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Pelagic ciliate communities within the Amundsen Sea polynya and adjacent sea ice zone, Antarctica

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ABSTRACT

Polynyas, areas of open water surrounded by sea ice, are sites of intense primary production and ecological hotspots in the Antarctic Ocean. This study determined the spatial variation in communities of pelagic ciliates in an Amundsen Sea polynya (ASP) and adjacent sea ice zones (SIZ) during austral summer from February to March 2012, and the results were compared with biotic and abiotic environmental factors. The species number, abundance and biomass were higher in the ASP than SIZ. Canonical analysis indicated that the communities in the ASP were distinct from those under the sea ice. The pelagic ciliate community structure was closely correlated with environmental variability. Several primary environmental variables, both alone and in combination, were found to affect community spatial patterns. The ciliate biomasses in the ASP and SIZ areas were both significantly correlated with total and nano-Chl *a*. This analysis of the ciliated microzooplankton communities associated with high primary production provides new insights into the roles of ciliates in biogeochemical cycles in high-latitude polynyas. Additionally, our findings provide detailed data on the composition, distribution, and structure of polynya ciliate communities in the Amundsen Sea.

1. Introduction

In most pelagic ecosystems, including different areas of the Southern Ocean, microzooplankton (20–200 μm in size) have long been recognized as important consumers of primary production in biogeochemical cycles (Calbet and Landry, 2004). Pelagic ciliates form a fundamental component of microzooplankton, and have also been found to be pivotal to the function of the overall marine food web (Dolan and Marrase, 1995; Yang et al., 2004; Dolan et al., 2013; Jiang et al., 2013a, c). They have long been considered to be important mediators of energy transfer from pico- and nano-planktonic production to higher trophic levels (Stoecker et al., 1994, Wickham et al., 2011; Jiang et al., 2011b; 2014a, b). Although the importance of planktonic ciliate ecology is being increasingly recognized, there have been few studies that combine quantitative abundance and biomass data with high taxonomic resolution for ciliates, particularly in the Southern Ocean, a region experiencing increasing climate influences (Wickham et al., 2011, Jiang et al., 2014a).

Polynyas, recurring areas of seasonally open water surrounded by sea ice, are foci for energy and material transfer between the atmosphere and the polar ocean (Smith and Barber, 2007; Yager et al., 2012). The Amundsen Sea is one of the most productive areas in the Southern Ocean (Smith et al., 2011; Arrigo and Alderkamp, 2012; Fragoso and Smith, 2012), and extensive phytoplankton blooms have been observed near the coast using satellite-based ocean color sensors (Arrigo and Alderkamp, 2012). A number of coastal polynyas exist in the Amundsen Sea. The high productivity in this region is mostly attributed to two polynyas, the Amundsen Sea polynya (ASP) and the Pine Island polynya (Arrigo and Alderkamp, 2012). The ASP is a polynya driven by katabatic winds blowing northward from the continental interior, and surrounded by pack ice and the Dotson and Getz ice shelves located off Marie Byrd Land (La et al., 2015). It is generally restricted to the period from October through March, and is defined as a region characterized by the absence of sea ice; i.e., where ice concentrations are lower than 10% (Arrigo and Alderkamp, 2012).

Sea ice influences microzooplankton distribution and production, and the rapid melting of glaciers and loss of sea ice results in a change in habitat conditions that may force substantial changes in microzooplankton. To predict the impact of these changes on the ecosystem, it is important to understand the structure of the pelagic ciliate community. However, to date, few studies have been

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published on the distribution and structure of ciliate communities in the ASP (Jiang et al., 2014a).

Previous studies (e.g., Song and Wilbert, 2000; Garrison et al., 2005; Santoferrara and Alder, 2009) on ciliates in the Southern Ocean have generally focused on sea ice/ice edge communities. Moreover, many studies only calculated the total abundance and/or biomass of assemblages (tintinnids or oligotrichs), and lacked sufficient taxonomic detail to identify the loss of ecologically relevant species. To our knowledge, only Wickham et al. (2011) have reported data that provide a detailed species list, which was pooled from nine stations in Bellinghausen and the Amundsen Sea. Jiang et al. (2014a) supplied further community information from 18 stations in the Amundsen Sea in 2011, and found that the community structures were diverse across various habitats. However, detailed information on ASP communities, and comparison between ASP communities and those of the surrounding sea ice zone (SIZ) is still scant. To improve our knowledge of this biological hot spot, analyses were conducted during a revisit cruise of the icebreaker *Araon* to the Amundsen Sea from February to March in 2012.

The primary objectives of this study were to characterize the composition and distribution of pelagic ciliates in a polynya, reveal the patterns of ciliate community structure at spatial scales, compare the differences in communities between the ASP and SIZ, and determine the linkages between the community structure and environmental conditions.

2. Materials and methods

2.1. Study stations

A multidisciplinary survey was conducted onboard the Korean Research icebreaker RV *Araon* in the Amundsen Sea during austral summer from February to March 2012 (Fig. 1). Conductivity, temperature, and depth (CTD) casts were conducted during the cruise. In the present study, 11 sampling stations were selected: 6 stations from ASP; other 5 sites as control which were surrounding ASP and located in SIZ areas (transitional area as connections between oceanic areas and polynya; sea ice area under pack ice to the east and west of the polynya; glacial edge close to the edges of the Dotson glaciers) (Fig. 1). Areas of sea ice and concentrations were based on data from the National Snow and Ice Data Center in Boulder, Colorado, that corresponded to the cruise period, and previous references such as Yager et al. (2012), Dolan et al. (2013), Lee et al. (2012, 2013) and La et al. (2015).

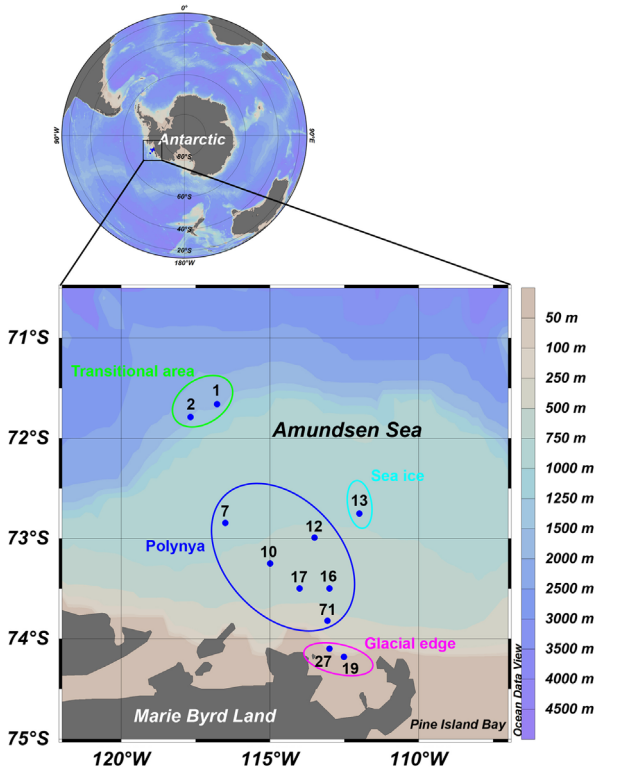

Fig. 1. 11 Sampling stations in the Amundsen Sea polynya and adjacent sea ice zone (western Antarctica) during early austral summer from February to March 2012.

2.2. Sampling and sample processing

Vertical profiles of seawater potential temperature, salinity, water pressure, and dissolved oxygen (DO) were obtained using a CTD-Rosette system (SeaBird Electronics, SBE-911+) at each sampling station basically following a depth gradient of 0 m, 10 m, 20 m, 40 m, 70 m, and 100 m.

Water samples (500–1000 mL) for the determination of total chlorophyll *a* (Chl *a*) were taken from each depth and immediately filtered through glass fiber filter paper (47 mm; Gelman). Size-fractionated Chl *a* was determined on samples passed sequentially through 20 and 3 μm polycarbonate membrane filters (47 mm) and glass fiber filters (47 mm). The three Chl *a* size fractions obtained were referred to as micro-fraction Chl *a* (>20 μm), nano-fraction Chl *a* (3–20 μm), and pico-fraction Chl *a* (<3 μm). Although picoplankton has been defined as being between 0.2 and 2 μm (Sieburth et al., 1978), here we defined picophytoplankton as <3 μm. All filtrations were performed under low vacuum pressure (<100 mm Hg) or by gravity (when using 20-μm mesh and 3-μm filter paper). Each concentration of Chl *a* was measured onboard using a Turner design trilogy fluorometer after extraction with 90% acetone (Parsons et al., 1984). The fluorometer was previously calibrated against pure Chl *a* (Sigma).

In total, 66 water samples were collected using a Niskin rosette sampler from six depths at 11 stations. For quantitative studies and the identification of ciliates, 500-ml seawater samples were fixed with Lugol's iodine solution (4% final concentration, volume/volume); these were then stored at 4 °C in darkness until analysis (Yang et al., 2012). Preserved samples were allowed to settle in the mass cylinder for at least 48 h. The upper water was then siphoned off, leaving 20 ml. A 1-ml aliquot of each concentrated sample was placed in a Perspex chamber and the ciliates were counted under a light microscope (Olympus BX51) at magnifications of 200× to 400×. Tintinnids were identified using lorica morphology and the species descriptions of Kofoid and Campbell (1929, 1939); other ciliates were identified by performing protargol staining according to Montagnes and Humphrey (1998), and based on the published references to keys and guides such as Montagnes and Lynn (1991) and Strüder-Kypke and Montagnes (2002). The taxonomic scheme used was according to Lynn (2008).

The biovolumes of naked ciliate cell or tintinnid lorica were determined from measurements of their linear dimensions and the volumes were calculated from standard geometric shapes (Hillebrand et al., 1999) and carbon content estimated from relationships described in Menden-Deuer and Lessard (2000). Hereinafter, the term biomass refers to carbon biomass.

2.3. Data analysis of samples

Multivariate analyses of spatial pattern in ciliate communities were conducted using the PRIMER v6.1 package (Clarke and Gorley, 2006) and PERMANOVA+ for PRIMER (Anderson et al., 2008). The contribution of each species to the average Bray–Curtis similarity

within each group and the dissimilarity among groups was summarized using the Similarity Percentage Analysis (SIMPER) program (Clarke and Gorley, 2006). The spatial environmental status of the sampling region was summarized using principal components analysis (PCA) based on log-transformed/normalized abiotic data and differences between groups of samples were tested with the submodule PERMANOVA (Clarke and Gorley, 2006; Anderson et al., 2008). The spatial differences in ciliate communities were summarized using the submodule CAP (canonical analysis of principal coordinates) of PERMANOVA+ with Bray–Curtis similarities from log-transformed species-abundance data and using PERMANOVA to test differences between sample clouds which were separated by two CAP axes (Anderson et al., 2008; Xu et al., 2013). The significance of biota–environment correlations was tested using the routine RELATE (Mantel test). Submodule Biota–Environment (BIOENV) was used to explore potential multivariate relationships between biotic parameters and the abiotic data (Clarke and Gorley, 2006).

Linear regression analysis between ciliate biomass and Chl *a* concentration was done using the statistical program SigmaPlot v10.0 based on the statistical significance ($P < 0.05$). Geographical map and figures were created using ODV software (R. Schlitzer, Ocean Data View, 2003, http://www.awi-bremerhaven.de/GEO/ODV).

3. Results

3.1. Hydrographical conditions

The ranges of physicochemical parameters among six sampling depths at 11 stations are summarized in Fig. 2.

Salinity was largely determined by meltwater from sea ice, which resulted in regional differences. At almost all stations, salinity increased with water depth, except at glacial edge and sea ice edge stations, which did not show clear vertical changes (Fig. 2A). A pronounced halocline layer occurred between 20 and 40 m in the transitional and polynya areas, with little vertical change below the halocline until the maximum at 100 m (Fig. 2A). No apparent halocline layer was observed in the glacial edge and sea ice edge areas, although the upper depths had relatively lower salinity values. Below the upper depths, salinity values increased slightly, but significant stratification was not observed (Fig. 2A).

Antarctic Surface Water (AASW) occupied the sampled water column. In the polynya and glacial edge areas, seawater temperature decreased with increasing depth and was markedly higher than in other areas (Fig. 2B). In the glacial edge area, surface temperatures were lower than in most of the polynya, but increased with depth (Fig. 2B). In the sea ice and transitional areas, temperatures were lowest and showed no clear vertical change from the surface to 100-m depth (Fig. 2B).

All stations showed similar gradual changes in water pressure from surface to greater depths (Fig. 2C). The spatial patterns in dissolved oxygen (DO) decreased with increasing depth, and could be divided into two layers by the pycnocline, which appeared at depths ranging from ~20 to 40 m following a deepening of the pycnocline, as shown most clearly in the salinity plot (Fig. 2A and D).

Of particular note is the trend in total and nano-chlorophyll-*a* (Chl *a*), which varied among the stations and decreased with increasing depth, with higher concentrations at the ASP stations compared with those at the SIZ stations (Fig. 2E and G). In the glacial edge and sea ice areas, concentrations of Chl *a* showed more even vertical distributions and decreased only slightly with depth (Fig. 2E–G). Notably, concentrations of pico-Chl *a* in the polynya and transitional areas were considerably higher, and increased from the surface to distinct maxima at 40–60 m, and decreasing below this depth (Fig. 2F).

Principal components analyses (PCAs) using 66 samples are shown in Fig. 3. The two principal components discriminated the

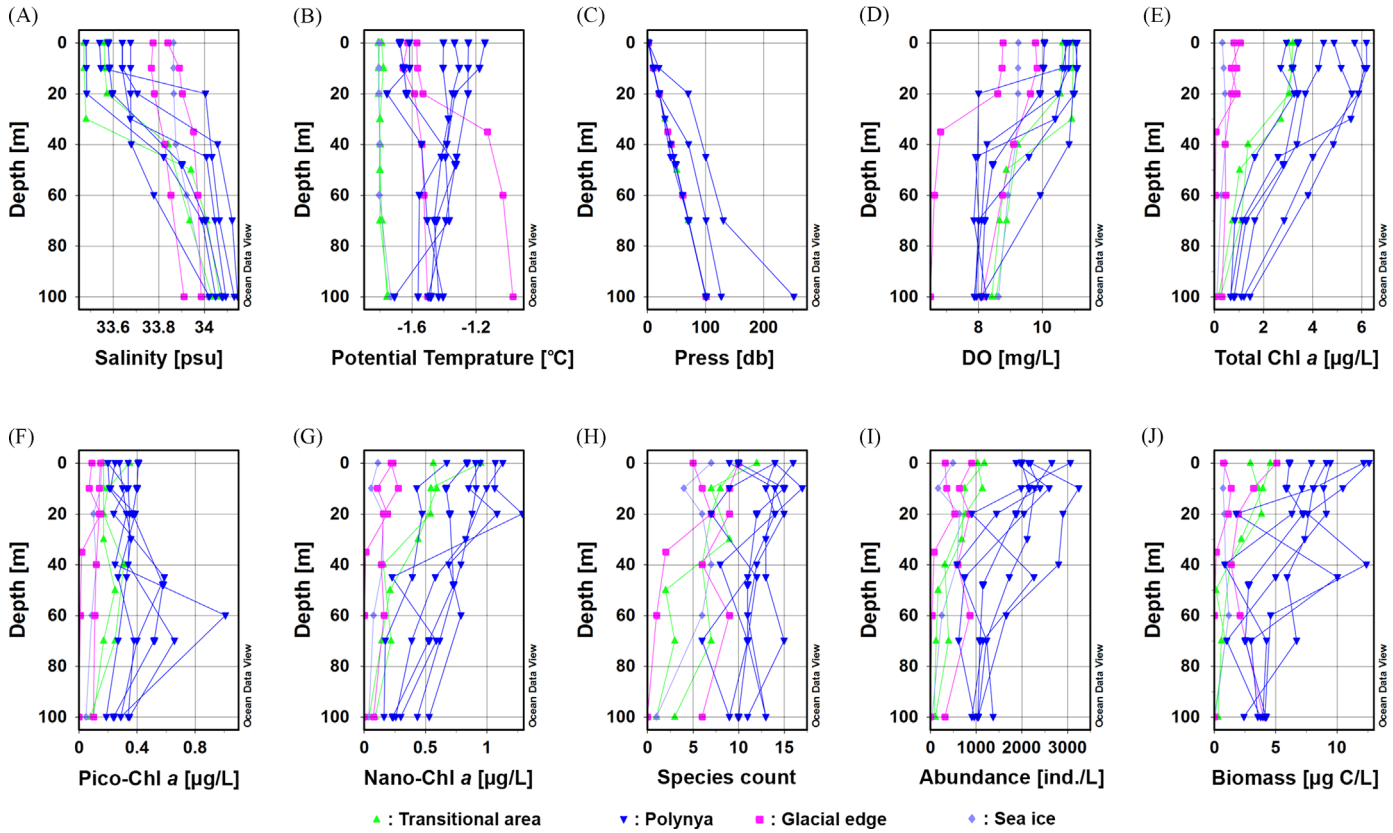

Fig. 2. Spatial distribution patterns of seven environmental variables (A–G) and species number (H), abundance (I), biomass (J) of planktonic ciliates, monitored at 11 sampling stations in four areas. DO, dissolved oxygen; Chl *a*, chlorophyll *a*.

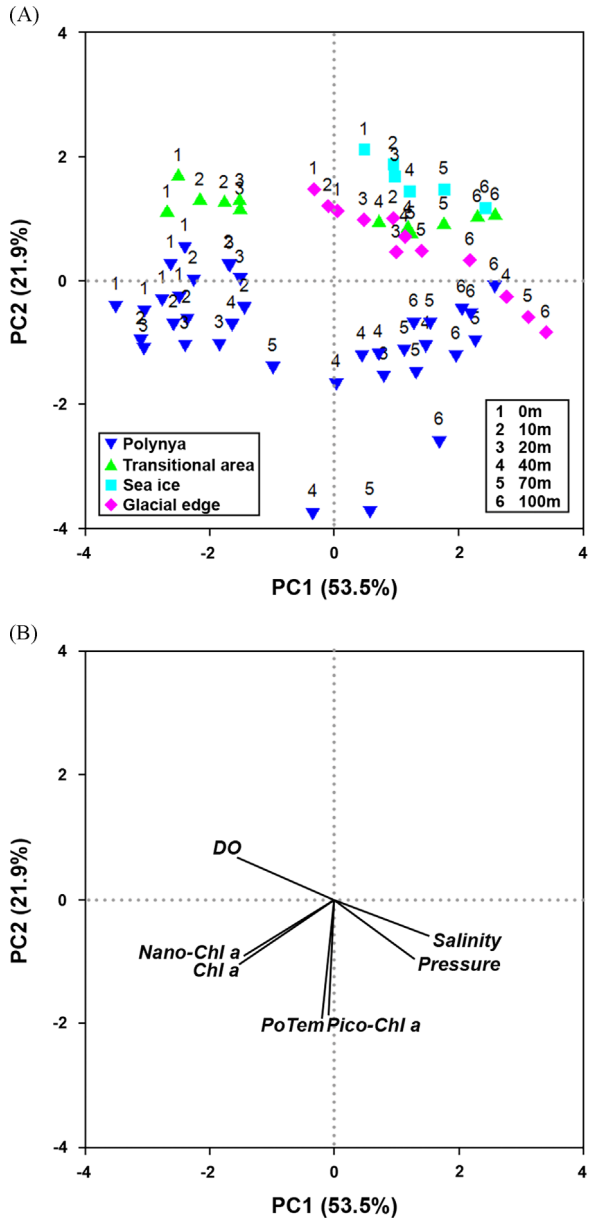

Fig. 3. Principal component analysis (PCA) plots based on log-transformed environmental variable data for spatial distribution in four areas.

environmental conditions at the four sampling areas with the apparent horizontal variation. The first PCA axis in the plot explained a large proportion (53.5%) of the total environmental variability, and separated most samples from the surface depths from those of the deeper depths. The second axis explained 21.9% of the environmental variability and discriminated polynya areas from sea ice areas (Fig. 3A). The vectors of total Chl *a*, pico-Chl *a*, and nano-Chl *a* all indicated sample clouds from the polynya (Fig. 3A and B). Among these, total Chl *a* and nano-Chl *a* showed close relationships with depth near the surface, while pico-Chl *a* showed a close relationship with depth at deeper depths (Fig. 3A and B). A permutational multivariate analysis of variance (PERMANOVA) test revealed significant differences among sample clouds from the four areas (pseudo-$F=8.406$, $P=0.001$), and clear distinctions between each pair of areas were also found by pair-wise test ($P<0.001$), with only one exception, the transitional area and sea ice ($P>0.05$) (Table 1). Notably, a significant difference existed between samples from the ASP and SIZ (pseudo-$F=15.241$, $P=0.001$). There were, however, distinct differences among the six sampling depths (pseudo-$F=8.18$, $P=0.001$), but no clear distinction between each pair of depths was found by pair-wise test ($P>0.05$), with the exception of between the third (20 m) and fourth depths (40 m) ($P=0.018<0.05$) (Table 1).

Table 1
Results of PERMANOVA based on Euclidean distance matrices derived from log-transformed data of environmental variables among (*F*) and between (pair-wise tests) groups. TA: transitional areas; PA: polynya areas; GE: glacial edge; SI: sea ice; 1: 0 m; 2: 10 m; 3: 20 m; 4: 40 m; 5: 70 m; 6: 100 m.

PERMANOVA among habitats					PERMANOVA among depths				
	df	MS	*F*	*P*		df	MS	*F*	*P*
Groups	3	43.9	8.406	0.001	Groups	5	36.9	8.18	0.001
Residual	62	5.22			Residual	60	4.51		
Total	65				Total	65			
Pair-wise tests					Pair-wise tests				
	df	*t*	*P*			df	*t*	*P*	
PA and TA	46	2.67	0.001		1 and 2	20	1.33	0.174	
PA and GE	46	3.30	0.001		2 and 3	20	0.84	0.533	
PA and SI	40	3.03	0.001		3 and 4	20	1.81	0.018	
TA and GE	22	2.99	0.004		4 and 5	20	0.71	0.716	
TA and SI	16	1.85	0.079		5 and 6	20	1.11	0.304	
GE and SI	16	2.17	0.016						

3.2. Taxonomic composition and spatial variations in community

The taxonomic composition of the ciliate communities observed during the survey is summarized in Table 2. In total, 34 ciliated species were recorded during the survey (Table 2). Their mean abundances and occurrences are summarized in Table 2, with their presence/absence in each area. The top 14 contributing species, which individually represented more than 1% of, and provided a cumulative contribution of 98.74% to, the ciliate communities, were summarized using the SIMPER analysis and defined as "dominant/common" (Table 2). Most of the dominant species were distributed primarily in the ASP, although several species provided noticeable contributions to other areas, such as *Strombidium dalum*, with higher numbers in transitional areas (Table 2).

The spatial distributions of species number, abundance, and biomass for the ciliate communities are shown in Fig. 2H–J. The species counts showed a spatial pattern, with higher values at the ASP stations (Fig. 2H). The maximum species numbers occurred at the subsurface at the ASP stations, while minimum numbers were found at deep sampling depths at the SIZ stations (Fig. 2H). At all stations, the counts decreased from the surface to 100-m depth, and no vertical stratification was observed, although counts in the SIZ were lower than in the ASP at all depths. Ciliate abundance and biomass showed similar patterns to the species counts, the highest values occurring at ASP stations (Fig. 2I and J).

Based on the significant consistency between the abundance and biomass data (Mantel test: global $R=0.867$, $P=0.001$), discrimination among the 66 samples from the four sampling areas was plotted by a canonical analysis of principal coordinates (CAP) using the Bray–Curtis similarities from log-transformed species-abundance data (Fig. 4). The plot revealed a clear spatial zonation pattern, and the communities could be separated roughly into two groups (Fig. 4A). The results produced a large first squared canonical correlation ($\delta^2=0.618$). The first canonical axis separated ciliate communities in the polynya (on the right of the plot) from communities in the other areas (on the left of the plot), while the second canonical axis, which had a very low eigenvalue ($\delta^2=0.094$), failed to discriminate further communities from the SIZ (Fig. 4A). The vectors of species count, abundance, biomass, and almost all environmental variables

Table 2
List of the 34 species recorded in 66 samples at 11 sampling stations from February to March 2012, including taxonomy (*Taxon*, Order), mean abundances in 66 samples (*Av. Abund.*, ind l^{-1}), occurrence in samples (*Occu.*, %), average Bray–Curtis similarity (*Av.Sim.*), contribution (*Cont.*, %), Cumulative contribution (*Cum.*, %) in communities, and mean abundance of each species in four sampling areas.

Species	*Taxon*, Order	*Av.Abund.*, ind l^{-1}	*Occu.*, %	*Av.Sim.*	*Cont.*, %	*Cum.*, %	Polynya	Transitional area	Sea ice	Glacial edge
Tontonia gracillima[a]	Oligotrichida	272	75.76	6.67	20.69	20.69	++++	++++	+++	+++
Lohmanniella oviformis[a]	Choreotrichida	110	86.36	5.68	17.6	38.28	++++	+++	+++	+++
Pelagostrobilidium spiralis[a]	Choreotrichida	143	80.30	4.68	14.5	52.79	++++	++	+++	+++
Strombidium antarcticum[a]	Oligotrichida	113	78.79	4.18	12.95	65.73	++++	++	+++	+++
Pelagostrobilidium neptuni[a]	Choreotrichida	112	74.24	4.01	12.44	78.17	++++	++	++	++
Balanion comatum[a]	Prorodontida	49	56.06	1.38	4.27	82.44	+++	++	+++	++
Leegaardiella ovalis[a]	Choreotrichida	42	54.55	1.17	3.64	86.08	+++	++	++	+
Cymatocylis cf. drygalskii[a]	Tintinnida	52	51.52	1.03	3.2	89.28	+++	++		+
Leegaardiella sol[a]	Choreotrichida	30	42.42	0.8	2.48	91.75	++	++	+	+
Strombidium acutum[a]	Oligotrichida	47	37.88	0.51	1.57	93.32	+++	+		+
Strombidium dalum[a]	Oligotrichida	32	34.85	0.48	1.49	94.82	++	+++		+
Mesodinium rubrum[a]	Cyclotrichiida	30	31.82	0.47	1.45	96.27	++	+	++	++
Laackmanniella prolongate[a]	Tintinnida	24	33.33	0.42	1.3	97.57	++	++	+	++
Pseudotontonia cornuta[a]	Oligotrichida	16	30.30	0.37	1.16	98.74	++	+	+	++
Strombidinopsis acuminatum	Choreotrichida	10	13.64	0.06	0.19	98.93	+	++		
Strombidium wulffi	Oligotrichida	11	16.67	0.06	0.19	99.12	++	+		+
Strombidium capitatum	Oligotrichida	7	13.64	0.06	0.18	99.3	++	+		
Askenasia sp.	Cyclotrichiida	7	12.12	0.04	0.12	99.42	++			
Didinium gargantua	Haptorida	6	12.12	0.04	0.11	99.53	+			+
Uronema marinum	Philasterida	8	9.09	0.03	0.09	99.62	++			
Laboea strobila	Oligotrichida	6	9.09	0.03	0.08	99.71	+	++	+	
Mesodinium pulex	Cyclotrichiida	5	9.09	0.02	0.07	99.78	+	+		
Strombidium emergens	Oligotrichida	7	9.09	0.02	0.05	99.83	++			
Tontonia antarctica	Oligotrichida	3	6.06	0.01	0.04	99.87	+	++		+
Rimostrombidium caudatum	Choreotrichida	4	6.06	0.01	0.03	99.9	+	+		
Pseudotontonia cf. simplicidens	Oligotrichida	8	6.06	0.01	0.03	99.93	++			
Strombidium styliferum	Oligotrichida	1	3.03	0	0.01	99.94	+		++	
Salpingella decurtata	Tintinnida	2	4.55	0	0.01	99.96	+			+
Strombidium cf. syowaense	Oligotrichida	2	4.55	0	0.01	99.97	+			
Salpingella faurei	Tintinnida	2	4.55	0	0.01	99.98	+			
Euplotes cf. antarcticus	Euplotida	3	4.55	0	0.01	99.99	+			
Cymatocylis cf. affinis	Tintinnida	1	3.03	0	0	100	+			
Codonellpsis gaussi	Tintinnida	2	3.03	0	0	100	+			
Strombidium cf. epidemum	Oligotrichida	< 1	1.52	0	0	100	+			

Abundances (ind ml^{-1}): + = 0–10, ++ = 10–50, +++ = 50–100, ++++ = over 100.

[a] Top 14 contributors of ciliate communities in all samples.

indicated sample clouds from the polynya, except those of salinity and water pressure (Fig. 4B). A PERMANOVA test demonstrated a significant effect of the groups (pseudo-F = 3.714, P = 0.001), and pair-wise comparisons in the PERMANOVA test showed fairly strong evidence against the null hypothesis, suggesting that all communities in the ASP differed from those in other areas ($P < 0.05$), but that there was no obvious difference between each pair from the SIZ (Table 3). A further PERMANOVA test revealed significant differences among the depths (pseudo-F = 1.621, P = 0.013), but pair-wise comparison between each pair of depths failed to show evidence against the null hypothesis ($P > 0.05$).

In addition, SIMPER analysis revealed that the species composition differed between the samples from the ASP and SIZ at a 73.77% dissimilarity level with respect to both abundance and occurrence (Table 4). There were 15 species at the 90% level of cumulative contribution percentage between the ASP and SIZ samples involving all dominant species in Table 1 (e.g., *Tontonia gracillima*, *Pelagostrobilidium spiralis*, *Pelagostrobilidium neptuni*, *Strombidium antarcticum*, *Lohmanniella oviformis*). These were the primary contributors to the dissimilarity of the two groups due to their much higher abundance and/or occurrence in the ASP samples than in the SIZ samples (Table 4).

3.3. Relationships between biotic and abiotic data

To achieve consistency in the spatial variability in the environmental and biotic data from the above PCA and CAP analyses, a further Mantel test was conducted to reveal the potential linkages. The results showed that, regardless of the spatial variation, significant correlations (P = 0.002) occurred between the variation in pelagic ciliate communities and changes in environmental variables across the entire study region (Table 5). In the ASP and SIZ, similar significant correlations were detected between the communities and environmental variables ($P < 0.05$) (Table 5).

The correlations between the ciliate community structures and environmental variables were established by a multivariate biota–environment (BIOENV) analysis (Table 6). BIOENV was used to select the subset of environmental variables that 'best' correlated with the ciliate faunal similarities. The best match with the ciliate spatial distribution was a combination of potential temperature and total Chl *a* (ρ = 0.368, P = 0.001); for communities in the ASP, it was salinity, potential temperature, total Chl *a*, pico-Chl *a*, and nano-Chl *a* (ρ = 0.359, P = 0.001); in the SIZ, it was salinity, potential temperature, DO, and pico-Chl *a* (ρ = 0.533, P = 0.024) (Table 6).

In the ASP, the ciliate biomass showed significant relationships with the bulk total Chl *a* (P = 0.001) and nano-Chl *a* (P = 0.036) (Fig. 5A and C), but was not related to pico-Chl a (Fig. 5B). In the SIZ, there were also significant relationships between the ciliate biomass and the concentrations of total Chl *a* ($P < 0.0001$) and nano-Chl *a* (P = 0.0001) (Fig. 5D and F). There was, however, only a weak positive trend between the ciliate biomass and pico-Chl *a*, but there was no significant linear relationship (Fig. 5E).

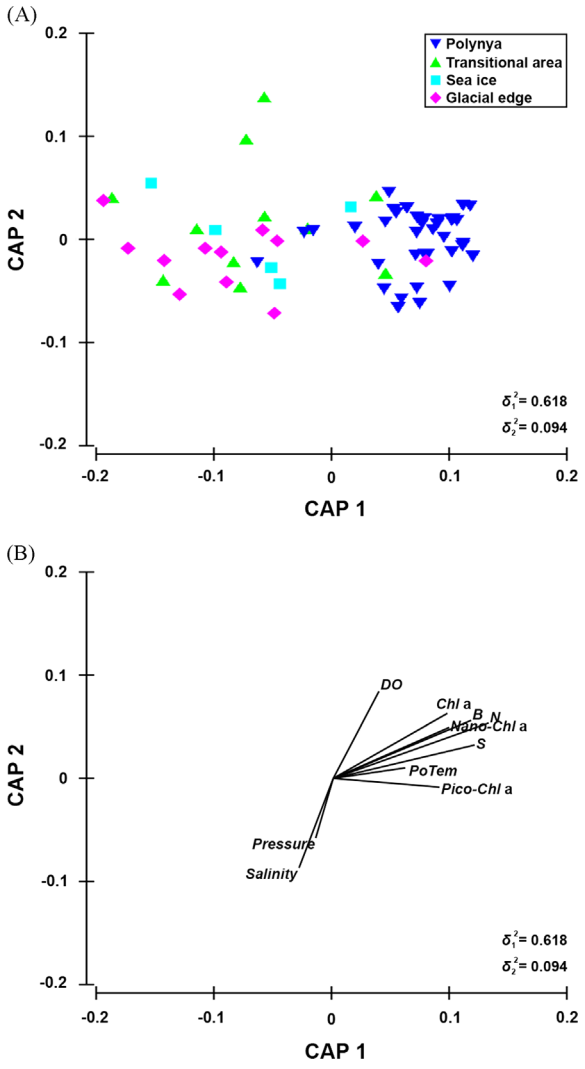

Fig. 4. Canonical analysis of principal coordinates (CAP) on Bray–Curtis similarities from log-transformed species-abundance data of 66 samples from four areas.

Table 3
Results of PERMANOVA based on Bray–Curtis dissimilarity matrices derived from log-transformed species abundance data among (F) and between (pair-wise tests) groups. TA: transitional area; PA: polynya; GE: glacial edge; SI: sea ice.

PERMANOVA among habitats				
	df	MS	F	P
Groups	3	5636.1	3.714	0.001
Residual	62	1517.5		
Total	65			
Pair-wise tests				
	df	t	P	
PA and TA	46	2.70	0.001	
PA and GE	46	2.59	0.001	
PA and SI	40	2.33	0.001	
TA and GE	22	0.75	0.813	
TA and SI	16	0.86	0.658	
GE and SI	16	0.78	0.745	

4. Discussion

Our physicochemical measurements from 11 sampling stations were consistent with former studies (e.g., Lee et al., 2012; Jiang et al., 2014a). The ASP area was characterized by distinct maximum Chl *a* concentrations and high primary production. Transitional areas within the SIZ were connected to the oceanic area and ASP with cold water of intermediate Chl *a*. Sea ice stations were located within the border of the SIZ and affected by the ASP. Glacial edge stations close to glacier margins were under the ice pack and subjected to the influence of ice shelf melting. Stations in the sea ice and glacial edge areas displayed considerably higher salinity, and lower water temperature and Chl *a* concentrations.

The pelagic ciliate community was diverse, and 34 species were identified during the survey. The taxonomic composition was comparable to published studies from the Amundsen Sea (Wickham et al., 2011; Dolan et al., 2013; Jiang et al., 2014a). For example, most of the taxa from our study were found by Wickham et al. (2011) and Jiang et al. (2014a), and the dominant species in our data (e.g., *Tontonia gracillima*, *Pelagostrobilidium neptuni*, *Strombidium antarcticum*, *Leegaardiella sol*, *Mesodinium rubrum*, and *Lohmanniella oviformis*) also showed high abundances in late austral summer 2006 (Wickham et al., 2011) and austral summer 2011 (Jiang et al., 2014a). The tintinnids observed in our study (*Codonellpsis gaussi*, *Cymatocylis* cf. *drygalski*, *Cymatocylis* cf. *affinis*, *Laackmanniella prolongata*, *Salpingella*

Table 4
Contribution of the top 15 species to the average Bray–Curtis dissimilarity (73.77%) in both occurrence and abundance between the samples of the ASP and SIZ. ASP: Amundsen Sea polynya; SIZ: sea ice zone.

Species	ASP Av.Abund	SIZ Av.Abund	Av.Diss	Contrib%	Cum.%
Tontonia gracillima	416	100	15.45	20.94	20.94
Pelagostrobilidium spiralis	228	41	8.94	12.12	33.06
Pelagostrobilidium neptuni	177	35	7.38	10.01	43.07
Strombidium antarcticum	163	52	5.93	8.04	51.1
Lohmanniella oviformis	136	79	5.21	7.06	58.17
Cymatocylis cf. drygalskii	86	11	3.56	4.82	62.99
Strombidium acutum	83	3	3.28	4.44	67.43
Leegaardiella ovalis	66	13	3.27	4.44	71.86
Balanion comatum	68	27	3.14	4.26	76.12
Leegaardiella sol	45	11	2.39	3.24	79.36
Strombidium dalum	41	21	2.14	2.91	82.27
Mesodinium rubrum	38	21	2.11	2.86	85.13
Laackmanniella prolongate	27	21	1.61	2.18	87.31
Pseudotontonia cornuta	21	10	1.28	1.73	89.04
Strombidium wulffi	18	3	0.77	1.04	90.08

Av. Diss.: average dissimilarity.

Table 5
Results of Mantel test showing the linkages between variations in planktonic ciliate communities and environmental variables. ASP: Amundsen Sea polynya; SIZ: sea ice zone.

	Sample ρ	No. of permutations	No. of permuted $\geq \rho$	P
Spatial variation	0.208	999	1	0.002
ASP	0.330	999	0	0.001
SIZ	0.326	999	4	0.005

Table 6
Summary of results from biota–environment (BIOENV) analysis showing the best matches of combinations of environmental variables with variations in ciliate abundances.

	ρ	Best combination of variables	P
Spatial variation	0.368	Tem, Total Chl *a*	0.001
ASP	0.359	Sal, Tem, Total Chl *a*, pico-Chl *a*, nano-Chl *a*	0.001
SIZ	0.533	Sal, Tem, DO, pico-Chl *a*	0.024

ρ: Spearman correlation coefficient; Tem: potential temperature; ASP: Amundsen Sea polynya; SIZ: sea ice zone.

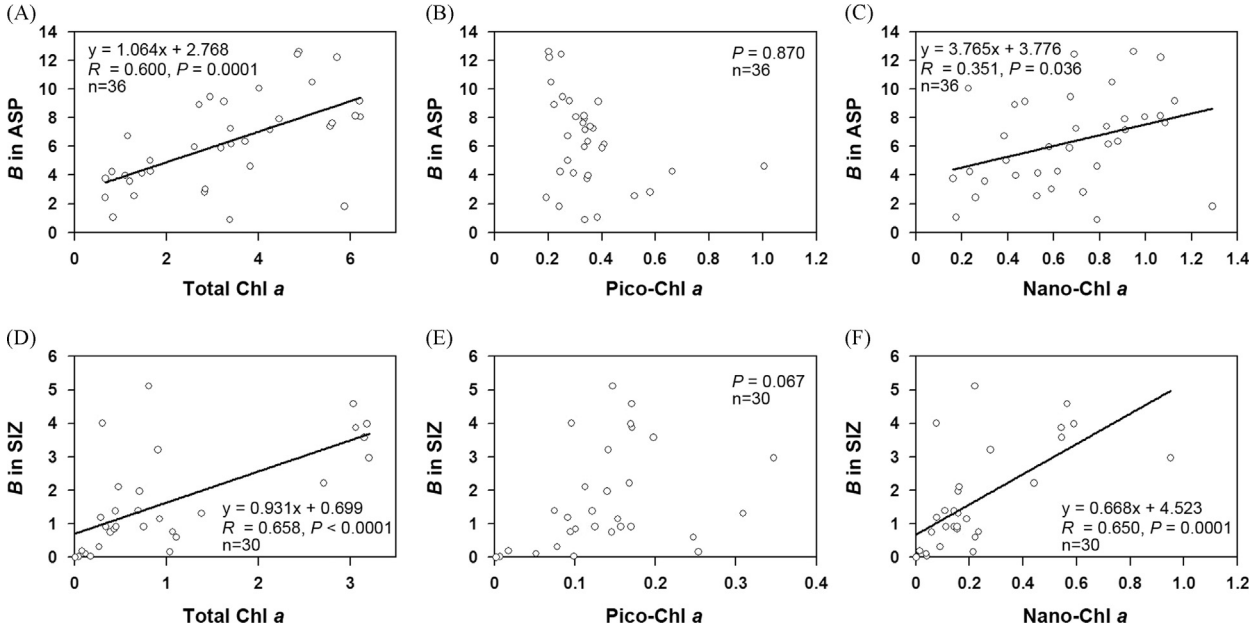

Fig. 5. Scatter plots with fitted linear regression lines showing the relationships between ciliate biomass (B, μg C l^{-1}) and concentrations (μg l^{-1}) of total Chl *a*, pico-Chl *a*, and nano-Chl *a*, respectively, in the top 100 m in an Amundsen Sea polynya (ASP) and surrounding sea ice zone (SIZ).

decurtata, and *Salpingella faurei*) were all recorded in net samples by Dolan et al. (2013), and fixed water samples by Jiang et al. (2014a) during the *Araon* maiden expedition in the Amundsen Sea. As shown by the dominant species in our results, an overwhelming dominance of aloricate oligotrichs was evident, which is consistent with many other studies in broad-scale habitats in marine ecosystems (e.g., Sherr et al., 1986; Klaas, 1997; Elloumi et al., 2006; Santoferrara and Alder, 2009; Wickham et al., 2011; Xu et al., 2011b; Jiang et al., 2012b). Aloricate oligotrich groups in our study (choreotrichids and oligotrichids) also had greater species numbers than other assemblages, which was generally consistent with previous reports (e.g., Agatha, 2011). However, comparing the species number in the ASP to previous studies is difficult because most previous work at detailed species-level resolution from the Southern Ocean focused on sea ice/ice edge communities, total abundance/biomass, or only tintinnids (e.g., Garrison and Buck, 1989; Garrison et al., 1993; Santoferrara and Alder, 2009). To date, the only available detailed study related to the ASP is from Jiang et al. (2014a), who found 44 species in the Amundsen Sea, including 35 species in the ASP during a 2011 cruise, which is highly consistent with our results. Eight ASP species (*Tontonia* sp., *Strombidiu globosaneum*, *Strombidium crassulum*, *Strombidinopsis* sp., *Strombidium sulcatum*, *Strombidum lynni* and *Holosticha cf. diademata*) from the 2011 cruise had disappeared in our study, while six species observed in our study (*Leegaardiella ovalis*, *Pseudotontonia cornuta*, *Laboea strobila*, *Strombidium emergens*, *Salpingella decurtata*, and *Euplotes cf. antarcticus*) were absent on the 2011 cruise (Jiang et al., 2014a). Thus, it appears that the diversity in the ASP is stable, although minor changes have occurred. However, we sampled pelagic communities in the ASP during austral summer over a period of only 2 years; further monitoring studies over extended time periods are needed to provide further information and corroborate the findings of the present study.

Ciliate abundance and biomass in our study were roughly comparable to the values reported in previous studies, for both the Antarctic (e.g., Wickham et al., 2011) and Arctic (Sherr et al., 1997; Jiang et al., 2013c). In four sampling areas, the abundance, biomass, and dominant species abundance had their maximum average values in the ASP stations, and all were higher than those of the other three sampling areas. Between the surface and a depth of 100 m, the species number, abundance, and biomass all decreased with increasing depth. Typically, deep-sea communities show a trend of decreasing density and biomass with increasing depth and our results in the Amundsen Sea were consistent with this trend.

In the vertical dimension, multidimensional PCA analysis of the environmental variables divided the water column into two major groups, 0–20 m and 40–100 m, which was consistent with the observed halocline layer. However, PERMANOVA analysis provided no evidence to clearly discriminate the communities into groups, which indicates that there was no clear vertical variation in the communities, which contrasted with the vertical changes observed in the environmental parameters. In contrast, on the horizontal scale, PERMANOVA analysis divided all 66 samples into groups, and all groups differed from each other, with the exception of between groups from the transitional and sea ice areas. Despite the fact that statistical evidence was found to support the differences, all measurements of the environmental variables were instantaneous, and might not accurately reflect the true environmental variability. Thus, we used CAP analysis to clearly divide the SIZ samples from those from the ASP, and found that 15 species contributed most to the dissimilarity between the ASP and SIZ communities. The PERMANOVA tests provided further support for this discrimination: all communities in the SIZ were highly similar to each other, but significantly different from those in the ASP. Therefore, overall, our results demonstrate that the pelagic ciliate community in the ASP consisted of a unique structure compared to the SIZ communities, and that, regardless of the distance between each other, all the communities in the SIZ, possessed a similar structure. Although limnological and physicochemical variability can be measured easily using modern techniques, instantaneous measurements do not provide sufficient information to understand how environmental changes influence the environmental conditions that are experienced by living creatures (Carmack et al., 2006; Hourston et al., 2009; Xu et al., 2011a; Jiang et al., 2013b, c). Stoecker et al. (1994) hypothesized that the taxonomic composition of pelagic ciliates follows the environmental status of the water mass rather than a traditional zoogeographic distribution pattern. Since that study, an increasing number of studies have found strong relationships between ciliates and environmental conditions (e.g., Elloumi et al., 2006; Jiang et al., 2011a, 2012a, 2013c, 2014a, b; Wickham et al.,

2011; Xu et al., 2011a, c, 2013). The present study provides further evidence to support these findings.

Additionally, a Mantel test demonstrated significant linkages between spatial variation in the ciliate community structure and certain environmental variables on a spatial scale. Moreover, considering the ASP and SIZ areas separately, significant linkages between ciliates and environmental variables also existed. Multivariate correlation analysis (biota and environment matching routine) was used to identify the specific relationships between the environmental variables and ciliates for all components that passed the Mantel test. The results suggest that the spatial variation in the ciliate communities was significantly correlated with temperature and total Chl *a*. It is no surprise that these two variables were the major contributors to the differences in the ASP and SIZ. While, for the ASP, a combination of salinity, temperature, total, pico-, and nano-Chl *a* most affected the communities, in the SIZ, the combination of salinity, temperature, and pico-Chl *a* most affected the communities, which indicates that, for a specific habitat, the best matched combinations were diverse.

The Chl *a* gradients between and within the sampling stations were the major drivers of most ciliate community structures and their spatial variation in species number, abundance, and biomass. Although positive chlorophyll and abundance/biomass relationships have been found in planktonic ciliate communities in both our and previous studies (Dolan and Marrase, 1995; Pitta et al., 2001; Zingel et al., 2002; Wickham et al., 2011, Jiang et al., 2014b), the relationships between Chl *a* and ciliate biomass are not always clear in polynya habitats. Our study showed strong positive relationships between ciliate biomass and total/nano-Chl *a* in both the ASP and SIZ. Thus, nano-Chl *a* is probably the major prey item for ciliates in this region. Note that, although pico-Chl *a* was a clear driver of variation in the SIZ community structure, nano-Chl *a* correlated most highly to their biomass. Ciliate distribution is often associated with nanophytoplankton (Yang et al., 2012) and is consistent with the present study. It is known that ciliates are filter feeders, and prey size is probably the most important factor in determining the ciliate distribution (Dolan et al., 2013). Nano-size phytoplankton comprises larger prey compared to those of pico-size, and is more easily encountered and grazed. This might explain the preference of nano-size phytoplankton as prey in ASP and SIZ ciliates. Further studies are necessary in the ASP, including dilution experiments, to improve our understanding of the predation selectivity of ciliates. Moreover, bulk primary production is possibly transferred by ciliates and heterotrophic dinoflagellates to the mesozooplankton. Hence, the trophic pathways in the ASP between sea-ice algae, microzooplankton, and mesozooplankton should also be investigated in detail.

To predict the impacts of environmental changes on ecosystems, it is important to understand the conditions under which the communities are exposed in the habitat (Jiang et al., 2014a). Sea ice influences biodiversity and species distributions, and rapid melting of glaciers and loss of sea ice will result in changes in environmental conditions that may drive substantial changes in communities (Griffiths, 2010; Jiang et al., 2013c, 2014a). Although most species inhabit a wide range of habitat conditions and have global distributions, and marine planktonic ciliates can be found almost anywhere where there is seawater, different forms predominate in different habitats (Agatha, 2011). Because of ease of sampling, relative immobility, increasing availability of easily used taxonomic references, and standardized methods for temporal and spatial comparisons, pelagic ciliates should be widely used in ecological investigations, especially in Southern Ocean polynya areas, which are being increasingly affected by climate change (Jiang et al., 2014a).

In summary, the results of this study demonstrated the diversity of pelagic ciliate communities in the ASP in 2012, and showed no obvious differences to those observed in 2011, but did differ from those in the SIZ, and, also, that variations in the ciliate community structure accurately reflected environmental variability. Furthermore, the primary environmental variables that described ciliate community spatial variation in the ASP were a combination of salinity, temperature, and Chl *a*. The biomass in both the ASP and SIZ showed strong relationships with total Chl *a* and nano-Chl *a*. Thus, our findings provide useful information to increase our understanding of pelagic ciliates living in Amundsen Sea polynyas.

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