

Vertical profiles of zooplankton community structure in Prydz Bay, Antarctica, during the austral summer of 2012/2013

Guang Yang¹ · Chaolun Li^{1,2,3} · Yanqing Wang¹ · Ye Zhang^{1,2}

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Abstract The abundance and vertical distribution of zooplankton in the mesopelagic zone are important to better understand their role in carbon and energy transfer in the Southern Ocean ecosystem. In the austral summer of 2012/2013, in Prydz Bay, Antarctica, the vertical profiles of zooplankton community structures between 0 and 1500 m were investigated by multivariate analysis of samples collected using a Hydro-Bios MultiNet (200- μ m mesh, 0.5 m² mouth size). Four zooplankton communities belonging to distinct water strata were identified. Group 1 contained samples collected from the surface water strata (<100 m) of four shelf and neritic stations. Group 2 was composed of samples collected from the neritic and shelf regions (<500 m) and the upper layers (0–200 m) of the oceanic region. Group 3 mainly comprised samples collected from the mesopelagic and upper bathypelagic zones (200–1500 m) of shelf and oceanic stations north of the shelf break edge. Group 4 consisted of samples in the 1000–1500 m water stratum of three oceanic stations. The four groups differed more in animal abundance than in

species composition. Similarity percentage analysis (SIMPER) showed that zooplankton communities in the upper depth strata (0–200 m) had higher abundance and more pronounced dissimilarity within samples than those below 200 m. A few species (*Metridia gerlachei*, *Rhincalanus gigas*, *Alacia* spp.) showed significant diel vertical migration based on quadratic regression analysis. Sampling depth was the strongest differentiating factor between samples. These results suggest that depth-related differences in environmental characteristics of water masses, such as temperature and salinity, may have the greatest effect upon community structure.

Keywords Vertical distribution · Zooplankton · Community composition · Prydz Bay · Water masses

Introduction

Zooplankton vertical distribution profiles have been examined in different regions of the world's oceans to study the impact of environmental factors on the patterns in these profiles, as well as the role of zooplankton in biogeochemical cycles (Schmidt et al. 2011; Schulz et al. 2012). In the Southern Ocean, euphausiids and copepods are critical components of both the abundance and biomass of the planktonic community and act as a link between primary production and higher trophic levels (Hunter et al. 2007). Much of the work on the vertical distribution of zooplankton has focused on krill and copepod species (Daly and Macaulay 1991; Schnack-Schiel and Hagen 1994; Atkinson 1998). A large number of researchers have also studied the vertical distribution of the entire zooplankton community (Hopkins 1985a; Atkinson and Peck 1988; Hopkins and Torres 1988; Ward et al. 2014).

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✉ Chaolun Li
lcl@qdio.ac.cn

¹ Key Laboratory of Marine Ecology and Environmental Sciences, Institute of Oceanology, Chinese Academy of Sciences, 7 Nanhai Road, Qingdao 266071, People's Republic of China

² University of Chinese Academy of Sciences, 19 Yuquan Road, Beijing 100049, People's Republic of China

³ Laboratory for Marine Ecology and Environmental Science, Qingdao National Laboratory for Marine Science and Technology, Qingdao 266071, People's Republic of China

Environmental factors (temperature and salinity), food availability, lipid store biophysical properties, and diel and ontogenetic vertical migrations are considered to be the main factors influencing zooplankton vertical distribution patterns (Atkinson et al. 1992; Atkinson 1998; Brugnano et al. 2010; Pond and Tarling 2011).

Prydz Bay is the largest incursion into the East Antarctic land mass. Previous studies have identified that several water masses exist in this region during the summer: Antarctic Surface Water, Circumpolar Deep Water, Antarctic Bottom Water, Winter Water, and Shelf Water (Smith et al. 1984; Williams et al. 2010; Shi et al. 2013). Zooplankton community structures in the epipelagic zones, as well as interannual dynamics, have been systematically studied in this region (Hosie and Cochran 1994; Hosie et al. 1997, 2003; Swadling et al. 2010; Yang et al. 2011a). An oceanic community, a neritic community, and a krill-dominated community in a latitudinal distribution pattern have been identified (Hosie et al. 1997; Yang et al. 2011a). To date, most zooplankton community research in Prydz Bay has been limited to samples collected from 200 m to the surface water (epipelagic zones), whereas vertical profiles of zooplankton community structures in the mesopelagic and bathypelagic zones of Prydz Bay have been less reported (Hosie and Stolp 1989; Terazaki 1989). It is unclear whether the latitudinal distribution patterns of epipelagic zooplankton communities also exist in the mesopelagic and bathypelagic zones. Moreover, it is necessary to obtain more information about the abundance and vertical distribution of zooplankton in the mesopelagic zone to better understand their role in carbon and energy transfer in the Prydz Bay ecosystem.

To address this shortage of information, zooplankton samples from discrete depths throughout the water column to 1500 m were collected from 11 stations distributed in the oceanic, shelf, and neritic regions of Prydz Bay using a Hydro-Bios MultiNet during the austral summer of 2012/2013. The main objectives of this work are to describe the composition and vertical profile of zooplankton community structures relative to environmental factors, with emphasis on the vertical distribution and stage composition of dominant copepods.

Materials and methods

During the 29th Chinese National Antarctic Research Expedition (CHINARE) cruise, zooplankton were collected on board the R.V. *Xuelong* using a Hydro-Bios MultiNet (200- μ m mesh, 0.5 m² mouth size) at 11 stations in Prydz Bay, Antarctica, during the austral summer of 2012/2013 (Fig. 1). Sampling was conducted as the ship arrived at each station, irrespective of time of day. Stations were numbered

in chronological order according to sampling date (Table 1). These 11 stations represent the oceanic region (stations 2, 3, 4, 8, and 9), shelf region (stations 10 and 11), and neritic region (stations 1, 5, 6, and 7) of Prydz Bay. Station 7 was located in the polynya region, where higher productivity is usually found (Arrigo and van Dijken 2003). The MultiNet was towed vertically using a winch with 3000 m of wire. At stations deeper than 2000 m (stations 2, 3, 4, 8, 9, and 10), samples were taken to depth of 1500 m (Table 1). The net could reach only 1600 m when the winch wire was paid out to lengths of 2900 m due to unfavorable field conditions. For stations 1, 5, 6, and 7 with depths less than 1000 m, the lowest depth of the fifth sample was set 150 m above the bottom to ensure that the net could reach the triggering depth but avoid touching the seafloor. Net intervals were designed as 0, 100, 200, 500, 1000, and 1500 m for the oceanic stations and 0, 50, 100, 200, 300, and 500 m for the neritic stations (Table 1). The MultiNet was equipped with a multiparameter probe system to simultaneously measure physico-chemical and biological factors (temperature, salinity, and fluorescence). The chlorophyll *a* (chl *a*) data used in this study were derived from the calibrated fluorescence sensor. Zooplankton from five water strata at each station were collected (Table 1), and the samples were preserved in 5 % buffered formalin solution.

In the laboratory, large (total length >3 mm) macrozooplankton species were counted in each entire sample. For all other species, aliquots from 1/2 to 1/32 were counted. Aliquots were divided according to the numerical density of individuals using a Folsom plankton splitter. Subsamples with approximately 500 specimens were counted using a dissecting microscope (Nikon SMZ 745T).

Multivariate analyses were performed using the analysis of similarity (ANOSIM), similarity percentages analysis (SIMPER), and Biota-Environmental matching procedure (BIO-ENV) tools in the PRIMER software package (Plymouth, UK) version 6 (Clarke and Ainsworth 1993; Clarke and Gorley 2006). The analyses were similar to those outlined by Yang et al. (2011a). Zooplankton abundance data were fourth-root-transformed and subjected to q-type cluster analysis (samples or stations were arranged into groups) based on the Bray–Curtis dissimilarity index and group average linkage classification (Field et al. 1982). Nonmetric multidimensional scaling (NMDS) was also performed to replicate the station groupings produced by cluster analysis (Hunt et al. 2007). ANOSIM was used to test for differences between resultant groups. The clustered groups were then subjected to SIMPER routines to determine the species contribution to the similarity within and differences between groups. Meanwhile, ANOSIM analysis using sampling depth (0, 100, 200, 500, 1000, 1500 m) as a factor was also conducted to determine differences between samples collected from various depth strata.

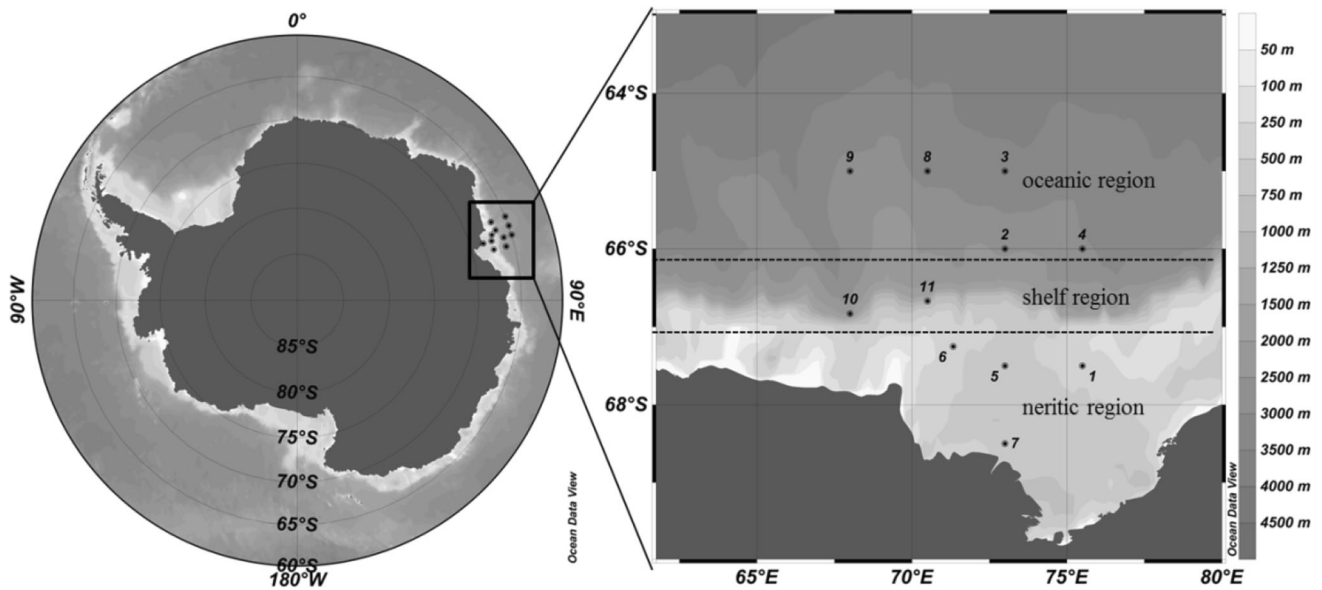


Fig. 1 Location of study area and stations of MultiNet hauls during austral summer of 2012/2013. Oceanic, shelf, and neritic regions are differentiated by *dashed lines* based on bathymetric data

Table 1 Sampling stations, date, time (local time), and strata of collected samples

Station	Date	Sampling time	Sampling strata
1	12/02/2013	15:30 (day)	0–50 m 50–100 m 100–200 m 200–300 m 300–350 m
2	13/02/2013	19:40 (twilight)	0–100 m 100–200 m 200–500 m 500–1000 m 1000–1500 m
3	14/02/2013	11:10 (day)	0–100 m 100–200 m 200–500 m 500–1000 m 1000–1500 m
4	15/02/2013	12:05 (day)	0–100 m 100–200 m 200–500 m 500–1000 m 1000–1500 m
5	17/02/2013	22:30 (night)	0–50 m 50–100 m 100–200 m 200–300 m 300–480 m
6	20/02/2013	13:30 (day)	0–50 m 50–100 m 100–200 m 200–300 m 300–450 m
7	26/02/2013	23:30 (night)	0–50 m 50–100 m 100–200 m 200–300 m 300–500 m
8	28/02/2013	13:00 (day)	0–100 m 100–200 m 200–500 m 500–1000 m 1000–1500 m
9	01/03/2013	00:30 (night)	0–100 m 100–200 m 200–500 m 500–1000 m 1000–1500 m
10	02/03/2013	02:10 (night)	0–100 m 100–200 m 200–500 m 500–1000 m 1000–1500 m
11	03/03/2013	04:30 (twilight)	0–100 m 100–200 m 200–500 m 500–800 m 800–1000 m

A series of quadratic regression analyses of $[\ln(x + 1)$ -transformed] abundance of all species over different sampling depths (0–100, 100–200, 200–500, 0–200, 0–500 m) against sampling time was conducted to determine the impact of diel vertical migration of zooplankton caused by arbitrary sampling time on the data (Daase and Eiane 2007).

Indicator value (IndVal) analysis was applied to identify the indicator species of each station cluster (Dufrene and Legendre 1997). The IndVal method combines measures of group specificity (A_{ij}) and group fidelity (B_{ij}):

$$A_{ij} = N \text{ individuals}_{ij} / N \text{ individuals}_i,$$

and

$$B_{ij} = N \text{ samples}_{ij} / N \text{ samples}_j,$$

where $N \text{ individuals}_{ij}$ is the mean number of individuals of species i in the sample of group j , while $N \text{ individuals}_i$ is the sum of the mean numbers of individuals of species i over all groups. $N \text{ samples}_{ij}$ is the number of samples in group j where species i is present, while $N \text{ samples}_j$ is the number of samples in group j . Subsequently, the IndVal was calculated as

$$\text{IndVal} = A_{ij} \times B_{ij} \times 100.$$

The values of A and B are multiplied because they represent independent information about species distribution and are multiplied by 100 to produce

percentages. $\text{IndVal} \geq 25\%$ was selected as the cutoff point for an indicator taxon using this method, meaning that such a taxon was mainly present in $\geq 50\%$ of samples in a group and that its relative abundance in that group was mostly $\geq 50\%$. Species with IndVal higher than 25% in two or more groups were considered indicator species for these groups in the study (Table 2). Generally, the abundance of species with higher IndVal in one community was usually higher across the samples in the same group.

Species associations were investigated using inverse (r -type) analysis (grouping of species). To avoid the random association of rare, low-abundance species, 21 species that contributed $>2\%$ to the intracommunity similarity on SIMPER analysis or having $\text{IndVal} > 25\%$ were chosen. Most of these species satisfied the criterion for selection proposed by Field et al. (1982) of having more than an arbitrary percentage dominance (2% in this study) at any one station.

The BIO-ENV procedure was used to estimate which set of environmental variables (temperature, salinity, chlorophyll a , and sampling depth) best explained the zooplankton community structure. BIO-ENV analysis is based on determining the Spearman's rank correlation coefficient (ρ_w) between the biological and environmental similarity matrices. A value of $\rho_w = 0$ would imply no match between the two matrices, while a value of $\rho_w = 1$ means a perfect match (Clarke and Ainsworth 1993).

Results

Environmental conditions

The ice had mainly retreated at all stations before our sampling. In general agreement with previously reported hydrographic studies of Prydz Bay (Smith et al. 1984; Nunes Vaz and Lennon 1996; Williams et al. 2010; Shi et al. 2013), four principal water masses in the shelf and oceanic regions were found (Fig. 2a). Summer Surface Water (SSW) with relatively high temperature and low salinity existed in the surface layer at all stations (Fig. 2b, c). SSW is mainly formed by ice melting and solar heating. Underneath the SSW of the shelf and neritic region, Shelf Water (SW) characterized by colder temperature (near freezing point) and salinity ranging from 34.4 to 34.6 was found (Fig. 2b, c). Relatively warm (near $1\text{ }^\circ\text{C}$) and salty ($S > 34.5$) Circumpolar Deep Water (CDW) was found at oceanic stations (Fig. 2). CDW can upwell to nearly 200 m in oceanic regions (Fig. 2b, c). Cold and salty Winter Water (WW), formed by wintertime convection, was found above the CDW, approximately above 200 m.

Dominant species

Different vertical profiles of abundance of the dominant species are given in Online Resource 1. The numerical abundances of the species were highly variable but were mainly concentrated in the upper layers and decreased with depth (Online Resource 1).

Calanoides acutus abundance was maximum in the 0–100 m layer but sharply decreased below this (Online Resource 1a). The late copepodite stages (CIV and CV) and females comprised the majority of the population, and the early copepodite stages (CI–CIII) were mainly found in the 0–200 m water strata (Online Resource 1a). *Calanus propinquus* showed a distribution pattern similar to *C. acutus*, with higher abundances in the epipelagic zones (Fig. 2b). However, the *C. propinquus* population was much younger and dominated by the early copepodite stages (CI–CIII), which accounted for more than 50% of the population in most samples of the upper 500-m stratum (Online Resource 1b). In contrast to *C. acutus* and *C. propinquus*, the vertical profile of *Metridia gerlachei* abundance showed a deeper distribution and peaked in the upper mesopelagic layer at 200–500 m (Online Resource 1c). The abundance of *M. gerlachei* was higher in the neritic region than the oceanic and shelf regions (Online Resource 1c). *Rhincalanus gigas* was almost entirely distributed in oceanic regions, and the bulk of the population was composed of the late copepodite stages CIV–CV and females (Online Resource 1d).

Euphausia superba was mainly distributed in the upper 100 m, and the population was mainly composed of juveniles and adults below 200 m (Online Resource 1e). *E. crystallorophias* was only found in the neritic regions (Online Resource 1f). The population of *E. crystallorophias* was dominated by the late furcilia stages FIV–VI, juveniles, and adults in the upper 200 m, while the early calytopis stages CI–CIII made a large contribution to the population structure of the 200–500-m strata (Online Resource 1f). The population structure of *Thysanoessa macrura* showed significant regional variation in the upper 100-m strata, with the young stages CI–CIII, FI–FIII, juveniles, and adults being mainly distributed in the oceanic, neritic, and shelf regions, respectively (Online Resource 1g).

Although undersampled using the 200- μm mesh net in this study, the copepods *Oithona similis*, *O. frigida*, *Oncaea curvata*, and *Triconia antarctica* and *Ctenocalanus citer* were the most dominant zooplankton species (Table 2). The abundance of *O. similis*, *O. curvata*, and *C. citer* was higher in the neritic regions than in the shelf and oceanic regions in the same water strata, while *O. frigida* showed higher abundance in the shelf and oceanic regions (Online Resource 1).

Table 2 Average similarity (%) from SIMPER analysis and average abundances (ind 1000 m⁻³) for identified species (>90 % total abundance of zooplankton in any sample) in different clusters

	Group 1	Group 2a	Group 2b	Group 3	Group 4
Average similarity (%)	52.83	65.05	67.42	68.06	69.57
<i>Calanoides acutus</i> (Ca)					
Ca CI–III	30	89.4	76.92	6.3	0
Ca CIV–V	10	320.78 ^a	1066.15 ^{a,b}	203.19 ^a	8.00 ^a
Ca Fe	10	3.14	347.69 ^{a,b}	156.00 ^{a,b}	0
<i>Calanus propinquus</i> (Cp)					
Cp CI–III	270.00 ^a	250.59 ^a	604.62 ^{a,b}	21.11	0
Cp CIV–V	20	77.25	481.54 ^{a,b}	9.78	1.33
Cp Fe	0	1.83	166.15 ^b	10.04	0
<i>Metridia gerlachei</i> (Mg)					
Mg CI–III	0	6669.41 ^{a,b}	3184.62 ^{a,b}	453.96 ^a	0
Mg CIV–V	5	6498.3 ^{a,b}	2512.31 ^{a,b}	716.78 ^a	4
Mg Fe	210	421.44 ^a	1035.38 ^{a,b}	181.19 ^a	0
<i>Rhincalanus gigas</i> (Rg)					
Rg CI–III	0	0	10.77 ^b	1.56	0
Rg CIV–V	5	0	95.38 ^b	28.15	0
Rg Fe	0	0	49.23 ^b	36.15 ^{a,b}	1.33
<i>Euphausia crystallorophias</i> (Ec)					
Ec CI–III	0	12.35 ^b	0	0	0
Ec FIV–VI	0	4.71	0	0	0
Ec juvenile + Fe	0	11.76 ^b	0	0	0
<i>Euphausia superba</i> (Es)					
Es CI–III	0	9.02	10.77	0	0
Es FIV–VI	10	0	1.54	0	0
Es J + Fe	100	5.49	6.15	1.11	0
<i>Thysanoessa macrura</i> (Tm)					
Tm CI–III	0	0	6.15	0	0
Tm FI–III	0	2.35	3.08	0	0
Tm FIV–VI	0	0	7.69	0	0
Tm J + Fe	0	0	32.31 ^b	0.22	0
<i>Aetideopsis minor</i> (Am)	0	0.65	0	113.33 ^{a,b}	1.33
<i>Alacia</i> spp. (Al)	15	72.16	501.54 ^{a,b}	585.29 ^{a,b}	8
<i>Bathycalanus richardi</i> (Br)	0	0	3.08	229.70 ^b	176.00 ^{a,b}
<i>Candacia falcifera</i>	0	0	0	11.7	2.67
<i>Clio pyramidata</i>	0	0.59	0	0	0
<i>Clione antarctica</i>	10	0	12.31	0	0
<i>Ctenocalanus citer</i> (Cc)	1400.00 ^a	9863.4 ^{a,b}	6730.77 ^{a,b}	1047.22 ^a	8.00 ^a
<i>Diphyes antarctica</i>	5	2.35	7.69	4.44	0
<i>Eukrohnia hamata</i> (Eh)	15	27.84	270.77 ^{a,b}	247.00 ^{a,b}	5.33
<i>Haloptilus ocellatus</i> (Ho)	0	0	27.69 ^b	2.89	0
<i>Heterorhabdus austrinus</i> (Ha)	0	0	36.92 ^b	11.04	0
<i>Marrus antarcticus</i>	0	4.71	0	0.74	0
<i>Megacalanus princeps</i> (Mp)	0	0	0	6.37 ^{a,b}	0
<i>Muggiaea bargmannae</i>	0	11.76	6.15	8.52	0
<i>Oikopleura</i> sp.	2.5	0	0	0	0
<i>Oithona frigida</i> (Of)	0	161.11	1246.15 ^{a,b}	192.96 ^a	0
<i>Oithona similis</i> (Os)	24,140.01 ^{a,b}	39,447.71 ^{a,b}	27,923.08 ^{a,b}	794.89 ^a	16.00 ^a
<i>Oncaea curvata</i> (Oc)	290.24 ^a	16,424.26 ^{a,b}	2003.92 ^a	4375.24 ^{a,b}	50.00 ^a
<i>Paraeuchaeta antarctica</i> (Pa)	0	170.20 ^a	555.38 ^{a,b}	76.41 ^a	6.67 ^a
<i>Pelagobia longicirrata</i>	30	568.17	204.62	24.59	0

Table 2 continued

	Group 1	Group 2a	Group 2b	Group 3	Group 4
<i>Pleurogramma antarcticum</i>	0	1.18	3.08	0	0
<i>Proboloides dentimanus</i>	15	1.18	61.54	20.37	1.33
<i>Rhynchonerella petersii</i>	15	0	16.92	4.81	0
<i>Salpa thompsoni</i>	0	25.88	0	0	0
<i>Scolecithricella minor</i> (Sm)	200	1488.24 ^{a,b}	715.38	18.15	0
<i>Stephos longipes</i>	0	1.18	0	0	0
<i>Tomopteris carpenteri</i>	30	7.06	36.92	7.63	0
<i>Travisiopsis levinseni</i>	0	1.18	0	0	0
<i>Triconia antarctica</i> (Ta)	179.76	2991.36 ^{a,b}	288.39 ^a	3799.02 ^{a,b}	26.00
<i>Vibilia antarctica</i>		1.18	0	0.22	0

Species abbreviations given in parentheses

^a The cumulative contribution of these species exceeds 90 % of similarity within groups from SIMPER analysis

^b Species identified by IndVal > 25 %

Community structure

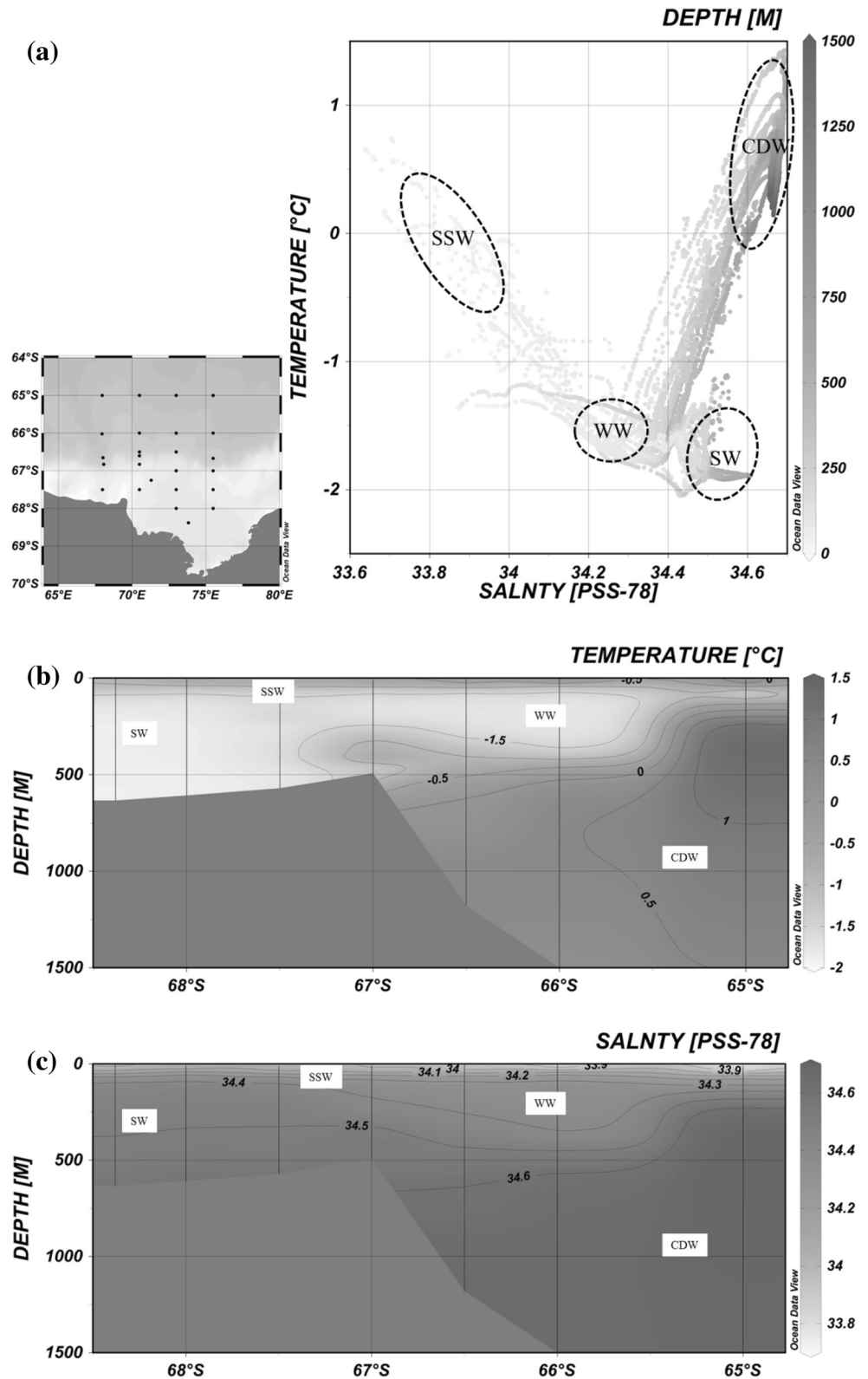
Four distinct communities were identified by cluster analysis, each one mainly identifying a different depth layer (Fig. 3). ANOSIM results indicated that the four clusters were significantly different at $p < 0.05$. The upper epipelagic water strata (0–50 or 0–100 m) samples of stations 1, 4, 5, and 6 were inconsistent with other samples and were placed into one group (Fig. 3). This group was typified by moderate abundance (mean 27,020 ind 1000 m⁻³) and mainly included the early copepodites CI–III of *C. propinquus* and the small copepods *O. similis*, *O. curvata*, *T. antarctica*, and *C. citer*. Group 2 mainly comprised zooplankton from the upper water strata (Fig. 3). This group also showed clear horizontal zonation and could be divided into two subgroups: subgroup 2a, which was mainly composed of samples collected from the neritic stations, and subgroup 2b, which comprised the zooplankton from the shelf and oceanic regions (Fig. 3). The mean abundance of group 2a was the highest (88,220 ind 1000 m⁻³), and the indicator species were *E. crystallorophias*, *M. gerlachei*, and the small abundant copepods *C. citer*, *O. similis*, *O. curvata*, *T. antarctica*, and *Scolecithricella minor* (Table 2). Group 2b also showed relatively high abundance (50,350 ind 1000 m⁻³), and the indicator species were *T. macrura*, *C. acutus*, *C. propinquus*, *M. gerlachei*, *R. gigas*, *Paraeuchaeta antarctica*, *Eukrohnia hamata*, *Haloptilus ocellatus*, *Heterorhabdus austrinus*, *Alacia* spp., and small copepods such as *O. similis*, *O. frigida*, and *C. citer* (Table 2). Group 3 mainly contained samples collected from the mesopelagic and upper bathypelagic zones (200–1500 m) of shelf and oceanic stations north of the shelf break edge (Fig. 3). The average abundance (13,410 ind 1000 m⁻³) was lower than that recorded in group 1 or 2. Group 3 was

characterized by high proportions of *Aetideopsis minor*, *Bathycalanus richardi*, *Megacalanus princeps*, the late copepodite stages of *C. acutus* and *R. gigas*, *P. antarctica*, *M. gerlachei*, *Eukrohnia hamata*, *Alacia* spp., and the small copepods *O. similis*, *O. frigida*, *O. curvata*, *T. antarctica*, and *C. citer* (Table 2). Group 4 comprised samples in the upper bathypelagic zone (1000–1500 m) of three oceanic stations (3, 8, and 9; Fig. 3); the average abundance was the lowest (316 ind 1000 m⁻³), and the assemblage was dominated by *B. richardi* and two small copepods, *O. curvata* and *O. similis* (Table 2).

Species assemblages

To identify assemblages of species with similar vertical and spatial distribution patterns, 21 taxa identified by SIMPER analysis as being principally responsible for community similarities or having IndVal >25 % in the four community groups were subjected to r-type cluster analysis (Fig. 4). The three krill species, *E. superba*, *E. crystallorophias*, and *T. macrura*, were mainly divided from other species due to their patchy distribution. Moreover, the MultiNet could not collect krill effectively compared with copepods. Excluding the krill species, four main zooplankton assemblages were identified (Fig. 4). Species in assemblage A were abundant in zooplankton community groups 1, 2, and 3, especially group 2a (Table 2). Species in assemblage B were mainly concentrated in groups 2 and 3 (Table 2). *C. acutus*, *P. antarctica*, and *O. frigida* occurred most frequently in community group 2, while the other three species were found in high abundance in community group 3 (Table 2). Assemblage C included two copepods, *H. ocellatus* and *H. austrinus*, indicator species of group 2b (Table 2). Species in assemblage D were widely distributed throughout groups 3 and 4 (Table 2).

Fig. 2 Temperature–salinity diagram for all conductivity–temperature–depth (CTD) stations in the upper 1500 m (a) and vertical profiles of temperature (b) and salinity (c) of the 73°E section. SSW, SW, WW, and CDW represent Summer Surface Water, Shelf Water, Winter Water, and Circumpolar Deep Water

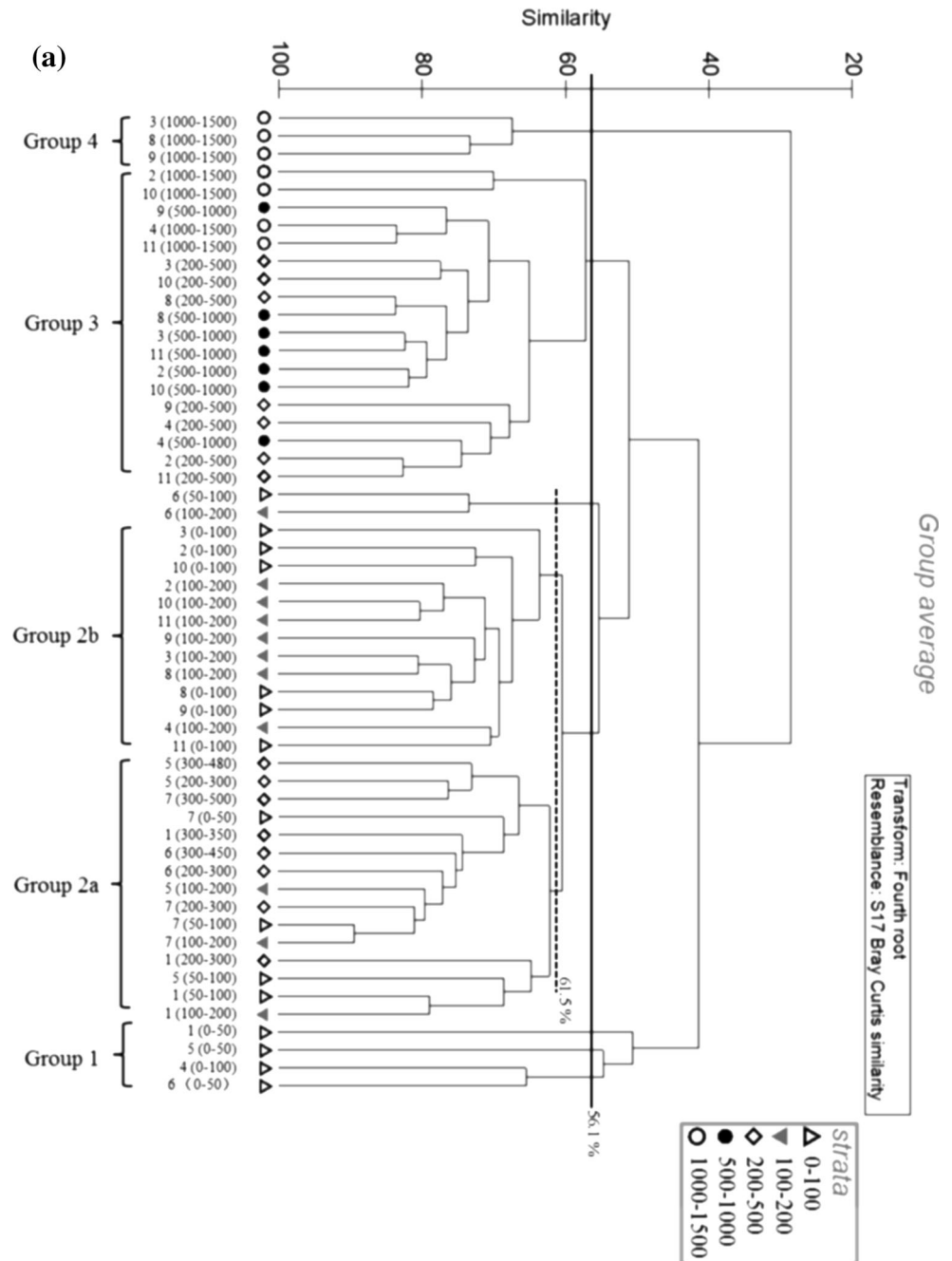


Factors affecting community structure

Cluster analysis based on the Bray–Curtis dissimilarity index showed that sampling depth was by far the strongest

differentiating factor between samples (Fig. 3). The results of BIO-ENV analysis (Table 3) also identified sampling depth as the largest single contributor to the zooplankton community ($\rho = 0.619$), followed by salinity, temperature,

Fig. 3 Cluster analysis (a) and nonmetric multidimensional scaling (b) performed on abundance datasets of all depth intervals for every station. Environmental factors depth, chlorophyll *a* (chl *a*), temperature (Tem), and salinity (Sal) are shown as vectors in (b)



and chl *a* ($\rho = 0.456$, $\rho = 0.398$, and $\rho = 0.297$). Sampling depth and chl *a* gave the best rank correlation coefficient ($\rho = 0.678$).

ANOSIM analysis using sampling time (day or night) as a factor showed a value of $R = 0.022$ ($p > 0.05$), while the larger magnitude of R ($R = 0.74$, $p < 0.001$) for sampling depth indicated that sampling time had slight influence on the cluster analysis compared with water stratum.

Over different sample depths (0–100, 100–200, 200–500, 0–200, 0–500 m), significant results ($p < 0.05$) for quadratic regression analysis of [ln($x + 1$)-transformed] species abundance against sampling time were found for *R. gigas*

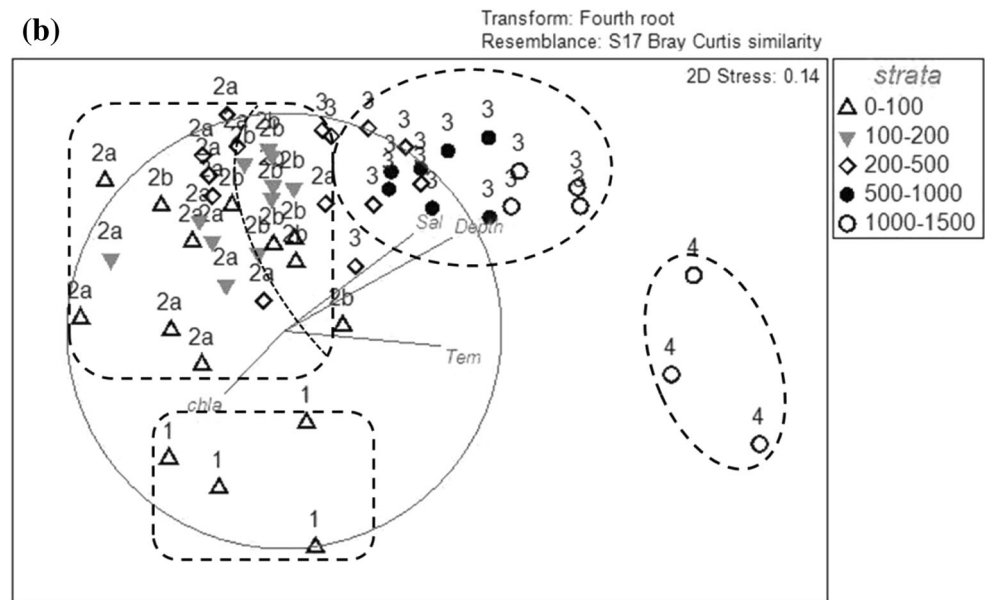
and *Alacia* spp. in the 0–100 m water strata and for *M. gerlachei* in the 200–500 m water strata. No significant relationship was found for the other cases ($p > 0.05$).

Discussion

Community structure

All species examined in this study are common in the Southern Ocean, and most have a wide distribution range. Similar to zooplankton vertical structure research

Fig. 3 continued



conducted in the polar ocean (Kosobokova and Hirche 2000; Hunt and Hosie 2003; Kosobokova and Hopcroft 2010; literature in Table 4), communities were also broadly associated with different depth layers in this study (Fig. 3). Differences in vertical community structure were largely attributable to variation in species abundance rather than variation in species composition per se (Table 2). Zooplankton could benefit from aggregating at particular depths to reduce intra- and interspecific competition and decrease predation risk (Schulz et al. 2012). Most species have characteristic but wide vertical distribution ranges, inhabiting two or more of the defined water masses. This was demonstrated by the r-type cluster analysis, in which most species failed to cluster at distinct water strata (Fig. 4). Kosobokova and Hopcroft (2010) also found a similar phenomenon in the Arctic Ocean, and suggested that species composition between layers was determined gradually rather than abruptly. Another explanation is that the towing depth strata in our study may include different water masses to varying degree. The main sampling strata design could not determine to which water masses the majority of species were confined. It has been suggested that the warm nutrient-rich upper CDW may contribute to a favorable zooplankton environment in Marguerite Bay, Western Antarctic Peninsula (Marrari et al. 2011). Many mesopelagic species, such as *A. minor*, *B. richardi*, and *M. princeps*, with high abundances in the 500–1000 m layer also occupy waters both above and below this layer (data not shown). Therefore, it is not surprising that the zooplankton from water strata C (200–500 m), D (500–1000 m), and E (1000–1500 m) of most stations clustered together (Fig. 3). It should be noted that the deep-water samples (1000–1500 m) from the three northernmost

stations (3, 8, and 9) showed the lowest abundances (Table 2). The Antarctic Circumpolar Current (ACC) at these stations at 1000–1500 m had stronger flow than at other oceanic stations (unpublished data). Further field sampling should be conducted in the future to determine whether the relatively stronger flow has a negative effect on zooplankton distribution. Upwelling in the CDW cannot reach the shelf region in Prydz Bay (Fig. 2; Shi et al. 2013). Accordingly, zooplankton from 200 to 500 m of the shelf and neritic region did not cluster together with those collected in the same stratum of the oceanic region (Fig. 3). Affected by air–sea (summer heating, wind) and sea–ice interactions, the water masses above 200 m were complex and highly variable (Williams et al. 2010; Michels et al. 2012), while the water masses at mid-water depth showed relatively stable temperature and salinity (Fig. 2). Correspondingly, the dissimilarity of zooplankton community was more pronounced in the upper strata, while the assemblages of zooplankton were more similar in the deeper strata (Fig. 3). Less pronounced differences between deeper zooplankton clusters compared with epipelagic clusters were also reported in the northern Mid-Atlantic Ridge, the Arctic’s Canada Basin, and the 80°W sector of the Southern Ocean west of the Drake Passage (Hosia et al. 2008; Kosobokova and Hopcroft 2010; Ward et al. 2014). Zooplankton communities in the epipelagic layer and especially the surface layer are highly dynamic in relation to environmental forces, such as global warming and changing ice conditions, and more attention should be paid to understand the susceptibility of Antarctic pelagic ecosystems (Flores et al. 2014).

With respect to defining the zooplankton community structure in the epipelagic zone, the neritic and oceanic

Fig. 4 Inverse (r-type) analysis of 21 species that contributed >2 % to intracommunity similarity on SIMPER analysis or had indicator value >25 %

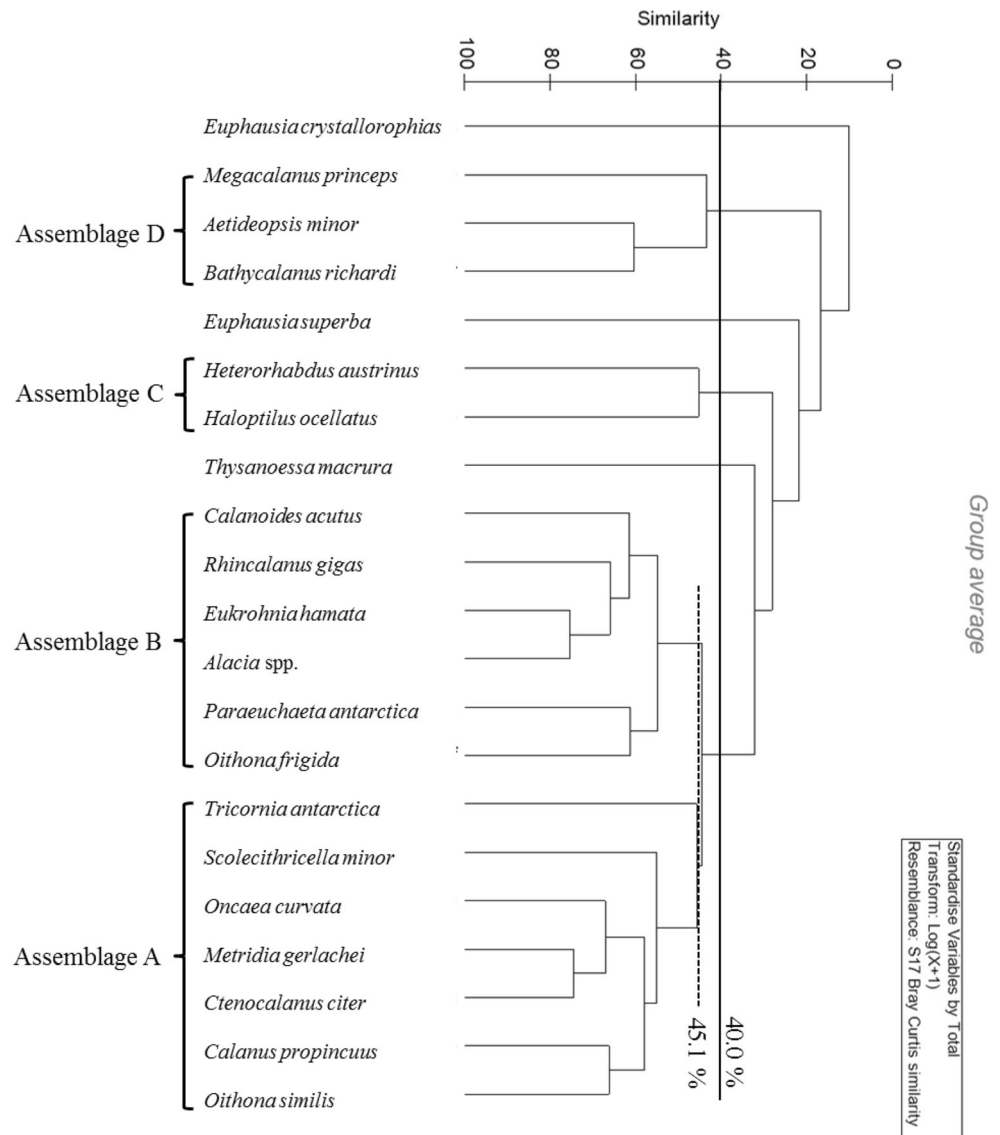


Table 3 Results of BIO-ENV analysis

K^a	ρ_w^b	Factors
1	0.619	Sampling depth
1	0.456	Salinity
1	0.398	Temperature
1	0.297	Chl <i>a</i>
2	0.678	Sampling depth, chl <i>a</i>
3	0.677	Sampling depth, salinity, chl <i>a</i>
Best	0.678	Sampling depth, chl <i>a</i>

^a Means combination of k variables

^b The largest Spearman rank correlations (ρ_w) between zooplankton and environmental similarity matrices

communities were also clearly divided in this study (Fig. 3), in agreement with numerous studies conducted in Prydz Bay and other regions of the Southern Ocean (Hosie

et al. 1997, 2000; Chiba et al. 2001; Hunt et al. 2007). The continental shelf edge has usually been identified as the main boundary between these two communities in Prydz Bay (Hosie and Cochran 1994; Yang et al. 2011a). The geographic distinction of the community structure may be due in part to the different indicator species of each community (such as *E. crystallophias* for neritic group 2a, *R. gigas*, *H. ocellatus*, and *H. austrinus* for oceanic group 2b; Table 2), as well as the higher abundances found in the neritic regions. Compared with a 6-year dataset for zooplankton in Prydz Bay collected with a 330- μm mesh NORPAC net (Yang et al. 2011a), the abundance of oceanic community group 2b (50,350 ind 1000 m^{-3}) was similar to that of previous works, while the abundance of neritic community group 2a (88,220 ind 1000 m^{-3}) was lower in this study than in previous studies. A latent-heat-type coastal polynya formed by substantial katabatic wind

Table 4 Vertical zooplankton community research in other regions of the Southern Ocean

Region	Sampling date	Sampling gear	Net strata (m)	Accompanying variables
South Georgia ^a	Nov. 1981, Jul. 1983	RMT 1, 330 μm	10–250–500–1000	Temperature (T), salinity (S)
Weddell Sea ^b	Mar. 1986	Collapsible nets, 162 μm	0–100–200–500–1000	T, S
Antarctic Peninsula ^c	Mar. 1983	Collapsible, 162 μm	0–100–200–300–500–1000	T, S
Five transects along 80°W ^d	Dec. 1933, Mar. 1934, Nov. 1934	N70 V net, 195 μm	0–50–100–250–500–750–1000	T, S, water mass
Lazarev Sea ^e	Nov. 2007, Mar. 2004, Jun. 2006	SUIT, 300 μm ; RMT 1, 330 μm ;	0–2; 0–200; 500–2500	T, S, solar radiation, sea ice
Gerlache and Bransfield Straits ^f	Feb. 1993	BIONESS net, 200 μm	0–20–50–100–200–400–600	T, S, chl <i>a</i>
Scotia Sea ^g	Series of transects from 1928 to 1951	Nansen closing net, ~200 μm	0–50–100–250–500–750–1000	T
Antarctic Polar Front (9.5–11.5°E) ^h	Dec. 1995/Jan. 1996	Multinet, 100 μm	0–25–50–100–300	T, S, chl <i>a</i>
Indian sector of Antarctic Ocean ⁱ	Mar. 1977	WP II net, 200 μm	0–100, 0–200, 0–600	T, S, chl <i>a</i>
Along 140°E ^j	Nov. 2001	NORPAC net, 270 μm	0–20–50–100–150	T, S

^a Atkinson and Peck (1988)

^b Hopkins and Torres (1988)

^c Hopkins (1985a)

^d Ward et al. (2014)

^e Flores et al. (2014)

^f Hernandez-Leon et al. (2001)

^g Atkinson and Sinclair (2000)

^h Dubischar et al. (2002)

ⁱ Errhif et al. (1997)

^j Hunt and Hosie (2003)

activity from the Amery Ice Shelf (Williams et al. 2007) often appears in Prydz Bay. The phytoplankton biomass of the neritic regions was usually higher than that in the oceanic regions (Fig. 3b; Arrigo and van Dijken 2003; Yang et al. 2011a). In this study, station 7, located in the polynya region, showed high chl *a* concentration. The other stations, 1, 5, and 6, in group 2a were located in the shelf region and had lower zooplankton densities.

Diel vertical migration (DVM) is a common behavior of many Southern Ocean copepod species (Atkinson et al. 1992; Lopez and Huntley 1995; Hernandez-Leon et al. 2001; Hosie et al. 2003; Hunt and Hosie 2003, 2005). Thus, the observed vertical differences in species composition and abundance may be influenced by DVM of different zooplankton species. However, based on the series of quadratic regression analyses, no significant relationship between sampling time and abundance was found for most species. These results indicate that, despite the arbitrary differences in sampling time, DVM did not severely affect the observed distributional patterns of community structure

between depth layers in this study. In the future, sampling should be adjusted according to hydrography and should be performed at similar times to reduce potential bias introduced by diel vertical migration of zooplankton.

Dominant species

The large copepods *C. acutus*, *C. propinquus*, *M. gerlachei*, and *R. gigas* are known to account for a large proportion of the total zooplankton abundance in Prydz Bay and other parts of the Southern Ocean (Hopkins and Torres 1988; Schnack-Schiel and Hagen 1994; Hosie et al. 1997; Schnack-Schiel et al. 2008; Yang et al. 2011a). The success of these numerically dominant species is likely due to their different life strategies (Atkinson 1998). *C. acutus* was considered herbivorous in summer and in diapause at depth in winter, and *C. propinquus* and *M. gerlachei*, omnivorous and less reliant on depth diapause during their life cycles, while *R. gigas* showed an intermediate life strategy (Atkinson 1998).

The vertical patterns in the abundance and population structure of these copepods are mainly in agreement with those of previous research (Schnack-Schiel et al. 1991; Schnack-Schiel and Hagen 1994; Yang et al. 2011b). The young stages of herbivorous *C. acutus* in this study, mainly concentrated in the upper layers (Online Resource 1a), may have found smaller food at shallower depths (Laakmann et al. 2009). The small proportion of the late copepodite stages (CIV and CV) and females distributed below 500 m (Online Resource 1a) may indicate that winter descent for a percentage of the *C. acutus* population had already started (Marin 1988; Schnack-Schiel et al. 1991). The dominance of the early stages (CI and CII) of *C. propinquus* and *M. gerlachei* in the surface water (Online Resource 1b, c) corroborates the results from other regions of the Southern Ocean and indicates that spawning of these two species may have still been underway (Schnack-Schiel and Hagen 1994). It should be noted that the diel vertical migration of *M. gerlachei* in the 200–500 m layer is significant ($p < 0.05$), which can also be observed in the high standard error of the mean in the total abundance of *M. gerlachei* in Online Resources 1 and 2. Atkinson (1998) reported that egg laying of *R. gigas* peaked prior to December and occurred later in the season within the Scotia Sea. The lack of offspring of *R. gigas* in this study (Online Resources 1 and 2) may indicate that main reproduction had finished long before our sampling.

The overwhelming numerical dominance of small copepods, such as *C. citer*, *O. frigida*, *O. similis*, *T. antarctica*, and *O. curvata*, in the upper and mesopelagic zone (Online Resource 1) is similar to that previously reported in the Southern Ocean (Errhif et al. 1997; Dubischar et al. 2002; Hunt and Hosie 2006; Schnack-Schiel et al. 2008; Ward et al. 2014). However, these small species are too small to be retained by the 200- μm mesh, and the net used in this study would have lost over 90 % of them (Metz 1995; Smith et al. 1998; Dubischar et al. 2002; Jonasdottir et al. 2013).

Eukrohnia hamata, *Alacia* spp., *P. antarctica*, *O. frigida*, *A. minor*, *B. richardi*, and *M. princeps* are mainly omnivorous or even carnivorous (Hopkins 1985b; Albers et al. 1996; Blachowiak-Samolyk and Angel 2007; Ikeda et al. 2006; Laakmann and Auel 2010). The deeper distribution trend of these species is likely due to their consumption of microzooplankton as important prey items, as indicated by isotope $\delta^{15}\text{N}$ values (Ikeda et al. 2006; Laakmann and Auel 2010).

In conclusion, the general results of this research reveal some associations between vertical zooplankton community structure and depth-related environmental factors. Nevertheless, the vertical zooplankton community structure and individual distribution patterns discussed in this study may be regarded only as preliminary findings for

Prydz Bay. More frequent sampling according to each specific water mass and better depth resolution are necessary to systematically analyze the zooplankton distribution with respect to different hydrological and biotic factors. Significant interannual variation in summer zooplankton community structure has been reported based on samples collected in the epipelagic zones (0–200 m) of Prydz Bay (Yang et al. 2011a). Additionally, forthcoming expeditions should conduct greater sampling for zooplankton in the mesopelagic and bathypelagic zones. Additionally, food supply and feeding strategy studies of zooplankton from different water strata, especially at greater depths, may shed new light on vertical distribution patterns and the role that zooplankton plays in the biogeochemical cycles and trophodynamic processes of Prydz Bay.

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