

RESEARCH LETTER

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Key Points:

- In the Arctic Ocean, sea ice is in decline, and ice-free duration is lengthening
- Ecosystem function under sea-ice-covered and sea-ice-free conditions governs phytoplankton community composition
- A future Chukchi Sea with less sea ice cover will exhibit lower phytoplankton carbon biomass, impacting the food web and carbon export

Supporting Information:

- Data Set S1
- Supporting Information S1

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Unraveling Phytoplankton Community Dynamics in the Northern Chukchi Sea Under Sea-Ice-Covered and Sea-Ice-Free Conditions

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Abstract The timing of sea ice retreat, light availability, and sea surface stratification largely control the phytoplankton community composition in the Chukchi Sea. This region is experiencing a significant warming trend, an overall decrease in sea ice cover, and a documented decline in annual sea ice persistence and thickness over the past several decades. The consequences of earlier seasonal sea ice retreat and a longer sea-ice-free season on phytoplankton community composition warrant investigation. We applied multivariate statistical techniques to elucidate the mechanisms that relate environmental variables to phytoplankton community composition in the Chukchi Sea using data collected during a single field campaign in the summer of 2011. Three phytoplankton groups emerged that were correlated with sea ice, sea surface temperature, nutrients, salinity, and light. Longer ice-free duration in a future Chukchi Sea will result in warmer sea surface temperatures and nutrient depletion, which we conclude will favor other phytoplankton types over larger diatoms.

Plain Language Summary In the Chukchi Sea, the seasonality of sea ice shapes ecosystem structure of the water column under both sea-ice-covered and sea-ice-free conditions. As such, phytoplankton community composition under both conditions responds to water column structure and nutrient availability. Owing to recent warming in the Arctic, sea ice is thinner and retreats earlier. To date, we do not fully understand the long-term consequences of earlier sea ice retreat on phytoplankton community composition and carbon biomass. To this end, we used environmental and phytoplankton data to relate how differences in ecosystem function under sea-ice-covered and sea-ice-free conditions govern phytoplankton communities. The results from this data set suggest that a future, sea-ice-free Chukchi Sea will exhibit lower phytoplankton biomass, impacting the food web and carbon export.

1. Introduction

In the Arctic Ocean, seasonal sea ice cover shapes the ecosystem structure of the water column by influencing light, nutrients, and density-driven stratification. In turn, ecosystem structure shapes pelagic phytoplankton community composition and spatial distribution under both sea-ice-cover and sea-ice-free conditions. Sea ice extent in the Arctic Ocean is declining rapidly, leading to predictions that the Arctic will be sea-ice-free in the summer as early as 2040 (Overland & Wang, 2013). Enhanced stratification from freshwater input and warming is expected to limit the advection of nutrients into the euphotic zone of ice-free regions (Mathis et al., 2014; J. É. Tremblay et al., 2008). The expected consequences of ice-free summers are longer open water duration and an extended growth season for pelagic phytoplankton. While recent work has focused on our still needed understanding of sea ice algae dynamics (Selz et al., 2017), it is also timely to consider how phytoplankton communities will respond to longer periods of seasonally open water.

Under sea-ice-free conditions, water column structure (stratification or vertical mixing) across the Chukchi Sea (Figure 1) is influenced by a number of factors, including inflow of Pacific water to the Arctic Ocean (Mathis et al., 2014), vertical mixing through wind events (Nishino et al., 2015) and upwelling (e.g., Barrow Canyon; Grebmeier et al., 2015; Hill & Cota, 2005), and the presence of nutrient rich Winter Water (Lowry et al., 2015; Woodgate et al., 2005). Vertical mixing events can influence the magnitude of primary production in the Arctic by replenishing nutrients to the euphotic zone, thereby creating an environment favorable to

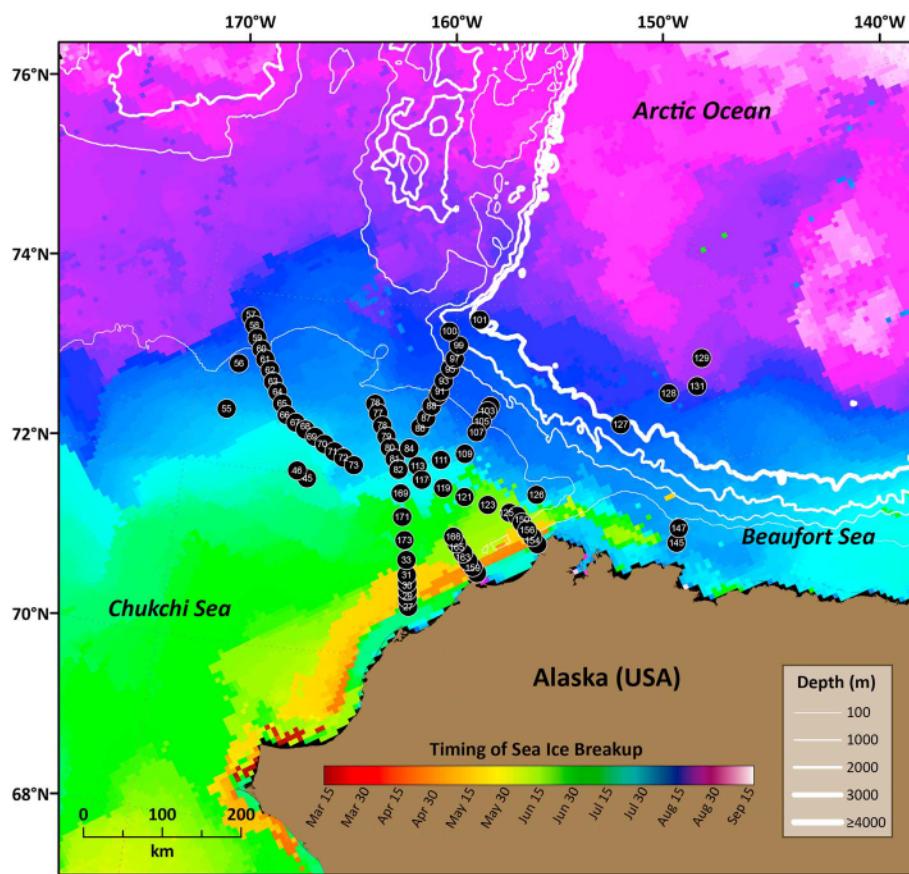


Figure 1. Map of Impacts of Climate on EcoSystems and Chemistry of the Arctic Pacific Environment 2011 sampling sites. Location of each sampling site has been superimposed on the bathymetry (white lines) and timing of sea ice breakup (colors). Each pixel represents the day of breakup during the study period in 2011 determined from the timing of when Advanced Microwave Scanning Radiometer for the Earth Observing System sea ice concentrations fall below a threshold of 15%.

larger phytoplankton such as chain-forming diatoms (Ardyna et al., 2011; Carmack, 2007). In contrast, stratification limits mixing, creating nutrient-depleted conditions that favor a community of smaller, less productive phytoplankton that exhibit lower nutrient requirements (e.g., cyanobacteria and pico-eukaryotes; Lee et al., 2007; Li et al., 2009). Recent studies have focused on the fate of net primary production (Arrigo & van Dijken, 2015; Hill et al., 2017) and spatial distribution of phytoplankton communities (Ardyna et al., 2011; G. Tremblay et al., 2009) in response to longer open water duration and nutrient availability. The magnitude of primary production is affected by phytoplankton community composition, where diatoms are responsible for new primary production fueled by upwelled nutrients, while autotrophic picoplankton and nanoflagellate production is supported by regenerated nutrients (Ardyna et al., 2011). Considering that the impact of local processes on the spatial distribution of phytoplankton communities throughout the Chukchi Sea will likely be heterogeneous under scenarios of future climate change, the question of how earlier sea ice retreat and longer ice-free conditions will affect phytoplankton production is difficult to answer.

Gaining an enhanced understanding of the mechanisms that drive the relationship between the environment and phytoplankton community composition under sea-ice-covered and sea-ice-free conditions is important to understand the implications of longer open water duration, increased stratification, and warmer sea surface temperature (SST) that will change the ecological niches that define the habitats to which the phytoplankton are adapted. To address the question of how phytoplankton will respond to a new Arctic system that describes the potential for an ice-free summer (Overpeck et al., 2005), we must first characterize phytoplankton communities in their current habitats of sea-ice-covered and sea-ice-free waters.

Margalef's (1978) mandala is a conceptual model of phytoplankton succession that describes mechanisms by which nutrients and turbulence drive phytoplankton dynamics. Within this framework, smaller phytoplankton dominate in calm, low nutrient environments, while larger phytoplankton succeed in areas of higher turbulence and greater nutrient concentrations. Since its inception, this model has been updated so that it may be applied to more complex ecosystems, such as that of harmful algal blooms (Glibert, 2016). As with Margalef's mandala, when we understand the underlying mechanisms that influence the ecological niches of Arctic phytoplankton under sea-ice-covered and sea-ice-free conditions, we may be able to predict responses of the phytoplankton communities to changes in the Arctic environment thereby creating new model for that ecosystem.

A number of synthesis papers have recently emerged using data collected during the NASA-funded Impacts of Climate on EcoSystems and Chemistry of the Arctic Pacific Environment (ICESCAPE) field campaigns that took place in 2010 and 2011 (Arrigo, 2015). One such study characterized the ecological drivers of the sea-ice algae community (Selz et al., 2017). Another important study characterized phytoplankton community composition of an under-ice bloom during the 2011 field campaign but did not provide a detailed discussion of the ecological drivers that shape the pelagic phytoplankton communities (Laney & Sosik, 2014; Selz et al., 2017). Here we present a parallel study applying similar approaches to that of Selz et al. (2017) to compare phytoplankton communities present in two different systems: sea-ice-free and sea-ice-covered. Using data collected in the summer of 2011, our goals in this study were two-fold: (1) characterize phytoplankton communities and abundances across the northern Chukchi Self and western Beaufort Sea and (2) determine which environmental drivers influence phytoplankton assemblages. Studies such as these are particularly timely in light of substantial changes in sea ice cover discussed earlier in this paper.

2. Materials and Methods

2.1. Study Site

Environmental and phytoplankton taxonomic data were collected as part of the NASA funded ICESCAPE field campaign on the U.S. Coast Guard Cutter Healy. The phytoplankton taxa and environmental parameters used in this study with their abbreviations are listed in supporting information Tables S1 and S2. Here we focus on a subset of the samples ($n = 380$; 81 stations) collected during the summer season between 2 July and 24 July 2011 in the northern Chukchi and western Beaufort Seas (Figure 1).

2.2. Sample Collection and Analysis

Water column profiles were collected using a rosette equipped with a Sea-bird Electronics conductivity-temperature-depth sensor package (SBE 911+, Sea-bird Electronics): a SBE9Plus CTD with dual pumps and dual temperature (SBE3plus), dual conductivity (SBE4C) sensors. Additional instruments included a Chelsea Technologies fluorometer (AQIII) and a Biospherical Instruments (QSP2300) photosynthetically active radiation (PAR) sensor. Samples were collected for analysis of nutrients, phytoplankton taxonomy, and chlorophyll *a* (Chla) at discrete depths of just below the surface, 10, 25, 50, 100, 150, and 200 m (depending on total water depth) and at the Chla maximum using a rosette of twelve 30-L Niskin bottles. Nitrate (NO_3^-), Nitrite (NO_2^-), and Silicate (Si) concentrations were determined using a modification of the Armstrong et al. (1967) method. Ammonium (NH_4^+) concentrations were measured fluorometrically (Kérrouel & Aminot, 1997). Phosphate (P) concentrations were measured following the Bernhardt and Wilhelms (1967) method. Chla was determined using high performance liquid chromatography (Hooker et al., 2005; Van Heukelem & Thomas, 2001). Subsurface PAR (light) was calculated as a fraction of the incoming surface PAR at each discrete sampling depth. Simulated in situ net primary productivity was measured using shipboard, 24-hr ^{14}C -bicarbonate incubations (Arrigo et al., 2014).

Phytoplankton taxonomy data (Table S1) were collected at each station using an Imaging FlowCytobot that collects images of particles greater than $\sim 8 \mu\text{m}$ (Olson & Sosik, 2007). A Beckman-Coulter Accuri C6 flow cytometer was used to enumerate particles between 2 and $14 \mu\text{m}$ (Laney & Sosik, 2014; Text S1). Phytoplankton biovolume was calculated using the method of Moberg and Sosik (2012). Phytoplankton carbon biomass from each taxon was estimated using the method of Menden-Deuer and Lessard (2000). It is important to note that the data are classified to the rank of genus or size class.

Sea ice cover and extent were determined at 6.25-km resolution using data collected by the Advanced Microwave Scanning Radiometer for the Earth Observing System on the Earth-observing satellite platform Aqua (Spreen et al., 2008). Timing of sea ice break-up was determined based on a sea ice concentration threshold of 15% (e.g., Frey et al., 2015). The sea ice index or *ICE presence*, similar to that of Lowry et al. (2015), was defined as the number of days since sea-ice breakup, where positive values represent locations still covered in ice, and negative values represent locations no longer covered with sea ice.

2.3. Statistics

To address our goals, we applied three multivariate statistical techniques, cluster analysis (CA), principle component analysis (PCA), and canonical correspondence analysis (CCA), to the phytoplankton taxonomic composition data and environmental variables (Tables S1 and S2, respectively) collected in the northern Chukchi and western Beaufort Seas (Figure 1). CA was applied to the phytoplankton data to group the taxa based on similar distribution and abundance patterns. CCA was applied to the taxonomic and environmental data to explain possible relationships between phytoplankton community composition and the environmental parameters (Ter Braak & Verdonschot, 1995). PCA was applied to the environmental data to elucidate distributional patterns across the study site. We also considered community richness in the samples (the count of phytoplankton taxa). From these analyses, we evaluated how water column properties under sea-ice-covered and sea-ice-free conditions impacted phytoplankton community composition. CA was performed using Primer-E version 7 software, a Bray-Curtis distance matrix, and group average linkage. Prior to CA, the phytoplankton data were transformed by dividing the value within each variable column (phytoplankton taxon) by the sum of the values. PCA and CCA were performed using the statistical software package Canoco version 5. Because PCA gives more weight to variables with higher variances, the environmental variables were both centered and standardized so that the mean was equal to 0 and the standard deviation was equal to 1 (Z scores). PCA was based on the correlation matrix. PCs were not rotated because the results were interpretable. CCA and CA were applied to the derived carbon abundances. For CCA, taxonomic carbon data were log transformed ($\log(X + 1)$) to reduce the bias associated with extreme values, the environmental variables were centered and standardized, and rare taxa were downweighted within Canoco. Because some of the environmental variables could be highly correlated, we also performed an interactive stepwise selection method in Canoco, which performs CCA on each variable separately and determines whether the fit of the variable is significant to $p < 0.05$ (with Bonferroni correction).

3. Results and Discussion

3.1. Phytoplankton Community Structure by CCA

In this study, we wanted to characterize the spatial variability and underlying patterns of the environmental variables across the study region by applying multivariate statistical analyses to the environmental and phytoplankton community composition data. We aimed to group the phytoplankton based on presence and abundance and define possible relationships between the environmental parameters and the phytoplankton community composition.

CA separated the taxa into four clusters (Figure 2). The first cluster included three diatom taxa, *Coscinodiscus*, *Odontella*, and *Thalassionema*, which were observed in <1.6% of all samples in this study. Because this cluster contributed a small percentage to phytoplankton communities in the samples, we consider these rare taxa and, for the sake of brevity, will not discuss them in this study.

The second cluster, phytoplankton group A (PGA; *ice-bloomers*) was composed of six diatom taxa (*Bacteriosira*, *Fragilariopsis*, *Detonula*, *Pleurosigma*, *Nitzschia*, and *Navicula*), a green alga (*Pyramimonas*), and a colonial haptophyte with and without diatoms (*Phaeocystis*). From the CCA biplot (Figure 3a), there is a clear distribution of the vectors along the CCA-axis 1, which explains 22.4% of the variation (Table S3a). Interactive-forward CCA revealed that these taxa exhibited a significant, positive relationship ($p < 0.05$; Table S3b) with the vectors silica (Si; an essential nutrient for diatoms) and ICE presence (Figure 3a; red symbols). The low turbulence and high nutrient environment (particularly Si; Table S4) created by sea ice and meltwater formed eutrophic-like conditions that are favorable for these taxa (Ardyna et al., 2011). Based on historical observations, these taxa are commonly associated with the sea ice edge and under-ice blooms in the Arctic (Selz et al., 2017; von Quillfeldt, 2000a; von Quillfeldt et al., 2003). This group also exhibited the highest Chla biomass, second highest carbon abundance, and highest median community richness (11 taxa) in samples

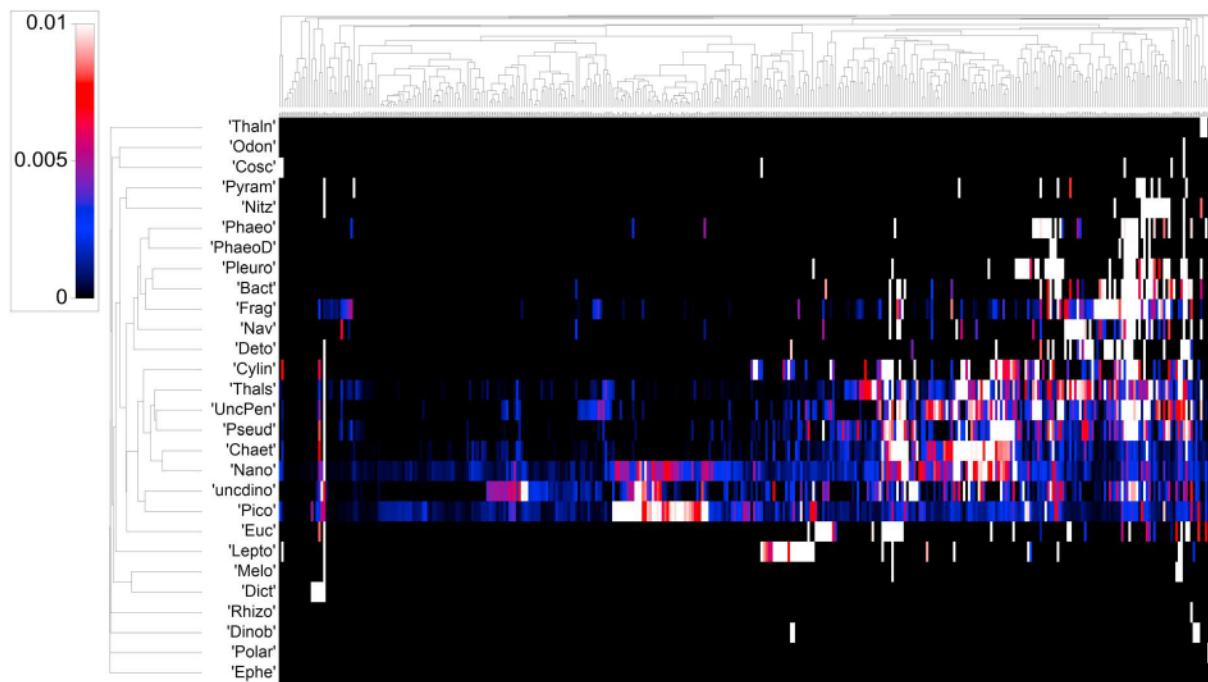


Figure 2. Cluster analysis generated four clusters (y-axis dendrogram): rare taxa and phytoplankton groups A, B, and C. Within in the heatmap, warmer colors (red to white) and cooler colors (blue to black) represent the relative greater presence or lower presence of a taxon, respectively. The x-axis dendrogram represents sample clusters.

where PGA was dominant (Table S4 and Text S2). The relationship of sea ice and Si is important to note because Si is regenerated in pack ice or sea-ice brine channels during the winter and released to the ocean surface when sea ice melts (Fripiat et al., 2014; Werner et al., 2007). In parallel studies to that presented here, Selz et al. (2017) and Laney and Sosik (2014) also found that the under-ice phytoplankton community accumulated in the late spring and was dominated by the same community of diatoms described in this study. Selz et al. (2017) concluded that water column phytoplankton were taxonomically distinct from the ice algae during the under-ice bloom.

The third cluster, phytoplankton group B (PGB; Figure 2), included six diatom taxa (*Eucampia*, Unclassified Pennates, *Pseudonitzschia*, *Chaetoceros*, *Thalassiosira*, and *Cylindrotheca*), nanophytoplankton, picophytoplankton, and unclassified dinoflagellates. PGB exhibited the highest carbon abundance and second highest Chla biomass and median community richness (10 taxa) in samples where PGB was dominant. Interactive-forward CCA revealed that these taxa (Figure 3a, green symbols) exhibited a significant, positive relationship ($p < 0.05$) with density, salinity, and depth where dissolved inorganic nitrogen (DIN) and P concentrations were higher (Table S4). Like PGA, many of these taxa are commonly associated with spring blooms (Daubjerg, 2000; Gradinger, 1996; von Quillfeldt, 2000b). Brown et al. (2015) observed that during ICESCAPE 2010 and 2011, the subsurface chlorophyll maximum SCM formed at least 1 month prior to sea ice retreat and was seeded by some members of the under-ice phytoplankton bloom (PGA). Once sea ice had fully retreated, the SCM was found at a depth of 15–30 m, deeper than the net primary productivity maximum (Brown et al., 2015). Nanophytoplankton and picophytoplankton were observed in 99% of the samples, under both sea-ice-covered and sea-ice-free conditions and may be considered cosmopolitan within this region (Text S2).

The fourth cluster, phytoplankton group C (PGC; Figure 2) or oligotrophic-type taxa included a chrysophyte (*Dinobryon*), four diatom taxa (*Thalassionema*, *Leptocylindrus*, *Melosira*, and *Rhizosolenia*), a dinoflagellate (*Polarella*), and a silicoflagellate (*Dictyocha*). Interactive-forward CCA revealed that these taxa (Figure 3a, orange symbols) exhibited a significant, positive relationship ($p < 0.05$) with the vectors *Temp* and *Light*. This group was also characterized with the lowest mean Chla biomass, carbon abundance, and median community richness (3) in samples where PGC was dominant. PGC was observed at sampling sites no longer

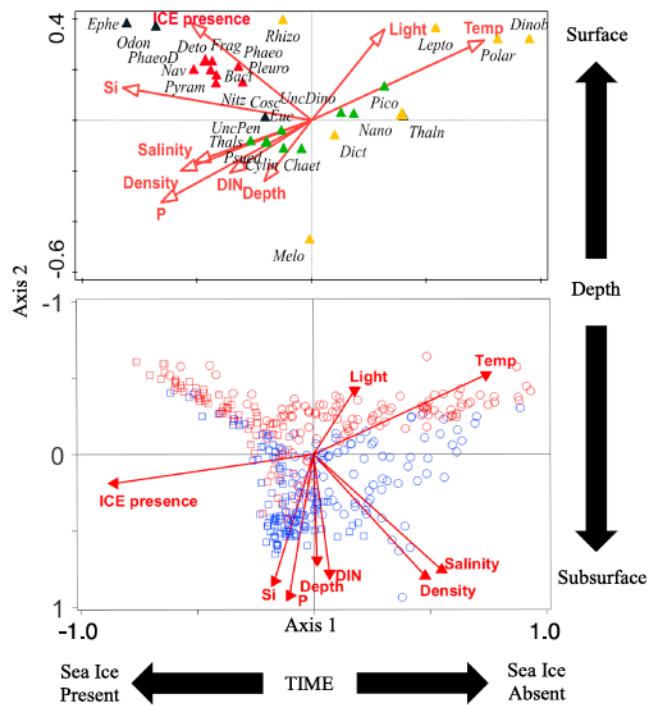


Figure 3. (a) The canonical correspondence analysis biplot shows the relationships between observed phytoplankton taxa and the environmental variables where black triangles represent rare taxa, red triangles represent phytoplankton group A, green triangles represent phytoplankton group B, and orange triangles represent phytoplankton group C as determined from cluster analysis. (b) The principle component analysis biplot shows the relationship between samples and the environmental variables where red squares represent samples collected at depths shallower than 25 m near the ice edge or underneath the ice, blue squares represent samples collected at depths deeper than 25 m near the ice edge or underneath the sea ice, blue circles represent samples collected at depths deeper than 25 m in a location no longer covered by sea ice, and red circles represent samples collected at depths shallower than 25 m in a location no longer covered by sea ice. Axes were flipped to match the canonical correspondence analysis biplot.

where red symbols represent depths shallower than 25 m and blue symbols represent samples collected deeper than 25 m. We found that samples collected at depths shallower than 25 m (red symbols) or in a sea-ice-free location (circles) were associated with higher water temperatures and greater light. Samples collected at depths greater than 25 m (blue symbols) and those collected underneath the ice (squares) were positively associated with nutrients, salinity, density, and depth (PC-axis 2). Density and salinity followed similar patterns as salinity drives stratification in high latitude seas, while subtropical seas are stratified by temperature (Carmack, 2007). The parameter ICE presence explained the variability of the sampling sites across the PC-axis 1, where sites collected underneath the ice (squares) are found along the left side of the plot and sites no longer covered by sea ice (circles) were distributed along the right side of the plot. Our inclusion of an index for sea ice presence in the statistical analyses proved to be a necessary explanatory factor to group the samples.

3.3. Environmental Forcing and Phytoplankton Spatial Distribution

CA and CCA revealed three major phytoplankton groups based on the distributional patterns of the phytoplankton taxa related to nutrients (particularly Si), temperature, light, and sea ice. Based on PCA, we concluded that the distributional pattern of the environmental variables was related to both sample depth and sea ice extent. These patterns were evident both vertically in the water column and horizontally in space. Therefore, the PCA and CCA biplots reflect spatial variations related to sea ice extent. CCA-axis 1 is representative of the effect of time or the seasonal transition of sea ice cover (negative CCA-axis 1) to

covered with sea ice, with the exception of *Rhizosolenia*. These taxa represent remnants of sea-ice-presence, such as *Polarella*, found in sea ice and can form cysts (Montresor et al., 2003) and taxa that are typically found in fresher, low-nutrient conditions, that is, *Rhizosolenia* (e.g., Villareal, 1990), *Dinobryon* (e.g., Balzano et al., 2012), and *Leptocylindrus* (e.g., Davis et al., 1980). An oligotrophic-type ecosystem (depleted nitrate) was created when the spring under-ice bloom depleted the nutrients in the surface waters supporting lower phytoplankton biomass similar to that described in Ardyna et al. (2011) and G. Tremblay et al. (2009) for the Canadian High Arctic.

From these analyses, we separated the phytoplankton assemblages into four groups. PGA was found as part of the under-ice blooms, in the presence of sea ice and greater Si. PGB dominated the SCM associated with greater DIN and P and was partially seeded by the under-ice phytoplankton community. PGC was found primarily in warm, nutrient-depleted, sea-ice-free waters. Next, we discuss the environmental forcing that shaped the spatial distribution of these groups.

3.2. Water Column Structure Explained by PCA

Using PCA, the measured environmental variables (Table S2) in samples collected from CTD profiles were grouped based on similar environmental characteristics and, using vectors to represent the environmental parameters, produced an ordination diagram or biplot to illustrate the relationship between the samples and environmental parameters. The direction and length of the vectors determine the direction at which each parameter increased the most and the rate of change of each parameter with the samples. At first glance, we see a clear distribution of the vectors along the PC-axis 2 of the biplot, explaining 48% of the variation (Figure 3b), where the magnitude of light and temperature increase in one direction and all other parameters, except ICE presence, increase in the opposite direction. The ICE presence vector explained 21% of the variation in the direction of PC-axis 1. We went a step further to distinguish each sample based on whether they were collected underneath the sea ice (squares) or in open water (circles) and if there was a depth dependence to the distribution of the samples,

open water (positive CCA-axis 1). The CCA-axis 2 dictates the vertical distribution of phytoplankton taxa in the water column in response to nutrient availability. Sea ice extent, and its effect on nutrient availability, SST, and stratification, is clearly a major driver of the dynamics of the three phytoplankton groups in this study.

The presence of PGA appears to be driven by the favorable conditions created by sea ice, such as meltwater-induced stratification (allows them to stay at the surface to access light) and higher Si and DIN concentrations, indicated by the median ratios of P:Si and DIN:Si (0.041 and 0.339, respectively, at under-ice bloom stations 56–101; Laney & Sosik, 2014). Large diatoms, particularly *Bacteriosira*, *Fragilaropsis*, *Detonula*, *Pleurosigma*, and *Navicula*, flourish in the high nutrient, low turbulence environment created by the presence of sea ice and melting ice. Margalef's original schematic placed large diatoms in the top right-hand corner of the diagram associated with high nutrients and low turbulence. The redrawn version of the schematic by Balch (2004) includes harmful algal bloom dinoflagellates in the top left-hand corner associated with high nutrients and low turbulence. Since there are no harmful algal bloom dinoflagellates observed in these waters, we can replace this group with the large diatoms observed in this study. In contrast, when the nutrients become depleted at the surface by the spring phytoplankton bloom, PGB forms an SCM deeper in the water column where nutrients are more abundant. PGB includes some taxa from the under-ice phytoplankton community already acclimated to low light conditions at depth. As open water duration lengthens, the surface ocean warms and become depleted of nutrients. PGC is observed in the warmer, nutrient depleted surface ocean as indicated by the median ratios of P:Si and DIN:Si (0.182 and 0.022, respectively). By characterizing phytoplankton dynamics relative to the presence or absence of sea ice using statistical tools, we have uncovered feedback mechanisms of climate change on critical features of the water column in the Chukchi Sea. Moreover, a new interpretation of Margalef's mandala using the results from this study highlights the continued importance of Margalef's conceptual model in understanding environmental drivers on phytoplankton communities.

3.4. Feedbacks of Climate Change

Using the output of these analyses, we can begin to elicit the implications of earlier sea ice retreat, thinning ice, reduction of sea ice extent and their feedbacks of warmer SST, and enhanced stratification in this system. Through our knowledge of ecosystem function and the structure of phytoplankton communities, we can make a prediction about how the three phytoplankton groups revealed in this study will behave in the future northern Chukchi and western Beaufort Seas and make inferences regarding the transfer pathways of phytoplankton carbon. Based on the current trajectory of Arctic climatology, we expect to see a lengthening of open water duration where PGC will be favored for a longer period than PGA and PGB. The fate of phytoplankton carbon will be determined by the productivity rates and total biomass of each phytoplankton group present in the system. Within our current framework of understanding, an ecosystem characterized by low chlorophyll and carbon biomass and depleted nutrients will subsist on regenerated production, while an ecosystem dominated by large diatoms and replete with nutrients represents new production (Hill et al., 2005). With the new analyses, the biomass of PGC will be lower than the diatom-rich groups PGB and PGC. We expect to see lower net primary productivity rates of PGC resembling those observed in the summer of 2011, where lower simulated in situ net primary productivity (e.g., $0.484 \text{ g-C-m}^{-2}\text{-day}^{-1}$) was measured in a region dominated by PGC compared to the region dominated by PGA and PGB (e.g., 6.726 and $1.275 \text{ g-C-m}^{-2}\text{-day}^{-1}$). Recent work by Ardyna et al. (2017) characterized shifts from eutrophic to oligotrophic conditions in the Canadian Arctic that were also driven by sea ice cover and nutrient depletion. We believe this study and others mentioned throughout this paper (Ardyna et al., 2011; Hill et al., 2005; Selz et al., 2017) improve our understanding of this ecosystem.

4. Conclusions

The objective of this study was to uncover the underlying mechanisms that drive phytoplankton community richness and spatial patterns in the northern Chukchi and western Beaufort Seas comparing rare data collected during a single field campaign in sea-ice-cover and sea-ice-free conditions. We went beyond Chla to consider carbon quantity and phytoplankton phenotypes by including phytoplankton taxonomic data in the analyses. It is important to emphasize the paucity of high resolution phytoplankton community data in this region with coincident measurements of hydrochemistry, making this a unique data set. We

confirmed that phytoplankton community structure was driven by stratification, nutrients, and light. We identified three major phytoplankton groups related to environmental variables in the Chukchi Sea. This study identifies a group of phytoplankton, PGC, typical of open water that adds to previously published identification of communities more likely to be found in sea ice PGA and PGB. Longer open water duration and lower phytoplankton carbon biomass could have implications for the upper trophic level consumers of the food web that rely on phytoplankton carbon for food. A shift in food web dynamics related to changes in phytoplankton community composition is likely to impact both food quantity and quality, comparable to those observed in the northern Bering Sea (Grebmeier et al., 2006) and western Antarctic Peninsula where the phytoplankton community has shifted from mainly large diatoms to picophytoplankton and nanoflagellates (Moline et al., 2004; Montes-Hugo et al., 2009; Smith et al., 2012). Notably, we applied a sea ice index that served as a proxy for the seasonality that controls phytoplankton life strategies in this region. Our hope is that the results from this study will assist the community in generating accurate models of phytoplankton community composition in the global ocean in response to climate change.

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References

- Ardyna, M., Gosselin, M., Michel, C., Poulin, M., & Tremblay, J. (2011). Environmental forcing of phytoplankton community structure and function in the Canadian High Arctic contrasting oligotrophic and eutrophic regions. *Marine Ecology Progress Series*, 442, 37–57.
- Ardyna, M., Babin, M., Devred, E., Forest, A., Gosselin, M., Raimbault, P., & Tremblay, J. É. (2017). Shelf-basin gradients shape ecological phytoplankton niches and community composition in the coastal Arctic Ocean (Beaufort Sea). *Limnology and oceanography*, 62(5), 2113–2132.
- Armstrong, F., Steams, C., & Strickland, J. (1967). The measurement of upwelling and subsequent biological process by means of the Technicon Autoanalyzer® and associated equipment. Paper presented at the Deep Sea Research and Oceanographic Abstracts.
- Arrigo, K. R. (2015). Impacts of climate on ecosystems and chemistry of the Arctic Pacific Environment (ICESCAPE). *Deep-Sea Research Part I*, 118, 1–6.
- Arrigo, K. R., Perovich, D. K., Pickart, R. S., Brown, Z. W., van Dijken, G. L., Lowry, K. E., et al. (2014). Phytoplankton blooms beneath the sea ice in the Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 105, 1–16.
- Arrigo, K. R., & van Dijken, G. L. (2015). Continued increases in Arctic Ocean primary production. *Progress in Oceanography*, 136, 60–70.
- Balch, W. M. (2004). Re-evaluation of the physiological ecology of coccolithophores. In *Coccolithophores* (pp. 165–190). Berlin, Heidelberg: Springer.
- Balzano, S., Gourvil, P., Siano, R., Chanoine, M., Marie, D., Lessard, S., et al. (2012). Diversity of cultured photosynthetic flagellates in the northeast Pacific and Arctic Oceans in summer. *Biogeosciences*, 9(11), 4553.
- Bernhardt, H., & Wilhelms, A. (1967). The continuous determination of low level iron, soluble phosphate and total phosphate with the autoanalyzer. Paper presented at the Technicon Symposia.
- Brown, Z. W., Lowry, K. E., Palmer, M. A., van Dijken, G. L., Mills, M. M., Pickart, R. S., & Arrigo, K. R. (2015). Characterizing the subsurface chlorophyll a maximum in the Chukchi Sea and Canada Basin. *Deep Sea Research Part II: Topical Studies in Oceanography*, 118, 88–104.
- Carmack, E. C. (2007). The alpha/beta ocean distinction: A perspective on freshwater fluxes, convection, nutrients and productivity in high-latitude seas. *Deep Sea Research Part II: Topical Studies in Oceanography*, 54(23), 2578–2598. <https://doi.org/10.1016/j.dsro.2007.08.018>
- Daugbjerg, N. (2000). *Pyramimonas tychotreta*, sp. nov. (Prasinophyceae), a new marine species from Antarctica: Light and electron microscopy of the motile stage and notes on growth rates. *Journal of Phycology*, 36(1), 160–171.
- Davis, C. O., Hollibaugh, J. T., Seibert, D. L., Thomas, W. H., & Harrison, P. J. (1980). Formation of resting spores by *Leptocylindrus danicus* (Bacillariophyceae) in a controlled experimental ecosystem 1. *Journal of Phycology*, 16(2), 296–302.
- Frey, K. E., Moore, G., Cooper, L. W., & Grebmeier, J. M. (2015). Divergent patterns of recent sea ice cover across the Bering, Chukchi, and Beaufort seas of the Pacific Arctic Region. *Progress in Oceanography*, 136, 32–49.
- Fripijat, F., Tison, J.-L., André, L., Notz, D., & Delille, B. (2014). Biogenic silica recycling in sea ice inferred from Si-isotopes: Constraints from Arctic winter first-year sea ice. *Biogeochemistry*, 119(1–3), 25–33.
- Glibert, P. M. (2016). Margalef revisited: A new phytoplankton mandala incorporating twelve dimensions, including nutritional physiology. *Harmful Algae*, 55, 25–30. <https://doi.org/10.1016/j.hal.2016.01.008>
- Gradinger, R. (1996). Occurrence of an algal bloom under Arctic pack ice. *Marine Ecology Progress Series*, 301–305.
- Grebmeier, J. M., Bluhm, B. A., Cooper, L. W., Danielson, S. L., Arrigo, K. R., Blanchard, A. L., et al. (2015). Ecosystem characteristics and processes facilitating persistent macrobenthic biomass hotspots and associated benthivory in the Pacific Arctic. *Progress in Oceanography*, 136, 92–114.
- Grebmeier, J. M., Overland, J. E., Moore, S. E., Farley, E. V., Carmack, E. C., Cooper, L. W., et al. (2006). A major ecosystem shift in the northern Bering Sea. *Science*, 311(5766), 1461–1464.
- Hill, V., Ardyna, M., Lee, S. H., & Varela, D. E. (2017). Decadal trends in phytoplankton production in the Pacific Arctic Region from 1950 to 2012. *Deep Sea Research Part II: Topical Studies in Oceanography*.
- Hill, V., & Cota, G. (2005). Spatial patterns of primary production on the shelf, slope and basin of the Western Arctic in 2002. *Deep Sea Research Part II: Topical Studies in Oceanography*, 52(24), 3344–3354.
- Hill, V., Cota, G., & Stockwell, D. (2005). Spring and summer phytoplankton communities in the Chukchi and Eastern Beaufort Seas. *Deep Sea Research Part II: Topical Studies in Oceanography*, 52(24), 3369–3385.
- Hooker, S. B., Van Heukelem, L., Thomas, C. S., Claustre, H., Ras, J., Barlow, R. et al. (2005). The second SeaWiFS HPLC analysis round-robin experiment (SeaHARRE-2). NASA Technical Memorandum, 212785, 124.
- Kérouel, R., & Aminot, A. (1997). Fluorometric determination of ammonia in sea and estuarine waters by direct segmented flow analysis. *Marine Chemistry*, 57(3–4), 265–275.
- Laney, S. R., & Sosik, H. M. (2014). Phytoplankton assemblage structure in and around a massive under-ice bloom in the Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 105, 30–41.

- Lee, S. H., Whittlestone, T. E., & Kang, S.-H. (2007). Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea. *Continental Shelf Research*, 27(17), 2231–2249.
- Li, W. K., McLaughlin, F. A., Lovejoy, C., & Carmack, E. C. (2009). Smallest algae thrive as the Arctic Ocean freshens. *Science*, 326(5952), 539–539.
- Lowry, K. E., Pickart, R. S., Mills, M. M., Brown, Z. W., van Dijken, G. L., Bates, N. R., & Arrigo, K. R. (2015). The influence of winter water on phytoplankton blooms in the Chukchi Sea. *Deep Sea Research Part II: Topical Studies in Oceanography*, 118, 53–72.
- Margalef, R. (1978). Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta*, 1(4), 493–509.
- Mathis, J. T., Grebmeier, J. M., Hansell, D. A., Hopcroft, R. R., Kirchman, D. L., Lee, S. H., et al. (2014). Carbon biogeochemistry of the Western Arctic: Primary production, carbon export and the controls on ocean acidification. In *The Pacific Arctic Region* (pp. 223–268). Dordrecht, Heidelberg, New York, London: Springer.
- Menden-Deuer, S., & Lessard, E. J. (2000). Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology and Oceanography*, 45(3), 569–579.
- Moberg, E. A., & Sosik, H. M. (2012). Distance maps to estimate cell volume from two-dimensional plankton images. *Limnology and Oceanography: Methods*, 10(4), 278–288.
- Moline, M. A., Claustre, H., Frazer, T. K., Schofield, O., & Vernet, M. (2004). Alteration of the food web along the Antarctic Peninsula in response to a regional warming trend. *Global Change Biology*, 10(12), 1973–1980.
- Montes-Hugo, M., Doney, S. C., Ducklow, H. W., Fraser, W., Martinson, D., Stammerjohn, S. E., & Schofield, O. (2009). Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science*, 323(5920), 1470–1473.
- Montresor, M., Lovejoy, C., Orsini, L., Procaccini, G., & Roy, S. (2003). Bipolar distribution of the cyst-forming dinoflagellate *Polella glacialis*. *Polar Biology*, 26(3), 186–194.
- Nishino, S., Kawaguchi, Y., Inoue, J., Hirawake, T., Fujiwara, A., Futsuki, R., et al. (2015). Nutrient supply and biological response to wind-induced mixing, inertial motion, internal waves, and currents in the northern Chukchi Sea. *Journal of Geophysical Research: Oceans*, 120, 1975–1992. <https://doi.org/10.1002/2014JC010407>
- Olson, R. J., & Sosik, H. M. (2007). A submersible imaging-in-flow instrument to analyze nano-and microplankton: Imaging FlowCytobot. *Limnology and Oceanography: Methods*, 5(6), 195–203.
- Overland, J. E., & Wang, M. (2013). When will the summer Arctic be nearly sea ice free? *Geophysical Research Letters*, 40, 2097–2101. <https://doi.org/10.1029/grl50316>
- Overpeck, J. T., Sturm, M., Francis, J. A., Perovich, D. K., Serreze, M. C., Benner, R., et al. (2005). Arctic system on trajectory to new, seasonally ice-free state. *Eos, Transactions American Geophysical Union*, 86(34), 309–313.
- Selz, V., Laney, S., Arnsten, A. E., Lewis, K. M., Lowry, K. E., Joy-Warren, H. L., et al. (2017). Ice algal communities in the Chukchi and Beaufort Seas in spring and early summer: Composition, distribution, and coupling with phytoplankton assemblages: Ice algal-phytoplankton coupling in Chukchi Sea. *Limnology and Oceanography*, 63(3), 1109–1133. <https://doi.org/10.1002/lno.10757>
- Smith, C. R., DeMaster, D. J., Thomas, C., Sršen, P., Grange, L., Evrard, V., & DeLeo, F. (2012). Pelagic-benthic coupling, food banks, and climate change on the West Antarctic Peninsula Shelf. *Oceanography*, 25(3), 188–201.
- Spreen, G., Kaleschke, L., & Heygster, G. (2008). Sea ice remote sensing using AMSR-E 89-GHz channels. *Journal of Geophysical Research*, 113, C02S03. <https://doi.org/10.1029/2005JC003384>
- Ter Braak, C. J., & Verdonschot, P. F. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences*, 57(3), 255–289.
- Tremblay, G., Belzile, C., Gosselin, M., Poulin, M., Roy, S., & Tremblay, J.-É. (2009). Late summer phytoplankton distribution along a 3500 km transect in Canadian Arctic waters: Strong numerical dominance by picoeukaryotes. *Aquatic Microbial Ecology*, 54, 55–70.
- Tremblay, J.-É., Simpson, K., Martin, J., Miller, L., Gratton, Y., Barber, D., & Price, N. M. (2008). Vertical stability and the annual dynamics of nutrients and chlorophyll fluorescence in the coastal, southeast Beaufort Sea. *Journal of Geophysical Research*, 113, C07S90. <https://doi.org/10.1029/2007JC004547>
- Van Heukelem, L., & Thomas, C. S. (2001). Computer-assisted high-performance liquid chromatography method development with applications to the isolation and analysis of phytoplankton pigments. *Journal of Chromatography A*, 910(1), 31–49.
- Villareal, T. A. (1990). Laboratory culture and preliminary characterization of the nitrogen-fixing Rhizosolenia-Richelia symbiosis. *Marine Ecology*, 11(2), 117–132.
- von Quillfeldt, C. (2000a). Common diatom species in Arctic spring blooms: Their distribution and abundance. *Botanica Marina*, 43(6), 499–516.
- von Quillfeldt, C. H. (2000b). *Pleurosigma tenuiforme* spec. nov.; a marine Pleurosigma species with long, slender apices, occurring in Arctic regions. *Diatom Research*, 15(2), 221–236.
- von Quillfeldt, C. H., Ambrose, W. G., & Clough, L. M. (2003). High number of diatom species in first-year ice from the Chukchi Sea. *Polar Biology*, 26(12), 806–818.
- Werner, I., Ikävalko, J., & Schünemann, H. (2007). Sea-ice algae in Arctic pack ice during late winter. *Polar Biology*, 30(11), 1493–1504.
- Woodgate, R. A., Aagaard, K., Swift, J. H., Falkner, K. K., & Smethie, W. M. (2005). Pacific ventilation of the Arctic Ocean's lower halocline by upwelling and diapycnal mixing over the continental margin. *Geophysical Research Letters*, 32, L18609. <https://doi.org/10.1029/2005GL023999>