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Timing of sea ice retreat can alter phytoplankton community structure in the western Arctic Ocean

A. Fujiwara[1,2], T. Hirawake[2], K. Suzuki[3], I. Imai[2], and S.-I. Saitoh[2]

[1]Arctic Research Center, National Institute of Polar Research, 10-3, Midoricho, Tachikawa, Tokyo 190-8518, Japan
[2]Faculty/Graduate School of Fisheries Sciences, 3-1-1 Minatocho, Hakodate, Hokkaido 041-8611, Japan
[3]Faculty of Environmental Earth Science/Graduate School of Environmental Earth Sciences, Hokkaido 060-0810, Japan

Correspondence to: A. Fujiwara (fujiwara.amane@nipr.ac.jp)

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Timing of sea ice retreat can alter phytoplankton community structure

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Abstract

This study assesses the response of phytoplankton assemblages to recent climate change, especially with regard to the shrinking of sea ice in the northern Chukchi Sea of the western Arctic Ocean. Distribution patterns of phytoplankton groups in the late summers of 2008–2010 were analyzed based on HPLC pigment signatures and, the following four major algal groups were inferred via multiple regression and cluster analyses: prasinophytes, diatoms, haptophytes and dinoflagellates. A remarkable interannual difference in the distribution pattern of the groups was found in the northern basin area. Haptophytes dominated and dispersed widely in warm surface waters in 2008, whereas prasinophytes dominated in cold water in 2009 and 2010. A difference in the onset date of sea ice retreat was evident among years – the sea ice retreat in 2008 was 1–2 months earlier than in 2009 and 2010. The spatial distribution of early sea ice retreat matched the areas in which a shift in algal community composition was observed. Steel-Dwass's multiple comparison tests were used to assess the physical, chemical and biological parameters of the four clusters. We found a statistically significant difference in temperature between the haptophyte-dominated cluster and the other clusters, suggesting that the change in the phytoplankton communities was related to the earlier sea ice retreat in 2008 and the corollary increase in sea surface temperatures. Longer periods of open water during the summer, which are expected in the future, may affect food webs and biogeochemical cycles in the western Arctic due to shifts in phytoplankton community structure.

1 Introduction

The acceleration of warming and the shrinking of sea ice in the Arctic Ocean have been observed since the late 1990s (Steel et al., 2008; Perovich and Richter-Menge, 2009). The first dramatic sea ice reduction was observed in 2007. Thereafter, the Arctic sea ice area during the late summer has remained at similar levels as that of 2007

with a historical minimum in September 2012. Further sea ice reduction may occur, and the disappearance of summer Arctic sea ice has been predicted for the 2020s (Wang and Overland, 2009). Reductions in sea ice cover are significant on the Pacific side of the western Arctic (e.g., Perovich and Ritcher-Menge, 2009). Such reductions in sea ice have caused the freshening of seawater, along with a recent increase in river discharge into the Canada basin (Yamamoto-Kawai et al., 2009). Corresponding to a deepening nutricline, induced by increasing volumes of low-density water, a predominance of groups of small phytoplankton and reduced primary productivity can be expected in the Beaufort Sea (Li et al., 2009; McLaughlin and Carmack, 2010). On the other hand, it has been reported that a thinning or/and shrinking of sea ice improved underwater light conditions, which stimulated higher primary productivity, where phytoplankton were not strongly limited by nutrient availability (Lee and Whitledge, 2005; Nishino et al., 2011; Arrigo et al., 2012).

Arrigo et al. (2008) showed that a longer ice-free season led to a longer algal growth season, and wider open water areas resulted in an expansion of the phytoplankton growth area. However, the effects of the expansion of new opened water areas on phytoplankton community composition in the western Arctic remain unknown. It is important to understand the influence of sea ice reduction on phytoplankton community composition because different phytoplankton functional types such as large diatoms and small flagellates play important but different roles in biogeochemical cycles and ecosystems. Therefore, we examined the horizontal distribution patterns of phytoplankton assemblages as derived from algal pigment data collected from the western Arctic Ocean during the late summers of 2008–2010. And main objective is to understand how the spatial variability of sea ice distribution can affect phytoplankton community composition.

2   Materials and methods

2.1   Sampling and pigment analysis

Data were collected during cruises of the R/V *Mirai* (Japan Agency for Marine-Earth Science and Technology), primarily in September of 2008 (28 August–6 October), 2009 (11 September–10 October) and 2010 (4 September–13 October). During these three collection years, water sampling was conducted at 185, 64 and 119 stations, respectively. Surface seawater or near-surface water (sampled at 5 m depth) was collected using a clean plastic bucket and Niskin bottles, which were attached to the CTD/Carousel sampler, respectively. The temperature and salinity of surface waters were measured using a thermometer and a Guildline AUTOSAL salinometer, respectively, or by a CTD system (SeaBird Electronics Inc., SBE-9plus). Nutrient concentrations (NO_2, NO_3, NH_4, PO_4 and $Si(OH)_4$) were determined using auto-analyzers on board within 24 hours after the sampling (Shimada, 2008; Kikuchi, 2009; Itoh, 2010). These environmental parameters were measured at all of the stations.

Water samples were collected for phytoplankton pigments at 24, 15 and 37 stations, respectively, during the three cruises. For these samples, 1200–2400 mL of seawater were immediately filtered onto Whatman GF/F glass fiber filters (25 mm in diameter) using a gentle vacuum (< 0.013 MPa). Filtered samples were stored in liquid nitrogen or a deep freezer ($-80\,^\circ$C) until analysis on land. The extraction of phytoplankton pigments followed the method of Suzuki et al. (2005), who used N,N-dimethylformamide with sonication. The algal pigments were separated by high-performance liquid chromatography (HPLC), following the method of Van Heukelem and Thomas (2001), except that this study used a flow rate of 1.2 mL min^{-1}. The pigments used for the analysis were chlorophyll *c*3 (chl *c*3), peridinin (peri), 19′-hexanoyloxyfucoxanthin (hex), focuxanthin (fuco), 19′-butanoyloxyfucoxanthin (but), diadinoxanthin (diadino), alloxanthin (allo), zeaxanthin (zea), prasinoxanthin (prasi), lutein (lut), chlorophyll *b* (chl *b*) and chlorophyll *a* (chl *a*). These pigments are often used as diagnostic pigments to iden-

tify phytoplankton community composition (e.g., Jeffrey and Vesk, 1997; Jeffrey and Wright, 2006).

Size-fractionated chl*a* concentrations were measured using a fluorometric method with a Turner Designs 10-AU fluorometer (Welshmeyer et al., 1994) during the 2009 and 2010 cruises. The sample water was passed through Whatman Nuclepore and GF/F filters with pore sizes of 10, 5, 2, and 0.7 µm, respectively. A quantitative index of phytoplankton community size structure (F_L) was used, following Fujiwara et al. (2011); F_L indicates the ratio of the algal biomass attributed to cells larger than 5 µm relative to the total biomass (Eq. 1):

$$F_L = \frac{\text{chl } a_{>5\,\mu m}}{\text{chl } a_{total}} \times 100\,\%, \tag{1}$$

where chl a_{total} is the sum of chl a detected from filters of all pore sizes, while chl $a_{>5\,\mu m}$ is the chl a detected using meshes larger than 5 µm.

2.2 Clustering phytoplankton groups

Multiple regression analysis (MRA) and cluster analysis (CA) were applied to the phytoplankton pigment data to determine the most predominant phytoplankton group at each sampling station. MRA can assess the contributions of diagnostic pigment to chl*a* levels (Wright and Jeffrey, 2006) and does not require any assumptions about the pigment ratios of each algal group, as does Chemical Taxonomy (CHEMTAX) (Mackey et al., 1996); however, MRA cannot discriminate among taxonomic groups that have diagnostic pigments in common (e.g., prasinophytes and chlorophytes both contain chl *b*). In this study, MRA was conducted twice using the following method: the first MRA included all pigment data, then several pigments with large standard errors (> 1.0) or unrealistic partial regression coefficients when compared to previous studies (e.g., Suzuki et al., 2002; Vidussi et al., 2004) were excluded and a second MRA was performed on the confined dataset.

CA was used to infer algal community composition based on pigment data, with Ward's linkage method using Euclidean distance. The same pigments used for CHMETAX analysis for Baffin Bay, in the Arctic Ocean, by Vidussi et al. (2004) were chosen for CA because similar algal groups are expected to appear in our study region – chl $c3$, peri, but, fuco, prasi, hex, allo, zea, lut and chl b. We divided phytoplankton groups into several clusters by CA using the same pigments using the ratios of the accessory pigment to chl a.

2.3 Multiple comparison test

We conducted a multiple comparison test to examine the significant differences in environmental conditions among the phytoplankton clusters. Because a normal distribution could not be assumed for each environmental variable, the non-parametric Steel-Dwass's multiple comparison test was used with a 5 % confidence interval. The environmental variables included in the test were water temperature, salinity, nutrient concentrations (NO_2, NO_3, NH_4, PO_4 and $Si(OH)_4$) and timing of sea ice retreat (described in Sect. 2.4), with chl a and F_L as the algal parameters

2.4 Satellite data

Daily sea ice concentration (SIC) data were collected by the Advanced Microwave Scanning Radiometer for Earth Observing System (AMSR-E) and retrieved from the National Snow and Ice Data Center (NSIDC). SIC was calculated by NASA-Team algorithm 2 (Markus and Cavalieri, 2000). Open water area was defined as areas in which SIC pixel values were less than 10 %, following Arrigo et al. (2008). The onset date of the sea ice retreat was defined as the first day that the SIC of each pixel became < 10 %. The daily sea surface temperature data collected by MODIS-Aqua were downloaded from the Goddard Space Flight Center/National Aeronautics and Space Administration (GSFC/NASA) with 9 km spatial resolution.

3 Results and discussion

3.1 Horizontal distribution

3.1.1 Distribution of phytoplankton pigments

The distribution of phytoplankton pigments showed similar pattern among the years. Figure 1a–c shows percentage contribution of each accessory pigment to the total pigments. In general, Fuco and/or peri showed high contribution in shallow shelf region (~ 200 m) and their contribution decrease along with the depth increase. In contrast, chl b and Pras increased with the depth (Fig. 1a–c). The distribution patterns were almost consistent with surface pigment composition during summer of 2002 and 2004 in the Chukchi Sea that Hill et al. (2005) reported. However, we would like to note that inter-annual variability of pigment distribution was found: not only Pras and chl-b but also Hex and chl $c3$ increased with the depth in 2008 (Fig. 1a), but the pattern was not found in 2009 and 2010 (Fig. 1b and c).

3.1.2 Inference of dominant algal groups

Concentrations of chl$a$ were successfully expressed from MRA, which included six accessory pigments:

$$\text{chl } a = 1.49[\text{peri}] + 1.85[\text{fuco}] + 1.74[\text{hex}] + 5.88[\text{allo}] + 3.54[\text{zea}] + 1.31[\text{chl } b] + 0.02, \quad (2)$$

where the adjusted R^2 was 0.99, and all partial regression coefficients and Eq. (2) were statistically significant ($p < 0.001$ by t test and $p < 0.001$ by F test). Each partial coefficient was in a similar range as the reciprocals of the pigment/chl a ratio reported for Baffin Bay (Vidussi et al., 2004), the North Pacific and the Bering Sea (Suzuki et al., 2002). Surface phytoplankton groups were divided into 4 clusters using CA and their pigment compositions. Using CA, 45, 10, 13 and 8 samples were grouped into cluster 1, 2, 3 and 4, respectively. A similarity index of 0.57 was set as the threshold for the

clusters (Fig. 2). To determine the dominant phytoplankton group in each cluster, we confirmed the average pigment/chl *a* ratio (Table 1) and the average contribution to chl *a* of the major pigments, which was derived by MRA (Fig. 3), referring to Vidussi et al. (2004) and Hill et al. (2005), who used HPLC pigments to identify phytoplankton taxa in the Arctic Ocean.

Cluster 1 contained the highest contribution of chl *b* relative to chl *a* (37 %; Fig. 3). The highest prasi / chl *a* ratio was also observed in this cluster (Table 1). The high amounts of chl *b* and prasi relative to chl *a* indicated that large fractions of type I or II prasinophytes occurred in this cluster. Type I prasinophytes consist of prasinoxanthin containing Prasinophyceae, and the type II prasinophytes lack prasinoxanthin but still contain high amounts of chl *b*. An example is *Micromonas pusilla*, which is widely distributed throughout the Arctic (e.g., Lovejoy et al., 2006, 2007). Vidussi et al. (2004) reported that type I prasinophytes, type II prasinophytes and chlorophytes were the major chl *b*-containing groups in Baffin Bay. However, significantly lower lut / chl *a* and zea / chl *a* ratios than that of chlorophytes found in this study (0.001 ± 0.02 and 0.011 ± 0.09, respectively) suggested that there were small fractions of chlorophytes in this cluster. Moreover, the prasi / chl*b* ratio was within the range of type I prasinophytes (e.g., Schlüter et al., 2000; Schlüter and Møhlenberg, 2003). Therefore, we assumed that type I prasinophytes were the most dominant algal group in this cluster. On the other hand, fuco, which is a major pigment of diatoms and haptophytes, contributed 20 % to chl *a* (Fig. 3). In addition, fuco / hex > 1 and fuco $>$ but (Table 1), which indicated that diatoms were the secondary contributors of chl *a* (Hill et al., 2005), rather than haptophytes, in cluster 1.

Fuco contributed the most to chl *a* in cluster 2 (~ 45 %; Fig. 3). The highest values of fuco/hex and fuco/but among all clusters (Table 1) suggest that the fraction of haptophytes was relatively small compared to that of diatoms. Thus, we concluded that diatoms were the dominant group in this cluster compared to that of diatoms in cluster 2. On the other hand, a remarkably low fuco/chl*a* ratio was observed (0.25 ± 0.072), compared to the result for diatoms by Suzuki et al. (2002) and Vidussi et al. (2004).

The chl b / chl a ratio was also higher than that reported by Hill et al. (2005) in a diatom-dominated community (0.11 ± 0.04). Therefore, type I and/or II prasinophytes were the secondary groups in cluster 2. We also noted some fractions of cryptophytes due to the 15 % contribution of allo to chl$a$ (Jeffrey and Vesk, 1997).

5   Fuco and hex contributed equally to chl$a$ in cluster 3 ($\sim$ 20 %; Fig. 3). This result suggested that a larger fraction of haptophytes was present in cluster 3 compared to other clusters (Mackey et al., 1996; Schlüter and Møhlenberg, 2003; Hill et al., 2005). The lowest fuco / hex ratio was found in this cluster (Table 1). Additionally, hex / chl a, but / chl a and fuco/chl$a$ were within the range of type I and/or II haptophytes reported by

10 Vidussi et al. (2004). Hence, haptophytes dominated the phytoplankton assemblages in cluster 3. Because the fuco/hex ratio did not always exceed 1.0, and the prasi / chl a ratio was slightly higher than in clusters 2 and 4 (Table 1), some fractions of diatoms and type I prasinophytes occurred in cluster 3.

    The peri / chl a ratio is a marker for dinoflagellates (e.g., Mackey et al., 1996; Jeffrey

15 and Vesk, 1997). The maximum observed peri / chl a ratio (0.25 ± 0.11) and the $\sim$ 30 % contribution of peri to chl a (Fig. 3) suggested that dinoflagellates were dominant algal group in cluster 4. The chl b/chl a and prasi/chl$b$ ratios, which were similar to those in clusters 2 and 3, suggested that pasinophytes were the secondary groups (Table 1). The presence of cryptophytes was also expected based on the contribution of allo to

20 chl a(Fig. 3), but their abundance was most likely lower as estimated from MRA.

    We thus inferred dominant phytoplankton groups (prasinophytes, diatoms, haptophytes and dinoflagellates) using MRA and CA. The presence of these four groups was consistent with the four major algal groups in the Arctic Ocean described by Sakshaug (2004). Secondarily, prasinophytes, cryptophytes and diatoms occurred in some

25 fractions in the study area.

3.1.3   Horizontal distribution of phytoplankton groups, nutrients, SIC and SST

Figure 4a–c indicate the distributions of SIC and sea surface temperature (SST) as monitored by a satellite on 1 September 2008–2010, along with the dominant phy-

toplankton groups at the sea surface during the cruises in each year. The ice-edge retreated to $\sim 78°$ N throughout the study area in 2008, except the area of 170–175° W (Fig. 4a). However, in 2009 and 2010, the northernmost ice edge was located at a similar latitude as in 2008, though the sea ice retreat at such a high latitude was observed only in the narrow areas of 150–155° W in 2009 and 160–165° W in 2010 (Fig. 4b and c). The distribution of sea surface temperature (SST) also showed spatial variation. A relatively high SST ($> 3\,°C$) was common in the southern Chukchi Sea ($\sim 72°$ N), where open water area commonly spread during the three years, and extended to $\sim 75°$ N in the eastern Chukchi Sea in 2008 (Fig. 4a), where ice cover was observed in 2009 and 2010 (Fig. 4b and c).

The distribution of clustered phytoplankton communities was remarkably different among years and regions (Fig. 4a–c). Prasinophytes expected to be dominated the algal communities (cluster 1) mainly in the basin area of the northern Chukchi Sea and partly near the ice edge around Barrow Canyon. Diatoms and dinoflagellates inferred to be dominated communities, clusters 2 and 4, exhibited a similar pattern in horizontal distribution. These clusters tended to occur in waters that extended from the shelf region of the Bering Strait to Chukchi shelf break. The most distinct interannual difference in the distribution patterns was observed in the western Chukchi Sea. Although clusters 1 and 3 showed a similar horizontal distribution pattern, most of cluster 3 was sampled in 2008 (Fig. 4a).

The surface distribution of $NO_3 + NO_2$ concentrations sampled during the cruises is plotted in Fig. 5a–c. In contrast to the distribution of the phytoplankton groups, the horizontal distribution of surface nutrients did not vary much from year to year. In general, high concentration of $NO_3 + NO_2$ ($\sim 11.98\,\mu M$) was found in the Bering Strait and the Chukchi shelf and gradually decreased with increasing water depth. $NO_3 + NO_2$ was almost depleted ($< 0.1\,\mu M$) where depths exceeded 100 m (Fig. 5a–c).

3.2 Favorable environmental conditions for the phytoplankton communities

We applied Steel-Dwass's multiple comparison test to the environmental and algal variables of the four clusters. The resulting box plots are shown in Fig. 6a–i. Statistically significant differences in temperature were observed between cluster 1 and the others. The temperature ranges observed in clusters 1, 2, 3 and 4 were -1–$1\,^{\circ}$C, 1.5–3.5$\,^{\circ}$C, 2.7–4.5$\,^{\circ}$C and 3.0–5.2$\,^{\circ}$C, respectively (Fig. 6a). Salinity differed significantly between the pairs of clusters 1 and 3 and clusters 2 and 4 (Fig. 6b). Clusters 1 and 3, in which prasinophytes and haptophytes were expected to dominate, showed lower salinity (24.5–27.5). Clusters 2 and 4, in which diatoms and dinoflagellates were expected to dominate, showed higher salinity (> 28.5). As for the chl a, the index of algal biomass, statistically significant differences were observed between the same pairs as for salinity (Fig. 6c). That is to say, prasinophytes and haptophytes tended to dominate with a relatively lower biomass ($< 0.4\,\mathrm{mg\,m^{-3}}$), while diatoms and dinoflagellates tended to dominate with a higher biomass ($> 0.8\,\mathrm{mg\,m^{-3}}$) (Fig. 6c). The contribution to chl a of phytoplankton cells larger than 5 µm (F_{L}) showed a similar pattern (Fig. 6d). Clusters 2 and 4 exhibited significantly higher fractions of large-celled phytoplankton than cluster 1. Note that we excluded cluster 3 from the analysis because we obtained only one size-fractionated chl a that sampled separated into cluster 3. Therefore, the community size composition of cluster 3 was uncertain.

Figure 6e–h indicate the results of multiple comparison tests performed on the nutrients, $NO_3 + NO_2$, NH_4, PO_4 and $Si(OH)_4$. All nutrients except PO_4 exhibited wide variation and significantly higher concentrations in cluster 2 than in the other clusters. The statistical difference of the timing of sea ice retreat observed by satellite remote sensing was also examined where the pigment sampled station between the clusters (Fig. 6i). Note that advection of sea surface water was omitted for this analysis but the timing of sea ice retreat at the stations where the cluster 1 was found showed significantly later ice retreat.

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3.3 Spatial distribution of phytoplankton communities and sea ice

We analyzed the interannual variability of SIC from 2008 to 2010, assuming that sea ice distribution was one of the determining factors of algal taxonomic distribution. Figure 7a–c show the distribution of sea ice on the dates that SIC became < 10 %, the criterion that defined the onset date of open water area (Arrigo et al., 2008). In the study area, sea ice retreat generally begins in May or June in the shelf, and the shrinking continues until August or September, when the ice edge reaches the basin. However, there was temporal and spatial variability in the onset date of sea ice retreat, especially in the eastern Chukchi Sea (140–160° W), where the algal assemblages of cluster 3 were observed. The onset date in that area occurred in June in 2008 (Fig. 7a); however, sea ice retreat occurred in July and August in 2009 and 2010, respectively (Fig. 7b and c). In short, 1–2 months earlier sea ice retreat observed in 2008 than in 2009 and 2010 (Fig. 7c and d).

4 Discussion

4.1 Inference of dominant phytoplankton groups

In this study, phytoplankton assemblages at the sea surface were clustered according to similarities in pigment composition, and the dominant algal groups of each cluster were inferred. However, the community structure of phytoplankton groups cannot be determined perfectly using pigment compositions. For example, Vidussi et al. (2004) found a nonsignificant relationship between the dinoflagellate biomass estimated by counting under a microscope and the same biomass estimated using CHEMTAX. They attributed this result to the presence of fuco-containing dinoflagellates instead of peri or mixotrophic dinoflagellates. Unfortunately, a quantitative relationship between phytoplankton pigment composition and the microscopically identified has not been established, and in addition, such data were unavailable either in this study. Nevertheless,

pigment-based identification is widely used because it provides the advantage of detecting small phytoplankton, which often cannot be quantified by microscopy (Mackey et al., 1996). In fact, Hill et al. (2005) have provided important information about the surface and vertical distribution of phytoplankton assemblages in the Arctic region using composition of algal pigments. Our result was also consistent with general distribution of phytoplankton communities that Hill et al. (2005) had shown; Fuco containing assemblage increased in shallow water and chl *b* containing flagellates was predominant in deeper water during summer (Figs. 1a–c and 4a–c). We believe that it is reasonable to discuss the distribution of dominant phytoplankton groups using algal pigment composition.

4.2 Response of phytoplankton communities to environmental conditions

We found some significant differences among the phytoplankton clusters in terms of environmental conditions. The results of the multiple comparison test revealed that cluster 1 exhibited significantly lower temperatures than the other clusters (Fig. 6a). Clusters 1 and 3 contained less saline water than the other two clusters (Fig. 6b). Low salinity is typical of the sea ice meltwater in the Arctic Ocean (Macdonald et al., 2004). Due to a strong halocline, nutrients are generally depleted at the surface layer during summer, especially in the basin area (Fig. 5a–c). The horizontal distribution patterns of the dominant phytoplankton groups and nutrients showed good agreement (Figs. 4 and 5). Hill et al. (2005) reported that reproductive phytoplankton groups, such as prasinophytes and haptophytes, were prevalent at the surface instead of diatoms and dinoflagellates, which favored nutrient-rich water. Because the western Arctic is limited in inorganic nitrogen relative to phosphorus (Yamamoto-Kawai et al., 2006), nitrogen can be a major factor limiting phytoplankton growth. Cluster 2, which was dominated by diatoms, showed a significantly higher nitrogen level than the other clusters, which contains oligotrophic-adapted groups (Fig. 6e and f). Dinoflagellates (cluster 4) were associated with intermediate nutrient conditions and chl *a* (Fig. 6a and e–h). Sakshaug (2004) reported a wide distribution of mixotrophic dinoflagellates such as

Ceratium arctium and *C. longipes* in the Arctic. In short, diatoms and dinoflagellates with greater biomass and larger cell sizes dominated the shelf and shelf break region, where lower levels of sea-ice melt water and nutrients occurs even during the summer. In contrast, prasinophytes and haptophytes with lower biomass and/or smaller cell sizes dominated the deeper basin area (Fig. 4a–c), where the strong halocline due to the large volume of low-salinity water limits replenishment of nutrients from underlying waters (Fig. 5a–c). Although haptophytes are widely distributed in open oceans (Liu et al., 2009), it is interesting to note that they prefer higher temperatures compared to prasinophytes in the Arctic Ocean (Fig. 6a).

4.3 Responses of phytoplankton groups to sea ice distribution

Cluster 3 dominated by haptophytes was observed only in 2008 in the eastern Chukchi Sea, where prasinophytes were dominant in the other two years. To understand the reason for this difference among the years, we focused on the inter-annual variability of open water area and the temporal variability of the onset date of sea ice melt. As indicated in Fig. 7a–e, there were significant differences in the onset date among the three years. In particular, an earlier onset of 1 to 2 months was observed in the eastern Chukchi Sea in 2008 (Fig. 7d and e). We hypothesize that this earlier sea ice melt and longer ice-free periods reduced the ice albedo in 2008, and warm water ($\sim 5\,^\circ$C) consequently distributed in the eastern Chukchi Sea. The locations of haptophyte-dominated samples showed good agreement with early open water and warm water (Figs. 4a and 7a, d and e). Such relatively warm and oligotrophic water conditions should be favorable for haptophytes (Fig. 6a, e and f). Haptophytes are known as mixotrophic organisms and can survive in nutrient-depleted waters by grazing bacteria or mixotrophic nanoflagellates (Estep et al., 1986; Porter, 1988). In addition, an earlier sea ice retreat might release phytoplankton from light limitation. Under light-limited conditions, phytoplankton tend to synthesize chl *b* and chl *a* to increase their photosynthesis efficiency (Giesks and Kraay, 1986). In the Arctic Ocean, phytoplankton often experience light limitation due to the presence of sea ice (e.g., Sakshaug, 2004; Hill et al., 2005).

Therefore, prasinophytes, which contain more chl *b* due to low-light acclimation, are distributed widely in the Arctic. However, the longer ice-free period in 2008 may have triggered a shift in the phytoplankton community from domination by prasinophytes to haptophytes due to improved light conditions. Thus, we suggest that the dominance of
5 haptophytes observed only in 2008 was due to the spread of warm, nutrient-depleted water and/or changing light conditions, all of which likely follow an early sea ice retreat.

Lovejoy et al. (2007) reported that, during late summer, the Arctic marine food web is supported by low temperature, low light and oligotrophic-adapted prasinophytes. Our results, however, revealed a shift in community composition in area of earlier sea ice
10 retreat; such changes in phytoplankton communities have the potential to trigger the dramatic changes in the Arctic marine food web. Reduction in sea ice are expected to increase in the future (Perovich and Richter-Menge, 2009). We note that the earlier and broader distribution of open water areas can result in a larger area in which shift in phytoplankton community structure, from prasinophytes to haptophytes, may occur. Few
15 studies exist showing that phytoplankton community shifts actually affect biogeochemical cycles or higher trophic levels in the western Arctic. However, a high-resolution time series observation conducted in Svalbard revealed that changes in phytoplankton community composition alter food quality for copepods (Søreide et al., 2010; Leu et al., 2011). Leu et al. (2011) reported that phytoplankton bloom dominated by diatoms con-
20 tains higher quality of polyunsaturated fatty acids (PUFAs) than other flagellates. On the other hand, it has been reported that diatoms can reduce their nutritional quality in lower nutrient conditions (Ban et al., 1997). It has not been reported what will happen if the switching of dominant algal groups from prasinophytes to haptophytes occur in a large temporal and spatial scale. As Leu et al. (2011) have noted, process studies are
25 the only way to determine how the spatiotemporal variability of sea ice affects lower trophic levels. However we suggest that the ecosystem can be more heterotrophic and reproductive along with increase of mixotrophic haptophytes in the western Arctic. Therefore, further studies are required to assess the biogeochemical and ecological impacts of the shifts in phytoplankton community composition in the western Arctic.

Our study revealed the horizontal distribution of major phytoplankton groups during the summer in the western Arctic and differences in the environmental conditions they favor. Because we could use in situ data from only three years, and we analyzed only the surface phytoplankton pigments, variability across long periods of time and the vertical phytoplankton community structure were not evaluated here. However, our data suggest that the phytoplankton community structure may shift due to interannual variability in the spatiotemporal distribution of sea ice. A remarkable shift was observed in the present study in regions containing significantly low nutrients and low chl*a*. By analyzing longer time-series data, Li et al. (2009) have reported that phytoplankton community size structure is decreasing due to a deepening nutricline. In addition to their report, our findings indicate that phytoplankton community shifts can occur even in the nutrient-depleted surface water associated with early expansions of open water. In situ and satellite observations of the distribution of phytoplankton functional types are important because functional types differ in their impacts on biogeochemical cycles and/or marine food webs (e.g., Lochte et al., 1993; Sunda et al., 2002; Bopp et al., 2005). Although the impact of phytoplankton community shift on biogeochemical cycles and food webs might be small, the longer ice-free periods and larger open water areas predicted for the future (Perovich and Richter-Menge, 2009) may amplify the spatial and temporal influence of algal community shifts. Therefore, the spatiotemporal patterns and changes in phytoplankton community structure should be taken into account when assessing biogeochemical cycles and food webs in the western Arctic Ocean.

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Timing of sea ice retreat can alter phytoplankton community structure

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Table 1. Means and standard deviations of pigment/chl*a* and pigment/pigment ratios that were used in this study to determine the dominant phytoplankton groups in each cluster. Standard deviations are shown in parentheses.

Pigment	Cluster 1	Cluster 2	Cluster 3	Cluster 4
peri / chl *a*	0.023 (0.025)	0.060 (0.025)	0.041 (0.036)	0.249 (0.105)
but / chl *a*	0.030 (0.011)	0.016 (0.018)	0.029 (0.017)	0.011 (0.003)
fuco / chl *a*	0.125 (0.034)	0.25 (0.072)	0.122 (0.037)	0.096 (0.022)
hex / chl *a*	0.060 (0.022)	0.025 (0.026)	0.129 (0.060)	0.014 (0.006)
prasi / chl *a*	0.065 (0.019)	0.022 (0.007)	0.040 (0.012)	0.026 (0.011)
zea / chl *a*	0.011 (0.009)	0.011 (0.006)	0.012 (0.013)	0.009 (0.005)
lut / chl *a*	0.001 (0.002)	0.001 (0.001)	0.001 (0.002)	0.001 (0.001)
chlb / chl *a*	0.293 (0.064)	0.105 (0.039)	0.097 (0.067)	0.118 (0.039)
pras / chl *b*	0.227 (0.076)	0.222 (0.086)	0.296 (0.065)	0.210 (0.042)
fuco / hex	2.37 (1.24)	19.4 (22.5)	1.30 (0.965)	7.79 (3.93)
fuco / but	4.76 (2.50)	24.8 (24.3)	5.03 (3.28)	9.73 (3.84)
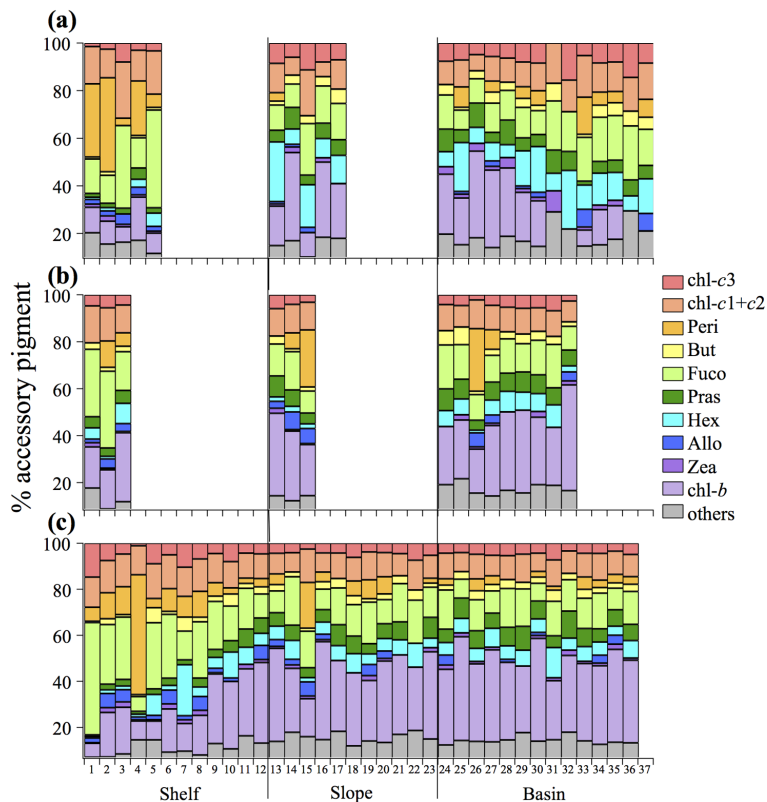
Fig. 1. Percentage contribution of major algal pigment detected by HPLC for all pigment sampled station in **(a)** 2008, **(b)** 2009 and **(c)** 2010. Data were sorted by station depths and divided into shelf (∼ 200 m), slope (200–500 m) and basin area (∼ 500 m).

Fig. 2. Dendrogram showing phytoplankton groups that were separated by cluster analysis using pigment composition data. The red line indicates the location of the similarity index (= 0.57) that divided the clusters into four groups. Numbers on the *x* axis indicate the sample IDs.
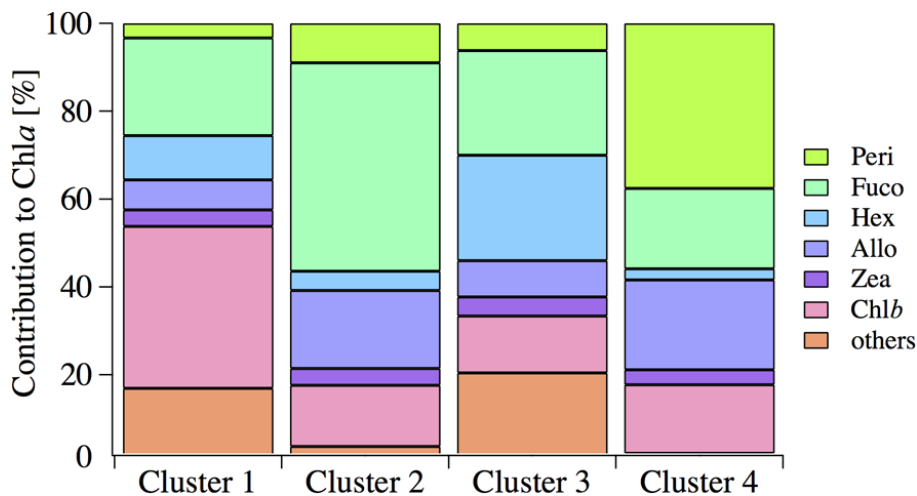
Fig. 3. Average percent contribution to chl *a* of major algal accessory pigments for each cluster. These contributions were determined by multiple regression analysis.
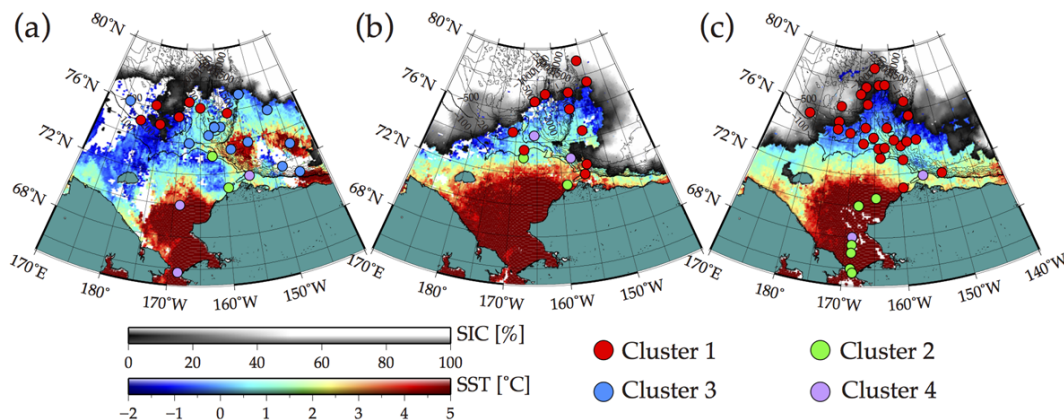
Fig. 4. Distribution of dominant phytoplankton groups at the surface layer in **(a)** 2008, **(b)** 2009 and **(c)** 2010. Clusters were identified by cluster analysis. SIC data were collected by AMSR-E on 1 September; SST data were collected by MODIS on September 1 of each year. Depth contours indicate 100-, 200-, 500-, 1000-, 1500-, and 2000-m intervals, respectively.
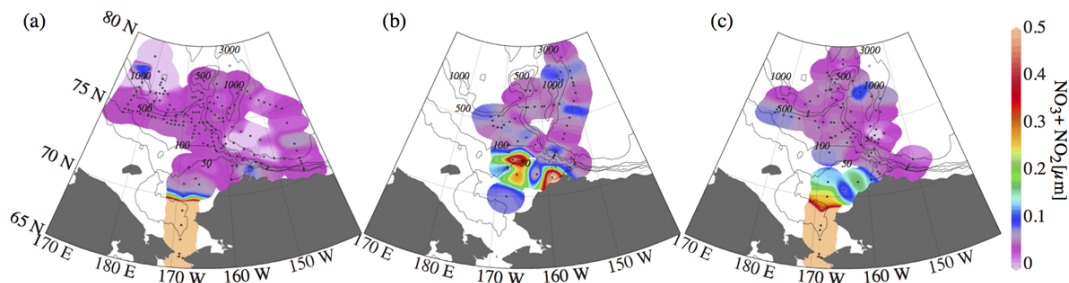
Fig. 5. Surface distribution of NO_3+NO_2 in the western Arctic Ocean during late summer in **(a)** 2008, **(b)** 2009 and **(c)** 2010. Black dots indicate the sampling stations visited during the cruises. Depth contours indicate 50-, 100-, 500-, 1000- and 3000-m intervals.
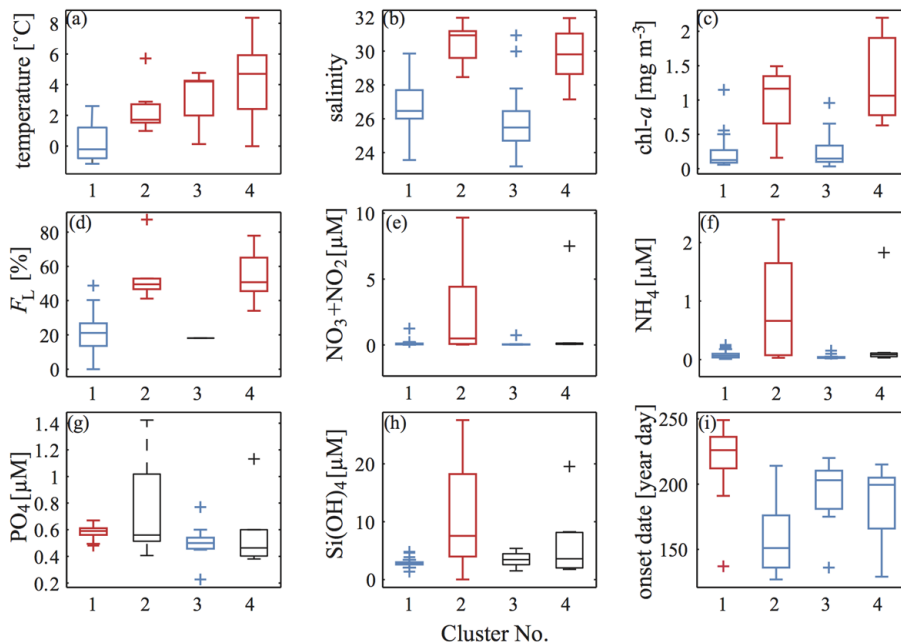
Fig. 6. Boxplots of **(a)** temperature, **(b)** salinity, **(c)** chl$a$, **(d)** F_L, **(e)** NO_3+NO_2, **(f)** NH_4, **(g)** PO_4, **(h)** $Si(OH)_4$ and **(i)** onset date of sea ice retreat for the four clustered phytoplankton groups. Significant differences were detected by Steel-Dwass's multiple comparison test between blue and red plots. Plots of the same color and black plots are not significantly different. Note that the multiple comparison test was not conducted for F_L in cluster 3 because only one data point exists for that variable in that cluster.
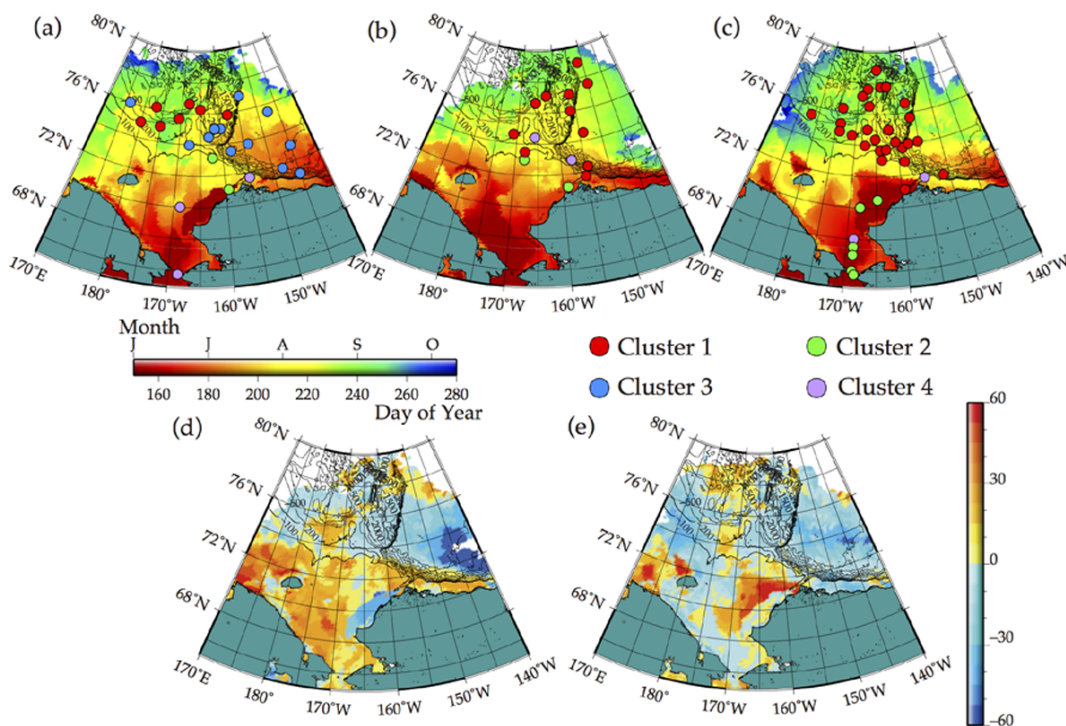
Fig. 7. Distribution of the clusters across Julian day when the area became open water in **(a)** 2008, **(b)** 2009 and **(c)** 2010. Clusters were identified by cluster analysis. White indicates areas where no open water appeared during the entire year. Differences of sea ice retreat timing between **(d)** 2008 and 2009, and between **(e)** 2008 and 2010 were also calculated subtracting Fig. 7b and c from Fig. 7a. Depth contours indicate 100-, 200-, 500-, 1000-, 1500-, and 2000-m intervals, respectively.