Available online at www.sciencedirect.com

ScienceDirect

Polar Science 4 (2010) 387−404

http://ees.elsevier.com/polar/

Structure of the pelagic cnidarian community in Lützow−Holm Bay in the Indian sector of the Southern Ocean

R. Toda, M. Moteki*, A. Ono, N. Horimoto, Y. Tanaka, T. Ishimaru

Department of Ocean Sciences, Tokyo University of Marine Science and Technology, 4-5-7 Konan, Minato, Toyko 108-8477, Japan

Received 30 November 2009; revised 26 April 2010; accepted 11 May 2010
Available online 23 June 2010

Abstract

The structure of the pelagic cnidarian community in Lützow−Holm Bay in the Indian sector of East Antarctica was investigated in January 2005 and 2006. Zooplankton samples from six discrete depths (surface to 2000 m) obtained using an RMT-8 yielded 4666 individuals of 31 species of cnidarian. Cnidarian abundance and carbon biomass were far greater in 2005 than in 2006. The biomass of macrozooplankton was large in the upper 200 m in 2005, but concentrated at 200−500 m in 2006, except for Euphausiacea. The most dominant species was *Diphyes antarctica*, followed by *Dimophyes arctica* and *Muggiaea bargmannae*. Four species had never been collected from East Antarctica; of these, *Solmissus incisa* was a first record in the Southern Ocean. Cluster analysis revealed the following three major communities: the epipelagic (0−200 m), in summer surface, winter, and upper modified circumpolar deep waters (MCDW); the upper mesopelagic (200−500 m), in upper MCDW; and the lower meso- and bathypelagic (500−2000 m), in lower MCDW. The epipelagic and lower meso- and bathypelagic communities are likely reduced in abundance/biomass when primary production is low, due to bottom-up control, while the upper mesopelagic community remains stable.

Keywords: Antarctic pelagic cnidarians; Community structure; Indian sector; Zooplankton; Medusae

1. Introduction

Pelagic cnidarians prey on zooplankton and fish larvae, and this may affect the meso- and bathypelagic ecosystems (Larson et al., 1991; Vinogradov and Shushkina, 2002; Lindsay and Hunt, 2005; Youngbluth et al., 2008; Stemmann et al., 2008). However, very few studies have focused on the role of cnidarians in the pelagic ecosystem of the Weddell Sea (Pagès and Kurbjeweit, 1994; Pagès et al., 1994; Pagès and Schnack-Schiel, 1996; Pugh et al., 1997; Pagès, 1997). The lack of information on cnidarians is most likely due to the difficulty of quantifying these creatures due to their vulnerability to net sampling. Furthermore, some analyses separated large scyphozoans from other zooplankton samples (Pagès, 1997).

In the last two decades, Antarctic zooplankton communities have been studied mainly in West Antarctica, including the Weddell Sea, Scotia Sea, Antarctic Peninsula Archipelago, and Ross Sea (Hopkins, 1985, 1987; Hopkins and Torres, 1988; Hopkins et al., 1993; Hubold et al., 1988; Atkinson and Peck, 1988; Boysen-Ennen and Piatkowski,

* Corresponding author. Tel.: +81 3 54630527; fax: +81 3 54630523.
E-mail address: masato@kaiyodai.ac.jp (M. Moteki).

1873-9652/$ - see front matter © 2010 Elsevier B.V. and NIPR. All rights reserved.
doi:10.1016/j.polar.2010.05.007

1988; Boysen-Ennen et al., 1991). In contrast, very few studies have been conducted in East Antarctica, and those that have been done there have targeted the epipelagic community (Hosie et al., 2000; Chiba et al., 2001; Takahashi et al., 2002; Hunt and Hosie, 2003; Hunt et al., 2007).

The Cosmonaut Sea including Lützow–Holm Bay has a complicated and dynamic oceanographic environment affected interannual variation of Antarctic Circumpolar Current and Coastal Current (Hunt et al., 2007). Thus, macrozooplankton assemblages in the Cosmonaut Sea exhibit interannual variation in zooplankton density, biomass, and assemblages, and that this variation reflected the different histories of spatially and temporally separated water masses, which were structured by a combination of bottom-up and top-down processes (Hunt et al., 2007).

This study sought to clarify the structure of the pelagic cnidarian community in Lützow–Holm Bay in the Indian Ocean sector during January 2005 and 2006. We also examined other macrozooplankton assemblages and vertical distribution patterns to estimate the determinants of the cnidarian distribution.

2. Materials and methods

2.1. Net sampling

We conducted research cruises from 6 to 13 January 2005 and 12 to 17 January 2006 on the Training and Research Vessel (TR/V) *Umitaka-maru* of Tokyo University of Marine Science and Technology (TUMSAT) in Lützow–Holm Bay (Table 1; Fig. 1). In both years, zooplankton were sampled at five stations using a rectangular midwater trawl (RMT)-1+8 equipped with three sets of opening/closing nets systems (Baker et al., 1973). The sampling stations in 2006 were located about one degree north of those in 2005 due to the delayed ice edge retreat in 2006 (Fig. 1). The northern two stations in 2005 (Stns. 05-L1 and -L9) were located offshelf, and the remaining stations (Stns. 05-L4, -L8, and -L12) were situated along the continental slope at the ice edge (Fig. 1). In contrast, in 2006, all five stations were located far from the slope water, although 06-L4, -L8, and -L12 were situated near the ice edge (Fig. 1). Two tows were deployed at each station, one from 200 to 0 m depth (0–50–100–200 m) and a second from 2000

Table 1
Sampling data of a RMT-1+8 off Lützow–Holm Bay, Indian sector, by TR/V *Umitaka-maru* in 2005 and 2006.

Stn.	Date	Time (UTC)	Position		Bottom		Vol filtered (m^3) (bottom, middle, top)
			Lat. (S)	Long. (E)	Depth (m)	Sampling depth (m)	
2005							
05-L1	6 Jan.	15:10–16:49	66–29.5	36–00.0	4535–4551	1800–1000–500–200	13,395, 13,910, 10,819
	6 Jan.	17:33–18:41	66–35.3	35–54.8	4490	200–100–50–0	7212, 6697, 6182
05-L4	7 Jan.	19:59–22:43	67–43.3	35–50.6	2821–3264	2000–1000–500–200	19,577, 16,486, 12,879
	7 Jan.	23:20–00:55	67–45.0	35–30.0	3156	200–100–50–0	6697, 7212, 7212
05-L8	9 Jan.	18:52–20:22	67–38.5	38–25.8	1693–1817	1750–1000–500–200	17,516, 13,910, 8243
	9 Jan.	21:13–23:05	67–31.6	38–26.0	1793	200–100–50–0	12,879, 9273, 9788
05-L12	12 Jan.	14:10–15:43	67–18.3	40–54.2	3490–3681	2000–1000–500–200	18,548, 10,819, 7728
	12 Jan.	16:19–17:54	67–12.0	40–54.4	3567	200–100–50–0	9273, 10,819, 9788
05-L9	13 Jan.	05:48–07:17	66–33.9	41–00.2	4152–4268	2000–1000–500–200	18,031, 11,849, 10,303
	13 Jan.	07:50–09:38	66–28.0	41–00.3	4152–4181	200–100–50–0	10,819, 9273, 9273
2006							
06-L4	12 Jan.	14:30–16:05	66–09.7	36–10.3	4495–4639	200–100–50–0	9273, 8758, 8243
	12 Jan.	18:10–19:37	66–05.0	36–09.2	4313–4404	2000–1000–500–200	7212, 10,819, 18,546
06-L1	13 Jan.	13:36–15:09	65–00.0	36–00.8	4334–4639	200–100–50–0	9273, 8758, 9273
	13 Jan.	16:56–18:29	64–59.6	36–01.0	4634–4647	2000–1000–500–200	8243, 12,364, 15,970
06-L5	14 Jan.	09:54–12:28	65–00.3	38–01.8	4858–4860	200–100–50–0	9273, 9788, 10,303
	14 Jan.	14:22–16:16	65–00.4	38–08.6	4860–4869	2000–1000–500–200	10,303, 13,395, 19,061
06-L8	15 Jan.	12:58–14:31	66–50.8	37–48.8	4504	200–100–50–0	9788, 9273, 10,819
	15 Jan.	16:10–17:40	66–47.9	37–36.7	4347–4443	2000–1000–500–200	8758, 11,849, 17,516
06-L12	17 Jan.	13:10–14:10	65–58.9	40–59.3	4230–4321	200–100–50–0	104,303, 11,334, 11,849
	17 Jan.	16:49–18:17	66–07.7	41–06.3	3913–4217	2000–1000–500–200	13,910, 22,668, 10,303

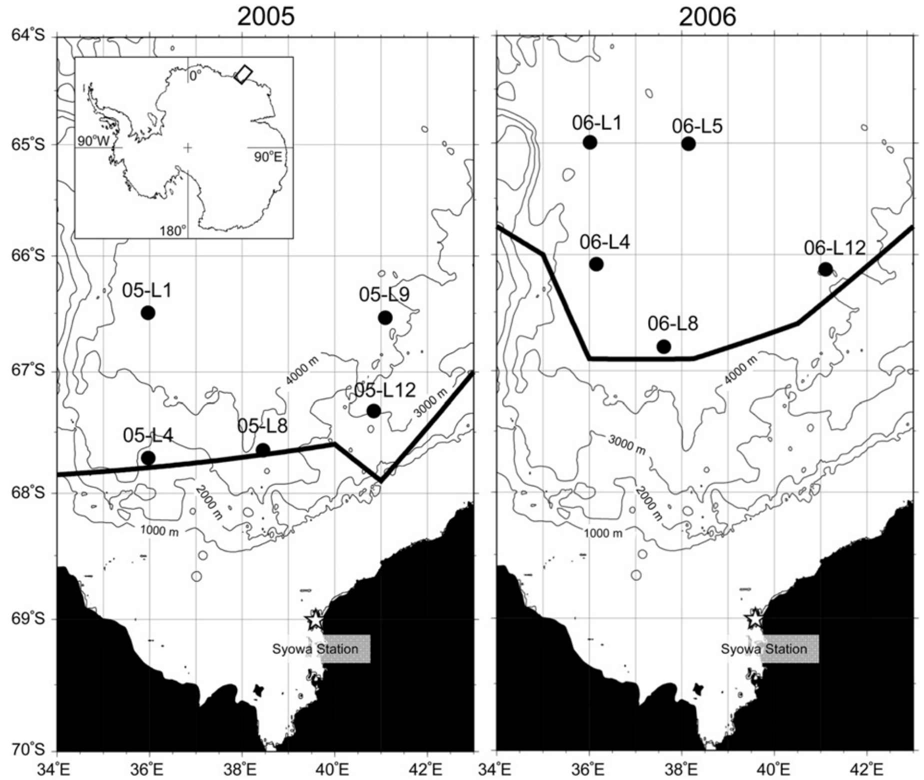

Fig. 1. Sampling stations off Lützow–Holm Bay, Indian sector, in 2005 and 2006. The thick line denotes the pack-ice edge estimated roughly from SeaWiFS satellite images.

to 200 m depth (200–500–1000–2000 m) (Table 1), although the maximum depth at stations 05-L1 and 05-L8 was 1800 and 1750 m, respectively. The protocols used for net towing and for calculating the filtered water volume are described in Moteki et al. (2009). This study did not design a net sampling program to collect gelatinous species. This study examined only the samples from RMT-8 (8-m^3 nominal mouth opening with 4.5-mm mesh). The samples were fixed in 5% buffered formaldehyde seawater solution onboard.

2.2. Hydrographic observations

Salinity and temperature data were collected at each sampling station before the RMT tow using a conductivity/temperature/depth (CTD) profiler (Sea-Bird Electronics, SBE911), except in the upper 200 m in 2006, which was not sampled because the instrument was not working properly in the epipelagic layer that year. Therefore, CTD data from another profiler (Falmouth Scientific, Inc., ICTD) were used for our analysis at 0–200 m depths for 2006. Both CTD instruments were calibrated, although the degree of accuracy was lower for the ICTD. The terminology of the water masses follows Bindoff et al. (2000) and Tomczak and Liefrink (2005).

2.3. Sample analysis

The zooplankton were divided into the following 11 taxa: Salpidae, Medusae, Siphonophorae, Polychaeta, Chaetognatha, Euphausiacea, Amphipoda, Decapoda, Copepoda, Ostracoda, and Pteropoda; the number of individuals and wet weight to the nearest 0.01 g were determined for each taxon. Before wet weight was determined with an electric balance, samples were filtered using a vacuum pump and then a filter paper dewatering process was repeated several times until the filter paper was not wet. For fragile gelatinous plankton, water was removed on a Petri dish with filter paper or a paper towel until water did not leach out. The conversion factors from wet weight to carbon weight used in this study followed those in Davis and Wiebe (1985). Pelagic cnidarians (Medusae and Siphonophorae) were identified to the lowest possible taxon. Abundances are shown as the number per 1000 m^3 water.

Pelagic cnidarians were identified and counted under a binocular dissecting microscope. The numbers

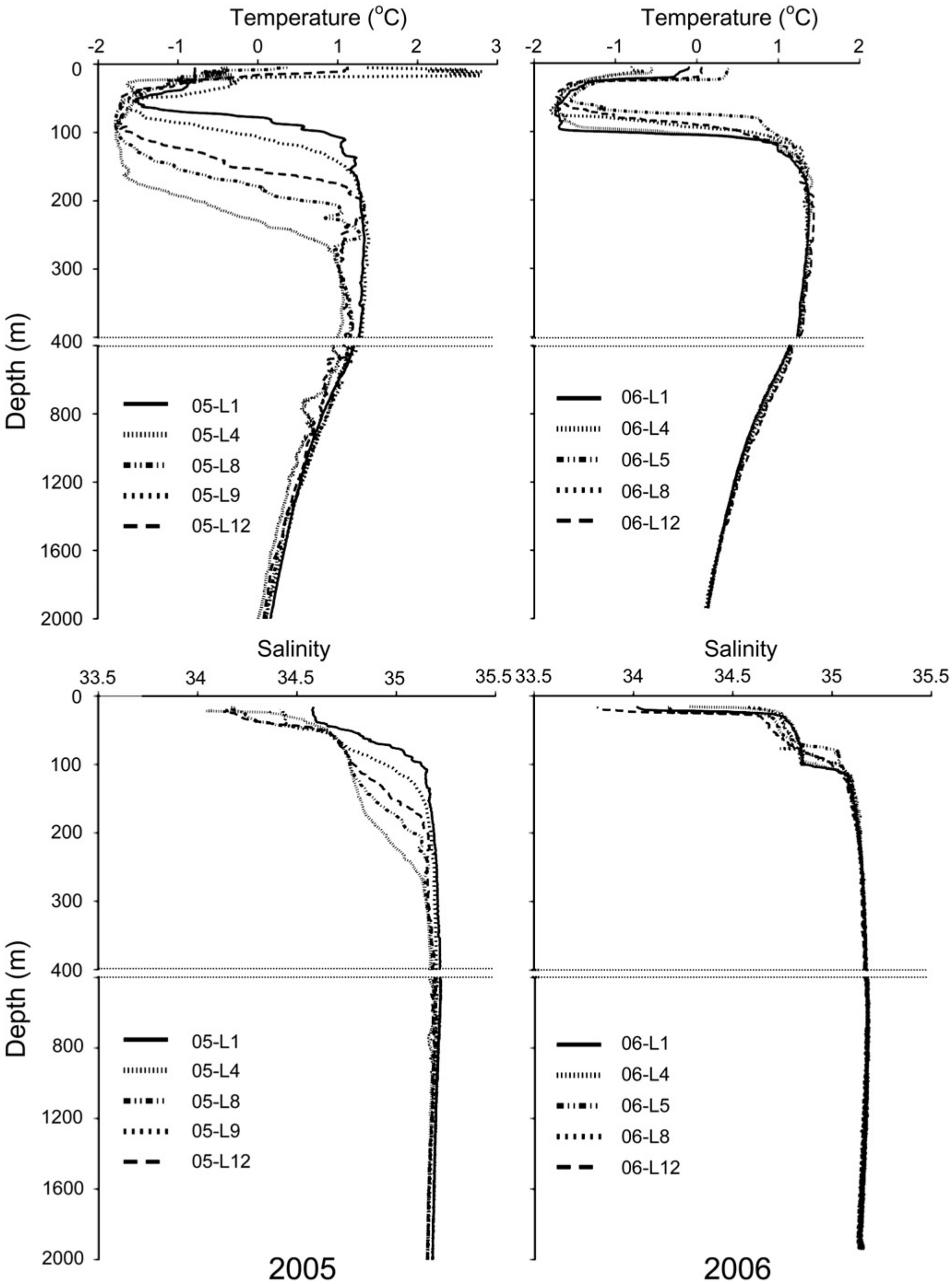

Fig. 2. Vertical profiles of water temperature (top) and salinity (bottom) off Lützow−Holm Bay, Indian sector, in 2005 and 2006. For the station names, see Fig. 1 and Table 1.

of physonects and calycophoran *Vogtia serrata* colonies were roughly estimated by assuming that ten nectophores represented a single colony, according to Pagès et al. (1996) and Hosia et al. (2008). Therefore, any number of nectophores from 1 to 10 was 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 for two nectophores. For the remaining siphonophores, the number of anterior nectophores was used to estimate the number of colonies. The scientific names follow 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 the genus *Rosacea* of Siphonophorae, we followed Haddock et al. (2005).

Chlorophyll *a* (Chl-*a*) concentrations were determined by the fluorometric method (Strickland and Parsons, 1972) using a Turner Design Model 10-AU fluorometer calibrated with commercial Chl-*a* (Wako Pure Chemical Industries, Osaka, Japan) and a Welshmayer filter set according to the method of Parsons et al. (1984). Seawater samples were collected at almost the same time as the CTD cast, from 12 depths above 200 m using a Niskin bottle. Chl-*a* was immediately extracted by immersing the filter in *N*, *N*-dimethylformamide (Suzuki and Ishimaru, 1990), and the samples were preserved at −4 °C until analysis. Photosynthetic pigments on the filter were extracted with 6 ml *N*, *N*-dimethylformamide for 1 day at −20 °C.

2.4. 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 were excluded from this analysis. Unweighted-pairs group linkage and non-metric multidimensional scaling (nMDS) were performed based on similarity. The SIMPER (similarity percentage) routine identified the species contributing to similarity within the observed clusters. These statistical analyses were conducted using the software package PRIMER v6 (PRIMER-E; Clarke and Gorley, 2006).

3. Results

3.1. Hydrography and primary production

In 2005, winter water (WW) at a temperature of less than −1.5 °C was observed at about 30–180 m (Fig. 2). The depth of the permanent thermocline varied among stations. The depths of 0 °C water ranged from 78 to 230 m, being deeper for the stations near the ice edge (Stns. 05-L4, -L8). Below the WW was modified circumpolar deep water (MCDW) with a maximum temperature of about 1.3 °C. The WW was covered by warm summer surface water (SSW). In 2006, the basic structure was similar to that in 2005, although the depth range of WW was narrower than that in 2005, with the depths of 0 °C water ranging from 76 to 105 m.

The epipelagic layer had a lower Chl-*a* concentration in 2006; the mean ± SD of the cumulative Chl-*a* concentration (0–200 m depth) was 5.86 ± 2.27 vs. 1.38 ± 0.28 μg L^{-1} in 2005 and 2006, respectively.

3.2. Zooplankton vertical distribution

The carbon biomass of the total macrozooplankton and the assemblages of the major taxa are shown in Fig. 3. The cumulative biomass (0–2000 m) in 2006 was very small compared to that in 2005 (5702 vs. 17,797 mgC).

In 2005, greater biomass percentages were observed in the 0–50 and 100–200 m layers (mean ± SD: 1520 ± 855 and 1012 ± 434 mgC, respectively), in which Euphausiacea (41.3%) and Medusae (53.5%) were dominant, respectively (Fig. 3). Medusae were observed in all layers, constituting 5.0–57.1% of the biomass, and especially dominated the 100–500 m layers. Siphonophores were also found in all layers and constituted a greater percentage in the 0–100 m layers.

In 2006, the greatest biomass was recorded at 0–50 m (866 ± 1685 mg), where Euphausiacea dominated (88.1% of the total carbon biomass; Figs. 3, 4). The biomass at 200–500 m exhibited another small peak, excluding Euphausiacea. Unlike in 2005, copepods occupied a greater biomass percentage in all layers except for 0–50 m (40.8–84.5% in 50–2000 m; pteropods dominated at 0–50 m, 59.4%). Siphonophores were found in all layers (Figs. 3, 4), but were mainly distributed in the upper 500 m (2.3–3.0% in 0–200 m). Medusae were found at higher percentages at 200–500 and 1000–2000 m, constituting 27.3% and 7.7% of the total carbon biomass, respectively.

In 2006, Medusae, Siphonophorae, Copepoda, and Salpida had a peak in abundance and biomass at 200–500 m depth, whereas these animals were mainly distributed in the upper 200 m layers in 2005 (Fig. 4). Euphausiacea was distributed mainly in the upper 50 m, although they were found in the 50–500 m layers in 2005. The carbon biomass of Medusae from the 0 to 50 m, 100–200 m, and 200–500 m layers was very high in 2005 compared to 2006, due to the occurrence of a large number of *Peryphylla peryphylla* (Fig. 4).

3.3. Overview of the cnidarian community

In 2005 and 2006, 31 and 20 species were recorded, respectively (Tables 2 and 3). In 2006, the total abundance was very small compared to that in 2005 (77.1 vs. 390.8 individuals/1000 m^3; Tables 2 and 3).

In all, 28 species (taxa) of hydrozoans and 3 species of scyphozoans were identified (Tables 2 and 3). Within the

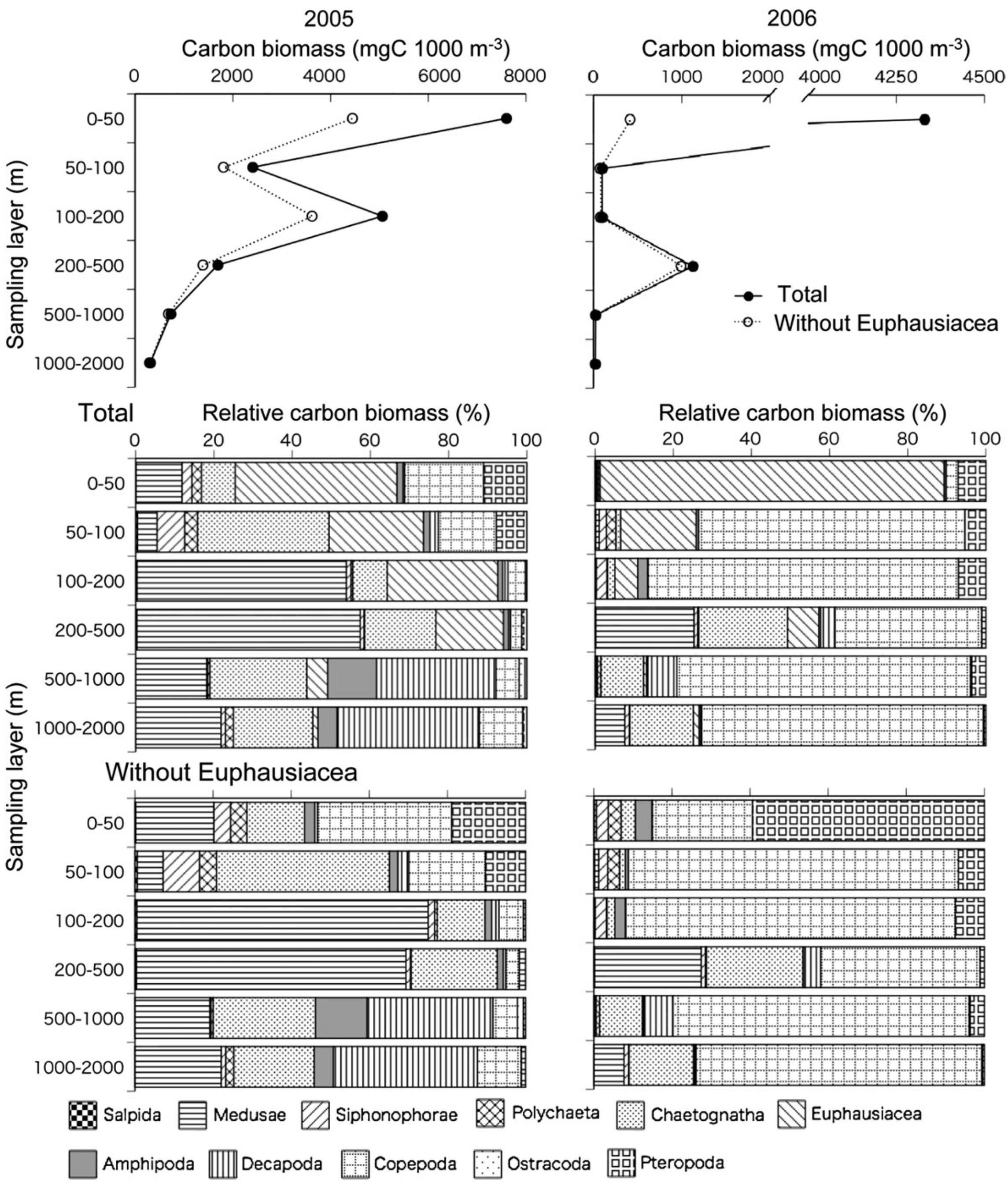

Fig. 3. Vertical distributions of total carbon biomass (top) and the relative abundance of major mesozooplankton taxa (middle, total biomass; bottom, without Euphausiacea) off Lützow–Holm Bay, Indian sector, in 2005 and 2006.

Hydrozoa, the greatest number of species (12) were from the order Siphonophorae, followed by Anthomedusae (5), Trachymedusae (5), Leptomedusae (3), and Narcomedusae (3). Two suborders of siphonophore were identified: Physonectae (2 species) and Calycophorae (10).

In 2005, 31 (20–24 species per station) species were identified at the five stations versus 20 (12–16 per station) in 2006 (Tables 2 and 3). Leptomedusae and Semaeostomeae did not occur in 2006, whereas two and one species, respectively, occurred in 2005. Only one species of anthomedusan was observed in 2006, whereas six species occurred in 2005.

In 2005, *Diphyes antarctica* (Calycophorae) was the most dominant species, contributing 27.9% of the total

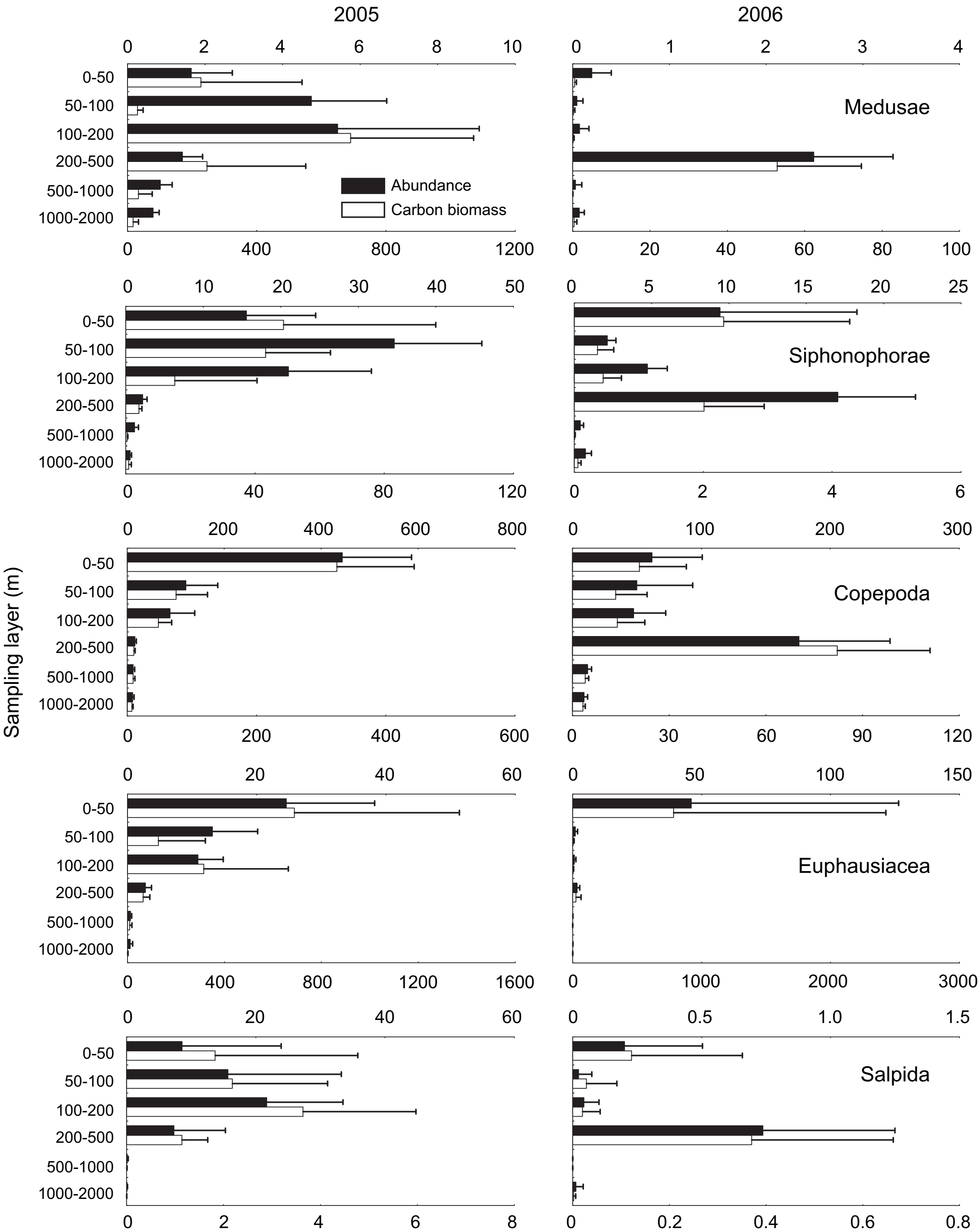

Fig. 4. Abundance (top horizontal axis; $n/1000\ m^3$) and carbon biomass (bottom axis; $mgC/1000\ m^3$) of Medusae, Siphonophorae, Copepoda, Euphausiace, and Salpida off Lützow−Holm Bay, Indian sector, in 2005 and 2006.

cnidarian abundance, followed by the siphonophores *Dimophyes arctica* (Calycophorae, 20.2%), *Muggiaea bargmannae* (Calycophorae, 18.3%), and *Pyrostephos vanhoeffeni* (Physophora, 9.9%) (Table 2). Siphonophorae contributed 82.2% of the total abundance. The abundance of Trachymedusae followed that of siphonophores and was 8.3% of the total. *Haliscera conica* constituted 80.5% of the total

Table 2
List, abundance (n/1000 m^3), and number of species of cnidarians collected off Lützow–Holm Bay, Indian sector, in 2005.

Station (total no. of species at each station)	05-L1 (24)						05-L4 (22)						05-L8 (21)					
Sampling depth (m)	0–50	50–100	100–200	200–500	500–1000	1000–1800	0–50	50–100	100–200	200–500	500–1000	1000–2000	0–50	50–100	100–200	200–500	500–1000	1000–1750
Hydrozoa																		
Anthomedusae																		
Calycopsis borchgrevinki Browne, 1910	0.65	2.54		0.18	0.07			3.33	1.49	0.23	0.06		2.04	2.91	0.78			0.06
Russellia mirabilis Kramp, 1957			0.14						0.15									
Koellikerina maasi Browne, 1910										0.16								
Euphysora sp.													0.10					
? *Bythotiara* sp.													0.10	0.11	0.16			
Anthomedusae sp.																		
Trachymedusae																		
Haliscera conica Vanhöffen, 1902		1.49	1.53	0.74	0.22	0.22	0.14	0.28	0.60	1.48	0.12			1.08	9.08	0.61	0.22	0.11
Halicreas minimum Fewkes, 1882				0.14	0.30					0.06	0.46					0.07	0.06	
Botrynema brucei Browne, 1908				0.07	0.37					0.06	0.15						0.17	
Pantachogon haeckeli Maas, 1893			0.18	0.36	0.07					0.36	0.15					0.29	0.06	
Crossota brunnea Vanhöffen, 1902				0.22	0.07				0.08	0.06								
Narcomedusae																		
Pegantha martagon Haeckel, 1879	0.32	0.30	0.55	0.09			0.28	0.28	0.15				0.10	0.11				
Aegina citrea Eschscholtz, 1829										0.08								
Solmissus incisa Fewkes, 1886				0.46							0.55			0.11				
Leptomedusae																		
Chromatonema rubrum Fewkes, 1882																		
Leptomedusae sp.													0.10					0.06
Siphonophora																		
Physonectae																		
Pyrostephos vanhoeffeni Moser, 1925	0.32						24.54	0.42	0.45	0.23	0.06	0.26	5.72	0.11	0.31	0.24	0.07	0.06
Marrus antarcticus Totton, 1954					0.07					0.08								
Calycophorae																		
Diphyes antarctica Moser, 1925	3.72	19.26	0.69	0.92			3.19	4.30	26.73	0.70			8.38	2.60	2.72	0.49	0.72	
Dimophyes arctica (Chun, 1897)	0.49	7.32	7.21	0.92		0.75	1.19	11.92	8.67	0.47		0.12	1.12	9.60	8.39	0.12	0.72	0.58
Muggiaea bargmannae Totton, 1954	1.13	14.36	1.68	0.18		0.15	0.83	4.71	1.49	0.39	0.12	0.24	0.52	5.68	11.41	0.12		0.11
Vogtia serrata (Moser, 1925)			0.14	0.92						0.62	0.18				0.08	0.97	0.07	
Crystallophyes amygdalina Moser, 1925				0.37	0.14	0.75						0.52				0.24	0.72	0.58
Clausophyes moserae Margulis, 1988					0.72	0.75												
Chuniphyes moserae Totton, 1954						0.22												
Lensia havock Totton, 1941					0.29						0.12	0.12					0.22	0.11
Lensia achilles Totton, 1941				0.92	0.72	0.22				0.78	0.12	0.52				0.24	0.29	0.11
Rosacea plicata Quoy and Gaimard, 1827				0.09														
Scyphozoa																		
Coronatae																		
Atolla wyvillei Haeckel, 1880					0.07	0.07												0.06
Periphylla periphylla (Péron and Lesueur, 1809)			0.14	0.09	0.07	0.07	0.14		0.15	0.23	0.06		0.10					0.11
Semaeostomeae																		
Diplulmaris antarctica Maas, 1908				0.09				0.14					0.10					
Total abundance	8.13	45.30	11.48	6.27	3.20	3.12	30.45	25.69	40.83	4.63	2.04	1.78	19.48	30.30	24.45	3.00	3.20	2.28
Total no. of individuals	41	301	152	35	35	27	218	183	267	61	23	30	180	372	423	25	20	21
Total no. species	7	6	9	17	13	9	7	8	10	16	11	6	12	9	8	10	11	11

Table 2 (*continued*)

Station (total no. of species at each station)	05-L9 (20)						05-L12 (23)						Total abundance
Sampling depth (m)	0–50	50–100	100–200	200–500	500–1000	1000–2000	0–50	50–100	100–200	200–500	500–1000	1000–2000	
Hydrozoa													
Anthomedusae													
Calycopsis borchgrevinki Browne, 1910	0.54	4.96	0.28	0.19			2.35	2.40	0.22	0.26			25.54
Russellia mirabilis Kramp, 1957													0.29
Koellikerina maasi Browne, 1910										0.13			0.28
Euphysora sp.													0.10
? *Bythotiara* sp.													0.37
Anthomedusae sp.											0.09		0.09
Trachymedusae													
Haliscera conica Vanhöffen, 1902	0.43		2.03	0.39	0.17			0.92	3.34	0.91	0.09		26.19
Halicreas minimum Fewkes, 1882					0.22					0.09	0.11		1.51
Botrynema brucei Browne, 1908			0.10	0.17	0.11						0.16		1.37
Pantachogon haeckeli Maas, 1893			0.19	0.51	0.11				0.26	0.28			2.83
Crossota brunnea Vanhöffen, 1902					0.11					0.09			0.63
Narcomedusae													
Pegantha martagon Haeckel, 1879	0.43	0.86	0.18	0.10			0.10	0.09	0.32	0.39			4.67
Aegina citrea Eschscholtz, 1829													0.08
Solmissus incisa Fewkes, 1886		0.86									0.18		2.16
Leptomedusae													
Chromatonema rubrum Fewkes, 1882						0.06				0.13			0.18
Leptomedusae sp.													0.16
Siphonophora													
Physonectae													
Pyrostephos vanhoeffeni Moser, 1925	1.40	0.22	0.18		0.08		3.37	0.09	0.11	0.13		0.16	38.54
Marrus antarcticus Totton, 1954													0.15
Calycophorae													
Diphyes antarctica Moser, 1925	8.34	4.55	2.43	0.39			1.73	15.86	1.19	0.26			109.15
Dimophyes arctica (Chun, 1897)		2.59	2.96	0.29	0.17	0.12	0.24	8.41	3.88	0.52		0.18	78.95
Muggiaea bargmannae Totton, 1954	0.86	6.39	13.40	0.98		0.55		2.68	2.48	0.39		0.54	71.42
Vogtia serrata (Moser, 1925)	0.11		0.65	0.58	0.08		0.20	0.09	0.22	0.91	0.18	0.05	6.06
Crystallophyes amygdalina Moser, 1925				0.68						0.26		0.54	4.80
Clausophyes moserae Margulis, 1988					0.84					0.13	0.92	0.54	3.90
Chuniphyes moserae Totton, 1954													0.22
Lensia havock Totton, 1941					0.60	0.12					0.65		2.23
Lensia achilles Totton, 1941					0.56					0.13	0.74	0.18	5.54
Rosacea plicata Quoy and Gaimard, 1827										0.13			0.22
Scyphozoa													
Coronatae													
Atolla wyvillei Haeckel, 1880				0.19	0.17	0.11						0.22	0.89
Periphylla periphylla (Péron and Lesueur, 1809)			0.09	0.10	0.08	0.06			0.11	0.26			1.87
Semaeostomeae													
Diplulmaris antarctica Maas, 1908													0.33
Total abundance	11.68	22.47	20.85	4.34	3.15	1.02	8.92	32.98	9.69	4.57	3.04	2.41	390.75
Total no. of individuals	112	512	238	34	30	19	166	325	109	39	25	19	4042
Total no. species	6	8	11	12	12	6	7	8	10	18	8	8	31

Table 3
List, abundance (n/1000 m^3), and number of species of cnidarians collected off Lützow–Holm Bay, Indian sector, in 2006.

Station (total no. of species at each station)	06-L1 (12)						06-L4 (12)						06-L5 (14)					
Sampling depth (m)	0-50	50-100	100-200	200-500	500-1000	1000-2000	0-50	50-100	100-200	200-500	500-1000	1000-2000	0-50	50-100	100-200	200-500	500-1000	1000-2000
Hydrozoa																		
Anthomedusae																		
Calycopsis borchgrevinki Browne, 1910	0.22			0.19			0.24			0.05						0.26		
Trachymedusae																		
Haliscera conica Vanhöffen, 1902	0.11			1.06			0.12			0.11						0.21		
Halicreas minimum Fewkes, 1882																		
Botrynema brucei Browne, 1908																		
Pantachogon haeckeli Maas, 1893				0.06												0.10		
Narcomedusae																		
Pegantha martagon Haeckel, 1879	0.11															0.05		
Aegina citrea Eschscholtz, 1829				0.06														
Solmissus incisa Fewkes, 1886				0.13						0.16						0.21		
Siphonophora																		
Physonectae																		
Pyrostephos vanhoeffeni Moser, 1925	0.32						1.58											
Marrus antarcticus Totton, 1954																		
Calycophorae																		
Diphyes antarctica Moser, 1925	1.08	0.11	0.43	0.19			2.30	0.80	0.11					0.31	0.32	0.16		
Dimophyes arctica (Chun, 1897)	0.11		0.54		0.08	0.24	0.36	0.23	0.32	0.05	0.09			0.10	1.73	0.16	0.22	0.10
Muggiaea bargmannae Totton, 1954	0.32	0.80	2.70	0.31		0.24	0.12	0.34	1.62	0.49		0.42	0.19	1.02	2.37	0.16		0.97
Vogtia serrata (Moser, 1925)	0.11			0.94		0.12				0.27	0.09					0.63		
Crystallophyes amygdalina Moser, 1925				0.13						0.05						0.37	0.15	0.10
Lensia havock Totton, 1941					0.08													
Lensia achilles Totton, 1941																		0.10
Rosacea plicata Quoy and Gaimard, 1827										0.05						0.10		
Scyphozoa																		
Coronatae																		
Atolla wyvillei Haeckel, 1880				0.25						0.05						0.05		
Periphylla periphylla (Péron and Lesueur, 1809)										0.16						0.10		
Total abundance (n/1000 m^3)	2.37	0.91	3.67	3.32	0.16	0.61	4.73	1.37	2.05	1.46	0.18	0.42	0.19	1.43	4.42	2.57	0.37	1.26
Total no. of individuals	21	8	34	53	2	5	39	12	19	27	2	3	2	14	41	49	5	13
Total no. of species	8	2	3	10	2	3	6	3	3	10	2	1	1	3	3	13	2	4

Table 3 (*continued*)

Station (total no. of species at each station)	06-L8 (16)						06-L12 (15)						Total abundance
Sampling depth (m)	0-50	50-100	100-200	200-500	500-1000	1000-2000	0-50	50-100	100-200	200-500	500-1000	1000-2000	
Hydrozoa													
Anthomedusae													
Calycopsis borchgrevinki Browne, 1910		0.11	0.10	0.23			0.17		0.10	0.04			1.71
Trachymedusae													
Haliscera conica Vanhöffen, 1902				0.40						0.09			2.10
Halicreas minimum Fewkes, 1882										0.04			0.04
Botrynema brucei Browne, 1908						0.23				0.04	0.07	0.13	0.47
Pantachogon haeckeli Maas, 1893				0.06							0.07		0.30
Narcomedusae													
Pegantha martagon Haeckel, 1879				0.06									0.22
Aegina citrea Eschscholtz, 1829													0.06
Solmissus incisa Fewkes, 1886				0.17						0.31			0.98
Siphonophora													
Physonectae													
Pyrostephos vanhoeffeni Moser, 1925	0.55									0.18			2.63
Marrus antarcticus Totton, 1954				0.11								0.13	0.24
Calycophorae													
Diphyes antarctica Moser, 1925	1.57	0.11	0.31	0.06			0.68	0.26	0.29	0.04		0.13	9.26
Dimophyes arctica (Chun, 1897)	0.09		2.25				0.17	0.35	1.26	0.22	0.07		8.75
Muggiaea bargmannae Totton, 1954	0.18	1.08	2.55				0.08	1.15	2.23	0.13		0.13	19.62
Vogtia serrata (Moser, 1925)	0.09			0.57			0.08			0.26		0.13	3.30
Crystallophyes amygdalina Moser, 1925				0.34						0.09		0.13	1.35
Lensia havock Totton, 1941						0.11				0.09			0.28
Lensia achilles Totton, 1941													0.10
Rosacea plicata Quoy and Gaimard, 1827				0.11						0.04			0.32
Scyphozoa													
Coronatae													
Atolla wyvillei Haeckel, 1880				0.06									0.41
Periphylla periphylla (Péron and Lesueur, 1809)													0.27
Total abundance (n/1000 m^3)	2.50	1.29	5.21	2.17	0	0.34	1.18	1.76	3.88	1.59	0.22	0.78	52.42
Total no. of individuals	26	12	51	37	0	3	14	20	40	35	3	6	596
Total no. of species	5	3	4	11	0	2	5	3	4	13	3	6	20

trachymedusan abundance. Anthomedusae was the third dominant taxa (order), of which 96% was *Calycopsis borchgrevinki*.

In 2006, *M. bargmannae* was most dominant, with 25.4% abundance, followed by the siphonophores *D. arctica* (16.8%), *V. serrata* (12.4%), and *D. antarctica* (12.2%; Table 3). Siphonophores contributed 79.4% of the abundance.

3.4. Cluster analysis

Hierarchical clustering based on the Bray–Curtis similarities of the community at all sampling depth layers in both years revealed five groups (A–E) and two outliers (F, G) at 35% similarity (Fig. 5). The nMDS plots showed a clear dissociation among three major groups: the epipelagic groups (B and C), upper mesopelagic group (A), and lower mesopelagic and bathypelagic groups (D and E; Figs. 5, 6). Group C partly existed in the bathypelagic layer (Stns. 06-L5).

Group B contained all of the 0–200 m samples in 2005 and the 0–50 m samples for stations 06-L4 and -L8 in 2006 (Fig. 6). Group B had the largest average abundance (24.43), but only the third highest average species richness (7.5; Table 4). The species contributing most to the similarity within this group were *D. antarctica*, *M. bargmannae*, *D. arctica*, *C. borchgrevinki*, and *P. vanhoeffeni*, which contributed 91.2% of the similarity (Table 5). Of these species, *D. antarctica* contributed 38.0%. A higher value of *Si*/SD (*Si*) in Table 5 indicates that species *i* occurred more consistently in all samples within a group (Clarke and Warwick, 2001). This value was higher for *D. antarctica* (3.76; Table 5). Group C represented part of the epipelagic community together with group B (Figs. 5, 6), which consisted of the 0–200 m samples for all stations in 2006 except for the 0–50 m samples for stations 06-L4 and -L8 (Fig. 5). However, this group was also found in the bathypelagic layer at 06-L5, although the individual numbers were very small (13 individuals; Table 3). Group C had somewhat low average abundance (2.23) and average species richness (3.8; Table 4). The species in group C were similar to those in group B, excluding *C. borchgrevinki* and *P. vanhoeffeni*. Only three species contributed 98.7% of the similarity, although *M. bargmannae* had a higher value of *Si*/SD(*i*), indicating that this species was distributed more consistently in the samples (Table 5). Group A contained the 200–500 m samples in both years and exhibited the highest diversity in terms of total species number and average species richness, 25 and 12.0, respectively (Table 4, Fig. 5). However, the average abundance was very small compared to group B (4.36; Table 4). The species in this group were *V. serrata*, *H. conica*, and *Crystallophyes amygdalina*, which contributed 57.7% of the similarity (Table 5). The first two species were more common in the samples, indicated by the highest *Si*/SD(*Si*) values. Group D was found only in 500–2000 m samples in 2005 (Fig. 6), and consisted of 11 species, the main ones being *Lensia achilles*, *Pantachogon haeckeli*, *Lensia havock*, and *H. conica*. However, their contribution percentages and *Si*/SD(*Si*) values were low (Table 5). Group D had the second highest average species richness (11.1; the total was 22) after group A, although the average abundance was low (1.72; Table 4). Group E was composed of only two samples from the meso- and bathypelagic layers in 2006, with five individuals in both samples (Table 5).

Average temperature–salinity (T–S) plots for each group are shown in Fig. 7. Cnidarians belonging to groups B and C were in the SSW, WW, and upper MCDW of the epipelagic layer. Group A was found only in the warm, high-salinity, upper MCDW. Groups D and E were distributed only in the lower MCDW. Samples in which fewer than five individuals were caught were observed mostly in the lower MCDW and only in 2006.

4. Discussion

4.1. New geographic records for East Antarctica

Many recent studies have examined the cnidarian communities of the Southern Ocean, although mostly in West Antarctica (Pagès and Kurbjeweit, 1994; Pagès and Schnack-Schiel, 1996; Pagès et al., 1996; Pugh et al., 1997). Pagès et al. (1994) studied the eastern part of the Weddell Gyre in East Antarctica. Therefore, our study is the second intensive study of the cnidarian communities from the epi- to bathypelagic zone in East Antarctica, although several taxonomic studies have reported the distributions of some cnidarian species in East Antarctica (Totton, 1954; Kramp, 1968; Larson, 1986).

Of the 31 species that we collected in Lützow–Holm Bay, at least four were first records for East Antarctica: *Koellikerina maasi*, *Russellia mirabilis*, *Pegantha martagon*, and *Solmissus incisa*. *K. maasi* is known from the Weddell and Ross seas (Kramp, 1957; Larson and Harbison, 1990), and Kramp (1957, 1961) recorded *R. mirabilis* and *P. martagon* from the Atlantic sector, although several

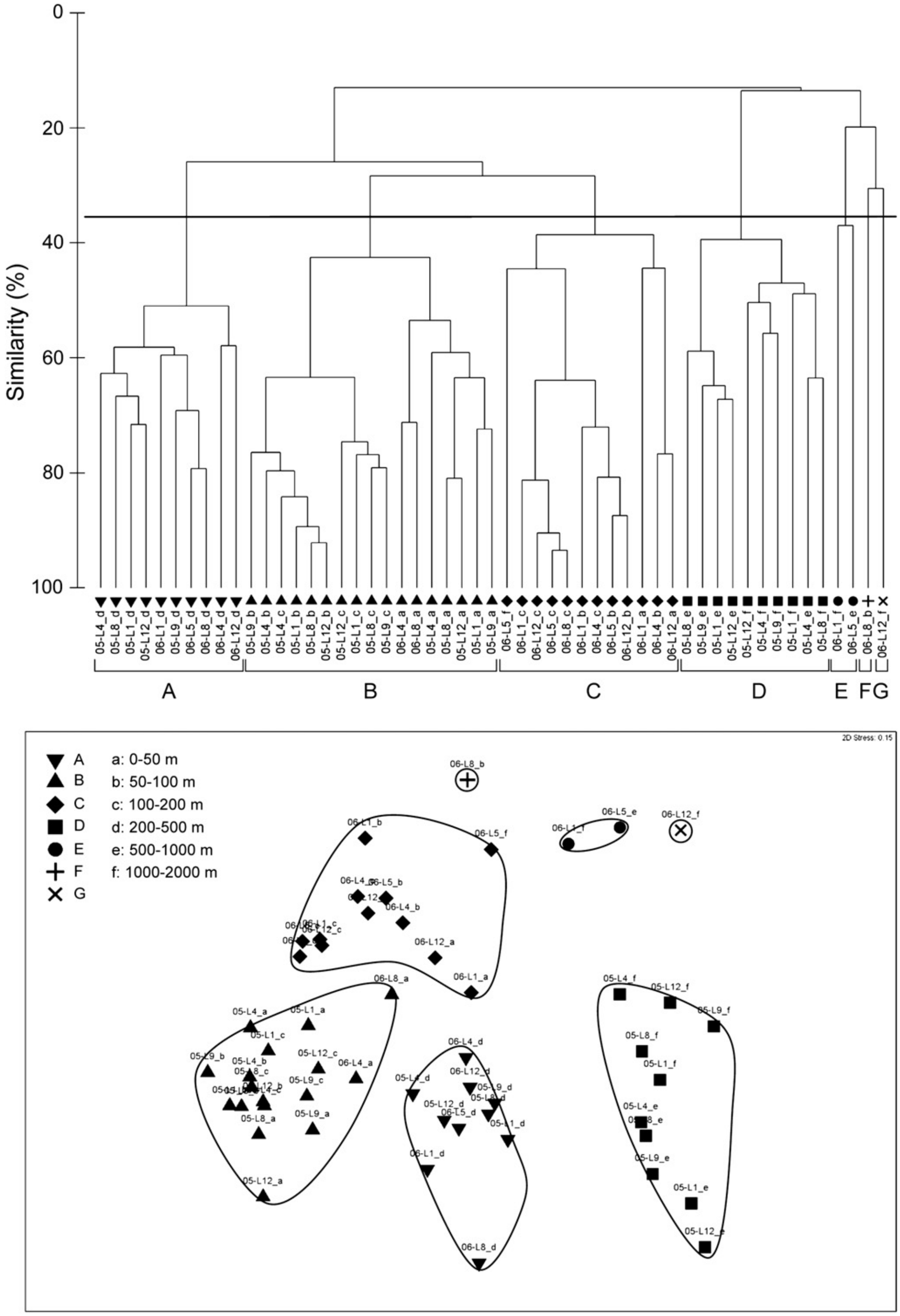

Fig. 5. Dendrogram (top) representing the classification of samples based on Bray–Curtis similarities for cnidarian species assemblages and nMDS plots (bottom) of the samples with clustering at 35% of similarity.

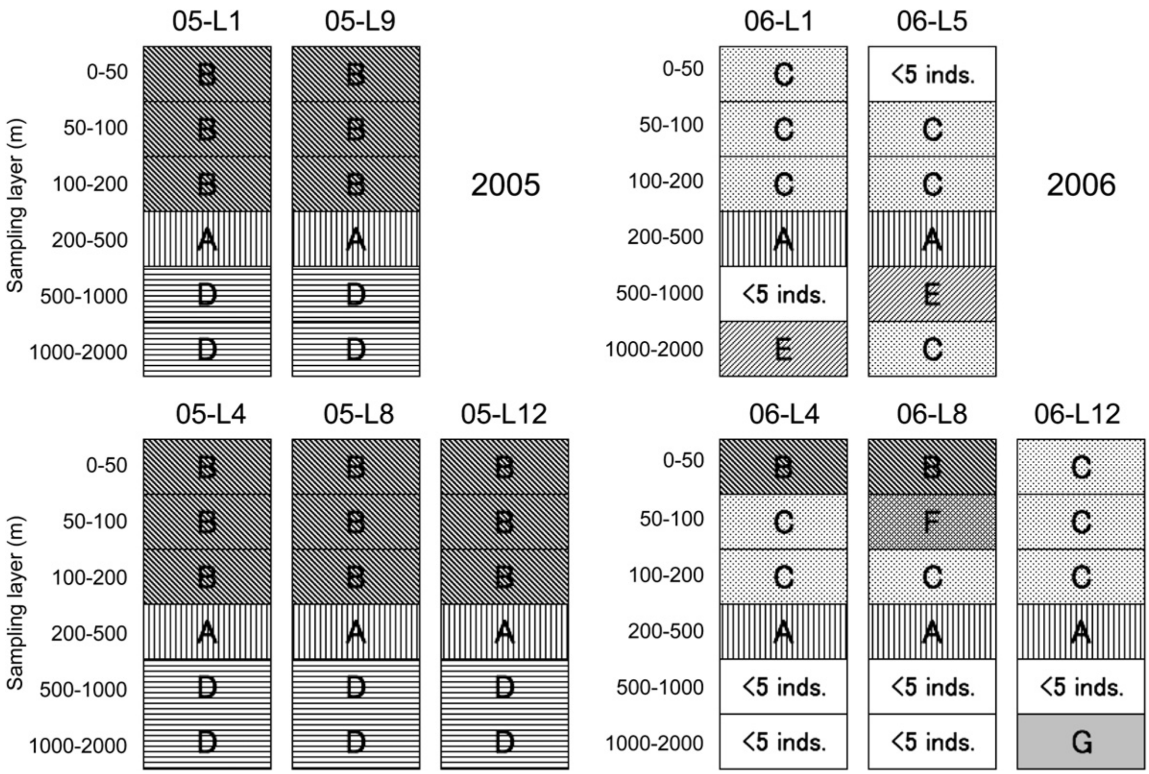

Fig. 6. Schematic of the cnidarian community structure off Lützow–Holm Bay, Indian sector, in 2005 and 2006. Capital letters denote the group name identified by the hierarchical clustering in Fig. 5.

comprehensive studies of the cnidarian community did not mention these species for East Antarctica.

We identified *S. incisa* in both years, and these constitute the first records for the species south of the Antarctic Polar Front. *S. incisa* is a mesopelagic species distributed from 45°S to 60°N in the Atlantic, Indian, and Pacific oceans (Kramp, 1965; Lindsay and Hunt, 2005; Hosia et al., 2008). We found this species mainly at 200–500 m, although it was distributed widely from 50 to 1000 m.

Table 4
Characteristics of each group identified by the hierarchical clustering.

Group	No. of samples	Average individual no.	Average abundance[a]	Average species richness	Total no. species
A	10	40.0	4.36	12.0	25
B	17	215.8	24.43	7.5	14
C	12	23.3	2.23	3.8	10
D	10	25.1	1.72	11.1	22
E	2	5.0	0.34	2.5	3
F	1	12.0	0.32	2.0	3
G	1	6.0	0.26	6.0	6

[a] Abundance, $n/1000\ m^3$.

4.2. Vertical distribution

Cnidarians undertake diel vertical migration (DVM; Pugh, 1984; Pagès et al., 1996; Youngbluth and Båmstedt, 2001), although we did not examine DVM in this study because the true night was very short in both years during the research period, 0–156 and 157–235 min in 2005 and 2006, respectively. Moreover, we conducted all samplings during daylight, although the samplings at stations 05-L4 and 05-L8 were partly conducted under the midnight sun. Furthermore, the sample sizes were too small to examine DVM. However, DVM has been observed in salps in a study conducted close to the midnight sun period in the Indian sector (Nishikawa and Tsuda, 2001). A detailed study of DVM by zooplankton is necessary to understand the pelagic ecosystem in the High-Antarctic Zone.

Pagès and Schnack-Schiel (1996) reported low abundance and species richness in the upper cold water (above the permanent thermocline), whereas we observed the highest abundance in the epipelagic layer (group B), where cold WW exists, as well as SSW. The permanent thermocline is considered an important

Table 5
Average abundance, similarity (Si), and related values within a cluster (SIMPER analysis).

Species	Contri.%	Cum.%	Av.Si	Si/SD(Si)	Av. abund. (inds 10^{-3} m^3)
Group A (Av. similarity: 57.6)					
Vogtia serrata	28.9	28.87	16.6	5.44	0.96
Haliscera conica	19.1	47.96	11.0	2.55	0.79
Crystallophyes amygdalina	9.8	57.72	5.6	1.40	0.36
Muggiaea bargmannae	8.0	65.69	4.6	1.40	0.37
Diphyes antarctica	7.1	72.81	4.1	1.25	0.28
Calycopsis borchgrevinki	6.9	79.73	4.0	1.64	0.24
Dimophyes arctica	5.6	85.28	3.2	1.01	0.26
Periphylla periphylla	3.1	88.37	1.8	0.86	0.14
Solmissus incisa	3.0	91.34	1.7	0.51	0.23
Group B (54.6)					
Diphyes antarctica	38.0	38.0	20.8	2.40	10.15
Dimophyes arctica	18.6	56.6	10.1	1.19	4.35
Muggiaea bargmannae	17.9	74.5	9.8	1.26	4.48
Calycopsis borchgrevinki	9.4	84.0	5.2	1.00	1.45
Pyrostephos vanhoeffeni	7.2	91.2	4.0	0.69	2.32
Group C (54.1)					
Muggiaea bargmannae	61.5	61.5	33.2	1.89	1.25
Diphyes antarctica	19.0	80.5	10.3	1.26	0.31
Dimophyes arctica	18.2	98.7	9.9	1.23	0.55
Group D (45.8)					
Lensia achilles	15.3	15.3	7.0	1.20	0.29
Pantachogon haeckeli	15.0	30.3	6.8	1.24	0.22
Lensia havock	11.8	42.1	5.4	1.08	0.22
Halicreas minimum	10.9	53.0	5.0	1.27	0.15
Botrynema brucei	9.6	62.6	4.4	1.03	0.13
Haliscera conica	7.5	70.1	3.4	0.86	0.12
Dimophyes arctica	5.6	75.7	2.6	0.85	0.07
Muggiaea bargmannae	4.4	80.1	2.0	0.65	0.07
Pyrostephos vanhoeffeni	3.7	83.8	1.7	0.62	0.07
Atolla wyvillei	3.7	87.5	1.7	0.62	0.07
Periphylla periphylla	2.9	90.4	1.3	0.69	0.05
Group E (37.0)					
Dimophyes arctica	100	100	37.0	–	0.17

Species list of each group is truncated when cumulative percentage of 90% 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.

factor restricting the vertical distribution; some studies have observed greater abundance and species richness below the thermocline (Pagès and Kurbjeweit, 1994; Pagès and Schnack-Schiel, 1996). In 2006, the thermocline was located at 50–100 m depths, and most of the communities in the 50–200 m layers represented group C, which exhibited low abundance and species richness. Furthermore, the vertical community structure was uniform across stations in 2005, although the development of the WW varied geographically. These observations indicate that the vertical distribution of cnidarians is not only determined by the existence of WW or a thermocline. Other factors may affect zooplankton prey or predators, as noted in Pagès and Kurbjeweit (1994) and Pugh (1991).

4.3. Differences in cnidarian community structure between 2005 and 2006

A community characterised by low abundance and a few species (group C) was identified mainly in the epipelagic layer and was also found at 1000–2000 m in 2006. Epipelagic group C was characterised by a negative factor, i.e., the absence of *C. borchgrevinki* and *P. vanhoeffeni* from the epipelagic community in 2005 (group B). Furthermore, bathypelagic group C

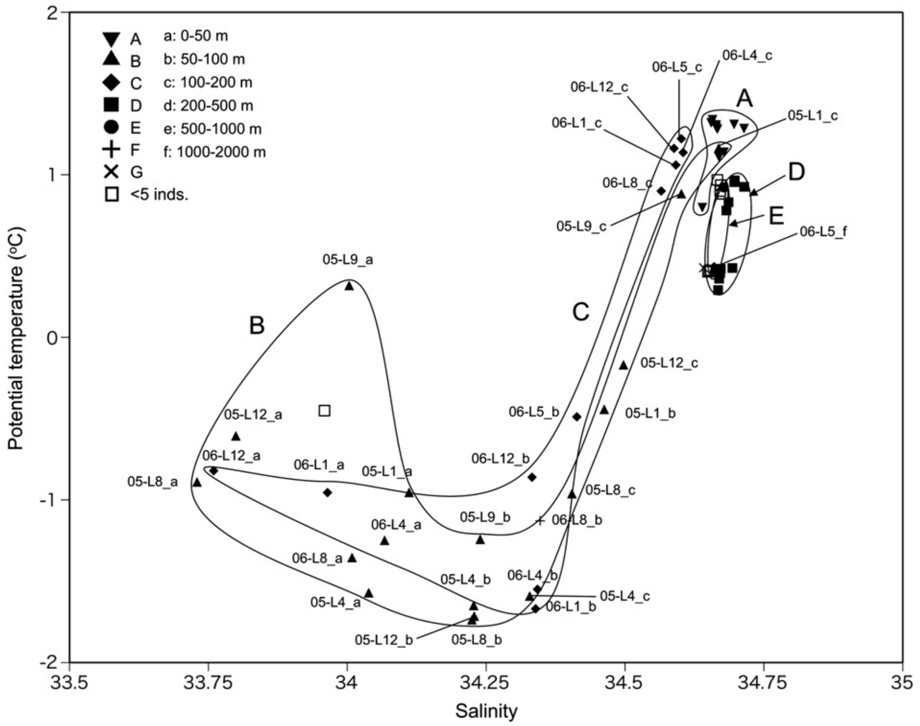

Fig. 7. Diagram of the average temperature and salinity at each sample. The station names and depth layer are indicated only for groups B and C.

was characterised by the absence of several species, including *L. achilles*, *L. havock*, *P. haeckeli*, and *Halicreas minimum* from bathypelagic group D in 2005. Furthermore, meso/bathypelagic samples in 2006 had a high frequency with less than five individuals.

A major factor for spatial and temporal variation in zooplankton density is bottom-up control through variation in the quantity of primary production (Richardson and Schoeman, 2004). Differences in abundance/biomass of cnidarians between years can be explained by the difference in the amount of primary production. Earlier and greater sea ice retreat and warmer surface water temperature in 2005 would may have generated higher primary production and more abundant herbivore copepods than in 2006, resulting in a large abundance/biomass of cnidarians. Pelagic cnidarians forage for zooplankton such as copepods or salps as well as other gelatinous plankton and fish eggs/larvae (Pagès and Schnack-Schiel, 1996; Costello and Colin, 2002; Purcell, 2003; Suchman et al., 2008).

In this study, the vertical distribution patterns of cnidarians were similar to those of copepods in both 2005 and 2006, although the main depth of distribution was different between the years. Vertical distribution patterns of copepods and salps are likely to be an important determinant of distribution and abundance/biomass of the pelagic cnidarians in Lützow–Holm Bay. However, the Euphausiacea has a negative impact on the distribution of other zooplankton through competition, as indicated by the krill-dominant assemblages associated with the low density of other zooplankton (Hunt et al., 2007). The large number of krill in surface waters in 2006 likely caused a low copepod density by competition. However, in 2005, the Euphausiacea had a reduced top-down impact resulting in a similar vertical distribution pattern to copepods. Higher primary production likely reduced competition with zooplankton in 2005.

5. Conclusion

The structure of the pelagic cnidarian community in Lützow–Holm Bay is typically divided vertically as follows: 1) the epipelagic community (0–200 m; observed in SSW, WW, and upper MCDW) is characterised by high abundance of *D. antarctica*, *D. arctica*, and *M. bargmannae*, with moderate species richness; 2) the upper mesopelagic community (200–500 m; upper MCDW) is characterised by high species richness and the two species *V. serrata* and *H. conica*, but low abundance; 3) the lower mesopelagic and bathypelagic community (500–2000 m; lower

MCDW) is characterised by high species richness but low abundance. *L. achlles*, *P. hackeli*, *L. havock*, and *H. minimum* are representative of this layer, although not in great numbers.

The abundance/biomass and assemblages of cnidarians in the epipelagic layer (0–200 m) and meso- and bathypelagic layers (500–2000 m) are most likely affected by the level of primary production, although these values were stable in the 200–500 m layer. The vertical distribution pattern in terms of abundance/biomass was also affected by a combination of bottom-up, top-down controls and competition in relation to the interannual variation in primary production.

Acknowledgments

We thank the officers and crew of the TR/V *Umitaka-maru* (TUMSAT) and all of the onboard cadets in the Advanced Course for Marine Science and Technology for their outstanding assistance in sample collection. We also thank our scientific colleagues from the National Institute of Polar Research (NIPR), Hokkaido University, and other institutes for help processing the samples and with the hydrographic observations onboard. We appreciate invaluable help in species identification of cnidarians given by Dhugal Lindsay (Japan Agency for Marine Earth Science and Technology). We also wish to thank Yukuya Yamaguchi for organizing the research cruise in 2006 as a cruise leader. This study was supported primarily by Grants-in-Aid for Scientific Research from the Japan Society for the Promotion of Science (Nos. 14255102 and 19255014 for T. Ishimaru and 16101001 for M. Fukuchi of the NIPR).

References

Atkinson, A., Peck, J.M., 1988. A summer–winter comparison of zooplankton in the oceanic area Around South Georgia. Polar Biol. 8, 463–473.

Baker, A., Baker, C., Clarke, M.R., Harris, M.J., 1973. The N.I.O. combination net (RMT 1+8) and further development of Rectangular Midwater Trawls. J. Mar. Biol. Ass. U.K. 53, 167–184.

Bindoff, N.L., Rosenberga, M.A., Warner, M.J., 2000. On the circulation and water masses over the Antarctic continental slope and rise between 80 and 150°E. Deep-Sea Res. II 47, 2299–2326.

Bouillon, J., 1999. Hydromedusae. In: Boltovskoy, D. (Ed.), South Atlantic Zooplankton. Backhuys Publishers, Leiden, pp. 385–465.

Bouillon, J., Medel, M.D., Pagès, F., Gili, J.M., Boero, F., Gravili, C., 2004. Fauna of the Mediterranean Hydrozoa. Scientia Marina 68, 1–438.

Boysen-Ennen, E., Piatkowski, U., 1988. Meso- and macrozooplankton communities in the Weddell Sea, Antarctica. Polar Biol. 9, 17–35.

Boysen-Ennen, E., Hagen, W., Hubold, G., Piatkowski, U., 1991. Zooplankton biomass in the ice-covered Weddell Sea, Antarctica. Mar. Biol. 111, 227–235.

Chiba, S., Ishimaru, T., Hosie, G.W., Fukuchi, M., 2001. Spatiotemporal variability of zooplankton community structure off east Antarctica (90 to 160°E). Mar. Ecol. Prog. Ser. 216, 95–108.

Clarke, K.R., Gorley, R.N., 2006. Primer v6: User Manual/Tutorial. Primer-E, Plymouth.

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

Costello, J.H., Colin, S.P., 2002. Prey resource use by coexistent hydromedusae from Friday Harbor, Washington. Limnol. Oceanogr. 47, 934–942.

Davis, C.S., Wiebe, P.H., 1985. Macrozooplankton biomass in warm-core Gulf Stream Ring: time series changes in size structure, taxonomic composition, and vertical distribution. J. Geophys. Res. 90, 8871–8884.

Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analyzing multispecies distribution patterns. Mar. Ecol. Prog. Ser. 8, 37–52.

Haddock, S.H.D., Dunn, C.W., Pugh, P.R., 2005. A re-examination of siphonophore terminology and morphology, applied to the description of two new prayine species with remarkable bio-optical properties. J. Mar. Biol. Ass. U.K. 85, 695–707.

Hopkins, T.L., 1985. Food web of an Antarctic midwater ecosystem. Mar. Biol. 89, 197–212.

Hopkins, T.L., 1987. Midwater food web in McMurdo Sound, Ross Sea, Antarctica. Mar. Biol. 96, 93–106.

Hopkins, T.L., Torres, J.J., 1988. The zooplankton community in the vicinity of the ice edge, western Weddell Sea, March 1986. Polar Biol. 9, 79–87.

Hopkins, T.L., Ainley, D.G., Torres, J.J., Lancraft, T.M., 1993. Trophic structure in open waters of the marginal ice zone in the Scotia-Weddell confluence region during spring (1983). Polar Biol. 13, 389–397.

Hosie, G.W., Schultz, M.B., Kitchener, J.A., Cochran, T.G., 2000. Macrozooplankton community structure off East Antarctica (80–150°E) during the Austral summer of 1995/1996. Deep-Sea Res. II 47, 2437–2463.

Hosia, A., Stemmann, L., Youngbluth, M., 2008. Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. Deep-Sea Res. II 55, 106–118.

Hubold, G., Hempel, I., Meyer, M., 1988. Zooplankton communities in the Southern Weddell Sea (Antartica). Polar Biol. 8, 225–233.

Hunt, B.P.V., Hosie, G.W., 2003. The continuous plankton recorder in the Southern Ocean: a comparative analysis of zooplankton communities sampled by the CPR and vertical net hauls along 140°E. J. Plankton Res. 25, 1561–1579.

Hunt, B.P.V., Pakhomov, E.A., Trotsenko, B.G., 2007. The macrozooplankton of the Cosmonaut Sea, east Antarctica (30°E–60°E), 1987–1990. Deep-Sea Res. I 54, 1042–1069.

Kramp, K.L., 1957. Hydromedusae from the discovery collections. Discovery Rep. 29, 1–128.

Kramp, K.L., 1959. The hydromedusae of the Atlantic Ocean and adjacent waters. Dana-Rep. 46, 1–283.

Kramp, K.L., 1961. Synopsis of the Medusae of the World. J. Mar. Biol. Ass. U.K. 40, 1–471.

Kramp, K.L., 1965. The hydromedusae of the Pacific and Indian Oceans. Dana-Rep. 63, 1–166. Sections.

Kramp, K.L., 1968. The hydromedusae of the Pacific and Indian Oceans. Dana-Rep. 72, 1–200. Sections II and III.

Larson, R.J., 1986. Pelagic Scyphomedusae (Scyphozoa: Coronatae and Semaeostomeae) of the Southern Ocean. Biol. Antarctic Seas XVI Antarctic Res. Series 41, 59–165.

Larson, R.J., Harbison, G.R., 1990. Medusae from McMurdo Sound, Ross Sea including the descriptions of two new species, Leuckartiara brownie and *Benthocodon hyalinus*. Polar Biol 11, 19–25.

Larson, R.J., Mills, C.E., Harbison, G.R., 1991. Western Atlantic midwater hydrozoan and scyphozoan medusae: in situ studies using manned submersibles. Hydrobiologia 216/217, 311–317.

Lindsay, D.J., Hunt, J.C., 2005. Biodiversity in midwater cnidarians and ctenophores: submersible-based results from deep-water bays in the Japan Sea and north-western Pacific. J. Mar. Biol. Ass. U.K. 85, 503–517.

Moteki, M., Horimoto, N., Nagaiwa, R., Amakasu, K., Ishimaru, T., Yamaguchi, Y., 2009. Pelagic fish distribution and ontogenetic vertical migration in common mesopelagic species off Lützow–Holm Bay (Indian Ocean sector, Southern Ocean) during austral summer. Polar Biol. 32, 1461–1472.

Nishikawa, J., Tsuda, A., 2001. Diel vertical migration of the tunicate *Salpa thompsoni* in the Southern Ocean during summer. Polar Biol. 24, 299–302.

Pagès, F., 1997. The gelatinous zooplankton in the pelagic system of the Southern Ocean: a review. Ann. l'Inst. Océanogr. 73, 139–158.

Pagès, F., Kurbjeweit, F., 1994. Vertical distribution and abundance of mesoplanktonic medusae and siphonophores from the Weddell Sea, Antarctica. Polar Biol. 14, 243–251.

Pagès, F., Pugh, P.R., Gili, J.M., 1994. Macro- and megaplanktonic cnidarians collected in the eastern part of the Weddell Gyre during summer 1979. J. Mar. Biol. Ass. U.K. 74, 873–894.

Pagès, F., Schnack-Schiel, S.B., 1996. Distribution patterns of the mesozooplankton, principally siphonophores and medusae, in the vicinity of the Antarctic Slope Front (eastern Weddell Sea). J. Mar. Syst. 9, 231–248.

Pagès, F., White, M.G., Rodhouse, P.G., 1996. Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Frontal Zone in summer 1994. Mar. Ecol. Prog. Ser. 141, 139–158.

Parsons, T.R., Maita, Y., Lalli, C.M., 1984. A Manual of Chemical and Biological Methods for Seawater Analysis. Pergamon Press, Oxford, 173 pp.

Pugh, P.R., 1984. The diel migrations and distributions within a mesopelagic community in the North East Atlantic. VII. Siphonophores. Prog. Oceanogr. 13, 461–489.

Pugh, P.R., 1991. Co-occurrence of hippopodiid siphonophores and their potential prey. Hydrobiologia 216/217, 327–334.

Pugh, P.R., 1999. Siphonophorae. In: Boltovskoy, D. (Ed.), South Atlantic Zooplankton. Backhuys Publishers, Leiden, pp. 467–511.

Pugh, P.R., Pagès, F., Boorman, B., 1997. Vertical distribution and abundance of pelagic cnidarians in the eastern Weddell Sea, Antarctica. J. Mar. Biol. Ass. U.K. 77, 341–360.

Purcell, J.E., 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequarea*, in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. 246, 137–152.

Richardson, A.J., Schoeman, D.S., 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science 305, 1609–1612.

Stemmann, L., Hosia, A., Youngbluth, M.J., Søiland, H., Picheral, M., Gorsky, G., 2008. Vertical distribution (0–1000 m) of macrozooplankton, estimated using the underwater video profiler, in different hydrographic regimes along the northern portion of the Mid-Atlantic Ridge. Deep-Sea Res. II 55, 94–105.

Strickland, J.D.H., Parsons, T.R., 1972. A practical handbook of seawater analysis. Fish. Res. Board Canada Bull. 167 310pp.

Suchman, L.S., Daly, E.A., Kleister, J.E., Peterson, W.T., Brodeur, R.D., 2008. Feeding patterns and predation potential of scyphomedusae in a highly productive upwelling region. Mar. Ecol. Prog. Ser. 358, 161–172.

Suzuki, R., Ishimaru, T., 1990. An improved method for the determination of phytoplankton chlorophyll using N, N-Dimethylformamide. J. Oceanogr. 46, 190–194.

Takahashi, K., Kawaguchi, S., Kobayashi, M., Hosie, G.W., Fukuchi, M., Toda, T., 2002. Zooplankton distribution patterns in relation to the Antarctic Polar Front Zones recorded by Continuous Plankton Recorder (CPR) during 1999/2000 Kaiyo Maru cruise. Polar Biosci. 15, 97–107.

Tomczak, M., Liefrink, S., 2005. Interannual variations of water mass volumes in the Southern Ocean. J. Atmos. Ocean Sci. 10, 31–42.

Totton, A.K., 1954. Siphonophora of the Indian Ocean, together with systematic and biological notes on related specimens from other oceans. Discovery Rep. 27, 1–162.

Vinogradov, M.E., Shushkina, E.A., 2002. Vertical distribution of gelatinous macroplankton in the North Pacific observed by manned submersibles Mir-1 and Mir-2. J. Oceanogr. 58, 295–303.

Youngbluth, M., Båmstedt, U., 2001. Distribution, abundance, behavior and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord. Hydrobiologia 451, 321–333.

Youngbluth, M., Sørnes, T., Hosia, A., Stemmann, L., 2008. Vertical distribution and relative abundance of gelatinous zooplankton, in situ observations near the Mid-Atlantic Ridge. Deep-Sea Res. II 55, 119–125.

NiPR
National Institute of Polar Research

INTERNATIONAL POLAR YEAR 2007-2008