscholtz, 1825 spp. | x | x |
| 70 | *Vanadis antarctica* (McIntosh, 1885) | | x |
| 71 | Other / Unidentified | x | x |
| | | | |
| 72 | Radiozoa | x | x |
| | | | |
| 73 | Scyphozoa Goette, 1887 | x | |
| | | | |
| 74 | Siphonophorae Eschscholtz, 1829 | x | x |
| | | | |
| 75 | Sipuncula Stephen, 1964 | x | x |
| | | | |
| | Tunicata Lamarck, 1816 | | |
| 76 | Appendicularia (Larvacea) Fol, 1874 | | |
| 77 | *Salpa thompsoni* Foxton, 1961 | x | x |
| 78 | *Ihlea racovitzai* (Van Beneden & De Selys Longchamp, 1913) | x | x |

1213
1214

4

**Supplemental Table 3** Winter cluster mean abundances, se (in parentheses) and frequency of occurrence for taxa with highest abundance (bold names) or with indicator values within any cluster higher than 25% (p < 0.05; square brackets). PL=post-larvae, L=larvae, F=furcilia

| | 1 | 2a | 2b | 3a | 3b |
|---|---|---|---|---|---|
| Crustaceans | | | | | |
| Copepoda | | | | | |
| *Calanoides acutus* | 3.71 | 10.77 | 1.06 | 101.05 | 13.61 |
| | (0.84) | (2.69) | (0.37) | (36.9) | (8.62) |
| | 42% | 32% | 25% | 77% | 43% |
| | | | | [60%] | |
| *Calanus propinquus* | 39.52 | 104.06 | 5.3 | 35.18 | 25.78 |
| | (4.31) | (13.55) | (1.05) | (9.2) | (7.98) |
| | 95% | 97% | 83% | 83% | 83% |
| | | [48%] | | | |
| **Metridia spp.** | 422.56 | 2043.16 | 10.71 | 3464.52 | 950.83 |
| | (56.14) | (315.21) | (2.18) | (482.14) | (440.39) |
| | 97% | 98% | 93% | 100% | 93% |
| | | | | [50%] | |
| *Paraeuchaeta* spp. | 3.72 | 13.82 | 0.19 | 10.79 | 0.4 |
| | (0.79) | (2.09) | (0.11) | (1.68) | (0.15) |
| | 40% | 60% | 13% | 83% | 28% |
| | | | | [31%] | |
| *Pleuromama* spp. | 0.69 | 27.7 | 0.2 | 1.18 | 2.93 |
| | (0.19) | (4.71) | (0.09) | (0.72) | (1.89) |
| | 14% | 51% | 15% | 9% | 15% |
| | | [43%] | | | |
| *Rhincalanus* spp. | 2.78 | 51.73 | 4.14 | 7.73 | 3.12 |
| | (0.83) | (12.45) | (1.38) | (2.12) | (1.93) |
| | 41% | 55% | 65% | 63% | 25% |
| | | [41%] | | | |
| Euphausiidae | | | | | |
| *E. crystallorophias* PL | 2.62 | 0.24 | 0.01 | 3.48 | 11.93 |
| | (0.99) | (0.15) | (0.01) | (1.48) | (6.79) |
| | 24% | 8% | 3% | 49% | 50% |
| | | | | | [33%] |
| *E. frigida* (PL) | 9.33 | 39.13 | 1.02 | 0.25 | 3.29 |
| | (1.78) | (3.78) | (0.34) | (0.23) | (1.28) |
| | 65% | 85% | 38% | 6% | 50% |
| | | [76%] | | | |
| *E. frigida* (L) | 5.85 | 151.76 | 26.85 | 0.16 | 2.73 |
| | (1.08) | (22.98) | (5.24) | (0.16) | (2.39) |
| | 46% | 94% | 85% | 3% | 13% |
| | | [76%] | | | |
| **E. superba (PL)** | 171.67 | 2.31 | 0.11 | 64.57 | 2288.21 |
| | (51.36) | (0.92) | (0.03) | (45.46) | (846.67) |
| | 79% | 40% | 28% | 71% | 100% |
| | | | | | [91%] |
| **E. superba (L-F)** | 116.78 | 71.13 | 13.1 | 74.41 | 75.74 |
| | (24.72) | (38.06) | (8.82) | (42.18) | (16.98) |
| | 87% | 72% | 60% | 66% | 93% |
| *E.triacantha* (PL) | 0.44 | 9.35 | 0.13 | 0.09 | 0.14 |
| | (0.14) | (1.16) | (0.09) | (0.09) | (0.06) |
| | 22% | 66% | 8% | 3% | 20% |
| | | [61%] | | | |

5

| | 1 | 2a | 2b | 3a | 3b |
|---|---|---|---|---|---|
| ***Thysanoessa macrura*** (**PL**) | 90.14 (6.39) 99% | 170.04 (9.22) 100% | 193.34 (31.91) 100% [37%] | 5.78 (1.52) 86% | 66.26 (11.26) 100% |
| Amphipoda | | | | | |
| *Hyperiella* spp. | 0.32 (0.07) 38% | 0.09 (0.02) 23% | 0.11 (0.06) 23% | 0.7 (0.17) 63% [29%] | 0.31 (0.09) 35% |
| *Primno macropa* | 1.35 (0.16) 58% | 7.9 (0.91) 77% [42%] | 4.55 (0.54) 93% | 0.47 (0.2) 40% | 0.2 (0.11) 13% |
| *Themisto gaudichaudii* | 0.39 (0.08) 44% | 3.08 (0.73) 73% [30%] | 3.04 (1.08) 73% | 0.03 (0.02) 9% | 0.85 (0.49) 28% |
| *Vibilia antarctica* | 0.98 (0.13) 61% | 1.43 (0.26) 80% [36%] | 0.16 (0.05) 28% | 0.26 (0.08) 31% | 0.37 (0.18) 30% |
| *Pseudorchomene* spp. | 0.17 (0.04) 21% | 0 (0) 2% | 0.01 (0.01) 3% | 0.58 (0.12) 69% [31%] | 0.54 (0.19) 50% |
| **Ostracoda** | 68.24 (9.88) 90% | 111.2 (10.33) 98% | 8.6 (1.72) 93% | 133.16 (25.81) 94% [36%] | 28.02 (12.89) 73% |
| Isopoda | 1.55 (0.32) 42% | 0.9 (0.36) 13% | 0.16 (0.06) 20% | 6.26 (1.54) 57% [33%] | 1.99 (0.51) 40% |
| Gastropoda | | | | | |
| *Clio pyramidata* | 0.26 (0.08) 21% | 0.08 (0.03) 12% | 0.01 (0.01) 5% | 0.98 (0.38) 37% [27%] | 0.03 (0.01) 10% |
| *Clione limac*ina | 3.93 (0.49) 85% [29%] | 2.96 (0.44) 77% | 1.02 (0.34) 58% | 2.88 (0.62) 89% | 0.71 (0.15) 50% |
| ***Limacina helicina*** | 44.12 (7.84) 95% | 188.26 (23.2) 98% [49%] | 133 (42.77) 98% | 6.44 (1.73) 63% | 3.52 (1.49) 48% |
| *Spongiobranchaea australis* | 0.84 (0.19) 51% | 3.85 (0.58) 77% [34%] | 1.66 (0.45) 80% | 2.03 (0.46) 94% | 0.22 (0.1) 20% |
| Polychaeta | | | | | |

6

| | 1 | 2a | 2b | 3a | 3b |
|---|---|---|---|---|---|
| *Pelagobia* spp. | 0.05 (0.02) 8% | 0.01 (0) 2% | 0.01 (0.01) 3% | 0.5 (0.26) 40% [27%] | 0.18 (0.14) 10% |
| *Rhynchonereella bongraini* | 1.62 (0.24) 46% | 0.97 (0.45) 13% | 0.08 (0.04) 15% | 3.23 (1.4) 37% | 6.37 (2.88) 55% [29%] |
| *Tomopteris* spp. | 0.68 (0.13) 36% | 1.86 (0.39) 72% | 0.4 (0.09) 60% | 3.03 (0.85) 66% [28%] | 1.25 (0.44) 25% |
| *Vanadis antarctica* | 0.17 (0.08) 15% | 0.05 (0.02) 9% | 0.01 (0.01) 8% | 1.11 (0.46) 40% [33%] | 0 (0) 0% |
| Polychaeta, Other | 1.09 (0.17) 46% | 4.75 (2.13) 23% | 0.33 (0.12) 28% | 7.04 (1.5) 77% [38%] | 1.09 (0.38) 33% |
| **Chaetognatha** | 26.4 (3.27) 98% | 122.77 (26.71) 97% | 13.71 (3.33) 98% | 288.18 (32.58) 100% [61%] | 24.43 (9.52) 80% |
| Sipuncula | 0.35 (0.04) 52% | 0.04 (0.01) 13% | 0.11 (0.08) 15% | 2.02 (0.96) 74% [52%] | 0.36 (0.14) 38% |
| Tunicata | | | | | |
| *Salpa thompsoni* | 8.83 (1.57) 81% [34%] | 4.08 (0.54) 85% | 0.38 (0.12) 40% | 1.41 (1.08) 26% | 6.13 (2.26) 75% |
| Radiozoa | 8.68 (1.44) 72% | 164.14 (35.06) 91% [66%] | 18.16 (4.73) 93% | 35.37 (13.17) 71% | 1.12 (0.64) 13% |
| Hydromedusae | | | | | |
| *Pegantha martagon* | 0.03 (0.02) 5% | 0.33 (0.06) 35% [30%] | 0 (0) 3% | 0 (0) 0% | 0.02 (0.02) 3% |
| Siphonophorae | 8.61 (1.2) 77% | 9.91 (1.59) 52% | 4.62 (1.71) 55% | 63.4 (5.84) 100% [71%] | 3.05 (0.96) 58% |
| Pisces | | | | | |
| Myctophidae L | 0.36 (0.1) 25% | 3.82 (0.94) 72% [55%] | 0.82 (0.27) 43% | 0 (0) 0% | 0.01 (0.01) 3% |

7

|  | 1 | 2a | 2b | 3a | 3b |
|---|---|---|---|---|---|
| Nototheniidae L | 0.15 | 0.07 | 0.02 | 1.37 | 0.12 |
|  | (0.05) | (0.03) | (0.01) | (0.45) | (0.05) |
|  | 15% | 12% | 10% | 60% | 18% |
|  |  |  |  | [47%] |  |
| *Pleuragramma antarctica* L | 0.02 | 0 | 0 | 0.22 | 0.04 |
|  | (0.02) | (0) | (0) | (0.08) | (0.03) |
|  | 3% | 1% | 0% | 34% | 10% |
|  |  |  |  | [26%] |  |
| Pisces, Other L | 0.29 | 4.01 | 1.32 | 0.11 | 0.19 |
|  | (0.08) | (0.98) | (0.23) | (0.04) | (0.13) |
|  | 20% | 48% | 70% | 20% | 13% |
|  |  | [31%] |  |  |  |

1218
1219

8

**Supplemental Table 4** Summer cluster mean abundances, se (in parentheses) and frequency of occurrence for taxa with highest abundance (bold names) or indicator values within any cluster higher than 25% (p<0.05; square brackets). PL=post-larvae, L=larvae, C=calyptopis

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| **Crustaceans** | | | | | | | |
| Copepoda | | | | | | | |
| ***Calanoides acutus*** | 45.86 | 73.93 | 5032.39 | 188.59 | 140.24 | 16.86 | 49.65 |
| | (13.38) | (16.05) | (1851.66) | (39.55) | (12.46) | (2.12) | (6.13) |
| | 80% | 99% | 94% | 100% | 99% | 98% | 99% |
| | | | [85%] | | | | |
| *Calanus propinquus* | 29.91 | 30.08 | 292.45 | 89.05 | 31.83 | 18.39 | 34.76 |
| | (4.88) | (5.4) | (49.62) | (16.41) | (3.35) | (2.24) | (3.38) |
| | 78% | 92% | 81% | 97% | 90% | 100% | 95% |
| | | | [45%] | | | | |
| *Haloptilus* spp. | 0.04 | 0.01 | 16.97 | 2.85 | 0.27 | 0.07 | 0.43 |
| | (0.04) | (0.01) | (4.51) | (0.86) | (0.08) | (0.07) | (0.34) |
| | 1% | 1% | 37% | 25% | 12% | 2% | 7% |
| | | | [30%] | | | | |
| ***Metridia* spp.** | 134.27 | 5.23 | 572.45 | 1426.23 | 397.89 | 15.21 | 210.69 |
| | (50.16) | (2.38) | (103.46) | (299.9) | (103.37) | (6.57) | (38.35) |
| | 60% | 41% | 77% | 98% | 79% | 79% | 91% |
| | | | | [51%] | | | |
| *Paraeuchaeta* spp. | 15.97 | 1.63 | 232.61 | 178.36 | 59.58 | 0.79 | 30.01 |
| | (3.23) | (0.65) | (33.34) | (19.57) | (7.6) | (0.4) | (6.53) |
| | 48% | 25% | 81% | 100% | 82% | 16% | 67% |
| | | | [36%] | | | | |
| *Rhincalanus* spp. | 10.14 | 7.83 | 471.93 | 67.22 | 35.59 | 4.67 | 15.98 |
| | (3.29) | (1.88) | (127.47) | (9.11) | (6.12) | (2.28) | (3.74) |
| | 45% | 63% | 81% | 90% | 89% | 56% | 72% |
| | | | [62%] | | | | |
| Euphausiidae | | | | | | | |
| *E. frigida* (PL) | 9.86 | 1.36 | 4.83 | 27.31 | 7.49 | 0.93 | 15.71 |
| | (2.39) | (0.65) | (1.81) | (4.13) | (2.06) | (0.42) | (3.25) |
| | 34% | 25% | 32% | 90% | 54% | 23% | 60% |
| | | | | [36%] | | | |
| *E. frigida* (L) | 0.4 | 0.08 | 59.4 | 7.36 | 0.23 | 0.14 | 0.97 |
| | (0.2) | (0.05) | (16.03) | (2.63) | (0.1) | (0.09) | (0.65) |
| | 6% | 5% | 37% | 31% | 6% | 5% | 10% |
| | | | [32%] | | | | |
| ***E. superba* (L-C)** | 2.87 | 3.8 | 234.76 | 1029.95 | 20.59 | 2.66 | 6.46 |
| | (1.11) | (1.79) | (161.73) | (383.17) | (7.29) | (1.23) | (2.62) |
| | 23% | 28% | 47% | 67% | 55% | 49% | 50% |
| | | | | [53%] | | | |
| ***Thysanoessa macrura* (PL)** | 86.07 | 95 | 14.83 | 150.76 | 196.31 | 137.48 | 146.73 |
| | (12.58) | (16.9) | (3.05) | (39.9) | (20.29) | (17.27) | (19.34) |
| | 91% | 93% | 79% | 98% | 99% | 100% | 99% |
| ***Thysanoessa macrura* (L)** | 170.01 | 18.31 | 3303.81 | 31.89 | 12.97 | 0.64 | 2.84 |
| | (39.47) | (6.72) | (714.46) | (11.09) | (2.83) | (0.16) | (0.59) |
| | 84% | 63% | 100% | 70% | 58% | 33% | 49% |
| | | | [93%] | | | | |
| Amphipoda | | | | | | | |
| *Cyllopus magellanicus* | 7.41 | 0.08 | 5.36 | 0.87 | 0.08 | 2.33 | 2.03 |
| | (1.03) | (0.03) | (0.87) | (0.22) | (0.02) | (0.93) | (0.77) |
| | 76% | 15% | 84% | 49% | 14% | 61% | 55% |
| | [31%] | | | | | | |

9

|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| *Cyllopus lucasii* | 0.39 | 0.23 | 0.07 | 0.28 | 0.04 | 0.21 | 1.26 |
|  | (0.07) | (0.04) | (0.03) | (0.11) | (0.01) | (0.05) | (0.25) |
|  | 25% | 39% | 8% | 20% | 9% | 32% | 51% |
|  |  |  |  |  |  |  | [26%] |
| *Primno macropa* | 3.06 | 3.4 | 20.95 | 6.03 | 3.87 | 3.28 | 2.79 |
|  | (0.31) | (0.8) | (4.96) | (1.25) | (0.47) | (0.44) | (0.33) |
|  | 65% | 80% | 68% | 74% | 71% | 86% | 69% |
|  |  |  | [33%] |  |  |  |  |
| *Themisto gaudichaudii* | 11.43 | 2.28 | 11.14 | 3.15 | 3.54 | 13.57 | 7.13 |
|  | (1.46) | (0.92) | (2.08) | (0.93) | (1.28) | (2.5) | (1.31) |
|  | 95% | 64% | 95% | 62% | 40% | 98% | 81% |
|  |  |  |  |  |  | [26%] |  |
| *Vibilia antarctica* | 11.75 | 0.92 | 7.73 | 4.07 | 0.29 | 1.97 | 1.84 |
|  | (1.3) | (0.35) | (1.14) | (0.76) | (0.05) | (0.28) | (0.22) |
|  | 93% | 53% | 89% | 74% | 36% | 82% | 77% |
|  | [38%] |  |  |  |  |  |  |
| Isopoda | 0.03 | 0.41 | 0.34 | 0.24 | 2.73 | 0.03 | 0.15 |
|  | (0.02) | (0.14) | (0.27) | (0.12) | (0.54) | (0.02) | (0.05) |
|  | 2% | 25% | 3% | 8% | 43% | 5% | 11% |
|  |  |  |  |  | [30%] |  |  |
| Gastropoda |  |  |  |  |  |  |  |
| *Clione limacina* | 1.45 | 1.82 | 4.88 | 0.38 | 0.89 | 0.11 | 0.41 |
|  | (0.29) | (0.89) | (1.57) | (0.16) | (0.14) | (0.04) | (0.09) |
|  | 41% | 65% | 81% | 36% | 66% | 19% | 46% |
|  |  |  | [40%] |  |  |  |  |
| *Limacina helicina* | 52.08 | 24.88 | 190.11 | 7.21 | 19.38 | 0.58 | 7.15 |
|  | (7.82) | (2.94) | (32.4) | (3.2) | (1.84) | (0.13) | (1.77) |
|  | 73% | 99% | 100% | 69% | 87% | 40% | 63% |
|  |  |  | [63%] |  |  |  |  |
| *Spongiobranchaea australis* | 1.26 | 0.92 | 3.96 | 1.66 | 0.96 | 0.31 | 1.5 |
|  | (0.18) | (0.14) | (0.79) | (0.24) | (0.16) | (0.05) | (0.2) |
|  | 58% | 73% | 89% | 85% | 71% | 58% | 72% |
|  |  |  | [33%] |  |  |  |  |
| Polychaeta |  |  |  |  |  |  |  |
| *Tomopteris* spp. | 1.75 | 0.91 | 13.09 | 3.03 | 1.92 | 0.69 | 1.21 |
|  | (0.41) | (0.22) | (3.86) | (0.46) | (0.43) | (0.13) | (0.16) |
|  | 42% | 59% | 90% | 90% | 61% | 70% | 54% |
|  |  |  | [53%] |  |  |  |  |
| **Chaetognatha** | 20.71 | 20.71 | 24.57 | 544.22 | 104.37 | 40.49 | 4.95 |
|  | (4.27) | (4.27) | (9.21) | (81.59) | (13.57) | (4.93) | (0.88) |
|  |  | 72% | 91% | 92% | 98% | 97% | 89% |
|  |  |  |  | [65%] |  |  |  |
| Sipuncula | 0.01 | 0.01 | 1.42 | 0 | 0.43 | 6.85 | 0.01 |
|  | (0.01) | (0.01) | (0.51) | (0) | (0.34) | (2.02) | (0.01) |
|  |  | 1% | 43% | 0% | 16% | 52% | 4% |
|  |  |  |  |  |  | [40%] |  |
| Tunicata |  |  |  |  |  |  |  |
| ***Salpa thompsoni*** | 1412.94 | 17.35 | 277.23 | 135.69 | 9.34 | 93.06 | 250.78 |
|  | (178.32) | (3.8) | (52.36) | (42.41) | (3.74) | (22.83) | (61.25) |
|  | 100% | 76% | 100% | 89% | 41% | 89% | 94% |
|  | [64%] |  |  |  |  |  |  |

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|
| Radiozoa | 0.94 (0.2) | 0.94 (0.2) 30% | 1.81 (0.49) 55% | 262.63 (80.63) 81% [77%] | 4.35 (1.15) 61% | 2.75 (0.7) 56% | 0.79 (0.24) 39% |
| Pisces | | | | | | | |
| *Notolepis* spp. (L) | 0.04 (0.02) 5% | 0.09 (0.04) 15% | 0.03 (0.02) 8% | 0.88 (0.26) 44% [39%] | 0.1 (0.02) 20% | 0.06 (0.02) 14% | 0.15 (0.04) 21% |

1223

Numbers in left margin:
1 2 3 4 5 6 7 8 9 10 11 ... 65

4 1224
5 1225
6 1226
7 1227

**Supplemental Table 5** Seasonal mean abundances, se (in parentheses) and frequency of occurrence. Bold font indicates season significantly greater than other season; normal font seasons not significantly different than other season; Season+NT night tows significantly greater than other season; -NT night tows did not differ among seasons. PL=post-larvae, L=larvae, C=calyptopis, F=furcilia

| | Summer | Winter | Night only |
|---|---|---|---|
| Amphipoda | | | |
| *Cyllopus lucasi* | **0.42** **(0.06)** **27%** | 0.02 (0) 8% | |
| *Cyllopus magelanicus* | **2.64** **(0.3)** **48%** | 0.19 (0.05) 26% | |
| *Cyllopus* spp. | **0.38** **(0.09)** **13%** | 0.01 (0.01) 2% | |
| *Eusirus* spp. | 0.04 (0.01) 6% | **0.23** **(0.04)** **22%** | Winter +NT |
| *Hyperiella* spp. | **0.57** **(0.09)** **46%** | 0.26 (0.03) 34% | |
| *Primno macropa* | **5.18** **(0.54)** **72%** | 3.64 (0.35) 62% | |
| *Pseudorchomene* spp. | 0.1 (0.04) 10% | **0.17** **(0.03)** **20%** | -NT |
| *Scina* spp. | 0.13 (0.05) 3% | **0.24** **(0.09)** **7%** | -NT |
| *Themisto gaudichaudii* | **7.18** **(0.59)** **74%** | 1.56 (0.28) 52% | |
| *Vibilia antarctica* | **4.06** **(0.33)** **70%** | 0.92 (0.1) 58% | |
| Chaetognatha | 81.58 (9.78) 89% | 79.96 (10.2) 96% | |
| Copepoda | | | |
| *Calanus propinquus* | 60.22 (5.86) 89% | 55.56 (5.2) 92% | |

12

| | Summer | Winter | Night only |
|---|---|---|---|
| *Calanoides acutus* | **545.43** **(180.06)** **95%** | 15.42 (3.74) 40% | |
| *Metridia* spp. | 342.46 (41.56) 75% | **1239.32** **(132.91)** **97%** | Winter +NT |
| *Paraeucheata* spp. | **60.59** **(5.06)** **62%** | 6.99 (0.81) 46% | |
| *Pleuromamma robusta robusta* | 2.7 (0.54) 14% | **9.82** **(1.69)** **26%** | -NT |
| *Rhincalanus* spp. | **64.44** **(12.98)** **71%** | 19.55 (4.27) 48% | |
| Ctenophora | | | |
| *Beroe* spp. | **0.08** **(0.02)** **12%** | 0.03 (0.01) 6% | |
| Mertensiidae | 0.1 (0.03) 9% | **0.11** **(0.02)** **17%** | |
| Other / Unidentified | 1.14 (1.07) 11% | 0.07 (0.01) 17% | |
| Euphausiidae | | | |
| *Euphausia superba* PL | 38.36 (9.16) 84% | **303.74** **(93.6)** **62%** | -NT |
| *E. superba* L(C) | **123.26** **(39.63)** **45%** | 0.02 (0.01) 1% | |
| *E. superba* L(F) | 2.16 (0.78) 4% | **83.26** **(16.24)** **78%** | |
| *E. crystallorophias* PL | 4.76 (1.64) 19% | 2.59 (0.81) 22% | |
| *E. frigida* | 9.94 (1.05) 47% | **16.9** **(1.63)** **62%** | -NT |

13

| | Summer | Winter | Night only |
|---|---|---|---|
| *E. frigida* Larvae | 6.55 (1.65) 12% | **55.3** **(8.34)** **58%** | Winter +NT |
| *E. triacantha* | 0.71 (0.13) 13% | **3.29** **(0.44)** **33%** | -NT |
| *Thysanoessa macrura* | **127.49** **(8.03)** **95%** | 117.06 (5.88) 98% | Summer +NT |
| *T. macrura* Larvae | **348.71** **(75.97)** **64%** | 3.32 (0.62) 22% | |
| **Gastropoda** | | | |
| *Clio pyramidata* | 0.38 (0.09) 16% | 0.21 (0.05) 17% | |
| *Clione limacina* | 1.26 (0.19) 52% | **2.9** **(0.25)** **76%** | |
| *Limacina helicina* | 36.96 (3.97) 76% | **93.23** **(9.98)** **88%** | Winter +NT |
| *Spongiobranchaea australis* | 1.41 (0.11) 71% | 1.96 (0.22) 63% | |
| **Hydrozoa** | | | |
| *Pegantha martagon* | 0.06 (0.01) 7% | **0.12** **(0.02)** **14%** | |
| Other / Unidentified | 0.28 (0.09) 17% | 0.21 (0.07) 22% | |
| **Isopoda** | 0.74 (0.13) 17% | **1.66** **(0.23)** **31%** | |
| **Ostracoda** | 7.87 (1.04) 46% | **78.04** **(5.99)** **92%** | Winter +NT |
| **Pisces** | | | |
| Eggs | 0 (0) 0% | **0.7** **(0.07)** **51%** | |

| | Summer | Winter | Night only |
|---|---|---|---|
| **Larvae** | | | |
| Bathydraconidae | 0 | **0.04** | |
| | (0) | **(0.01)** | |
| | 0% | **7%** | |
| Bathylagidae | 0 | 0.01 | |
| | (0) | (0.01) | |
| | 1% | 1% | |
| Channichthyidae | 0.01 | **0.05** | |
| | (0) | **(0.01)** | |
| | 4% | **12%** | |
| Myctophidae | 0.6 | **1.48** | |
| | (0.1) | **(0.32)** | |
| | 25% | **38%** | |
| Nototheniidae | **1.16** | 0.22 | |
| | **(0.14)** | (0.05) | |
| | **48%** | 18% | |
| *Notolepis* spp. | **0.16** | 0.07 | |
| | **(0.03)** | (0.02) | |
| | **17%** | 8% | |
| *Pleuragramma antarctica* | 0.18 | 0.03 | |
| | (0.11) | (0.01) | |
| | 7% | 5% | |
| Other / Unidentified | 0.68 | **1.6** | |
| | (0.13) | **(0.34)** | |
| | 24% | **34%** | |
| **Adult** | | | |
| Myctophidae | 0.04 | **0.05** | -NT |
| | (0.01) | **(0.01)** | |
| | 7% | **10%** | |
| **Polychaeta** | | | |
| *Pelagobia longicirrata* | 0.06 | **0.08** | |
| | (0.02) | **(0.03)** | |
| | 5% | **9%** | |
| *Rhynchonereella bongraini* | 0.29 | **1.88** | |
| | (0.05) | **(0.37)** | |
| | 131% | **733%** | |
| *Tomopteris* spp. | **2.66** | 1.31 | |
| | **(0.4)** | (0.17) | |
| | **62%** | 52% | |

15

| | Summer | Winter | Night only |
|---|---|---|---|
| *Vanadis antarctica* | 0.04 (0.01) 5% | **0.18** **(0.05)** **13%** | |
| Radiozoa | 26.36 (8.01) 51% | **62.54** **(12.17)** **74%** | |
| Siphonophorae | 2.39 (0.36) 41% | **12.93** **(1.19)** **67%** | |
| Sipuncula | 1.75 (0.46) 22% | 0.37 (0.09) 36% | |
| Tunicata | | | |
| *Salpa thompsoni* | **372.98** **(42.04)** **81%** | 5.47 (0.68) 73% | Summer +NT |
| *Ihlea racovitzai* | **3.68** **(1.06)** **16%** | 0.03 (0.01) 5% | |

1228
1229

16
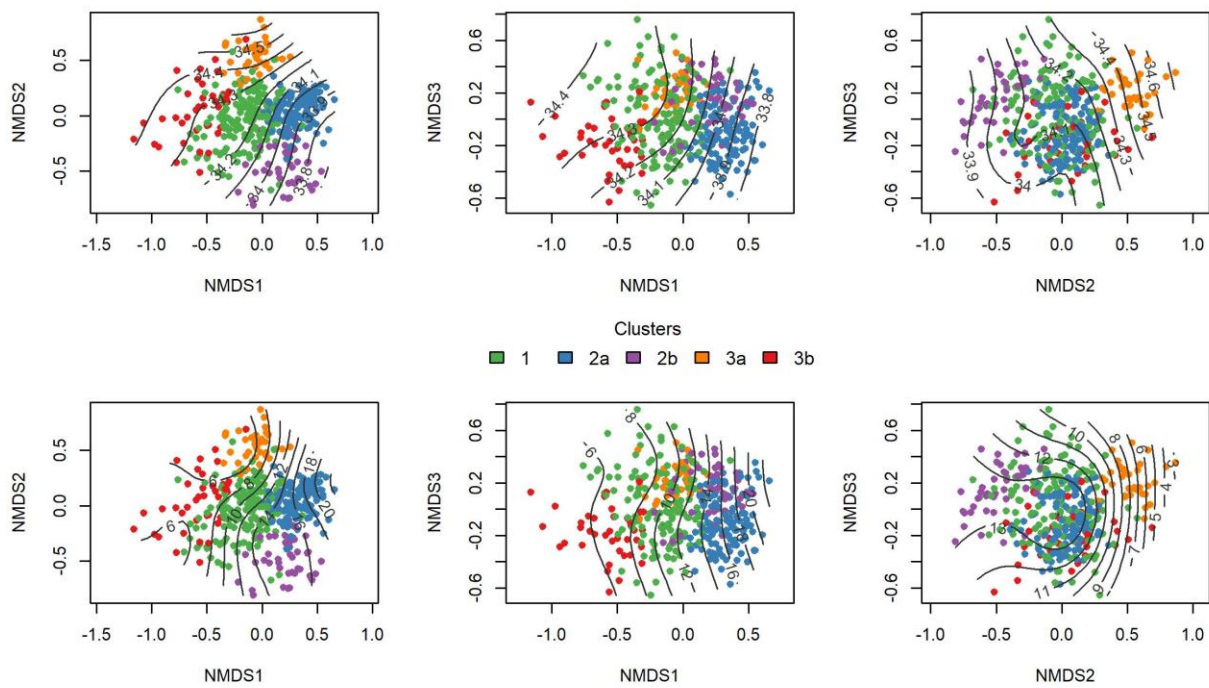
**Supplemental Fig. 1** Contours of salinity (top panels) and average integrated Chl *a* to 100 m (bottom panels) plotted onto winter NMDS ordination.
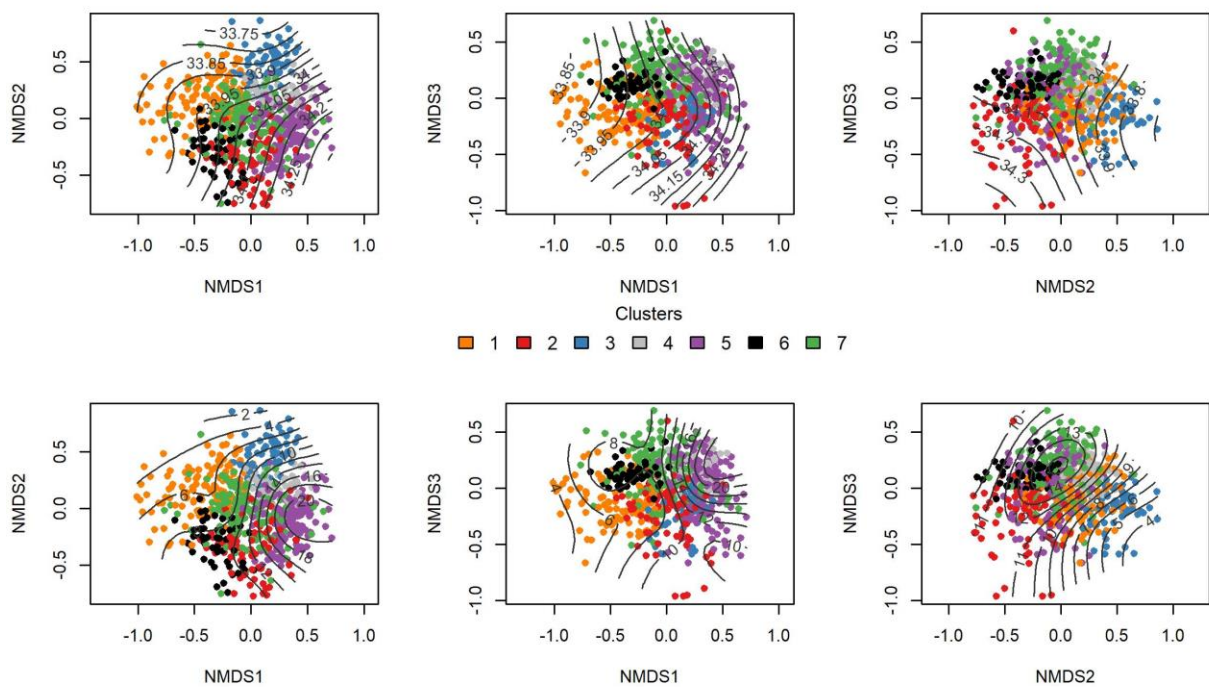


**Supplemental Fig. 2** Contours of UML salinity (top panels) and integrated phaeopigment to 100 m (bottom panels) plotted onto summer NMDS ordination.

17

Figure 1　　　　　　　　　　　　　Click here to access/download;Figure;Fig 1.jpg ⬇
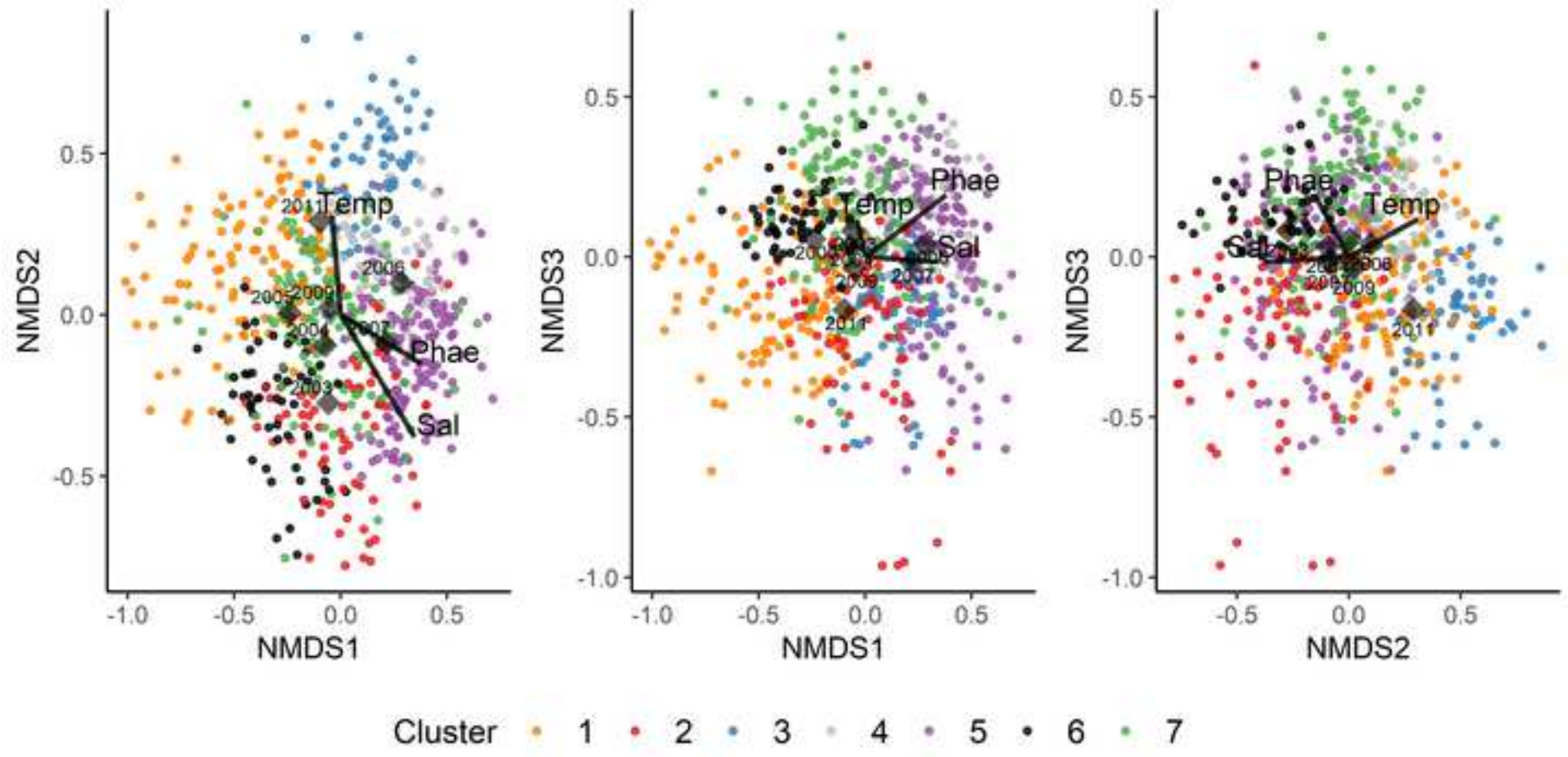
Fig 4

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Fig 6                    Click here to access/download;Figure;Fig 6.jpg ±

Suppl Fig 1

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Suppl Fig 2

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