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Antarctic sympagic meiofauna in winter: comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions

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Abstract

This study of Antarctic sympagic meiofauna in pack ice during late winter compares communities between the perennially ice-covered western Weddell Sea and the seasonally ice-covered southern Indian Ocean. Sympagic meiofauna (proto- and metazoans $> 20\,\mu$m) and eggs $> 20\,\mu$m were studied in terms of diversity, abundance and carbon biomass, and with respect to vertical distribution. Metazoan meiofauna had significantly higher abundance and biomass in the western Weddell Sea (medians: $31.1 \times 10^3\,\mathrm{m}^{-2}$ and $6.53\,\mathrm{mg\,m}^{-2}$, respectively) than in the southern Indian Ocean (medians: $1.0 \times 10^3\,\mathrm{m}^{-2}$ and $0.06\,\mathrm{mg\,m}^{-2}$, respectively). Metazoan diversity was also significantly higher in the western Weddell Sea. Furthermore, the two regions differed significantly in terms of meiofauna community composition, as revealed

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through multivariate analyses. The overall diversity of sympagic meiofauna was high, and integrated abundance and biomass of total meiofauna were also high in both regions (0.6–$178.6 \times 10^3 \, \mathrm{m}^{-2}$ and 0.02–$89.70 \, \mathrm{mg} \, \mathrm{m}^{-2}$, respectively), mostly exceeding values reported earlier from the western Weddell Sea in winter. We attribute the differences in meiofauna communities between the two regions to the older first-year ice and multi-year ice that is present in the western Weddell Sea, but not in the southern Indian Ocean. Our study indicates the significance of perennially ice-covered regions for the establishment of diverse and abundant meiofauna communities. Furthermore, it highlights the potential importance of sympagic meiofauna for the organic matter pool and trophic interactions in sea ice.

Keywords: sympagic meiofauna, sea ice, abundance, biomass, WWOS, SIPEX, Antarctica: western Weddell Sea: 60–65° S, 41–57° W, Antarctica: southern Indian Ocean: 64–65° S, 116–129° E

1. Introduction

The Southern Ocean is characterised by two profoundly different types of pack ice: first- and multi-year ice. The mainly divergent drift patterns of sea ice in the Southern Ocean cause large portions of the ice to be exported (Gow and Tucker III, 1990), and this results in strong seasonality in sea-ice cover: in winter, up to $19 \times 10^6 \, \mathrm{km}^2$ of the Southern Ocean are covered by sea ice, while the ice-covered area in summer can be as low as $2 \times 10^6 \, \mathrm{km}^2$ (Comiso and Nishio, 2008). Seasonally ice-covered areas thus make up the major part of the Antarctic sea-ice zone, and 90 % of the Antarctic sea-ice cover is first-year ice (Brierley and Thomas, 2002). A typical example of a seasonally ice-covered region is the southern Indian Ocean, where sea ice is confined to a narrow band that extends to a maximum of no more than 300 km from the continent in some locations (Worby et al., 1998). Sea ice in this area is

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31 highly dynamic, characterised by a divergent net drift, and it is generally thinner

32 than sea ice in the Weddell Sea (Worby et al., 1998). The Weddell Sea, in contrast,

33 is one of the few Antarctic regions where geographic, oceanographic and meteorolog-

34 ical conditions cause convergent sea-ice drift patterns, resulting in a perennial sea-ice

35 cover (Brierley and Thomas, 2002). Ice concentrations in the Weddell Sea are high,

36 large proportions of thick multi-year ice and deformed ice are found (Gordon, 1993;

37 Haas et al., 2008, 2009), and the snow cover is comparatively thick (Massom et al.,

38 2001; Haas et al., 2008; Nicolaus et al., 2009), particularly in the western regions

39 (Willmes et al., in press). We hypothesise that these different sea-ice regimes—

40 seasonal ice cover with young and first-year ice on one hand, perennial ice cover

41 with multi-year ice on the other—host different communities of sympagic (sea-ice

42 associated) organisms.

43 Sea ice is permeated with a system of brine channels that develops during its

44 formation and growth when salt ions are rejected from the crystal lattice of water

45 molecules; brine thus collects in between the ice crystals (Weissenberger et al., 1992;

46 Cottier et al., 1999). These brine channels are inhabited by viruses, bacteria, fungi,

47 microalgae, protozoans and metazoans, which, together with under-ice organisms,

48 constitute the sympagic community (Brierley and Thomas, 2002; Schnack-Schiel,

49 2003). The metazoans and larger protozoans ($> 20\,\mu$m) living inside the brine chan-

50 nels of sea ice are referred to as sympagic meiofauna (Gradinger, 1999a).

51 Protozoan meiofauna in Antarctic sea ice comprises mainly foraminiferans and

52 ciliates (Garrison and Buck, 1989; Gradinger, 1999a; Schnack-Schiel et al., 2001),

53 with heliozoans being reported only once (Garrison and Buck, 1989). Metazoan

54 meiofauna comprises mainly harpacticoid and calanoid copepods and acoel platy-

55 helminthes (commonly referred to as "turbellarians") (Gradinger, 1999a; Schnack-Schiel et al.,

56 2001; Guglielmo et al., 2007). Ctenophores (Dahms et al., 1990; Kiko et al., 2008b)

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57 and nudibranchs (Kiko et al., 2008a,b) have been reported in very few studies from
58 the Weddell Sea, and never from the eastern part of the southern Indian Ocean.

59   In comparison to sea-ice algae, sympagic meiofauna has received only little at-
60 tention, and studies during winter are particularly scarce. Antarctic sympagic meio-
61 fauna studies have usually focused on copepods (Swadling, 2001; Guglielmo et al.,
62 2007; Kiko et al., 2008b; Schnack-Schiel et al., 2008), with few publications dealing
63 with other specific taxa (Janssen and Gradinger, 1999; Kiko et al., 2008a). The only
64 two general studies on Antarctic sympagic meiofauna communities by Gradinger
65 (1999a) and Schnack-Schiel et al. (2001) focus on integrated abundance and biomass
66 and summarise results from several cruises to the Weddell Sea, including one expe-
67 dition in late winter. The present study aims to expand our knowledge of Antarctic
68 sympagic meiofauna diversity, abundance, carbon biomass and vertical distribution
69 patterns in late winter.

70   Given the large proportion of seasonally ice-covered regions in the Southern Ocean
71 (Brierley and Thomas, 2002), knowledge of the sympagic communities in these re-
72 gions is of central importance for understanding the Antarctic sympagic ecosystem.
73 Sympagic communities in seasonally and perennially ice-covered regions obviously
74 have different options to colonise sea ice and are likely characterised by different
75 successional histories. We therefore hypothesised that substantial differences exist
76 between sympagic meiofauna communities in seasonally and perennially ice-covered
77 regions. To test this hypothesis, we compare meiofauna communities between the
78 seasonally ice-covered southern Indian Ocean and the perennially ice-covered western
79 Weddell Sea.

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2. Materials and methods

2.1. Field work

Analyses of Antarctic sympagic meiofauna communities in late winter were based on samples from the perennially ice-covered western Weddell Sea and the seasonally ice-covered southern Indian Ocean (Fig. 1, online supplementary Suppl. 1). Samples in the western Weddell Sea were taken during the RV *Polarstern* cruise ANT–XXIII / 7 ("WWOS", Aug 24 to Oct 29, 2006), while sea ice in the southern Indian Ocean was sampled during the SIPEX expedition on RSV *Aurora Australis* (voyage 1, Sep 5 to Oct 17, 2007). Due to logistic constraints, and since winter cruises are scarce, sampling had to be conducted in two consecutive years, but took place during the same season.

In the western Weddell Sea, sea ice was sampled near the South Orkney Islands and east of the tip of the Antarctic Peninsula. Air temperatures during the study period were usually between -10 °C and -2 °C (Willmes et al., in press). The ice edge retreated southward during the period of the cruise, from 58–60 °S on Aug 24 to 59–65 °S on Oct 29 (cf. AMSR-E sea-ice maps from www.seaice.de, data not shown here). Ice concentration in most parts of the study area was above 9 / 10 (Haas et al., 2009). Modal ice thickness (from electro-magnetics) was 1.2–1.4 m (first-year ice), with secondary modes between 2.5 m and 3.0 m (multi-year ice); mean ice thickness was 2.1 m due to large amounts of ice thicker than 3 m (Haas et al., 2009). Modal snow thickness (from ground-penetrating radar) was 5–10 cm, with secondary modes between 30 cm and 45 cm (Haas et al., 2009) indicating second-year snow (Nicolaus et al., 2009). While thin and medium first-year ice with thin snow cover prevailed in the southern part of the study area, the northern part was characterised by deformed first- and second-year ice with thick snow cover (Haas et al.,

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105 2009; Willmes et al., in press). The sampling stations in the western Weddell Sea
106 (Fig. 1 a, Suppl. 1) were pack ice, most of which probably originated from the Larsen
107 and Ronne polynyas (Haas et al., 2009). The samples from stations WS–4, WS–7,
108 WS–11 and WS–21 were multi-year ice covered with second-year snow, whereas the
109 samples from all other stations were first-year ice (Haas et al., 2009; Willmes et al.,
110 in press). Snow stratigraphies, sea-ice textures and bulk salinity profiles are shown
111 in Willmes et al. (in press); information on biogeochemical conditions and ice algal
112 photosynthetical parameters are given in Meiners et al. (2009).

113   In the southern Indian Ocean, sea ice was sampled in the 115–130 °E sector off
114 Wilkes Land, East Antarctica. Air temperatures during the study period usually
115 remained between -16 °C and -9 °C (Meiners et al., 2010). The ice edge was located
116 at 62–64 °S and retreated southward only slightly during the period of the cruise
117 (cf. AMSR-E sea-ice maps from www.seaice.de, data not shown here). Ice concen-
118 tration was usually between 8 / 10 and 9 / 10 (Worby et al., 2010). Modal ice thick-
119 ness (from laser altimetry) was about 0.8 m with no strong secondary modes; mean
120 ice thickness was 2.0 m due to the high percentage of surface ridging (Worby et al.,
121 2010). The eastern part of the study area was characterised by high proportions of
122 new and young ice with no or little snow cover, the northwestern part by thin first-
123 year ice, while thicker first-year ice, thicker snow cover and strong deformation were
124 recorded in the southwestern part (Worby et al., 2010). Sampled sea ice (Fig. 1 b,
125 Suppl. 1) was drifting pack ice except for station IO–5, which was offshore fast
126 ice hemmed in by large icebergs. All sampled ice was first-year ice, which was often
127 rafted (Meiners et al., 2010; Worby et al., 2010). The ice close to the coast had prob-
128 ably formed east of the study region, while ice floes close to the ice edge were from
129 different origin (T. Worby, pers. comm.). Information on ice physics, biogeochemical
130 parameters and ice algal biomass and composition are given in Meiners et al. (2010)

Figure 1: Stations sampled for community analyses of Antarctic sympagic meiofauna during SIPEX and ANT–XXIII / 7. **A** Overview with all stations from both cruises; areas for enlarged station maps (B and C) are highlighted. **B** Stations sampled in the western Weddell Sea during ANT–XXIII / 7 (Aug 24 to Oct 29, 2006) with sea-ice concentration from Sep 20, 2006. **C** Stations sampled in the southern Indian Ocean during SIPEX (Sep 5 to Oct 17, 2007) with sea-ice concentration from Sep 20, 2007. All sea-ice concentration data are based on AMSR-E data and were re-plotted in grey scale from www.seaice.de (Spreen et al., 2008). The legend refers to both B and C; MF := meiofauna full cores, MB := meiofauna bottom-ice sections, EF := environmental full cores. Note different scales in B and C.

131   and Worby et al. (2010).

132   Level ice was sampled with an engine-powered KOVACS ice corer (inner diameter
133   9 cm) at 21 stations in the western Weddell Sea and 14 stations in the southern
134   Indian Ocean (Fig. 1, Suppl. 1). At each station, snow thickness, ice thickness and
135   freeboard were determined, air and snow temperatures were measured, and at least
136   one full ice core (environmental full core EF) was taken for determination of ice *in*
137   *situ* temperature, bulk salinity, brine salinity, relative brine volume, concentration
138   of chlorophyll *a* (chl *a*) and phaeopigment *a* (phaeo), and ratio phaeo / chl *a* over
139   the entire ice column. Another full core (meiofauna full core MF) was taken at six
140   stations during ANT–XXIII / 7 and 12 stations during SIPEX for determination of
141   abundance and carbon biomass of sympagic meiofauna taxa and eggs over the entire
142   ice column on fixed samples. During ANT–XXIII / 7, an additional three bottom-
143   ice sections of 5 cm length (meiofauna bottom-ice sections MB) were taken at nine
144   stations for live counts of sympagic metazoan meiofauna.

145   *2.2. Determination of environmental parameters*

146   At each sampling station, snow and ice thickness as well as freeboard at the coring
147   site were determined as the median of up to 10 measurements. Air temperature

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148 close to the snow surface, snow temperature above the snow-ice interface, and ice *in*

149 *situ* temperatures were measured using a handhold thermometer (Testotherm 720,

150 Pt 100 sensor, accuracy $0.2\,°C$). Ice temperature was measured on full core EF in

151 intervals of 5–10 cm by inserting the temperature probe into small holes drilled with

152 an electric drill. Subsequently, core EF was cut into sections of usually 5–10 cm

153 length directly in the field. The sections were melted in the dark at $+4\,°C$, and bulk

154 salinity was measured with a conductivity meter (WTW microprocessor conductivity

155 meter LF 196, accuracy 0.2). Brine salinity (accuracy better than 4) was calculated

156 from ice temperature according to Assur (1958) and Frankenstein and Garner (1967).

157 Relative brine volume (accuracy better than 4%) was calculated from ice temperature

158 and bulk salinity according to Frankenstein and Garner (1967), the ice temperature

159 for the calculation being adjusted to the values expected for the middle point of each

160 section by calculating the weighted average of the two nearest measurements.

161   For chl *a* and phaeo measurements, subsamples of at least 250 mL of the melted

162 sections of core EF were filtered on Whatman GF / F filters within 24 h after melting.

163 Pigments were extracted in 90 % acetone for 6–12 h at -25 °C (Gradinger, 1999b) af-

164 ter ultrasonic cell disruption during ANT–XXIII / 7 or in 100 % methanol for 24 h at

165 $0\,°C$ (McMinn et al., 2007) without cell disruption during SIPEX. Pigment concen-

166 trations were determined by fluorometric measurements (Turner 10-AU fluorometer,

167 detection limit $0.1\,\mu g\,L^{-1}$) before and after acidification with 0.1 N HCl. The different

168 methodologies, particularly the use of different extraction agents, might have slightly

169 impacted the data, but the effect is assumed to be small (Buffan-Dubau and Carman,

170 2000).

171 *2.3. Meiofauna community analyses*

172 *Sample processing and species identification*

173   Core MF was cut into sections of usually 5–10 cm length directly after coring. The

174 ice samples for meiofauna analyses (MF and MB) were melted in the dark at $+4\,°C$

175 in a surplus of $0.2\,\mu$m filtered seawater (200 ml per 1 cm core length, Gradinger,

176 1999a). This method considerably reduces osmotic stress for the organisms dur-

177 ing melting (Garrison and Buck, 1986); although very delicate organisms, such as

178 aloricate ciliates and acoel platyhelminthes, may be disrupted even under moderate

179 osmotic stress, this method is generally accepted (Horner et al., 1992) and commonly

180 applied in studies on sympagic organisms (Nozais et al., 2001; Schnack-Schiel et al.,

181 2001; Gradinger et al., 2005; Schünemann and Werner, 2005), so that our data is

182 readily comparable with previous literature. Within 24 h after complete melting of

183 the ice, organisms were enriched over a $20\,\mu$m gauze. MB samples were transferred

184 into petri dishes for live counts of metazoan meiofauna performed immediately at

185 $0\,°C$. MF samples were fixed with borax-buffered formaldehyde (2 % in sea water).

186 These samples were later rinsed with water (MilliQ : tap water, v:v = 1:1) and trans-

187 ferred into petri dishes for abundance and biomass analyses.

188   Meiofauna and eggs were sorted and counted using a stereomicroscope equipped

189 with transmitted and impinging light (Leica WILD MZ 12.5, 20–100× magnifica-

190 tion; Leica MZ 16 F, 20–115× magnification). For identification and further char-

191 acterisation of specific taxa and eggs, light and electron microscopes were also used

192 (see Suppl. 4 for details). Protozoans were grouped into ciliates, foraminiferans and

193 radiolarians; other protozoans, such as heterotrophic flagellates, were not consid-

194 ered. Within ciliates, the tintinnids were distinguished; foraminiferans were iden-

195 tified to species level whenever possible. Copepods were identified to species level

196 as far as possible. For the platyhelminthes acoels and rhabditophors were distin-
197 guished. Nudibranchs (juveniles and adults) were identified to species level. Eggs
198 and veliger larvae of *Tergipes antarcticus* were identified using the description given
199 by Kiko et al. (2008a); eggs and veligers were assessed together, since late egg stages
200 and early veliger stages could not be distinguished from one another in some of the
201 fixed samples. Eggs of acoel platyhelminthes were identified by morphological com-
202 parison of the fixed eggs with (i) eggs from specimens collected during ANT–XXIII / 7
203 which reproduced in culture and (ii) eggs observed in the bodies of fixed sympagic
204 acoels from ANT–XXIII / 7 (scanning electron microscopic images, see Suppl. 4.2 for
205 details).

206 *Assessment of abundance, carbon biomass and diversity*

207 Abundance and carbon biomass of protozoans, metazoans and eggs were deter-
208 mined as bulk values (i. e. in relation to volume of melted ice) for each ice-core section.
209 Integrated abundance and carbon biomass of the full cores MF (i. e. in relation to
210 ice area) were also calculated in order to compare the stations and regions.

211 For calculation of carbon biomass, the carbon contents of meiofauna and eggs
212 were determined from length and width principally according to Gradinger et al.
213 (1999)—see Suppl. 2.1 for details.

214 For the assessment of metazoan diversity, the absolute number of species $\hat{S}$, Mar-
215 galef's species richness d, Pielou's evenness J', Shannon-Wiener diversity H' and the
216 expected species number in a sample of 100 individuals ES_{100} were calculated from
217 integrated abundance (Clarke and Warwick, 2001). For these calculations, it was
218 assumed that the ctenophores, the acoel and rhabditophor platyhelminthes, the cy-
219 clopoid copepods and the harpacticoid copepods *Drescheriella* spp., *Ectinosoma* sp.,
220 *Diarthrodes* cf. *lilacinus*, *Harpacticus* sp. and "harpacticoid species 1" represented

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221 only one species each. Eggs and larvae were not included in the calculations. The
222 data are thus conservative estimates.

223 *2.4. Comparison of the two study areas*

224 Two-tailed Mann-Whitney U-tests were performed to test for differences between
225 the two regions in terms of (1) integrated abundance and carbon biomass of proto-
226 zoans, metazoans and eggs and (2) metazoan diversity measures.

227 Integrated abundance of meiofauna, including eggs, was further analysed by
228 means of non-parametric multivariate statistics to investigate patterns in meiofauna
229 community structure. To test for differences between the two regions, a global
230 one-way analysis of similarities (ANOSIM, Clarke and Warwick, 2001) was applied.
231 Meiofauna taxa discriminating between the two regions and typifying taxa for each
232 region were identified by the one-way similarity percentages method (SIMPER;
233 Clarke and Warwick, 2001). To visualize and further investigate grouping patterns
234 of the stations, hierarchical agglomerative clustering with group-average linkage was
235 performed, and significance of clustering was tested with a similarity profile test
236 (SIMPROF, Clarke and Warwick, 2001). Furthermore, non-metric multi-dimensional
237 scaling (MDS) to two dimensions was conducted (Clarke and Warwick, 2001).

238 Comparison of vertical meiofauna abundance profiles between stations and re-
239 gions was complicated by the inherent differences in ice thicknesses as well as by
240 the different cutting schemes applied during the two expeditions. To overcome these
241 problems, each core was divided into five theoretical sections of $1/5$ of the total core
242 length, and average bulk abundance was calculated for each theoretical section (as
243 weighted arithmetic means of the abundances in the comprised sections). These were
244 used in second-stage analyses (Clarke and Warwick, 2001), defining the theoretical
245 sections as inner factors and the stations as outer factors, thus investigating simi-

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246 larities and differences between stations in terms of vertical meiofauna distribution.

247 A second-stage ANOSIM (ANOSIM2) as well as second-stage cluster analysis and

248 MDS (Clarke and Warwick, 2001) were conducted.

249   Environmental variables were investigated with the focus on relationships to pat-

250 terns seen in meiofauna communities. In a first approach, vertical profiles of sea-ice

251 parameters were disregarded, using integrated pigment concentrations as well as

252 average values of ice temperature, bulk salinity and derived measures. To investi-

253 gate whether inter-regional differences in terms of integrated meiofauna communi-

254 ties were also reflected by environmental variables, two-tailed Mann-Whitney U-tests

255 were applied to each environmental variable. Subsets of environmental variables best

256 matching the grouping of stations based on meiofauna data were identified using the

257 BIO-ENV procedure (Clarke and Warwick, 2001), which was applied to similarity

258 matrices from analysis of both integrated meiofauna communities and vertical meio-

259 fauna profiles. The environmental variables entered in the procedure were ice and

260 snow thickness, bulk salinity, ice temperature, brine volume and chl a concentration;

261 the variables excluded were considered to be either of minor relevance to integrated

262 meiofauna abundance or highly correlated with the above-mentioned variables. In

263 a second approach, vertical profiles of environmental sea-ice parameters were anal-

264 ysed: average values were calculated for theoretical core sections as described for the

265 meiofauna analyses. Dissimilarities of stations in terms of profiles of different sub-

266 sets of environmental sea-ice variables were calculated using the above-mentioned

267 second-stage routine. The sub-sets analysed included (i) the full set, (ii) all abiotic

268 variables, (iii) all biotic variables, (iv-x) all possible sub-sets of the set sea-ice temper-

269 ature, relative brine volume and chl a concentration. Correlations with the pattern

270 based on vertical meiofauna profiles were calculated using the RELATE procedure

271 (Clarke and Warwick, 2001).

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272   All multivariate analyses were based on Bray-Curtis similarities or dissimilarities

273   (Bray and Curtis, 1957) calculated from fourth-root transformed abundance data, or

274   on euclidean distances of z-standardised environmental variables. The significance

275   level for all statistical tests was 5 %. Details of the statistical procedures are given

276   in Suppl. 3.

277   **3. Results**

278   All data sets from this study are available online, doi:10.1594/PANGAEA.734773.

279   *3.1. Environmental parameters*

280   Level-ice thickness, snow thickness and freeboard on the sampling stations were

281   significantly higher in the western Weddell Sea than in the southern Indian Ocean

282   (Table 1). Negative freeboard was measured at stations WS–1, IO–3 and IO–10.

283   Air and snow temperatures during sampling were significantly higher in the western

284   Weddell Sea than in the southern Indian Ocean (Table 1).

285   Sea-ice temperature and, consequently, brine salinity (averaged over the full cores)

286   did not differ significantly between the study regions (Table 1). Also the vertical

287   profiles were generally similar in both regions, with temperatures usually increasing

288   from the ice surface to the bottom-ice layer, where temperatures were at the freezing

289   point of sea water. At a few stations in the western Weddell Sea there was also a slight

290   increase in temperature near the ice surface, and at two stations the temperature was

291   almost constant throughout the ice column. Bulk salinity and brine volume of the

292   full cores were significantly lower in the western Weddell Sea than in the southern

293   Indian Ocean (Table 1). Also the shapes of the bulk salinity profiles were different.

294   In the southern Indian Ocean, all bulk salinity profiles were generally C-shaped; at

295   most stations, the profiles were very smooth. In the western Weddell Sea, C-shaped

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Table 1: Medians and ranges of environmental parameters measured at the sampling stations in the western Weddell Sea and southern Indian Ocean. In case of sea-ice parameters, medians and ranges of point values calculated for each station (i. e. values averaged or integrated over full cores) as well as ranges of bulk values measured for each ice-core section are given—note the different units for integrated and bulk values in case of pigment concentrations ($mg\,m^{-2}$ and $\mu g\,L^{-1}$, respectively). Overall medians of point values are given where no significant difference was detected; significant differences in point values are marked with $\star$ (U-test, significance level 5 %). n denotes the number of stations where the respective parameter was measured. The full data sets, including vertical profiles, are available online, doi:10.1594/PANGAEA.734773.

| | Mediands and ranges of point values for stations (i. e. average or integrated values for full ice cores) | | | | | | Ranges of bulk values for ice-core sections | |
| | Weddell Sea | | | Southern Indian Ocean | | Overall | Weddell Sea | Southern Indian Ocean |
Parameter	Med	Range	n	Med	Range	n	Med	Range	Range
Level-ice thickness [cm]	125	63–244	22	81	37–210	15	$\star$	—	—
Snow thickness [cm]	17	0–105	22	5	0–9	15	$\star$	—	—
Freeboard [cm]	+8	-2 to +23	22	3	-4 to +8	15	$\star$	—	—
Air temperature [$^{\circ}$C]	-6.0	-16.0 to +6.1	22	-11.1	-20.1 to -5.6	15	$\star$	—	—
Snow temperature [$^{\circ}$C]	-6.5	-10.9 to -0.3	22	-9.6	-15.7 to -5.5	11	$\star$	—	—
Sea-ice temperature [$^{\circ}$C]	-4.5	-6.3 to -2.8	22	-4.5	-6.9 to -2.8	13	-4.5	-10.5 to -1.8	-11.9 to -1.7
Brine salinity	76.0	49.0–102.3	22	75.6	48.8–111.2	13	75.6	32.2–162.5	30.5–180.3
Bulk salinity	5.1	1.1–6.5	22	7.2	5.0–10.0	15	$\star$	0.0–14.0	2.1–18.7
Relative brine volume [%]	6.3	2.0–9.9	22	9.8	6.6–13.7	13	$\star$	0.0–33.6	2.2–29.5
Chl a [$mg\,m^{-2}$] or [$\mu g\,L^{-1}$]	8.0	1.2–70.8	19	1.2	0.1–13.6	15	$\star$	0.0–1339.8	0.0–74.8
Phaeo [$mg\,m^{-2}$] or [$\mu g\,L^{-1}$]	1.5	0.1–11.3	19	0.5	0.0–3.9	15	$\star$	0.0–192.5	0.0–36.8
Phaeo / chl a or [$\mu g\,L^{-1}$]	0.2	0.1–0.5	19	0.3	0.2–0.5	15	0.3	0.0–1.0	0.0–0.6

296 profiles prevailed, but at most stations the profiles were irregular and the C-shape
297 less distinct. Stations WS–4, WS–7, WS–11 and WS–21 exhibited I-shaped (linear)
298 bulk salinity profiles.

299 Integrated concentrations of chl a and phaeo in the ice were significantly higher
300 in the western Weddell Sea than in the southern Indian Ocean (Table 1). The
301 ratio phaeo / chl a, in contrast, did not differ significantly between the two regions
302 (Table 1).

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303   *3.2. Meiofauna communities*

304   *Taxonomic composition*

305   In total 20 sympagic meiofauna taxa were recorded in this study, and different

306   types of eggs were distinguished (Table 2). The eggs and several meiofauna taxa

307   occurred frequently in the ice in both western Weddell Sea and southern Indian

308   Ocean (Table 2), including acoel platyhelminthes and an unidentified ctenophore

309   (see Suppl. 4.4 for photographs and further information). Others occurred mainly or

310   exclusively in one of the two regions (Table 2): tintinnid ciliates, the foraminiferan

311   *Turborotalita quinqueloba*, radiolarians and the harpacticoid copepod *Microsetella*

312   *rosea* in the southern Indian Ocean; rhabditophor platyhelminthes (see Suppl. 4.1–

313   4.3 for photographs and further information), the nudibranch *Tergipes antarcticus*,

314   several harpacticoid copepod species, the calanoid copepod *Stephos longipes* and

315   cyclopoid copepods in the western Weddell Sea.

316   *Integrated abundance and carbon biomass, metazoan diversity*

317   For most meiofauna taxa and eggs, individuals from the western Weddell Sea were

318   generally bigger than individuals from the southern Indian Ocean, resulting in higher

319   individual carbon contents for animals from the western Weddell Sea (Suppl. 2.2).

320   Abundance of sympagic meiofauna in total did not differ significantly between

321   the western Weddell Sea and the southern Indian Ocean (Mann-Whitney U-test,

322   significance level 5 %), whereas total meiofauna carbon biomass was significantly

323   higher in the western Weddell Sea than in the southern Indian Ocean (Table 3).

324   Protozoans usually dominated the meiofauna communities in the southern Indian

325   Ocean, while in the western Weddell Sea metazoans were usually dominant in terms

326   of both abundance and biomass (Table 4).

327   Abundance and carbon biomass of protozoans in total, as well as of ciliates,

15

Table 2: Qualitative information on taxonomic composition of sympagic meiofauna and eggs in the western Weddell Sea and southern Indian Ocean (+++ abundant, ++ not abundant but frequent, + occasional occurrence, — not recorded) and on vertical distribution (x occurrence in internal or surface layers, o occurrence only in bottom layers, i.e. lowermost 20 cm).

Taxon	Occurrence Weddell Sea	Occurrence Southern Indian Ocean	Vertical distribution
Ciliata	+++	+++	
Tintinnida indet.	+	+++	x
Other Ciliata	+++	+++	x
Foraminifera	++	+++	
Neogloboquadrina pachyderma	++	+++	x
Turborotalita quinqueloba	—	+	x
Radiolaria	+	++	x
Ctenophora	++	++	x
Plathelminthes	+++	++	
Acoela indet.	+++	++	x
Rhabditophora indet.	++	—	o
Nudibranchia	++	+	
Tergipes antarcticus ad.	+[a]	—	
T. antarcticus juv.	++	+	x
Harpacticoida	+++	++	
Drescheriella glacialis, *D. racovitzai*	+++	—	x
Drescheriella spp. nauplii	+++		x
Ectinosoma sp.	+	—	o
Idomene antarctica	++	—	x
Diarthrodes cf. *lilacinus*	+	—	o
Nitokra gracilimana	+++	+	x
Microsetella rosea	—	+	x
Harpacticus sp.	+++	+	x
"Harpacticoida species 1"	+	—	x
Calanoida	++	+	
Paralabidocera antarctica	+	+	o
P. antarctica nauplii		+	o
Stephos longipes	++	—	x
S. longipes nauplii		+	o
Cyclopoida	+	—	x
Eggs	+++	+++	
Eggs and veliger larvae of *T. antarcticus*	+++	+++	x
Eggs of Acoela	+++	+++	x
Other eggs	+++	+++	x

[a]in non-quantitative large-volume samples only

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328 foraminiferans and radiolarians separately did not differ significantly between the
329 two regions (Fig. 2, Table 3). In the western Weddell Sea, ciliates dominated the
330 protozoan community in terms of abundance and usually also in terms of biomass, fol-
331 lowed by foraminiferans (Fig. 3, Table 4). In the southern Indian Ocean, abundance
332 contributions from ciliates and foraminiferans were almost equal, and foraminiferans
333 were usually dominant in terms of biomass. Radiolarian contribution to total proto-
334 zoan abundance was always low, but they could contribute substantially to protozoan
335 biomass.

336 Metazoan abundance and carbon biomass were significantly higher in the western
337 Weddell Sea than in the southern Indian Ocean (Table 3). This trend was found
338 for platyhelminthes as well as for copepodids (Fig. 2, Table 3). Abundance and
339 biomass of copepod nauplii did not differ significantly between the two regions (Fig. 2,
340 Table 3). Ctenophores appeared to be more abundant in the western Weddell Sea
341 than in the southern Indian Ocean (up to four individuals in three out of six full
342 cores and 11 out of 23 bottom-ice sections in the western Weddell Sea; up to three
343 individuals in two out of 12 full cores in the southern Indian Ocean). Juveniles of
344 *Tergipes antarcticus* were found in very low numbers in both regions (one individual
345 in one full core and two bottom-ice sections from the western Weddell Sea and in one
346 full core from the southern Indian Ocean). In both regions, metazoans were always
347 dominated by either copepods or platyhelminthes, in terms of both abundance and
348 biomass (Fig. 3, Table 4). In the western Weddell Sea, platyhelminthes usually
349 made lower contributions to abundance than copepods, but higher contributions to
350 biomass. Contributions of both *Tergipes antarcticus* and ctenophores to metazoan
351 abundance and biomass were always low.

352 The total abundance of eggs (including nudibranch veliger larvae) did not dif-
353 fer significantly between the two regions, whereas carbon biomass was significantly

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Table 3: Medians and ranges of integrated abundance and carbon biomass of sympagic meiofauna and eggs from six full cores from the western Weddell Sea and ten full cores from the southern Indian Ocean. Overall medians are given where no significant difference was detected; significant differences are marked with $\star$ (U-test, significance level 5 %). The full data sets, including vertical profiles, are available online, doi:10.1594/PANGAEA.734773.

| | Abundance in $10^3\,\mathrm{m}^{-2}$ | | | | | Carbon biomass in $\mathrm{mg\,m}^{-2}$ | | | | |
| Taxon | Weddell Sea | | Southern Indian Ocean | | Overall | Weddell Sea | | Southern Indian Ocean | | Overall |
	Med	Range	Med	Range	Med	Med	Range	Med	Range	Med
Meiofauna total	62.6	12.7–178.6	15.0	0.6–163.4	31.0	10.90	3.99–89.70	1.89	0.02–28.28	$\star$
Protozoa total	20.7	2.5–85.0	14.0	0.2–139.2	14.0	3.91	2.76–8.47	1.85	0.00–28.23	3.53
Ciliata	20.0	1.4–84.9	6.1	0.2–63.7	9.2	2.38	0.13–6.27	0.18	0.00–4.49	0.48
Foraminifera	0.7	0.2–3.1	8.8	0.0–117.8	2.0	1.14	0.02–2.62	1.06	0.00–26.83	1.14
Radiolaria	0.2	0.0–0.9	0.3	0.0–9.9	0.2	0.01	0.00–2.20	0.04	0.00–2.17	0.01
Metazoa total	31.1	10.2–146.0	1.0	0.0–53.4	$\star$	6.53	1.23–81.23	0.06	0.00–1.10	$\star$
Copepoda CI–CVI	8.0	3.0–16.7	0.0	0.0–0.3	$\star$	3.01	0.32–4.98	0.00	0.00–0.21	$\star$
Copepoda NI–NVI	2.8	0.8–19.3	0.5	0.0–49.6	0.9	0.19	0.03–1.83	0.04	0.00–1.04	0.05
Plathelminthes	10.5	6.3–132.7	0.4	0.0–4.5	$\star$	1.83	0.26–76.22	0.02	0.00–0.21	$\star$
Eggs total	253.1	7.2–7064.3	20.1	6.6–217.7	31.5	35.90	0.50–5089.23	0.63	0.13–9.00	$\star$
Eggs and veliger larvae of *Tergipes antarcticus*	4.9	0.0–17.4	3.1	0.2–32.8	4.5	0.07	0.00–0.52	0.03	0.00–0.44	0.04
Eggs of Acoela	225.3	0.0–7000.5	4.2	0.9–148.5	6.7	32.38	0.00–5083.09	0.18	0.03–6.67	0.27
Other eggs	13.7	0.3–46.4	9.6	3.4–36.4	10.6	2.48	0.06–5.62	0.41	0.08–2.48	0.98

354 higher in the western Weddell Sea than in the southern Indian Ocean (Table 3). Nei-
355 ther abundance nor biomass of nudibranch eggs and veligers, acoel eggs or uniden-
356 tified eggs differed significantly between the two regions (Fig. 2, Table 3). In the
357 western Weddell Sea, in particular, eggs were often considerably more abundant than
358 meiofauna, and egg biomass could be more than 200 times higher than meiofauna
359 biomass (Fig. 2, Table 3).

360 Metazoan diversity in the ice was significantly higher in the western Weddell
361 Sea than in the southern Indian Ocean (Mann-Whitney U-test) in terms of several
362 measures (species number S, Margalef's index d, expected species number in a sample
363 of 100 individuals ES_{100} and Shannon-Wiener diversity H'; Table 5). Evenness in
364 distribution of individuals across the species present was not significantly different
365 between the two regions (Pielou's index J'; Table 5).

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Table 4: Contributions by several meiofauna taxa to integrated abundance and carbon biomass of total protozoans, metazoans or meiofauna, given in %. The full data sets are available online, doi:10.1594/PANGAEA.734773.

Contribution in terms of	Abundance				Carbon biomass			
	Weddell Sea		Southern Indian Ocean		Weddell Sea		Southern Indian Ocean	
Contribution by	Med	Range	Med	Range	Med	Range	Med	Range
Protozoa to meiofauna	28	18–71	92	32–100	40	9–69	96	3–100
Metazoa to meiofauna	72	29–82	8	0–68	60	31–91	4	0–97
Ciliata to Protozoa	95	52–100	50	1–100	63	5–100	25	0–100
Ciliata to meiofauna	26	11–71	39	1–73	9	3–47	12	0–63
Foraminifera to Protozoa	4	0–44	46	0–99	30	0–95	62	0–100
Foraminifera to meiofauna	2	0–9	43	0–94	10	0–66	59	0–98
Radiolaria to Protozoa	0	0–6	1	0–10	0	0–45	1	0–42
Radiolaria to meiofauna	0	0–1	1	0–9	0	0–18	0	0–41
Copepoda to Metazoa	52	9–73	50	15–93	46	6–94	65	35–95
Copepoda to meiofauna	23	7–58	3	0–34	24	6–49	2	0–63
Nauplii to Copepoda	23	8–84	100	77–100	11	1–40	100	30–100
Plathelminthes to Metazoa	48	25–91	50	6–85	53	6–94	35	5–65
Plathelminthes to meiofauna	33	10–74	3	0–34	22	3–85	1	0–34
Tergipes antarcticus to Metazoa	0	0–1	0	0–0	0	0–3	0	0–0
Tergipes antarcticus to meiofauna	0	0–1	0	0–0	0	0–3	0	0–0
Ctenophora to Metazoa	1	0–2	0	0–1	0	0–4	0	0–0
Ctenophora to meiofauna	0	0–1	0	0–0	0	0–2	0	0–0

Figure 2: Boxplots of integrated abundance (top) and carbon biomass (bottom) of sympagic protozoan meiofauna, metazoan meiofauna and eggs in the two study regions, showing medians, quartiles and ranges from six stations in the western Weddell Sea and ten stations in the southern Indian Ocean. Outliers (with distance from quartiles being more than 1.5 times the interquartile distance) are not displayed. The metazoan taxa with very low abundance and biomass (ctenophores and juvenile *Tergipes antarcticus*) are not included. Significant differences are marked with ⋆. Note different scaling of abundance and biomass axes.

Figure 3: Integrated abundance (top) and carbon biomass (bottom) of sympagic protozoan meiofauna, metazoan meiofauna and eggs at each station, with contributions by the major taxa. Note different scaling of abundance and biomass axes.

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Table 5: Medians and ranges of metazoan diversity and evenness measures calculated from abundances in six full cores from the western Weddell Sea and ten full cores from the southern Indian Ocean. Overall medians are given where no significant difference was detected; significant differences are marked with $\star$ (U-test, significance level 5 %).

| Diversity measure | Metazoan diversity and evenness | | | | |
| | Weddell Sea | | Southern Indian Ocean | | Overall |
	Med	Range	Med	Range	Med
Species number S	8.5	3.0–10.0	1.0	0.0–3.0	$\star$
Margalef's index d	0.7	0.2–0.9	0.0	0.0–0.2	$\star$
Expected species number ES_{100}	6.5	2.8–8.7	1.0	0.0–2.9	$\star$
Shannon-Wiener diversity H'	1.0	0.4–1.7	0.0	0.0–0.6	$\star$
Pielou's index J'	0.6	0.2–0.7	0.6	0.3–0.8	0.6

366   The two study regions further differed significantly in terms of meiofauna com-
367 munity composition including eggs (global one-way ANOSIM). This pattern was
368 also clearly seen in cluster analyses (Fig. 4 a), revealing similarities of only 44 %
369 between the regions, and illustrated by MDS (Fig. 4 b). The best discriminating
370 taxa (SIMPER; average contribution to between-group dissimilarity > 5 % and av-
371 erage divided by standard deviation > 2) were *Drescheriella* spp. and unidentified
372 harpacticoid copepods, both of which were abundant in the western Weddell Sea but
373 absent or extremely rare in the southern Indian Ocean, as well as tintinnid ciliates,
374 which showed an opposite pattern. Acoel platyhelminthes and unidentified ciliates
375 were the most typifying for the western Weddell Sea, while unidentified eggs, eggs
376 of acoels, eggs and veliger larvae of *Tergipes antarcticus* and tintinnid ciliates typ-
377 ified the community in the southern Indian Ocean (SIMPER; average contribution
378 to within-group similarity > 10 % and average divided by standard deviation > 2).
379   Clustering and MDS (Fig. 4 a, b) further revealed that the meiofauna commu-
380 nity at stations IO–1, IO–2, IO–10 and IO–13 (cluster α) differed from the six
381 other stations (cluster β) in the southern Indian Ocean (significant differences, SIM-
382 PROF), with similarities of only 59 %. The α stations were generally characterised

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Figure 4: Grouping patterns of stations in terms of integrated abundance (**A**, **B**) and vertical abundance profiles (**C**, **D**) of sympagic meiofauna, including eggs. Cluster dendograms (**A**, **C**): hierarchical agglomerative; bold lines in A indicating significant clusters (SIMPROF, significance level 5 %). MDS plots (**B**, **D**): non-metric, with similarity levels from clustering (lines). See Suppl. 3 for details on statistical procedures.

383   by intermediate total abundance and were usually dominated by protozoans (mainly
384   foraminiferans), with high contributions from eggs. The β stations, in contrast, were
385   characterised by low total abundance, with eggs being dominant and protozoans
386   (mainly ciliates) also contributing considerably to total abundance. The discriminat-
387   ing taxa between the two clusters (SIMPER; average contribution to between-group
388   dissimilarity > 10 % and average divided by standard deviation > 2) were tintinnids
389   and radiolarians, both of which were abundant at the α stations, but absent or rare
390   at the β stations. Within the western Weddell Sea, two groups could be discerned:
391   station WS–4 (cluster γ), characterised by high total abundance, pronounced dom-
392   inance of eggs, low contribution from metazoans and very low contribution from
393   protozoans as well as low metazoan diversity; and stations WS–6, WS–9, WS–12,
394   WS–11 and WS–15 (cluster δ) with intermediate or high total abundance, higher
395   contributions from proto- and metazoans and comparatively high metazoan diver-
396   sity. The groups within the regions did not seem to be related to geographic position
397   (cf. Fig.1).
398   Several subsets of sea-ice environmental variables (averaged or integrated over
399   the full cores) matched well with the grouping patterns of stations based on meio-
400   fauna communities, with correlation coefficients for similarity matrices above 0.50
401   (BIO-ENV). Amongst these best-matching subsets, none contained the sea-ice tem-
402   perature. The best-matching subset of three variables, with a correlation coefficient

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403 of 0.57, comprised snow thickness, ice thickness and bulk salinity.

404 *Vertical distribution*

405   Meiofauna in both regions was not restricted to the bottom-ice layer. Internal and

406 surface communities were found at many stations, at times exceeding the abundance

407 in bottom layers at the respective station (Fig. 5, Suppl. 5). Occurrence in internal

408 or surface layers was most obvious for protozoans, but was also observed for several

409 metazoan taxa, while others occured exclusively in bottom layers (Table 2, Fig. 5,

410 Suppl. 5).

411   Maximum bulk abundance of protozoans was found in a surface layer (uppermost

412 20 cm) in the western Weddell Sea and in bottom ice (lowermost 20 cm) in the south-

413 ern Indian Ocean. Maximum metazoan and egg abundance was found in bottom ice

414 in both regions.

415   Vertical carbon biomass profiles generally followed abundance profiles; only at

416 some stations, biomass profiles were distinctly different from abundance profiles,

417 mainly due to the relatively low biomass contributions of ciliates and of eggs and

418 veliger larvae of *Tergipes antarcticus*. Highest bulk biomass of protozoans, metazoans

419 and eggs was recorded in bottom layers in both the western Weddell Sea and the

420 southern Indian Ocean.

421   Vertical meiofauna abundance profiles did not differ significantly between the two

422 regions (ANOSIM2). Second-stage cluster analyses and MDS revealed five clusters,

423 reflecting different types of vertical profiles (Fig. 4 c, d). The grouping patterns were

424 not related to geographic positions of the stations (cf. Fig. 1). The environmental

425 variables assessed during this study matched the grouping of vertical meiofauna

426 profiles very poorly (BIO-ENV, RELATE), with exception of the subset of vertical

427 pigment profiles (RELATE).

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Figure 5: Examples of vertical bulk abundance profiles of sympagic protozoan meiofauna, metazoan meiofauna and eggs in sea ice in the western Weddell Sea (left) and southern Indian Ocean (right). Note different scaling of abundance axes. Vertical bulk abundance profiles of all stations are shown in Suppl. 5.

4. Discussion

We have found significant differences in sympagic meiofauna communities between the perennially sea-ice covered western Weddell Sea and the seasonally sea-ice covered southern Indian Ocean, which we attribute mainly to the presence of older ice in the western Weddell Sea, thus supporting our hypothesis. Our study has further revealed that in both regions sympagic meiofauna diversity, abundance and carbon biomass were higher than expected from literature (Gradinger, 1999a; Schnack-Schiel et al., 2001). The study indicates the significance of regions with perennial ice cover and old ice for the development of abundant and diverse sympagic communities and highlights the potential importance of meiofauna in the sympagic ecosystem.

4.1. Significance of old ice and perennial ice cover to sympagic metazoan meiofauna

Significant differences between sympagic meiofauna communities in the western Weddell Sea and the southern Indian Ocean were particularly obvious in metazoans, which were more diverse and abundant and had accordingly higher carbon biomass in the western Weddell Sea. We attribute these differences to the different sea-ice regimes of the two regions, the western Weddell Sea being characterised by perennial ice cover (Brierley and Thomas, 2002) and older ice, the southern Indian Ocean by seasonal ice cover (Worby et al., 1998) and younger ice.

Generally, differences in abundance and biomass of sympagic meiofauna can be seasonal (Schünemann and Werner, 2005) or spacial (Swadling et al., 1997). In this

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449 study, samples from both regions were taken during the same months of two consec-
450 utive years and at quite similar latitudes. Although the lower air and snow temper-
451 atures in the southern Indian Ocean might indicate more hibernal conditions during
452 sampling than in the western Weddell Sea, sea-ice temperature profiles were gener-
453 ally similar and average temperatures of full cores did not differ significantly between
454 the two regions. We thus assume that sympagic organisms were not exposed to more
455 hibernal conditions in the southern Indian Ocean than in the western Weddell Sea,
456 and consequently that the observed differences were spacial rather than seasonal.

457   The significantly higher ice and snow thickness and lower bulk salinity in the
458 western Weddell Sea compared to the southern Indian Ocean, as well as the irreg-
459 ularly C-shaped and I-shaped bulk salinity profiles in the former region compared
460 to the distinctly C-shaped profiles in the latter, indicate that the ice sampled in the
461 western Weddell Sea was generally older (Weeks, 2001; Nicolaus et al., 2009). Also
462 the significantly higher brine volumes in the southern Indian Ocean are related to the
463 younger age of the ice, since brine volume is positively correlated with bulk salinity (if
464 temperatures are constant) (Frankenstein and Garner, 1967). Hence, although most
465 of the ice sampled for meiofauna analyses in the western Weddell Sea was first-year
466 ice, it was older than the ice sampled in the southern Indian Ocean—a difference that
467 can be attributed to the fact that most of the pack ice in the western Weddell Sea
468 is formed in polynyas much further to the south (Haas et al., 2009; Willmes et al.,
469 in press), where the onset of ice formation is earlier in autumn.

470   Space limitation due to low relative brine volumes did obviously not strongly
471 affect meiofauna, since the bigger metazoan meiofauna was more abundant in the
472 western Weddell Sea in spite of smaller brine volume fractions. Freeboard, which
473 can affect the development of surface communities (Horner et al., 1992), is also con-
474 sidered to be of minor significance for integrated meiofauna communities in winter.

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475 Given the good match between integrated meiofauna communities and the environ-
476 mental parameters indicating sea-ice age, we suggest that the different age of the
477 ice sampled is one of the main reasons for the observed differences in meiofauna
478 communities. Communities in older ice have had more time to colonise the habitat
479 and to further develop than communities in younger ice. The observed differences
480 might partly be features of a succession in first-year ice, with a shift from communi-
481 ties characterised by protozoans, acoels and harpacticoids to communities with lower
482 protozoan contributions a more diverse metazoan fauna. To further investigate this
483 issue, future studies should include time series in growing first-year ice as well as
484 comparisons of first- and multi-year ice sampled within one region.

485 Besides the age of the actual ice floes, we suggest that general differences in the
486 sea-ice regimes give additional explanation to the observed differences in meiofauna
487 communities: perennial ice cover and high proportions of multi-year ice in the Wed-
488 dell Sea (more than 40 % of the total sea-ice cover, S. Schwegmann, pers. comm.),
489 particularly in its western regions (Brierley and Thomas, 2002), standing in con-
490 trast to seasonal ice cover and almost exclusively young and first-year ice in the
491 southern Indian Ocean (Worby et al., 1998), as observed also during the present
492 study (Haas et al., 2009; Worby et al., 2010). In seasonally ice-covered regions, the
493 ice needs to be newly colonised each winter when formed and is accessible only to
494 species which can, at least during part of their life cycle, survive longer periods in
495 the water column. In perennially ice-covered regions, in contrast, the large amounts
496 of multi-year ice provide a stable habitat particularly to species which spend all
497 phases of their life cycle in the ice and cannot survive longer periods in the water.
498 We consider it probable that this multi-year ice serves as a refuge during summer
499 from which newly forming sea ice can be colonised in winter, as suggested for sym-
500 pagic copepods by Schnack-Schiel et al. (1998). To further address this issue, future

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501   studies should compare areas with different amounts of multi-year ice (e. g. west-

502   ern and eastern Weddell Sea) and experimentally investigate swimming ability and

503   colonisation mechanisms of sympagic meiofauna.

504   Generalising our results, we suggest that at least sympagic metazoan meiofauna

505   is more diverse and abundant in perennially ice-covered regions (even in first-year

506   ice). Rhabditophores as well as several copepod species presumably rely on perennial

507   ice cover—particularly some harpacticoids, which were amongst the discriminating

508   taxa. Furthermore, platyhelminthes, copepods and ctenophores seem to reach higher

509   abundance in older sea ice or perennially ice-covered regions. Sympagic protozoans,

510   in contrast, appear to be less influenced by the age of the ice and sea-ice regime,

511   at least in terms of total abundance; however, species-level analyses of ciliates may

512   reveal differences also in protozoan communities.

513   *4.2. High meiofauna diversity, abundance and biomass in winter*

514   Our study has revealed that Antarctic sympagic meiofauna communities are more

515   diverse than previously reported, reflected by the high number of different taxa found

516   in both regions. Our study is the first to report sympagic occurrence of radiolari-

517   ans, rhabditophor platyhelminthes and the harpacticoid copepod *Microsetella rosea*.

518   Rhabditophors seem to be an important component of the sympagic meiofauna com-

519   munity in perennially ice-covered regions: in spite of low abundance, they can, due to

520   their high individual carbon content, reach similarly high biomass to the acoels (this

521   study, data not shown). Judging from morphology and anatomy, the rhabditophors

522   were probably rhabdocoels (see Suppl. 4.3 for details). Several other taxa we found in

523   sea ice have rarely been reported from this habitat before. The frequent occurrence

524   of ctenophores and of the nudibranch *Tergipes antarcticus* in sea ice is particularly

525   interesting regarding the functioning of the sympagic ecosystem: both ctenophores

526 (Ju et al., 2004; Scolardi et al., 2006) and nudibranchs (Kiko et al., 2008a) are prob-

527 ably carnivores and might thus, in spite of low abundance and biomass, play a partic-

528 ularly important role in the sympagic food web. Sympagic ctenophores can obviously

529 colonise different porous ice habitats in winter, such as bottom ice and slush layers.

530 Judging from general morphological features, we assume that the ctenophores we

531 found were not of the species *Callianira antarctica* reported from summer sea ice by

532 Kiko et al. (2008b), but rather *Euplokamis* sp. (see Suppl. 4.4 for details).

533   Abundance and carbon biomass of Antarctic sympagic meiofauna in winter have

534 been underestimated so far, since previous studies, based on principally similar meth-

535 ods, reported substantially lower abundance and biomass from a winter expedition to

536 the northern Weddell Sea (Gradinger, 1999a; Schnack-Schiel et al., 2001) than found

537 in our study for both western Weddell Sea and southern Indian Ocean. Meiofauna

538 abundance in our study mostly exceeded abundance reported earlier from the north-

539 ern Weddell Sea in winter (Gradinger, 1999a) (median 14-fold higher in the western

540 Weddell Sea, 3-fold higher in the southern Indian Ocean). The difference was even

541 more distinct for meiofauna biomass (Gradinger, 1999a) (median 27-fold higher in

542 the wester Weddell Sea, 5-fold higher in the southern Indian Ocean). For the west-

543 ern Weddell Sea, these findings can be attributed particularly to the high abundance

544 and biomass of ciliates (medians 11-fold and 119-fold higher, respectively, than in

545 the previous study (Schnack-Schiel et al., 2001)), but also to the high abundance of

546 platyhelminthes (median 3-fold higher) and copepods (median 2-fold higher). For

547 the southern Indian Ocean, the differences to the previous study were particularly

548 due to high ciliate abundance and biomass (medians 4-fold and 9-fold higher, re-

549 spectively), but also due to high foraminiferan biomass (median 2-fold higher). In

550 the western Weddell Sea, we further found contributions of ciliates to total meio-

551 fauna abundance and biomass to be generally higher than previously reported from

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552 winter (2-fold and 4-fold higher contributions, respectively, regarding median abun-
553 dance and biomass), while foraminiferan contributions to meiofauna abundance and
554 biomass were substantially lower compared to the previous study (44-fold lower and
555 4-fold lower, respectively) (Gradinger, 1999a). Metazoan contribution to total meio-
556 fauna abundance was distinctly higher than in the previous study (2-fold higher for
557 total metazoans as well as for platyhelminthes and copepods) (Gradinger, 1999a).
558 In terms of biomass, total metazoan and platyhelminth contributions were slightly
559 higher during the previous expedition (Gradinger, 1999a); this is probably due to the
560 fact that biomass calculations in the previous study were mainly based on carbon
561 content data of Arctic sea-ice meiofauna (Gradinger, 1999a) instead of size measure-
562 ments of the actual individuals studied.

563   There are many possible explanations for the differences between our data and
564 those from the previous studies, including differences in sea-ice conditions between
565 western and northern Weddell Sea (Eicken, 1992; Schnack-Schiel et al., 2008) and
566 inter-annual variability (Eicken, 1992) as well as the generally observed heterogene-
567 ity of sympagic communities (Swadling et al., 1997; Schnack-Schiel et al., 2008). Re-
568 gardless of the reason for differences, our study indicates that the role of Antarctic
569 sympagic meiofauna in the sympagic ecosystem has been underestimated so far.
570 Both contribution of meiofauna to sea-ice particulate organic carbon (POC) and
571 feeding impact of meiofauna are essentially functions of carbon biomass. The high
572 meiofauna biomass we report thus implies an accordingly high POC contribution
573 and feeding impact, questioning previous findings by Gradinger (1999a), according
574 to which sympagic meiofauna does not control accumulation of ice algae.

4.3. Occurrence of meiofauna internal and surface communities in winter

Our study contradicts previous observations that sympagic meiofauna is mainly restricted to the bottom ice in winter (Schnack-Schiel et al., 2001), since we found sympagic meiofauna to frequently occur in internal and surface layers. A restriction to bottom ice was only found for some metazoan taxa and is thus probably related to physiological limitations and life-cycle strategies of specific taxa, as has been proposed in earlier studies from summer (Kiko et al., 2008b; Kiko, 2009; Schnack-Schiel et al., 2008).

Our data suggest that, other than integrated abundance, vertical distribution of sympagic meiofauna is not strongly influenced by the age of the ice or the sea-ice regime, but rather controlled by other factors. Vertical distribution of meiofauna was correlated with vertical pigment profiles, which might either be an indication of trophic relationships, or a consequence of common factors controlling vertical distribution of both ice algae and sympagic meiofauna. However, vertical meiofauna distribution was not correlated with any of the abiotic variables measured, nor was it related to geographic positions. It does not seem to be related to ice textures, either (cf. Meiners et al., 2010). It is therefore still a matter of question which factors control vertical distribution of sympagic organisms.

4.4. Conclusions

Multi-year ice and old first-year ice are probably of central importance for the establishment of diverse and abundant sympagic communities, at least in the case of metazoan meiofauna. If the observed warming in the region of the Antarctic Peninsula (Solomon et al., 2007) results in a loss of multi-year ice in the western Weddell Sea, this may drive sympagic meiofauna communities into a state more similar to that in the southern Indian Ocean. In the Arctic Ocean, a reduction

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600 in sea-ice age has already been observed (Rigor and Wallace, 2004; Maslanik et al.,
601 2007; Nghiem et al., 2007), and the complete loss of multi-year ice has been predicted
602 to occur before the middle of this century (Stroeve et al., 2007; Wang and Overland,
603 2009). We assume that this development will result in a loss in diversity, abundance
604 and biomass of sympagic meiofauna.

605   Diversity, abundance and biomass of Antarctic sympagic meiofauna have been
606 underestimated so far. The high meiofauna diversity implies that interactions within
607 the sympagic community, such as feeding and competition, are probably more com-
608 plex than previously expected and ought to be taken into account in future ecological
609 studies. Due to their high carbon biomass and potentially high contributions to total
610 sea-ice POC, sympagic meiofauna and eggs are a potentially important food source
611 for under-ice organisms such as krill. On the other hand, these may also have to
612 compete with meiofauna for food, particularly since meiofauna ingestion rates are
613 likely to be higher than previously assumed. Our study thus highlights the im-
614 portance of sympagic meiofauna in sympagic and adjacent ecosystems. Hence, if a
615 reduction in sea-ice age and loss of multi-year sea ice due to global warming result
616 in reduced abundance and diversity of sympagic meiofauna, this will probably affect
617 other components of the polar marine ecosystems.

638   **References**

639   **References**

640   Assur, A., 1958. Composition of sea ice and its tensile strength. National Research

641   Council Publications 598, 106–138.

642   Bray, J. R., Curtis, J. T., 1957. An ordination of the upland forest of Southern

643   Wisconsin. Ecological Monographs 27, 225–349.

644   Brierley, A. S., Thomas, D. N., 2002. The ecology of Southern Ocean pack ice.

645   Advances in Marine Biology 43, 171–278.

646   Buffan-Dubau, E., Carman, K. R., 2000. Extraction of benthic microalgal pigments

647   for HPLC analyses. Marine Ecology Progress Series 204, 293–297.

31

648 Clarke, K. R., Warwick, R. M., 2001. Change in marine communities: an approach to
649   statistical analysis and interpretations, 2nd Edition. PRIMER-E Ltd, Plymouth.

650 Comiso, J. C., Nishio, F., 2008. Trends in the sea ice cover using enhanced and
651   compatible AMSR-E, SSM/I, and SMMR data. Journal of Geophysical Research
652   – Oceans 113, C02S07.

653 Cottier, F., Eicken, H., Wadhams, P., 1999. Linkages between salinity and brine
654   channel distribution in young sea ice. Journal of Geophysical Research 104 (C7),
655   15859–15871.

656 Dahms, H.-U., Bergmans, M., Schminke, H. K., 1990. Distribution and adaptations
657   of sea ice inhabiting Harpacticoida (Crustacea, Copepoda) of the Weddell Sea
658   (Antarctica). Marine Ecology 11 (3), 207–226.

659 Eicken, H., 1992. The role of sea ice in structuring Antarctic ecosystems. Polar
660   Biology 12 (1), 3–13.

661 Frankenstein, G., Garner, R., 1967. Equations for determining the brine volume of
662   sea ice from -0.5° to -22.9°C. Journal of Glaciology 6 (48), 943–944.

663 Garrison, D. L., Buck, K. R., 1986. Organism losses during ice melting: a serious
664   bias in sea ice community studies. Polar Biology 6 (4), 237–239.

665 Garrison, D. L., Buck, K. R., 1989. The biota of Antarctic pack ice in the Weddell
666   Sea and Antarctic Peninsula regions. Polar Biology 10 (3), 211–219.

667 Gordon, A. L., 1993. Weddell Sea exploration from ice station. EOS, Transactions,
668   American Geophysical Union 74 (11), 121, 124–126.

32

669 Gow, A. J., Tucker III, W. B., 1990. Sea ice in the polar regions. In: Smith Jr, W. O.
670   (Ed.), Polar oceanography, Part A: Physical science. Academic Press, San Diego,
671   pp. 47–122.

672 Gradinger, R., 1999a. Integrated abundance and biomass of sympagic meiofauna in
673   Arctic and Antarctic pack ice. Polar Biology 22 (3), 169–177.

674 Gradinger, R., 1999b. Vertical fine structure of the biomass and composition of algal
675   communities in Arctic pack ice. Marine Biology 133 (4), 745–754.

676 Gradinger, R., Friedrich, C., Spindler, M., 1999. Abundance, biomass and composi-
677   tion of the sea ice biota of the Greenland Sea pack ice. Deep Sea Research Part II:
678   Topical Studies in Oceanography 46 (6-7), 1457–1472.

679 Gradinger, R. R., Meiners, K., Plumley, G., Zhang, Q., Bluhm, B. A., 2005. Abun-
680   dance and composition of the sea-ice meiofauna in off-shore pack ice of the Beaufort
681   Gyre in summer 2002 and 2003. Polar Biology 28 (3), 171–181.

682 Guglielmo, L., Zagami, L., Saggiomo, V., Catalano, G., Granata, A., 2007. Copepods
683   in spring annual sea ice at Terra Nova Bay (Ross Sea, Antarctica). Polar Biology
684   30 (6), 747–758.

685 Haas, C., Friedrich, A., Li, Z., Nicolaus, M., Pfaffling, A., Toyota, T., 2009. Regional
686   variability of sea ice properties and thickness in the northwestern Weddell Sea
687   obtained by in-situ and satellite measurements. In: Lemke, P. (Ed.), The expedi-
688   tion of the research vessel "Polarstern" to the Antarctic in 2006 (ANT-XXIII/7).
689   Vol. 586 of Berichte zur Polar- und Meeresforschung. Alfred-Wegener-Institut für
690   Polar- und Meeresforschung, Bremerhaven, pp. 36–74.

691 Haas, C., Nicolaus, M., Willmes, S., Worby, A., Flinspach, D., 2008. Sea ice and
692   snow thickness and physical properties of an ice floe in the western Weddell Sea
693   and their changes during spring warming. Deep Sea Research Part II: Topical
694   Studies in Oceanography 55, 963–974.

695 Horner, R., Ackley, S. F., Dieckmann, G. S., Gulliksen, B., Hoshiai, T., Legendre,
696   L., Melnikov, I. A., Reeburgh, W. S., Spindler, M., Sullivan, C. W., 1992. Ecology
697   of sea ice biota. 1. Habitat, terminology, and methodology. Polar Biology 12 (3-4),
698   417–427.

699 Janssen, H. H., Gradinger, R., 1999. Turbellaria (Archoophora: Acoela) from Antarc-
700   tic sea ice endofauna: examination of their micromorphology. Polar Biology 21 (6),
701   410–416.

702 Ju, S.-J., Scolardi, K., Daly, K. L., Harvey, H. R., 2004. Understanding the trophic
703   role of the Antarctic ctenophore, *Callianira antarctica*, using lipid biomarkers.
704   Polar Biology 27 (12), 782–792.

705 Kiko, R., 2009. Acquisition of freeze protection in a sea-ice crustacean through hor-
706   izontal gene transfer? Polar Biology doi:10.1007/s00300-009-0732-0.

707 Kiko, R., Kramer, M., Spindler, M., Wägele, H., 2008a. *Tergipes antarcticus* (Gas-
708   tropoda, Nudibranchia): distribution, life cycle, morphology, anatomy and adap-
709   tation of the first mollusc known to live in Antarctic sea ice. Polar Biology 31,
710   1383–1395.

711 Kiko, R., Michels, J., Mizdalski, E., Schnack-Schiel, S. B., Werner, I., 2008b. Living
712   conditions, abundance and composition of the metazoan fauna in surface and sub-

713   ice layers in pack ice of the western Weddell Sea during late spring. Deep Sea
714   Research Part II: Topical Studies in Oceanography 55, 1000–1014.

715   Maslanik, J. A., Fowler, C., Stroeve, J., Drobot, S., Zwally, J., Yi, D., Emery, W.,
716   2007. A younger, thinner Arctic ice cover: increased potential for rapid, extensive
717   sea-ice loss. Geophysical Research Letters 34, L24501.

718   Massom, R. A., Eicken, H., Haas, C., Jeffries, M. O., Drinkwater, M. R., Sturm,
719   M., Worby, A. P., Wu, X., Lyle, V. I., Ushio, S., Morris, K., Reid, P. A., Warren,
720   S. G., Allison, I., 2001. Snow on Antarctic sea ice. Reviews of Geophysics 39 (3),
721   413–445.

722   McMinn, A., Ryan, K., Ralph, P., Pankowski, A., 2007. Spring sea ice photosynthesis,
723   primary productivity and biomass distribution in eastern Antarctica, 2002–2004.
724   Marine Biology 151 (3), 985–995.

725   Meiners, K. M., Norman, L., Granskog, M. A., Krell, A., Heil, P., Thomas, D. N.,
726   2010. Physico-ecobiogeochemistry of East Antarctic pack ice during the winter-
727   spring transition. Deep Sea Research Part II: Topical Studies in Oceanography
728   this volume.

729   Meiners, K. M., Papadimitriou, S., Thomas, D. N., Norman, L., Dieckmann, G. S.,
730   2009. Biogeochemical conditions and ice algal photosynthetic parameters in Wed-
731   dell Sea ice during early spring. Polar Biology 32 (7), 1055–1065.

732   Nghiem, S. V., Rigor, I. G., Perovich, D. K., Clemente-Colón, P., Weatherly, J. W.,
733   Neumann, G., 2007. Rapid reduction of Arctic perennial sea ice. Geophysical Re-
734   search Letters 34, L19504.

735 Nicolaus, M., Haas, C., Willmes, S., 2009. Evolution of first- and second-year snow
736   properties on sea ice in the Weddell Sea during spring-summer transition. Journal
737   of Geophysical Research 114, D17109.

738 Nozais, C., Gosselin, M., Michel, C., Tita, G., 2001. Abundance, biomass, compo-
739   sition and grazing impact of the sea-ice meiofauna in the North Water, northern
740   Baffin Bay. Marine Ecology Progress Series 217, 235–250.

741 Rigor, I., Wallace, J. M., 2004. Variations in the age of Arctic sea-ice and summer
742   sea-ice extent. Geophysical Research Letters 31, L09401.

743 Schnack-Schiel, S. B., 2003. The macrobiology of sea ice. In: Thomas, D. N., Dieck-
744   mann, G. S. (Eds.), Sea ice – an introduction to its physics, chemistry, biology
745   and geology. Blackwell Science Ltd, Oxford, pp. 211–239.

746 Schnack-Schiel, S. B., Dieckmann, G. S., Gradinger, R., Melnikov, I. A., Spindler,
747   M., Thomas, D. N., 2001. Meiofauna in sea ice of the Weddell Sea (Antarctica).
748   Polar Biology 24 (10), 724–728.

749 Schnack-Schiel, S. B., Haas, C., Michels, J., Mizdalski, E., Schünemann, H., Steffens,
750   M., Thomas, D. N., 2008. Copepods in sea ice of the western Weddell Sea during
751   austral spring 2004. Deep Sea Research Part II: Topical Studies in Oceanography
752   55 (8-9), 1056–1067.

753 Schnack-Schiel, S. B., Thomas, D., Dahms, H.-U., Haas, C., Mizdalski, E., 1998.
754   Copepods in Antarctic sea ice. Antarctic Research Series 73, 173–182.

755 Schünemann, H., Werner, I., 2005. Seasonal variations in distribution patterns of
756   sympagic meiofauna in Arctic pack ice. Marine Biology 146 (6), 1091–1102.

757 Scolardi, K. M., Daly, K. L., Pakhomov, E. A., Torres, J. J., 2006. Feeding ecology
758   and metabolism of the Antarctic cydippid ctenophore *Callianira antarctica*. Marine
759   Ecology Progress Series 317, 111–126.

760 Solomon, S., Qin, D., Mannin, M., Chen, Z., Marquis, M., Averty, K. B., Tignor, M.,
761   Miller, H. L., 2007. Climate change 2007: the physical science basis. Contribution
762   of working group I to the fourth assessment report of the Intergovernmental Panel
763   on Climate Change. Tech. rep., Cambridge.

764 Spreen, G., Kaleschke, L., Heygster, G., 2008. Sea ice remote sensing using AMSR-E
765   89-GHz channels. Journal of Geophysical Research 113 (C2), C02S03.

766 Stroeve, J., Holland, M. M., Meier, W., Scambos, T., Serreze, M., 2007. Arctic sea
767   ice decline: Faster than forecast. Geophysical Research Letters 34, L09501.

768 Swadling, K. M., 2001. Population structure of two Antarctic ice-associated cope-
769   pods, *Drescheriella glacialis* and *Paralabidocera antarctica*, in winter sea-ice. Ma-
770   rine Biology 139 (3), 597–603.

771 Swadling, K. M., Gibson, J. A. E., Ritz, D. A., Nichols, P. D., 1997. Horizontal
772   patchiness in sympagic organisms of the Antarctic fast ice. Antarctic Science 9 (4),
773   399–406.

774 Wang, M., Overland, J. E., 2009. A sea ice free summer Arctic within 30 years?
775   Geophysical Research Letters 36, L07502.

776 Weeks, W. F., 2001. Growth conditions and the structure and properties of sea ice. In:
777   Leppäranta, M. (Ed.), Physics of ice-covered seas, 2nd Edition. Vol. 1. University
778   of Helsinki Press, Helsinki, pp. 25–104.

779 Weissenberger, J., Dieckmann, G., Gradinger, R., Spindler, M., 1992. Sea ice: a cast
780   technique to examine and analyze brine pockets and channel structure. Limnology
781   and Oceanography 37 (1), 179–183.

782 Willmes, S., Haas, C., Nicolaus, M., Bareiss, J., in press. High radar-backscatter
783   regions on Antarctic sea ice and their relation to sea-ice and snow properties and
784   meteorological conditions. International Journal of Remote Sensing in press.

785 Worby, A., Steer, A., Lieser, J., Galin, N., Yi, D., Allison, I., Heil, P., Massom, R. A.,
786   Zwally, J., 2010. Regional-scale sea ice and snow thickness distributions from in
787   situ and satellite measurements over East Antarctica during the Sea Ice Physics
788   and Ecosystem eXperiment (SIPEX). Deep Sea Research Part II: Topical Studies
789   in Oceanography this volume.

790 Worby, A. P., Massom, R. A., Allison, I., Lytle, V. I., Heil, P., 1998. East Antarc-
791   tic sea ice: a review of its structure, properties and ice drift. In: Jeffries, M.
792   (Ed.), Antarctic sea ice: physical processes, interanctions and variability. Vol. 74
793   of Antarctic Research Series. American Geophysical Union, Washington, DC, pp.
794   41–67.

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A

B ANT-XXIII/7

C SIPEX

Legend:
- O — MF, MB, EF
- □ — MF, EF
- △ — MB, EF
- ☆ — EF

Sea-ice concentration
0% — 100%

Map C (SIPEX) station labels: IO-1, IO-2, IO-3, IO-5, IO-6, IO-7, IO-8, IO-9, IO-10, IO-11, IO-12, IO-13, IO-14, IO-15a&b

Map B (ANT-XXIII/7) station labels: WS-1, WS-2, WS-3, WS-4, WS-5, WS-6, WS-7, WS-8, WS-9, WS-10, WS-11, WS-12, WS-13, WS-14, WS-15, WS-16, WS-17, WS-18, WS-19, WS-20, WS-21, WS-22

Map A labels: Antarctica, Weddell Sea, Indian Ocean, Antarctic Peninsula

A

B

C

D

E

F

B

C

D

E

F

A

B