Progress in Oceanography 128 (2014) 49–59

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Spatial patterns in pelagic ciliate community responses to various habitats in the Amundsen Sea (Antarctica)

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ARTICLE INFO

Article history:
Received 26 August 2013
Received in revised form 12 August 2014
Accepted 12 August 2014
Available online 18 September 2014

ABSTRACT

To investigate the impacts of climate change on environmental conditions and pelagic biodiversity, spatial patterns in pelagic ciliate communities were studied at 18 stations from five habitats in the Amundsen Sea (western Antarctic) during austral summer from December 2010 to January 2011. Clear spatial patterns were observed in community structure, and significant differences were found among the various habitats. The species number, abundance, biomass and biodiversity indices (Shannon diversity H', Pielou's evenness J', and Margalef richness D) also showed clear spatial trends. Pelagic ciliate community structure accurately reflected environmental variability. Alone or in combination, several primary environmental variables were found to affect community spatial patterns in specific habitats. Shannon H' and Margalef D showed strong relationships with spatial changes in chlorophyll *a* and might be better predictors in future Antarctic studies. This study presents the first detailed description of spatial patterns in pelagic ciliate communities and their correlations with environmental variability in habitats in the Amundsen Sea during early austral summer. Our findings provide detailed and basic data on the composition, distribution, and variation of ciliate communities in the Amundsen Sea, and will help answer important questions about polar ecosystems.

1. Introduction

As a part of the Southern Ocean located off Marie Byrd Land, the Amundsen Sea is historically known as a region with a relatively narrow continental shelf and several coastal polynyas that are located adjacent to large ice shelves (Fragoso and Smith, 2012). Sea ice extent in the Amundsen Sea has been decreasing over the last few decades (Arrigo and Alderkamp, 2012; Yager et al., 2012) and primary production studies show that it is probably the most productive area in Antarctica (Yager et al., 2012). Therefore, the Amundsen Sea has been described as one of the most productive and dynamic pelagic systems in Antarctica (Smith et al., 2011). Being the most poorly sampled area of the Southern Ocean, increasing attention has recently focused on this region (Griffiths, 2010; De Broyer et al., 2011; Dolan et al., 2013).

Although limnological and physicochemical variability can be easily measured using modern techniques, instantaneous measurements cannot provide enough information to understand how environmental changes influence the habitat conditions that are experienced by living creatures. Therefore, investigations of biota are still essential (Carmack et al., 2006; Hourston et al., 2009; Xu et al., 2011a; Jiang et al., 2013b,c). In most pelagic ecosystems, planktonic ciliates can form a substantial proportion of microplankton and play a crucial role in the functioning of the pelagic food web (Dolan and Marrase, 1995; Yang et al., 2004; Wickham et al., 2011; Dolan et al., 2013; Jiang et al., 2013a). With their rapid growth and delicate external membranes, ciliates react more quickly to environmental changes than most other eukaryotic organisms (Gong et al., 2005). 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 then, more and more studies have found strong relationships between ciliates and environmental conditions (e.g., Elloumi et al., 2006; Kchaou et al., 2009; Jiang et al., 2011a, 2012a, 2013c; Wickham et al., 2011; Xu et al., 2011a,c, 2013).

Although the importance of planktonic ciliate ecology is being increasingly recognized, studies that combine quantitative abundance and biomass data with good taxonomic resolution for ciliates, particularly in the Southern Ocean, which is experiencing increasing climate influences, are quite rare (Wickham et al.,

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http://dx.doi.org/10.1016/j.pocean.2014.08.006
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2011). Moreover, previous studies on ciliates in the Southern Ocean have generally concentrated on sea ice/ice edge communities or calculated the total abundance and/or biomass of assemblages (tintinnids or oligotrichs) and have lacked sufficient taxonomic detail to identify the loss of ecologically relevant species (e.g., Song and Wilbert, 2000; Garrison et al., 2005; Santoferrara and Alder, 2009). As far as we know, Wickham et al. (2011) have reported the only existing data that provide a species list, which was pooled from nine stations in Bellinghausen and the Amundsen Sea. Furthermore, the quantitative importance of identifying spatial patterns in pelagic ciliate communities in response to habitat conditions has still received little attention. To improve our knowledge of this biological hot spot and assess environmental heterogeneity in the sea ice melting region, a maiden expedition was conducted by the icebreaker *Araon* in the Amundsen Sea from December 2010 to January 2011.

The primary objectives of this study were to characterize the composition and distribution of pelagic ciliates, determine forcing factors that influence ciliate spatial distributions, reveal spatial patterns in ciliate community structure in various habitats, and investigate linkages between community structure and environmental conditions in habitats.

2. Materials and methods

2.1. Study stations

A multidisciplinary survey was conducted onboard the Korean Research icebreaker RV *Araon* in the Amundsen Sea between 64 and 74°S during early austral summer from December 2010 to January 2011 (Fig. 1). Conductivity, temperature, and depth (CTD) casts were conducted at 30 stations during the cruise. In the present study, 18 sampling stations were selected from five areas: oceanic stations 27–30 located in open oceanic water; stations 8, 9, 18, 21, and 29 in polynya; transitional area stations 6, 7, 22, 24, and 26 in sea ice areas as connections between oceanic areas and polynya; stations 10 and 11, which were also in polynya but were very close to the edges of the Getz and Dotson glaciers, respectively, and were affected by ice shelf melting and thought to be specific habitat with different environmental conditions and community characteristics than polynya; and sea ice edge stations 16 and 17 as habitats under sea ice to the east and west of the polynya that were thought to be affected by polynya. 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. The classification of habitats follows Yager et al. (2012), Dolan et al. (2013), and Lee et al. (2012, 2013).

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, 5 m, 15 m, 25 m, 35 m, 50 m, 75 m, 100 m and 150 m.

Water samples for nutrient analysis were collected using the CTD/rosette sampler holding 24 10-l Niskin bottles. Nutrient samples (100 ml) for measuring nitrate + nitrite nitrogen ($NO_2 + NO_3$), ammonium nitrogen (NH_4), phosphate (PO_4), and silicate concentrations (SiO_2) were analyzed onboard the ship using a Bran and Luebbe model Quatro AA (Auto Analyzer), according to the manufacturer's manual.

Water samples (500–1000 ml) for chlorophyll *a* (Chl *a*) concentration were taken from each depth and immediately filtered through glass fiber filter paper (47 mm; Gelman GF/F). Concentration of Chl *a* was measured onboard using a Turner design trilogy fluorometer after extraction with 90% acetone (Parsons et al., 1984).

In total, 130 water samples were collected using a Niskin rosette sampler from depths at 18 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 carbon biomass of ciliate cells was determined from measurements of their linear dimensions and by using volume equations for their appropriate geometric shapes (Winberg, 1971). Conversion factors of carbon biomass were 0.19 pg C μm^{-3} for aloricate ciliates and 0.053 pg C μm^{-3} for loricate cells (Putt and Stoecker, 1989; Stoecker et al., 1994).

2.3. Data analysis of samples

The diversity parameters species diversity (Shannon-Wiener H'), evenness (Pielou's J') and richness (Margalef D) were computed following the equations:

$$H' = -\sum_{i=1}^{S} Pi(\ln\ Pi)$$

$$J' = H' / \ln\ S$$

$$D = (S-1)/\ln/N$$

where Pi = proportion of the total count arising from the ith species, S = total species, and N = total individuals.

Univariate spearman correlation analyses were carried out using the statistical program SPSS v16.0. Data were log-transformed before analyses.

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 ciliate communities was summarized using the SIMPER (Similarity Percentage Analysis) program (Clarke and Gorley, 2006). The spatial environmental status of the 5 habitats was summarized using principal components analysis (PCA) based on log-transformed/normalized abiotic data from 130 samples and differences between groups of samples were tested with the submodule ANOSIM (Clarke and Gorley, 2006). 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).

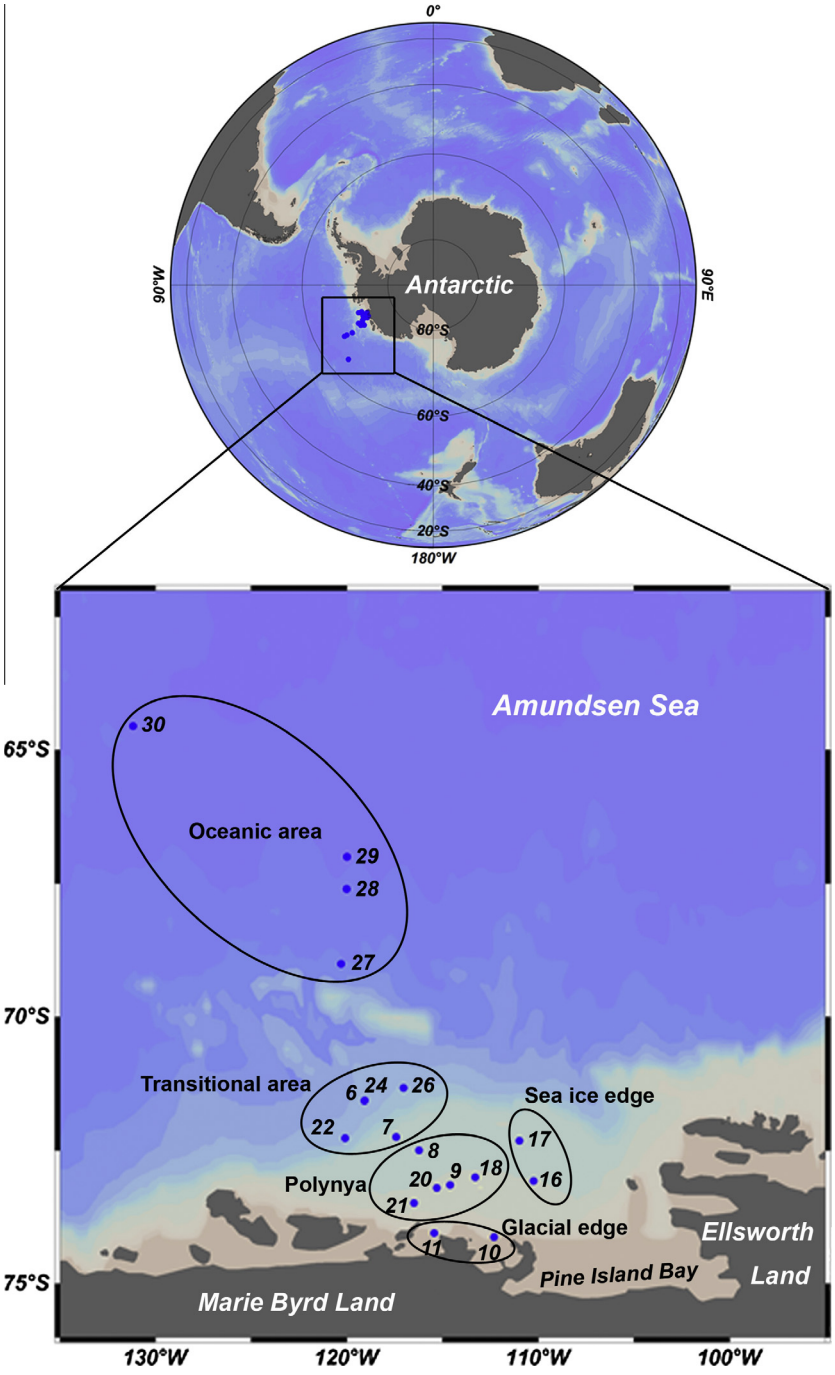

Fig. 1. 18 Sampling stations in the Amundsen Sea (western Antarctica) during the early austral summer from December 2010 to January 2011. Samples are coded for stations.

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. Spatial hydrologic structure of the water mass

The ranges in physicochemical parameters among nine sampling depths at 18 stations are summarized in Fig. 2. Antarctic Surface Water (AASW) occupied the surface layer, with a decreasing temperature trend that reached a minimum at 35–100 m in the oceanic area (Sts. 27–30); the water below was influenced by Circumpolar Deep Water (CDW) with an increasing trend with depth (Fig. 2a). A colder water mass extended from the surface to 150 m in transitional areas (Sts. 6, 7, 22, 24 and 26) (Fig. 2a). In the polynya (Sts. 8, 9, 18, 20 and 21) and glacial edge (Sts. 10, 11), seawater temperature decreased with depth but was obviously higher than in transitional areas, and the surface water temperature was higher than in both oceanic and transitional areas (Fig. 2a). In the sea ice areas (St. 16 and 17), temperatures were lower than in polynyas but higher than in transitional areas and showed an increasing trend from the surface to 150 m (Fig. 2a).

Salinity was largely determined by melt from sea ice, which resulted in regional differences. At almost all stations, salinity

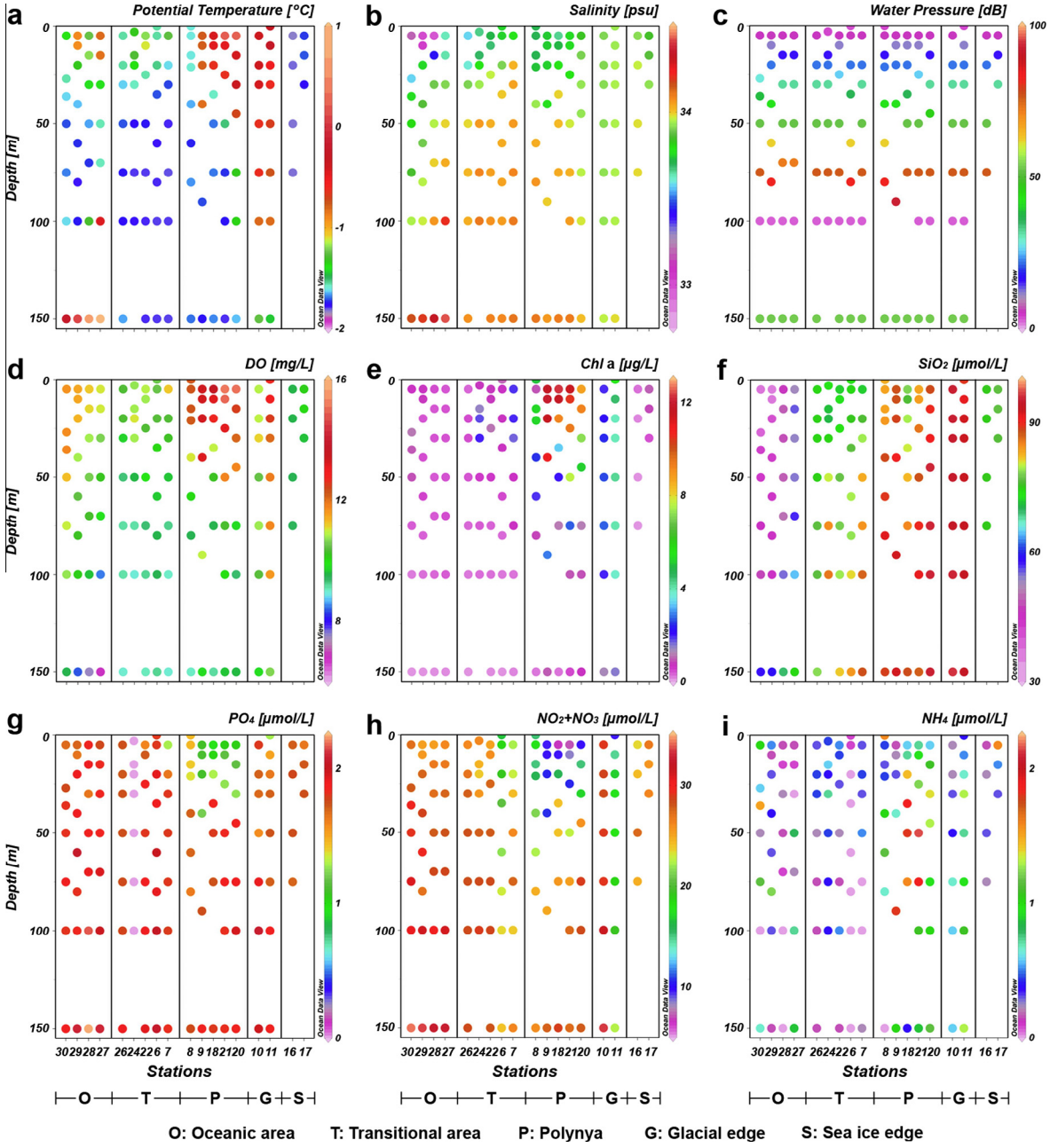

Fig. 2. Spatial distribution pattern of nine environmental variables monitored at 18 sampling stations from five habitats. DO, dissolved oxygen; Chl *a*, chlorophyll *a*; SiO_2, silicate concentrations; PO_4, phosphate; $NO_2 + NO_3$, nitrate + nitrite nitrogen; NH_4, ammonium nitrogen.

increased with water depth, except at glacial edge and sea ice edge stations (St. 10, 11, 16, and 17), which did not show clear vertical changes (Fig. 2b). The most significant vertical variation occurred in the oceanic area, with maximum values at approximately 150 m and minimum values at the surface (Fig. 2b). A pronounced halocline layer occurred between 15 and 35 m in the oceanic area, with little vertical change below the halocline until the maximum at 150 m (Fig. 2b). No apparent halocline layer was observed in transitional and polynya areas, although the upper depths (0–35 m) had relatively lower salinity values. Below the upper depths, salinity values increased slightly but significant stratification was not observed (Fig. 2b).

Water pressure was stratified and increased gradually with depth but a minimum depth of about 100 m (Fig. 2c). Spatial patterns in dissolved oxygen (DO) were similar to patterns in temperature, with maximum values in polynya and values differing among areas (Fig. 2d). Silicate concentrations (SiO_2) were varied and increased from oceanic open water to inner polynya, with no obvious vertical distribution except in the oceanic area, which had the lowest concentrations and clear vertical distributions (Fig. 2f). The highest values were observed at Sts. 10, 11, 20, and 21, while values in transitional areas and in the upper 0–100 m at sea ice edges were lower and similar (Fig. 2f).

Concentrations of Chl *a* varied across the stations and decreased with depth, with the highest concentrations were observed in polynya stations (Fig. 2e). In the oceanic area, concentrations of Chl *a* showed more even vertical distributions and decreased slightly with depth. In transitional areas, the decreasing trend in Chl *a* was disturbed at 15–35 m and the concentration increased toward the inner part of the continental slope. The polynya areas

were characterized by high primary production with considerably higher Chl *a* concentrations and distinct maximums at 0–25 m. Because of their proximity to polynya and influences from glacial shelf melting, Sts. 10 and 11 had higher Chl *a* values than other sampling regions but their values were still less than at polynya stations. At sea ice edge stations (Sts. 16 and 17), Chl *a* concentrations were similar to oceanic and transitional areas (Fig. 2f).

Although the vertical trend of nutrient was opposite to that of Chl *a*, with concentrations increasing with depth, phosphate (PO_4) and nitrate nitrogen + nitrite nitrogen ($NO_3 + NO_2$) still showed highly similar horizontal variation patterns and could be separated into different regions (Fig. 2g and h). Spatial patterns in ammonium nitrogen (NH_4) appeared complex and irregular, with higher values at depths of 35–100 m at polynya stations compared to the other regions, but values could essentially be characterized into five different areas (Fig. 2i).

Principal components analyses (PCAs) using 130 samples are shown in Fig. 3. The two principal components discriminated the environmental conditions at the five habitats with apparent horizontal variation. In the plot, the first PCA axis explained a large proportion (38.5%) of the total environmental variability and separated the polynya areas (including two habitats: polynya at Sts. 8, 9, 18, 20, and 21 and glacial edge at Sts. 10 and 11) from the others. The second axis explained 15.3% of the environmental variation and discriminated oceanic areas (Sts. 27–30) from sea ice areas (including transitional areas at Sts. 6, 7, 22, 24, and 26 and sea ice edge at Sts. 16 and 17) (Fig. 3). Analysis of similarities (ANOSIM) revealed significant differences among sample clouds of the five habitats (global $R = 0.194$, $P = 0.001$) and clear distinctions between each pair of habitats were also found by pair-wise tests ($P < 0.001$), with several notable exceptions; e.g., the transitional area & the sea ice edge ($P > 0.05$), and the polynya & the glacial edge ($P > 0.05$).

3.2. Taxonomic composition

The taxonomic composition of ciliate communities observed during the survey is summarized in Table 1. In total, 44 ciliated species, representing 21 genera and 11 orders (Cyclotrichiida, Choreotrichida, Euplotida, Haptorida, Oligotrichida, Peniculida, Philasterida, Prorodontida, Sporadotrichida, Tintinnida, and Urostylida), were recorded during the survey (Table 1). Their mean abundances and occurrences are summarized in Table 1, and presence/absence in habitats are shown. Of these, the top 12 contributing species, which represented more than 2% individually and had a cumulative contribution of 93.57% to ciliate communities, were summarized using the SIMPER program and defined as "dominant/common" (Table 1). Most of the dominant species were distributed primarily in polynya, although several species provided noticeable contributions to specific habitats, including *Strombidium wulffi* with higher numbers at glacial edges and in transitional areas, *Mesodinium rubrum* in transitional areas, and *Totonia* sp. in oceanic areas (Table 1).

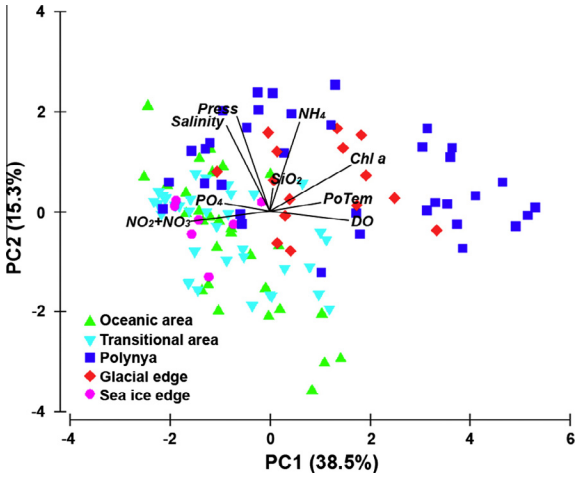

Fig. 3. Principal component analysis (PCA) plots based on log-transformed environmental variable data for spatial distribution of five habitats.

3.3. Spatial variations in species number, abundance, biomass and biodiversity parameters

The spatial distributions of species number, abundance, biomass, and three biodiversity parameters (D, J', and H') for ciliate communities are shown in Fig. 4. Species counts showed a spatial pattern, with higher values at polynya stations and at depths of 0–35 m at transitional stations (Fig. 4a). The maximum species numbers occurred at 75 m at St. 18 and at 0–15 m at St. 21, while minimum numbers were found at deeper sampling depths at oceanic Sts. 29 and 30 (Fig. 4a). In oceanic and transitional areas, species counts showed obvious decreasing gradients from the surface to 150 m; counts in the first area were lower than at the second at comparable depths. Regarding polynya and glacial edges, no vertical distributions or stratification was observed, although counts at glacial edges were lower than in polynya at all depths. Counts at sea ice edges were lower than at glacial edges, and the decreasing gradient was disturbed by a lower record at about 75 m (Fig. 4a). Ciliate abundance and biomass showed similar patterns to species number, the highest values occurred at the surface at polynya stations (Fig. 4b and c). The spatial patterns in Margalef richness (D) and Shannon–Wiener diversity index (H') results were highly consistent with that of species number, abundance and biomass (Fig. 4d and f). Pielou's evenness (J') was irregular and no obvious pattern was observed in variation among stations, (Fig. 4e).

3.4. Spatial patterns in pelagic ciliate communities

Discrimination among the 130 samples from the five habitats was plotted by a canonical analysis of principal coordinates (CAP) using Bray–Curtis similarities from log-transformed species–abundance data (Fig. 5). The resulting spatial zonation pattern was clear, and the communities were separated into five groups (Fig. 5). The results demonstrated that the first squared canonical correlation was large ($\delta^2 = 0.765$). The first canonical axis separated ciliate communities in transitional, polynya and glacial edge areas (on the right) from communities in the oceanic area, and sea ice edges (on the left), while the second canonical axis, which also had a large eigenvalue ($\delta^2 = 0.660$), clearly discriminated communities in the transitional area (upper) from the others (lower; Fig. 5). Although no clear separation occurred between sample clouds from the polynya and the glacial edge (upper right), or those from the oceanic area and the sea ice edge (upper left) in the two-dimensional plot (Fig. 5). A permutational multivariate analysis of variance (PERMANOVA) test demonstrated a significant effect of the habitats (pseudo-$F = 5.81$, $P = 0.001$), and pair-wise comparisons in the PERMANOVA test showed fairly strong evidence against the null hypothesis, suggesting that all of five habitats differed from one another ($P < 0.05$) (Table 2).

3.5. Relationship between spatial community structure patterns and environmental structure

To achieve consistency in the spatial variability in environmental and biotic data from the above PCA and CAP analyses, a further Mantel test (RELATE analysis) was conducted to reveal potential

Table 1
List of the 44 species recorded in 130 samples at 18 sampling stations in the Amundsen Sea from December 2010 to January 2011, including taxonomy (*Taxon*, Order), mean abundances in 130 samples (*N*, ind. l^{-1}), occurrence in samples (*Occu*, %), contribution (*Cont*, %), Cumulative contribution (*Cumu*, %) in communities, and mean abundance in five habitats.

Species	*Taxon*	*N*	*Occu*	*Cont*	*Cumu*	Oceanic area	Transitional area	Polynya	Glacial edge	Sea ice edge
*Strombidium antarcticum**	Oligotrichida	165	76	21.29	21.29	++++	++++	+++++	+++	++
*Lohmanniella oviformis**	Choreotrichida	117	82	20.73	42.02	+++	+++	+++++	++	++
*Tontonia antarctica**	Oligotrichida	168	50	8.06	50.08	++	++	+++++	+++	++
*Leegaardiella sol**	Choreotrichida	45	54	7.43	57.51	++	++	+++	++	
*Strombidium wulffi**	Oligotrichida	113	54	7.24	64.74	++	++++	+++	+++++	++
*Tontonia gracillima**	Oligotrichida	72	52	5.98	70.73	+	+++	+++	++	++
*Mesodinium rubrum**	Cyclotrichiida	174	48	5.91	76.63	++	+++++	++	+++	++++
*Pelagostrobilidium spiralis**	Choreotrichida	49	53	5.44	82.08	++	++	++++	++	++
*Pelagostrobilidium neptuni**	Choreotrichida	32	47	3.86	85.94	++	++	+++	++	+
Tontonia sp.*	Oligotrichida	36	36	2.87	88.81	++	++	++	++	
*Strombidium acutum**	Oligotrichida	33	38	2.40	91.21	++	++	++	+	
*Pseudotontonia cf. simplicidens**	Oligotrichida	27	37	2.36	93.57	+	++	++	++	
Mesodinium pulex	Cyclotrichiida	13	21	1.31	94.87	++	+	+		+++
Laackmanniella prolongate	Tintinnida	14	23	0.61	95.48		++	++	++	++
Leegaardiella ovalis	Choreotrichida	6	12	0.59	96.07	+	++			++
Askenasia sp.	Cyclotrichiida	10	18	0.59	96.66	+	++	+	+	
Cymatocylis cf. drygalskii	Tintinnida	13	22	0.51	97.17		+	++	++	
Balanion comatum	Prorodontida	9	15	0.48	97.66	+	++	+	+	
Strombidium capitatum	Oligotrichida	9	15	0.46	98.11	++	+	+	++	
Strombidium cf. syowaensis	Oligotrichida	10	18	0.40	98.52			++	++	+
Strombidium globosaneum	Oligotrichida	8	15	0.32	98.83	+	+	++	+	
Strombidium emergens	Oligotrichida	5	12	0.22	99.06	++	+		++	
Uronema marinum	Philasterida	5	12	0.17	99.22		+	++		+
Strombidium conicum	Oligotrichida	12	12	0.16	99.39	+	+	++	++	
Strombidium crassulum	Oligotrichida	5	11	0.13	99.51	+	+	++		
Didinium gargantuan	Haptorida	6	11	0.10	99.61		+	+	+	+
Strombidium cf. epidemum	Oligotrichida	7	8	0.08	99.69		+	+	+	
Strombidinopsis acuminatum	Choreotrichida	4	7	0.07	99.76		+	+	+	
Strombidinopsis sp.	Choreotrichida	4	7	0.06	99.81		+	+	+	
Rimostrombidium caudatum	Choreotrichida	3	7	0.05	99.86		+	+		
Strombidium styliferum	Oligotrichida	5	5	0.03	99.89	+	+	+		
Euplotes cf. antarcticus	Euplotida	2	5	0.03	99.93		+			
Strombidium sulcatum	Oligotrichida	3	5	0.02	99.95		+	+		
Cymatocylis cf. affinis	Tintinnida	2	4	0.01	99.96			+		
Salpingella faurei	Tintinnida	2	3	0.01	99.97			+		
Strombidium dalum	Oligotrichida	2	4	0.01	99.98		+	+		
Salpingella decurtata	Tintinnida	1	2	0.01	99.98	+				
Uronema sp.	Philasterida	<1	2	0.00	99.99	+				
Strombidium lynni	Oligotrichida	1	2	0.00	99.99			+		
Frontonia cf. frigida	Peniculida	<1	2	0.00	100.00		+			+
Laboea strobila	Oligotrichida	2	2	0.00	100.00		+			
Pseudotontonia cornuta	Oligotrichida	<1	2	0.00	100.00	+				
Holosticha cf. diademata	Urostylida	<1	1	0.00	100.00			+		
Laackmanniella naviculaefera	Tintinnida	<1	1	0.00	100.00		+			

* Top 12 contributors of ciliate communities in all samples. +: 0–10 ind. l^{-1}; ++: 10–50 ind. l^{-1}; +++: 50–100 ind. l^{-1}; ++++: 100–200 ind. l^{-1}; +++++: over 200 ind. l^{-1}.

linkages. The results showed that regardless of variations in spatial dimension or in various habitats, significant correlations ($P < 0.05$) occurred between variation in planktonic ciliate communities and changes in environmental variables (Table 3). The only exception was observed at the sea ice edge (Sts. 16 and 17), where no significant correlations were detected between communities and environmental variables ($P > 0.05$) (Table 3).

Correlations between ciliates and environmental variables were established by a multivariate biota–environment (BIOENV) analysis (Table 4). BIOENV was used to select the subset of environmental variables that 'best' correlated with ciliate faunal similarities. The best match with the ciliate spatial distribution was the combination of salinity, potential temperature, DO and Chl *a* ($\rho = 0.508$, $P = 0.002$); for communities in oceanic areas, it was Chl *a* and $NO_3 + NO_2$; in transitional areas, it was SiO_2; in polynyas, it was salinity and Chl *a*; and at glacial edges, it was salinity, temperature, DO, PO_4, and $NO_3 + NO_2$ (Table 4).

Notably, a Spearman correlation analysis (Table 5) also determined that the spatial distributions of species number, abundance, biomass, richness (*D*) and diversity (*H′*) were positively correlated with Chl *a*, DO and SiO_2 ($P < 0.01$) but negatively correlated with $NO_3 + NO_2$ ($P < 0.01$). In addition, species number, abundance, and biomass were negatively correlated with salinity and temperature ($P < 0.05$) (Table 5).

4. Discussion

Based on sea ice concentration, location, and references (e.g., Lee et al., 2012, 2013; Dolan et al., 2013), five habitats were selected. In the present study, physicochemical measurements from 18 sampling stations in these habitats supported the classification and were consistent with former studies (e.g., Lee et al., 2012). Among these habitats, the oceanic area was in deep offshore open waters (free of sea ice) and had comparatively low concentrations of Chl *a*. Transitional areas within the sea ice zone were connected to the oceanic area and polynya with cold water, intermediate salinity and Chl *a*, and the lowest PO_4 and NH_4 concentrations were recorded. The polynya area was characterized by having distinct maximum Chl *a* concentrations and high primary production. Glacial edge stations close to glacier margins, without sea ice at all but under the influence of ice shelf melting,

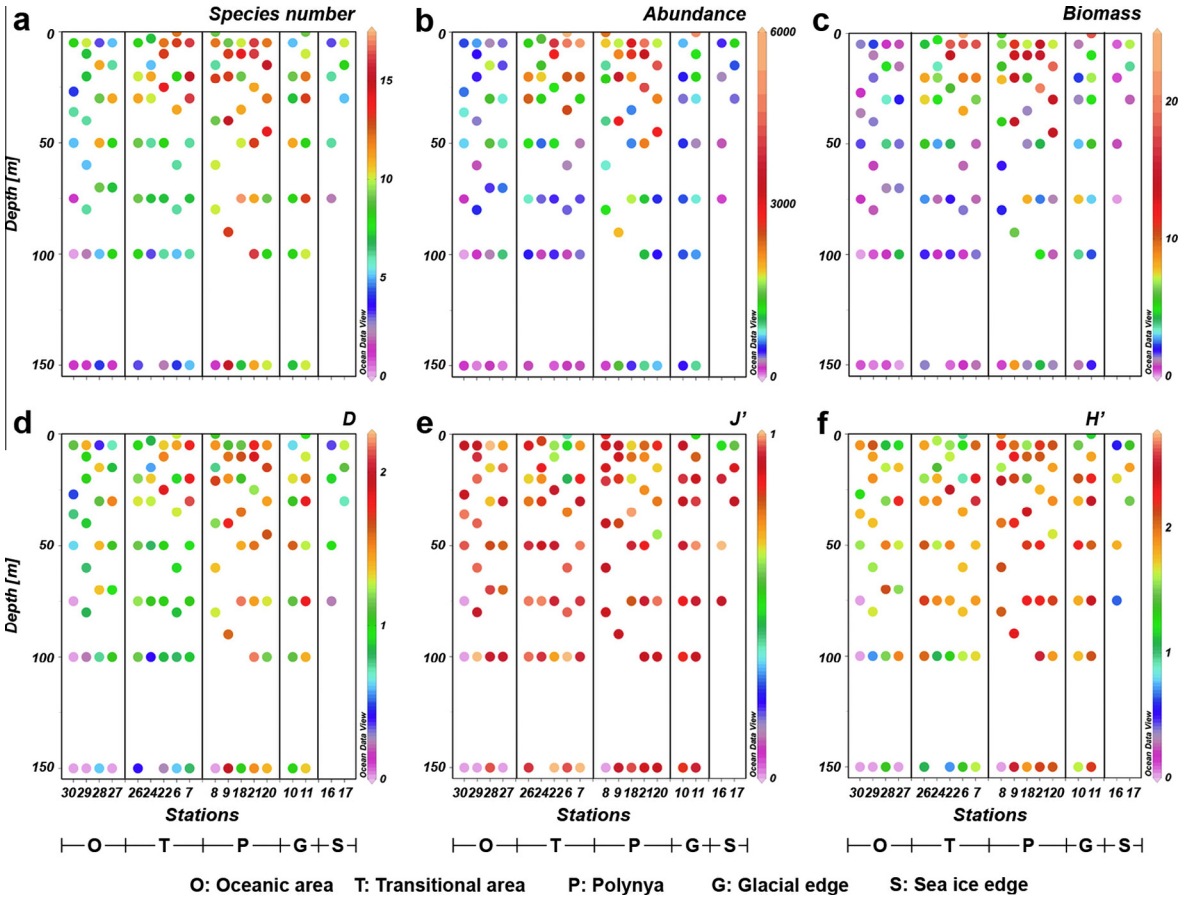

Fig. 4. Spatial variations in species number (a), abundance (b), biomass (c), Margalef *D* (d), Pielou's *J′* (e) and Shannon-Wiener *H′* (f) of planktonic ciliates from 18 stations.

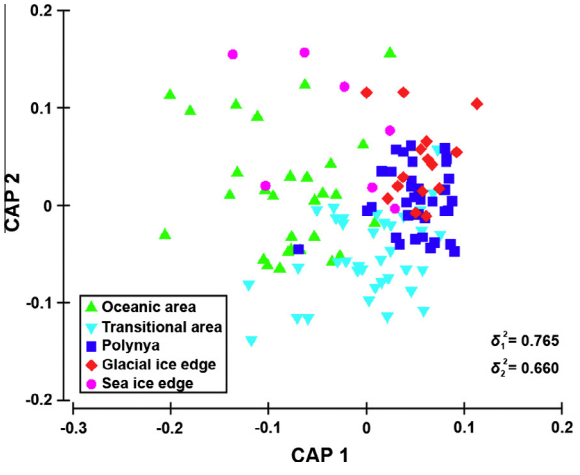

Fig. 5. Canonical analysis of principal coordinates (CAP) on Bray-Curtis similarities from log-transformed species-abundance data of 130 samples from five habitats.

had considerably higher water temperature, salinity, and Chl *a* concentrations. Sea ice edge stations were under the border of the sea ice zone and affected by polynya (Lee et al., 2012).

The pelagic ciliate community in the Amundsen Sea was diverse and 44 species representing 21 genera and 11 orders were identified during the survey. Comparing the species number to previous studies is difficult because most previous work with detailed species-level resolution from the Southern Ocean concentrated on sea ice/ice edge communities, total abundance/biomass, or only

Table 2
Results of PERMANOVA based on Bray Curtis dissimilarity matrices derived from log-transformed species abundance data among (*F*) and between (pair-wise tests) habitats, and dissimilarity between each pair of habitats. OA: Oceanic area; TA: Transitional area; PA: Polynya; GE: Glacial edge; SE: Sea ice edge.

	df	MS	*F*	*P*
PERMANOVA among habitats				
Habitats	4	11932	5.81	0.001
Residual	117	2052		
Total	121			
	df	*t*	*P*	
Pair-wise tests				
OA & TA	63	2.42	0.001	
OA & PA	62	3.10	0.001	
OA & GE	42	2.31	0.001	
OA & SE	34	1.62	0.013	
TA & PA	69	2.82	0.001	
TA & GE	49	2.28	0.001	
TA & SE	41	2.02	0.001	
PA & GE	48	1.88	0.001	
PA & SE	40	2.87	0.001	
GE & SE	20	2.29	0.001	
	OA	TA	PA	GE
Dissimilarity between habitats				
TA	75.20			
PA	70.99	62.89		
GE	73.19	65.94	54.36	
SE	76.29	73.48	70.09	70.79

tintinnids (e.g., Garrison and Buck, 1989; Garrison et al., 1993; Santoferrara and Alder, 2009). For now, the only available detailed

Table 3
Results of Mantel test showing the linkages between variations in planktonic ciliate communities and environmental variables.

	Sample ρ	No. of permutations	No. of permuted $\geqslant \rho$	P
Spatial variation	0.394	999	3	0.002
Oceanic area	0.391	999	0	0.001
Transitional area	0.164	999	24	0.025
Polynya	0.279	999	0	0.001
Glacial edge	0.439	999	0	0.001
Sea ice edge	0.326	999	78	0.079

Table 4
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	0.508	Sal, Tem, DO, Chl *a*	0.002
Oceanic area	0.576	Chl *a*, $NO_3 + NO_2$	0.01
Transitional area	0.334	SiO_2	0.01
Polynya	0.406	Sal, Chl *a*	0.01
Glacial edge	0.533	Sal, Tem, DO, PO_4, $NO_3 + NO_2$	0.01

ρ: Spearman correlation coefficient; Tem: potential temperature; Press: water pressure; see Fig. 2 for other abbreviations and units.

Table 5
Spearman correlations analysis between environmental variables and ciliate species number (S), abundance (N), biomass (B), species richness (D), species evenness (J'), and species diversity (H') of pelagic ciliates.

	Horizontal variation					
	S	N	B	D	J'	H'
Salinity	−0.187*	−0.299**	−0.231*	−0.136	−0.109	−0.146
Tem	−0.185*	−0.302**	−0.252**	−0.132	−0.071	−0.126
DO	0.475**	0.555**	0.597**	0.437**	0.105	0.345**
Press	−0.031	−0.128	−0.195*	0.000	0.055	0.050
Chl *a*	0.540**	0.571**	0.656**	0.508**	0.094	0.388**
SiO_2	0.345**	0.262**	0.345**	0.353**	0.123	0.279**
PO4	−0.112	−0.233*	−0.238*	−0.060	−0.062	−0.089
NO_3–NO_2	−0.440**	−0.550**	−0.641**	−0.383**	0.027	−0.257**
NH_4	0.343*	0.298*	0.230*	0.350*	0.033	0.258*

See Fig. 2 and Table 3 for abbreviations and units.
* $P < 0.05$.
** $P < 0.01$.

study from Amundsen Sea is Wickham et al. (2011) found 70 species in all of the Amundsen and Bellingshausen seas. In temperate waters, Kchaou et al. (2009) and Jiang et al. (2011b) found 56 and 64 planktonic ciliates, respectively, while the observed diversity in the Arctic Ocean was 55 species (Jiang et al., 2013c). Compared to the Arctic region and more temperate habitats, ciliate communities during austral summer in the Amundsen Sea are not species-poor. The taxonomic composition in the current collections was comparable with available studies from the Amundsen Sea (Wickham et al., 2011; Dolan et al., 2013). For example, most taxa could be found in Wickham et al. (2011) and the present dominant species (e.g., *L. sol*, *Lohmanniella oviformis*, *M. rubrum*, and *Strombidium antarcticum*) were also top ranked with high abundance in late summer 2006 (Wickham et al., 2011). The tintinnids that were found in the present study (e.g., *Cymatocylis* cf. *drygalski*, *Laackmanniella prolongata*, and *Salpingella faurei*) were all recorded in net samples from the same cruise by Dolan et al. (2013). 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 basically consistent with previous reports (e.g., Agatha, 2011).

Variations in abundance in various habitats ranged from 369 to 4227 ind. L^{-1}, which is closely comparable with other Antarctic studies (e.g., Wickham et al., 2011) and Arctic reports (e.g., Sherr et al., 1997) and as high as in temperate waters (Sorokin, 1977; Smetacek, 1981; Levinsen et al., 1999; Moritz et al., 2006; Jiang et al., 2011b). Biomass also showed a similar pattern to those listed above. In summary, ciliate abundance and biomass in the current study were roughly comparable to values reported in previous research.

Community structure parameters (species number, abundance, biomass, diversity H', evenness J', and richness D) are commonly used in community-level investigations. In five habitats, almost all parameters (except J') and dominant species abundance had maximum average values in polynya, which is consistent with the high Chl *a* concentrations typical in polynya (Lee et al., 2012). From the surface to 150 m, species number, abundance, biomass, and parameters (D and H') by depth all followed a decreasing trend. Typically, deep-sea communities show a trend of decreasing density and biomass with depth. Our analyses in the Amundsen Sea confirmed this trend. As shown by Wickham et al. (2011), Chl *a* is a better predictor of ciliate abundance and biomass in this region. According to the above coincident variations in community structure parameters and Chl *a*, we suggest that spatial diversity in ciliate communities was mainly correlated with Chl *a*. Otherwise, all of the results demonstrated that ciliate communities exhibited very similar spatial patterns to those of environmental variables. Our results indicate that pelagic ciliate community structure in specific station/depth accurately reflects different environmental conditions. The similar result has also been found in other protozoan groups, for instance heterotrophic flagellates (Tikhonenkov, 2013), which could be distinguished due to vertical gradient of environmental condition.

Although the five habitats had unique environmental conditions and clear spatial variation was observed in some environmental variables (e.g., temperature, SiO_2, and Chl *a*), multidimensional PCA analysis of environmental variables divided all of the 130 samples into three major groups only: oceanic areas, sea ice areas, and polynya areas. No evidence was found to support further separation within the three sample clouds. As we know, all of the measurements of environmental variables were instantaneous and might not have accurately reflected habitat variability. For both transitional areas and sea ice edges, all of the stations were under sea ice and might have had some similar values. Important information, such as combined influences from the open sea and polynya on habitats in transitional areas, were completely obscured in the mixture with sea ice edge stations that were located a long distance away. The lack of discrimination between polynya and glacial edge stations might have occurred for the same reason.

However, clear evidence from the CAP analysis divided the glacial edge samples from polynya, and sea ice edge samples also differed significantly from transitional ones. In addition, the PERMANOVA tests provide further support for this finding: All five habitats were clearly separated from each other, and the communities in the habitats were highly similar but significantly different from those in other habitats. Therefore, all of these results demonstrate that pelagic ciliate community structure varied among the habitats studied.

Furthermore, a Mantel test demonstrated significant linkages between spatial variation in ciliate community structure and certain environmental variables, which supports above findings. Moreover, in each habitat, significant linkages between ciliates and environmental variables also existed, except in sea ice edge sites, where environmental effects appeared to be weak. Multivariate correlation analysis was used to identify specific relationships

between environmental variables and ciliates for all components that passed the Mantel test. The results demonstrated that spatial variation in ciliate communities was significantly related to various parameters (a combination of salinity, temperature, dissolved oxygen and Chl *a*), which means that not only the establishment and discrimination of habitats but also relationships between environmental conditions and communities are multivariate. Because of collinearity between DO and Chl *a*, we suggest that Chl *a* had a significant influence on the spatial distribution of ciliate communities in this study. For specific habitats, the best match combinations were diverse. Notably, Chl *a* was included in the combinations of parameters for oceanic areas and polynya, but was absent in parameter combinations for transitional areas and glacial edges. In the report by Lee et al. (2013) from the same cruise, mesozooplankton also followed a horizontal distribution, with copepods dominating in the oceanic area and euphausiids dominating in polynya. The greater biomass of euphausiids *Euphausia crystallorophias* in polynya was associated with lower salinity and higher Chl *a* (Lee et al., 2013), which is very similar to the present ciliate community study, where the best parameter combination also included salinity and Chl *a*.

Diversity (Shannon H'), evenness (Pielou's J'), and richness (Margalef D) indices are amenable to simplifying statistical analyses (Connell, 1978; Magurran, 1991; Gong et al., 2005; Jiang et al., 2012b). Generally, higher values for these three indices indicate better environmental conditions (Ismael and Dorgham, 2003). In the present study, diversity and richness indices had maximum values in polynya, and values were clearly higher in connected areas (transitional areas and glacial edges) than in the oceanic area and sea ice edges. According to measures of two indices in five habitats, their values followed a decreasing gradient: polynya > glacial edge > transitional area > oceanic sea > sea ice edge. This suggests that polynya habitats are the best for ciliates among all of the habitats in the Amundsen Sea. Furthermore, their spatial distributions suggest that the indices were correlated with environmental variables, especially Chl *a*. The Spearman correlation analysis supported our hypothesis that strong correlations exist between environmental variables and structure parameters. Among these correlations, spatial variation in structure parameters, especially species number, abundance, and biomass were significantly correlated with Chl *a*, DO and SiO_2, and negative correlations with salinity, temperature and nutrients. Regarding variation of D and H', significant correlations were also found, including positive correlations with Chl *a*, DO and SiO_2, and negative correlations with nutrients. Note that for J', no reasonable relationship was found with respect to spatial variation; it seems to be irregular and useless for characterizing community variation along spatial environmental gradients, which has been found in previous studies (e.g., Gong et al., 2005; Jiang et al., 2011b). This suggests that D and H' are more appropriate for comparing spatial variation among habitats.

Because nutrients and salinity are both important for phytoplankton growth, Chl *a* is a key factor affecting vertical variation in structure parameters. Thus, Chl *a* gradients between and within sampling stations were the major drivers of most ciliate community structure parameters (spatial variation in species number, abundance, biomass, D and H'). Although positive chlorophyll abundance/biomass relationships have been found in planktonic ciliate communities in the present and previous studies (Dolan and Marrase, 1995; Pitta et al., 2001; Zingel et al., 2002; Wickham et al., 2011), relationships between Chl *a* and biodiversity indices (D, J', and H') are not always clear. For example, strong positive relationships between tintinnid abundance and Chl *a* have been found in the equatorial Pacific and the Mediterranean, but unlike the current study, no relationship was found between tintinnid species diversity/richness and Chl *a* (Dolan et al., 2007). Thus, although Chl *a* was a clear driver of variation in D and H', these relationships with biodiversity indices are far from being a general phenomenon. The potential of using these indices for pelagic ciliate communities to assess spatial changes in phytoplankton biomass remains to be studied in the future. These findings suggest that structure parameters might be useful for determining environmental conditions in habitats and understanding relationships between pelagic ciliate communities and environmental conditions in the Southern Ocean. However, we only sampled pelagic communities in the Amundsen Sea during austral summer; further investigations of broad Antarctic regions over extended time periods are needed to provide further information and evidence.

Sea ice influences biodiversity and species distributions, and rapid melting of glaciers and losses of sea ice will result in changes in habitat conditions that may drive substantial changes in communities (Griffiths, 2010; Jiang et al., 2013c). To predict the impacts of these changes on ecosystems, understanding spatial distribution patterns within communities is important. Because of easy sampling, relative immobility, increasing availability of easily used taxonomic references, and standardization methods for temporal and spatial comparisons, ciliates have been widely used in ecological investigations (Jiang et al., 2013c). Although most species are cosmopolitan and have global distributions, and marine planktonic ciliates can be found almost anywhere with liquid water, different forms predominate in different habitats (Agatha, 2011). This may be an important and often overlooked approach to thinking about environmental variability in marine ecosystems, especially in the Southern Ocean, which is being increasingly affected by climate changes. However, to date, few studies have been published on the distribution of pelagic ciliates in the Amundsen Sea (Wickham et al., 2011). To our knowledge, this is the first report on variation in spatial patterns in community structure in relation to habitat conditions in the Amundsen Sea.

In the present case study, uni-/multivariate analyses all supplied positive evidence and sufficient information to reveal strong correlations between spatial or habitat variations in environmental conditions and those in ciliate communities. Thus, all of our results point to one conclusion: pelagic ciliate community structure accurately and effectively reflects habitat characteristics in the Amundsen Sea and can be used to investigate environmental heterogeneity over broad habitats.

In summary, the results of this study demonstrated that pelagic ciliate communities in the Amundsen Sea are diverse and dominated by 12 aloricate forms and show clear spatial patterns that can be divided among five habitats; also, variation in the ciliate community structure accurately reflects environmental variability. Furthermore, the primary environmental variables that describe ciliate community spatial variation or specific habitats, either alone or in combination were also supplied. Note that spatial variations of community structure or structure parameters both showed strong relationships with Chl *a*. Thus, our findings provide basic data and a better understanding of spatial variation in pelagic ciliates living in various habitats in the Amundsen Sea. These results have considerable potential to help answer questions of importance for polar research about the effects of increasing climate changes.

Acknowledgements

This work was supported by the Korea Polar Research Institute Project (KOPRI; PP 14020). Partial support was provided by grants from the K-PORT Program (KOPRI; PM13020) funded by the Ministry of Oceans and Fisheries, Korea. We thank the captain and crew of the Korean Research Icebreaker, *Araon*, for their outstanding assistance during the cruise; Dong-Jin Lee, for his great help with sampling, sample processing and data collection. We greatly appre-

ciate the constructive comments by three anonymous reviewers, which dramatically improve the quality of the manuscript.

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