

# Distribution patterns of micro- and meso-zooplankton communities in sea ice regions of Lützow-Holm Bay, East Antarctica

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Received: 19 September 2012/Revised: 21 May 2013/Accepted: 22 May 2013/Published online: 31 May 2013  
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**Abstract** In the Southern Ocean, zooplankton research has focused on krill and macro-zooplankton despite the high densities of micro- and meso-zooplankton. We investigated their community structure in relation to different sea ice conditions around Japan's Syowa Station in Lützow-Holm Bay, in the summers of 2011 and 2012. Zooplankton samples were collected using vertical hauls (0–150 m), with a closing net of 100- $\mu$ m mesh size. The results of cluster analysis showed that the communities in this region were separated into fast ice, pack ice, and open ocean fauna. The fast ice fauna had lower zooplankton abundance (393.8–958.9 inds.  $m^{-3}$ ) and was dominated by cyclopoid copepods of *Oncaea* spp. (54.9–74.8 %) and *Oithona similis* (6.6–19.9 %). Deep-water calanoid copepods were also found at the fast ice stations. Pack ice and open ocean fauna had higher zooplankton abundance (943.6–2,639.8 inds.  $m^{-3}$ ) and were characterized by a high density of foraminiferans in both years (6.6–61.9 %). Their test size distribution indicated that these organisms were possibly released from melting sea ice. The pteropod *Limacina* spp. was a major contributor to total abundance of zooplankton in the open ocean zone in 2012 (26.4 %).

Part of this research was supported by the National Institute of Polar Research (NIPR) through Project Research no. KP-4. The study is also part of the Science Program of JARE AMB-2. It was supported by the NIPR under MEXT

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The physical and/or biological changes between 2 years may affect the abundance and distribution of the dominant zooplankton taxa such as cyclopoid copepods, foraminiferans, and pteropods. Information on the relationships between the different species associated with sea ice will help to infer the possible future impacts of climate change on the sea ice regions.

**Keywords** Southern Ocean · Sea ice ·  
Micro- and meso-zooplankton · Foraminiferans

## Introduction

Zooplankton are secondary producers in marine ecosystems and play an important role as food for pelagic fish and air-breathing predators such as seals, whales, and penguins in the Southern Ocean (e.g. Hempel 1985a). While various factors defining zooplankton distribution in the Southern Ocean have been discussed, sea ice plays a crucial, highly dynamic, and variable role in the life cycles of organisms including zooplankton in the sea ice region (Massom and Stammerjohn 2010). In fact, Antarctic zooplankton communities are usually divided into three ice-associated faunal zones: (1) the northern ice-free zone, dominated by copepods and *Salpa thompsoni*; (2) the seasonal pack ice zone, dominated by Antarctic krill *Euphausia superba*; and (3) the fast ice zone, where the ice krill *Euphausia crystallorophias* is dominant (Hempel 1985b; Hosie 1994; Loeb 2007). However, these distributional data for macro-zooplankton are mostly based on information obtained from sampling with 200–500  $\mu$ m nets or coarser nets such as the RMT (Rectangular Mid-water Trawl) 8. Recently, the increasing use of finer plankton nets (60–200  $\mu$ m) has provided a more realistic view of the ecological

significance of meso- (200–2,000  $\mu\text{m}$ ) and micro-zooplankton (20–200  $\mu\text{m}$ ), such as small calanoid and cyclopoid copepods, foraminiferans, and appendicularians (Metz 1996; Atkinson 1998; Schnack-Schiel et al. 1998; Atkinson and Sinclair 2000; Dubischar et al. 2002). Micro- and meso-zooplankton have been estimated to have a high abundance in the seasonal ice zone (Chiba et al. 2001; Swadling et al. 2010). Although their roles in the pelagic food web under sea ice are being gradually identified, the dynamics of these smaller zooplankton communities within the sea ice regions are still poorly understood.

Lützow-Holm Bay, where Japan's Syowa Station is located, is a region where fast ice cover persists during summer, and some studies have been made of the zooplankton community structure around the shore-based stations of this bay (e.g. Fukuchi and Sasaki 1981; Fukuchi and Tanimura 1981; Fukuchi et al. 1985; Tanimura et al. 1986; Tanimura et al. 2008). The marine biological monitoring program of the sea ice region by ship-based sampling began with the 52nd Japanese Antarctic Research Expedition (JARE-52; 2010/2011 season). The aim of this program was to investigate biological production and mechanisms in relation to sea ice. The objectives of the present study were to examine the abundance and distribution patterns of micro- and meso-zooplankton communities in Lützow-Holm Bay

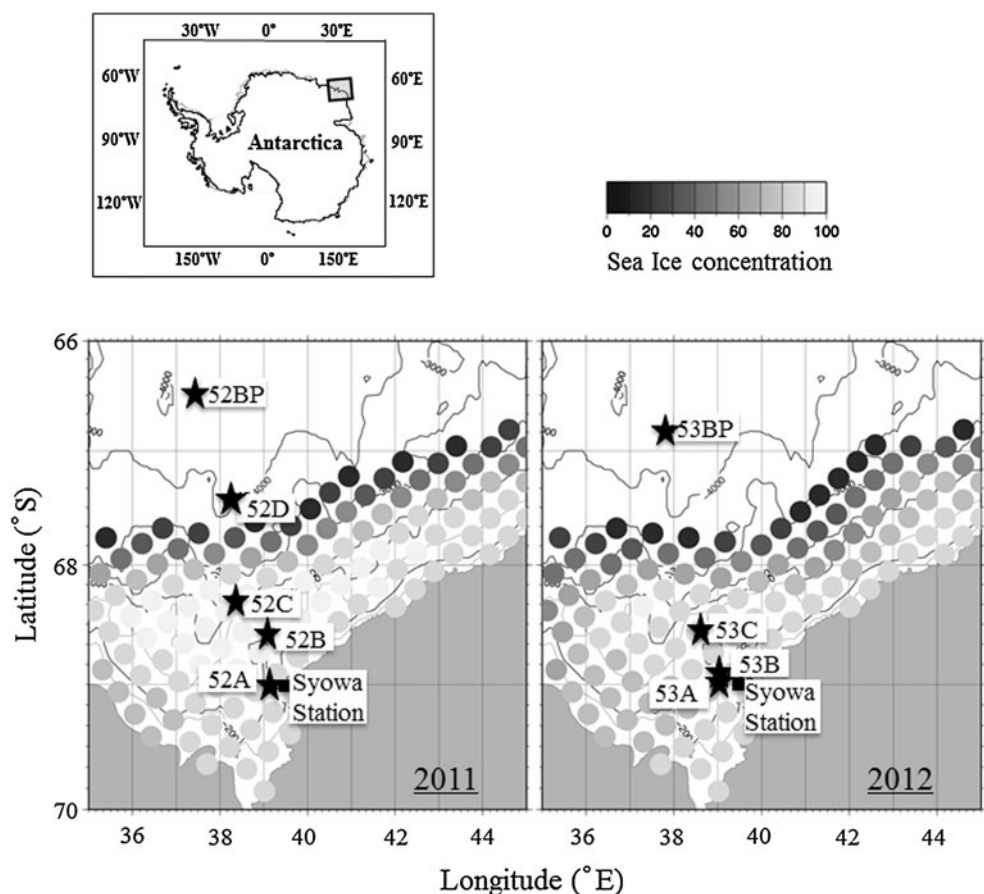
during the austral summer, and their relationship to sea ice distribution. To achieve this objective, it was assumed that sea ice distribution would affect the distribution of micro- and meso-zooplankton communities in the sea ice regions as well as that of macro-zooplankton.

## Materials and methods

### Sampling

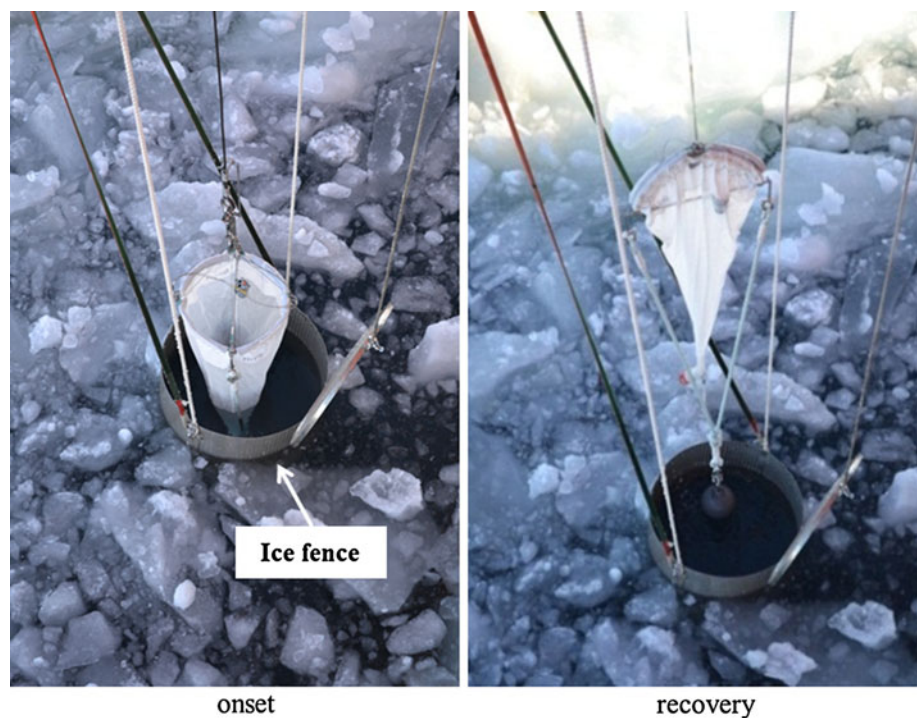
The survey was conducted during two cruises of the Japanese icebreaker *Shirase* through the sea ice zone in Lützow-Holm Bay. The first took place from February 9 to 24, 2011 (JARE-52) and the second from February 14 to March 4, 2012 (JARE-53; Fig. 1). Zooplankton samples were collected using a closing net (mouth diameter 0.75 m, mesh size 100  $\mu\text{m}$ ; Table 1) at nine stations (five in 2011 and four in 2012) with contrasting sea ice environments (Fig. 1): fast ice (four stations: 52A, 52B, 53A, and 53B), pack ice (three stations: 52C, 52D, and 53C), and ice-free open ocean (two stations: 52BP and 53BP). To prevent the sea ice from being mixed into the net, an ice fence was employed and the net was closed as it reached the surface (Fig. 2; Takahashi et al. 2012). The net was equipped with

**Fig. 1** Spatial and temporal variability in sea ice distribution around Syowa Station in the austral summers of 2011 (a) and 2012 (b). Stars indicate sampling stations



**Table 1** Sampling locations and environmental information

Station	Location		Date (LMT)	Sampling depth (m)	Sea-ice distribution	$S_{\text{average}}$ [min, max] (PSU)	$T_{\text{average}}$ [min, max] (°C)	Chl. <i>a</i> (mg m <sup>-2</sup> )
	Lat. (S)	Long. (E)						
52A	69°03'	39°20'	February 9, 2011	75-0	Fast ice	33.97 [31.76, 34.15]	-1.72 [-1.81, -1.64]	9.78
52B	68°59'	39°11'	February 12, 2011	135-0	Fast ice	34.12 [33.98, 34.22]	-1.72 [-1.86, -1.64]	1.08
52C	68°31'	38°42'	February 18, 2011	150-0	Pack ice	34.06 [33.71, 34.22]	-1.80 [-1.85, -1.76]	12.48
52D	67°43'	38°18'	February 23, 2011	150-0	Pack ice	34.07 [33.27, 34.43]	-1.51 [-1.78, -0.84]	30.01
52BP	66°50'	37°49'	February 24, 2011	150-0	Open ocean	34.45 [34.07, 34.68]	0.63 [-0.52, 1.44]	80.13
53A	68°57'	39°05'	February 14, 2012	150-0	Fast ice	34.00 [32.27, 34.26]	-1.76 [-1.85, -1.71]	1.46
53B	68°56'	39°05'	February 17, 2012	150-0	Fast ice	No data	-1.74 [-1.82, -1.71]	1.16
53C	68°34'	38°39'	March 1, 2012	150-0	Pack ice	No data	No data	12.26
53BP	66°50'	37°51'	March 4, 2012	150-0	Open ocean	34.33 [33.88, 34.77]	0.17 [-1.73, 1.31]	28.74

**Fig. 2** Zooplankton sampling in the pack ice using an “ice-fence” to guard against net closing due to sea ice

a flow meter to estimate the volume of water filtered and was vertically hauled from a depth of 150 m to the surface at stations where the bottom was deeper than 150 m, or from 5 m above the bottom to the surface at stations where the bottom was shallower than 150 m (Table 1). All samples were fixed immediately with buffered 5 % formaldehyde and seawater solution.

A number of environmental variables were also measured during the cruise. Temperature and salinity were measured at 1-m intervals down to the seafloor using a CTD (SBE 55 ECO, Sea-Bird Electronics, Bellevue, Washington, DC, USA). Water samples for measurement of chlorophyll *a* (Chl *a*) concentration were collected from three to seven depths in the upper 150 m with a Niskin

bottle mounted on the CTD. Chl *a* concentration was determined fluorometrically with a Turner Designs fluorometer (model 10AU). For the purpose of comparison with zooplankton data, temperature and salinity data were averaged across the sampling layers. And Chl *a* concentrations were integrated vertically (e.g. Suzuki et al. 1998; Uitz et al. 2006).

Daily values of sea ice concentration were obtained from the National Snow and Ice Data Center (NSIDC) in Boulder, Colorado, USA. These data were derived from passive microwave data collected by the Special Sensor Microwave Imager (SSM/I) (Cavalieri et al. 1996) and the Advanced Microwave Scanning Radiometer for EOS (AMSR-E) (Cavalieri et al. 2004).

## Analysis

In the laboratory, zooplankton samples were split using a Motoda box splitter (Motoda 1959) so that approximately 1,000 individuals were counted per sample. The samples were identified to the lowest possible taxonomic level (generally species or genus) with a stereomicroscope. Members of the Ostracoda, Polychaeta, Salpa, Foraminifera, Chaetognatha, and Echinodermata were not identified to species level (Table 2). The copepods *Oithona similis* and *Oncaea* spp. were classed as adult or copepodite, with adult *Oncaea* spp. further identified to species level and classified as male or female. The maximum diameter of the test was measured for individual foraminiferans because the test size gives an indication of the growth stage. The test sizes of approximately 100 foraminiferans were measured per sample, except in cases where there were <100 individuals. Individual counts were converted to the number of individuals per 1 m<sup>3</sup> for each station.

Abundance data were log-transformed ( $\log_{10} [n + 1]$ ) to decrease any bias in abundance, and a similarity matrix was constructed using the Bray–Curtis similarity index (Field et al. 1982). For grouping the samples, group average linkage was performed based on similarity. The SIMPER (similarity percentage) routine identified those species contributing to the similarity within the observed clusters. These statistical analyses were conducted using the PRIMER v6 software package (Clarke and Gorley 2006). The Shannon index ( $H'$ ) was chosen to show the species diversity in each cluster group.

## Results

### Environmental variables

The average temperature and salinity ranged from –1.80 to 0.63 °C and 33.97 to 34.45 PSU, respectively (Table 1). A few stations contributed no data as the CTD did not work. Vertically integrated Chl *a* concentrations ranged from 1.08 to 80.13 mg m<sup>-2</sup> (Table 1). Both temperature and salinity tended to increase from the fast ice stations to the open ocean stations each year, Chl *a* concentration showed a similar trend, with the exception of station 52A.

### Community structure

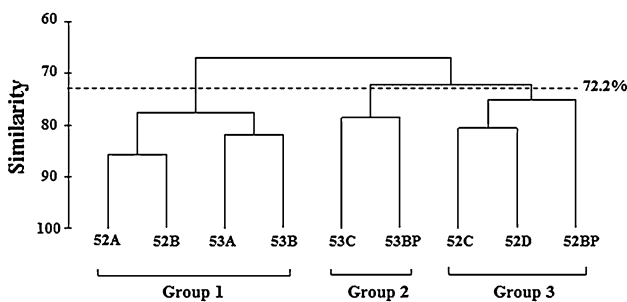
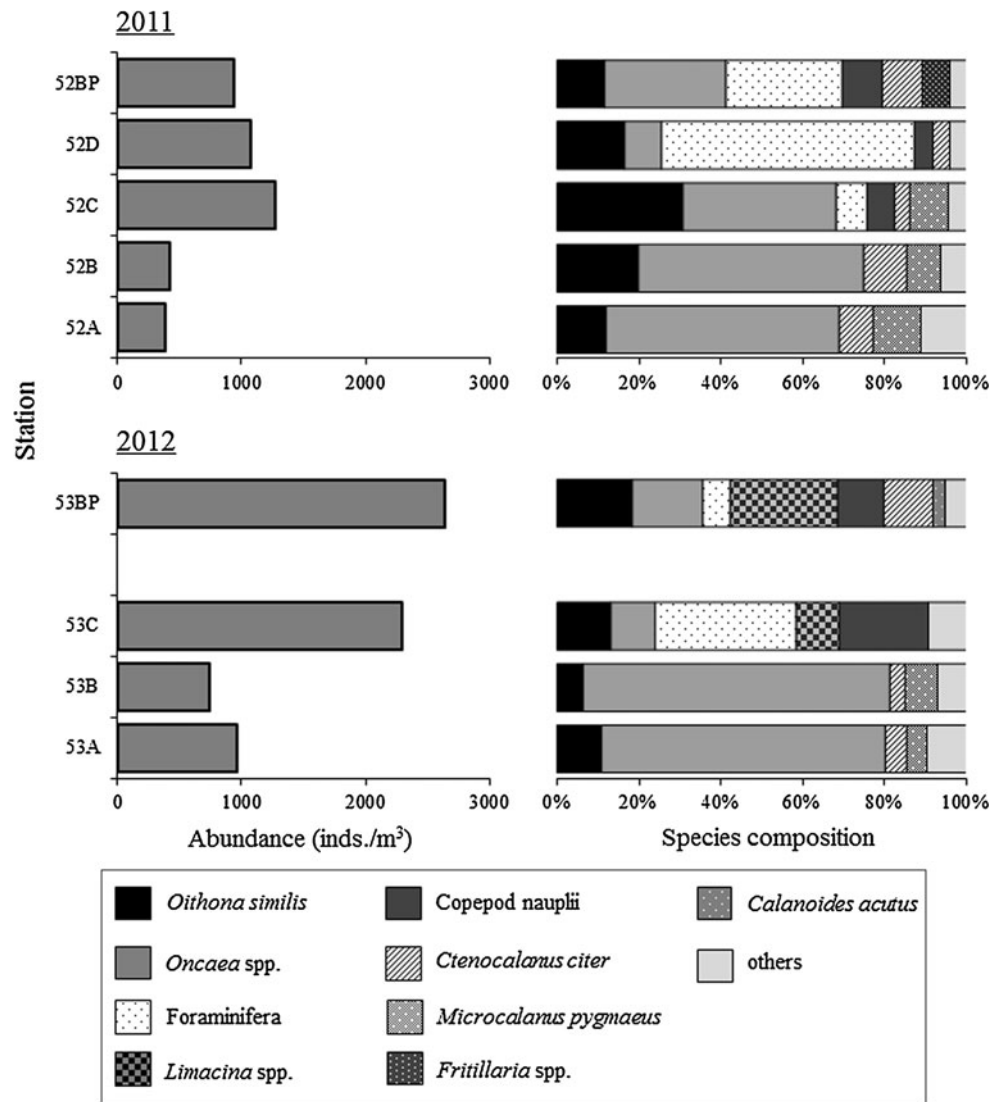
A total of 42 zooplankton species/taxa were identified from the nine stations (Table 2). Zooplankton abundance ranged from 393.8 to 2,639.8 inds. m<sup>-3</sup> (Fig. 3). Values were lower at the stations under fast ice and greater at those under pack ice or in the open ocean. Copepods (including nauplius stages) were generally the dominant zooplankton

**Table 2** Zooplankton taxa/species recorded in this study

Copepoda	Aetideidae
	<i>A. antarctica</i>
	Amalothrix sp.
	Calanoida
	<i>C. acutus</i>
	<i>Calanus propinquus</i>
	<i>Clausocalanus laticeps</i>
	<i>C. citer</i>
	Euchaetidae
	<i>Euchirella rostromagna</i>
	<i>Haloptilus oxycephalus</i>
	Harpacticoida
	Heterorhabdidae
	<i>Heterorhabdus austrinus</i>
	<i>Metridia gerlachei</i>
	<i>M. pygmaeus</i>
	<i>Oithona frigida</i>
	<i>O. similis</i>
	<i>Oncaea</i> spp.
	<i>Paraeuchaeta antarctica</i>
	<i>Paraeuchaeta biloba</i>
	<i>Racovitzanus antarcticus</i>
	<i>Rhincalanus gigas</i>
	<i>S. minor</i>
	Scolecitrichidae
	Spinocalanidae
Copepod nauplii	
Amphipoda	<i>Themisto</i> spp.
Euphausiacea	Euphausiidae
	<i>E. superba</i>
	<i>Thysanoessa macrura</i>
Ostracoda	
Polychaeta	
Appendicularia	<i>Fritillaria</i> spp.
	<i>Oikopleura</i> spp.
Salpa	<i>Salpa</i> spp.
Chaetognatha	
Siphonophorae	
Echinodermata	
Pteropoda	<i>Limacina</i> spp.
Foraminifera	
Fish egg	

component, with the copepods *O. similis* and *Oncaea* spp. being the most abundant copepod taxa at all stations. For example, at the fast ice stations (52A, 52B, 53A, and 53B), *Oncaea* spp. accounted for 54.9–74.8 % of the total zooplankton abundance. Foraminiferans were also highly abundant at pack ice and open ocean stations, comprising 6.6–61.9 % of the total zooplankton community. *Limacina*

**Fig. 3** Abundance (inds. m<sup>-3</sup>) and species composition of zooplankton at all stations in 2011 and 2012



**Fig. 4** Dendrogram of the cluster analysis based on the Bray–Curtis similarity index with UPGMA linkage

spp. occurred in high numbers at pack ice and open ocean stations in 2012 (10.3 and 26.4 %, respectively). Copepod nauplii were also abundant, accounting for 4.3–21.8 % under pack ice and in the open ocean (Fig. 3).

Cluster analysis revealed three groups at  $\geq 72.2\%$  similarity (Fig. 4). The groups were clearly separated by

the interface between fast ice and pack ice. Group 1 comprised all four stations located under fast ice in 2011 and 2012. Groups 2 and 3 comprised the five stations located under pack ice or in the open ocean, Group 2 with the two stations in 2012 and Group 3 with the three stations in 2011.

The species contributing most to the similarity within Group 1 was *Oncaea* spp., followed by *O. similis*, *Microcalanus pygmaeus*, and *Ctenocalanus citer* (Table 3). Group 2 was characterized by *O. similis*, copepod nauplii, *Oncaea* spp., *Limacina* spp., and foraminiferans. Group 3 was mainly composed of foraminiferans, *Oncaea* spp., *O. similis*, copepod nauplii, and *C. citer*. The values for average abundance and species diversity were the highest in samples within Group 2, followed by Group 3 and then Group 1 (Table 3; Fig. 4). The average abundance of zooplankton in samples within Group 2 was more than triple that of samples within Group 1, while the species

richness of samples within each group was almost the same (Table 3). The organisms contributing most to the difference between Groups 1 and 3 were foraminiferans, followed by copepod nauplii, *Fritillaria* spp., *M. pygmaeus*, *O. similis*, and echinoderms (Table 4). For Groups 1 and 2, *Limacina* spp. and foraminiferans were the most influential contributors to the dissimilarity. The species causing most of the dissimilarity between Groups 2 and 3 was *Limacina* spp., followed by *Fritillaria* spp., *Calanoides acutus*, *Scolecithricella minor*, copepod nauplii, and polychaetes (Table 4).

#### Population structure

The abundance of *O. similis* ranged from 47.9 to 491.4 inds. m<sup>-3</sup> (Fig. 5a), and their pattern of abundance follows a similar pattern to that of total zooplankton abundance in this study (Fig. 3). Copepodite stages were dominant at all stations, accounting for 65.5–94.2 % of total abundance (Fig. 5a). The abundance of *Oncaea* spp. varied from 96.0 to 670.0 inds. m<sup>-3</sup> (Fig. 5b). It was highest at pack ice station 52C in 2011 (472.0 inds. m<sup>-3</sup>), while in 2012, the highest value occurred at fast ice station 53A (670.0 inds. m<sup>-3</sup>). The species distribution and stage composition at each station were similar between 2011 and 2012: adults were dominant under fast ice, contributing 50.4–76.5 %, and adult abundance gradually decreased toward the open ocean. In contrast, copepodites were most abundant at the open ocean stations (79.4 % in 2011 and 83.7 % in 2012) and decreased in abundance toward the fast ice. Adult *Oncaea antarctica* occurred in abundance only at the northern pack ice and open ocean stations, while adult *Oncaea curvata* occurred at the southern pack ice and fast ice stations. Adult male *O. curvata* tended to be dominant in the fast ice area.

The test size distribution patterns for foraminiferans in 2011 and 2012 were similar (Fig. 6). At the open ocean stations, 52BP and 53BP, size ranges were 77.8–320.4 and 86.4–330.2 μm, respectively, and a peak in abundance occurred at approximately 175 μm. The peak at pack ice station 52D was the same as that found at the open ocean stations. However, at this station, the size range was 110–354.8 μm. The smaller individuals found at the open ocean stations were not present at station 52 D, and the largest sizes found were greater than those found at open ocean stations. At pack ice stations 52C and 53C, larger individuals were even more abundant in the samples (105.7–419.4 and 103.1–407.0 μm, respectively) and two peaks in size occurred, at approximately 200 and 300 μm (Fig. 6).

**Table 3** Average abundance (inds. m<sup>-3</sup>), species richness (*r*), and diversity (*H'*) for the three clusters identified by cluster analysis

Species/taxa	Group 1	Group 2	Group 3
<i>C. acutus</i>	0.67	42.66	2.78
<i>C. propinquus</i>	0.59	4.99	1.77
Chaetognatha	0.94	2.33	2.70
Copepod nauplii	12.69	<b>393.53</b>	<b>74.74</b>
<i>C. citer</i>	<b>38.86</b>	182.88	<b>59.89</b>
Euchaetidae	2.83	0.10	1.82
Foraminifera	5.01	<b>484.16</b>	<b>342.89</b>
<i>Fritillaria</i> spp.	0.48	23.44	21.43
<i>H. oxycephalus</i>	0.03	1.39	0.20
Harpacticoida	1.98	1.50	1.89
<i>Limacina</i> spp.	0.93	<b>466.04</b>	1.11
<i>M. gerlachei</i>	4.17	28.17	5.24
<i>M. pygmaeus</i>	<b>46.91</b>	43.72	47.64
<i>O. frigida</i>	8.97	5.30	10.54
<i>O. similis</i>	<b>72.30</b>	<b>396.85</b>	<b>227.77</b>
<i>Oncaea</i> spp.	<b>420.73</b>	<b>350.72</b>	<b>281.82</b>
Ostracoda	0.26	0.24	1.07
Polychaeta	4.74	9.49	1.71
<i>R. gigas</i>	0.02	3.89	0.87
<i>S. minor</i>	0.53	16.40	1.92
Siphonophorae	1.81	1.62	1.52
<i>Themisto</i> spp.	0.02	0.05	0.06
Aetideidae	0.02	2.31	
<i>P. antarctica</i>	0.37	1.18	
<i>Salpa</i> spp.	0.02	1.59	
Heterorhabdidae	0.51		0.02
<i>Oikopleura</i> spp.	0.03		0.14
<i>C. laticeps</i>		2.27	2.51
Euphausiidae		0.05	0.01
<i>T. macrura</i>		0.05	0.09
<i>A. antarctica</i>	0.48		
Calanoida	0.06		
Echinodermata	2.12		
Spinocalanidae	0.48		
<i>E. rostromagna</i>		0.05	
<i>E. superba</i>		1.44	
Fish egg		0.05	
<i>H. austrinus</i>		0.19	
<i>Amallothrix</i> sp.			0.02
<i>P. biloba</i>			0.01
<i>R. antarcticus</i>			0.53
Scolecitrichidae			0.28
Total abundance (ind m <sup>-3</sup> )	629.53	2,468.56	1,094.99
Species richness ( <i>r</i> )	31	32	31
Diversity ( <i>H'</i> )	1.84	2.98	2.60

Abundance of major contributor species/taxa are in bold

**Table 4** Average abundance (inds. m<sup>-3</sup>) and contribution (%) within each cluster group as a result of SIMPER

Species/taxon	Av. Abund Group 1	Av. Abund Group 3	Contrib. (%)	Cum. (%)
Groups 1 and 3 (average dissimilarity 28.75)				
Foraminifera	5.01	342.89	18.35	18.35
Copepod nauplii	12.69	74.74	8.57	26.92
<i>Fritillaria</i> spp.	0.48	21.43	6.77	33.69
<i>M. pygmaeus</i>	46.91	47.64	5.56	39.25
<i>O. similis</i>	72.30	227.77	4.65	43.90
Echinodermata	2.12	0.00	4.17	48.07
	Group 1	Group 2		
Groups 1 and 2 (average dissimilarity 38.94)				
<i>Limacina</i> spp.	0.93	466.04	14.61	14.61
Foraminifera	5.01	484.16	11.76	26.37
Copepod nauplii	12.69	393.53	9.43	35.80
<i>C. acutus</i>	0.67	42.66	6.44	42.25
<i>S. minor</i>	0.53	16.40	6.30	48.54
	Group 2	Group 3		
Groups 2 and 3 (average dissimilarity 27.82)				
<i>Limacina</i> spp.	466.04	1.11	17.89	17.89
<i>Fritillaria</i> spp.	23.44	21.43	7.19	25.08
<i>C. acutus</i>	42.66	2.78	6.16	31.23
<i>S. minor</i>	16.40	1.92	5.99	37.23
Copepod nauplii	393.53	74.74	5.58	42.81
Polychaeta	9.49	1.71	4.84	47.64

## Discussion

Community structure of micro- and meso-zooplankton in sea ice regions

Information on micro- and meso-zooplankton community structure in sea ice regions, including those of the Southern Ocean, is sparse. The present study is one of few to try to assess variations in distribution and abundance of zooplankton under different sea ice conditions using ship-based sampling. This study indicates that micro- and meso-zooplankton community structures vary according to sea ice distribution. Two characteristic distribution patterns of zooplankton occurred in both years: (1) the ubiquitous distribution of *O. similis* and *Oncaea* spp.; and (2) the regional distribution of foraminiferans which contributed highly to the separate characterization of zooplankton communities in this sea ice region.

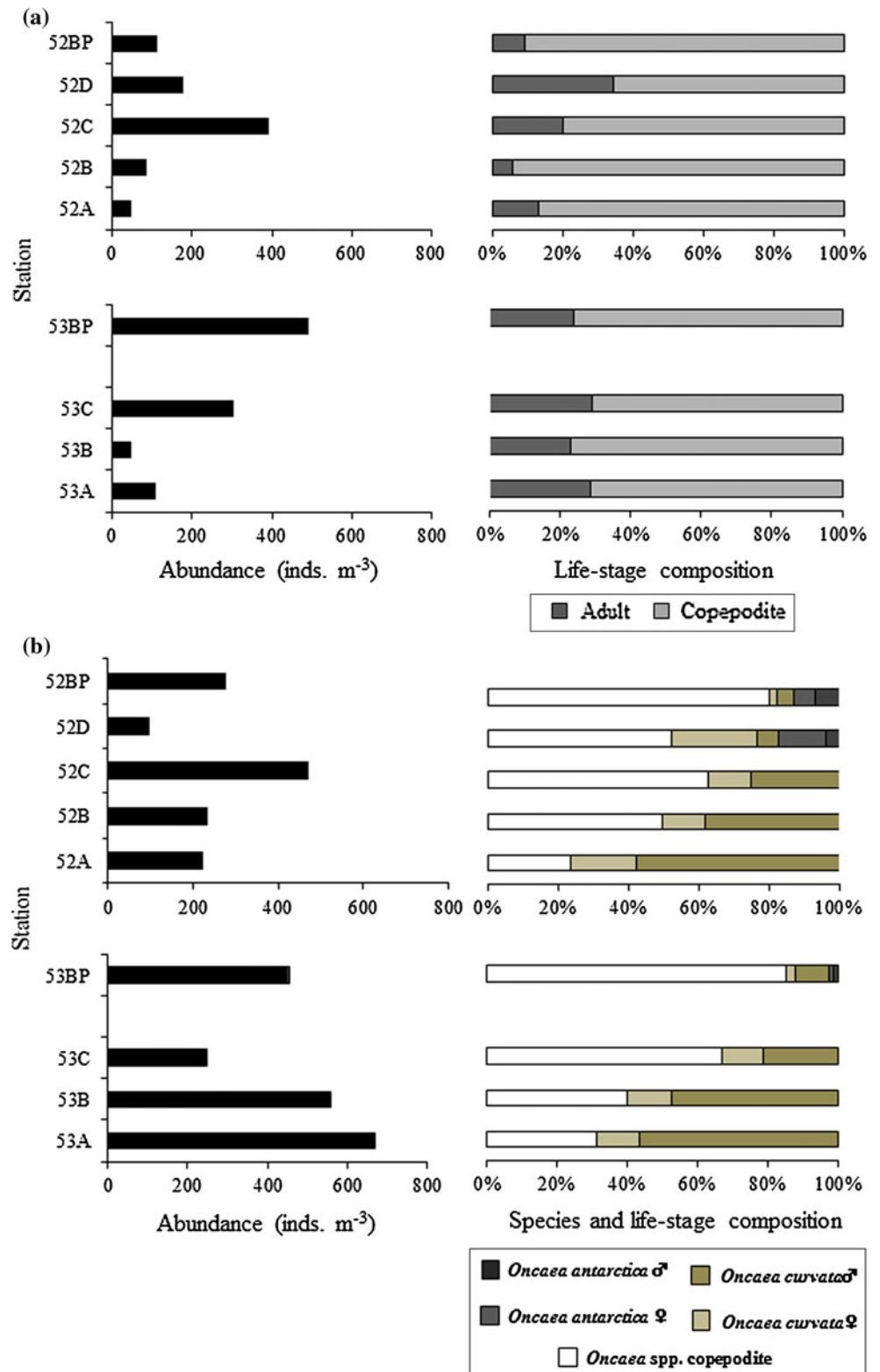
In addition, the pteropod *Limacina* spp. was the major contributor to total zooplankton abundance in the open ocean zone in 2012 (Fig. 3). Pteropods are ubiquitous components of Southern Ocean zooplankton communities and are extremely abundant regionally in the meso-zooplankton size fractions (Hunt et al. 2008). Regional and inter-annual variation in primary production is probably the

major determinant of spatial and temporal variability in pteropod densities (Seibel and Dierssen 2003). In the present study, no relationship between pteropod density and Chl *a* concentration could be found. Thus, factors other than primary production may also play a role in determining the occurrence of pteropods in sea ice regions.

### Mesh size effects on zooplankton sampling

The mesh size used for plankton sampling is a major factor affecting plankton selection and thus sample composition. In the Southern Ocean, several studies using plankton nets with 100- $\mu$ m mesh size have indicated that small copepods exceed the abundance, and sometimes the biomass, of larger species (Metz 1996; Atkinson and Sinclair 2000; Dubischar et al. 2002; Schnack-Schiel et al. 2008). Makabe et al. (2012) noted that a 100- $\mu$ m mesh net is suitable sampling gear to determine meso-zooplankton (200–2,000  $\mu$ m) community structure in the northern region of Lützw-Holm Bay, although it was not appropriate for copepod nauplii. In their study, the average abundance of zooplankton was  $2,664 \pm 1,991$  inds. m<sup>-3</sup>, and our data were within this range. In addition, Fukuchi and Tanimura (1981) observed a meso-zooplankton abundance of  $2,495.7 \pm 1,935.2$  inds. m<sup>-3</sup> at a fast ice station near St. 52A, a value also similar to

**Fig. 5** Abundance (inds. m<sup>-3</sup>) and life stage composition of *O. similis* (a) and *Oncaea* spp. (b) at all stations in 2011 and 2012

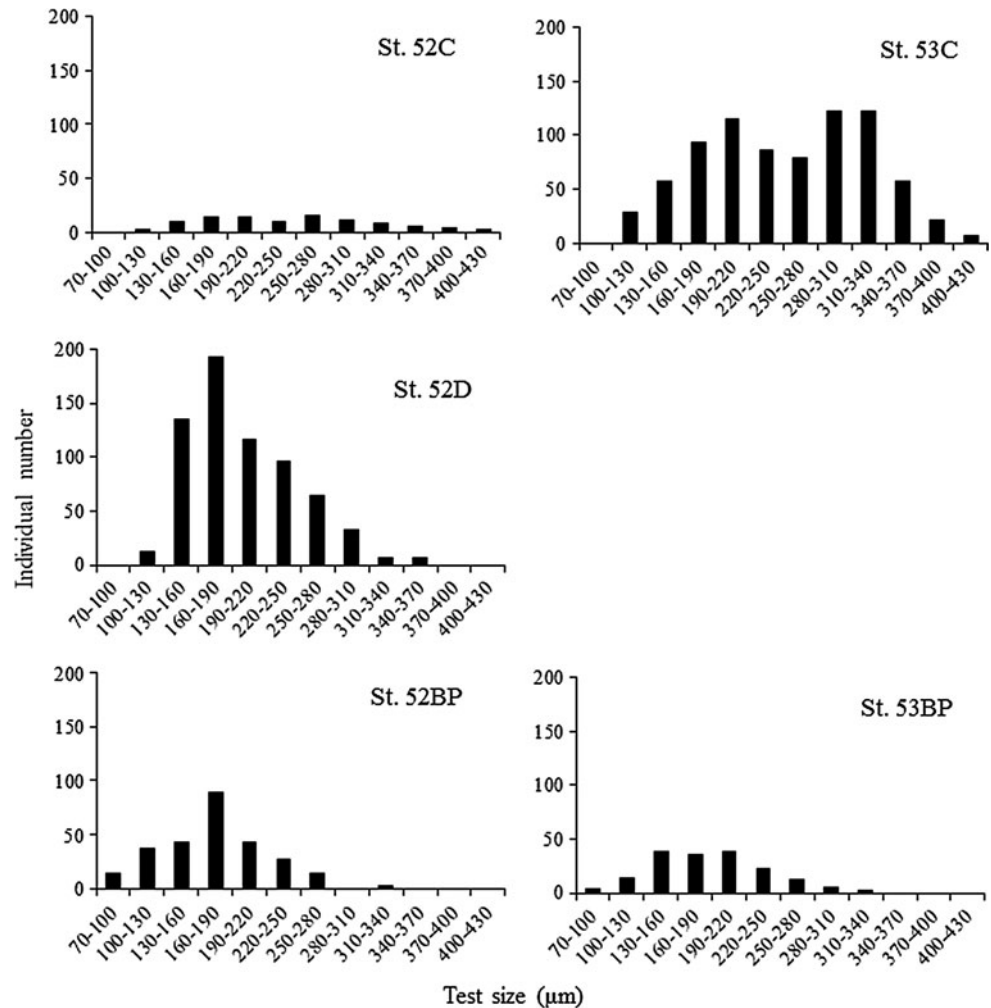


our own for the fast ice stations. Therefore, the present data seem appropriate for the sea ice regions of the Southern Ocean.

Nonetheless, it is likely that the abundance of some taxa has been underestimated. Over 80 % of planktonic foraminiferans are smaller than 100 μm, and only adults



**Fig. 6** Size frequency distribution of foraminifera at northern stations in 2011 and 2012



are larger than 200  $\mu\text{m}$  (Berger 1971; Brummer et al. 1986; Spindler and Dieckmann 1986). Similarly, for *O. similis* and *Oncaea* spp., it is difficult to assess the population structure for copepodite stages I(CI) and II (CII) or for copepod nauplius stages, as the body size of these juveniles is often  $<100 \mu\text{m}$ . Thus, the sampling regime used in the present study cannot fully represent micro-zooplankton and may underestimate the juvenile stages of meso-zooplankton. However, foraminiferans and copepods, including individuals smaller than 100  $\mu\text{m}$ , were clearly abundant within the samples at pack ice and open ocean stations where Chl *a* concentrations were higher in both years (Table 3). Thus, despite their underestimate, a clear distribution pattern could be discerned.

The ubiquitous distribution of *Oithona similis* and *Oncaea* spp.

*Oithona similis* and *Oncaea* spp. are considered to be key components of the planktonic food web of the Southern Ocean (Atkinson 1998). They are the most numerically

abundant copepod genera (Hunt and Hosie 2006a, b) and can form a significant proportion of the zooplankton biomass despite their small size ( $<1 \text{ mm}$ ). For example, they form up to 20 % of the total copepod biomass in the Weddell Sea (Schnack-Schiel et al. 1998). In the present study, they were the most abundant organisms in all cluster groups (Table 3).

*Oithona* spp. and *Oncaea* spp. are known to be omnivorous (Lampitt and Gamble 1982; Turner 1986). *O. antarctica* has been observed feeding on small copepods (Hopkins et al. 1993). *O. similis* are able to adapt to the low phytoplankton densities of the permanent open ocean zone (Takahashi et al. 2010). In the present study, *Oncaea* spp. occurred in high densities in the fast ice area where the Chl *a* concentration was the lowest. The omnivorous nature of these species may thus allow them to exploit areas of relatively low primary productivity, unavailable to purely herbivorous species. In addition to omnivory, these species have a behavioral strategy which may increase their intake of available microalgae. These copepods have been found to exhibit diel vertical migration synchronized with the

sinking of microalgae from melting sea ice (Tanimura et al. 2008). The range of possible food sources and the feeding behavior of these copepods make them highly adaptable and thus lead to their ubiquitous distribution throughout the sea ice region.

*Oncaea curvata* is regarded as a deep-water species (Hardy and Gunther 1935; Seno et al. 1963). In ice-covered surface waters, Ainley et al. (1986) noted an abundance of crustacean species thought to occur only below 300 m. They suggested that the physical environment, in particular light intensity and quality, immediately beneath the ice was reminiscent of a mesopelagic environment. The pelagic environment in the fast ice area of our study would be similar to that of the deeper water where *Oncaea* spp. is generally found. The deep-water calanoid copepods, *Aetideopsis antarctica* and *Spinocalanus* sp. (Schnack-Schiel et al. 2008), were also found only at the fast ice stations in our study (Table 3).

#### The regional distribution of foraminiferans

Cluster analysis clearly separated groups according to the presence or absence of foraminiferans, which were in high abundance at the northern stations, in particular, the pack ice stations. Only one species of planktonic foraminiferans, *Neogloboquadrina pachyderma* Ehrenberg, lives in Antarctic waters, and the occurrence of this species in Lützow-Holm Bay was noted in the first JARE (Uchio 1960). Lipps and Krebs (1974) reported a high density of *N. pachyderma* in Antarctic floating ice, although it was not certain whether they were alive or merely preserved in the ice. Further studies by Spindler and Dieckmann (1986) revealed that only juveniles and sub-adults were found in high densities and that they were alive in the sea ice. Subsequently, Dieckmann et al. (1991) showed that foraminiferans in ice cores were mainly found in granular ice and that their numbers were much higher in the pack ice. Foraminiferans attach to frazil ice whose growth result in granular ice using their rhizopods and stay in the sea ice as part of their life cycle in the Southern Ocean (Eicken 1992). The ice community with its high density of foraminiferans is released into the water column as the sea ice melts. In the present study, the northern stations were areas where sea ice was melting or had recently melted. The high densities of foraminiferans found at these stations seem likely to reflect the release of foraminiferans from the ice.

Analysis of the size distribution of foraminiferans tests in sea ice cores has indicated that large living individuals (200–300  $\mu\text{m}$ ) are found in the lower part of the core (Spindler and Dieckmann 1986). Thus, it seems likely that in areas where the sea ice is in the process of melting the size of foraminiferans would be larger. Indeed, at the pack ice stations (52C and 53C), where the ice was just melting,

a greater proportion of larger individuals was recorded. In addition, a trend in foraminiferans size distribution seemed apparent among stations with a greater proportion of smaller individuals at the open ocean stations (Fig. 6). If foraminiferans were released from melting sea ice, it might also be expected that their abundance would increase from the pack ice stations toward the open ocean stations. However, the densities at open ocean stations varied between years, and in 2012, the density at station 53BP was less than half of that at the pack ice station 53C. In addition, the numbers of larger individuals at open ocean stations were markedly less than those at the pack ice stations in both years. Adult specimens are mainly found below 200 m (Spindler and Dieckmann 1986); therefore, larger individuals may have sunk to deeper levels than the 150 m depth from which hauls were taken at the open ocean stations at the time of sampling. Another possibility is that the distribution of foraminiferans was related to Chl *a* concentration. The polar species *N. pachyderma* is known to be omnivorous but to exhibit a strong preference for phytoplankton (Hemleben et al. 1989; Lee and Anderson 1991). Bergami et al. (2009) and Takahashi et al. (2010) found correlations between foraminiferans abundance and Chl *a* concentration. In the present study, the Chl *a* concentration generally increased from fast ice to pack ice to open ocean stations. Thus, although melting ice and increased phytoplankton abundance may reflect the occurrence of foraminiferans at pack ice and open ocean stations compared with the fast ice stations, it does not explain variations between pack ice and open water stations. Foraminiferans did not show a clear distribution pattern in response to environmental conditions as identified by Hunt and Hosie (2006a) and Swadling et al. (2010).

The dynamics of sea ice around Antarctica is a major factor affecting the distribution and composition of zooplankton communities in these areas. This preliminary study indicates that, like macro-zooplankton, the distribution of micro- and meso-zooplankton varies between fast ice, pack ice and open ocean areas. While in general, *O. similis* and *Oncaea* spp. were ubiquitous, being able to adapt to fast ice, pack ice or open ocean, differences were observed in the distributions of copepodite stages compared with adults. Foraminiferans were only found in pack ice and open ocean stations. Foraminiferans have been found in the guts of higher trophic level organisms, such as polychaetes, fish, and tunicates (Hemleben et al. 1989), and they feed on phytoplankton, ciliates, and some copepods (Hemleben et al. 1989; Lee and Anderson 1991). The life cycle of these foraminiferans may be dependent on sea ice. Changes in sea ice dynamics and coverage because of climate change have major implications for the distribution of micro- and meso-zooplankton and for the ecology of the sea ice regions as a whole. Given this and the

scarcity of studies of micro- and meso-zooplankton communities in sea ice regions, much more extensive and ongoing research is required in this field in the future.

**Acknowledgments** We would like to thank the officers and crew of the icebreaker *Shirase* and the expedition members of the Japanese Antarctic Research Expedition (JARE) cruises 52 and 53 for collecting data and zooplankton samples along with the CTD data.

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## References

- Ainley DG, Fraser WR, Sullivan CW, Torres JJ, Hoplins TL, Smith WO (1986) Antarctic mesopelagic micronekton: evidence from seabirds that pack ice affects community structure. *Science* 232:847–849
- Atkinson A (1998) Life cycle strategies of epipelagic copepods in the Southern Ocean. *J Mar Syst* 15:289–311
- Atkinson A, Sinclair JD (2000) Zonal distribution and seasonal vertical migration of copepod assemblages in the Scotia Sea. *Polar Biol* 23:46–58
- Bergami C, Capotondi L, Langone L, Giglio F, Ravaioi M (2009) Distribution of living planktonic foraminifera in the Ross Sea and the Pacific sector of the Southern Ocean (Antarctica). *Mar Micropaleontol* 73:37–48
- Berger WH (1971) Sedimentation of planktonic foraminifera. *Mar Geol* 11:325–358
- Brummer GJA, Hemleben C, Spindler M (1986) Planktonic foraminiferal ontogeny and new perspectives for micropaleontology. *Nature* 319:50–52
- Cavaliere DJ, Parkinson CL, Gloersen P, Zwally HJ (1996) Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS passive microwave data. Version 1.0. NSIDC, Colorado
- Cavaliere DJ, Markus T, Comiso JC (2004) AMSR-E/aqua daily L3 12.5 km brightness, temperature, sea ice concentration, and snow depth polar grids V002. NSIDC, Colorado
- Chiba S, Ishimaru T, Hosie GW, Fukuchi M (2001) Spatio-temporal variability of zooplankton community structure off east Antarctica (90 to 160°E). *Mar Ecol Prog Ser* 216:95–108
- Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth
- Dieckmann GS, Spindler M, Lange MA, Ackley SF, Eicken H (1991) Antarctic sea ice: a habitat for the foraminifer *Neogloboquadrina pachyderma*. *J Foraminifer Res* 21:182–189
- Dubischar CD, Lopes RM, Bathmann UV (2002) High summer abundances of small pelagic copepods at the Antarctic polar front—implications for ecosystem dynamics. *Deep-Sea Res II* 49:3871–3887
- Eicken H (1992) The role of sea ice in structuring Antarctic ecosystems. *Polar Biol* 12:3–13
- Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analyzing multispecies distribution patterns. *Mar Ecol Prog Ser* 8:37–52
- Fukuchi M, Sasaki H (1981) Phytoplankton and zooplankton standing stocks and downward flux of particulate material around fast ice edge of Lützow-Holm Bay, Antarctica. *Mem Natl Inst Polar Res Ser E (Biol Med Sci)* 34:13–36
- Fukuchi M, Tanimura A (1981) A preliminary note on the occurrence of copepods under sea ice near Syowa Station, Antarctica. *Mem Natl Inst Polar Res Ser E (Biol Med Sci)* 34:37–43
- Fukuchi M, Tanimura A, Ohtsuka H (1985) Zooplankton community conditions under sea ice near Syowa Station, Antarctica. *Bull Mar Sci* 37:518–528
- Hardy C, Gunther ER (1935) The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927. University Press, Cambridge
- Hemleben C, Spindler M, Anderson OR (1989) Modern planktonic foraminifera. Springer, New York
- Hempel G (1985a) Antarctic marine food web. In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic nutrient cycles and food webs. Springer, Berlin, pp 266–270
- Hempel G (1985b) On the biology of polar seas, particularly the Southern Ocean. In: Gray JS, Christiansen ME (eds) Marine biology of polar regions and effects of stress on marine organisms. Wiley, Chichester, pp 3–34
- Hopkins TL, Lancraft TM, Torres JJ, Donnelly J (1993) Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988). *Deep-Sea Res I* 40:81–105
- Hosie GW (1994) The macrozooplankton communities in the Prydz Bay region, Antarctica. In: El-Sayed SZ (ed) Southern ocean ecology: the BIOMASS perspective. University Press, Cambridge, pp 93–123
- Hunt BPV, Hosie GW (2006a) The seasonal succession of zooplankton in the Southern Ocean south of Australia, part I: the seasonal ice zone. *Deep-Sea Res I* 53:1182–1202
- Hunt BPV, Hosie GW (2006b) The seasonal succession of zooplankton in the Southern Ocean south of Australia, part II: the sub-Antarctic to polar frontal zones. *Deep-Sea Res I* 53:1203–1223
- Hunt BPV, Pakhomov EA, Hosie GW, Siegel V, Ward P, Bernard K (2008) Pteropods in Southern Ocean ecosystems. *Prog Oceanogr* 78:193–221
- Lampitt RS, Gamble JC (1982) Diet and respiration of the small planktonic marine copepod *Oithona nana*. *Mar Biol* 66:185–190
- Lee JJ, Anderson OR (1991) Biology of foraminifera. Academic Press, New York
- Lipps JH, Krebs WN (1974) Planktonic foraminifera associated with Antarctic sea ice. *J Foraminifer Res* 4:80–85
- Loeb V (2007) Environmental variability and the Antarctic marine ecosystem. In: Vasseur DA, McCann KS (eds) The impact of environmental variability on ecological systems. The Peter Yodzis fundamental ecology series, vol 2, pp 197–225
- Makabe R, Tanimura A, Fukuchi M (2012) Comparison of mesh size effects on mesozooplankton collection efficiency in the Southern Ocean. *J Plankton Res* 34:432–436
- Massom RA, Stammerjohn SE (2010) Antarctic sea ice change and variability—physical ecological implications. *Polar Sci* 4:149–186
- Metz C (1996) Lebensstrategien dominanter antarktischer Oithonidae (Cyclopoida, Copepoda) und Oncaeidae (Poecilostomatoida, Copepoda) im Bellingshausenmeer. *Ber Polarforsch* 207:1–123
- Motoda S (1959) Devices of simple plankton apparatus. *Mem Fac Fish Hokkaido Univ* 7:73–94
- Schnack-Schiel SB, Hagen W, Mizdalski E (1998) Seasonal carbon dynamics of Antarctic copepods in the eastern Weddell Sea. *J Mar Syst* 17:305–311
- Schnack-Schiel SB, Michels J, Mizdalski E, Schodlok MP, Schröder M (2008) Composition and community structure of zooplankton in the sea ice-covered western Weddell Sea in spring 2004—with emphasis on calanoid copepods. *Deep-Sea Res II* 55:1040–1055
- Seibel BA, Dierssen HM (2003) Cascading trophic impacts of reduced biomass in the Ross Sea Antarctica: just the tip of the iceberg? *Biol Bull* 205:93–97

- Seno J, Komaki Y, Takeda A (1963) Reports on the biology of the “Umitaka-Maru” expedition. Plankton collected by the “Umitaka-Maru” in the Antarctic and adjacent waters, with special references to copepod. *J Tokyo Univ Fish* 49:53–62
- Spindler M, Dieckmann GS (1986) Distribution and abundance of the planktic foraminifer *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea (Antarctica). *Polar Biol* 5:185–191
- Suzuki K, Kishino M, Sasaoka K, Saitoh S, Saino T (1998) Chlorophyll-specific absorption coefficients and pigments of phytoplankton off Sanriku, Northwestern North Pacific. *J Oceanogr* 54:517–526
- Swadling KM, Kawaguchi S, Hosie GW (2010) Antarctic mesozooplankton community structure during BROKE-west (30°E–80°E), January–February 2006. *Deep-Sea Res II* 57:887–904
- Takahashi KT, Hosie GW, Kitchener JA, McLeod DJ, Odate T, Fukuchi M (2010) Comparison of zooplankton distribution patterns between four seasons in the Indian Ocean sector of the Southern Ocean. *Polar Sci* 4:317–331
- Takahashi KT, Iida T, Hashida G, Odate T (2012) Field test of “ice-fence” for oceanographic observation in the sea-ice zone. *Antarct Rec* (in press)
- Tanimura A, Fukuchi M, Hoshiai T (1986) Seasonal change in the abundance of zooplankton and species composition of copepods in the ice-covered sea near Syowa Station, Antarctica. *Mem Natl Inst Polar Res Spec Issue* 40:212–220
- Tanimura A, Hattori H, Miyamoto Y, Hoshiai T, Fukuchi M (2008) Diel changes in vertical distribution of *Oithona similis* (Cyclopoida) and *Oncaea curvata* (Poecilostomatoida) under sea ice in mid-summer near Syowa Station, Antarctica. *Polar Biol* 31:561–567
- Turner JT (1986) Zooplankton feeding ecology: contents of fecal pellets of the cyclopoid copepods *Oncaea venusta*, *Corycaeus amazonicus*, *Oithona plumifera*, and *O. simplex* from the Northern Gulf of Mexico. *Mar Ecol* 7:289–302
- Uchio T (1960) Planktonic foraminifera of the Antarctic Ocean. Biological results of the Japanese Antarctic research expedition 11. Seto Mar Biol Lab, Wakayama
- Uitz J, Claustre H, Morel A, Hooker SB (2006) Vertical distribution of phytoplankton communities in open ocean: an assessment based on surface chlorophyll. *J Geophys Res C Oceans* 111:C08005. doi:10.1029/2005JC003207