

1 **Zooplankton abundance and biomass size spectra in the East Antarctic sea-**
2 **ice zone during the winter-spring transition**

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4 Jake R. Wallis¹, Kerrie M. Swadling^{1,2}, Jason D. Everett^{3,4}, Iain M. Suthers^{3,4}, Hugh J. Jones¹,
5 Pearse J. Buchanan¹, Christine M. Crawford¹, Lainey C. James¹, Robert Johnson^{2,5}, Klaus M.
6 Meiners^{2,6}, Patti Virtue^{1,2}, Karen Westwood⁶, So Kawaguchi^{2,6}

7
8 ¹Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart,
9 Tasmania 7001, Australia

10 ²Antarctic Climate and Ecosystems Cooperative Research Centre, University of Tasmania,
11 Private Bag 80, Hobart, Tasmania 7001, Australia

12 ³Evolution and Ecology Research Centre, School of Biological, Earth and Environmental
13 Sciences, University of New South Wales, Sydney, NSW 2052, Australia

14 ⁴Sydney Institute of Marine Science, Building 22, Chowder Bay Road, Mosman NSW 2088,
15 Australia

16 ⁵Bureau of Meteorology, 700 Collins Street, Docklands, Victoria 3001, Australia

17 ⁶Australian Antarctic Division, Department of the Environment, 203 Channel Highway,
18 Kingston, Tasmania 7050, Australia

19 *Corresponding author email address: jrwallis@utas.edu.au

20 **Abstract**

21 Sea ice is an influential feature in Southern Ocean- Antarctic marine environments creating a
22 2-phase vertical ecosystem. The lack of information on how this system influences
23 community structure during the winter-spring transition however is largely lacking.
24 Zooplankton form the link that bridges these environments, with the meiofaunal and algal
25 communities within sea ice directly influencing the epipelagic zooplankton community at the
26 ice-water interface. A combination of methods including sea ice coring, umbrella net
27 sampling and Laser Optical Plankton Counter were used to describe the vertical structure of
28 zooplankton and meiofaunal communities. The distribution of meiofauna and chlorophyll *a*
29 both played important roles in structuring the zooplankton community within this dynamic
30 region. Many dominant taxa, including *Calanus propinquus* and *Oithona similis*, directly
31 responded to the high availability of algae present within the bottom strata of sea ice. The
32 sea-ice associated species *Stephos longipes* represented a strong link between this 2-phase
33 ecosystem. Observations of the vertical distribution of biomass obtained from the LOPC
34 suggests that the responses of these species to the sea ice directly influences the vertical
35 structure of zooplankton during the winter-spring transition.

36 Key words: Antarctica, sea ice, cryo-pelagic coupling, *Calanus propinquus*, *Oithona similis*,
37 *Stephos longipes*, optical plankton counter

39 **1. Introduction**

40 Zooplankton play an integral role in Southern Ocean ecosystem structure and function, yet
41 limited work has been undertaken to describe and understand patterns in their distribution in
42 the Antarctic sea-ice zone, especially during the winter-spring transition when sea ice is at its
43 maximum extent. This period is critical for the establishment and recruitment of many
44 dominant zooplankton species, with the convergence of abiotic and biotic cues triggering the
45 cessation of diapause in some species and initiating reproduction in preparation for the spring
46 phytoplankton bloom (Hunt and Hosie, 2006a).

47 Sea ice has a dynamic role in Southern Ocean physical processes. Its optical and
48 insulative properties, combined with its freeze and melt cycles, strongly affect physical
49 characteristics of the water column below, regulating light availability, temperature, salinity
50 and stratification (Massom and Stammerjohn, 2010). Vast regions of the Southern Ocean are
51 seasonally ice-covered, with winter extent reaching $19 \times 10^6 \text{ km}^2$ and decreasing to
52 approximately $4 \times 10^6 \text{ km}^2$ during summer. There is a high degree of regional variation in
53 both sea-ice extent and duration due to prevailing differences in wind, oceanic circulation and
54 bathymetry (Stammerjohn et al., 2012; Massom et al., 2013). Sea ice harbours a network of
55 micro-environments for ice-associated (=sympagic) organisms, including bacteria, algae and
56 metazoans, which form communities in different depth horizons of the ice (Kramer et al.,
57 2011).

58 The number of studies on the diversity of ice-associated metazoans ($> 20 \mu\text{m}$, hereafter
59 referred to as meiofauna) is limited, particularly during the winter months. This impedes our
60 ability to understand how these communities intersect with the pelagic environment; e.g.
61 there is evidence to suggest that grazing on ice-associated detritus, algae and meiofauna
62 forms an important trophic pathway for some pelagic zooplankton groups (Werner, 2005;
63 Kramer et al., 2011). Therefore intra-regional and inter-annual variation in sea-ice physical

64 properties have the potential to alter both sea-ice meiofaunal and under-ice epipelagic
65 zooplankton communities.

66 The timing of sea-ice advance and retreat, and spatial variation in thickness and age, are
67 controlling factors of annual patterns of primary and secondary production (Thomas and
68 Dieckmann, 2010). The biomass of the standing stock of epipelagic zooplankton varies in
69 response to these patterns in sea-ice growth and decay. Zooplankton presence and activity in
70 the vicinity of the sea ice-water interface have been shown to increase during the onset of
71 spring, when environmental signals trigger the end of diapause events and the beginning of
72 breeding (Schnack-Schiel and Hagen, 1994). The seasonal succession of zooplankton is an
73 important regulator of ecosystem processes such as grazing and biogeochemical flux,
74 however, zooplankton, in turn, are controlled by the physical environment and primary
75 producers. This ‘bottom-up’ control is characteristic of the Southern Ocean (Hunt and Hosie,
76 2006a; b). Bottom ice-algal communities occurring at the sea ice – water interface are
77 influential in shaping the community of epipelagic zooplankton communities, presenting a
78 resource that is up to 50 times more concentrated than that found within the upper water
79 column (Arrigo and Thomas, 2004), with the out-flux of biogenic particles from ageing and
80 decaying sea ice most likely adding to resource availability (Lizotte, 2001; Kramer et al.,
81 2011). Pack ice often drifts up to 20 km day⁻¹, whilst the water column beneath can reach
82 speeds in excess of 17 km day⁻¹ with varied directionality due to mesoscale currents, eddies
83 and wind stress (Williams et al., 2011). Consequently, the sea ice and water column move
84 independently of one another, yet the movements and behaviour of zooplankton within and
85 between these dynamic environments directly couples this 2-phase ecosystem.

86

87 The aims of this study were to identify drivers of, and describe patterns in, the
88 distribution of sea-ice meiofauna and under-ice zooplankton, at both the community and
89 individual taxon levels, off the Budd/Sabrina coast of East Antarctica. Sea-ice cores and net
90 tows were used to describe community composition during the winter-spring transition in
91 2007 and 2012. To assess how the biomass of plankton was distributed vertically in the
92 surface waters under the sea ice, we deployed a Laser Optical Plankton Counter (LOPC), in
93 conjunction with our net sampling. The LOPC has rarely been deployed in Southern Ocean
94 waters yet it provides a relatively rapid means of comparing plankton biomass and
95 community size structure between sites, independent of the species present.

96

97 **2. Methods**

98 *2.1 Field*

99 Sea ice was sampled between 114°E and 130°E (Fig. 1), from mid-September to early
100 October 2007, and again from late September to the end of October 2012, as part of the Sea
101 Ice Physics and Ecosystems eXperiment (SIPEX) and SIPEX-2 voyages. During both years
102 sea ice was encountered at ~61°S, extending as first-year pack until fast ice occurred at
103 ~65.5°S. The maximum extent of sea ice for this area is characteristically small compared
104 with flanking regions to the east and west, with the sea-ice zone reaching only 300 km off the
105 coastline as it is constricted by high wind and water velocities (Williams et al., 2011;
106 Massom et al., 2013).

107 Twelve sites were sampled in 2007 and eight in 2012 (Fig. 1). Of the 12 sites in 2007,
108 11 were sampled for epipelagic zooplankton and 12 for sea-ice meiofauna. In 2012, seven
109 sites were sampled for epipelagic zooplankton whilst only five were accessible for sea-ice
110 coring due to thick, rafted sea ice in excess of 2 m. All ice cores were taken from within a 4

111 m² area at each site using a SIPRE ice corer with a 0.02 m internal diameter. A single sea- ice
112 core was taken from each site during 2007 for quantifying meiofauna abundance and
113 distribution, while two to six ice cores were collected during 2012. All cores were sectioned
114 (at 0.1 m intervals) and melted in filtered seawater at 4 °C. Afterwards the contents of each
115 segment were concentrated using a 20 µm sieve to collect meiofauna above this size. During
116 2012, sites 2 and 3 were pre-drilled with a Jiffy drill and only cores for the bottom 0.02 and
117 0.03 m, respectively, were processed.

118 Epipelagic zooplankton were sampled using an umbrella net (mouth opening:
119 0.078 m², mesh size: 100 µm) deployed through holes widened after sea ice coring took
120 place (Loots et al. 2009). Due to heavy ice conditions encountered during 2012 some sites
121 were sampled from the trawl deck of *RV Aurora Australis*. Zooplankton were collected by
122 vertical hauls through the top 50 m of the water column during 2007 and 60 m during 2012.
123 All zooplankton collected were preserved in 4% borax-buffered formaldehyde.

124 A Laser Optical Plankton Counter (LOPC; Herman, 2004) was deployed vertically at
125 sites 3, 4, 6, 7 and 8 during 2012, accompanying umbrella net sampling at each site. The
126 LOPC was lowered from the surface to 60 m at a rate of 1 m s⁻¹. At sites 7 and 8 the LOPC
127 was deployed manually through a hole drilled in the sea ice, while at sites 3, 4 and 6 it was
128 lowered from the stern of the vessel. The LOPC was housed within a steel frame, and
129 consisted of a 7 x 7 cm sampling tunnel, with a 35 mm x 1 mm laser that was reflected back
130 onto a 35 element (1 mm spacing) photo-diode array by a prism. When a particle passed
131 through the emitted or reflected beam, the size of the shadow was detected and recorded as
132 the corresponding equivalent spherical diameter (ESD) of the particle. The data were
133 recorded on a data-logger (ODIM Brooke Ocean, Dartmouth, Canada) housed within the
134 frame, and a conductivity–temperature–depth (CTD) sensor (Model SBE- 37, Sea-Bird
135 Electronics, Inc., Washington, U.S.A) measured the depth profile.

136 Environmental variables were recorded during both voyages. The thickness of the sea
137 ice and the snow cover were measured at the site of each ice core. Chlorophyll *a*
138 concentration and salinity and temperature of the sea ice cores were profiled as per Meiners
139 et al. (2011). Brine volumes were calculated from the temperature and salinity profiles using
140 the equations of Cox and Weeks (1983).

141 A ship-based CTD-rosette was used to measure temperature, salinity, fluorescence and
142 PAR of the top 200 m of the water column. Chlorophyll *a* concentrations of the upper water
143 column were determined by High Performance Liquid Chromatography (HPLC) at depth
144 intervals of approximately 15 m, according to methods described by Wright and van den
145 Enden (2000). Linear regressions were established between chlorophyll *a* measurements and
146 CTD fluorescence measurements at the same depths. The regression equations were then
147 used to convert the remaining fluorescence data in order to obtain high-resolution profiles of
148 the water-column. Integrated measurements were calculated for the top 150 m.

149

150 *2.2 Laboratory*

151 Preserved zooplankton and meiofauna were identified to the lowest taxonomic level possible.
152 Replicate umbrella net samples collected in 2012 were used to estimate biomass (dry weight)
153 by filtering zooplankton onto pre-combusted (450 °C for 12 h) 50 µm pore-size glass-fibre
154 filters (Macherey-Nagel) and dried at 60 °C until constant mass was reached. Additional
155 biomass estimates for both years, expressed as mg C m⁻³ were calculated by multiplying the
156 abundance of each zooplankton species by its carbon content (determined by Jia et al., this
157 volume).

158 The LOPC particle sizes were classified into size bins from 306 µm–3080 µm. The size bins
159 were calculated based on the geometric mean of the squares of two consecutive whole

160 numbers from 17 to 55 (Moore and Suthers, 2006). Size bins from the first zero-count and
161 larger were removed from the analysis. Biomass of zooplankton measured using the LOPC
162 was estimated using the method of (Suthers et al., 2004). ESD values (μm) were converted to
163 biomass assuming the volume of a sphere and the density of water ($\rho = 10^9 \text{ mg m}^{-3}$) using:

$$164 \quad \text{Biomass (mg m}^{-3}\text{)} = \frac{4}{3} \pi \left(\frac{\text{ESD}}{2} \right)^3 \rho$$

165 Normalised biomass (NB; m^{-3}) was calculated by dividing the biomass of each bin by the mass
166 range of that bin (Platt, 1985; Platt and Denman, 1978). The normalised biomass is independent
167 of any specified body size interval, allowing for comparison across systems and studies
168 (Krupica et al., 2012). The normalised biomass $\beta(w)$ is the total biomass $b(w)$ in the size class
169 characterised by weight (w) divided by the width of the size class Δw :

$$170 \quad \beta(w) = b(w) / \Delta w$$

171 The linear slope and intercept is given by the least-squares linear regression of the \log_{10} NB
172 against the \log_{10} body mass (mg). Due to the dominance of crustaceans identified in umbrella
173 net samples, total biomass derived from LOPC was then converted to a dry weight using the
174 conversion factor of 0.171 outlined by Young et al. (1996).

175

176 *2.3 Statistical analysis*

177 Analyses were performed using the statistical packages PRIMER 6 (version 6.1.13) and R
178 (version 3.1.1). To explore the relationships between epipelagic zooplankton assemblages
179 and sampling sites, a canonical analysis of principal coordinates (CAP) was used to find the
180 axes that best discriminated between the samples from the two years, while a vector overlay
181 showed which species were responsible for differences in the years. SIMPER (similarity

182 percentages) analysis was conducted to determine which species contributed to greater than
183 10% of total abundance in each year.

184 Environmental data at each site were summarised, and tested for statistical differences
185 in the means between years using Welch's t-test; this test was chosen due to heterogeneity in
186 the variances. There was a high degree of variability in brine and chlorophyll *a* content over
187 the depth of the sea ice; therefore, brine volume and chlorophyll *a* concentration in the
188 bottom 0.01 m of the sea ice were analysed separately to the remainder of the core (hereafter
189 referred to as 'bottom ice chlorophyll' and 'bottom ice brine volume', respectively).

190 R-mode analysis (PRIMER) was undertaken on 17 epipelagic taxa that were common
191 to both sampling periods based upon cluster analysis performed using unweighted pair-group
192 arithmetic averages (UPGMA). Non-metric Dimensional Scaling (NMDS) was then used to
193 provide zooplankton associations defined by the cluster analysis. Indicator Value (IndVal)
194 analysis was performed to identify 'indicator' species within each sampling year. Each
195 IndVal was calculated as:

$$196 \quad \text{IndVal}_{ij} = A_{ij} * B_{ij} * 100$$

197 Where $A_{ij} = N_{\text{individuals}_{ij}}/N_{\text{individuals}_i}$ and $B_{ij} = N_{\text{sites}_{ij}}/N_{\text{sites}_j}$

198 A_{ij} is a measure of specificity, where $N_{\text{individuals}_{ij}}$ is the mean number of individuals of
199 species *i* across all sites and $N_{\text{individuals}_i}$ is the sum of the mean of species *i* across all sites.

200 B_{ij} is a measure of fidelity where $N_{\text{sites}_{ij}}$ is the number of sites where species *i* is present,
201 with N_{sites_j} the total number of sites sampled in that year (Dufrêne and Legendre, 1997). A
202 taxon with an IndVal of 25% or greater was considered to be indicative of a community,
203 showing that it was present in at least 50% of the samples for 50% of the time.

204 A BIOENV (biological-environmental) analysis using Spearman's rank correlation and
205 Euclidean distance was used to describe the environmental variables which were associated
206 with the patterns in zooplankton community structure identified. Due to missing variables,
207 site 7 from 2007 and sites 5, 7 and 8 from 2012 were omitted from the BIOENV analysis.

208 To understand how environmental variables influenced individual taxa, generalised
209 linear models (GLM) were applied to the numerically abundant genera or species common to
210 both years. A generalised additive model (GAM) with all predictor variables was initially
211 used to assess the relationship of each predictor variable to each taxon's abundance to assess
212 the need to incorporate polynomial terms in subsequent GLM. GLM used a Poisson
213 distribution and when tests indicated that abundance data were overdispersed a negative
214 binomial model was used instead. Backwards selection was used to select the most
215 parsimonious model based upon Akaike Criterion Information (AIC), with the model
216 presenting the lowest AIC deemed the most appropriate. The goodness-of-fit of the simplified
217 model was then tested for using a Pearson's chi-squared test based upon the residual deviance
218 and degrees of freedom of the model.

219

220 **3. Results**

221 *3.1 Environmental variation*

222

223 Environmental variables that were measured during both years are summarised in Table 1.

224 The water column features that differed significantly between years were temperature, depth
225 and chlorophyll *a* concentration. Water temperatures were slightly warmer, surface layer
226 chlorophyll *a* concentrations were higher and mean depth of sampling sites deeper in 2012
227 than in 2007. Both snow depth and ice thickness were also greater in 2012, although these

228 features were more variable between sites, ranging between 0.008 m and 0.1 m for snow
229 cover and from 0.075 m to 2.5 m for ice thickness.

230

231 3.2 Epipelagic zooplankton community composition and species assemblages

232 Twenty-one taxa were identified in 2007 and 38 in 2012 from epipelagic umbrella net
233 samples. Copepods, including nauplii, contributed the most to total abundance (63-96%) at
234 most sites during 2007, with the exception of sites 1 and 3, where they contributed 13 and
235 41%, respectively (Fig. 2a). Tintinnids, dominated by members of the genus *Cymatocylis*,
236 accounted for 57% of total abundance at site 1 and 84% at site 3; they comprised from 1 to
237 35% of abundance at the other sites. The foraminifera *Neogloboquadrina pachyderma* and
238 radiolarians comprised 1-8% of overall abundance, with all other groups, including
239 euphausiids, ostracods and pteropods, accounting for less than 1%. In 2012, copepods were
240 the most abundant group at all sites, comprising 68-97% of total abundance (Fig. 2b). Those
241 samples also contained protists (0-21%) and pteropods (0-7%). All other taxonomic groups,
242 including ostracods, polychaetes, chaetognaths, siphonophores, euphausiids and
243 appendicularians contributed less than 3%. Total abundance did not differ significantly
244 between years (p -value = 0.18), based on a non-parametric Welch's test.

245 Seventeen taxa co-occurred in net samples from both SIPEX voyages (Table 2). These
246 included the numerically abundant cyclopoid *Oitona similis*, the harpacticoid *Microsetella*
247 *norvegica*, the small calanoid *Microcalanus pygmaeus* and copepod nauplii. The large
248 calanoid copepods, *Calanus propinquus* and *Calanus simillimus*, were present in relatively
249 low abundances. Total zooplankton abundance showed little variation between years,
250 however, there was high spatial variability, with large ranges for each site in both years. Six
251 distinctive assemblages were identified at 40% similarity, although *Stephos longipes*,

252 *Ctenocalanus* sp., *Thysanoessa macrura* and *Neocalanus tonsus* each formed solitary clusters
253 (clusters C-F). *Maupasia* sp. and *Calanus simillimus* formed a single cluster, B, and the
254 remaining 11 taxa grouped to form the largest cluster, A (Fig. 3a). Whilst group A consisted
255 of the most individuals, several sub-clusters were evident at 70% similarity.

256

257 3.3 Environmental drivers of epipelagic community composition

258 Results from the CAP comparing water column communities between years are shown in Fig.
259 3b. A clear distinction between years is evident based upon species composition and
260 abundance. BIOENV indicated that the environmental variables that best described the
261 community composition of epipelagic zooplankton were longitude, snow thickness and
262 chlorophyll *a* concentration in the water column, with a correlation of 0.384.

263 GAM indicated that all predictor variables had a linear relationship with species
264 abundance and therefore no polynomial terms were used in fitting each GLM. The taxa
265 assessed were *Calanus propinquus*, *Microsetella norvegica*, *Oithona similis*,
266 *Neogloboquadrina pachyderma* and tintinnids (Table 3). Due to the lack of sufficient data
267 from both years, *Microcalanus pygmaeus*, *Stephos longipes* and *Limacina helicina* could not
268 be assessed. In each case, the most parsimonious model, as selected by AIC, provided a better
269 fit than the saturated model.

270 *Calanus propinquus* was mainly influenced by total sea-ice chlorophyll *a*
271 concentration, with its abundance increasing with increasing chlorophyll *a* content.
272 *Microsetella norvegica* was influenced by bottom-ice chlorophyll *a*, with an increase in
273 abundance corresponding to increased chlorophyll *a* concentration. *Oithona similis* was
274 influenced by the depth of the site, snow thickness, sea ice chlorophyll *a* concentration and
275 latitude, whereby its abundance increased with a decrease in snow depth, and increased

276 latitude and sea ice chlorophyll *a* content. *Neogloboquadrina pachyderma* responded to snow
277 depth, chlorophyll *a* concentrations within the sea ice and latitude, with abundances
278 increasing with deeper snow, less sea-ice chlorophyll *a* and a decrease in latitude. Tintinnids
279 were most influenced by bottom-ice chlorophyll concentration, latitude and longitude. As
280 bottom-ice chlorophyll concentration increased so did the abundance of tintinnids, with
281 abundances also being higher close to the coast on the western boundary of the sampling
282 region (corresponding to an increase in longitude and a decrease in latitude).

283

284 *3.4 Sea-ice meiofauna: temporal variation and vertical structure*

285 Ten taxa were identified in sea-ice cores collected during 2007 and five in 2012. Of these
286 taxa, *N. pachyderma*, *Paralabidocera antarctica*, *Drescheriella glacialis*, *Stephos longipes*
287 and copepod nauplii were common to both years. Integrated abundances of each species
288 across the length of their respective ice core tended to be higher in 2007 than in 2012 (Fig 4).
289 During 2007, *N. pachyderma* was the most abundant species, accounting for 42 to 100% of
290 total integrated abundance. A variable number of nauplii was found (0-58%), and all other
291 taxa contributed less than 12% together. In 2012, *N. pachyderma* contributed from 22 to 98%
292 to total abundance. Copepod nauplii and *D. glacialis* were present in approximately equal
293 proportions, contributing 1-38 and 3-30%, respectively. *Stephos longipes* reached its highest
294 proportion at site 6 (10%), and contributed less than 1% at all other sites, while *P. antarctica*
295 represented less than 2% at all sites. Total meiofauna abundance did not differ significantly
296 between years ($p = 0.231$), based on a non-parametric Welch's test.

297 Figure 5 a-c depicts representative cores from 2007 and figure 5 d and e from 2012.
298 During 2007 meiofaunal communities just below the snow-ice interface were observed at
299 sites 1, 3, 8 and 13 (Fig. 5 and b). The surface communities tended to be dominated by *N.*

300 *pachyderma* and nauplii, when present. *Neogloboquadrina pachyderma* dominated the
301 bottom 50% of sea ice cores at all sites except 3 and 8. When present, *D. glacialis*, *S.*
302 *longipes* and copepod nauplii also followed this trend but in lower abundances (Fig. 5 c). In
303 2012, surface communities were dominated by *N. pachyderma*, with low numbers of *P.*
304 *antarctica*, *D. glacialis* and *S. longipes* (Fig. 5d). Sites 2, 3 and 6 possessed very similar
305 meiofaunal communities, with approximately equal proportions of *N. pachyderma*, *D.*
306 *glacialis* and *P. antarctica* in the bottom 0.02 m of ice (Fig. 5e). Nauplii were also recorded
307 at site 2 whilst *S. longipes* were recorded at site 3.

308 Vertical profiles through the sea ice in 2007 showed L-shaped profiles with lowest
309 chlorophyll *a* concentrations at the surface of the ice, remaining low throughout the length of
310 each core and then increasing within the bottom 20% of each core (Fig. 6a). Sea ice sampled
311 during 2012 lacked a similar trend (Fig. 6b). Sites 2 and 3 had chlorophyll maxima mid-way
312 down the length of the core, whilst site 4 showed a reverse trend from that recorded during
313 2007, with the highest chlorophyll concentration at the surface of the core and decreasing to
314 the ice-water interface (Fig. 6b). Ice brine volumes showed generally C-shaped profiles, with
315 the lowest volumes occurring in the interior of the ice and higher volumes near the surface
316 and at the ice-water interface (Figs. 6c, d).

317

318 3.5 Carbon content and vertical biomass distribution of epipelagic communities

319 Carbon biomass did not differ significantly between years within the water column or the sea
320 ice ($p = 0.055$ and $p = 0.349$, respectively; Table 4), although carbon content was much
321 higher in the sea ice than the water column in both years. Biomass derived from the LOPC
322 deployments in 2012, was lowest at sites 3 and 6 (24 and 26 mg m⁻³, respectively), peaked at
323 site 4 (231 mg m⁻³) and remained relatively constant at sites 7 and 8 (70 and 48 mg m⁻³

324 respectively; Fig. 7). The normalised biomass size spectrum (NBSS) at site 7 indicated a
325 shallow slope (-0.59) while site 4 had a steeper slope (-1.06). Sites 3, 6 and 8 had slopes of -
326 0.63, -0.70 and -0.73, respectively. Sites 3, 6 and 8 had distinct nonlinearities (doming) at
327 sizes greater than 0.58 mm (Fig. 7), indicating an increased biomass at these larger sizes.

328 A breakpoint of 2 mm length was used to separate the zooplankton identified during
329 2012 into size classes, separating protists, molluscs and small copepods such as *O. similis*, *C.*
330 *citer* and *S. longipes* from larger, biomass dominating species including the copepod *C.*
331 *propinquus* and euphausiid, *T. macrura*. Assuming an elliptical shape and a 3:1 length:width
332 ratio of the zooplankton individuals, the ESD size classes of greater and less than 1.154 mm
333 were used to define this break allowing for an LOPC derived vertical structure of biomass at
334 each site . Integrated biomass of the upper 60 m of the water column indicated a clear
335 disjunction in the contribution of each of these size classes to overall biomass. The larger size
336 class contributed 38% or less to total biomass derived from LOPC deployments. The LOPC
337 data were used to examine vertical distributions of biomass over the sampling depth at five
338 sites. Most of the biomass was distributed in the top 20 m at sites 3, 4 and 6 (Fig. 8). At sites
339 7 and 8, however, the biomass was more evenly distributed, with the highest proportion
340 found at depth.

341

342 **4. Discussion**

343 *4.1 Drivers of the epipelagic zooplankton*

344 The composition of zooplankton collected during 2007 and 2012 was typical of the
345 Pacific/Indian sectors of the Southern Ocean (Hunt and Hosie, 2006a; Ojima et al., 2013).
346 The dominant taxa recorded from both years were indicative of Antarctic waters south of the
347 Southern Antarctic Circumpolar Current Front (SACCF) (Atkinson, 1991; Hunt and Hosie,
348 2006a), with copepods and protists forming the dominant taxonomic groups. Considerable

349 variability in these two groups was observed, with tintinnids contributing greater proportions
350 to total zooplankton abundance than copepods at the first three sites sampled in 2007.
351 However, while 21 and 38 taxa were identified during 2007 and 2012, respectively, the 17
352 taxa common to both years generally accounted for greater than 95% of total zooplankton
353 abundance. Therefore, the separation seen in epipelagic zooplankton assemblages in the two
354 years was likely due to changes in ratios of these common taxa rather than substantial
355 differences in the species collected; *e.g.* cluster B developed from the ordination analysis was
356 predominantly comprised of those species that contributed to greater than 10% of total
357 abundance for each year.

358 Over larger regions of the Southern Ocean distinct associations of species assemblages
359 with major water masses have been observed in large-scale synoptic surveys of the east
360 Antarctic SIZ, such as BROKE and BROKE-West (Hosie et al., 2000; Swadling et al., 2010).
361 The hydrography of this region of East Antarctica has been extensively studied over the past
362 20 years, with oceanographic features including the SACCF and the Southern Boundary of
363 the Antarctic Circumpolar Current (SBACC) well understood (Williams et al., 2011). There
364 were relatively small degrees of variation in both temperature and salinity of the upper water
365 column, both between sites and between years; however, the mixed layers were considerably
366 deeper in 2007 (100 – 400 m; Williams et al., 2011) than in 2012 (90 – 160 m; Schallenberg
367 et al., this volume). Water column characteristics, with temperatures below -1 °C and
368 salinities of 34.2 confirmed that epipelagic zooplankton communities were sampled south of
369 the SBACC (Hunt and Hosie, 2006a; Williams et al., 2011).

370 Meso-scale changes in water column chlorophyll *a* (a proxy for phytoplankton biomass
371 and available resources for grazers), snow depth and longitude were shown to be the
372 variables most likely driving the communities of zooplankton observed. Snow depth was

373 generally ten times higher in 2012 than in 2007. Given its high albedo and high attenuation
374 coefficient it is likely that snow depth was responsible for the changes observed in water
375 column chlorophyll *a* and thus was indicated as a driving feature of epipelagic zooplankton
376 communities. As snow significantly reduces the amount of photosynthetically active radiation
377 (PAR) that reaches the sea-ice interface, algal communities present in the bottom layers of
378 the ice are likely to be negatively impacted, reducing potential algal biomass despite low-
379 light adaptations of these algal communities (Smith et al., 2000). As the surface roughness
380 and structural heterogeneity of sea ice influences snow accumulation (Sturm and Massom,
381 2010), sea ice may have played an indirect role in under-ice zooplankton community
382 structure. Counter-intuitively, under-ice water chlorophyll *a* concentrations were higher
383 during 2012 when snow depth was significantly greater. However this could be an indication
384 of dark-adaptation, e.g. a higher cell-specific chlorophyll *a* content in phytoplankton.
385 Alternatively, it could reflect the slightly later sampling time in 2012, with phytoplankton
386 populations more developed.

387 Longitude also played an important role in zooplankton community composition,
388 chiefly for those taxa that grouped independently when the cluster analysis was applied.
389 *Maupausia* sp. and *C. simillimus* were found only at the longitudinal extremes of the study
390 region, while *S. longipes* and *T. macrura* possessed no pattern with longitude. 122°E formed
391 a breakpoint, with *Ctenocalanus* sp. found to the east of this point and *N. tonsus* to the west.
392 Whilst *N. tonsus* and *C. simillimus* are considered to be sub-Antarctic species, both occurring
393 north of the SB, the presence of *C. simillimus* in waters below this boundary is not
394 uncommon (Hunt and Hosie, 2006a). *Calanus simillimus* presence has been attributed to
395 southern eddy-transport from the SBACC; however, there was a lack of warm water “hot-
396 spots” that could explain its presence in 2007 and 2012, indicating that seeding of individuals
397 may have occurred from eddy activity earlier in both years.

398 Although BIOENV analysis revealed physical characteristics of the water column to be
399 important in structuring communities, individual taxon-based analysis using GLM
400 highlighted the influence of the sea ice as an important driver of populations. The results of
401 GLM indicated that two different aspects of sea ice properties influenced the dominant taxa
402 of the epipelagic communities below: (i) depth-integrated ice algal chlorophyll *a* (i.e. in the
403 entire ice cores), and bottom ice chlorophyll *a* (bottom 0.01 m in direct contact with the
404 under-ice realm). The abundances of *C. propinquus* and *O. similis* increased with an increase
405 in integrated sea-ice chlorophyll *a* content, whilst *N. pachyderma* decreased. *Microsetella*
406 *norvegica* and tintinnids, however, were only influenced by bottom ice chlorophyll. The
407 feeding of *C. propinquus* is not fully understood, with suggestions of ice algal grazing at the
408 ice-ocean interface as well as feeding in the water column ingesting pelagic phytoplankton,
409 protists and microzooplankton (Bathmann et al., 1993; Pasternak and Schnack-Schiel, 2001).
410 Jia et al. (this volume) found, via carbon and nitrogen isotope analysis, that *C. propinquus* fed
411 predominantly upon phytoplankton within the water column. Whilst our results of the GLM
412 indicate that *C. propinquus* was most influenced by the algae present within the sea ice, it is
413 likely, given these two pieces of information, that *C. propinquus* formed close associations
414 with the sea ice, feeding sporadically on ice algae at the sea-ice interface. Atkinson et al
415 (2001) described this species as an indiscriminate feeder favouring large, non-spinous
416 diatoms, and therefore algal composition of both the sea ice and water column may have
417 influenced these results. Ice algal bottom communities were dominated by pennate diatoms,
418 in particular *Fragilariopsis* spp., during both 2007 and 2012 (Meiners et al., 2011; Ugalde et
419 al., this volume).

420 The diet of *O. similis* is perhaps better understood than that of *C. propinquus*, and it is
421 known to rely upon microplankton (both autotrophic and heterotrophic) and detrital material
422 including faecal pellets, readily switching between any available resources. Consequently the

423 presence of a concentrated food source, which is often comprised of small diatoms and the
424 presence of large numbers of other species close to the sea-ice interface allow *O. similis* to
425 exploit its flexible diet and coprophagous nature (Pond and Ward, 2011). However, a lack of
426 stable isotope analysis for this species makes it unclear which of these potential factors
427 influenced the trend uncovered by GLM in the present study.

428 The negative relationship between integrated chlorophyll *a* in the sea ice and *N.*
429 *pachyderma* is interesting, and might point to strong grazing pressure. Conversely, the
430 positive relationship between abundance and snow depth suggests that *N. pachyderma*
431 accumulate in areas of low chlorophyll concentration where light attenuation by snow limits
432 algal growth. It is possible that, given their omnivorous diet, a shift is seen with the onset of
433 spring whereby individuals switch from grazing on phytoplankton to other protists.
434 Reproduction of *N. pachyderma* begins in spring, so this switch may occur in preparation for
435 coinciding with the mass release of entrained individuals during ice melt (Spindler and
436 Dieckmann, 1986).

437 Bottom ice chlorophyll *a* concentration was an important driver of *M. norvegica* and
438 tintinnid distribution. *Microsetella norvegica* is known to inhabit both the epipelagic and the
439 lower portion of sea ice; therefore it relies heavily upon sea-ice algal communities for its diet
440 (Dahms et al., 1990). The distribution and feeding ecology of tintinnids is poorly understood.
441 The tintinnid bloom recorded during 2007 points to their possible importance in the sea-ice
442 zone off East Antarctica. The tintinnids found within this bloom were predominantly of the
443 genus *Cymatocylis*, which are cosmopolitan filter feeders consuming phytoplankton of
444 approximately 30 µm (Dolan et al., 2012; Alder and Boltovskoy, 1991). The high abundances
445 of tintinnids associated with high bottom ice chlorophyll *a* suggests their ability to capitalise
446 on bottom-ice algal communities, with relatively stable water column environmental
447 conditions ideal for proliferation.

448 4.2 Distribution of sea-ice meiofauna

449 Our study suggests that a strong degree of coupling exists between the sea ice and epipelagic
450 environments. The environmental stability and supply of concentrated food resources
451 provided by sea ice during winter and early spring is a driving force in shaping sea-ice
452 associated zooplankton communities. Moreover, the presence, abundance and vertical
453 distribution of sea-ice meiofauna contributes to the coupling of this 2-phase system. The sea-
454 ice meiofaunal communities found during 2007 and 2012 are similar to previous studies off
455 East Antarctica during maximum sea-ice extent (Swadling et al., 1997; Loots et al. 2009).
456 Brine volume, an indicator of habitable space, was the dominant factor influencing meiofauna
457 distribution, with high brine volumes correlated with high abundances and diversity. Whilst
458 meiofauna abundances tend to increase with ice algal concentration (Kramer et al. 2011), our
459 study indicated that proximity to the ice-water interface was a key factor, confirming a
460 previous observation that sea-ice meiofauna maxima generally occur within this sea-ice strata
461 (Schnack-Schiel et al., 2001).

462 The vertical distribution of the three copepods identified in sea-ice cores reflects their
463 respective life histories. The low abundances of adult *P. antarctica* is a common observation
464 in sea ice (Swadling et al., 2004). Adults generally do not directly inhabit sea ice, although
465 their nauplii and young copepodid stages use it as the main overwintering habitat (Loots et al.
466 2009). Nauplii that were found at the ice-water interface were likely entrained during initial
467 sea-ice formation, e.g. in autumn (Swadling et al., 2004). *Stephos longipes* have been shown
468 to migrate actively between the water column and sea ice habitats, where naupliar stages are
469 able to move towards the interior of the sea ice when sufficient 'space' is available
470 (Kurbjeweit et al., 1993). In the present study *S. longipes* was only found within the water
471 column when it was also present within the sea ice above, demonstrating their ability to
472 migrate freely between the ice and the water, and therefore forming a substantial link

473 between the two habitats. In contrast, *D. glacialis* appears to be completely reliant upon the
474 sea ice as no individuals were identified within the water column from either year. Whilst
475 previous studies have demonstrated an active migration of this species between the sea ice,
476 pelagic realm and benthos this generally occurred in autumn, prior to sea-ice formation when
477 the nauplii migrate to the sea-ice interface and are likely scavenged during sea-ice formation
478 (Loots et al., 2009). The large numbers of *S. longipes* and *D. glacialis* nauplii in both the
479 lower and surface layers of sea ice suggests active breeding by these ice-associated species.
480 Given their small size, naupliar stages of these two species are able to inhabit sea-ice layers
481 with small brine volumes and correspondingly small brine channel diameters. The
482 distribution of *S. longipes* across distinct sea-ice layers and in the under-ice waters indicates
483 their ability to migrate to and within sea ice, therefore representing an, so far understudied,
484 link in cryopelagic coupling,

485

486 *4.3 Vertical distribution of biomass*

487 Despite variations in total zooplankton abundance and species composition, no statistical
488 difference in carbon biomass was recorded between 2007 and 2012. Dry weight and LOPC
489 derived biomass estimates were only conducted for 2012, and biomass calculated from the
490 LOPC were considerably higher than from the other methods applied. Given that LOPC
491 derived biomass is comparable to a 'wet-weight', higher LOPC estimates of biomass is not
492 unexpected, however when LOPC biomass is converted to a dry weight, biomass estimates
493 were considerably larger than the other methods applied. Trends in total biomass were
494 consistent between each of the three methods used for sites during 2012. Previous attempts to
495 use LOPC to quantify biomass of the water column *in situ* generally always yielded higher
496 values than those by traditional means and is attributed to the detection by the LOPC of non-

497 zooplankton particles, e.g. detritus and algal material (Herman and Harvey, 2006). The
498 separation of particles based upon size class in the present study, i.e. smaller and larger than 2
499 mm, reduces this problem for the larger size class at least, given that detrital and algal
500 material would rarely fall within that category. The vertical stratification of biomass based
501 upon this size class separation therefore provides a relatively robust insight into the
502 distribution of the dominant taxa in the upper water column. A dominant change in the
503 distribution of biomass in both size classes was seen at sites 7 and 8 during 2012. At these
504 sites *C. propinquus* was the most numerically abundant zooplankter within the greater than 2
505 mm size fraction. Its presence in abundances greater than 1 ind. m⁻³ coincided with the trend
506 seen in LOPC data at sites 3, 4 and 6 during 2012. High biomasses of particles within close
507 proximity to the sea-ice interface could not be directly resolved due to the interference of ice
508 particles with LOPC measurements.

509 In conclusion, our study suggests an effect of coupled sea ice physical-biological
510 properties on under-ice zooplankton abundance and species composition. Our study supports
511 the observations that copepod species *Oithona similis* and *Calanus propinquus* use the
512 pelagic habitat as well as the sea-ice interface, whilst *Stephos longipes* use both, as well as
513 the interior of the ice. We suggest that these species contribute significantly to exchange of
514 material and carbon flow across the sea ice – ocean interface. To our knowledge, this study
515 presents the first LOPC data on under-ice plankton in the high latitude Southern Ocean.
516 LOPC data, albeit providing larger estimates of biomass, demonstrated site specific trends
517 that were consistent with classical methods indicating that LOPC may provide a useful
518 method to study under-ice zooplankton in a cost- and time-effective manner. Our study
519 confirms previous findings that Antarctic sea ice supports dense communities of ice-
520 associated meiofauna.

521

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527

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652

653 Table 1. Environmental variables recorded for the water column and sea ice for 2007 and 2012 (showing means and ranges). F-values were
 654 calculated using Welch's tests to test for significant differences between years. *denotes p-value ≤ 0.05 and ** denotes p-value ≤ 0.005 for
 655 calculated F values.

	2007	2012	F value
Water column			
Number of samples	11	19	
Latitude °S	64.94 (64.23 – 65.58)	65.01 (64.4 – 65.26)	0.179
Longitude °E	121.93 (116.19 – 128.10)	119.52 (116.16 – 121.67)	2.913
Depth, m	2000 (750 – 3000)	3000 (2000 – 3500)	8.339*
Temperature, °C	-1.85 (-1.83 – -1.86)	-1.86 (-1.85 – -1.87)	11.69**
Salinity	34.24 (34.10 – 34.41)	34.28 (34.21 – 34.33)	0.166
Chlorophyll <i>a</i> , mg m ⁻³	0.05 (0.01 – 0.10)	0.15 (0.10 – 0.25)	19.087**
Sea ice			
Number of samples	12	5	
Latitude °S	64.97 (64.32 – 65.58)	64.91 (63.88 – 65.40)	0.047
Longitude °E	121.65 (116.82 – 128.10)	120.33 (119.91 – 120.92)	1.082
Snow depth, m	0.0035 (0 – 0.008)	0.0055 (0.008 – 0.1)	33.79**
Ice thickness, m	0.0078 (0.0058 – 0.132)	0.768 (0.075 – 2.5)	6.10*
Freeboard, m	0.0024 (-0.004 – 0.008)	0 (-0.009 – 0.005)	0.273
Chlorophyll <i>a</i> in bottom 0.01 m, mg m ⁻³	0.144 (0.0040 – 0.647)	0.089 (0.00036 – 0.318)	0.483
Integrated chlorophyll <i>a</i> , mg m ⁻²	2.14 (0.08 – 8.43)	3.02 (0.41 – 1.06)	0.013
Brine volume - bottom 0.01 m, %	20.04 (13.24 – 34.82)	18.26 (8.64 – 26.92)	0.19
Brine volume - remainder, %	7.60 (5.37 – 11.79)	11.40 (6.69 – 14.57)	4.047

656

657 Table 2. List of the common zooplankton taxa. Abundances are means for all sites within
 658 each sampling year (ind. m⁻³). **Bold** indicates a statistically significant Indicator Value of
 659 greater than 25% for that year. *distinguishes those species that contributed ≥10% to
 660 abundance for that year (SIMPER analysis).

	2007	2012
<i>Calanus propinquus</i>	0.95	1.22
<i>Calanus simillimus</i>	0.05	0.53
<i>Ctenocalanus</i> sp.	0.05	0.05
<i>Microcalanus pygmaeus</i>	0.44	6.30*
<i>Microsetella norvegica</i>	1.09	3.47*
<i>Neocalanus tonsus</i>	0.72	0.04
<i>Oithona similis</i>	94.5*	58.5*
<i>Stephos longipes</i>	0.12	1.29
Nauplii	38.4*	34.4*
<i>Neogloboquadrina pachyderma</i>	1.99*	0.82
Radiolarians	2.55*	2.89
Tintinnids	85.0*	0.91
Gastropod veliger	0.09	2.16
<i>Limacina helicina</i>	0.26	2.59
<i>Maupasias</i> sp.	0.02	0.36
Ostracods	0.07	0.95
<i>Thysanoessa macrura</i>	0.05	0.19

661

662 Table 3. The most parsimonious GLM based upon AIC selection criteria. Predictor variables used are indicated and when appropriate, significant
 663 parameters ($p \leq 0.05$) are indicated. The fit of the model as determined by Chi-squared analysis is also provided.

Species	Model predictors	Significant Parameter/s	coeff	\pm SE	Z-value	AIC	Fit of model
<i>C. propinquus</i> ¹	Chl _a _{water} , snow depth, Chl _a _{ice} , Chl _a _{bottom 0.01 m} , longitude, year	Chl _a _{ice}	1.53	0.76	2.01	67.81	0.101
<i>M. norvegica</i> ¹	Chl _a _{water} , Chl _a _{bottom 0.01 m} , depth	Chl _a _{bottom 0.01 m} depth	0.98 -0.93	0.29 0.341	3.39 -2.72	76.02	0.039
<i>O. similis</i> ²	snow depth, Chl _a _{ice} , Chl _a _{bottom 0.01 m} , latitude	intercept snow depth Chl _a _{ice} latitude	76.69 -0.013 0.39 -1.12	22.48 0.01 0.15 0.35	3.42 -2.97 2.67 -3.24	215.1	0.143
<i>N. pachyderma</i> ¹	longitude, latitude, snow depth, Chl _a _{ice}	intercept snow depth latitude Chl _a _{ice}	106.6 0.03 -1.82 -37.12	33.86 0.01 0.54 15.91	3.14 2.09 -3.33 -2.33	56.92	0.913
Tintinnids ²	Chl _a _{water} , salinity, Chl _a _{bottom 0.01 m} , latitude, longitude	Chl _a _{bottom 0.01m} latitude longitude	0.625 -1.432 0.54	0.16 0.59 0.09	4.00 -2.41 5.60	108.5	0.092

664 ¹GLM based upon a Poisson distribution

665 ²GLM based upon a negative binomial distribution due to overdispersion of the abundance data

666

667

668 Table 4. Zooplankton and sea-ice meiofauna. Abundance and biomass in the water column and sea ice during winter 2007 and 2012 (showing
 669 means and ranges). F-values were calculated using Welch's tests.

	2007	2012	F value
Water column			
Total net zooplankton abundance, ind. m ⁻³	226.7 (33.9 – 725.8)	120.0 (30.1 – 315.1)	2.462
Total number of species per site, S	9 (6 – 15)	12 (6 – 20)	-
Dry weight (DW), mg m ⁻³	-	0.11 (0.00 – 20)	-
Carbon, mg m ⁻³	0.83 (0.041 – 2.77)	1.54 (0.23 – 4.44)	4.07
LOPC predicted biomass mg m ⁻³	-	80.89 (24.93 – 231.06)	-
LOPC converted biomass (DW) mg m ⁻³	-	13.65 (4.10 – 39.50)	
Sea ice			
Total meiofauna abundance, ind. m ⁻³	27483 (0 – 117472)	61189 (24036 – 140890)	1.797
Total number of species per site, S	3 (1 – 5)	4 (3 – 4)	2.233
Carbon, mg m ⁻³	61.07 (0 – 266.3)	114.8 (14.33 – 279.7)	1.031

670

671 **Figure Captions**

672 Figure 1. Map of the sites sampled during 2007 (solid) and 2012 (open) voyages, showing
673 features mentioned in the text.

674 Figure 2. Abundance (ind. m⁻³) of main epipelagic zooplankton groups identified from the
675 upper water column during (a) 2007 and (b) 2012.

676 Figure 3. Multivariate analyses of epipelagic species and sites for 2007 and 2012. (a) Species
677 assemblages identified by cluster analysis indicating those clusters identified at 40%
678 similarity and sub-clusters at 70% and (b) CAP analysis of sites, with dominant species as
679 vectors.

680 Figure 4. Sea-ice meiofauna integrated abundance (ind. m⁻²) during (a) 2007 and (b) 2012.

681 Figure 5. Vertical distribution and abundance of meiofauna in sea ice cores from the sea ice
682 surface from representative sea ice cores during 2007 (a-c) and 2012 (d, e).

683 Figure 6. Vertical distribution of brine volume and chlorophyll a (mg m⁻³) within sea ice
684 during 2007 (a, b) and 2012 (c, d).

685 Figure 7. Normalised Biomass Size Spectrum (NBSS) for each of the 5 sites (A-E) derived
686 from the LOPC deployments in 2012. Slope intercept, biomass and counts are shown on each
687 figure.

688 Figure 8. Vertical structure of epipelagic biomass (mg m⁻³) for zooplankton less than (solid)
689 and greater than (open) 2 mm length as derived from the vertical deployments of the LOPC in
690 2012.

