

Community structure of pelagic cnidarians off Adélie Land, East Antarctica, during austral summer 2008

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Abstract Some studies have suggested that pelagic cnidarians are important components of the Southern Ocean ecosystem due to their high abundance and diversity and their high predatory effects, although little information on these animals is available. Thus, we examined the spatial distribution of pelagic cnidarians from the oceanic to neritic zone off Adélie Land, East Antarctica. Discrete depth sampling was conducted from the surface to 2,000 m depth from late January to early February 2008. In total, 3347 individuals representing 45 species/taxa from eight orders were collected. Cluster analysis revealed three major clusters: (1) an epipelagic group in the oceanic zone composed mainly of *Peganthia martagon*, the abundance and species diversity of which were very low; (2) a meso- and bathy-pelagic group characterised by high abundance and species diversity with dominance of *Dimophyes arctica*, *Vogtia serrata*, and *Haliceas minimum*; and (3) a neritic group represented by a high abundance of *Diphyes antarctica*.

Cnidarian communities in the epipelagic zone were divided by hydrographic structures such as the Southern Boundary of the Antarctic Circumpolar Current and Antarctic Slope Front, whereas those in the meso- and bathy-pelagic layers dominated by circumpolar deep water were relatively stable with higher diversity throughout the oceanic zone.

Keywords Siphonophorae · Medusae · Spatial distribution · Vertical distribution · Cluster analysis · Discrete depth sampling

Introduction

In the last few decades, high abundances and biomass of pelagic cnidarians have been reported in the Southern Ocean. In particular, ecological and faunal aspects of those animals have been well documented in the Weddell Sea and west Antarctic Peninsular regions of west Antarctica (Pagès et al. 1994; Pagès and Schnack-Schiel 1996; Pugh et al. 1997; Panasiuk-Chodnicka and Żmijewska 2010). Some studies have also indicated that these organisms may have strong predatory effects on other zooplankton taxa and fish (Mackie et al. 1987; Pagès 1997; Panasiuk-Chodnicka and Żmijewska 2010). In addition, pelagic cnidarians exhibit high species diversity, especially in meso- and bathy-pelagic layers (Pagès and Kurbjeweit 1994; Pagès et al. 1994, 1997; Hosia et al. 2008). Discrete depth samplings from the surface to 2,000 m depth in Lützow–Holm Bay in the western part of East Antarctica have demonstrated high diversity of medusae at 200–2,000 m depth (Toda et al. 2010).

To date, data on the distribution of cnidarians are scarce, not only for the meso- and bathy-pelagic realm in the

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Southern Ocean, but also for the neritic zone. Swadling et al. (2011) analysed Bongo-net samples from Adélie Land from 2004 to 2008 and found that changes in the zooplankton community were related to the thickness and extent of sea ice cover, the position and extent of the Mertz Polynya, local wind conditions and bathymetric features, although very little attention was paid to cnidarians in this study, and they were identified only to higher taxa (e.g. Medusa, Siphonophora, *Diphyes* spp.).

In East Antarctica, BROKE and BROKE-west surveys by Australian researchers have demonstrated hydrographic features and associated distribution patterns of marine biota, although the surveys only focused on the epipelagic layer (Nicol and Raymond 2012). These surveys revealed that distances from the continent to the Southern Boundary (SB) of the Antarctic Circumpolar Current (ACC) differ substantially between the western and eastern part of East Antarctica, resulting in differences between regions in the extent of sea ice and the distribution patterns of animals (Nicol and Raymond 2012).

In the present study, we examined the spatial distribution of pelagic cnidarians from the oceanic to neritic zone off Adélie Land using discrete depth samplings from the surface to 2,000 m. The present study will provide new information on pelagic cnidarian distribution patterns from the neritic to oceanic zones in the eastern Indian sector, adding fundamental knowledge for a better understanding of Antarctic marine ecosystems. In addition, our results will offer a robust benchmark (baseline) to verify marine ecosystem changes associated with future global climate change (Hosie et al. 2011).

Materials and methods

Net sampling and hydrographic observation

This study was conducted as a part of the Collaborative East Antarctic Marine Census (CEAMARC). During CEAMARC, a multidisciplinary survey conducted off Adélie Land, discrete depth net samplings from the surface to 2,000 m depth were undertaken to examine zooplankton and fish assemblages and their spatial distribution patterns during summer (Hosie et al. 2011). Previous reports have already presented CEAMARC data on euphausiids and fish (Amakasu et al. 2011; Koubbi et al. 2011; Moteki et al. 2011; Ono et al. 2011). The CEAMARC survey covered regions from the oceanic to neritic zones off Adélie Land, where sea ice usually retreats to a large extent (Nicol and Raymond 2012).

The cruise was conducted on the Training and Research Vessel (TR/V) *Umitaka-Maru* of the Tokyo University of Marine Science and Technology (TUMSAT) from 28 January to 8 February 2008 off Adélie Land and its

adjacent waters in the Southern Ocean (Table 1; Fig. 1). Zooplankton were sampled at 16 stations. Six northern stations (Stns. 14–19) were located in the oceanic zone (bottom depth >3,000 m), two intermediate stations (Stns. 20 and 21) were situated along the continental slope (1,000–3,000 m) and the remaining southern stations (Stns. 11, 22–27, 42) were located in the neritic zone (<1,000 m; Fig. 1).

A rectangular midwater trawl (RMT) 1 + 8 equipped with three sets of opening/closing net systems (Baker et al. 1973) was used in this study. The present study only examined samples from the RMT 8 (8-m² nominal mouth opening with 4.5-mm mesh). Two tows were deployed at each station, one from 200 to 0 m depth (0–50–100–200 m) and a second from 2,000 to 200 m depth (200–500–1,000–2,000 m; Table 1), although the maximum sampling depths at stations 15, 17, 19, and 21 were 1,000 m. At the remaining stations where bottom depths were shallower than 1,000 m, maximum sampling depths were 200 m (Stns. 22–26) or 500 m (Stns. 42, 27 and 11). At Stns. 11 and 19, the RMT net did not open or close during the 0–200 m tows due to mechanical trouble. The protocols used for net towing and for calculating filtered water volume were described by Moteki et al. (2009). Filtered water volumes are shown in Table 1. Most of the gelatinous organisms were carefully sorted out from samples onboard; then, those were identified and counted. The remaining animals were fixed onboard in a 5 % buffered formalin seawater solution.

Salinity and temperature data were collected at each sampling station before the RMT tow using a conductivity/temperature/depth (CTD) profiler (SBE911; Sea-Bird Electronics, Bellevue, WA, USA). Terminology for water masses follows Bindoff et al. (2000) and Tomczak and Liefbrink (2005). The location of the SB was estimated from potential temperature, following Sokolov and Rintoul (2002).

Sample analysis

Pelagic cnidarians were identified and counted under a binocular dissecting microscope. The numbers of physonect colonies were roughly estimated by assuming that 20 nectophores represented a single colony, and for the calycophoran *Vogtia serrata* that 10 nectophores represented a single colony, following Pagès et al. (1996) and Hosia et al. (2008). Therefore, groups of nectophores numbering from 1 to 20 (or 1–10) were assumed to represent one animal. These estimates were used for the cluster analysis as the number of individual colonies. For the calycophoran siphonophore *Rosacea plicata*, the number of individuals (colonies) was estimated by assuming two nectophores per colony. For the remaining siphonophores, the greater number of either anterior or posterior nectophores was used to estimate the number of colonies. Scientific names follow

Table 1 Data of a rectangular midwater trawl samplings off Adélie Land and George V Land during austral summer in 2008

Stn.	Date	Time (UTC)	Bottom depth (m)	Latitude (S)	Longitude (E)	Net depth (m)	Day/night	Vol. filtered (m ³) (top, middle, bottom)
14	28 Jan.	23:13–00:10	4,275	61°59.79'	139°59.91'	0–50–100–200	D	6,182, 6,182, 7,212
	29 Jan.	02:00–03:40	4,252			200–500–1,000–2,000	D	10,819, 10,303, 10,303
15	29 Jan.	21:33–22:25	3,941	62°29.71'	140°00.35'	0–50–100–200	D	7,212, 6,181, 6,697
	29 Jan.	23:34–00:50	3,940			0–200–500–1,000	D	8,242, 9,273, 11,334
16	30 Jan.	15:01–16:03	3,778	62°59.88'	139°59.95'	0–50–100–200	N	7,212, 7,212, 8,242
	31 Jan.	19:06–20:34	3,804			200–500–1,000–2,000	DA	12,364, 9,273, 8,758
17	31 Jan.	06:53–08:05	3,804	63°30.06'	139°59.75'	0–50–100–200	D	7,728, 7,728, 9,788
	31 Jan.	09:19–10:53	3,807			0–200–500–1,000	D	8,758, 9,273, 10,819
18	1 Feb.	01:56–03:07	3,705	63°59.91'	140°00.01'	0–50–100–200	D	7,212, 7,728, 7,728
	1 Feb.	05:03–07:00	3,717			200–500–1,000–2,000	D	10,303, 9,788, 19,577
19	1 Feb.	16:59–18:47	3,357	64°30.07'	139°59.99'	0–200–500–1,000	DA	12,879, 16,486, 15,970
20	2 Feb.	15:49–17:01	2,797	65°07.09'	139°50.12'	0–50–100–200	N	7,121, 7,728, 9,273
	2 Feb.	19:40–20:50	2,843			200–500–1,000–2,000	D	7,728, 10,303, 19,061
21	3 Feb.	07:25–08:34	1,366	65°28.62'	139°51.66'	0–50–100–200	D	8,242, 8,758, 8,242
	3 Feb.	05:20–06:51	1,853			0–200–500–1,000	D	15,970, 6,182, 11,849
22	3 Feb.	18:23–19:18	291	65°44.45'	140°06.26'	0–50–100–200	DA	8,758, 7,728, 7,212
23	4 Feb.	08:00–09:02	193	65°59.96'	140°00.04'	0–50–100–175	D	7,212, 7,212, 7,728
42	6 Feb.	11:34–12:40	478	66°19.96'	139°59.70'	0–50–100–200	D*	6,697, 7,212, 8,758
	6 Feb.	09:57–10:56	450			0–200–425	D*	8,758, 8,758
24	6 Feb.	22:33–23:50	172	66°20.09'	140°40.44'	0–50–100–150	D*	7,212, 6,697, 6,697
25	7 Feb.	03:21–04:14	249	66°20.36'	141°22.83'	0–50–100–200	D*	9,273, 8,242, 8,758
26	7 Feb.	16:54–18:05	254	66°19.87'	142°00.06'	0–50–100–200	D*	8,758, 8,242, 8,242
27	8 Feb.	03:28–04:43	401	66°19.84'	142°40.38'	0–50–100–200	D*	8,242, 8,242, 9,788
	8 Feb.	01:52–02:57	422			0–200–390	D*	11,334, 10,303
11	8 Feb.	17:00–18:02	722	66°19.99'	143°19.91'	0–200–500	D*	10,303, 11,849

D day, N night, DA dawn, D* the sun never set all day

Kramp (1968) and Pugh (1999). Identifications were made following Kramp (1957, 1959, 1968) and Bouillon (1999) for medusae, and Pugh (1999) and Bouillon et al. (2004) for Siphonophorae. For *Leuckartiara brownei* reference was also made to Bouillon et al. (2000). For the siphonophore genus *Rosacea*, we followed Haddock et al. (2005) and Mapstone (2009), and for the siphonophore family Clausophyidae, we also referred to Pugh (2006). When these references were not sufficient, the original descriptions were consulted. Abundances are shown as the number/1,000 m³ water ($n \cdot 10^3 \text{ m}^{-3}$).

Data analysis

The Bray–Curtis dissimilarity index was used to compare cnidarian species composition with respect to station and depth (Field et al. 1982). Abundances were $\log_{10}(n + 1)$ -transformed to decrease the importance of dominant species. Samples for which fewer than five specimens were caught and species/taxa for which <1 % of the total number was recorded were excluded from this analysis.

Unweighted-pairs group linkage and non-metric multidimensional scaling (nMDS) were performed based on similarity. The similarity percentage (SIMPER) routine identified the species contributing to similarity within the observed clusters. $Si/SD(Si)$ values in the SIMPER analysis indicate levels that a given species is typical to all stations in the cluster (Clarke and Warwick 2001). These statistical analyses were conducted using the software package PRIMER v6 (PRIMER-E; Clarke and Gorley 2006).

Results

Hydrography

The SB, defined by the southern limit of maximum θ warmer than 1.5 °C (Sokolov and Rintoul 2002), was located at 63°30'–64°00'S (Fig. 2). Across the upper continental slope and shelf break, a sub-surface horizontal density gradient known as the Antarctic Slope Front (ASF; Jacobs 1991) was observed between Stns. 21 and 22 (Fig. 2). The ASF was

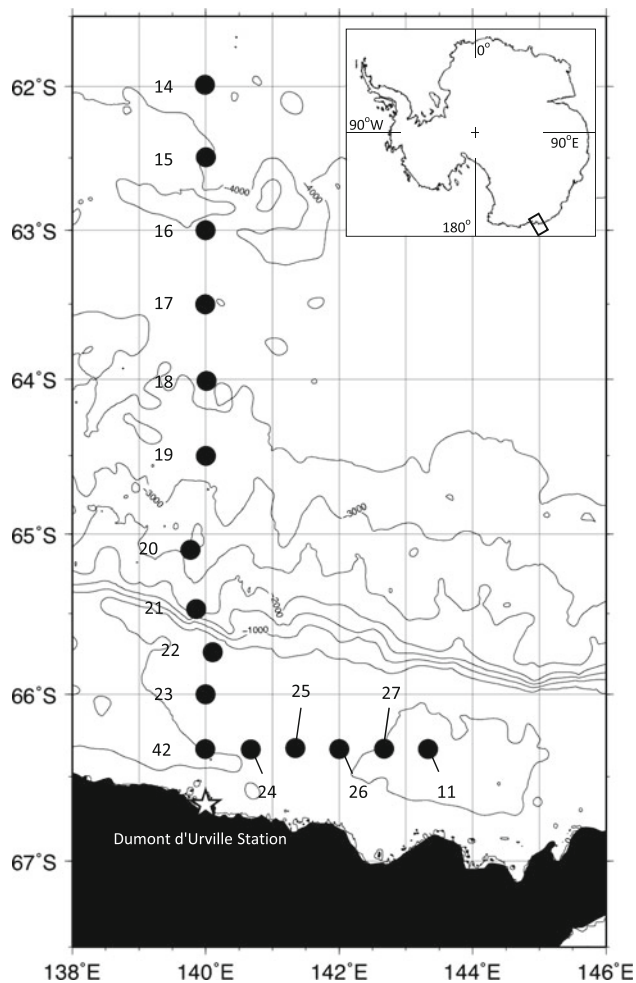


Fig. 1 Sampling stations (black circles) off Adélie Land during austral summer 2008

coincident with the 0 °C isotherm (Ainley and Jacobs 1981). Circumpolar deep water (CDW: $\theta > 1.8$ °C, salinity < 34.7 ; Bindoff et al. 2000) was distributed below about 200 m in the area north of the SB, and modified circumpolar deep water (MCDW: $\theta < 1.8$ °C, salinity < 34.7 ; Bindoff et al. 2000) was found south of the SB (Fig. 2). Antarctic winter water (WW), with θ between -1.9 and -1.5 °C and salinity between 34.2 and 34.5 (Tomczak and Liefink 2005), occurred near the continental slope. Antarctic Surface Water (AASW: $\theta = -1.8$ to 2.0 °C, salinity > 34.0 ; Bindoff et al. 2000) was observed in the neritic zone. Along 66°20'S, WW was found at three stations (Stns. 24–26), and shelf water (SW: $\theta < -1.7$ °C, salinity < 34.7 ; Bindoff et al. 2000) was observed at stations 27 and 11 (Fig. 2).

Overview of the cnidarian community

In total, 3,347 individuals representing 45 species/taxa from eight orders were collected (Table 2).

Siphonophorae contributed 35 % of the total abundance, and Narcomedusae contributed 21 % in the oceanic zone (Stns. 14–19). In the oceanic zone, *Pegantha martagon* (Narcomedusae) was dominant, comprising 20 % (3.7 individuals 10^3 m^{-3} per station) of the total abundance, followed by *Dimophyes arctica* (Siphonophorae, 11 %), *Haliscera conica* (Trachymedusae, 9.0), and *V. serrata* (Siphonophorae, 9.0 %) (Table 2). *P. martagon* contributed 94 % of the total narcomedusan abundance. The 13 rare species, which comprised < 0.1 % of the total, were primarily caught in the oceanic zone.

In the continental slope area (Stns. 20 and 21), *Diphyes antarctica* (Siphonophorae) was dominant, comprising 29 % (8.9 individuals 10^3 m^{-3} per station) of the total abundance, followed by *D. arctica* (22 %), *H. conica* (6.6 %), and *P. martagon* (6.5 %). These four species were caught at both stations (Table 2). Siphonophorae contributed 60 % of the total abundance, and Trachymedusae contributed 15 %. *H. conica* contributed 43 % of the total trachymedusan abundance.

In the neritic zone (Stns. 22–11), *D. antarctica* was dominant, comprising 73 % (19 individuals 10^3 m^{-3} per station) of the total abundance, followed by *D. arctica* (22 %), *P. martagon* (1.1 %), and *Pyrostephos vanhoeffeni* (Siphonophorae, 0.9 %). *D. antarctica* was caught at all stations, while *D. arctica* was also caught at all stations except Stn. 11. Siphonophorae contributed 97 % of the total abundance.

Cnidarian abundances in the 0–100-m layers were very low at all sampling stations (Figs. 3, 4), whereas high abundances were recorded in the 100–200-m layer in the neritic zone. The highest abundance was observed at 200–500 m at the deeper Stn. 42. Siphonophores accounted for a large proportion of the neritic cnidarians (Fig. 4). In the oceanic and continental slope zones, cnidarians were more abundant in 200–2,000-m layers than in epipelagic layers (Figs. 3, 4). In particular, high abundances were observed in the 200–500-m layer in the continental slope zone, where both medusae and siphonophores were abundant (Fig. 4). At 0–200 m at Stns. 16 and 20, where samplings were conducted at night, abundances were higher than values observed in the same layers at other stations. In the oceanic zone, siphonophores were abundant at depths below 200 m, and medusae were abundant deeper than 500 m.

High abundances were recorded widely on the right half (salinity $> \sim 34.2$) of the potential temperature and salinity diagram (T–S diagram) (Fig. 5, upper panel), with two main clusters being observed on the T–S diagram. A cluster near the bottom of the diagram (low temperature and moderate salinity water mass) showed high abundances in neritic waters, and another cluster plotted in the upper-right corner (warmer, higher salinity water mass) on the T–S diagram indicated high abundances in the meso- and bathypelagic waters associated with the MCDW and CDW.

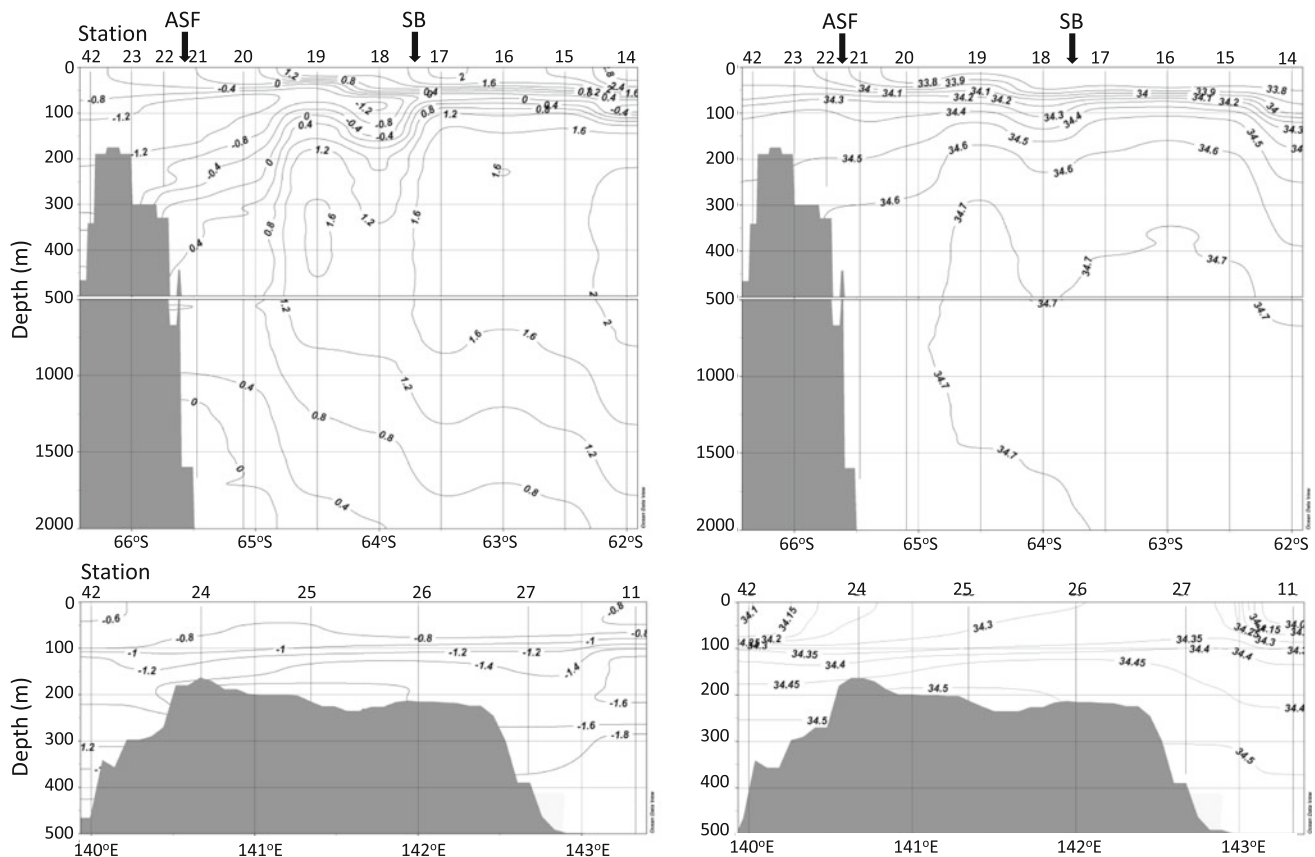


Fig. 2 Vertical sections of potential temperature (°C, left) and salinity (right) along the 140°E (top) and 66°20'S transects (bottom). SB Southern Boundary of the Antarctic Circumpolar Current, ASF Antarctic Slope Front

Remarkably high species numbers were recorded in the upper-right corner above 0 °C, whereas low values were observed for low-temperature, neritic waters (Fig. 5, bottom panel).

Cluster analysis

Hierarchical clustering based on Bray–Curtis similarities of cnidarian communities at all sampling depth layers revealed seven groups (A–G) at 54 % similarity (Fig. 6). The nMDS plots showed a clear dissociation among the four major groups at 46 %: the epipelagic groups (A and B), the meso- and bathy-pelagic group (C and D) and neritic groups (F and G; Figs. 6, 7). Group E partially occurred in the oceanic zone (Stns. 15 and 17).

Group A was composed of only one sample from the 0–50-m layer at Stn. 16, with only six individuals belonging to three species (Table 3; Fig. 7). Group A exhibited a low average abundance (0.8 individuals 10^3 m^{-3}). Group B was composed of two samples from the epipelagic layers of Stns. 14 and 16 (Fig. 7), with moderately high average abundance (5.1). Only one species, *P. martagon*, characterized this group (Table 4), but a few

individuals of *Calycopsis* sp. and *Solmundella bitentaculata* were also recorded (Tables 1 and 3) though they were excluded from the cluster analysis.

Group C represented the lower meso- and bathy-pelagic communities, which consisted of the 500–2,000-m samples for stations located in the oceanic and continental slope zones. This group had the third highest abundance and the highest species richness (Table 3). The representative species in this group were *Halicreas minimum*, *V. serrata*, *Periphylla periphylla*, *Pantachogon haeckeli*, and *H. conica*, which together contributed 63 % of the similarity (Table 4). However, lower *Si/SD(Si)* values were observed for these species, except for *P. periphylla* (Table 4), indicating that these species were distributed less consistently in samples with high abundance (Clarke and Warwick 2001; Table 4). Group D consisted of the upper mesopelagic community (200–500 m) of the oceanic and continental slope zones. Species richness was second highest (13) after the deeper community of Group C. *D. arctica* was typical and the most abundant species in this group and exhibited a high *Si/SD(Si)* value (1.9).

Group E was composed of stations in the epipelagic layers (100–200 m) north of the SB (Fig. 6). This group had the second lowest average abundance (1.7). The major

Table 2 List of cnidarians collected off Adelie Land, East Antarctica, during austral summer 2008 with abundances ($n\ 1,000\ m^{-3}$)

Station	14					15					
	0–50	50–100	100–200	200–500	500–1,000	1,000–2,000	0–50	50–100	100–200	200–500	500–1,000
Cluster ID*	–	–	B	D	C	C	–	–	E	D	C
Hydrozoa											
Anthomedusae											
<i>Calycopsis borchgrevinkii</i>				1.02	0.29	0.10		0.16	0.30	0.32	0.18
<i>Calycopsis</i> sp.		0.14						0.16	0.15		
<i>Pandea rubra</i>					0.10						0.09
<i>L. browni</i>											
<i>Zanclonia weldoni</i>											
<i>Koellikerina maasi</i>											
Leptomedusae											
<i>Modeeria rotunda</i>											
<i>Cosmetirella davisi</i>											
<i>Pychogena antarctica</i>											
Trachymedusae											
<i>Botrynema brucei</i>				0.09	0.19	0.87					0.18
<i>Crossota brunnea</i>				0.09	0.29	0.10					0.26
<i>H. minimum</i>					0.19	2.33				0.65	1.32
<i>H. conica</i>	0.16			0.74	3.11	0.29					2.21
<i>P. haeckeli</i>				0.55	0.58	1.36					
Rhopalonematidae sp.											
Narcomedusae											
<i>Solmissus incisa</i>											
<i>P. martagon</i>		0.97		0.55					0.15	3.56	0.35
Solmarisidae											
<i>S. bitentaculata</i>					0.10	0.10					
<i>Tetraplatia</i> sp.											
Siphonophorae											
Physonectae											
<i>P. vanhoeffeni</i>				0.09						0.07	
<i>Marrus antarcticus</i>					0.19	0.39			0.15	0.01	0.24
<i>Marrus</i> sp.											
<i>Bargmannia</i> sp.											
Calycophorae											
<i>D. antarctica</i>									0.75	0.22	0.35
<i>D. arctica</i>				1.02	0.19					0.75	
<i>Muggiaea bargmannae</i>											
<i>V. serrata</i>				1.75	1.57				0.26	0.38	0.72
<i>R. plicata</i>				0.74							
<i>Lenisia achilles</i>					0.39	0.10					0.62

Table 2 continued

Station	14						15					
	0–50	50–100	100–200	200–500	500–1,000	1,000–2,000	0–50	50–100	100–200	200–500	500–1,000	
Sampling depth (m)	–	–	B	D	C	C	–	–	E	D	C	
Cluster ID*												
<i>Lensia havock</i>				0.09							0.09	
<i>Heteropyramis cystallina</i>				0.18	1.07	0.97				0.11	0.35	
<i>Crystallaphyes amygdalina</i>					0.29	0.10						
<i>Chuniphyes multidentata</i>												
<i>Chuniphyes moserae</i>					0.10	0.29						
<i>Clausophyes moserae</i>				0.28	0.29	2.14				0.11	0.44	
<i>Nectopyramis larval nectophore</i>						0.10						
<i>Maresearsia praeclara</i>												
Scyphozoa												
Coronatae												
<i>Atolla</i> spp.					0.39	0.49				0.43	0.44	
<i>P. periphylla</i>					0.97	0.39					0.53	
Semaeostomae												
<i>Diplumaris antarctica</i>												
<i>Poralia rufescens</i>												
<i>Stygiomedusa gigantea</i>			1.11	7.20	10.30	9.62		0.32	1.50	0.11	8.02	
Total abundance (m/1,000 m ³)	0.16	0.00					0.00					
Total no. of individuals	1	0	8	78	106	99	0	2	10	65	91	
Total no. of species	1	0	2	13	18	16	0	2	5	13	15	
Station	16						17					
Sampling depth (m)	0–50	50–100	100–200	200–500	500–1,000	1,000–2,000	0–50	50–100	100–200	200–500	500–1,000	
Cluster ID*	A	B	G	C	C	C	–	–	E	D	C	
Hydrozoa												
Anthomedusae												
<i>Calyropsis borchgrevinkii</i>				0.08	0.22	0.11		0.26	0.10		0.09	
<i>Calyropsis</i> sp.									0.41			
<i>Pandea rubra</i>												
<i>L. browni</i>												
<i>Zanclonia weldoni</i>												
<i>Koellikerina maasi</i>												
Leptomedusae												
<i>Modeeria rotunda</i>				0.08								
<i>Cosmetirella davisi</i>												
<i>Pychogena antarctica</i>												
Trachymedusae												
<i>Botrynema brucei</i>	0.14			0.08	0.54	1.03						
<i>Crossota brunnea</i>					0.32	0.46					0.09	

Table 2 continued

Station	16							17				
	Sampling depth (m)							Sampling depth (m)				
	Cluster ID*	0-50 A	50-100 B	100-200 G	200-500 C	500-1,000 C	1,000-2,000 C	0-50 -	50-100 -	100-200 E	200-500 D	500-1,000 C
<i>H. minimum</i>					0.11	0.57						
<i>H. conica</i>					0.40	0.23						0.28
<i>P. haeckeli</i>					0.24	1.19	0.34				0.11	0.37
Rhopalonematidae sp.												
Narcomedusae												
<i>Solmissus incisa</i>												
<i>P. martagon</i>	0.55	8.32	5.58	0.24				0.13	0.92			
Solmarisidae						0.11						
<i>S. bitentaculata</i>		0.69										
<i>Tetraplata</i> sp.												
Siphonophorae												
Physonectae												
<i>P. vanhoeffeni</i>							0.35		0.01			
<i>Marrus antarcticus</i>							0.05					0.28
<i>Marrus</i> sp.												
<i>Bargmannia</i> sp.												
Calycophorae												
<i>D. antarctica</i>			1.33	0.08	0.11				0.31	0.11		
<i>D. arctica</i>	0.14		3.03	0.24	0.11		0.43	0.13			1.08	
<i>Muggitaea bargmannae</i>												
<i>V. serrata</i>			0.05	1.03	0.68		0.02		0.10	0.27	0.32	1.40
<i>R. plicata</i>												0.01
<i>Lensia achilles</i>				0.08								
<i>Lensia havock</i>							0.22					
<i>Heteropyramis cyistallina</i>				0.08						0.22		
<i>Crystalliphyes amygdalina</i>												
<i>Chuniphyes multidentata</i>												
<i>Chuniphyes moserae</i>							0.22					
<i>Clausophyes moserae</i>							1.08					
<i>Nectopyramis</i> larval nectophore												
<i>Maresearsia praeclara</i>												
Scyphozoa												
Coronatae												
<i>Atolla</i> spp.				0.32	0.32	0.11				0.32		0.18
<i>P. periphylla</i>				0.24	0.54	0.34				0.22		0.65
Semaeostomae												
<i>Diplumaris antarctica</i>												
<i>Porolia rufescens</i>					0.11							0.09

Table 2 continued

Station	16										17																			
	0-50		50-100		100-200		200-500		500-1,000		1,000-2,000		0-50		50-100		100-200		200-500		500-1,000									
Cluster ID*	A	B	G	C	C	C	C	C	C	C	C	C	-	-	-	-	E	D	D	C	C	C								
<i>Stygiomedusa gigantea</i>	0.83	9.01	9.99	3.13	4.57	5.57							0.13	0.39	1.85	0.11														
Total abundance (n/1,000 m ³)	6	65	82	39	42	49							1	3	18	25						3.44								
Total no. of individuals	3	2	4	12	13	15							1	2	6	9						37								
Total no. of species																						10								
Station	18										19										20									
Sampling depth (m)	0-50		50-100		100-200		200-500		500-1,000		1,000-2,000		0-200		200-500		500-1,000		100-200		200-500		500-1,000		1,000-2,000					
Cluster ID	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-				
Hydrozoa																														
Anthomedusae																														
<i>Calyropsis borchgrevinkii</i>		0.13	0.19	0.51									0.08	0.12	0.25				0.11	1.29	0.29									
<i>Calyropsis</i> sp.																														
<i>Pandea rubra</i>							0.10																							
<i>L. browni</i>																														
<i>Zanclonia weldoni</i>																			0.11	0.13										
<i>Koellikerina maasi</i>																														
Leptomedusae																														
<i>Modeeria rotunda</i>																														
<i>Cosmetirella davisi</i>																														
<i>Pychozena antarctica</i>											0.05									0.78						0.05				
Trachymedusae																														
<i>Botrynema brucei</i>							0.61				0.10									1.16										
<i>Crossota brunnea</i>							0.10																			0.05				
<i>H. minimum</i>							0.10																		1.36	0.47				
<i>H. conica</i>							2.66												0.22	1.29					0.10	0.16				
<i>P. haeckeli</i>							1.43																							
Rhopalonematidae sp.																														
Narcomedusae																														
<i>Solmissus incisa</i>							0.10																							
<i>P. martagon</i>							0.29												2.16	0.52										
Solmarisidae																														
<i>S. bidentaculata</i>																														
<i>Tetraplatia</i> sp.																														
Siphonophorae																														
Physonectae																														
<i>P. vanhoffeni</i>							0.09												0.11	0.03					0.45	0.01				
<i>Marrus antarcticus</i>							0.61																			0.43				

Table 2 continued

Station		18					19					20					
		0–50	50–100	100–200	200–500	500–1,000	1,000–2,000	0–200	200–500	500–1,000	1,000–2,000	0–50	50–100	100–200	200–500	500–1,000	1,000–2,000
Cluster ID	Sampling depth (m)	–	–	–	D	C	C	–	D	C	C	–	–	G	D	C	C
<i>Marnus</i> sp.																	
<i>Bargmannia</i> sp.																	
Calycophorae																	
<i>D. antarctica</i>																	
<i>D. arctica</i>																	
<i>Muggiata bargmannae</i>																	
<i>V. serrata</i>																	
<i>R. plicata</i>																	
<i>Lensia achilles</i>																	
<i>Lensia havock</i>																	
<i>Heteropyramis cystallina</i>																	
<i>Crystallophyes amygdalina</i>																	
<i>Chuniphyes multidentata</i>																	
<i>Chuniphyes moserae</i>																	
<i>Clausophyes moserae</i>																	
<i>Nectopyramis larval nectophore</i>																	
<i>Maresearsia praeclara</i>																	
Scyphozoa																	
Coronatae																	
<i>Atolla</i> spp.																	
<i>P. periphylla</i>																	
Semaestomae																	
<i>Diplalmaris antarctica</i>																	
<i>Poralia rufescens</i>																	
<i>Stygiomedusa gigantea</i>																	
Total abundance (n/1,000 m ³)																	
Total no. of individuals																	
Total no. of species																	
Station		21					22										
Sampling depth (m)		0–50	50–100	100–200	200–500	500–1,000	1,000–2,000	0–200	200–500	500–1,000	1,000–2,000	0–50	50–100	100–200	200–500	500–1,000	1,000–2,000
Cluster ID		–	–	–	D	C	C	–	D	C	C	G	G	G	G	G	G
Hydrozoa																	
Anthomedusae																	
<i>Calycopsis borchgrevinkii</i>																	
<i>Calycopsis</i> sp.																	
<i>Pandea rubra</i>																	
<i>L. browni</i>																	

Table 2 continued

Station	21				22			
	0–50	50–100	100–200	200–500	500–1,000	0–50	50–100	100–200
Sampling depth (m)	Cluster ID	–	–	D	C	G	G	G
<i>Zanclonia weldoni</i>								
<i>Koellikerina maasi</i>								
Leptomedusae								
<i>Modeeria rotunda</i>				0.32	0.25			
<i>Cosmetirella davisi</i>								
<i>Psychoгена antarctica</i>				0.16	0.17			
Trachymedusae								
<i>Botrycnema brucei</i>								
<i>Crossota brunnea</i>				0.16				
<i>H. minimum</i>				0.32	1.35			
<i>H. conica</i>				1.62	0.93			
<i>P. haeckeli</i>				0.16	0.08			
Rhopalonematidae sp.								
Narcomedusae								
<i>Solmisus incisa</i>								
<i>P. maritagon</i>				1.29				0.28
Solmarisidae								
<i>S. bitentaculata</i>								
<i>Tetraplatia</i> sp.								
Siphonophorae								
Physonectae								
<i>P. vanhoeffeni</i>	0.01			1.26	0.34			
<i>Marrus antarcticus</i>					0.41			
<i>Marrus</i> sp.								
<i>Bargmannia</i> sp.								
Calycophorae								
<i>D. antarctica</i>				3.24	0.59	0.34	0.39	8.60
<i>D. arctica</i>				7.28	0.59	0.46	0.39	2.91
<i>Muggiaea bargmannae</i>								
<i>V. serrata</i>				1.36	1.57			
<i>R. plicata</i>				0.08				
<i>Lensia achilles</i>				0.16				
<i>Lensia havock</i>								
<i>Heteropyramis cystallina</i>								
<i>Crystallophyes amygdalina</i>								
<i>Chuniphyes multidentata</i>								
<i>Chuniphyes moserae</i>								
<i>Clausophyes moserae</i>								

Table 2 continued

Station	21	22				
Sampling depth (m)	0–50	50–100	100–200	200–500	500–1,000	100–200
Cluster ID	–	–	–	D	C	G
<i>Nectopyramis</i> larval nectophore						
<i>Maresearsia praeclara</i>						
Scyphozoa						
Coronatae						
<i>Atolla</i> spp.					0.08	
<i>P. periphylla</i>			0.12		0.17	
Semaecostomae						
<i>Diplulmaris antarctica</i>						
<i>Poralia rufescens</i>						
<i>Stygiomedusa gigantea</i>						
Total abundance ($m/1,000\ m^3$)	0.01	0.00	0.12	19.53	6.96	0.80
Total no. of individuals	1	0	1	120	80	7
Total no. of species	1	0	1	15	15	2
Station	23	42				
Sampling depth (m)	0–50	50–100	100–200	50–100	100–200	200–500
Cluster ID	G	G	G	G	G	G
Hydrozoa						
Anthomedusae						
<i>Calycopsis borchgrevinki</i>	0.28	0.14	0.13	0.15		0.57
<i>Calycopsis</i> sp.						0.11
<i>Pandea rubra</i>						
<i>L. browni</i>			0.13			0.23
<i>Zanclonia weldoni</i>						
<i>Koellikerina maasi</i>			0.13			
Leptomedusae						
<i>Modeeria rotunda</i>						
<i>Cosmetirella davisi</i>						
<i>Pychogena antarctica</i>						
Trachymedusae						
<i>Borynema brucei</i>						
<i>Crossota brunnea</i>						
<i>H. minimum</i>						
<i>H. conica</i>						
<i>P. haeckeli</i>						
Rhopalonematidae sp.						
24						
Sampling depth (m)	0–50	50–100	100–200	50–100	100–200	200–500
Cluster ID	F	G	G	G	G	G
0.28						
0.30						

Table 2 continued

Station	23			42			24		
	0–50 G	50–100 G	100–200 G	0–50 G	50–100 G	100–200 G	0–50 F	50–100 G	100–200 G
Narcomedusae									
<i>Solmisus incisa</i>									
<i>P. maritagon</i>	0.28		0.39			0.91			
Solmarisidae									
<i>S. bitentaculata</i>									
<i>Tetraplatia</i> sp.									
Siphonophorae									
Physonectae									
<i>P. vanhoeffeni</i>	0.04		0.36		0.64	0.37		0.11	0.15
<i>Marrus antarcticus</i>									
<i>Marrus</i> sp.									
<i>Bargmannia</i> sp.									
Calycophorae									
<i>D. antarctica</i>	2.20	3.74	15.79	0.60	1.39	17.13	1.53	1.10	25.24
<i>D. arctica</i>	0.42	0.83	6.47	0.45	0.14	10.96		1.10	7.20
<i>Muggiaea bargmannae</i>			0.13						
<i>V. serrata</i>						0.02			
<i>R. plicata</i>									
<i>Leusia achilles</i>									
<i>Leusia havock</i>									
<i>Heteropyramis cystallina</i>									
<i>Crystalliphyes amygdalina</i>									
<i>Chuniphyes multidentata</i>									
<i>Chuniphyes moserae</i>									
<i>Clausophyes moserae</i>									
<i>Nectopyramis larval nectophore</i>									
<i>Maresearsia praedara</i>									
Scyphozoa									
Coronatae									
<i>Atolla</i> spp.									
<i>P. periphylla</i>									
Semaeostomae									
<i>Diplulmaris antarctica</i>						0.23			0.75
<i>Poralia rufescens</i>			0.13						
<i>Stygiomedusa gigantea</i>									
Total abundance (n/1,000 m ³)	3.22	4.71	23.66	1.20	2.17	30.53	1.81	2.31	33.64
Total no. of individuals	23	34	183	8	16	267	13	15	225
Total no. of species	5	3	9	3	3	9	2	3	5

Table 2 continued

Station	25			26			27			11		
Sampling depth (m)	0–50	50–100	100–200	0–50	50–100	100–200	0–50	50–100	100–200	200–500	0–200	200–500
Cluster ID	G	F	F	G	F	F	–	F	F	G	F	F
Hydrozoa												
Anthomedusae												
<i>Calycopsis borchgrevinkii</i>			0.11							0.19		
<i>Calycopsis</i> sp.												
<i>Pandea rubra</i>												
<i>L. browni</i>												
<i>Zanclonia weldoni</i>												
<i>Koellikerina maasi</i>												
Leptomedusae												
<i>Modeeria rotunda</i>												
<i>Cosmetirella davisi</i>												
<i>Psychogena antarctica</i>								0.12				0.17
Trachymedusae												
<i>Botrynema brucei</i>												
<i>Crossota brunnea</i>												
<i>H. minimum</i>												
<i>H. conica</i>												
<i>P. haeckeli</i>												
Rhopalonematidae sp.												
Narcomedusae												
<i>Solmissus incisa</i>												
<i>P. martagon</i>					0.12	0.24					0.10	
Solmarisidae												
<i>S. bitentaculata</i>												
<i>Terraplatia</i> sp.												
Siphonophorae												
Physonectae												
<i>P. vanhoeffeni</i>												
<i>Marrus antarcticus</i>												
<i>Marrus</i> sp.												
<i>Bargmannia</i> sp.												
Calycophorae												
<i>D. antarctica</i>	0.65	0.98	20.56	0.34	2.67	12.62	0.12	0.49	4.90	3.98	11.16	2.40
<i>D. arctica</i>	0.33		5.14	0.22	0.12	3.16				2.62		
<i>Muggiata bargmannae</i>						0.13					0.78	0.20

Table 2 continued

Station	25			26			27			11		
Sampling depth (m)	0–50	50–100	100–200	0–50	50–100	100–200	0–50	50–100	100–200	0–200	200–500	
Cluster ID	G	F	F	G	F	F	–	F	F	F	F	
<i>V. serrata</i>												
<i>R. plicata</i>												0.25
<i>Lenisia achilles</i>												0.85
<i>Lenisia havock</i>												0.17
<i>Heteropyramis cystallina</i>												0.17
<i>Crystallallophyes amygdalina</i>												0.17
<i>Chumiphyes multidentata</i>												
<i>Chumiphyes moserae</i>												
<i>Clausophyes moserae</i>												
<i>Nectopyramis larval nectophore</i>												
<i>Maresearsia praeclara</i>												
Scyphozoa												
Coronatae												
<i>Atolla</i> spp.												
<i>P. periphylla</i>												
Semaeostomae												
<i>Diplulmaris antarctica</i>		0.12					0.12	0.12				
<i>Poralia rufescens</i>												
<i>Stygionedusa gigantea</i>												
Total abundance (n/1,000 m ³)	0.98	1.10	25.81	0.56	2.91	16.38	0.24	0.73	4.90	6.79	12.04	4.21
Total no. of individuals	9	9	226	5	24	135	2	6	48	70	124	48
Total no. of species	2	2	3	2	3	6	2	3	1	3	3	7

Cluster ID: defined by the hierarchical clustering in Fig. 6, – removed from the cluster analysis due to low abundance

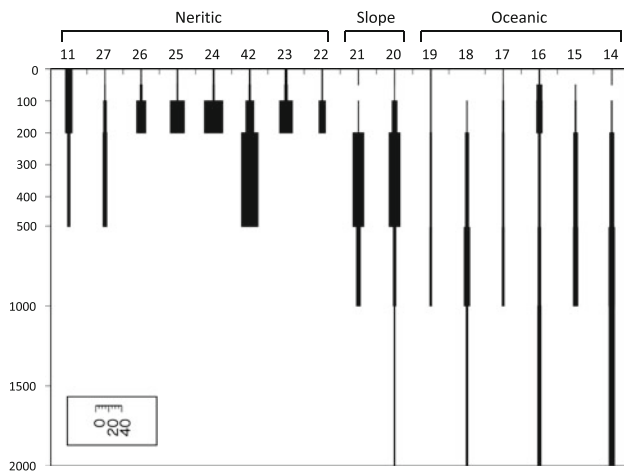


Fig. 3 Vertical distributions of total cnidarian abundance at each station off Adélie Land during summer 2008

species in this group were *D. antarctica* and *P. martagon*, which together contributed 82 % of the similarity (Table 4). Group F represented part of the neritic community together with group G, which consisted of 0–500-m samples for stations located mainly in the eastern part of the neritic zone (Fig. 7). *D. antarctica* was the sole dominant species in group F with a high *Si*/*SD*(*Si*) value. Group G was composed of 19 samples from primarily the western part of the neritic waters, with one exception in the 100–200-m sample at Stn. 20. This group was characterised by the dominance of only two species, *D. antarctica* and *D. arctica*, which together contributed 98 % of the similarity. This group exhibited the highest abundance (10).

Pegantha martagon was the most abundant species in the epipelagic communities (Groups A, B and E) except for Group G (Tables 2, 4). Meso- and bathy-pelagic

communities (Groups C and D) in the oceanic zone exhibited high species diversity. *D. antarctica* was the most abundance species in the neritic zone (Groups F and G).

In the T–S plots (Fig. 8), only Groups F and G were positioned below 0 °C, whereas the other groups, except for Stn. 17 (100–200 m), were positioned above 0 °C. Groups E, C, and D were found in the CDW or MCDW with relatively high temperature and high salinity, and Groups A and B occurred in the high temperatures region of the AASW. Group A was the only communities at <34.0 salinity (0–50 m, Stn. 16).

Discussion

The mesh size of 4.5 mm used in this study was somewhat large to collect small species. Many studies on gelatinous plankton have used smaller-mesh nets (e.g. Boysen-Ennen and Piatkowski 1988; Hosia et al. 2008; Panasiuk-Chodnicka and Żmijewska 2010). Therefore, we likely underestimate abundances and species numbers of small deformable or fragile cnidarians. However, some important literature in the Southern Ocean is based on samples collected by a RMT8 or RMT25 (5-mm mesh size) (Pagès et al. 1994, 1996; Pugh et al. 1997), allowing the results of the present study using a RMT8 to be compared with those of these study.

We were unable to identify a simple positive relationship between water temperature and cnidarian abundance, with high abundances being observed both in neritic waters at relatively low temperatures and in meso- and bathy-pelagic waters with warm water masses. However, Pagès and Schnack-Schiel (1996) noted that very low abundances

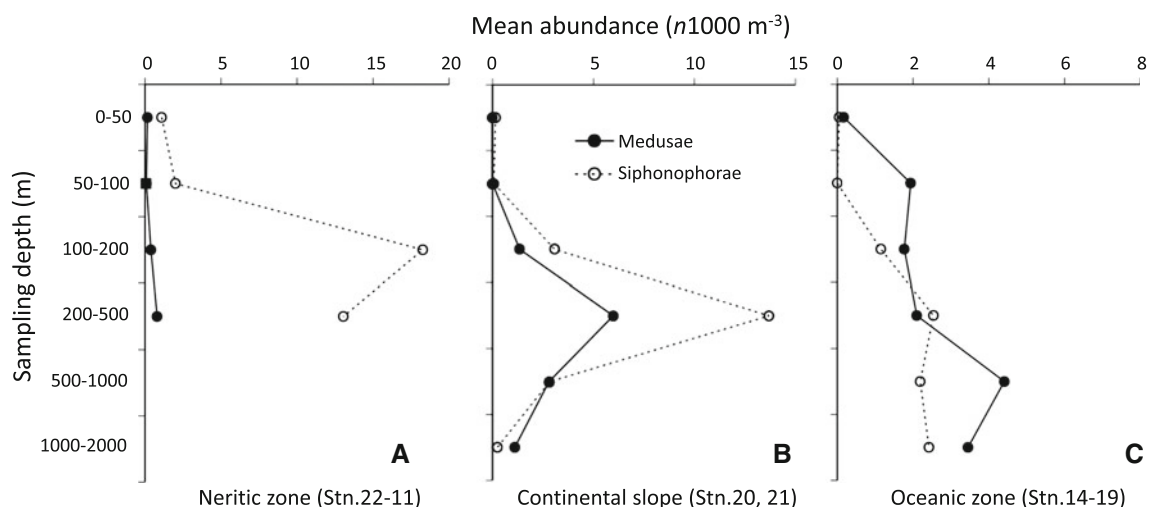


Fig. 4 Vertical profiles of cnidarian abundance in the neritic zone (a), continental shelf (b), and oceanic zone (c) off Adélie Land during summer 2008

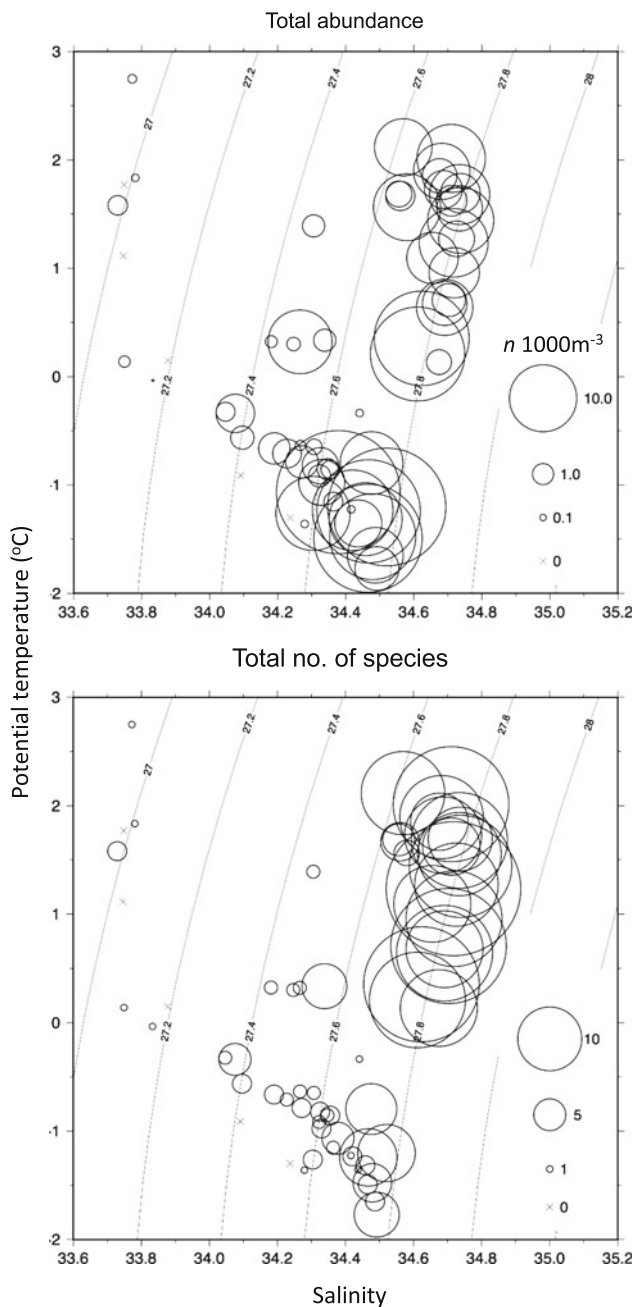


Fig. 5 Bubble plots of total abundance (top) and species number (bottom) for each sample on the potential temperature and salinity diagram. Curved lines denote isopycnal lines

of pelagic cnidarians occur in cold epipelagic waters. We observed very low abundances in the warm AASW (0–50 m) lying over the cold WW layer (~ 50–100 m). Furthermore, in the neritic zone, where the very cold AASW and SW were dominant, siphonophores were abundant in the 100–500-m layers, and numerically very few cnidarians were collected in the 0–50-m layer. Off Lützow–Holm Bay in the western part of East Antarctica, Toda et al. (2010) found no correlation between cnidarian

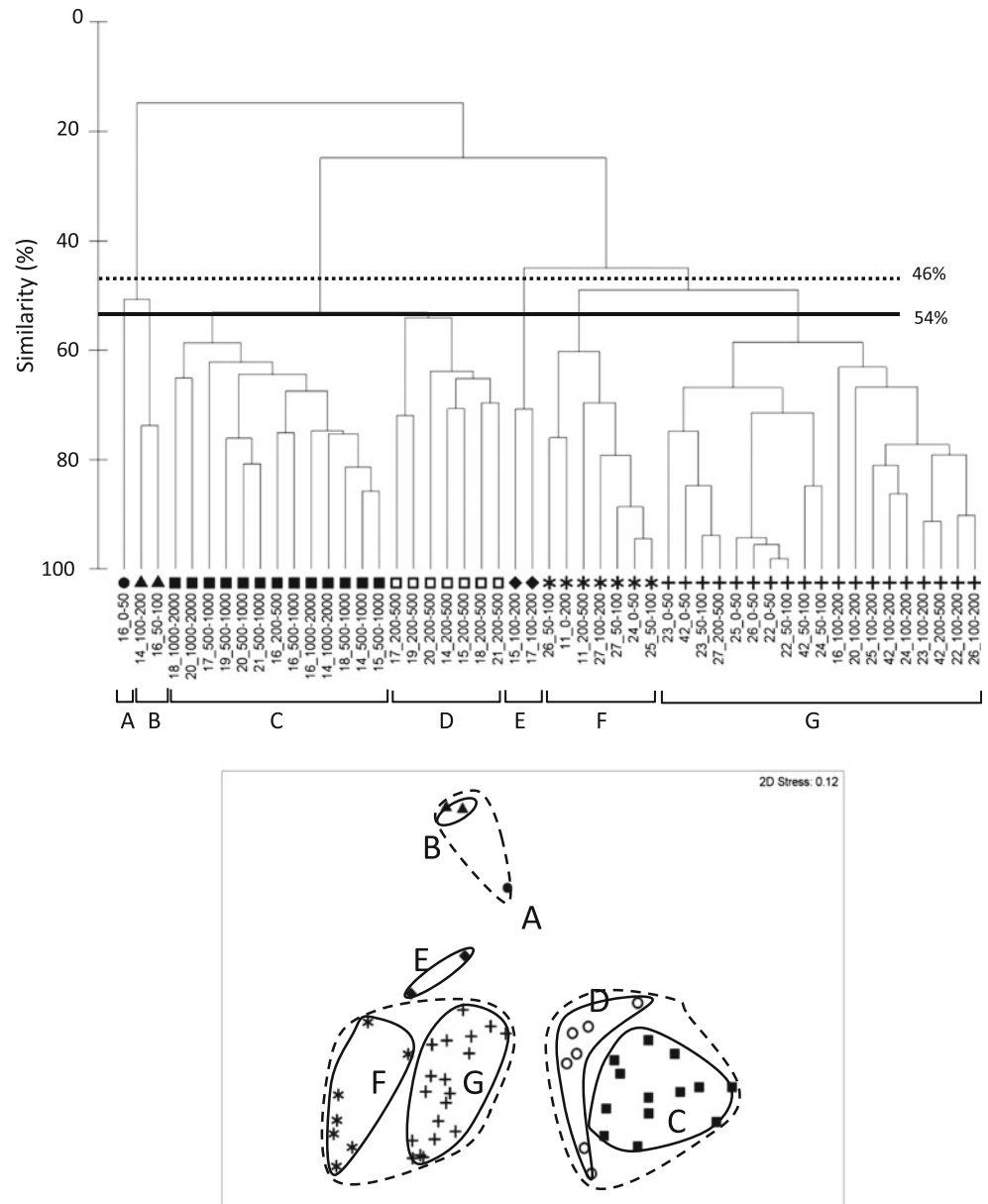
abundance and the presence of cold water masses. In the eastern Weddell Sea also, no clear relationship between abundance and water temperature was observed in the epipelagic layer (Pugh et al. 1997).

Remarkably high numbers of species were observed in the MCDW and CDW, with warmer and more saline waters in the meso- and bathy-pelagic layers. Greater species diversity of pelagic cnidarians in the meso- and bathy-pelagic layers compared to epipelagic layers, has been recorded across oceans worldwide (Pagès et al. 1994, 1996; Lindsay and Hunt 2005; Hosia et al. 2008; Toda et al. 2010). Pagès et al. (1994), who studied the vertical distribution of zooplankton in the Weddell Sea, indicated that the stable water temperature of the CDW leads to high species richness. Similarly, high species richness in communities associated with the MCDW has been recorded in Lützow–Holm Bay (Toda et al. 2010). The relative stability of environmental factors such as temperature, salinity, and water density in the CDW and MCDW seems to lead to high diversity not only of gelatinous plankton but also of other organisms such as fish and copepods in the Southern Ocean (Moteki et al. 2011, Tachibana et al., unpublished data).

We found that cnidarians were sparsely distributed in the epipelagic layer of the oceanic zone, likely due to daytime sampling to some degree. In fact, at Stns. 16 and 20, where net tows of the 0–200-m layers were conducted at night, *D. antarctica* and *D. arcica* appeared to slightly ascend to join community group G at 100–200 m, and *P. martagon* ascended to join groups A and B (Table 4; Fig. 7). At both stations, diel vertical migration (DVM) was also observed in terms of total abundance (Fig. 3). Some gelatinous zooplankton species have been observed to exhibit DVM north of the South Georgia Islands (Pagès et al. 1996). However, in the study performed off Lützow–Holm Bay, most samplings were conducted during the midnight sun period, and cnidarians were abundant in the epipelagic layers in 2005 (Toda et al. 2010). In this case, *D. antarctica* was recorded at high abundance in the well-developed WW in the epipelagic layer. This species is endemic to high Antarctic zones of the Southern Ocean and is usually found mainly in cold neritic waters (Swadling et al. 2011; present study).

In the oceanic zone, the 200–500 and 500–2,000-m layers exhibited very similar cnidarian communities across sampling stations, regardless of the SB, except for Stn. 16, where DVM may have been observed. Community groups C and D identified in the present study are likely to be typical of the CDW and MCDW. This pattern of spatial distribution is very similar to that observed in Lützow–Holm Bay in January 2005 (Toda et al. 2010). In Lützow–Holm Bay, communities at 200–500 m were recognised as the same community in both 2005 and 2006 according to a cluster analysis. This homogeneity across SB in the

Fig. 6 Dendrogram based on the similarity of cnidarian communities (*top*) off Adélie Land during summer 2008, and nMDS plots (*bottom*) of the samples with clustering at 54 % (*solid line*) and 46 % (*dashed line*). Sample codes below symbols denote the station number (*left*) and depth range (*right*)



cnidarian community is likely to be attributable to the stability of the CDW and MCDW among oceanic sampling stations.

Most of the species contributing to each cluster in the SIMPER analysis in the meso- and bathy-pelagic layers were common between the waters off Adélie Land and Lützow–Holm Bay, except for *V. serrata*, *Atolla* spp., *Calycopsis borchgrevinki*, and *P. martagon*, which did not contribute to meso- and bathy-pelagic clusters in Lützow–Holm Bay. *D. arctica*, one of the main components in the 200–500-m communities (Group D), was also dominant in the 100–800-m layers in Croker passage on the west Antarctic Peninsula (Panasiuk-Chodnicka and Żmijewska 2010). *V. serrata*, *P. haeckeli*, and *P. periphylla*, which

occurred at relatively high abundances in meso- and bathy-pelagic communities (Groups C and D), were dominant in the same layers in the Weddell Sea (Pagès and Kurbjewit 1994; Pagès et al. 1994; Pagès et al. 1996) and Lützow–Holm Bay (Toda et al. 2010).

The ASF served as a strong barrier dividing cnidarian communities into the neritic and oceanic zones off Adélie Land, similar to patterns observed for euphausiids and fish in the same area and in the Ross Sea (Donnelly et al. 2004; Moteki et al. 2011; Ono et al. 2011). In the neritic zone, two community groups (F and G) associated with the cold AASW and SW were observed despite a less varied physical environment. However, diversity in these communities was low, with siphonophores such as *D.*

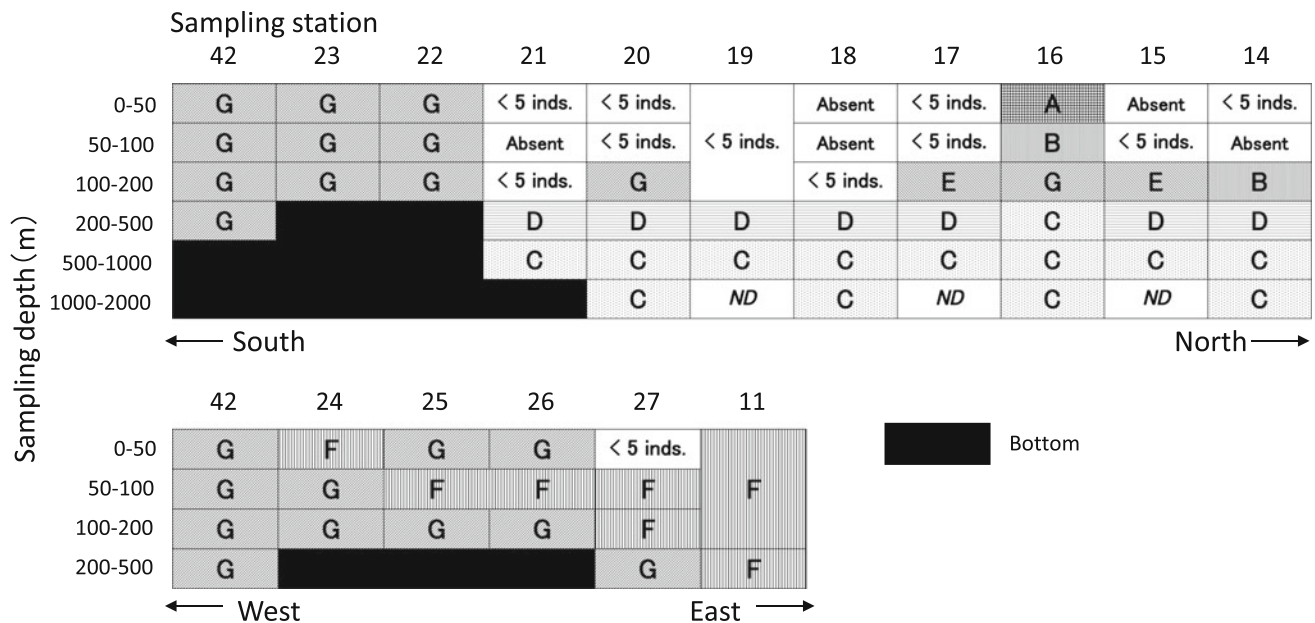


Fig. 7 Schematic of the distribution of cnidarian communities off Adélie Land during summer 2008. Capital letters denote the group name identified by hierarchical clustering in Fig. 6. ND no data. <5 inds., fewer than 5 individuals sampled were excluded from this analysis

Table 3 Characteristics of each group identified by the hierarchical clustering

Group	No. of samples	Average individual number	Average abundance ^a	Average species richness	Total no. spp.
A	1	6.0	0.8	3.0	3
B	2	36.5	5.1	2.0	3
C	13	61.9	5.6	14.6	34
D	7	76.4	9.2	12.7	30
E	2	14.1	1.7	5.5	7
F	7	39.1	4.0	3.0	11
G	19	84.5	10.4	4.1	16

^a Abundance, $n/1,000 \text{ m}^{-3}$

antarctica and *D. arctica* dominating. These species were especially abundant in the neritic zone, although *D. arctica* was widely distributed in the upper mesopelagic layer (200–500 m) in the oceanic zone off Adélie Land. However, in the Weddell Sea and west Antarctic Peninsular region, where there is a transition zone between oceanic and neritic conditions for the zooplankton and fish fauna (Lancraft et al. 2004; Donnelly and Torres 2008; Panasiuk-Chodnicka and Żmijewska 2010), *D. arctica* exhibits epi- and meso-pelagic distribution patterns in Antarctic waters (Boysen-Ennen and Piatkowski 1988; Panasiuk-Chodnicka and Żmijewska 2010). *D. antarctica* is primarily found in cold water masses and is potentially a “key species” in the high Antarctic zone (Pagès et al. 1994; Boysen-Ennen and Piatkowski 1988; Hunt et al. 2007), while low abundances

of this species were observed in Weddell Sea and west Antarctic Peninsula areas (Boysen-Ennen and Piatkowski 1988; Panasiuk-Chodnicka and Żmijewska 2010). However, it remains unclear whether dominance by this species is universal in the neritic zone of the Southern Ocean, as cnidarian communities of the neritic zone are understudied.

Cnidarian communities in the epipelagic layer are affected by hydrographical structures such as the SB, whereas those in the meso- and bathy-pelagic layers are likely stable and maintain higher diversity throughout the oceanic zone in East Antarctica. The SB likely divides the cnidarian communities of the epipelagic layer, in a similar way to patterns observed in other zooplankton (Tanimura et al. 2008; Ono et al. 2011). Groups A, B, and E associated with warmer AASW in the oceanic zone and defined by dominance of *P. martagon*, were only observed north of the SB. The distance from Antarctica to the SB differs greatly between the eastern and western East Antarctic Ocean, and this distance is very short off Adélie Land (Nicol and Raymond 2012). The ACC, which is characterised by low chlorophyll, runs close to the continental slope off Adélie Land ($\sim 140^\circ\text{E}$), with maximum sea ice extent lying closer to Antarctica. In contrast, the area north of Lützow–Holm Bay, which is located in the western part of East Antarctica, contains the chlorophyll-rich Coastal Current. Epipelagic species such as *P. martagon*, which is distributed mainly at 50°S – 60°S in the Southern Ocean (Kramp 1957; O’Sullivan 1982), were abundant north of the SB in the oceanic zone in the present study, likely due to the close proximity of the ACC to the continental slope region.

Table 4 Average abundance, similarity (*Si*), and related values within a cluster (SIMPER analysis)

Species	Av. abund. (n/1,000 m ⁻³)	Av. <i>Si</i>	<i>Si</i> /SD (<i>Si</i>)	Contri. %	Cum. %
Group B (Av. similarity: 20.9)					
<i>P. martagon</i>	4.65	20.9	–	100	100
Group C (39.3)					
<i>H. minimum</i>	0.68	6.42	0.88	16.39	16.39
<i>V. serrata</i>	0.64	5.32	0.73	13.59	29.98
<i>P. periphylla</i>	0.38	4.95	1.92	12.63	42.61
<i>Pantachogon haeckeli</i>	0.62	4.14	0.89	10.57	53.18
<i>H. conica</i>	0.71	4.1	0.96	10.46	63.64
<i>Atolla</i> spp.	0.24	3.03	1.81	7.73	71.37
<i>D. arctica</i>	0.27	2.46	1.13	6.29	77.66
<i>Calycopeis borchgrevinki</i>	0.18	1.86	1.12	4.74	82.39
<i>Marrus antarcticus</i>	0.21	1.6	0.8	4.08	86.47
<i>Clausophyes moserae</i>	0.37	1.32	0.37	3.36	89.84
<i>Botrynema brucei</i>	0.26	1.12	0.44	2.87	92.7
Group D (36.4)					
<i>D. arctica</i>	2.36	12.38	1.9	34.04	34.04
<i>V. serrata</i>	0.82	6.3	1.84	17.34	51.38
<i>R. plicata</i>	0.36	4.27	0.91	11.73	63.11
<i>Calycopeis borchgrevinki</i>	0.7	2.51	0.99	6.9	70
<i>D. antarctica</i>	1.86	2.47	0.65	6.78	76.78
<i>P. martagon</i>	0.89	2.26	0.77	6.21	83
<i>H. conica</i>	0.6	1.97	0.68	5.42	88.41
<i>Atolla</i> spp.	0.25	1.64	0.65	4.51	92.93
Group E (42.4)					
<i>D. antarctica</i>	0.53	23.48	–	55.36	55.36
<i>P. martagon</i>	0.54	11.36	–	26.79	82.14
<i>Calycopeis borchgrevinki</i>	0.2	7.58	–	17.86	100
Group F (47.9)					
<i>D. antarctica</i>	3.45	47.81	2.13	99.86	99.86
Group G (37.0)					
<i>D. antarctica</i>	7.01	24.45	1.27	66.11	66.11
<i>D. arctica</i>	2.58	11.64	1.25	31.47	97.57

Species list of each group is truncated when cumulative percentage of 80 % is reached

Av. *Si* average contribution of species *i* to the similarity within the cluster, *SD(Si)* standard deviation of *Si*, high *Si*/*SD(Si)* ratio indicates that a given species is typical to all stations in the cluster, *Contri. %* percentage of Av. *Si* to the similarity within the cluster, *Cum. %* cumulative percentage of *Contri. %*

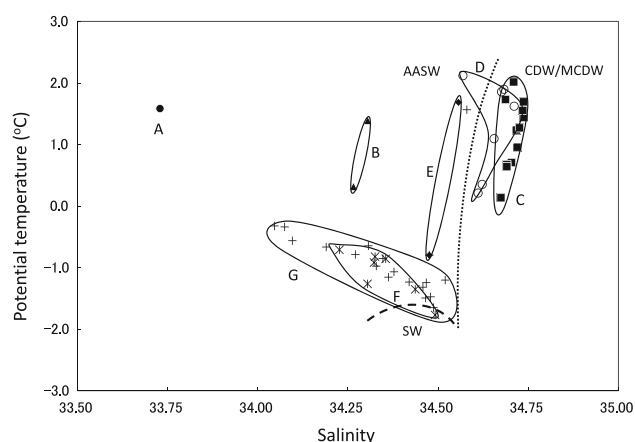


Fig. 8 Diagram of the average potential temperature and salinity during each sampling event. Symbols follow those identified by the hierarchical clustering in Fig. 6. Dotted line denotes the rough border between the Antarctic Surface Water (AASW) and circumpolar deep water (CDW)/modified CDW (MCDW), and shelf water (SW) was present below the broken line

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