ARTICLE IN PRESS

Deep-Sea Research II ∎ (∎∎∎∎) ∎∎∎–∎∎∎

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

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

Maike Kramer [a],*, Kerrie M. Swadling [b], Klaus M. Meiners [c,d], Rainer Kiko [e], Annette Scheltz [a], Marcel Nicolaus [f], Iris Werner [a]

[a] *Institute for Polar Ecology (IPÖ), Wischhofstr. 1–3, Geb. 12, 24148 Kiel, Germany*
[b] *Institute of Marine and Antarctic Studies, University of Tasmania, Private Bag 49, Hobart, Tasmania 7001, Australia*
[c] *Australian Antarctic Divison (AAD), Department of the Environment, Water, Heritage and the Arts, 203 Channel Highway, Kingston, Tasmania 7050, Australia*
[d] *Antarctic Climate & Ecosystems Cooperative Research Centre (ACE CRC), Private Bag 80, Hobart, Tasmania 7001, Australia*
[e] *IFM-GEOMAR Leibniz Institute of Marine Sciences, Biological Oceanography, Hohenbergstr. 2, 24105 Kiel, Germany*
[f] *Alfred Wegener Institute for Polar and Marine Research, Bussestr. 24, 27570 Bremerhaven, Germany*

ARTICLE INFO

Article history:
Received 20 October 2010
Accepted 20 October 2010

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

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: $31.1\times10^3\,m^{-2}$ and $6.53\,mg\,m^{-2}$, respectively) than in the southern Indian Ocean (medians: $1.0\times10^3\,m^{-2}$ and $0.06\,mg\,m^{-2}$, 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 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–$178.6\times10^3\,m^{-2}$ and 0.02–$89.70\,mg\,m^{-2}$, respectively), mostly exceeding values reported earlier from the northern 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.

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, 1990), and this results in strong seasonality in sea-ice cover: in winter, up to $19\times10^6\,km^2$ of the Southern Ocean is covered by sea ice, while the ice-covered area in summer can be as low as $2\times10^6\,km^2$ (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 highly dynamic, characterised by a divergent net drift, and it is generally thinner than sea ice in the Weddell Sea (Worby et al., 1998). The Weddell Sea, in contrast, is one of the few Antarctic regions where geographic, oceanographic and meteorological conditions cause convergent sea-ice drift patterns, resulting in a perennial sea-ice cover (Brierley and Thomas, 2002). Ice concentrations in the Weddell Sea are high, large proportions of thick multi-year ice and deformed ice are found (Gordon, 1993; Haas et al., 2008, 2009), and the snow cover is comparatively thick (Massom et al., 2001; Haas et al., 2008; Nicolaus et al., 2009), particularly in the western regions (Willmes et al., in press). We hypothesise that these different sea-ice regimes—seasonal ice cover with young and first-year ice on one hand, perennial ice cover with multi-year ice on the other—host different communities of sympagic (sea-ice associated) organisms.

Sea ice is permeated with a system of brine channels that develops during its formation and growth when salt ions are rejected from the crystal lattice of water molecules; brine thus collects in between the ice crystals (Weissenberger et al., 1992; Cottier et al., 1999). These brine channels are inhabited by viruses, bacteria, fungi, microalgae, protozoans and metazoans, which,

---

* Corresponding author.
E-mail address: mkramer@ipoe.uni-kiel.de (M. Kramer).

0967-0645/$ - see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2010.10.029

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

together with under-ice organisms, constitute the sympagic community (Brierley and Thomas, 2002; Schnack-Schiel, 2003). The metazoans and larger protozoans (>20 μm) living inside the brine channels of sea ice are referred to as sympagic meiofauna (Gradinger, 1999a).

Protozoan meiofauna in Antarctic sea ice comprises mainly foraminiferans and ciliates (Garrison and Buck, 1989; Gradinger, 1999a; Schnack-Schiel et al., 2001), with heliozoans being reported only once (Garrison and Buck, 1989). Metazoan meiofauna comprises mainly harpacticoid and calanoid copepods and acoel platyhelminthes (commonly referred to as “turbellarians”) (Gradinger, 1999a; Schnack-Schiel et al., 2001; Guglielmo et al., 2007). Ctenophores (Dahms et al., 1990; Kiko et al., 2008b) and nudibranchs (Kiko et al., 2008a, b) have been reported in very few studies from the Weddell Sea, and never from the eastern part of the southern Indian Ocean.

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

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

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 R.V. *Polarstern*

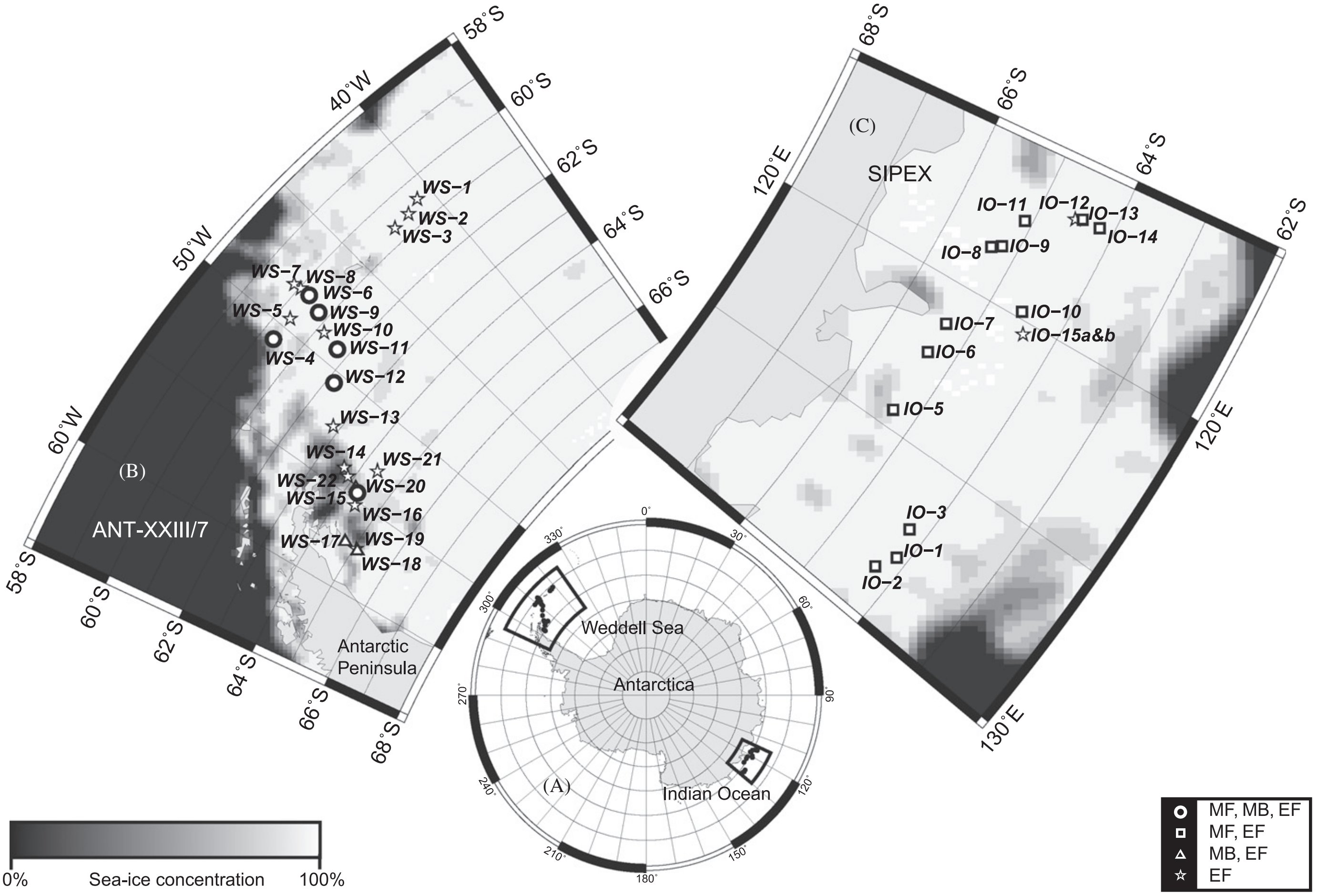

Fig. 1. Stations sampled for community analyses of Antarctic sympagic meiofauna during SIPEX and ANT-XXIII/7. (A) Overview with all stations from both cruises; areas for enlarged station maps (B) and (C) are highlighted. (B) Stations sampled in the western Weddell Sea during ANT-XXIII/7 (August 24 to October 29, 2006) with sea-ice concentration from September 20, 2006. (C) Stations sampled in the southern Indian Ocean during SIPEX (September 5 to October 17, 2007) with sea-ice concentration from September 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 the different scales in (B) and (C).

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

cruise ANT-XXIII/7 (“WWOS”, August 24 to October 29, 2006), while sea ice in the southern Indian Ocean was sampled during the SIPEX expedition on R.S.V. *Aurora Australis* (voyage 1, September 5 to October 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 August 24 to 59−65°S on October 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., 2009; Willmes et al., in press). The sampling stations in the western Weddell Sea (Fig. 1A, Suppl. 1) were pack ice, most of which probably originated from the Larsen and Ronne polynyas (Haas et al., 2009). The samples from stations WS-4, WS-7, WS-11 and WS-21 were multi-year ice covered with second-year snow, whereas the samples from all other stations were first-year ice (Haas et al., 2009; Willmes et al., in press). Snow stratigraphies, sea-ice textures and bulk salinity profiles are shown in Willmes et al. (in press); information about biogeochemical conditions and ice algal photosynthetical parameters are given in Meiners et al. (2009).

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

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

2.2. *Determination of environmental parameters*

At each sampling station, snow and ice thickness as well as freeboard at the coring site were determined as the median of up to 10 measurements. Air temperature close to the snow surface, snow temperature above the snow-ice interface and ice *in situ* temperatures were measured using a handhold thermometer (Testotherm 720, Pt 100 sensor, accuracy 0.2 °C). Ice temperature was measured on full core EF in intervals of 5–10 cm by inserting the temperature probe into small holes drilled with an electric drill. Subsequently, core EF was cut into sections of usually 5–10 cm length directly in the field. The sections were melted in the dark at +4 °C, and bulk salinity was measured with a conductivity meter (WTW micro-processor conductivity meter LF 196, accuracy 0.2). Brine salinity (accuracy better than 4) was calculated from ice temperature according to Assur (1958) and Frankenstein and Garner (1967). Relative brine volume (accuracy better than 4%) was calculated from ice temperature and bulk salinity according to Frankenstein and Garner (1967), the ice temperature for the calculation being adjusted to the values expected for the middle point of each section by calculating the weighted average of the two nearest measurements.

For chl *a* and phaeo measurements, subsamples of at least 250 mL of the melted sections of core EF were filtered on Whatman GF/F filters within 24 h after melting. Pigments were extracted in 90% acetone for 6–12 h at −25 °C (Gradinger, 1999b) after ultrasonic cell disruption during ANT-XXIII/7 or in 100% methanol for 24 h at 0 °C (McMinn et al., 2007) without cell disruption during SIPEX. Pigment concentrations were determined by fluorometric measurements (Turner 10-AU fluorometer, detection limit 0.1 $\mu g\,L^{-1}$) before and after acidification with 0.1 N HCl. The different methodologies, particularly the use of different extraction agents, might have slightly impacted the data, but the effect is assumed to be small (Buffan-Dubau and Carman, 2000).

2.3. *Meiofauna community analyses*

2.3.1. *Sample processing and species identification*

Core MF was cut into sections of usually 5–10 cm length directly after coring. The ice samples for meiofauna analyses (MF and MB) were melted in the dark at +4 °C in a surplus of 0.2 μm filtered seawater (200 ml per 1 cm core length, Gradinger, 1999a). This method considerably reduces osmotic stress for the organisms during melting (Garrison and Buck, 1986); although very delicate organisms, such as aloricate ciliates and acoel platyhelminthes, may be disrupted even under moderate osmotic stress, this method is generally accepted (Horner et al., 1992) and commonly applied in studies on sympagic organisms (Nozais et al., 2001; Schnack-Schiel et al., 2001; Gradinger et al., 2005; Schünemann and Werner, 2005), so that our data are readily comparable with the previous literature. Within 24 h after complete melting of the ice, organisms were enriched over a 20 μm gauze. MB samples were transferred into petri dishes for live counts of metazoan meiofauna performed immediately at 0 °C. MF samples were fixed with borax-buffered

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

formaldehyde (2% in sea water). These samples were later rinsed with water (MilliQ:tap water, v:v = 1:1) and transferred into petri dishes for abundance and biomass analyses.

Meiofauna and eggs were sorted and counted using a stereomicroscope equipped with transmitted and impinging light (Leica WILD MZ 12.5, 20–100 × magnification; Leica MZ 16 F, 20–115 × magnification). For identification and further characterisation of specific taxa and eggs, light and electron microscopes were also used (see Suppl. 4 for details). Protozoans were grouped into ciliates, foraminiferans and radiolarians; other protozoans, such as heterotrophic flagellates, were not considered. Within ciliates, the tintinnids were distinguished; foraminiferans were identified to species level whenever possible. Copepods were identified to species level as far as possible. For the platyhelminthes acoels and rhabditophors were distinguished. Nudibranchs (juveniles and adults) were identified to species level. Eggs and veliger larvae of *Tergipes antarcticus* were identified using the description given by Kiko et al. (2008a); eggs and veligers were assessed together, since late egg stages and early veliger stages could not be distinguished from one another in some of the fixed samples. Eggs of acoel platyhelminthes were identified by morphological comparison of the fixed eggs with (i) eggs from specimens collected during ANT-XXIII/7 which reproduced in culture and (ii) eggs observed in the bodies of fixed sympagic acoels from ANT-XXIII/7 (scanning electron microscopic images, see Suppl. 4.2 for details).

2.3.2. Assessment of abundance, carbon biomass and diversity

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

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

For the assessment of metazoan diversity, the absolute number of species $\hat{S}$, Margalef's species richness d, Pielou's evenness J', Shannon–Wiener diversity H' and the expected species number in a sample of 100 individuals ES_{100} were calculated from integrated abundance (Clarke and Warwick, 2001). For these calculations, it was assumed that the ctenophores, the acoel and rhabditophor platyhelminthes, the cyclopoid copepods and the harpacticoid copepods *Drescheriella* spp., *Ectinosoma* sp., *Diarthrodes* cf. *lilacinus*, *Harpacticus* sp. and "harpacticoid species 1" represented only one species each. Eggs and larvae were not included in the calculations. The data are thus conservative estimates.

2.4. Comparison of the two study areas

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

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

Comparison of vertical meiofauna abundance profiles between stations and regions was complicated by the inherent differences in ice thicknesses as well as by the different cutting schemes applied during the two expeditions. To overcome these problems, each core was divided into five theoretical sections of 1/5 of the total core length, and the average bulk abundance was calculated for each theoretical section (as weighted arithmetic means of the abundances in the comprised sections). These were used in second-stage analyses (Clarke and Warwick, 2001), defining the theoretical sections as inner factors and the stations as outer factors, thus investigating similarities and differences between stations in terms of vertical meiofauna distribution. A second-stage ANOSIM (ANOSIM2) and also a second-stage cluster analysis and MDS (Clarke and Warwick, 2001) were conducted.

Environmental variables were investigated with the focus on relationships to patterns seen in meiofauna communities. In a first approach, vertical profiles of sea-ice parameters were disregarded, using integrated pigment concentrations as well as average values of ice temperature, bulk salinity and derived measures. To investigate whether inter-regional differences in terms of integrated meiofauna communities were also reflected by environmental variables, two-tailed Mann–Whitney *U*-tests were applied to each environmental variable. Subsets of environmental variables best matching the grouping of stations based on meiofauna data were identified using the BIO-ENV procedure (Clarke and Warwick, 2001), which was applied to similarity matrices from analysis of both integrated meiofauna communities and vertical meiofauna profiles. The environmental variables entered in the procedure were ice and snow thickness, bulk salinity, ice temperature, brine volume and chl *a* concentration; the variables excluded were considered to be either of minor relevance to integrated meiofauna abundance or highly correlated with the above-mentioned variables. In a second approach, vertical profiles of environmental sea-ice parameters were analysed: average values were calculated for theoretical core sections as described for the meiofauna analyses. Dissimilarities of stations in terms of profiles of different sub-sets of environmental sea-ice variables were calculated using the above-mentioned second-stage routine. The sub-sets analysed included (i) the full set, (ii) all abiotic variables, (iii) all biotic variables, (iv)–(x) all possible sub-sets of the set sea-ice temperature, relative brine volume and chl *a* concentration. Correlations with the pattern based on vertical meiofauna profiles were calculated using the RELATE procedure (Clarke and Warwick, 2001).

All multivariate analyses were based on Bray–Curtis similarities or dissimilarities (Bray and Curtis, 1957) calculated from fourth-root transformed abundance data, or on euclidean distances of *z*-standardised environmental variables. The significance level for all statistical tests was 5%. Details of the statistical procedures are given in Suppl. 3.

3. Results

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

3.1. Environmental parameters

Level-ice thickness, snow thickness and freeboard on the sampling stations were significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 1). Negative freeboard was measured at stations WS-1, IO-3 and IO-10. Air and snow

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

Table 1
Medians and ranges of environmental parameters measured at the sampling stations in the western Weddell Sea and southern Indian Ocean.

Parameter	Medians 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
	Med	Range	*n*	Med	Range	*n*	Med	Range	Range
Level-ice thickness (cm)	125	63–244	22	81	37–210	15	⋆	—	—
Snow thickness (cm)	17	0–105	22	5	0–9	15	⋆	—	—
Freeboard (cm)	+8	−2 to +23	22	3	−4 to +8	15	⋆	—	—
Air temperature (°C)	−6.0	−16.0 to +6.1	22	−11.1	−20.1 to −5.6	15	⋆	—	—
Snow temperature (°C)	−6.5	−10.9 to −0.3	22	−9.6	−15.7 to −5.5	11	⋆	—	—
Sea-ice temperature (°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	⋆	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	⋆	0.0–33.6	2.2–29.5
Chl *a* (mg m^{-2}) or (µg L^{-1})	8.0	1.2–70.8	19	1.2	0.1–13.6	15	⋆	0.0–1339.8	0.0–74.8
Phaeo (mg m^{-2}) or (µg L^{-1})	1.5	0.1–11.3	19	0.5	0.0–3.9	15	⋆	0.0–192.5	0.0–36.8
Phaeo/chl *a*	0.2	0.1–0.5	19	0.3	0.2–0.5	15	0.3	0.0–1.0	0.0–0.6

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 µg L^{-1}, respectively). Overall medians of point values are given where no significant difference between the regions was detected; significant differences in point values are marked with ⋆ (*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.

temperatures during sampling were significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 1).

Sea-ice temperature and, consequently, brine salinity (averaged over the full cores) did not differ significantly between the study regions (Table 1). Also the vertical profiles were generally similar in both regions, with temperatures usually increasing from the ice surface to the bottom-ice layer, where temperatures were at the freezing point of sea water. At a few stations in the western Weddell Sea there was also a slight increase in temperature near the ice surface, and at two stations the temperature was almost constant throughout the ice column. Bulk salinity and brine volume of the full cores were significantly lower in the western Weddell Sea than in the southern Indian Ocean (Table 1). Also the shapes of the bulk salinity profiles were different. In the southern Indian Ocean, all bulk salinity profiles were generally C-shaped; at most stations, the profiles were very smooth. In the western Weddell Sea, C-shaped profiles prevailed, but at most stations the profiles were irregular and the C-shape less distinct. Stations WS-4, WS-7, WS-11 and WS-21 exhibited I-shaped (linear) bulk salinity profiles.

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

3.2. *Meiofauna communities*

3.2.1. *Taxonomic composition*

In total 20 sympagic meiofauna taxa were recorded in this study, and different types of eggs were distinguished (Table 2). The eggs and several meiofauna taxa occurred frequently in the ice in both the western Weddell Sea and the southern Indian Ocean (Table 2), including acoel platyhelminthes and an unidentified ctenophore (see Suppl. 4.4 for photographs and further information). Others occurred mainly or exclusively in one of the two regions (Table 2): tintinnid ciliates, the foraminiferan *Turborotalita quinqueloba*, radiolarians and the harpacticoid copepod *Microsetella rosea* in the southern Indian Ocean; rhabditophor platyhelminthes (see Suppl. 4.1–4.3 for photographs and further information), the nudibranch *Tergipes antarcticus*, several harpacticoid copepod species, the calanoid copepod *Stephos longipes* and cyclopoid copepods in the western Weddell Sea.

3.2.2. *Integrated abundance and carbon biomass, metazoan diversity*

For most meiofauna taxa and eggs, individuals from the western Weddell Sea were generally bigger than individuals from the southern Indian Ocean, resulting in higher individual carbon contents for animals from the western Weddell Sea (Suppl. 2.2).

Abundance of sympagic meiofauna in total did not differ significantly between the western Weddell Sea and the southern Indian Ocean (Mann–Whitney *U*-test, significance level 5%), whereas total meiofauna carbon biomass was significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 3). Protozoans usually dominated the meiofauna communities in the southern Indian Ocean, while in the western Weddell Sea metazoans were usually dominant in terms of both abundance and biomass (Table 4).

Abundance and carbon biomass of protozoans in total, as well as of ciliates, foraminiferans and radiolarians separately did not differ significantly between the two regions (Fig. 2, Table 3). In the western Weddell Sea, ciliates dominated the protozoan community in terms of abundance and usually also in terms of biomass, followed by foraminiferans (Fig. 3, Table 4). In the southern Indian Ocean, abundance contributions from ciliates and foraminiferans were almost equal, and foraminiferans were usually dominant in terms of biomass. Radiolarian contribution to total protozoan abundance was always low, but they could contribute substantially to protozoan biomass.

Metazoan abundance and carbon biomass were significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 3). This trend was found for platyhelminthes as well as for copepodids (Fig. 2, Table 3). Abundance and biomass of copepod nauplii did not differ significantly between the two regions (Fig. 2, Table 3). Ctenophores appeared to be more abundant in the western Weddell Sea than in the southern Indian Ocean (up to four individuals in three out of six full cores and 11 out of 23 bottom-ice sections in the western Weddell Sea; up to three individuals in two out of 12 full cores in the southern Indian Ocean). Juveniles of *Tergipes antarcticus* were found in very low numbers in both regions (one individual in one full core and two bottom-ice

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

Table 2
Qualitative information about taxonomic composition of sympagic meiofauna and eggs in the western Weddell Sea and the 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		Vertical distribution
	Weddell Sea	Southern Indian Ocean	
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.

sections from the western Weddell Sea and in one full core from the southern Indian Ocean). In both regions, metazoans were always dominated by either copepods or platyhelminthes, in terms of both abundance and biomass (Fig. 3, Table 4). In the western Weddell Sea, platyhelminthes usually made lower contributions to abundance than copepods, but higher contributions to biomass. Contributions of both *Tergipes antarcticus* and ctenophores to metazoan abundance and biomass were always low.

The total abundance of eggs (including nudibranch veliger larvae) did not differ significantly between the two regions, whereas carbon biomass was significantly higher in the western Weddell Sea than in the southern Indian Ocean (Table 3). Neither abundance nor biomass of nudibranch eggs and veligers, acoel eggs or unidentified eggs differed significantly between the two regions (Fig. 2, Table 3). In the western Weddell Sea, in particular, eggs were often considerably more abundant than meiofauna, and egg biomass could be more than 200 times higher than meiofauna biomass (Fig. 2, Table 3).

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

The two study regions further differed significantly in terms of the meiofauna community composition including eggs (global one-way ANOSIM). This pattern was also clearly seen in cluster analyses (Fig. 4A), revealing similarities of only 44% between the regions, and illustrated by MDS (Fig. 4B). The best discriminating taxa (SIMPER; average contribution to between-group dissimilarity $>5\%$ and average divided by standard deviation >2) were *Drescheriella* spp. and unidentified harpacticoid copepods, both of which were abundant in the western Weddell Sea but absent or extremely rare in the southern Indian Ocean, as well as tintinnid ciliates, which showed an opposite pattern. Acoel platyhelminthes and unidentified ciliates were the most typifying for the western Weddell Sea, while unidentified eggs, eggs of acoels, eggs and veliger larvae of *Tergipes antarcticus* and tintinnid ciliates typified the community in the southern Indian Ocean (SIMPER; average contribution to within-group similarity $>10\%$ and average divided by standard deviation >2).

Clustering and MDS (Fig. 4A and B) further revealed that the meiofauna community at stations IO-1, IO-2, IO-10 and IO-13 (cluster α) differed from the six other stations (cluster β) in the southern Indian Ocean (significant differences, SIMPROF), with similarities of only 59%. The α stations were generally characterised by intermediate total abundance and were usually dominated by protozoans (mainly foraminiferans), with high contributions from eggs. The β stations, in contrast, were characterised by low total abundance, with eggs being dominant and protozoans (mainly ciliates) also contributing considerably to total abundance. The discriminating taxa between the two clusters (SIMPER; average contribution to between-group dissimilarity $>10\%$ and average divided by standard deviation >2) were tintinnids and radiolarians, both of which were abundant at the α stations, but absent or rare at the β stations. Also, within the western Weddell Sea, two groups could be discerned: station WS-4 (cluster γ), characterised by high total abundance, pronounced dominance of eggs, low contribution from metazoans and very low contribution from protozoans as well as low metazoan diversity; and stations WS-6, WS-9, WS-12, WS-11 and WS-15 (cluster δ) with intermediate or high total abundance, higher contributions from proto- and metazoans and comparatively high metazoan diversity. The groups within the regions did not seem to be related to the geographic position (cf. Fig. 1).

Several subsets of sea-ice environmental variables (averaged or integrated over the full cores) matched well with the grouping patterns of stations based on meiofauna communities, with correlation coefficients for similarity matrices above 0.50 (BIO-ENV). Amongst these best-matching subsets, none contained the sea-ice temperature. The best-matching subset of three variables, with a correlation coefficient of 0.57, comprised snow thickness, ice thickness and bulk salinity.

3.2.3. *Vertical distribution*

Meiofauna in both regions was not restricted to the bottom-ice layer. Internal and surface communities were found at many stations, at times exceeding the abundance in bottom layers at the respective station (Fig. 5, Suppl. 5). Occurrence in internal or surface layers was most obvious for protozoans, but was also observed for several metazoan taxa, while other metazoans occurred exclusively in bottom layers (Table 2, Fig. 5, Suppl. 5).

Maximum bulk abundance of protozoans was found in a surface layer (uppermost 20 cm) in the western Weddell Sea and in bottom

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

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 10 full cores from the southern Indian Ocean.

Taxon	Abundance in 10^3 m^{-2}					Carbon biomass in mg m^{-2}				
	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	⋆
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	⋆	6.53	1.23–81.23	0.06	0.00–1.10	⋆
Copepoda CI–CVI	8.0	3.0–16.7	0.0	0.0–0.3	⋆	3.01	0.32–4.98	0.00	0.00–0.21	⋆
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	⋆	1.83	0.26–76.22	0.02	0.00–0.21	⋆
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	⋆
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

Overall medians are given where no significant difference between the regions was detected; significant differences are marked with ⋆ (U-test, significance level 5%). The full data sets, including vertical profiles, are available online, doi:10.1594/PANGAEA.734773.

Table 4
Contributions by several meiofauna taxa to integrated abundance and carbon biomass of total protozoans, metazoans or meiofauna, given in %.

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

The full data sets are available online, doi:10.1594/PANGAEA.734773.

ice (lowermost 20 cm) in the southern Indian Ocean. Maximum metazoan and egg abundance was found in bottom ice in both regions.

Vertical carbon biomass profiles generally followed abundance profiles; only at some stations, biomass profiles were distinctly different from abundance profiles, mainly due to the relatively low biomass contributions of ciliates and of eggs and veliger larvae of *Tergipes antarcticus*. Highest bulk biomass of protozoans, metazoans and eggs was recorded in bottom layers in both the western Weddell Sea and the southern Indian Ocean.

Vertical meiofauna abundance profiles did not differ significantly between the two regions (ANOSIM2). Second-stage cluster analyses and MDS revealed five clusters, reflecting different types of vertical profiles (Fig. 4C and D). The grouping patterns were not related to the geographic positions of the stations (cf. Fig. 1). The environmental variables assessed during this study matched the grouping of vertical meiofauna profiles very poorly (BIO-ENV, RELATE), with the exception of the subset of vertical pigment profiles (RELATE).

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.

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

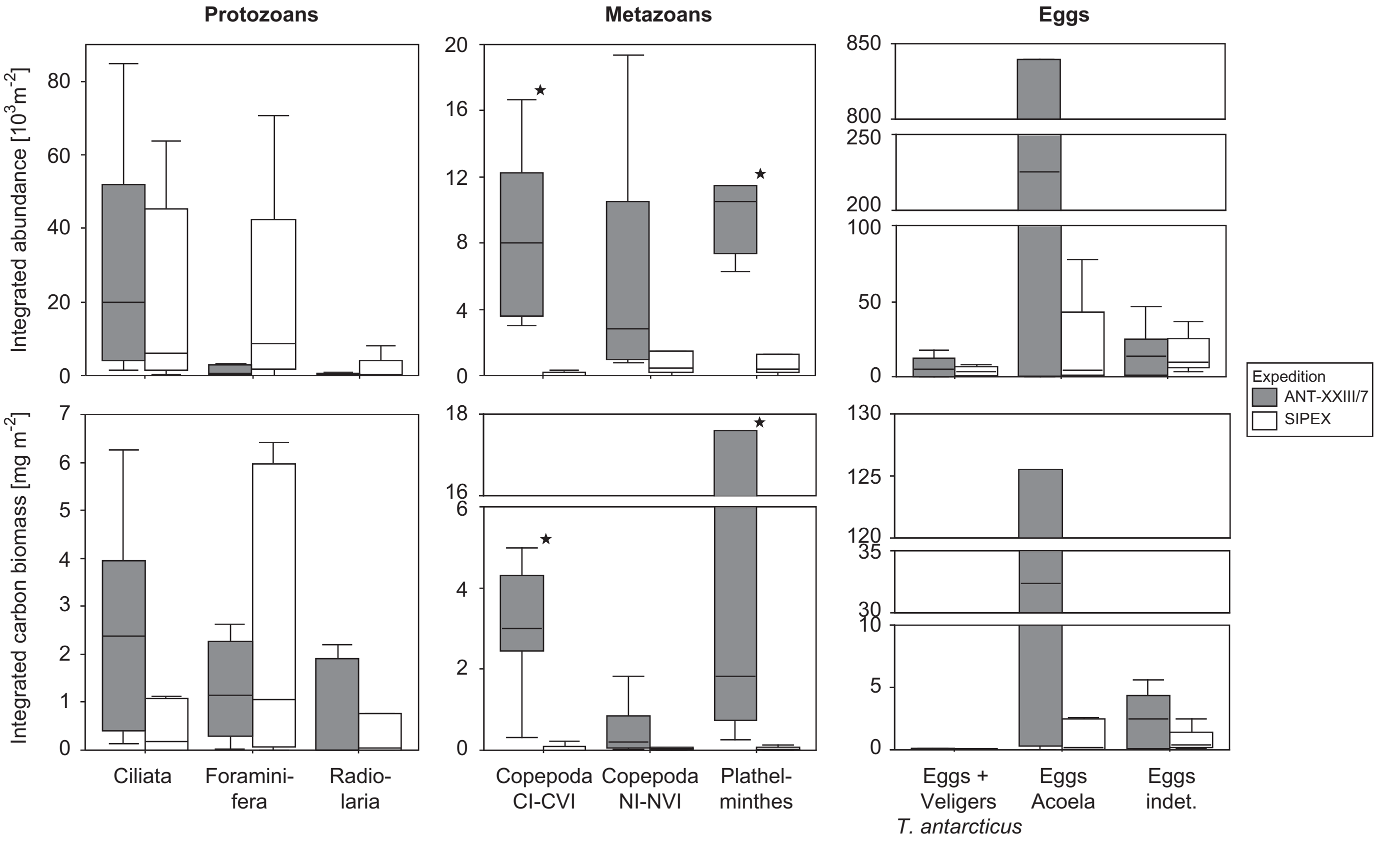

Fig. 2. Boxplots of integrated abundance (top) and carbon biomass (bottom) of sympagic protozoan meiofauna, metazoan meiofauna and eggs in the two study regions, showing medians, quartiles and ranges from six stations in the western Weddell Sea (ANT-XXIII/7) and 10 stations in the southern Indian Ocean (SIPEX). 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 between the regions are marked with ⋆. Note the different scaling of abundance and biomass axes.

Our study has further revealed that in both regions sympagic meiofauna diversity, abundance and carbon biomass were higher than expected from the 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 study, samples from both regions were taken during the same months of two consecutive years and at quite similar latitudes. Although the lower air and snow temperatures in the southern Indian Ocean might indicate more hibernal conditions during sampling than in the western Weddell Sea, sea-ice temperature profiles were generally similar and average temperatures of full cores did not differ significantly between the two regions. We thus assume that sympagic organisms were not exposed to more hibernal conditions in the southern Indian Ocean than in the western Weddell Sea, and consequently that the observed differences were spacial rather than seasonal.

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

Space limitation due to low relative brine volumes obviously did not strongly affect meiofauna, since the bigger metazoan meiofauna was more abundant in the western Weddell Sea in spite of smaller brine volume fractions. Freeboard, which can affect the development of surface communities (Horner et al., 1992), is also considered to be of minor significance for integrated meiofauna communities in winter. Given the good match between integrated meiofauna communities and the environmental parameters indicating sea-ice age, we suggest that the different age of the ice sampled is one of the main reasons for the observed differences in

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

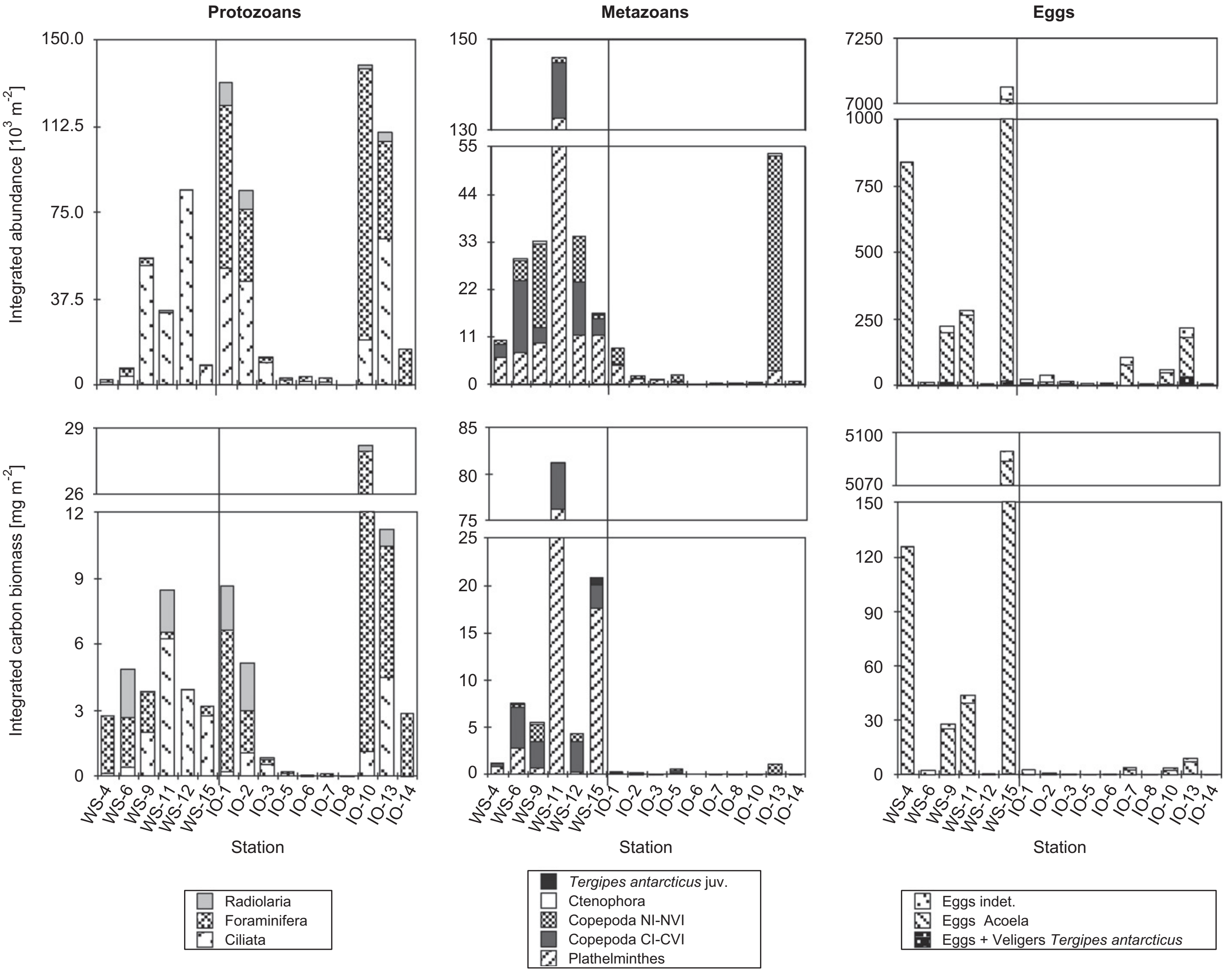

Fig. 3. Integrated abundance (top) and carbon biomass (bottom) of sympagic protozoan meiofauna, metazoan meiofauna and eggs at each station, with contributions by the major taxa. Note the different scaling of abundance and biomass axes.

meiofauna communities. Communities in older ice have had more time to colonise the habitat and to further develop than communities in younger ice. The observed differences might partly be features of a succession in first-year ice, with a shift from communities characterised by protozoans, acoels and harpacticoids to communities with lower protozoan contributions and a more diverse metazoan fauna. To further investigate this issue, future studies should include time series in growing first-year ice as well as comparisons of first- and multi-year ice sampled within one region.

Besides the age of the actual ice floes, we suggest that general differences in the sea-ice regimes give additional explanation to the observed differences in meiofauna communities: perennial ice cover and high proportions of multi-year ice in the Weddell Sea (more than 40% of the total sea-ice cover, S. Schwegmann, pers. comm.), particularly in its western regions (Brierley and Thomas, 2002), standing in contrast to seasonal ice cover and almost exclusively young and first-year ice in the southern Indian Ocean (Worby et al., 1998), as observed also during the present study (Haas et al., 2009; Worby et al., this issue). In seasonally ice-covered regions, the ice needs to be newly colonised each winter when formed and is accessible only to species that can, at least during part of their life cycle, survive longer periods in the water column.

Table 5
Medians and ranges of metazoan diversity and evenness measures calculated from abundances in six full cores from the western Weddell Sea and 10 full cores from the southern Indian Ocean.

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

Overall medians are given where no significant differences between the regions was detected; significant differences are marked with ⋆ (*U*-test, significance level 5%).

In perennially ice-covered regions, in contrast, the large amounts of multi-year ice provide a stable habitat particularly to species that spend all phases of their life cycle in the ice and cannot survive longer periods in the water column. We consider it probable that

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

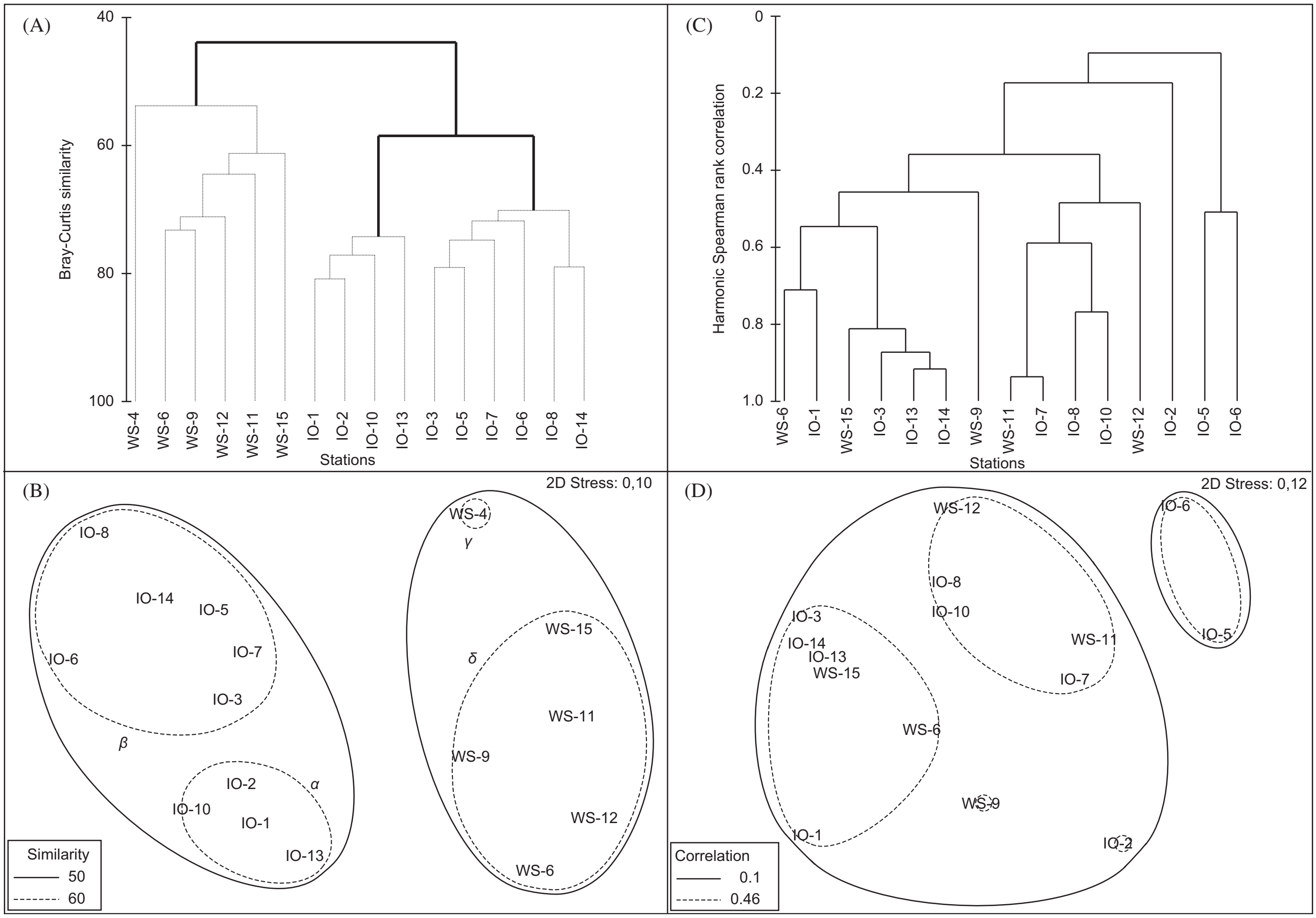

Fig. 4. Grouping patterns of stations in terms of integrated abundance (A, B) and vertical abundance profiles (C, D) of sympagic meiofauna, including eggs. Cluster dendograms (A, C): hierarchical agglomerative; bold lines in (A) indicating significant clusters (SIMPROF, significance level 5%). MDS plots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

this multi-year ice serves as a refuge during summer from which newly forming sea ice can be colonised in winter, as suggested for sympagic copepods by Schnack-Schiel et al. (1998). To further address this issue, future studies should compare areas with different amounts of multi-year ice (e.g. western and eastern Weddell Sea) and experimentally investigate swimming ability and colonisation mechanisms of sympagic meiofauna.

Generalising our results, we suggest that at least sympagic metazoan meiofauna is more diverse and abundant in perennially ice-covered regions (even in first-year ice). Rhabditophores as well as several copepod species presumably rely on perennial ice cover—particularly some harpacticoids, which were amongst the discriminating taxa. Furthermore, platyhelminthes, copepods and ctenophores seem to reach higher abundance in older sea ice or perennially ice-covered regions. Sympagic protozoans, in contrast, appear to be less influenced by the age of the ice and sea-ice regime, at least in terms of total abundance; however, species-level analyses of ciliates may reveal differences also in protozoan communities.

4.2. High meiofauna diversity, abundance and biomass in winter

Our study has revealed that Antarctic sympagic meiofauna communities are more diverse than previously reported, reflected by the high number of different taxa found in both regions. Our study is the first to report sympagic occurrence of rhabditophor platyhelminthes and the harpacticoid copepod *Microsetella rosea*. Rhabditophors seem to be an important component of the sympagic meiofauna community in perennially ice-covered regions: in spite of low abundance, they can, due to their high individual carbon content, reach similarly high biomass to the acoels (this study, data not shown). Judging from morphology and anatomy, the rhabditophors were probably rhabdocoels (see Suppl. 4.3 for details). Several other taxa we found in sea ice have rarely been reported from this habitat before. The frequent occurrence of ctenophores and of the nudibranch *Tergipes antarcticus* in sea ice is particularly interesting regarding the functioning of the sympagic ecosystem: both ctenophores (Ju et al., 2004; Scolardi et al., 2006) and nudibranchs (Kiko et al., 2008a) are probably carnivores and might thus, in spite of low abundance and biomass, play a particularly important role in the sympagic food web. Sympagic ctenophores can obviously colonise different porous ice habitats in winter, such as bottom ice and slush layers. Judging from general morphological features, we assume that the ctenophores we found were not of the species *Callianira antarctica* reported from summer sea ice by Kiko et al. (2008b), but rather *Euplokamis* sp. (see Suppl. 4.4 for details).

Abundance and carbon biomass of Antarctic sympagic meiofauna in winter have been underestimated so far, since previous studies, based on principally similar methods, reported substantially lower abundance and biomass from a winter expedition to the northern Weddell Sea (Gradinger, 1999a; Schnack-Schiel et al., 2001) than found in our study for both the western Weddell Sea and the southern Indian Ocean. Meiofauna abundance in our study mostly exceeded abundance reported earlier from the northern Weddell Sea in winter

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

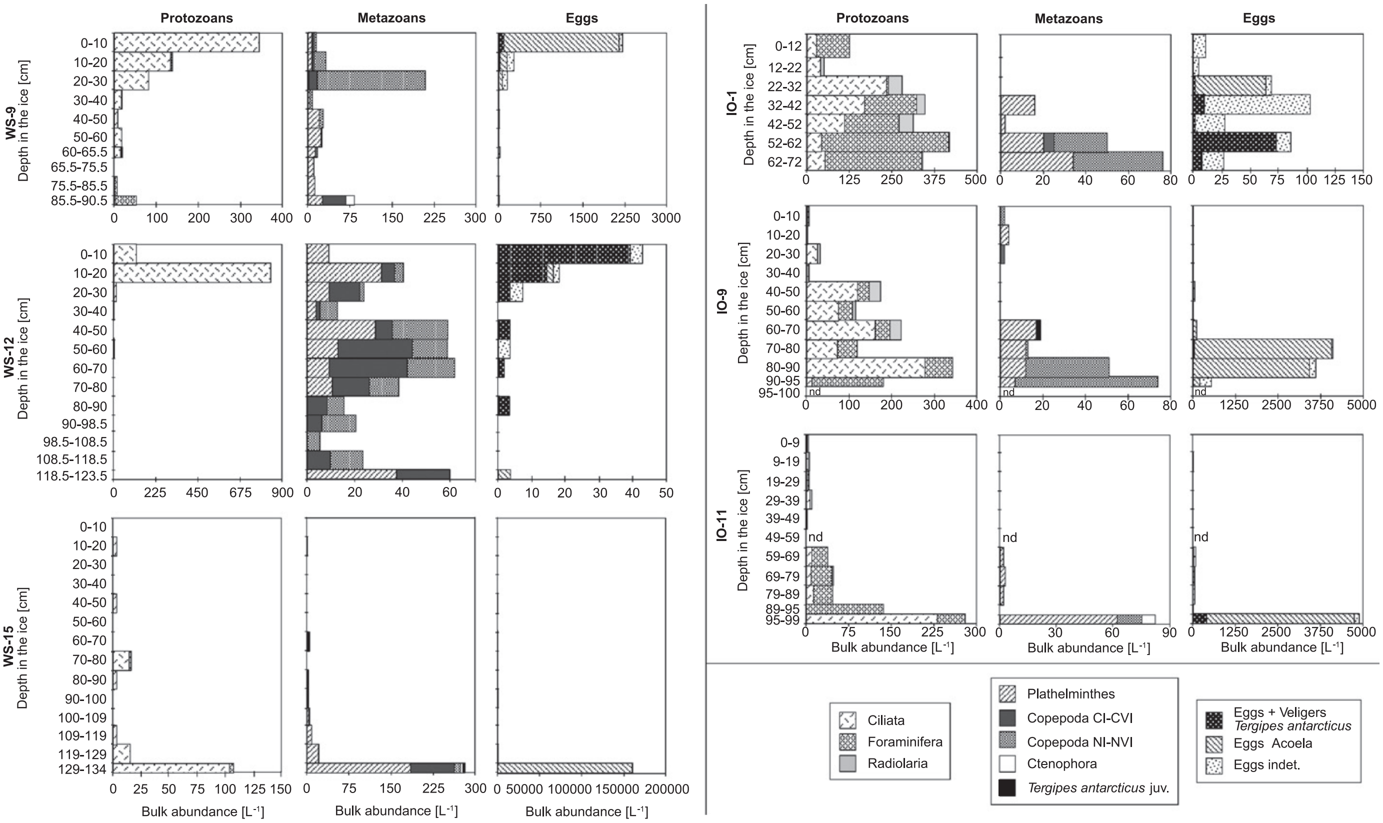

Fig. 5. Examples of vertical bulk abundance profiles of sympagic protozoan meiofauna, metazoan meiofauna and eggs in sea ice in the western Weddell Sea (left) and the southern Indian Ocean (right). Note the different scaling of abundance axes. Vertical bulk abundance profiles of all stations are shown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

(Gradinger, 1999a) (median 14-fold higher in the western Weddell Sea, threefold higher in the southern Indian Ocean). The difference was even more distinct for meiofauna biomass (Gradinger, 1999a) (median 27-fold higher in the wester Weddell Sea, fivefold higher in the southern Indian Ocean). For the western Weddell Sea, these findings can be attributed particularly to the high abundance and biomass of ciliates (medians 11-fold and 119-fold higher, respectively, than in the previous study, Schnack-Schiel et al., 2001), but also to the high abundance of platyhelminthes (median threefold higher) and copepods (median twofold higher). For the southern Indian Ocean, the differences from the previous study were particularly due to high ciliate abundance and biomass (medians fourfold and ninefold higher, respectively), but also due to high foraminiferan biomass (median twofold higher). In the western Weddell Sea, we further found contributions of ciliates to total meiofauna abundance and biomass to be generally higher than previously reported from winter (twofold and fourfold higher contributions, respectively, regarding median abundance and biomass), while foraminiferan contributions to meiofauna abundance and biomass were substantially lower compared to the previous study (44-fold lower and fourfold lower, respectively) (Gradinger, 1999a). Metazoan contribution to total meiofauna abundance was distinctly higher than in the previous study (twofold higher for total metazoans as well as for platyhelminthes and copepods) (Gradinger, 1999a). In terms of biomass, total metazoan and platyhelminth contributions were slightly higher during the previous expedition (Gradinger, 1999a); this is probably due to the fact that biomass calculations in the previous study were mainly based on carbon content data of Arctic sympagic meiofauna (Gradinger, 1999a) instead of size measurements of the actual individuals studied.

There are many possible explanations for the differences between our data and those from the previous studies, including differences in sea-ice conditions between western and northern Weddell Sea (Eicken, 1992; Schnack-Schiel et al., 2008) and interannual variability (Eicken, 1992) as well as the generally observed heterogeneity of sympagic communities (Swadling et al., 1997; Schnack-Schiel et al., 2008). Regardless of the reason for differences, our study indicates that the role of Antarctic sympagic meiofauna in the sympagic ecosystem has been underestimated so far. Both contribution of meiofauna to sea-ice particulate organic carbon (POC) and feeding impact of meiofauna are essentially functions of carbon biomass. The high meiofauna biomass we report thus implies an accordingly high POC contribution and feeding impact, questioning previous findings by Gradinger (1999a), according to which Antarctic sympagic meiofauna does not control the 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 recent studies from summer (Schnack-Schiel et al., 2008; Kiko, 2010).

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

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

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., this issue). 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 (IPCC, 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 in sea-ice age has already been observed (Rigor and Wallace, 2004; Maslanik et al., 2007; Nghiem et al., 2007; Drobot et al., 2008), and the complete loss of multi-year ice has been predicted to occur before the middle of this century (Stroeve et al., 2007; Wang and Overland, 2009). We assume that this development will result in a loss in diversity, abundance and biomass of sympagic meiofauna.

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

Acknowledgments

We thank all those who helped us in the field and lab during ANT-XXIII/7 and SIPEX, particularly Erika Allhusen (Alfred Wegener Institute, Bremerhaven) and Dai Fang-Fang (University of Zhejiang Wanli), who did most of the chlorophyll sampling and measurements during ANT-XXIII/7. We thank Heike Wägele (University of Bonn) for identification of the nudibranch *Tergipes antarcticus*, Sigrid Schiel (Alfred Wegener Institute, Bremerhaven) for her help with harpacticoid taxonomy, Ole Riemann (University of Würzburg Graduate School), Alexander Kieneke (German Center for Marine Biodiversity Research, Wilhelmshaven) and Wilko Ahlrichs (University of Oldenburg) as well as Bart Tessens (University of Hasselt) for their help with platyhelminth taxonomy and electron microscopy. Kerri Scolardi (Mote Marine Laboratory, Sarasota, Florida) is thanked for giving her opinion on the unidentified ctenophore and for providing information about Antarctic planktonic ctenophores. We thank Dieter Piepenburg (Institute for Polar Ecology, Kiel) for his advice concerning statistics. We further acknowledge the effort of two anonymous reviewers, whose constructive comments helped to improve the manuscript. The constant support by captains, officers and crews of R.V. *Polarstern* and R.S.V. *Aurora Australis* during the expeditions ANT-XXIII/7 and SIPEX is gratefully acknowledged. This research was supported by the Deutsche Forschungsgesellschaft WE 2536/11-1 (to IW, MK, AS) as well as by the Australian Government through the Antarctic Climate and Ecosystems Cooperative Research Centre (ACE CRC) and Australian Antarctic Science Project 2767 (to KM) and 1358 (to KS).

Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.dsr2.2010.10.029.

References

Assur, A., 1958. Composition of sea ice and its tensile strength. In: Arctic Sea Ice: Proceedings of the Conference Conducted by the Division of Earth Sciences and supported by the Office of Naval Research. Vol. 598 of National Research Council Publications. National Academy of Sciences, National Research Council, Washington, DC, pp. 106–138.

Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs 27 (4), 325–349.

Brierley, A.S., Thomas, D.N., 2002. The ecology of Southern Ocean pack ice. Advances in Marine Biology 43, 171–278.

Buffan-Dubau, E., Carman, K.R., 2000. Extraction of benthic microalgal pigments for HPLC analyses. Marine Ecology Progress Series 204, 293–297.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretations second ed. PRIMER-E Ltd, Plymouth.

Comiso, J.C., Nishio, F., 2008. Trends in the sea ice cover using enhanced and compatible AMSR-E, SSM/I, and SMMR data. Journal of Geophysical Research 113 (C2), C02S07.

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

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

Drobot, S., Stroeve, J., Maslanik, J., Emery, W., Fowler, C., Kay, J., 2008. Evolution of the 2007–2008 Arctic sea ice cover and prospects for a new record in 2008. Geophysical Research Letters 35 (19), L19501.

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

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

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

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

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

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

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

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

Gradinger, R., Friedrich, C., Spindler, M., 1999. Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. Deep Sea Research Part II 46 (6–7), 1457–1472.

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

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

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

Haas, C., Nicolaus, M., Willmes, S., Worby, A., Flinspach, D., 2008. Sea ice and snow thickness and physical properties of an ice floe in the western Weddell Sea and their changes during spring warming. Deep Sea Research Part II 55 (8–9), 963–974.

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

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029

IPCC, 2007. Climate change 2007: the physical science basis. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, New York.

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

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

Kiko, R., 2010. Acquisition of freeze protection in a sea-ice crustacean through horizontal gene transfer? Polar Biology 33 (4), 543–556.

Kiko, R., Kramer, M., Spindler, M., Wägele, H., 2008a. *Tergipes antarcticus* (Gastropoda, Nudibranchia): distribution, life cycle, morphology, anatomy and adaptation of the first mollusc known to live in Antarctic sea ice. Polar Biology 31 (11), 1383–1395.

Kiko, R., Michels, J., Mizdalski, E., Schnack-Schiel, S.B., Werner, I., 2008b. Living conditions, abundance and composition of the metazoan fauna in surface and sub-ice layers in pack ice of the western Weddell Sea during late spring. Deep Sea Research Part II 55 (8–9), 1000–1014.

Maslanik, J.A., Fowler, C., Stroeve, J., Drobot, S., Zwally, J., Yi, D., Emery, W., 2007. A younger, thinner Arctic ice cover: increased potential for rapid, extensive sea-ice loss. Geophysical Research Letters 34 (24), L24501.

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

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

Meiners, K.M., Norman, L., Granskog, M.A., Krell, A., Heil, P., Thomas, D.N. Physico-ecobiogeochemistry of East Antarctic pack ice during the winter-spring transition. Deep Sea Research Part II, this issue [doi:10.1016/j.dsr2.2010.10.033].

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

Nghiem, S.V., Rigor, I.G., Perovich, D.K., Clemente-Colón, P., Weatherly, J.W., Neumann, G., 2007. Rapid reduction of Arctic perennial sea ice. Geophysical Research Letters 34 (19), L19504.

Nicolaus, M., Haas, C., Willmes, S., 2009. Evolution of first- and second-year snow properties on sea ice in the Weddell Sea during spring-summer transition. Journal of Geophysical Research 114 (D17), D17109.

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

Rigor, I., Wallace, J.M., 2004. Variations in the age of Arctic sea-ice and summer sea-ice extent. Geophysical Research Letters 31 (9), L09401.

Schnack-Schiel, S.B., 2003. The macrobiology of sea ice. In: Thomas, D.N., Dieckmann, G.S. (Eds.), Sea Ice—An Introduction to its Physics, Chemistry, Biology and Geology. Blackwell Science Ltd, Oxford, pp. 211–239.

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

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

Schnack-Schiel, S.B., Thomas, D., Dahms, H.-U., Haas, C., Mizdalski, E., 1998. Copepods in Antarctic sea ice. In: Lizotte, M.P., Arrigo, K.R. (Eds.), Antarctic Sea Ice: Biological Processes, Interactions and Variability. Vol. 73 of Antarctic Research Series. American Geophysical Union, Washington, DC, pp. 173–182.

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

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

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

Stroeve, J., Holland, M.M., Meier, W., Scambos, T., Serreze, M., 2007. Arctic sea ice decline: faster than forecast. Geophysical Research Letters 34 (9), L09501.

Swadling, K.M., 2001. Population structure of two Antarctic ice-associated copepods, *Drescheriella glacialis* and *Paralabidocera antarctica*, in winter sea-ice. Marine Biology 139 (3), 597–603.

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

Wang, M., Overland, J.E., 2009. A sea ice free summer Arctic within 30 years? Geophysical Research Letters 36 (7), L07502.

Weeks, W.F., 2001. Growth conditions and the structure and properties of sea ice. In: Leppäranta, M. (Ed.), Physics of Ice-Covered Seas, second ed., vol. 1. University of Helsinki Press, Helsinki, pp. 25–104.

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

Willmes, S., Haas, C., Nicolaus, M., Bareiss, J., in press. High radar-backscatter regions on Antarctic sea ice and their relation to sea-ice and snow properties and meteorological conditions. International Journal of Remote Sensing, doi:10.1080/01431161003801344.

Worby, A.P., Steer, A.D., Lieser, J.L., Heil, P., Yi, D., Markus, T., Allison, I., Massom, R.A., Galin, N., Zwally, H.J. Regional-scale sea ice and snow thickness distributions from *in situ* and satellite measurements over East Antarctic pack ice during SIPEX 2007. Deep-Sea Research II, this issue.

Worby, A.P., Massom, R.A., Allison, I., Lytle, V.I., Heil, P., 1998. East Antarctic sea ice: a review of its structure, properties and ice drift. In: Jeffries, M. (Ed.), Antarctic Sea Ice: Physical Processes, Interactions and Variability. Antarctic Research Series, vol. 74. American Geophysical Union, Washington, DC, pp. 41–67.

Please cite this article as: Kramer, M., et al., Antarctic sympagic meiofauna in winter: Comparing diversity, abundance and biomass between perennially and seasonally ice-covered regions. Deep-Sea Research II (2011), doi:10.1016/j.dsr2.2010.10.029