# 1 Short-term changes in a microplankton community in the

# 2 Chukchi Sea during autumn: Consequences of a strong

## 3 wind event

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#### 15 Abstract

- 16 This report presents an increase in atmospheric turbulence in the Chukchi Sea due to the
- 17 recent drastic sea-ice reduction during summer months. The importance of the effects of this
- 18 atmospheric turbulence on the marine ecosystem in this region, however, is not fully
- 19 understood. To evaluate the effects of atmospheric turbulence on the marine ecosystem, high-
- 20 frequency sampling (daily) from five layers of the microplankton community between 0 and
- 21 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.
- 23 The abundance of microplankton was 2.6 to 17.6 cells ml<sup>-1</sup>, with a maximum abundance
- 24 being reported at 20 m on 22 September, while diatoms were the most dominant taxa
- 25 throughout the study period. The abundances of diatoms, dinoflagellates and ciliates ranged

between 1.6 and 14.1 cells ml<sup>-1</sup>, 0.5 and 2.4 cells ml<sup>-1</sup> and 0.1 and 2.8 cells ml<sup>-1</sup>, respectively. 1 Diatoms belonging to seven genera consisting of 35 species (Cylindrotheca closterium and 2 3 Leptocylindrus danicus were dominant), dinoflagellates belonging to seven genera consisting of 25 species (Prorocentrum balticum and Gymnodinium spp. were dominant) and ciliates 4 5 belonging to seven genera consisting of eight species (Strobilidium spp. and Strombidium spp. were dominant) were identified. Within the microplankton species, there were 11 species 6 7 with abundances that increased after the SWE, while there was no species with an abundance 8 that decreased following the SWE. It is conjectured that atmospheric turbulences, such as that 9 of an SWE, may supply sufficient nutrients to the surface layer that subsequently enhance the 10 small bloom under the weak stratification of the Chukchi Sea shelf during the autumn months. 11 After the bloom, the dominant diatom community then shifts from centric-dominated to one 12 where centric/pennate are more equal in abundance.

#### 1 Introduction

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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., in press). 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 timeframe 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,
- 24 depth 56 m) between 10 and 25 September 2013 (Fig. 1). At approximately 9:30 am (local
- 25 time) every day, 12 L of seawater was collected from depths of 0, 5, 10, 20 and 30 m using a
- 26 rosette multi-sampler mounted on a CTD (Sea-Bird Electronics). A total of 80 samples were
- 27 collected (16 days × 5 depths). Temperature and salinity were measured using CTD, and 1-L
- water samples 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 autoanalyser (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<sup>-1</sup>) for more than 1 hour, 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, so 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<sup>-1</sup>) of diatoms was log-transformed (Log<sub>10</sub>[*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-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<sup>-1</sup>. To evaluate the effect of the SWE, the

- abundances of each microplankton taxon and species were compared "before the SWE (10–18
- 2 September)" and "after the SWE (19–25 September)" using the U test. This statistical
- analysis was performed using StatView.

#### 4 3 Results

## 5 3.1 Hydrography

- 6 Through the sampling period, temperatures ranged from -1.5 to 3.3°C (Fig. 2a). Cold water
- 7 below 0°C was observed at depths below 20 m, and thermocline occurred at approximately 25
- 8 m. The temperatures in the upper thermocline decreased from 3 to 1.5°C during the study
- 9 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: NO<sub>3</sub>+ NO<sub>2</sub>+ NH<sub>4</sub><sup>+</sup>)
- 15 concentration ranged from 0.02 to 18.1 µM, while the nutricline was observed at
- approximately 30 to 40 m (Fig. 2d). Silicates ranged from 0.5 to 32.3 μM, and their nutricline
- was observed at approximately 40 to 50 m. Compared with DIN, silicate concentration was
- relatively higher (> 2  $\mu$ M even at the surface layer) (Fig. 2e). Chl. a ranged from 0.1 to 3.2
- 19  $\mu$ g L<sup>-1</sup>, and relatively high chl. a was observed at depths less than 30 m (Fig. 2f). After the
- SWE, chl. a increased in the upper 30 m and remained high until the end of the study period.
- 21 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

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

#### 3.3 Diatoms

- 2 The mean abundance of diatoms (0 to 30 m) ranged from 1.6 to 14.1 cells ml<sup>-1</sup>. The dominant
- 3 species for centric diatoms was Leptocylindrus danicus, while the dominant species for
- 4 pennate diatoms was Cylindrotheca closterium (Fig. 3a). Centric diatoms showed a
- 5 maximum abundance on 16 September (before the SWE) (Fig. 3b), while pennate diatoms
- 6 increased in abundance throughout the water column after 20 September (after the SWE) (Fig.
- 7 3c). With respect to the diatoms, 5 species increased in abundance after the SWE -
- 8 Chaetoceros furcellatus (resting spore), Dactyliosolen fragilissimus and Rhizosolenia spp. for
- 9 centric diatoms, and Cylindrotheca closterium and Navicula spp. for pennate diatoms (Table
- 10 1).

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## 3.4 Dinoflagellates

- The mean abundance of dinoflagellates (0 to 30 m) ranged from 0.5 to 2.4 cells ml<sup>-1</sup>. 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 (Fig. 4b, c). Five thecate dinoflagellate species
- 17 increased in abundance after the SWE Alexandrium tamarense, Oxytoxum sp. 2,
- 18 Protoperidinium bipes, P. conicum, and P. pellucidum (Table 1).

#### 19 **3.5 Ciliates**

- 20 Mean abundance of ciliates (0 to 30 m) ranged from 0.1 to 2.8 cells ml<sup>-1</sup>. The dominant
- 21 species were the oligotrich ciliates Strobilidium spp. and Strombidium spp. (Fig. 5a).
- 22 Temporal changes in vertical distribution varied between oligotrich and tintinnid ciliates. For
- 23 oligotrich ciliates, high abundances were observed at four-day intervals until 20 September
- 24 (Fig. 5b). For tintinnid ciliates, high abundance was noted after 22 September (Fig. 5c). Only
- one ciliate species (tintinnid *Ptychocylis obtusa*) increased in abundance after the SWE (Table
- 26 1).

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## 3.6 Temporal and spatial changes in community structure

- 28 As a feature of microplankton assemblages in this study, diatoms were the dominant taxa
- 29 (comprising 68.0% of mean abundance). For dinoflagellates, the proportion of the

- 1 autotrophic species (such as P. balticum and A. tamarense) was low, while that of the
- 2 heterotrophic species (such as *Protoperidinium* spp. and *Gymnodinium* spp.) was high (Table
- 3 1). With this in mind, we conducted a cluster analysis based on the abundance of diatoms.
- 4 For other taxa (dinoflagellates and ciliates), their communities were evaluated based on the
- 5 relationship with communities of diatoms.
- A cluster analysis based on diatom abundance classified their community into 5
- 7 groups (A to E) at 46.1, 65.9 and 78.7% dissimilarity levels (Fig. 6a). Each group contained
- 8 between 7 and 24 samples. The highest abundance was observed for group C, followed by
- 9 groups B, E, A and D. Group A exhibited no distinct dominant species, while groups B and C
- 10 were dominated by L. danicus and C. closterium, and group E was dominated by C.
- 11 *closterium* (Fig. 6b).
- 12 Comparisons between and among groups indicated that there were 8 species with
- significantly different numbers from one group to another according to a one-way ANOVA, p
- 14 < 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
- 16 thecate dinoflagellate Protoceratium reticulatum; group C had a higher abundance of the
- 17 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.*
- 19 *obtusa* (Table 2). No species were found to dominate group D.
- With respect to temporal and vertical distribution of each group, group D dominated
- 21 the water column on 10 September (Fig. 6c). From 12 to 18 September, group B dominated
- 22 at the 0 to 20 m level in the water column, while other groups were observed to dominate on
- various occasions. For example, from 19 to 23 September, after the SWE, group C dominated
- 24 the water column group. After that, group E was found to be dominant on 24 and 25
- 25 September. At the greatest depth, 30 m, group A was dominant throughout most of the study
- 26 period.

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## 4 Discussion

#### 4.1 Characteristics of a microplankton community

29 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., in press) 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 5 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.  $a > 1 \, \mu g \, L^{-1}$  indicated that the microplankton community studied herein corresponds with group B of Matsuno et al. (2014). Matsuno et al.'s (2014) group had characteristics of high abundance (mean 31.0 cells ml<sup>-1</sup>), a predominance of diatoms (78% of mean total microplankton abundance), and the microplankton are found throughout the Chukchi Sea shelf (Matsuno et al., 2014). Comparing with values, this study found a slightly lower abundance (range 2.6 to 17.6 cells ml<sup>-1</sup>) 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. (in press) divided the microplankton community in this region into 3 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 with Yang et al.'s 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 characterised in Matsuno et al.'s (2014) groups.

With respect to seasonal changes, diatoms (> 5 µm) 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

2 the subsurface layer at a maximum depth of 20–30 m (Cota et al., 1996; Hill and Cota, 2005;

3 Sukhanova et al., 2009; Joo et al., 2012). In the present study, nutrient (DIN and silicate)

4 depletion and the occurrence of the sporadic subsurface chl. a maximum corresponded well

with the aforementioned studies (Fig. 2d, f). During winter months, diatoms (> 20 µm) and

pigmented dinoflagellates were less than 1 cell ml<sup>-1</sup> and ciliates (mostly oligotrich) ranged

from 0.1 to 2 cells ml<sup>-1</sup> (Sherr et al., 2003).

Compared with these seasonal patterns, the subsurface chl. *a* maximum in the present study corresponded with 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 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 be the results of the following process - 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 5 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 1 2 low, possibly due to the warm, low saline ice-melt water (phase 1). On 15 and 16 September, 3 the abundance of the centric diatoms C. convolutes and L. danicus increased (phase 2). This 4 sudden increase in diatom abundance in phase 2, which exceeded the range reported for diatom growth (0.35–0.4 d<sup>-1</sup>) in this region (Strom and Fredrickson, 2008; Sherr et al., 2009), 5 could not be explained by cell division growth within the same water masses. Accordingly, as 6 7 an alternative cause, Nishino et al. (2015) reported that the displacement of the ice-melt 8 seawater during this period caused the horizontal movement of water masses, which, in turn, 9 may have led to the sudden increase in diatoms during this phase.

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On 17 and 18 September, diatom abundance decreased while there was an increase in the thecate dinoflagellate *A. tamarense*, *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 abundance 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 characterised 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 sank, 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 characterised by low abundance throughout the study period (Fig. 6c). Because the pycnocline layer was observed at approximately 25 m (Fig. 2a, b, 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 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.

#### **Authors' contributions**

S.N., J.I. and T.K. designed and coordinated this research project. S.N. and J.I. were chief scientists during the MR13-06 cruise of R.V. *Mirai*. K.M. collected the water samples during the cruise. N.Y. conducted species identification and the enumeration of the microplankton

- samples in the land laboratory. M.I. and J.O. gave variable comments to analyse the
- 2 microplankton community. N.Y. and A.Y. wrote the manuscript with contributions from all
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#### References

- 2 Alcoverro, T., Conte, E., and Mazzella, L.: Production of mucilage by the Adriatic epipelic
- diatom Cylindrotheca closterium (Bacillariophyceae) under nutrient limitation, J.
- 4 Phycol., 36, 1087–1095, doi:10.1046/j.1529-8817.2000.99193.x, 2000.
- 5 Booth, B. C. and Horner, R. A.: Microalgae on the Arctic Ocean section, 1994: Species
- 6 abundance and biomass, Deep-Sea Res. II, 44, 1607–1622, doi:10.1016/S0967-
- 7 0645(97)00057-X, 1997.
- 8 Cota, G. F., Pomeroy, L. R., Harrison, W. G., Jones, E. P., Peters, F., Sheldon, W. J., and
- 9 Weingartner, T. R.: Nutrients, primary production and microbial heterotrophy in the
- southeastern Chukchi Sea: Arctic summer nutrient depletion and heterotrophy, Mar.
- Ecol. Prog. Ser., 135, 247–258, doi:10.3354/meps135247, 1996.
- 12 Coupel, P., Jin, H. Y., Joo, M., Horner, R., Bouvet, H. A., Sicre, M., and Ruiz-Pino, D.:
- Phytoplankton distribution in unusually low sea ice cover over the Pacific Arctic,
- Biogeosciences, 9, 4835–4850, doi:10.5194/bg-9-4835-2012, 2012.
- Davis, C. O., Hollibaugh, J. T., Seibert, D. L., Thomas, W. H., and Harrison, P. J.: Formation
- of resting spores by Leptocylindrus danicus (Bacillariophyceae) in a controlled
- 17 experimental ecosystem, J. Phycol., 16, 296–302, doi:10.1111/j.1529-
- 18 8817.1980.tb03034.x, 1980.
- 19 Field, J. G., Clarke, K. R., and Warwick, R. M.: A practical strategy for analyzing
- 20 multispecies distribution patterns, Mar. Ecol. Prog. Ser., 8, 37–52,
- 21 doi:10.3354/meps008037, 1982.
- Fritz, L. and Triemer, R. E.: A rapid simple technique utilizing Calcofluor white M2R for the
- visualization of dinoflagellate thecal plates, J. Phycol., 21, 662-664,
- 24 doi:10.1111/j.0022-3646.1985.00662.x, 1985.
- Fukuyo, Y., Inoue, H., and Takayama, H.: Class Dinophyceae, In: An illustrated guide to
- marine plankton in Japan, edited by: Chihara, M., Murano, M., Tokai University
- 27 Press, Tokyo, Japan, 31–112, 1997.
- Hansen, B. W. and Jensen, F.: Specific growth rates of protozooplankton in the marginal ice
- zone of the central Barents Sea during spring, J. Mar. Biol. Ass. U.K., 80, 37–44,
- 30 doi:10.1017/S002531549900154X, 2000.

- 1 Hasle, G. R. and Syvertsen, E. E.: Marine diatoms, In: Identifying marine phytoplankton,
- edited by: Tomas, C. R., Academic Press, San Diego, USA, 5–385, 1997.
- 3 Hill, V. and Cota, G.: Spatial patterns of primary production on the shelf, slope and basin of
- 4 the western Arctic in 2002, Deep-Sea Res. II, 52, 3344–3354,
- 5 doi:10.1016/j.dsr2.2005.10.001, 2005.
- 6 Hill, V., Cota, G., and Stockwell, D.: Spring and summer phytoplankton communities in the
- 7 Chukchi and eastern Beaufort Seas, Deep-Sea Res. II, 52, 3369-3385,
- 8 doi:10.1016/j.dsr2.2005.10.010, 2005.
- 9 Hoppenrath, M., Elbrächter, M., and Drebes, G. (Eds): Marine phytoplankton, E.
- Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany, 264 pp., 2009.
- Joo, H. M., Lee, S. H., Jung, S. W., Dahms, H., and Lee, J. H.: Latitudinal variation of
- phytoplankton communities in the western Arctic Ocean, Deep-Sea Res. II, 81–84, 3-
- 13 17, doi:10.1016/j.dsr2.2011.06.004, 2012.
- 14 Kawaguchi, Y., Nishono, S. and Inoue, J.: Fixed-point observation of mixed layer evolution
- in the seasonally ice-free Chukchi Sea: turbulent mixing due to gale winds and
- gravity waves, J. Phys. Oceanogr., 45, 836–853, doi:10.1175/JPO-D-14-0149.1,
- 17 2015.
- Lovejoy, C., Legendre, L., Martineau, M. J., Bâcle, J., and von Quillfeldt, C. H.: Distribution,
- phylogeny, and growth of cold-adapted picoprasinophytes in Arctic Seas, J. Phycol.,
- 20 43, 78–89, doi:10.1111/j.1529-8817.2006.00310.x, 2007.
- 21 Macdonald, R. W., McLaughlin, F. A., and Carmack, E. C.: Fresh water and its sources
- during the SHEBA drift in the Canada Basin of the Arctic Ocean, Deep-Sea Res. I,
- 23 49, 1769–1785, doi:10.1016/S0967-0637(02)00097-3, 2002.
- 24 Maeda, M.: Suborder Oligotrichida, In: An illustrated guide to marine plankton in Japan,
- edited by: Chihara, M., Murano, M., Tokyo University Press, Tokyo, Japan, 397–420,
- 26 1997.
- 27 Matsuno, K., Ichinomiya, M., Yamaguchi, A., Imai, I., and Kikuchi, T.: Horizontal
- distribution of microprotist community structure in the western Arctic Ocean during
- 29 late summer and early fall of 2010, Polar Biol., 37, 1185–1195, doi:10.1007/s00300-
- 30 014-1512-z, 2014.

- 1 Matsuno, K., Yamaguchi, A., Nishino, S., Inoue J. and Kikuchi T.: Short-term changes in the
- 2 mesozooplankton community and copepod gut pigment in the Chukchi Sea in
- autumn: reflections of a strong wind event, Biobeosciences 12, 4005-4015,
- 4 doi:10.5194/bg-12-4005-2015, 2015.
- 5 McCabe, G. J., Clark, M. P., and Serreze, M. C.: Trends in northern hemisphere surface
- 6 cyclone frequency and intensity, J. Clim., 14, 2763-2768, doi:10.1175/1520-
- 7 0442(2001)014<2763:TINHSC>2.0.CO;2, 2001.
- 8 Nishino, S., Itoh, M., Kawaguchi, Y., Kikuchi, T., and Aoyama, M.: Impact of an unusually
- 9 large warm-core eddy on distributions of nutrients and phytoplankton in the
- southwestern Canada Basin during late summer/early fall 2010, Geophys. Res. Lett.,
- 38, L16602, doi:10.1029/2011GL047885, 2011.
- 12 Nishino, S., Kawaguchi, Y., Inoue, J., Hirawake, T., Fujiwara, A., Futsuki, R., Onodera, J.,
- and Aoyama, M.: Nutrient supply and biological response to wind-induced mixing,
- intertial motion, and currents in the northern Chukchi Sea, J. Geophys. Res., C, 20,
- 15 1975–1992, doi:10.1002/2014JC010407, 2015.
- Olson, M. B. and Strom, S. L.: Phytoplankton growth, microzooplankton herbivory and
- 17 community structure in the southeast Bering Sea: Insight into the formation and
- temporal persistence of an Emiliania huxleyi bloom, Deep-Sea Res. II, 49, 5969–
- 19 5990, doi:10.1016/S0967-0645(02)00329-6, 2002.
- 20 Onodera, J. and Nishino, S.: Fixed-point observation of diatom biocoenosis and water mass
- 21 condition in the Northern Chukchi Sea during September 2013. JpGU Meeting 2014,
- 22 Abstract, ACG36-P20, 2014.
- Sepp, M. and Jaagus, J.: Changes in the activity and tracks of arctic cyclones, Clim. Change,
- 24 105, 577–595, doi:10.1007/s10584-010-9893-7, 2011.
- 25 Serreze, M. C., Walsh, J. E., Chapin III, F., Osterkamp, T., Dyurgerov, M., Romanovsky, V.,
- and Barry, R. G.: Observational evidence of recent change in the northern high-
- 27 latitude environment, Clim. Change, 46, 159–207, doi:10.1023/A:1005504031923,
- 28 2000.
- 29 Sherr, E. and Sherr, B.: Role of microbes in pelagic food webs: A revised concept, Limnol.
- 30 Oceanogr., 33, 1225–1227, doi:10.4319/lo.1988.33.5.1225, 1988.

- 1 Sherr, E. B., Sherr, B. F., and Fessenden, L.: Heterotrophic protists in the central Arctic
- Ocean, Deep-Sea Res. II, 44, 1665–1682, doi:10.1016/S0967-0645(97)00050-7,
- 3 1997.
- 4 Sherr, E. B., Sherr, B. F., Wheeler, P. A., and Thompson, K.: Temporal and spatial variation
- 5 in stocks of autotrophic and heterotrophic microbes in the upper water column of the
- 6 central Arctic Ocean, Deep-Sea Res. I, 50, 557–571, doi:10.1016/S0967-
- 7 0637(03)00031-1, 2003.
- 8 Sherr, E. B., Sherr, B. F., and Hartz, A. J.: Microzooplankton grazing impact in the western
- 9 Arctic Ocean, Deep-Sea Res. II, 56, 1264–1273, doi:10.1016/j.dsr2.2008.10.036,
- 10 2009.
- Steele, M., Ermold, W., and Zhang, J.: Arctic Ocean surface warming trends over the past 100
- 12 years, Geophys. Res. Lett., 35, L02614, doi:10.1029/2007GL031651, 2008.
- 13 Stroeve, J., Marika, M. H., Walt, M., Ted, S., and Mark, S.: Arctic sea ice decline!: Faster
- than forecast?, Geophys. Res. Lett., 34, L09501, doi:10.1029/2007GL029703, 2007.
- 15 Strom, S. L. and Fredrickson, K. A.: Intense stratification leads to phytoplankton nutrient
- limitation and reduced microzooplankton grazing in the southeastern Bering Sea,
- 17 Deep-Sea Res. II, 55, 1761–1774, doi:10.1016/j.dsr2.2008.04.008, 2008.
- Sukhanova, I. N., Flint, M. V., Pautova, L. A., Stockwell, D. A., Grebmeier, J. M., and
- 19 Sergeeva, V. M.: Phytoplankton of the western Arctic in the spring and summer of
- 20 2002: Structure and seasonal changes, Deep-Sea Res. II, 56, 1223–1236,
- 21 doi:10.1016/j.dsr2.2008.12.030, 2009.
- 22 Taniguchi, A.: Suborder Tintinnina, In: An illustrated guide to marine plankton in Japan,
- edited by: Chihara, M., Murano, M., Tokai University Press, Tokyo, Japan, 421–483,
- 24 1997.
- 25 Yang, E. J., Ha, H. K., and Kang, S.: Microzooplankton community structure and grazing
- impact on major phytoplankton in the Chukchi Sea and the western Canada Basin,
- 27 Arctic Ocean, Deep-Sea Res. II, in press.

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- Figure 1. Location of the sampling station in the Chukchi Sea. Depth contours at 50, 100 and 1000 m are superimposed.
- Figure 2. Temporal and vertical changes in temperature (°C) (a), salinity (b), sigma-T (c), dissolved inorganic nitrogen (μM) (d), silicate (μM) (e) and chlorophyll *a* (μg L<sup>-1</sup>) (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.
- Figure 3. Temporal changes in cell density and species composition of total diatoms (a), the vertical distribution of centric diatoms (cells ml<sup>-1</sup>) (b) and pennate diatoms (cells ml<sup>-1</sup>) (c) in the Chukchi Sea during the period 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.
  - **Figure 4.** Temporal changes in cell density and species composition of total dinoflagellates (a), vertical distribution of thecate dinoflagellates (cells ml<sup>-1</sup>) (b) and athecate dinoflagellates (cells ml<sup>-1</sup>) (c) in the Chukchi Sea for the period 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.
  - **Figure 5.** Temporal changes in cell density and species composition of total ciliates (a), the vertical distribution of oligotrich ciliates (cells ml<sup>-1</sup>) (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.
- 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% BrayCurtis 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.
  - **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.

**Table 1.** List of microplankton species and their mean cell densities (cells L<sup>-1</sup>) 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.

Chesics	Before SWE	After SWE	
Species	(10–18 Sep.)	(19–25 Sep.)	U-test
Centric diatoms			
Chaetoceros affinis	308	113	NS
Chaetoceros borealis	28	67	NS
Chaetoceros compressus	224	273	NS
Chaetoceros convolutus	120	237	NS
Chaetoceros concavicornis	424	730	NS
Chaetoceros decipience	52	77	NS
Chaetoceros furcellatus (resting spore)	12	252	**
Chaetoceros laciniosus	28	113	NS
Chaetoceros sp.	48	108	NS
Dactyliosolen fragilissimus	0	139	*
Leptocylindrus danicus	2068	2186	NS
Leptocylindrus danicus (resting spore)	84	5	NS
Leptocylindrus minimus	424	129	NS
Proboscia alata	316	617	NS
Rhizosolenia borealis	20	15	NS
Rhizosolenia setigera	172	118	NS
Rhizosolenia spp.	0	21	*
Pennate diatoms			
Cylindrotheca closterium	700	3111	***
Navicula spp.	0	15	*
Thecate dinoflagellates			
Alexandrium tamarense	68	157	*
Ceratium horridum	0	3	NS
Gonyaulax scrippsae	2	8	NS
Gonyaulax spp.	6	3	NS
Oxytoxum sp.1	98	72	NS
Oxytoxum sp.2	2	15	*
Prorocentrum balticum	192	203	NS
Prorocentrum compressum	0	5	NS
Prorocentrum minimum	16	36	NS
Protoceratium reticulatum	40	26	NS
Protoperidinium avellanum	68	95	NS
Protoperidinium bipes	56	177	**
Protoperidinium conicum	0	10	**
Protoperidinium leonis	0	3	NS
Protoperidinium marukawai	12	10	NS

Protoperidinium mite	0	3	NS
Protoperidinium monovelum	34	28	NS
Protoperidinium pellucidum	0	21	**
Protoperidinium punctulatum	96	90	NS
Protoperidinium subinerme	4	3	NS
Protoperidinium thorianum	76	80	NS
Protoperidinium sp.1	4	0	NS
Protoperidinium spp.	2	3	NS
Scripsiella crystallina	28	64	NS
Athecate dinoflagellates			
Gymnodinium spp.	628	573	NS
Oligotrich ciliates			
Lohmanniella spp.	16	21	NS
Strobilidium spp.	408	638	NS
Strombidium strobilum	56	26	NS
Strombidium spp.	720	962	NS
Tontonia gracillima	72	67	NS
Tintinnid ciliates			
Parafavella denticulata	4	0	NS
Ptychocylis obtusa	12	57	*
Tintinnopsis sp.	8	0	NS

Table 2. Mean cell densities (cells L<sup>-1</sup>) 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 number of samples included. Differences between groups were tested by one-way ANOVA and Tukey-Kramer tests. Any groups not connected by underlines are significantly different (p < 0.05). NS: not significant; \*: p < 0.05; \*\*: p < 0.01; \*\*\*: p < 0.001.

Species	Group					one-way	Tukey-Kramer test				
	A (14)	B (22)	C (24)	D (7)	E (13)	ANOVA		тикеу	-Kran	ier test	
Centric diatoms											
Chaetoceros affinis	475.7	458.2	45.0	0	0	NS					
Chaetoceros borealis	77.1	32.7	22.5	0	96.9	NS					
Chaetoceros compressus	77.1	343.6	457.5	0	0	NS					
Chaetoceros concavicornis	154.3	286.4	90.0	51.4	207.7	NS					
Chaetoceros convolutus	257.1	523.6	817.5	514.3	484.6	NS					
Chaetoceros decipience	38.6	81.8	112.5	0	0	NS					
Chaetoceros furcellatus (resting spore)	205.7	32.7	142.5	77.1	138.5	NS					
Chaetoceros laciniosus	25.7	90.0	120.0	0	0	NS					
Chaetoceros sp.	257.1	8.2	60.0	102.9	0	*		В	C	D	A
Dactyliosolen fragilissimus	192.9	98.2	0	0	0	NS					
Leptocylindrus danicus	90.0	2593.6	4590.0	25.7	69.2	***	D	E	A	В	C
Leptocylindrus danicus (resting spore)	192.9	0	52.5	0	0	NS					
Leptocylindrus minimus	90.0	310.9	585.0	77.1	0	**	E	D	A	В	C
Proboscia alata	64.3	310.9	1050.0	51.4	193.8	***	D	A	Е	В	C
Rhizosolenia borealis	12.9	8.2	30.0	25.7	13.8	NS				_	
Rhizosolenia setigera	205.7	90.0	180.0	102.9	152.3	NS					
Rhizosolenia spp.	12.9	8.2	7.5	0	13.8	NS					
Pennate diatoms											
Cylindrotheca closterium	205.7	1178.2	3060.0	411.4	2713.8	***	A	D	B	<u>E</u>	C
Navicula spp.	0	16.4	7.5	0	0	NS					
Thecate dinoflagellates											
Alexandrium tamarense	38.6	110.5	131.3	25.7	173.1	NS					
Ceratium horridum	0	0	0	0	6.9	NS					
Gonyaulax scrippsae	6.4	4.1	3.8	0	6.9	NS					
Gonyaulax spp.	0	12.3	0	0	6.9	NS					
Oxytoxum sp. 1	96.4	90.0	82.5	51.4	96.9	NS					
Oxytoxum sp. 2	0	4.1	7.5	0	27.7	NS					

Prorocentrum balticum	102.9	237.3	191.3	167.1	256.2	NS					
Prorocentrum compressum	6.4	0	3.8	0	0	NS					
Prorocentrum minimum	19.3	20.5	41.3	12.9	13.8	NS					
Protoceratium reticulatum	0	69.5	30.0	12.9	27.7	*		D	E	C	В
Protoperidinium avellanum	45.0	98.2	105.0	12.9	76.2	NS					
Protoperidinium bipes	12.9	130.9	168.8	0	124.6	**		A	E	В	С
Protoperidinium conicum	0	0	11.3	0	6.9	NS					
Protoperidinium leonis	0	0	3.8	0	0	NS					
Protoperidinium marukawai	0	24.5	7.5	0	13.8	NS					
Protoperidinium mite	0	0	3.8	0	0	NS					
Protoperidinium monovelum	19.3	61.4	33.8	0	6.9	NS					
Protoperidinium pellucidum	0.0	16.4	11.3	0	6.9	NS					
Protoperidinium punctulatum	25.7	143.2	97.5	0	124.6	NS					
Protoperidinium subinerme	0	8.2	0	12.9	0	NS					
Protoperidinium thorianum	12.9	106.4	82.5	51.4	103.8	NS					
Protoperidinium sp. 1	0	4.1	3.8	0	0	NS					
Protoperidinium spp.	0	4.1	0	0	6.9	NS					
Scripsiella crystallina	6.4	57.3	60.0	0	55.4	NS					
Athecate dinoflagellates											
Gymnodinium spp.	353.6	695.5	817.5	192.9	546.9	NS					
Oligotrich ciliates											
Lohmanniella spp.	12.9	8.2	30.0	25.7	13.8	NS					
Strobilidium spp.	360.0	515.5	757.5	308.6	304.6	NS					
Strombidium strobilum	0	0	105.0	51.4	41.5	NS					
Strombidium spp.	720.0	736.4	1087.5	180.0	955.4	NS					
Tontonia gracillima	64.3	49.1	135.0	0	27.7	NS					
Tintinnid ciliates											
Parafavella denticulata	0	0	7.5	0	0	NS					
Ptychocylis obtusa	12.9	16.4	30.0	0	96.9	*	A	В	C	<u>E</u>	
Tintinnopsis sp.	12.9	0	7.5	0	0.0	NS					

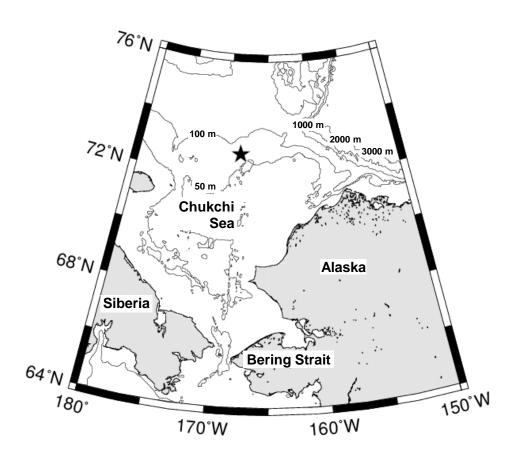
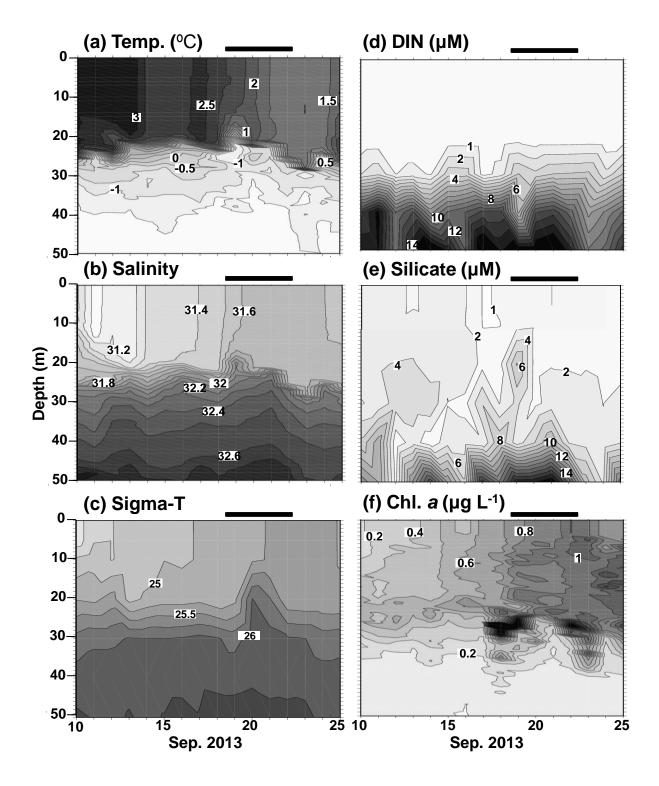


Fig. 1. (Yokoi et al.)



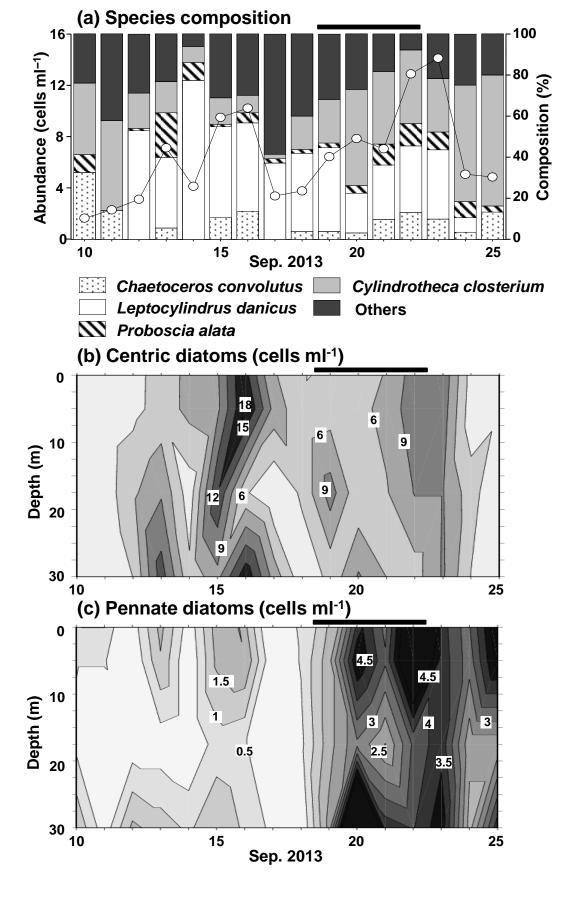


Fig. 3. (Yokoi et al.)

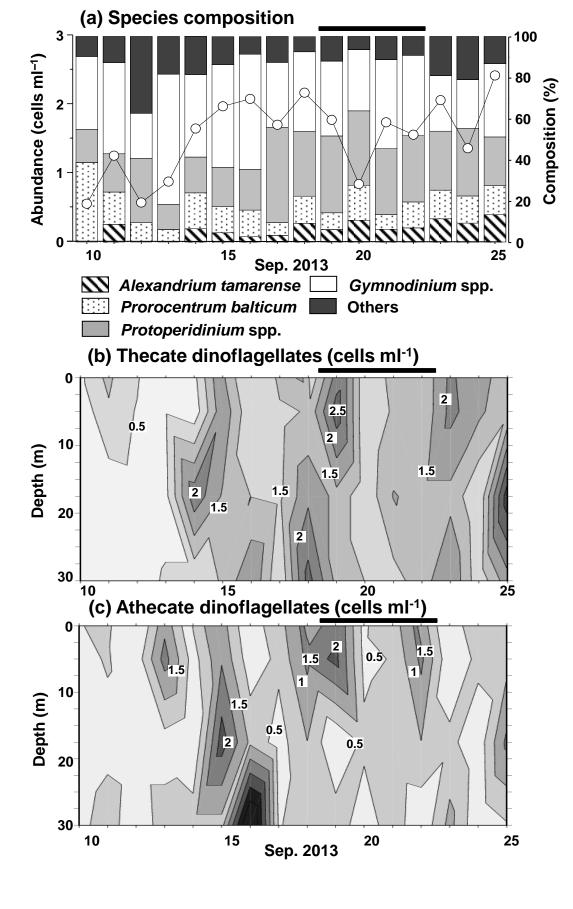


Fig. 4. (Yokoi et al.)

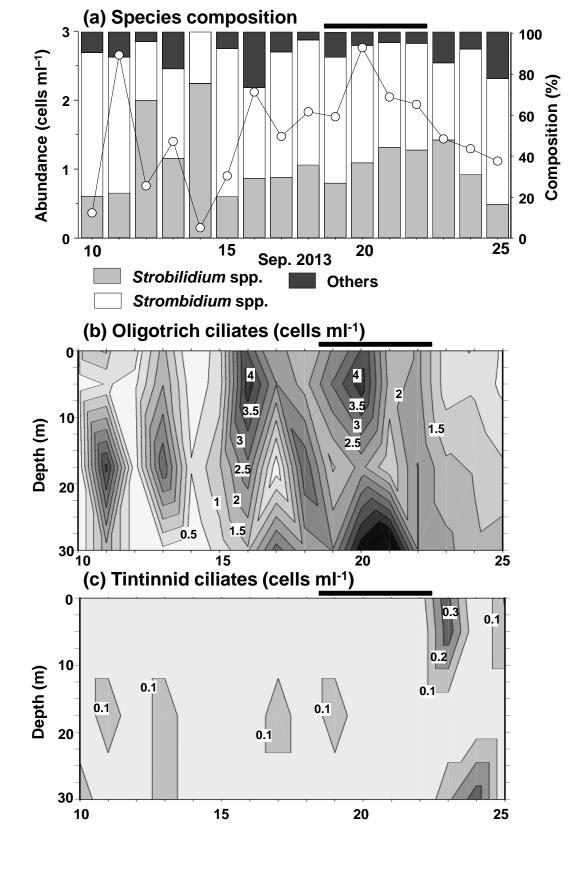


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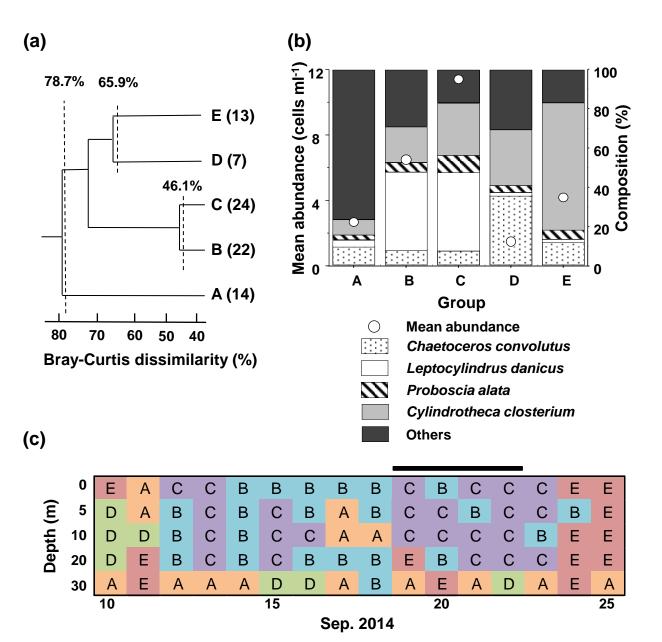


Fig. 6. (Yokoi et al.)

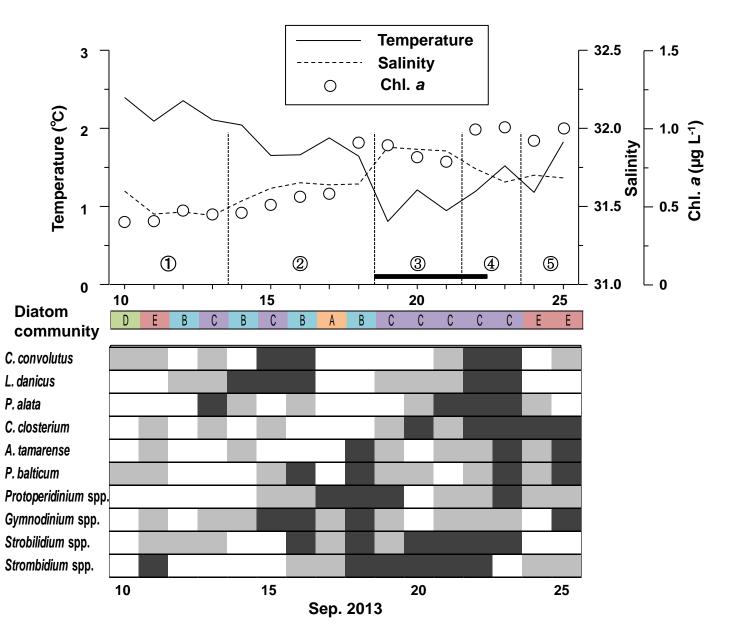


Fig. 7. (Yokoi et al.)