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Short-term changes in a microplankton community in the Chukchi Sea during autumn: consequences of a strong wind event

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Abstract. Recent studies indicate an increase in atmospheric turbulence in the Chukchi Sea due to the recent drastic sea-ice reduction during summer months. The importance of the effects of this atmospheric turbulence on the marine ecosystem in this region, however, is not fully understood. To evaluate the effects of atmospheric turbulence on the marine ecosystem, high-frequency sampling (daily) from five layers of the microplankton community between 0 and 30 m at a fixed station in the Chukchi Sea from 10 through 25 September 2013 was conducted. During the study period, a strong wind event (SWE) was observed on 18 and 19 September. The abundance of microplankton was 2.6 to 17.6 cells mL^{−1}, with a maximum abundance being reported at 20 m on 22 September, while diatoms were the most dominant taxa throughout the study period. The abundance of diatoms, dinoflagellates and ciliates ranged between 1.6 and 14.1, 0.5 and 2.4 and 0.1 and 2.8 cells mL^{−1}, respectively. Diatoms belonging to 7 genera consisting of 35 species (*Cylindrotheca closterium* and *Leptocylindrus danicus* were dominant), dinoflagellates belonging to 7 genera consisting of 25 species (*Prorocentrum balticum* and *Gymnodinium* spp. were dominant) and ciliates belonging to 7 genera consisting of 8 species (*Strobilidium* spp. and *Strombidium* spp. were dominant) were identified. Within the microplankton species, there were 11 species with abundances that increased after the SWE, while there was no species with an abundance that decreased following the SWE. It is conjectured that at-

mospheric turbulences, such as that of an SWE, may supply sufficient nutrients to the surface layer that subsequently enhance the small bloom under the weak stratification of the Chukchi Sea Shelf during the autumn months. After the bloom, the dominant diatom community then shifts from centric-dominated to one where centric/pennate are more equal in abundance.

1 Introduction

In the marine ecosystem of the western Arctic Ocean, microplankton, including diatoms, dinoflagellates and ciliates, play several roles, such as primary producers, consumers and food resources for mesozooplankton (Sherr and Sherr, 1988, Sherr et al., 1997; Olson and Strom, 2002). The microplankton community in the western Arctic Ocean is divided into three groups – shelf, continental slope and basin (Sukhanova et al., 2009; Matsuno et al., 2014). As a special characteristic, during the summer, the development of pycnocline prevents the supply of nutrients to the surface layer, and phytoplankton (as determined by chlorophyll *a*) form a maximum subsurface layer that may be between 20 and 30 m in depth (Hill and Cota, 2005; Sukhanova et al., 2009; Joo et al., 2012). With respect to the microplankton community on the shelf of the Chukchi Sea, diatoms are the dominant taxa both in abundance and biomass (Matsuno et

al., 2014; Yang et al., 2015). Regarding temporal changes in the microplankton community, seasonal comparisons with 3- to 4-month sampling intervals (Sukhanova et al., 2009) and year-round changes with 8-day intervals were reported (Sherr et al., 2003). As microplankton grow rapidly (Strom and Fredrickson, 2008; Sherr et al., 2009), fine temporal resolution (every day) is required to evaluate detailed temporal changes in their community. However, such high-frequency sampling of microplankton has not been conducted previously.

In recent years, a drastic decrease in sea ice has been reported for the western Arctic Ocean during the summer months, and even greater related changes in sea surface temperatures have been reported (Stroeve et al., 2007; Steele et al., 2008). The changes in sea surface temperatures, increases in the frequency and intensity of cyclones, and northward shifts from their tracks during the summer months as well as during other seasons have also been reported (Serreze et al., 2000; McCabe et al., 2001; Sepp and Jaagus, 2011). While these changes are important, little is known about the effects of atmospheric and oceanic changes on the marine ecosystem in the western Arctic Ocean. During the period from 10 to 25 September 2013, high-frequency (daily) sampling and observations were conducted at a fixed station in the western Arctic Ocean, and the occurrence of strong wind events (SWEs), vertical flux of nutrients and changes in primary production were reported (Nishino et al., 2015). However, it is not clear how the microplankton assemblages – diatoms, dinoflagellates, ciliates – respond to the SWEs and the changes in nutrient supply and primary production.

In the present study, we evaluate short-term changes in the microplankton community in the Chukchi Sea during the autumn months by quantification of both autotrophic and heterotrophic microplankton assemblages – diatoms, dinoflagellates, ciliates – based on the samples collected during the same time frame as Nishino et al. (2015). Note that we only observed microplankton and did not quantify nano- and pico-plankton in this paper. We conducted a cluster analysis based on microplankton abundance and evaluated the effect of SWEs on microplankton assemblages under weak stratification in the Chukchi Sea due to atmospheric cooling during the autumn months.

2 Materials and methods

2.1 Field sampling

Water samples were collected from a fixed station in the Chukchi Sea (72°45' N, 168°15' W; depth 56 m) between 10 and 25 September 2013 (Fig. 1). At approximately 09:30 (local time) every day, 12 L of seawater was collected from depths of 0, 5, 10, 20 and 30 m using a rosette multi-sampler mounted on a CTD (Sea-Bird Electronics). A total of 80 samples were collected (16 days × 5 depths). Temperature and salinity were measured using CTD, and 1 L water samples

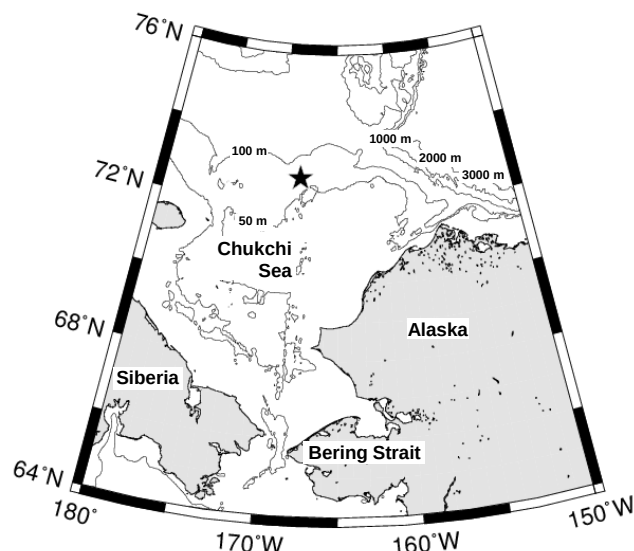


Figure 1. Location of the sampling station in the Chukchi Sea. Depth contours at 50, 100 and 1000 m are superimposed.

were preserved with 1 % glutaraldehyde and stored in a dark cold room. Nutrients (nitrate, nitrite, ammonium and silicic acid) were measured on 10 mL water samples using an auto-analyser (Bran + Luebbe GmbH, TRAACS-800). For each sample, duplicate 1 L seawater samples were filtered through a GF/F filter, and chlorophyll *a* (chl *a*) was measured with a fluorometer (Turner Design, Inc., 10-AU-005).

2.2 Microplankton analysis

In a land laboratory, 1 L preserved samples were concentrated to 18 mL with the settlement of microplankton cells at the bottom of the bottle, and a syphon was used to drain the clear water from the top. To obtain cell counts of diatoms and ciliates, subsamples (0.1 to 0.2 mL) were mounted on a glass slide and counted under an inverted microscope. For species identification, we referenced Hasle and Syvertsen (1997) and Hoppenrath et al. (2009) for diatoms and Maeda (1997) and Taniguchi (1997) for ciliates. To distinguish thecate and athecate forms for cell counts of dinoflagellates, after staining subsamples with calcofluor (1 mg mL⁻¹) for more than 1 h, subsamples (0.1 to 0.2 mL) were mounted on a glass slide and counted under an epifluorescence microscope with UV light excitation (Fritz and Triemer, 1985). For species identification of dinoflagellates, we referenced Fukuyo et al. (1997) and Hoppenrath et al. (2009). From each sample, we counted and identified cells that were larger than 10 µm. Because we did not check pigments in the cell, the nutrition of dinoflagellates (heterotrophs, autotrophs and mixotrophs) was not distinguishable in this study.

2.3 Statistical analysis

For cluster analysis, the abundance (X : cells L^{-1}) of diatoms was log-transformed ($\log_{10}[X+1]$) prior to the analysis to reduce any bias in abundances (Field et al., 1982). Similarities between samples were examined using the Bray–Curtis method (Bray and Curtis, 1957). To group the samples, similarity indices were coupled with hierarchical agglomerative clustering using a complete linkage method – the unweighted pair group method – using the arithmetic mean, UPGMA (Field et al., 1982). All analyses were performed using PRIMER v6 (PRIMER-E Ltd.). We evaluated differences in abundances of each species between groups using a one-way ANOVA and post hoc Tukey–Kramer tests. During the study period, a SWE was observed on approximately 19 to 22 September (Kawaguchi et al., 2015; Nishino et al., 2015). According to Kawaguchi et al. (2015), there were meteorologically and oceanographically distinct periods between 10 and 18 September and 19 and 26 September, represented as terms I and II, respectively. Term II was characterized by longer, stronger northeasterly winds, which continued for several days between 19 and 22 September, the average intensity of which was greater than 13 m s^{-1} . To evaluate the effect of the SWE, the abundances of each microplankton taxon and species were compared “before the SWE (10–18 September)” and “after the SWE (19–25 September)” using the U test. This statistical analysis was performed using StatView.

3 Results

3.1 Hydrography

Through the sampling period, temperatures ranged from -1.5 to 3.3°C (Fig. 2a). Cold water below 0°C was observed at depths below 20 m, and thermocline occurred at approximately 25 m. The temperatures in the upper thermocline decreased from 3 to 1.5°C during the study period. Salinity ranged from 31.0 to 32.7, and high-salinity water (>32) was observed at depths below 20 m. Halocline was observed at approximately 25 m, which paralleled that of the thermocline. Salinity in the upper halocline increased from 31.1 at the start of the sampling period (10 September) to 31.6 at the end of the sampling period (25 September) (Fig. 2b). From Sigma- T , the development of pycnocline was observed at approximately 20 to 30 m during the study period (Fig. 2c). DIN (dissolved inorganic nitrogen: $\text{NO}_3 + \text{NO}_2 + \text{NH}_4^+$) concentration ranged from 0.02 to $18.1 \mu\text{M}$, while the nutricline was observed at approximately 30 to 40 m (Fig. 2d). Silicates ranged from 0.5 to $32.3 \mu\text{M}$, and their nutricline was observed at approximately 40 to 50 m. Compared with DIN, silicate concentration was relatively higher ($>2 \mu\text{M}$ even at the surface layer) (Fig. 2e). Chl a ranged from 0.1 to $3.2 \mu\text{g L}^{-1}$, and relatively high chl a was observed at depths less than 30 m (Fig. 2f). After the

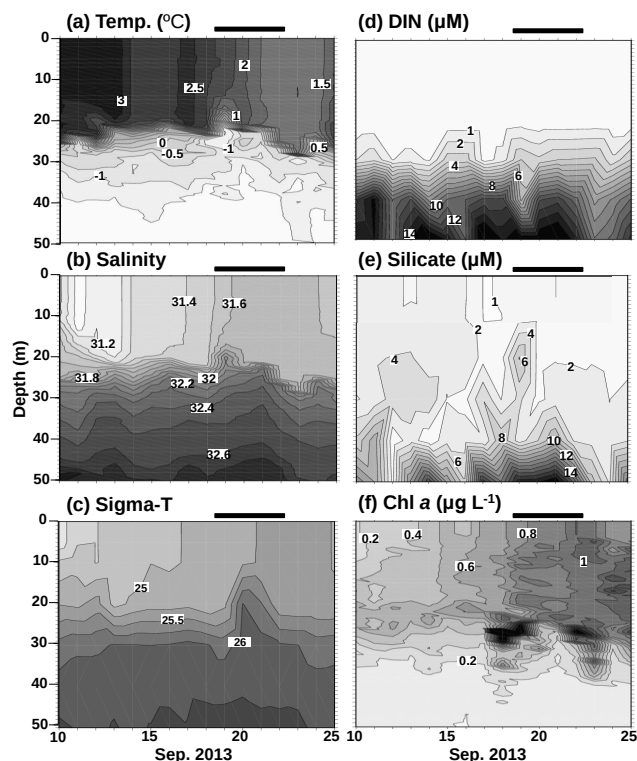


Figure 2. Temporal and vertical changes in temperature ($^\circ\text{C}$) (a), salinity (b), sigma- T (c), dissolved inorganic nitrogen (μM) (d), silicate (μM) (e) and chlorophyll a ($\mu\text{g L}^{-1}$) (f) at a fixed station in the Chukchi Sea between 10 and 25 September 2013. Solid bars indicate the timing of the strong wind event.

SWE, chl a increased in the upper 30 m and remained high until the end of the study period. It is notable that the sporadic high chl a was observed at approximately 25 m on 18, 19 and 22 September – the days following the SWE.

3.2 Microplankton assemblage

In the present study, diatoms belonging to 7 genera and 35 species, dinoflagellates belonging to 7 genera and 25 species, and ciliates belonging to 7 genera and 8 species were identified (Table 1). Within the microplankton species, 11 species increased in abundance after the SWE, while no species decreased in abundance after the SWE (Table 1).

3.3 Diatoms

The mean abundance of diatoms (0 to 30 m) ranged from 1.6 to $14.1 \text{ cells mL}^{-1}$. The dominant species for centric diatoms was *Leptocylindrus danicus*, while the dominant species for pennate diatoms was *Cylindrotheca closterium* (Fig. 3a). Centric diatoms showed a maximum abundance on 16 September (before the SWE) (Fig. 3b), while pennate diatoms increased in abundance throughout the water column after 20 September (after the SWE) (Fig. 3c). With

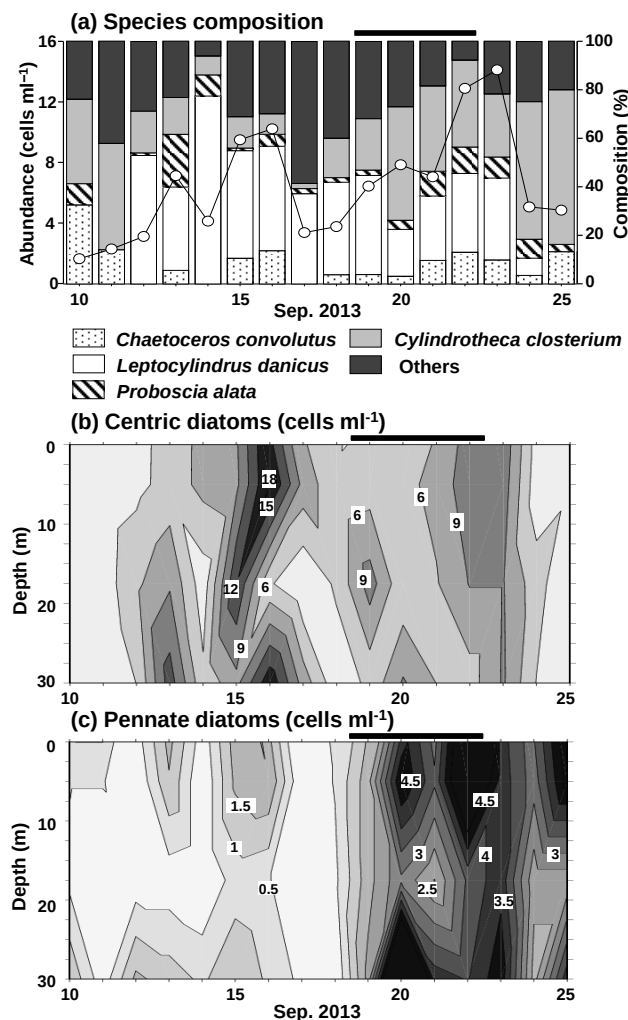


Figure 3. Temporal changes in cell density and species composition of total diatoms (a), the vertical distribution of centric diatoms (cells mL^{-1}) (b) and pennate diatoms (cells mL^{-1}) (c) in the Chukchi Sea during the period from 10 to 25 September 2013. In (a), values represent the mean of diatom abundance between 0 and 30 m. Solid bars indicate the timing of a strong wind event.

respect to the diatoms, five species increased in abundance after the SWE – *Chaetoceros furcellatus* (resting spore), *Dactyliosolen fragilissimus* and *Rhizosolenia* spp. for centric diatoms, and *Cylindrotheca closterium* and *Navicula* spp. for pennate diatoms (Table 1).

3.4 Dinoflagellates

The mean abundance of dinoflagellates (0 to 30 m) ranged from 0.5 to 2.4 cells mL^{-1} . The dominant species of thecate dinoflagellates was *Prorocentrum balticum* and *Gymnodinium* spp. for athecate dinoflagellates (Fig. 4a). Temporal changes in vertical distribution were similar for thecate and athecate dinoflagellates, with both exhibiting high abundance at 20 m on 15 September and at 5 m on 19 September

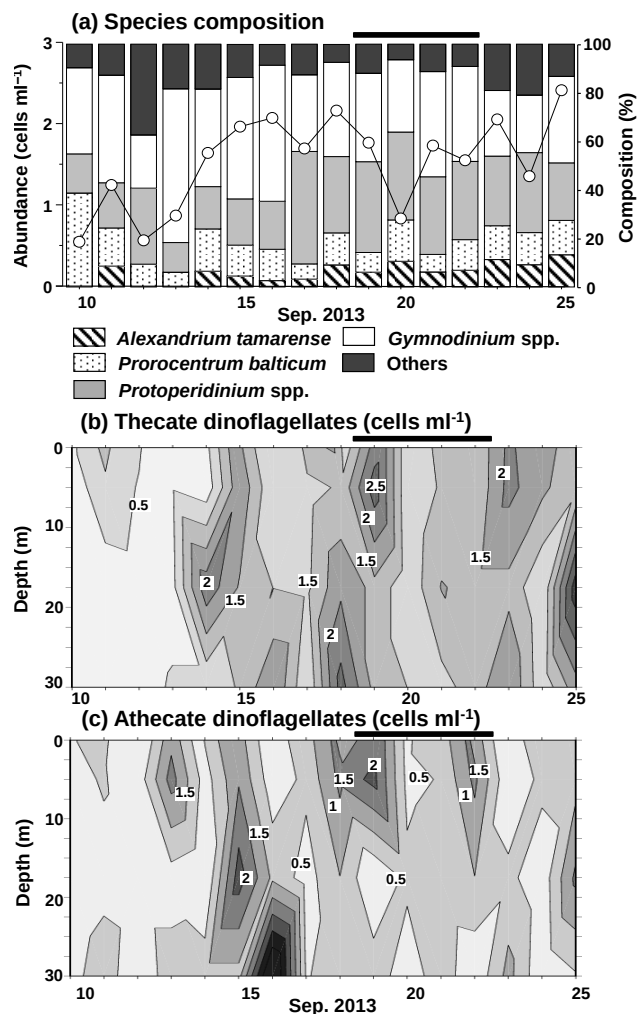


Figure 4. Temporal changes in cell density and species composition of total dinoflagellates (a), vertical distribution of thecate dinoflagellates (cells mL^{-1}) (b) and athecate dinoflagellates (cells mL^{-1}) (c) in the Chukchi Sea for the period from 10 to 25 September 2013. In (a), values represent the mean of dinoflagellate abundance between 0 and 30 m. Solid bars indicate the timing of a strong wind event.

(Fig. 4b, c). Five thecate dinoflagellate species increased in abundance after the SWE – *Alexandrium tamarens*, *Oxytoxum* sp. 2, *Protoperidinium bipes*, *P. conicum* and *P. pelucidum* (Table 1).

3.5 Ciliates

Mean abundance of ciliates (0 to 30 m) ranged from 0.1 to 2.8 cells mL^{-1} . The dominant species were the oligotrich ciliates *Strobilidium* spp. and *Strombidium* spp. (Fig. 5a). Temporal changes in vertical distribution varied between oligotrich and tintinnid ciliates. For oligotrich ciliates, high abundances were observed at 4-day intervals until 20 September (Fig. 5b). For tintinnid ciliates, high abundance was noted af-

Table 1. List of microplankton species and their mean cell densities (cells L⁻¹) at a single station in the Chukchi Sea between 10 and 18 September (before SWE) and 19 and 25 September (after SWE) 2013. NS: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Species	Before SWE (10–18 September)	After SWE (19–25 September)	U test
Centric diatoms			
<i>Chaetoceros affinis</i>	308	113	NS
<i>Chaetoceros borealis</i>	28	67	NS
<i>Chaetoceros compressus</i>	224	273	NS
<i>Chaetoceros convolutus</i>	120	237	NS
<i>Chaetoceros concavicornis</i>	424	730	NS
<i>Chaetoceros decipience</i>	52	77	NS
<i>Chaetoceros furcellatus</i> (resting spore)	12	252	**
<i>Chaetoceros laciniosus</i>	28	113	NS
<i>Chaetoceros</i> sp.	48	108	NS
<i>Dactyliosolen fragilissimus</i>		139	*
<i>Leptocylindrus danicus</i>	2068	2186	NS
<i>Leptocylindrus danicus</i> (resting spore)	84	5	NS
<i>Leptocylindrus minimus</i>	424	129	NS
<i>Proboscia alata</i>	316	617	NS
<i>Rhizosolenia borealis</i>	20	15	NS
<i>Rhizosolenia setigera</i>	172	118	NS
<i>Rhizosolenia</i> spp.		21	*
Pennate diatoms			
<i>Cylindrotheca closterium</i>	700	3111	***
<i>Navicula</i> spp.		15	*
Thecate dinoflagellates			
<i>Alexandrium tamarense</i>	68	157	*
<i>Ceratium horridum</i>		3	NS
<i>Gonyaulax scrippsae</i>	2	8	NS
<i>Gonyaulax</i> spp.	6	3	NS
<i>Oxytoxum</i> sp.1	98	72	NS
<i>Oxytoxum</i> sp.2	2	15	*
<i>Prorocentrum balticum</i>	192	203	NS
<i>Prorocentrum compressum</i>		5	NS
<i>Prorocentrum minimum</i>	16	36	NS
<i>Protoceratium reticulatum</i>	40	26	NS
<i>Protoperidinium avellanum</i>	68	95	NS
<i>Protoperidinium bipes</i>	56	177	**
<i>Protoperidinium conicum</i>		10	**
<i>Protoperidinium leonis</i>		3	NS
<i>Protoperidinium marukawai</i>	12	10	NS
<i>Protoperidinium mite</i>		3	NS
<i>Protoperidinium monovelum</i>	34	28	NS
<i>Protoperidinium pellucidum</i>		21	**
<i>Protoperidinium punctulatum</i>	96	90	NS
<i>Protoperidinium subinerme</i>	4	3	NS
<i>Protoperidinium thorianum</i>	76	80	NS
<i>Protoperidinium</i> sp.1	4	0	NS
<i>Protoperidinium</i> spp.	2	3	NS
<i>Scripsiella crystallina</i>	28	64	NS
Athecate dinoflagellates			
<i>Gymnodinium</i> spp.	628	573	NS
Oligotrich ciliates			
<i>Lohmanniella</i> spp.	16	21	NS
<i>Strobilidium</i> spp.	408	638	NS
<i>Strobilidium strobilum</i>	56	26	NS
<i>Strobilidium</i> spp.	720	962	NS
<i>Tontonia gracillima</i>	72	67	NS
Tintinnid ciliates			
<i>Parafavella denticulata</i>	4	0	NS
<i>Ptychocyclus obtusa</i>	12	57	*
<i>Tintinnopsis</i> sp.	8	0	NS

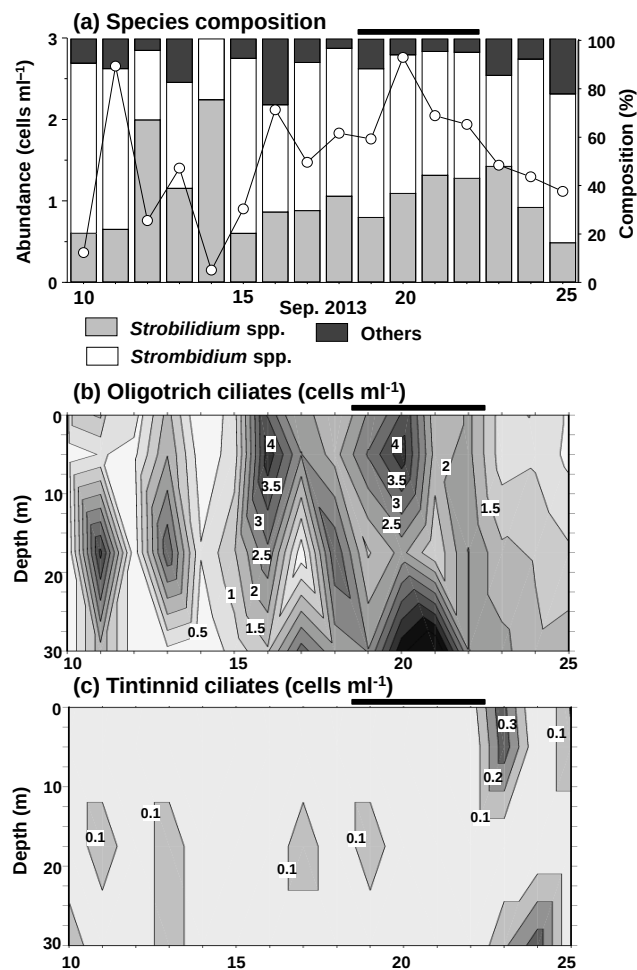


Figure 5. Temporal changes in cell density and species composition of total ciliates (a), the vertical distribution of oligotrich ciliates (cells mL^{-1}) (b) and tintinnid ciliates (cells mL^{-1}) (c) in the Chukchi Sea during the period from 10 to 25 September 2013. In (a), values represent the mean ciliate abundance between 0 and 30 m. Solid bars indicate the timing of a strong wind event.

ter 22 September (Fig. 5c). Only one ciliate species (tintinnid *Ptychocyclus obtusa*) increased in abundance after the SWE (Table 1).

3.6 Temporal and spatial changes in community structure

As a feature of microplankton assemblages in this study, diatoms were the dominant taxa (comprising 68.0 % of mean abundance). For dinoflagellates, the proportion of the autotrophic species (such as *P. balticum* and *A. tamarens*) was low, while that of the heterotrophic species (such as *Protoperdinium* spp. and *Gymnodinium* spp.) was high (Table 1). With this in mind, we conducted a cluster analysis based on the abundance of diatoms. For other taxa (dinoflag-

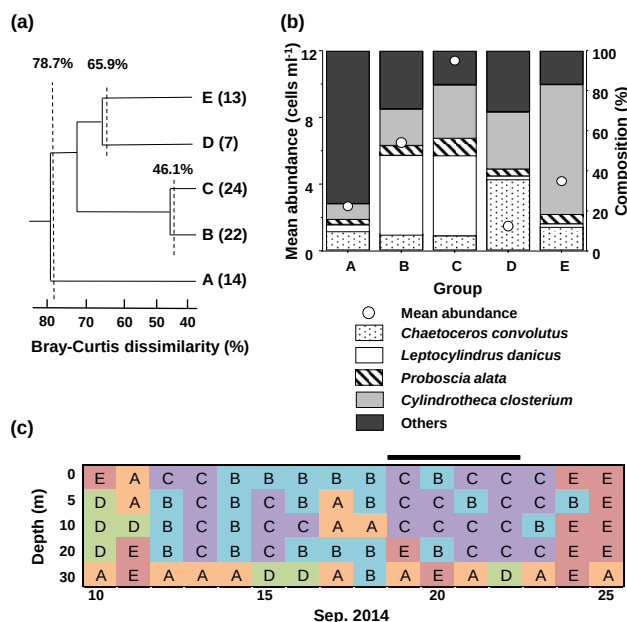


Figure 6. (a) Results of cluster analysis based on diatom cell density in the Chukchi Sea from 10 to 25 September 2013. Five groups (A to E) were identified at 46 to 78 % Bray-Curtis dissimilarity connected using UPGMA. Numbers in parentheses indicate the number of samples in each group. (b) Mean abundance and species composition of each group. (c) Vertical and temporal distribution of each group. Solid bar in (C) indicates the timing of a strong wind event.

ellates and ciliates), their communities were evaluated based on the relationship with communities of diatoms.

A cluster analysis based on diatom abundance classified their community into five groups (A to E) at 46.1, 65.9 and 78.7 % dissimilarity levels (Fig. 6a). Each group contained between 7 and 24 samples. The highest abundance was observed for group C, followed by groups B, E, A and D. Group A exhibited no distinct dominant species, while groups B and C were dominated by *L. danicus* and *C. closterium*, and group E was dominated by *C. closterium* (Fig. 6b).

Comparisons between and among groups indicated that there were eight species with significantly different numbers from one group to another according to a one-way ANOVA, $p < 0.05$, as presented in Table 2. Compared to the other groups, group A had a higher abundance of the centric diatom *Chaetoceros* sp.; group B had a higher abundance of the thecate dinoflagellate *Protoperdinium reticulatum*; group C had a higher abundance of the centric diatom *L. danicus*, *L. minimus* and *P. alata*, the pennate diatom *C. closterium*, and the thecate dinoflagellate *P. bipes*; and group E had a higher abundance of the tintinnid ciliate *P. obtusa* (Table 2). No species were found to dominate group D.

With respect to temporal and vertical distribution of each group, group D dominated the water column on 10 September (Fig. 6c). From 12 to 18 September, group B dominated at the 0 to 20 m level in the water column, while other groups

Table 2. Mean cell densities (cells L⁻¹) of microplankton in each group identified by cluster analysis (cf. Fig. 6) in the Chukchi Sea between 10 and 25 September 2013. Numbers in parentheses indicate the number of samples included. Differences between groups were tested by one-way ANOVA and the Tukey–Kramer test. Any groups not connected by the underlines are significantly different ($p < 0.05$). NS: not significant; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Species	Group A (14)	B (22)	C (24)	D (7)	E (13)	One-way ANOVA	Tukey–Kramer test
Centric diatoms							
<i>Chaetoceros affinis</i>	475.7	458.2	45.0	0	0	NS	
<i>Chaetoceros borealis</i>	77.1	32.7	22.5	0	96.9	NS	
<i>Chaetoceros compressus</i>	77.1	343.6	457.5	0	0	NS	
<i>Chaetoceros concavicornis</i>	154.3	286.4	90.0	51.4	207.7	NS	
<i>Chaetoceros convolutus</i>	257.1	523.6	817.5	514.3	484.6	NS	
<i>Chaetoceros decipience</i>	38.6	81.8	112.5	0	0	NS	
<i>Chaetoceros furcellatus</i> (resting spore)	205.7	32.7	142.5	77.1	138.5	NS	
<i>Chaetoceros laciniosus</i>	25.7	90.0	120.0	0	0	NS	
<i>Chaetoceros</i> sp.	257.1	8.2	60.0	102.9	0	*	<u>B</u> <u>C</u> <u>D</u> <u>A</u>
<i>Dactyliosolen fragilissimus</i>	192.9	98.2	0	0	0	NS	
<i>Leptocylindrus danicus</i>	90.0	2593.6	4590.0	25.7	69.2	***	<u>D</u> <u>E</u> <u>A</u> <u>B</u> <u>C</u>
<i>Leptocylindrus danicus</i> (resting spore)	192.9	0	52.5	0	0	NS	
<i>Leptocylindrus minimus</i>	90.0	310.9	585.0	77.1	0	**	<u>E</u> <u>D</u> <u>A</u> <u>B</u> <u>C</u>
<i>Proboscia alata</i>	64.3	310.9	1050.0	51.4	193.8	***	<u>D</u> <u>A</u> <u>E</u> <u>B</u> <u>C</u>
<i>Rhizosolenia borealis</i>	12.9	8.2	30.0	25.7	13.8	NS	
<i>Rhizosolenia setigera</i>	205.7	90.0	180.0	102.9	152.3	NS	
<i>Rhizosolenia</i> spp.	12.9	8.2	7.5	0	13.8	NS	
Pennate diatoms							
<i>Cylindrotheca closterium</i>	205.7	1178.2	3060.0	411.4	2713.8	***	<u>A</u> <u>D</u> <u>B</u> <u>E</u> <u>C</u>
<i>Navicula</i> spp.	0	16.4	7.5	0	0	NS	
Thecate dinoflagellates							
<i>Alexandrium tamarense</i>	38.6	110.5	131.3	25.7	173.1	NS	
<i>Ceratium horridum</i>	0	0	0	0	6.9	NS	
<i>Gonyaulax scrippsae</i>	6.4	4.1	3.8	0	6.9	NS	
<i>Gonyaulax</i> spp.	0	12.3	0	0	6.9	NS	
<i>Oxytoxum</i> sp. 1	96.4	90.0	82.5	51.4	96.9	NS	
<i>Oxytoxum</i> sp. 2	0	4.1	7.5	0	27.7	NS	
<i>Prorocentrum balticum</i>	102.9	237.3	191.3	167.1	256.2	NS	
<i>Prorocentrum compressum</i>	6.4	0	3.8	0	0	NS	
<i>Prorocentrum minimum</i>	19.3	20.5	41.3	12.9	13.8	NS	
<i>Protoceratium reticulatum</i>	0	69.5	30.0	12.9	27.7	*	<u>D</u> <u>E</u> <u>C</u> <u>B</u>
<i>Protoperidinium avellandum</i>	45.0	98.2	105.0	12.9	76.2	NS	
<i>Protoperidinium bipes</i>	12.9	130.9	168.8	0	124.6	**	<u>A</u> <u>E</u> <u>B</u> <u>C</u>
<i>Protoperidinium conicum</i>	0	0	11.3	0	6.9	NS	
<i>Protoperidinium leonis</i>	0	0	3.8	0	0	NS	
<i>Protoperidinium marukawai</i>	0	24.5	7.5	0	13.8	NS	
<i>Protoperidinium mite</i>	0	0	3.8	0	0	NS	
<i>Protoperidinium monovelum</i>	19.3	61.4	33.8	0	6.9	NS	
<i>Protoperidinium pellucidum</i>	0	16.4	11.3	0	6.9	NS	
<i>Protoperidinium punctulatum</i>	25.7	143.2	97.5	0	124.6	NS	
<i>Protoperidinium subinermis</i>	0	8.2	0	12.9	0	NS	
<i>Protoperidinium thorianum</i>	12.9	106.4	82.5	51.4	103.8	NS	
<i>Protoperidinium</i> sp. 1	0	4.1	3.8	0	0	NS	
<i>Protoperidinium</i> spp.	0	4.1	0	0	6.9	NS	
<i>Scripsiella crystallina</i>	6.4	57.3	60.0	0	55.4	NS	
Athecate dinoflagellates							
<i>Gymnodinium</i> spp.	353.6	695.5	817.5	192.9	546.9	NS	
Oligotrich ciliates							
<i>Lohmanniella</i> spp.	12.9	8.2	30.0	25.7	13.8	NS	
<i>Strobilidium</i> spp.	360.0	515.5	757.5	308.6	304.6	NS	
<i>Strombidium strobilum</i>	0	0	105.0	51.4	41.5	NS	
<i>Strombidium</i> spp.	720.0	736.4	1087.5	180.0	955.4	NS	
<i>Tontonia gracillima</i>	64.3	49.1	135.0	0	27.7	NS	
Tintinnid ciliates							
<i>Parafavelladenticulata</i>	0	0	7.5	0	0	NS	
<i>Ptychocyclus obtusa</i>	12.9	16.4	30.0	0	96.9	*	<u>A</u> <u>B</u> <u>C</u> <u>E</u>
<i>Tintinnopsis</i> sp.	12.9	0	7.5	0	0	NS	

were observed to dominate on various occasions. For example, from 19 to 23 September, after the SWE, group C dominated the water column group. After that, group E was found to be dominant on 24 and 25 September. At the greatest depth, 30 m, group A was dominant throughout most of the study period.

4 Discussion

4.1 Characteristics of a microplankton community

To obtain information on the microplankton community in the Chukchi Sea, geographical changes in community structure during the summer months (Joo et al., 2012; Matsuno et al., 2014; Yang et al., 2015) as well as seasonal and horizontal changes in diatoms (Sukhanova et al., 2009) were recorded. Because the study region and season were comparable to those in Matsuno et al. (2014), we compared the characteristics of the microplankton community in this study. Matsuno et al. (2014) classified the microplankton community into five groups (A to E) based on abundance and concluded that the grouping was strongly correlated with the environmental parameters, which varied by water mass. When comparing the findings of this study with the environmental parameters of Matsuno et al. (2014), ranges of surface salinity (31.0–32.7) and chl *a* ($> 1 \mu\text{g L}^{-1}$) indicated that the microplankton community studied herein corresponds to group B of Matsuno et al. (2014). Matsuno et al.'s (2014) group had characteristics of high abundance (mean $31.0 \text{ cells mL}^{-1}$), a predominance of diatoms (78 % of mean total microplankton abundance), and the microplankton are found throughout the Chukchi Sea Shelf (Matsuno et al., 2014). In comparison with the Matsuno et al. (2014) results, our study found a slightly lower abundance (range 2.6 to $17.6 \text{ cells mL}^{-1}$) and lower diatom composition (65 %). The variations between the two studies may be related to the current study's late sampling period (10 to 25 September).

In the biomass base, Yang et al. (2015) divided the microplankton community in this region into three groups – the diatom-dominated eutrophic Chukchi Sea Shelf, the picoplankton-dominated oligotrophic Northwind Abyssal Plain and the picoplankton- and diatom-dominated Northwind Ridge. Comparing the classifications, the diatom-dominated microplankton community of this study may correspond to Yang et al.'s (2015) Chukchi Sea Shelf group. The dominant species of this study – the pennate diatom *C. closterium*, the thecate dinoflagellate *P. balticum*, the athecate dinoflagellate *Gymnodinium* spp. and the oligotrich *Strombidium* spp. – are all species that have been listed as important and that are characterized in Matsuno et al.'s (2014) groups.

With respect to seasonal changes, diatoms ($> 5 \mu\text{m}$) and haptophytes dominated during the spring months, while small prasinophytes, larger haptophytes and diatoms dominated beneath the nitrate-depleted surface layer during the

summer months (Hill et al., 2005). As important species during the summer, *Chaetoceros* spp., *Thalassiosira* spp., *Fragilaria* sp. and *Fragilariopsis* sp. were reported to dominate at the chl *a* maximum layer (Booth and Horner, 1997; Coupel et al., 2012). In the autumn months, prasinophytes, which adapt to low temperatures, short daylight hours and an oligotrophic environment, were found to dominate (Lovejoy et al., 2007). At the ice-free surface layer without light limitations, due to the nutrient depletion at the surface layer, phytoplankton, mainly diatoms, are known to exist in the subsurface layer at a maximum depth of 20–30 m (Cota et al., 1996; Hill and Cota, 2005; Sukhanova et al., 2009; Joo et al., 2012). In the present study, nutrient (DIN and silicate) depletion and the occurrence of the sporadic subsurface chl *a* maximum corresponded well to the aforementioned studies (Fig. 2d, f). During winter months, diatoms ($> 20 \mu\text{m}$) and pigmented dinoflagellates were less than 1 cell mL^{-1} and ciliates (mostly oligotrich) ranged from 0.1 to 2 cells mL^{-1} (Sherr et al., 2003).

Compared with these seasonal patterns, the subsurface chl *a* maximum in the present study corresponded to the characteristics from summer to autumn, while the low abundance and dominant species of dinoflagellates and ciliates are similar to the characteristics exhibited during the winter. Given the occurrence of resting spores of diatoms, as referenced in this study (Table 1), the seasonal succession of the microplankton species and community from summer to winter began during the study period.

4.2 Short-term changes in the microplankton community

The hydrographic condition of the Arctic Ocean means that low salinity occurs at the surface layer due to the melting of sea ice during the summer months, while high salinity is the result of brine, which occurs during the formation of sea ice during winter months (Macdonald et al., 2002; Nishino et al., 2011). Throughout the study period, sea surface temperatures decreased while salinity gradually increased (Fig. 2). These environmental changes may result from the following processes – atmospheric cooling during autumn induces high-density sea surface water and weakens the density of the pycnocline layer, which then promotes the mixing of the cold and the saline deep water. From 10 to 14 September, less saline ice-melt water was found in the surface layer, the pycnocline layer formed at approximately 25 m, and nutrient-rich and saline Pacific summer water was found beneath the ice-melt water (Fig. 2c) (Nishino et al., 2015). It was noted that the SWE, which was observed from 18 to 19 September, temporally weakened the pycnocline layer, thus causing vertical mixing to occur, which then resulted in the supply of rich nutrients to the surface layer (Nishino et al., 2015).

A schematic diagram of short-term changes in the microplankton community and the dominant species during the study (10 to 25 September) is presented in Fig. 7. Based on

the dominant species and community structure during the study period, the microplankton community was classified into five phases, each of which occurred at 2- to 5-day intervals. Thus, from 10 to 14 September, the abundance of most species as well as the levels of chl *a* were low, possibly due to the warm, low-saline ice-melt water (phase 1). On 15 and 16 September, the abundance of the centric diatoms *C. convolutus* and *L. danicus* increased (phase 2). This sudden increase in diatom abundance in phase 2, which exceeded the range reported for diatom growth ($0.35\text{--}0.4\text{ day}^{-1}$) in this region (Strom and Fredrickson, 2008; Sherr et al., 2009), could not be explained by cell division growth within the same water masses. Accordingly, as an alternative cause, Nishino et al. (2015) reported that the displacement of the ice-melt seawater during this period caused the horizontal movement of water masses, which, in turn, may have led to the sudden increase in diatoms during this phase.

On 17 and 18 September, diatom abundance decreased, while there was an increase in the thecate dinoflagellate *A. tamarensis*, *P. balticum*, *Protoperidinium* spp., the athecate dinoflagellate *Gymnodinium* spp., and the oligotrich ciliates *Strobilidium* spp. and *Strombidium* spp. (Fig. 7). Within these species, the heterotrophic *Gymnodinium* spp. and *Protoperidinium* spp. are known to prey on diatoms and, thus, strongly regulate the phytoplankton community (Olson and Strom, 2002). Therefore, these increases in microzooplankton and the decrease in diatoms may be caused by microzooplankton grazing on diatoms.

In phase 3, 18 and 19 September, the SWE occurred (Nishino et al., 2015). Effects of the SWE included a decrease in temperature and an increase in salinity and chl *a* (Fig. 7). The dominant microplankton group also changed to group C, which was characterized by the high abundance of the majority of the species (Fig. 6b). Interestingly, chl *a* almost doubled from phase 2 to 3, while the abundance of diatoms (primary autotrophic taxa) increased only slightly during this phase. According to Onodera and Nishino (2014), the discrepancy between chl *a* and diatom abundance may be caused by the time lag in the physiological response of diatoms to the supply of nutrients. That is, diatoms may first use added nutrients from the increase in chl *a* pigment within the cell and then perform cell division, which is delayed due to the increase in chl *a*, within 3 to 4 days (Fig. 7). An additional characteristic of phase 3 was the remarkable and substantial increase in the abundance of oligotrich ciliates *Strobilidium* spp. and *Strombidium* spp. It is well known that the growth rate of heterotrophic microprotists varies with taxa. For example, the oligotrich ciliates grow faster than do the dinoflagellates (Hansen and Jensen, 2000). Thus, the oligotrich ciliates may respond more quickly than the dinoflagellates to an increase in autotrophs, an event that enhances the supply of nutrients caused by the SWE.

From 22 to 23 September, most of the microplankton species increased in abundance and formed a small bloom (phase 4). As a characteristic of this small bloom, the abun-

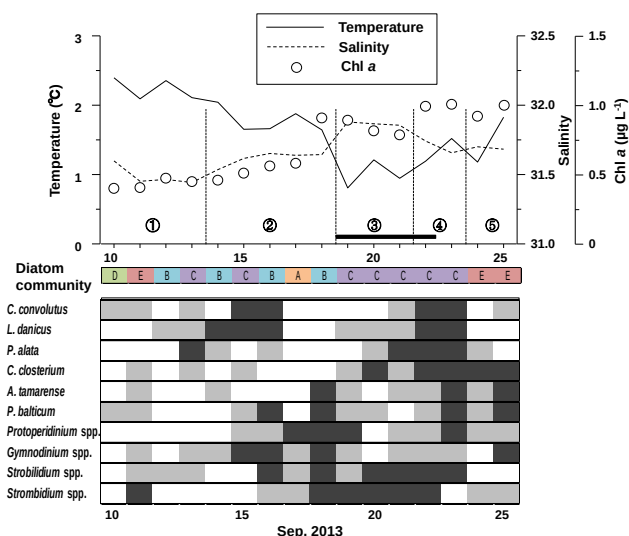


Figure 7. Schematic diagram of temporal changes in environmental parameters (upper panel), diatom community (middle bar) and abundance of dominant microplanktonic species (lower panel) at a water column of a single station in the Chukchi Sea from 10 to 25 September 2013. Values of the upper panel indicate integrated mean data. The solid bar indicates the timing of a strong wind event. Black, grey and white in the lower panel indicate relative abundance – high, middle and low, respectively – of each species in a 0 to 30 m column of water. Based on a dominant community and species, temporal changes in a microprotist community were divided into five phases, which are indicated by the circled numbers (1 to 5) and dashed lines in the upper panel. For details, see text.

dance of the pennate diatom *C. closterium* increased dramatically. While pennate diatoms were very low in abundance before the SWE, they increased significantly after the SWE (Fig. 3c, Table 1). This increase in pennate diatoms may imply that they respond to the supply of nutrients from the deeper layer through the pycnocline layer after the SWE (Alcoverro et al., 2000).

From 24 to 25 September, the dominant microplankton group shifted to group E, which is characterized by a high abundance of *C. closterium*, a diatom frequently observed in sea ice (Booth and Horner, 1997). Because of the nutrient depletion after the bloom, centric diatoms such as *L. danicus* may have formed resting spores (Davis et al., 1980) and sunk, thus causing the shift in dominant taxa from centric diatoms to pennate diatoms by the end of this study (phase 5). The microplankton community in the upper layer (0 to 20 m) demonstrated clear temporal changes within a 2- to 5-day interval. In contrast to the shallower layer, the microplankton community at the deepest sampling depth (30 m) was composed of groups A and D, both of which were characterized by low abundance throughout the study period (Fig. 6c). Because the pycnocline layer was observed at approximately 25 m (Fig. 2a–c), these two groups may form in that layer.

Throughout this study, it was revealed that atmospheric turbulence, such as SWE, may supply sufficient nutrients to the surface layer, which subsequently enhances a small bloom under the weak stratification of the Chukchi Sea Shelf during the autumn months. After the bloom, the dominant diatom community shifts from centric diatoms to pennate diatoms, thus suggesting that a SWE accelerates the seasonal succession of the microplankton community from summer to winter. Such a SWE-enhanced small bloom in autumn may be fed upon by copepods (*Calanus glacialis*) immediately (Matsuno et al., 2015). Thus, Matsuno et al. (2015) suggested that the temporal phytoplankton bloom caused by the atmospheric turbulence (SWE) during autumn may have had a positive indirect effect on the mesozooplankton (SWE → nutrient supply from the deep layer → small phytoplankton bloom → copepod feeding) within a short period.

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