Temporal and Light-Dependent Variability of Algal Communities In Land-Fast Arctic Sea Ice

by

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ABSTRACT

Sea ice algae dominated by diatoms inhabit the brine channels of the Arctic sea ice and serve as the base of the Arctic marine food web in the spring. I studied sea ice diatoms in the bottom 10 cm of first year land-fast sea ice off the coast of Barrow, AK, in spring of 2011, 2012, and 2013. I investigated the variability in the biomass and the community composition of these sea-ice diatoms between bloom phases, as a function of overlying snow depth and over time. The dominant genera were the pennate diatoms *Nitzschia, Navicula, Thalassiothrix,* and *Fragilariopsis* with only a minor contribution by centric diatoms. While diatom biomass as estimated by organic carbon changed significantly between early, peak, and declining bloom phases (average of 1.6 mg C L^{-1}, 5.7 mg C L^{-1}, and 1.0 mg C L^{-1}, respectively), the relative ratio of the dominant diatom groups did not change. However, after export, when the diatoms melt out of the ice into the underlying water, diatom biomass dropped by ~73% and the diatom community shifted to one dominated by centric diatoms. I also found that diatom biomass was ~77% lower under high snow cover (>20 cm) compared to low snow cover (<8 cm); however, the ratio of the diatom categories relative to particulate organic carbon (POC) was again unchanged. The diatom biomass was significantly different between the three sampling years (average of 2.4 mg C L^{-1} in 2011, 1.1 mg C L^{-1} in 2012, and 5.4 mg C L^{-1} in 2013, respectively) as was the contribution of all of the dominant genera to POC. I hypothesize the latter to be due to differences in the history of ice sheet formation each year. The temporal variability of these algal communities will influence their availability for pelagic or benthic consumers. Furthermore, in an Arctic that is changing rapidly with earlier sea ice and snowmelt, this time series study will constitute an important baseline

for further studies on how the changing Arctic influences the algal community immured in sea ice.

DEDICATION

I dedicate my thesis to my wife Alyson and to my family for their love and support throughout my education.

ACKNOWLEDGMENTS

I am grateful for the guidance and insight from Dr. Susanne Neuer and Dr. Andy Juhl who not only served on my committee but also helped me focus and provided me with opportunities to conduct fieldwork and gave me scholarly support when preparing for presentations as well as my thesis. I also thank Dr. Hilairy Hartnett for her commitment to serving on my committee as well as valuable input to my thesis. I also acknowledge Dr. Craig Aumack for support in the field and for supplying nutrient and chlorophyll data, as well as his perspective in regards to my thesis. Thanks to Anna Szymanski for help with identification of the diatoms. Thanks to the administration and students in the School of Life Sciences that have made earning my degree a pleasant experience. Thanks to the Neuer lab specifically Wei Deng, Francesca De Martini, and Demetra Hamill for providing support throughout this thesis as well as many presentations. Finally, I thank Mark Wiener and Cora McHugh for the many hours spent staring into a microscope to help with microscopic analyses of the sea ice samples.

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CHAPTER 1

INTRODUCTION

Sea ice serves as a vast habitat for organisms that reside in the brine channels of the ice (Horner & Schrader 1982, Bluhm et al. 2010). Ice algae dominate the primary production during the spring bloom in these ice-covered waters when there is relatively little phytoplankton in the water (Horner & Schrader 1982, Cota & Smith 1991). These ice algae are dominated by diatoms, both pennate and centric forms (Gradinger et al. 1999, Arrigo et al. 2010). The diatom assemblages are very diverse (731 individual species, von Quillfeldt et al. 2003, Poulin et al. 2011); however, the majority of the diatom biomass is dominated by a few genera of pennate diatoms (Horner 1985), mainly *Nitzschia frigida* in addition to *Navicula, Fragilariopsis, Thalassiothrix,* and *Fragilariopsis* (Horner et al. 1982, Hsaio 1980). Flagellated protists as well as invertebrate meiofauna graze on these primary producers, which serve as the base of the food web in the ice (Eddie et al. 2010, Gradinger et al. 1999b). The spring algal bloom is triggered by increasing solar radiation in the spring (Horner 1985, Cota and Smith, 1991) and the bloom continues until algae are exported out of the ice into the water column beneath (Horner 1985, Juhl et al. 2010, Juhl et al. 2011). Once exported, the sea ice algae are either grazed in the water column (Michel et al. 1996), or sink to the benthos where they are consumed by benthic animals or become part of a benthic algal community on the shallow shelf (Michel et al. 2002, McMahon et al. 2006).

In addition to the low sun angle in early spring, ice and overlying snow cover limit the amount of solar radiation that can penetrate to the bottom layer of the ice where most sea-ice algae are found (Gosselin et al. 1990, Mundy et al. 2005, Manes &

Gradinger 2009). Snow removal experiments have shown an increase in algal biomass in the bottom algal layer of the ice after removal of thin snow cover or partial removal of thick snow (≥9 cm, Juhl et al. 2010, Gradinger et al. 1991, Juhl & Krembs 2010, Lund-Hansen et al. 2014). While algae can proliferate under lower snow cover, this high light regime shortens the growing season by decreasing the insulation of the ice by the overlaying snow cover. This is important as snow cover in the Arctic has decreased 40% over the period of 1989 – 2009 (Screen & Simmonds 2012) and is predicted to continue along this trend (Overland et al. 2013). A decline in snow cover is further exacerbated by warming temperatures, changes in precipitation from snow to rain, and declining surface albedo (Screen & Simmonds 2011). Our ability to understand the community and the way it responds to the tightly coupled relationship with snow cover will help us predict how the bloom progression may change in coming years.

My research had three main objectives (based on results of previous studies) focused on the late spring bloom of sea ice algae in land-fast sea ice:

1. To understand the succession and community composition of sea ice algae among different phases of the bloom;
2. To understand the community composition of sea ice algae based on changes in snow cover; and
3. To understand the community composition of sea ice algae between three consecutive sampling years.

In this study I not only investigate bulk changes in sea ice algae, but also take into consideration the changes in community composition of the major taxa of diatoms in response to environmental conditions.

Numerous studies have described a consistent seasonal pattern in the biomass of ice algae in near-shore land-fast sea ice, as measured by chlorophyll a (hereafter referred to as chlorophyll) concentration (Horner et al. 1982, Gradinger et al. 1991, Juhl et al. 2011). In the spring, algal biomass begins to steadily increase with increasing light availability and declining snow cover, eventually reaching its greatest value during a peak bloom phase. As the spring temperatures continue to rise, the snow melts and the ice begins to ablate from the bottom of the ice and algae are released into the water column below (Juhl & Krembs 2010, Juhl et al. 2011, Aumack et al. 2014). This temporal succession has been well documented in terms of algal biomass (Clasby et al. 1976, Horner et al. 1982). Far fewer studies have focused on the composition of the ice algae community throughout the seasonal cycle.

Chlorophyll concentration has been found to be higher under lower snow cover compared to high snow; however when thick snow is removed, algal growth can be inhibited due to high light levels (Juhl & Krembs 2010, Lund-Hansen et al. 2014). Studies have also shown that diatoms are able to migrate vertically in the ice in response to changing light levels (Aumack et al. 2014). Lund-Hansen et al. (2014) found that abundance of most diatoms decreased when snow was removed, however since it was a low snow cover that was removed, the study attributed the decline in abundance to migration out of the ice. Understanding these community dynamics is important, as climate change has become an increasing concern in the high latitudes and more attention has been paid to the potential environmental impact in these environments. Numerous studies have focused on sea ice extent (Ogi & Rigor 2013, Zhang et al. 2013), temperature change (both atmospheric and water temperature increases; Arrigo et al.

2008, Comiso et al. 2014), diminishing snow coverage, or precipitation falling as rain instead of snow (Comiso et al. 2014). I am especially concerned with the results of climate models on future snow coverage and precipitation, which show that warming will lead to increased precipitation in the form of rain, as this will dramatically affect the snow cover which directly controls the length of the primary producers' growing season and the light availability for the sea ice algae (Horner et al. 1982, Juhl & Krembs 2010, Aumack et al. 2014).

The few Arctic time series studies that have been conducted in the same area have found spatial variability of algal biomass within very small areas, sometimes concentrations of biomass of an order of magnitude or more between adjacent ice cores (Eicken et al. 1991). Fewer studies have examined inter-annual differences at the same site. Studies in the Canadian Arctic and northern Alaska have reported large differences in chlorophyll concentration between sampling years (Horner et al. 1982, Arrigo et al. 2008, Lee et al. 2008). For example, Lee et al. (2008) found near Barrow, AK, that chlorophyll measured in 2003 was 2 to 3 times lower than it was when sampled the previous year at the same site.

I studied community changes and the composition of the dominant genera of sea ice algae (primarily diatoms) in the sea ice off the northern coast of Alaska near Barrow during the spring bloom. I pooled data from all three years of field sampling to make statistical inferences on the changes of community composition as a function of environmental conditions. This helps overcome the high degree of variability within the sea ice described above and allowed me to test changes in community composition as a function of bloom phases, snow depth and interannual differences. I used multiple

measures of ice algal community composition to determine changes in the composition of the dominant genera of sea ice algae (primarily diatoms) in the sea ice off the northern coast of Alaska near Barrow during the spring bloom. These measures included a) the relative ratio of the dominant diatoms found in the sea ice, b) the ratio of the biomass of centric to pennate diatoms, c) the ratio of small-to large-celled diatoms ($<5000\ \mu m^3$: $>5000\ \mu m^3$), d) the Shannon-Wiener index of species diversity, and e) heterotrophic protist biomass. My work can help form a baseline for how the diatom community develops in this habitat as conditions in the Arctic marine environment are predicted to change rapidly for the foreseeable future.

CHAPTER 2

METHODS

2.1 Field Sampling

Samples were collected from land-fast sea ice in the Chukchi Sea approximately 2 km northwest of Pt. Barrow, AK (71°23'3"N 156°32'1"W; Fig. 1) at a water depth of approximately 6-8 m during three consecutive field seasons (Spring of 2011, 2012, and 2013). The stations selected were free of rubble and pressure ridges, decreasing the chance of contaminating debris from the shore and/or re-suspended sediment. During 2011, field work was conducted from 5/3/11 to 5/26/11. Stations were selected and sampled at a range of snow depths (0 - 42 cm) in order to sample a range of light conditions. The snow depth at each station was measured with a meter stick and snow depth was consistent over all three years (± 2 cm) within a radius of approximately 2 m. In 2012, four stations were sampled during the spring (5/15/2012 – 6/4/2012) every 3 – 7 days. Initial snow depths varied among stations. Station 1 started with 5 cm, Station 2 with 1.5 cm, Station 3 with 21 cm, and Station 4 with 30 cm. In 2013, an artificial snow gradient was maintained to compare the effect of consistent snow cover on the sea ice algae community. Results from the initial sampling (5/11/13) and subsequent sampling (5/17/13) were included in the analysis of this study, in addition to natural snow depth sites. The original snow depth at the snow gradient site was between 12 and 15 cm, and the manipulated snow depths ranged from 0 to 25+ cm.

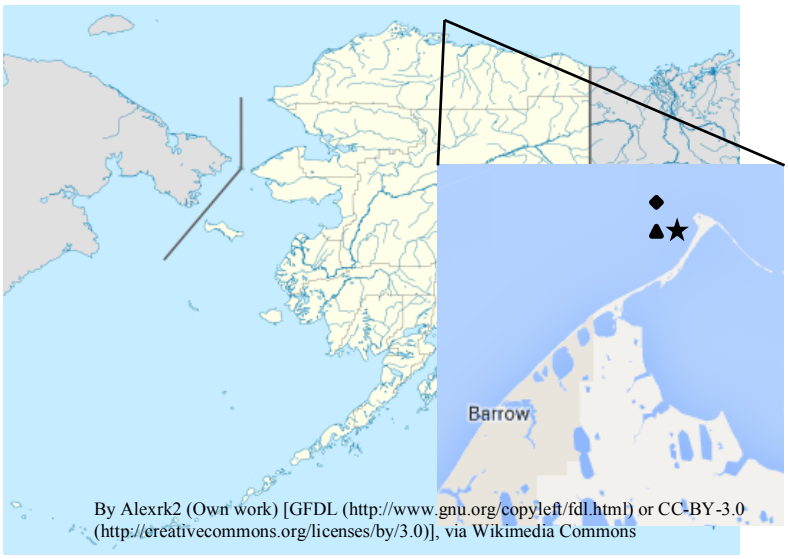

Fig. 1 Map of Alaska with an insert of Barrow and the general sampling locations for each field season (2011: triangle, 2012: diamond, 2013: star)

Before collecting ice cores, snow was cleared in an area of approximately 1 m^2 and cores were drilled using a hand powered portable drill attached to a 14-cm diameter ice corer (Kovacs, Roseburg, OR). After cores were removed from the ice, the bottom 10-cm section was sectioned off using a Bonesaw (G3, North Vancouver, BC) and immediately placed into polyethylene bags for transport in an insulated cooler to protect core sections from light and temperature changes. Two replicate cores were taken at each station (within 10 cm) for microscopy as well as bulk nutrients, which required separate processing techniques. All cores were taken to the Barrow Arctic Research Center (BARC) laboratory in Barrow, AK for processing. The first core from each station was melted at a ratio of 2:1 with particle free seawater. Seawater was collected from beneath the ice using a peristaltic pump by carefully lowering a weighted tube through the ice, making sure not to collect suspended ice or benthic sediment. The water was filtered in the laboratory using Sterivex™ capsules (pore size of 0.2 µm, Pall Corp. Port Washington, NY) and added to the sea ice to prevent osmotic shock to organisms during

melting (Gradinger et al. 1991, Juhl et al. 2011). The ice cores were melted in a dark walk-in incubator or refrigerator at 4˚C for approximately 48-72 hours, and then sampled for microscopy, chlorophyll, and particulate organic carbon (POC). The replicate core was melted without the addition of seawater, filtered, then frozen for nutrient and dissolved organic carbon (DOC) analyses after acidification with HCl.

2.2. Measurement of Particulate and Dissolved Constituents

Chlorophyll was determined by filtering the melted ice cores on to precombusted (6 h at 450° C) Whatmann GF/F filters until the filter began to turn green (volumes filtered ranged from 100 to 1000 mL). Filters were frozen (-20°C) until chlorophyll was extracted using 90% acetone for 24 h. A fluorometer (Turner Designs TD-700) was used to analyze chlorophyll fluorescence according to UNESCO (1994). POC samples were filtered onto precombusted (6 h at 450° C) Whatmann GF/F filters until the filter began to turn green (total volume filtered was typically 100 mL for sea ice samples and 1000 mL for sea water). Filters were then frozen (-20°C), and sent to Nutrient Analytical Services Laboratory at the Chesapeake Biological Laboratory of the University of Maryland for elemental analysis using a CE-440 Elemental Analyzer according to methods in USEPA (1997). Nutrient concentrations were measured colorimetrically using an Aquakem 250 for dissolved inorganic analytes following the methods set by the Technicon Corp.

2.3. Sample Preservation for Microscopy

For inverted light microscopy, melted sea ice samples were fixed with acid Lugol's solution (2.5% final concentration; Utermöhl 1931) in 20-ml scintillation vials.

The samples were kept at room temperature in darkness until they were transported to Arizona State University (ASU) for analysis. Concurrently, melted sea ice samples for epifluorescence microscopy were fixed with gluteraldehyde (0.1% final concentration) and refrigerated at 40°C for 24 hrs. Samples were then stained with 4', 6-diamidino-2-phenylindole (DAPI; 0.2% final concentration), a DNA binding agent, before 10 mL were filtered onto a polycarbonate filter (0.8µm pore size; GE Water & Process Technologies,). The filter was then sandwiched on a microscope slide with immersion oil and covered with a cover slip. The slides were kept frozen (-20˚C) and transport to ASU laboratory, where they were stored at -40˚C.

2.4. Microscopy

Samples fixed with Lugol's solution were settled for 24 hours using a 10-ml settling column (Utermöhl 1931) onto a slide chamber. The diatoms were counted using an Olympus inverted microscope and a 40x phase contrast objective. Diatoms were counted using 11 broad categories based on common Arctic diatom genera (as in Horner & Schrader 1982, Lund-Hansen et al, Hsaio 1980, Poulin et al. 2010, von Quillfeldt et al. 2003). These categories included: *Navicula, Amphiprora, Pinnularia, Cylindrotheca, Fragilariopsis, Luticola, Nitzschia, Gyrosigma, Pseudogomphonema,* and *Thalassiothrix* (Fig. 2). The centric diatoms, while only counted in one category ("centric"), included representatives of the genera *Melosira*, *Chaetoceros* and *Thalassiosira* (Fig. 2); the latter genus was the one most commonly found. In most cases a minimum of 30 cells in each category was counted. The categories were confirmed using scanning electron microscopy (SEM) as described below. The size range among all categories ranged from

5 µm to 210 µm, and was determined based on the largest dimension of the cell. Cell dimensions were measured in the x-y plane using a calibrated ocular grid. The hidden (z) dimension was calculated based on the geometric shape of the cell. To confirm that the hidden dimension was correctly calculated, some cells were turned using a fine needle and the third dimension was measured directly. The biovolume ($\mu m^3\ L^{-1}$) was calculated by multiplying cell abundance by the cell-specific biovolume. Using a carbon to volume factor specific for diatoms based on cell volume (<3000 μm^3 and >3000 μm^3), the biovolume was converted to biomass (mg C L^{-1}; Menden-Deuer et al. 2000).

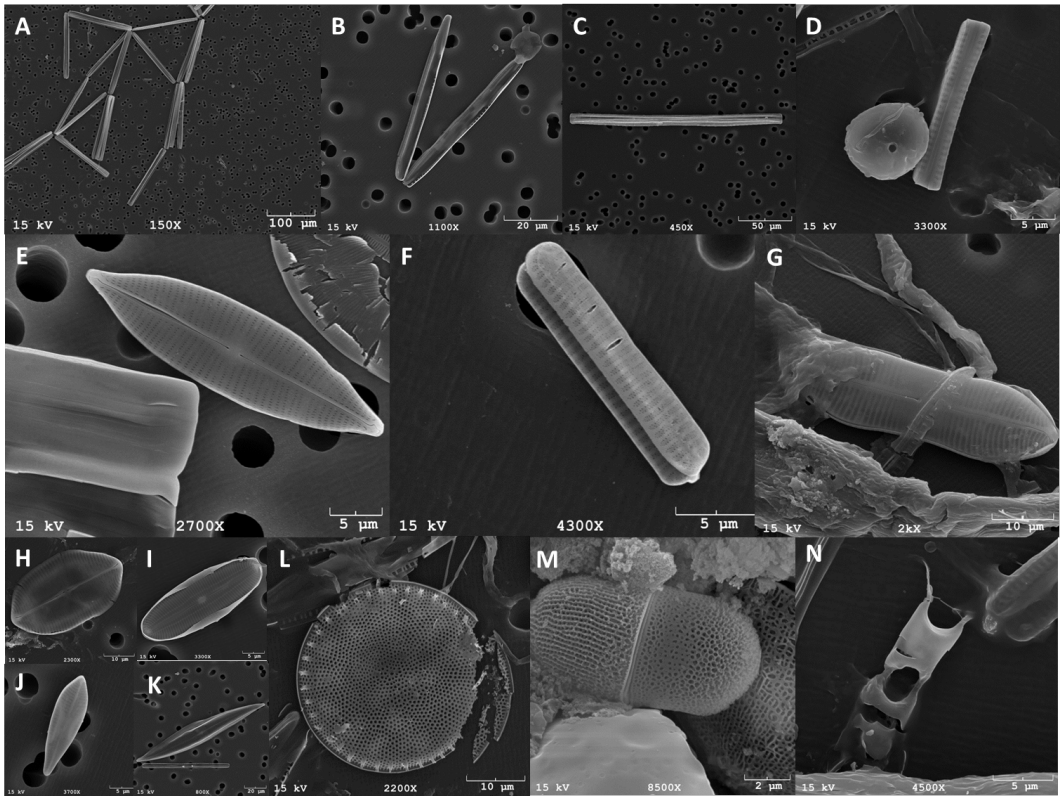

Fig. 2 SEM images of diatom categories. (A-K) Pennate diatoms: (A-C) *Nitzschia*, (D) *Thalassiothrix*, (E) *Navicula*, (F) *Fragilariopsis*, (G) *Pinnularia*, (H-I) *Luticola*, (J) Pseudogomphonema, (K) Gyrosigma; (L-N) Centric diatoms: (L) *Thalassiosira*, (M) *Melosira*, (N) *Chaetoceros*.

Epifluorescence microscopy was used to quantify the abundance and biovolume of heterotrophic protists (Fig. 3). All samples were counted using a Zeiss Axioscope A.1 epifluorescence microscope using a mercury short arc light source (OSRAM). Two different filter sets were used for microscopy, one for chlorophyll autofluorescence using Zeiss' filter combination Fs 09 (excitation wavelength 450-490 nm, emission wavelength >515 nm) and one for DAPI fluorescence using Zeiss' filter combination Fs 34 (excitation wavelength 375-400 nm, emission wavelength 420-480 nm). Heterotrophc protists consisted of nanoflagellates, as well as gymnodinoid and thecate dinoflagellates (Fig 3). Broad size categories were chosen for heterotrophic protists: <2 µm, 2-5 µm, 5-10 µm, 10-15 µm, and >15 µm (as in Eddie et al. 2010) and approximately 30 – 400 cells were counted in each size category. Biovolume ($\mu m^3 L^{-1}$) for each of the categories was calculated by averaging size in the respective size classes and approximating geometric shapes based on recommendations from HELCOM (Hillebrand et al.1999, Olenina et.al. 2006). Biovolume ($\mu m^3 L^{-1}$) was converted to biomass (mg C L^{-1}) using a conversion factor specific to heterotrophic protists (Menden-Deuer, et al. 2000).

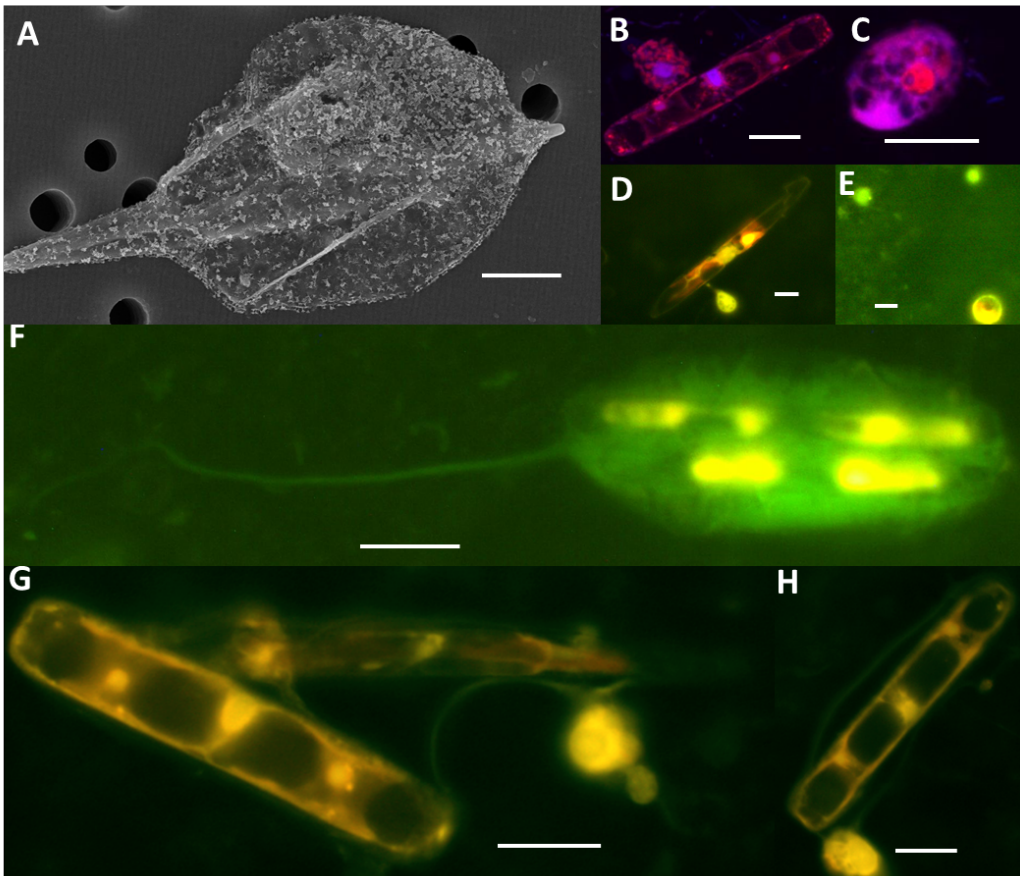

Fig. 3 SEM image of heterotrophic protist and their diatom prey (A), from laser confocal microscopy (B and C), and from epifluorescence microscopy with blue light excitation (C-G). 10 µm scale bar (white line).

Scanning electron microscopy (SEM) was used to obtain greater morphological differentiation of diatom frustules and to confirm the genus identified using inverted microscopy. I used a strong oxidizing agent (50% $KMnO_4$ and 16% HCl) or a combination of 50% (2:1) NO_4 and H_2SO_4 (Taylor et al. 2007) to remove organics. Enrichments from the field, as well as Lugol's iodine preserved samples, were used for SEM. The Lugol's preserved samples were filtered onto polycarbonate membrane filters (0.8 µm pore size), rinsed with 18.2 MΩ water to remove salt, and finally rinsed with 10 mL 6% H_2O_2 to remove organics. Samples were sputter-coated with a 10-15nm layer of

Au and analyzed using a JEOL 6300 SEM equipped with a LaB6 filament running at 12-18 kV. I compared diatom taxa in my SEM images with taxa described in Hsiao (1980), Horner et al. (1982), Round et al. (1990), and von Quillfeldt et al. (2003).

The diversity was calculated using the Shannon Wiener Index (H'):

$H' = \sum_i^S PilogePi$

where P is the fraction of the diatom biomass or abundance for each diatom taxon (i) identified, and S is the biomass or abundance of all taxa combined. All statistical tests were carried out using IBM SPSS 22 software. Further description on statistical analyses is provided in section 3.3.1.

CHAPTER 3

RESULTS

3.1. Environmental conditions

Air temperature data were collected by the Alaska Climate Research Center at Barrow Post Rogers AP (http://climate.gi.alaska.edu/acis_data). Temperatures varied between each year with coolest temperatures recorded in May 2012 compared to the same time-period in 2011 and 2013 (Table 1). Ice thickness was variable during the sampling period but was greatest in 2013. (Table 1).

Table 1. Sampling period, range of environmental temperatures (average for month of May) and ice thickness in each sampling year.

Year	Dates	Temperature (°C)	Ice Thickness (cm)
2011	5/1/11 - 5/31/11	-5.3	112 to 167
2012	5/1/12 - 6/4/12	-5.75	142 to 156
2013	5/1/13 - 6/4/13	-5.06	144 to 171

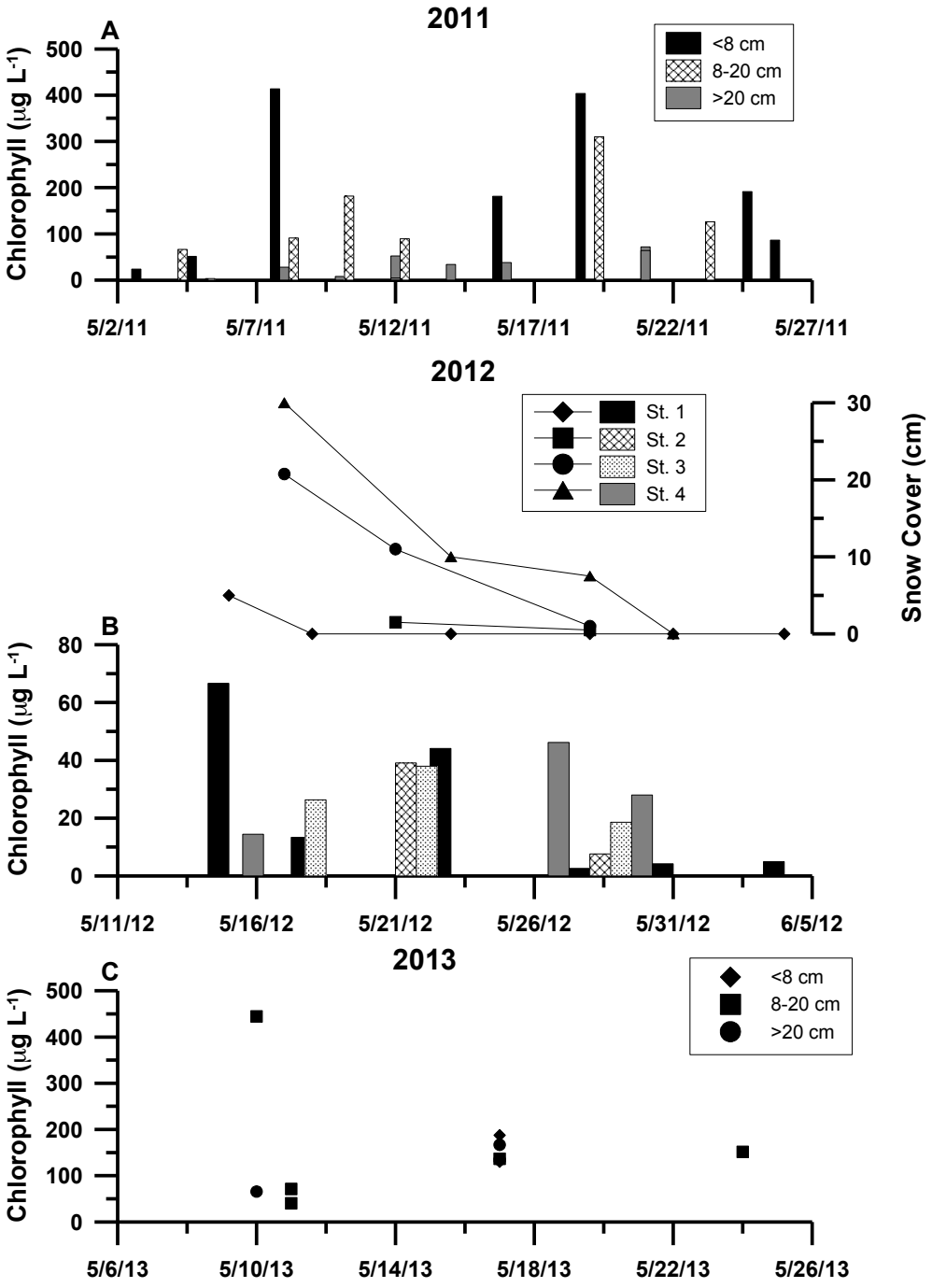

Fig. 4 Ice algal bloom development (as Chlorophyll a, ug L^{-1}) in each of the three years as function of snow depth. A. 2011. Stations separated by snow depth range. B. 2012. Chlorophyll a concentration and snow cover shown for each station sampled. C. 2013. Chlorophyll a shown for each station sampled. Symbol indicates snow depth range.

3.2 Dissolved and Particulate Matter in Sea Ice and Water Column

In 2011 Particulate Organic Carbon (POC), Dissolved Organic Carbon (DOC), Total N (Nitrogen), and P (Phosphorus) in the form of phosphate increased with decreasing snow cover (Table 2). Water column samples were less variable than ice samples and had generally higher nutrient concentrations compared to the lower sections of the sea ice (Table 2). Phosphate concentration was only measured in 2011 and was not found to be limiting in the water column based on Redfield ratio (C:N:P 39:6:1, compared to Redfield ratio of 106:16:1). Throughout the 2012 season, POC, DOC, Total N, and Silicate was greater in the ice with lower snow cover (Table 2). Throughout the spring bloom, POC and DOC decreased at stations 1 and 2 (lower snow sites) but increased at stations 3 and 4 (higher snow cover; Table 2). Dissolved Organic Nitrogen (DON) as well as Dissolved Inorganic Nitrogen (DIN) decreased at all stations. Silicate (SiO_4^{2-}) in the sea ice decreased at all stations to the detection limit by the end of sampling (0.83 μmol L^{-1}; Table 2). Based on modified Redfield ratios, which include silicate, there is evidence that silicate was limiting in 2012. The Redfield ratio for silicate is ~1:1 (N:Si), however, I found in 2012 that the ratio was closer to ~3:1 in the water column underneath the ice (Table 2; Brzezinski 1985). In 2013, POC was highest in the sea ice at intermediate snow depths with the second highest concentration under low snow cover. DON was highest at intermediate snow depths with the next highest concentration in the ice underneath the highest snow cover (Table 2). DIN was lowest at intermediate snow depths and highest in the ice underneath the greatest snow depth. Silicate concentration in the bottom ice was lower in 2013 (~0.1 μmol L^{-1}) than in 2012 (~3.0 μmol L^{-1}) and was lowest under the low snow cover sites. DOC was highest in

2013(~343 μmol L^{-1} initially) under intermediate snow cover with the lowest DOC concentration found at sites under the low snow cover (Table 2).

Table 2. Particulate Organic Carbon (POC), Total Nitrogen (N), Dissolved Organic Carbon (DOC), Dissolved Organic Nitrogen (DON), Dissolved Inorganic Nitrogen (DIN), Phosphorous (P, as PO_4^{3-}), Silicate (SiO_4^{2-}) determined in the 0-10 cm sections of the sea ice cores and water column throughout the field seasons (2011 – 2013). Values in 2011and 2013 based on snow cover range and average ± standard deviation is shown. Values from 2012 based on initial (T_0) and final values (T_f) at each station. Samples below detection limit indicated by *.

Station (2011)	Snow Cover (cm)	POC (mg L^{-1})	DOC (µmol L^{-1})	DON (µmol L^{-1})	DIN (µmol L^{-1})	P (µmol L^{-1})	SiO_4 (µmol L^{-1})	
N/A	< 8	3.38 ± 2.73	318.53 ± 360.71	N/A	N/A	3.39 ± 4.43	N/A	N/A
N/A	8 – 20	1.82 ± 1.64	257.37 ± 201.00	N/A	N/A	2.75 ± 6.05	N/A	N/A
N/A	>20	1.18 ± 0.93	97.41 ± 42.59	N/A	N/A	1.26 ± 1.16	N/A	N/A
N/A	Water	0.08 ± 0.02	117.33 ± 44.71	N/A	N/A	3.06 ± 0.18	N/A	N/A

Station (2012)	Snow Cover (cm)		POC (mg L^{-1})		DOC (µmol L^{-1})		DON (µmol L^{-1})		DIN (µmol L^{-1})		P (µmol L^{-1})		SiO_4 (µmol L^{-1})	
	T_0	T_f	T_0	T_f	T_0	T_f	T_0	T_f	T_0	T_f	T_0	T_f	T_0	T_f
1	5	0	1.4	0.29	139.88	57.45	12.77	4.72	2.94	0.28	N/A	N/A	1.66	0.83*
2	1.5	0.5	0.97	0.68	139.88	124.06	17.14	5.9	2.14	0.52	N/A	N/A	1.83	0.83*
3	20.75	1	0.63	1.12	91.59	180.67	14.9	10.81	2.24	0.62	N/A	N/A	7.49	0.83*
4	30	0	0.3	1.12	80.76	84.92	7.57	2.89	1	1.39	N/A	N/A	0.83	0.83*
Water	N/A	N/A	0.06	0.09	108.21	111.57	13.71	12.6	0.57	0.97	N/A	N/A	5.83	5.83

Station (2013)	Snow Cover (cm)	POC (mg L^{-1})	DOC (µmol L^{-1})	DON (µmol L^{-1})	DIN (µmol L^{-1})	P (µmol L^{-1})		SiO_4 (µmol L^{-1})
N/A	< 8	3.55 ± 0.28	268.51 ± 127.75	3.28 ± 0.99	0.70 ± 0.23	N/A	N/A	0.06 ± 0.03
N/A	8 – 20	3.84 ± 2.35	627.11 ± 472.62	4.18 ± 1.97	0.47 ± 0.17	N/A	N/A	0.24 ± 0.17
N/A	>20	2.94 ± 1.22	359.96 ± 42.59	3.80 ± 0.88	0.76 ± 0.44	N/A	N/A	0.11 ± 0.05
N/A	Water	0.12 ± 0.04	117.33 ± 45.95	1.00 ± 0.13	0.20 ± 0.04	N/A	N/A	0.81 ± 0.19

3.3 Development of sea ice communities

A greenish-brown layer was clearly visible in the bottom two to five centimeters of the ice cores (sea ice interface) indicative of the presence of sea ice algae (pigments were not seen anywhere else in the ice). Throughout the seasonal progression (specifically in 2012) the pigmented algal layer declined and was no longer visible towards the end of the sampling period at low snow sites.

3.3.1. Bloom Phase Determination and Statistical Testing

The spring algal bloom occurred each year in our study site and started with lower chlorophyll values and increased to a peak before declining (Fig. 5). To determine the effect of bloom phase on community composition, I separated the community development into five phases; early, intermediate, peak, declining, and post export. Phases were determined by taking into consideration the algal biomass (as chlorophyll, $\mu g\ L^{-1}$) of a given sample relative to the maximum biomass for that year, as well as snow cover (Table 3).

Table 3. Bloom phase determination based on the fraction of maximum chlorophyll concentration for a given field season and snow cover.

Bloom Phase	Chlorophyll (% of annual max)	Snow Cover (cm)
Early Bloom	<15	>5
Intermediate Bloom	15 - 50	>5
Peak Bloom	>50	n/a
Declining Bloom	15 - 50	<5
Post Export Bloom	<15	<5

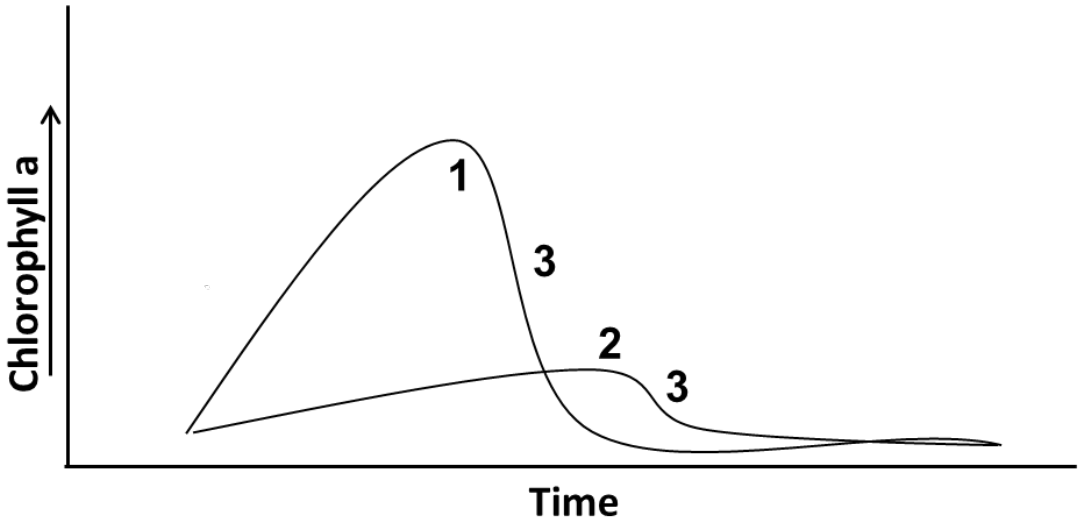

Fig. 5 Schematic representation of the sea ice algal bloom based on chlorophyll a at high and low snow cover site. (1) Typical low snow (high light) bloom development, (2), typical high snow (low light) bloom development; (3) export phases.

To compare the community composition under low and high snow cover (Fig. 5), peak bloom samples from all years were grouped by snow cover range (<8 cm, 8-20 cm and >20 cm). The low snow cover (<8 cm) and the high snow cover (>20 cm) conditions were compared using statistical tests described below. I chose these two snow depths because low snow cover (<8 cm) is considered to not impose light limitation with an approximate PAR (Photosynthetically Available Radiation) flux of >16 μmol photons m^{-2} s^{-1} (Aumack et. al. 2014) and high snow cover (>20 cm) is considered to result in light limitation with a PAR flux of ~3 μmol photons m^{-2} s^{-1} (Aumack et al. 2014). Light limiting snow covers were based on the light threshold known to initiate growth of sea ice diatoms (2.3 – 9.3 μmol photons m^{-2} s^{-1}, Horner 1985). Intermediate snow depths were excluded from analysis to avoid uncertainty regarding phase determinations. Statistical tests were used to test if significant differences existed in community

composition between bloom phases, snow depths and years. I compared the community composition between the three different years by grouping the three positive growth bloom phases defined previously (early, intermediate, and peak) together and separating them by year. My data were not normally distributed (Shapiro-Wilk test) and had unequal variance (F-test) so I used two non-parametric tests. For the two-sample tests I used the Wilcoxon Signed Ranked test and for the three-sample tests I used Kruskal-Wallis one-way analysis of variance. Kruskal-Wallis test results with significant outcomes were further tested using Dunn's multiple comparisons tests to find out which samples were different from each other.

3.3.2 Community Development

For each of the field seasons both pennate and centric diatoms were observed (Fig. 2). All of the pennate categories were represented (*Navicula, Amphiprora, Pinnularia, Cylindrotheca, Fragilariopsis, Luticola, Nitzschia, Gyrosigma, Pseudogomphonema,* and *Thalassiothrix)* and while I did not differentiate among centric diatoms, *Thalassiosira* was most commonly found in this category. I also observed heterotrophic protists (gymnodinoid, thecate dinoflagellates and pico- and nanoflagellates; Fig. 3) in high abundance (average of 1.7×10^{-7} cells L^{-1}) however they contributed relatively little to POC compared to diatoms (no more than 25%; see section 3.3.6). In 2012, I observed heterotrophic protist grazing, mainly by heterotrophic dinoflagellates, on diatoms with multiple types of feeding mechanisms (ingestion, pallium feeding, peduncle feeding; Fig. 3; Miller & Wheeler 2012) but not in 2013.

I observed the development of an algal bloom during each field season and under each snow depth. In 2011, I observed an algal bloom based on chlorophyll and biomass that increased in concentration up to the declining phase, however the sampling period concluded before the begin of the export phase. During the pre-bloom phase, chlorophyll concentration ranged from 3.4 to 52.3 μg L^{-1} (Table 4) with a snow depth range of 5 to 42 cm. Pennate diatoms dominated the diatom biomass (Table 4) with *Nitzschia* contributing 34% and *Navicula* contributing 21% of the total diatom biomass. During the peak bloom phase, chlorophyll concentration ranged from 310 - 414 μg L^{-1} (Table 4) with a snow depth range of 4 to 14 cm. Pennate diatoms again dominated the diatom biomass with *Nitzschia* contributing 54% to the total diatom biomass. During the declining phase, chlorophyll concentration ranged from 86 to 192 μg L^{-1} (Table 4) and snow cover ranged from 0 to 4.5 cm. Pennate diatoms continued to account for more of the diatom biomass than centric diatoms with the dominant taxa, *Nitzschia*, contributing 48%, and *Thalassiothrix* contributing 26% to total diatom biomass.

In 2012, data from the pre-bloom phase are not available because of the timing of the field season. While samples were collected earlier than a peak bloom phase, those samples were grouped into an intermediate phase because of the bloom development distinction. Most of the sampling in 2012 occurred later in the bloom, including the post export phase. During the peak bloom phase, chlorophyll concentration ranged from 37.9 - 66.7 μg L^{-1} with a snow depth range of 0 - 11 cm (Table 4). Pennate diatoms were dominant by *Nitzschia* contributing 42%, *Navicula* contributing 11%, and *Thalassiothrix* contributing 11% to the total diatom biomass. Heterotrophic protists were also present during the peak bloom phase and were found in all size ranges (<2 μm, 2-5 μm, 5-10 μm,

10-15 μm, and >15 μm) ranging from 0.03 - 0.17 mg C L^{-1}. During the declining phase, chlorophyll concentration ranged from 13.4 – 28.0 μg L^{-1} and snow cover ranged from 0 – 1 cm (Table 4). Pennate diatoms continued to dominate diatom biomass; however, the centric taxa category contributed 38% to total diatom biomass. Second, *Nitzschia* contributed 20% and *Navicula* contributed 16% to total diatom biomass. Heterotrophic protist biomass ranged from 0.09 – 0.10 mg C L^{-1}.

During the 2012 field season, the algal bloom occurred much earlier, which allowed for sampling after export. During the post export phase, chlorophyll concentration ranged from 2.3 - 7.6 μg L^{-1} with a snow depth range of 0 - 0.5 cm (Table 4). Centric diatoms were the dominant diatom (mostly contributed by *Thalassiosira)* category contributing 66% to the total diatom biomass, and *Nitzschia* and *Thalassiothrix* contributing 15% and 5%, respectively. Heterotrophic protists were also present in the post export phase ranging from 0.04 - 0.08 mg C L^{-1}.

In 2013, sampling occurred during the early to peak phase. During the pre-bloom phase, chlorophyll concentration ranged from 40.5 to 65.7 μg L^{-1} (Table 4) with a snow depth range of 11 to 30 cm. Pennate diatoms dominated the diatom biomass with *Nitzschia* contributing 56% and *Fragilariopsis* contributing 11% to the total diatom biomass. Heterotrophic protists were also present in the pre-bloom bloom phase ranging from 0.3 - 0.8 mg C L^{-1}. Only one sample from the peak bloom phase was collected (on 5-24-13) with a chlorophyll concentration of 444.7 μg L^{-1} (Table 4) and a snow depth of 10 cm. Pennate diatoms were dominant with *Nitzschia* and *Navicula* contributing 80% and 11% to total diatom biomass, respectively.

In the sections below, I will investigate differences in the development of the diatom community throughout the different bloom phases (3.3.3), the influence of snow cover on the biomass and composition of the diatom community (3.3.4) and the influence of interannual variability on the diatom community between each sampling year (3.3.5). Finally, in section 3.3.6, I test the influence of bloom phases, snow cover and interannual variability on the heterotrophic protist biomass and ratio of protist biomass to diatoms biomass.

3.3.3 Phase Dependent Community Composition

To test if diatom community composition was different between bloom phases, data from the respective bloom phases from all three years were pooled. To avoid error with sample selection, the extreme phases were compared first (Early, Peak, and Declining phases). Diatoms that contributed less than 5% on average to the total diatom biomass were grouped into an "other" pennate category. Results indicate that chlorophyll concentration and *Thalassiothrix* biomass were significantly different between the phases ($P = 0.025$ and 0.039, respectively calculated using Kruskal-Wallis tests; Table 4) and specifically Dunn's multiple comparison showed that chlorophyll ($\mu g\ L^{-1}$) and *Thalassiothrix* biomass were significantly higher between the early and peak bloom phases. Total diatom biomass (mg C L^{-1}) was highest during the peak bloom phase (Fig. 6A) however the high variability between samples resulted in non-significant differences (Table 4). The relative contribution of each of the pennate diatom categories showed slight changes between the three bloom phases but was also non-significant.

Table 4. Mean values and standard deviations (STD) of chlorophyll, diatom biomass, community composition, contribution of diatom biomass to overall particulate organic carbon (POC) and diversity between three bloom phases (Early, Peak, and Declining) of all sampling years. Kruskal-Wallis test results with P-value <0.05 indicated in bold specify significant differences between bloom phases.

Variable (unit)	Early Bloom		Peak Bloom		Declining		Kruskal Wallis
	mean	STD	mean	STD	mean	STD	H value Pr (>H)
Chlorophyll (μg L^{-1})	31.74	19.70	200.76	175.54	67.57	67.26	**0.025**
Diatom (mg C L^{-1})	1.61	1.76	5.73	6.30	1.02	0.55	0.153
Ratio of C:Chl	39.44	39.22	32.88	23.28	32.78	7.10	0.455
Pennate (mg C L^{-1})	1.41	1.52	5.33	6.13	0.80	0.62	0.182
Centric (mg C L^{-1})	0.20	0.27	0.40	0.31	0.23	0.10	0.173
Nitzschia (mg C L^{-1})	0.84	1.17	3.71	4.70	0.35	0.34	0.107
Navicula (mg C L^{-1})	0.17	0.11	0.61	0.73	0.13	0.05	0.630
Thalassiothrix (mg C L^{-1})	0.07	0.05	0.47	0.64	0.18	0.18	**0.039**
Fragilariopsis (mg C L^{-1})	0.14	0.20	0.23	0.34	0.04	0.02	0.727
Other Pennate (mg C L^{-1})	0.14	0.20	0.23	0.34	0.04	0.02	0.346
Diatom ratio (<5000 μm^3:>5000μm^3)	2.86	1.45	4.58	5.42	3.75	2.04	0.877
Diatom ratio (Pennate:Centric)	8.77	6.06	14.83	17.74	8.21	11.49	0.320
Diversity Index (H' by Abundance)	1.76	0.24	1.61	0.22	1.85	0.20	0.306
Diversity Index (H' by Biomass)	1.69	0.30	1.39	0.27	1.57	0.11	0.196
Nitzschia (Ratio of POC)	0.40	0.17	0.50	0.16	0.27	0.15	0.178
Navicula (Ratio of POC)	0.17	0.10	0.11	0.07	0.15	0.06	0.433
Thalassiothrix (Ratio of POC)	0.07	0.04	0.11	0.06	0.15	0.09	0.252
Fragilariopsis (Ratio of POC)	0.05	0.04	0.03	0.02	0.03	0.02	0.721

I compared the change in community composition between the post export phase and the peak bloom phase for 2012 because it was the only year where post export sampling occurred. Chlorophyll (μg L^{-1}), total diatom biomass (mg C L^{-1}), and C:Chl ratio were all significantly lower after export (P=0.009, 0.009, and 0.006 respectively; Table 5). The pennate diatom biomass dominated during the peak bloom phase with 1.30 mg C L^{-1}, then significantly decreased to 0.15 mg C L^{-1} during post export (P=0.009; Table 5). In contrast, centric diatom biomass decreased post export (0.37 to 0.30 mg C L^{-1}), but not significantly. Although the size ratio of the diatoms was not significantly different, the ratio of pennate:centric was significantly different with a change from 4.62 to 0.59 (P=0.009) from the bloom to post-export phase. The diversity index was not significantly different between phases; however, the ratio of *Nitzschia* and *Navicula* to total POC was significantly lower after export (Table 5).

Table 5. As in Table 4 for the comparison of the community between peak bloom and post export phase in 2012. Wilcoxon Signed-Rank test and P scores with significant values (P<0.05) in bold.

Variable (unit)	Peak Bloom		Post Export		Wilcoxon W
	mean	STD	mean	STD	W value Pr (>W)
Chlorophyll (μg L^{-1})	46.79	10.39	4.85	2.34	**0.009**
Diatom (mg C L^{-1})	1.67	0.93	0.45	0.05	**0.009**
Ratio of C:Chl	32.88	23.28	117.73	52.78	**0.006**
Pennate (mg C L^{-1})	1.30	0.82	0.15	0.05	**0.009**
Centric (mg C L^{-1})	0.37	0.20	0.30	0.09	0.754
Nitzschia (mg C L^{-1})	0.80	0.73	0.07	0.02	**0.009**
Navicula (mg C L^{-1})	0.16	0.13	0.02	0.01	**0.009**
Thalassiothrix (mg C L^{-1})	0.15	0.06	0.02	0.01	**0.009**
Fragilariopsis (mg C L^{-1})	0.05	0.06	0.01	0.01	0.117
Other Pennate (mg C L^{-1})	0.13	0.05	0.03	0.03	**0.016**
Diatom ratio (<5000 μm^3:>5000μm^3)	6.15	6.70	2.53	0.94	0.754
Diatom ratio (Pennate:Centric)	4.62	3.25	0.59	0.29	**0.009**
Diversity Index (H' by Abundance)	1.68	0.17	1.85	0.10	0.076
Diversity Index (H' by Biomass)	1.48	0.16	1.12	0.30	0.076
Nitzschia (Ratio of POC)	0.42	0.14	0.15	0.05	**0.009**
Navicula (Ratio of POC)	0.11	0.09	0.04	0.02	**0.047**
Thalassiothrix (Ratio of POC)	0.11	0.05	0.05	0.03	0.076
Fragilariopsis (Ratio of POC)	0.02	0.01	0.03	0.03	0.754

3.3.4 Light Dependent Community Composition

The effect of light availability (based on two snow depths (<8 cm and >20 cm) on community composition during peak bloom phases from all sampling years were tested using a non-parametric Wilcoxon signed rank test (Table 6). The lower snow depth was chosen as a depth where PAR was slightly above the threshold light level to initiate growth (2.3 and 9.3 μmol photons m^{-2} s^{-1}; Horner 1985). The higher snow cover (>20 cm) was chosen based on a lower PAR where light would limit growth (Mundy et al. 2005). Chlorophyll concentration and diatom biomass were significantly lower with high snow cover (P=0.047 and 0.008 respectively; Table 6). Between the two light conditions C:Chl was higher under low snow cover but the difference was not significant. Biomass (mg C L^{-1}) of the pennate and centric diatoms was significantly lower under light limiting snow cover (P= 0.008 and 0.047, respectively, Fig. 6). At the genus level, the biomass of *Nitzschia*, *Navicula*, and *Thalassiothrix* was significantly lower (P=0.008, 0.013, and 0.001 respectively) under high snow cover compared to low snow cover. Biomass of *Fragilariopsis* and the "other" pennate category was also lower but not significantly. The ratio of pennate:centric diatom biomass as well as small:large diatom sizes (<5000μm^3:>5000μm^3) showed no significant changes between snow depths. H' (by biomass) was significantly higher under high snow (P=0.026) and the ratio of *Nitzschia* to total POC was significantly lower under high snow cover (P=0.039).

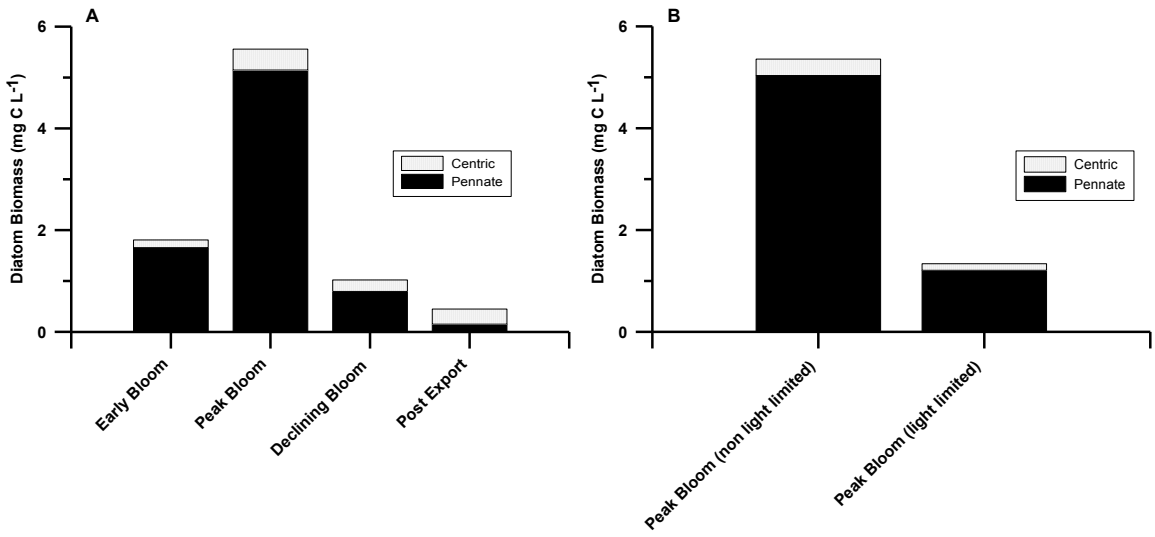

Fig. 6 A. Average diatom (pennate and centric) biomass (mg C L^{-1}) during all four bloom phases of all years (except post-bloom phase, only 2012 data could be used). B. Average diatom (Pennate and Centric) biomass (mg C L^{-1}) in the peak bloom phase of all three years under light limited or non-light limited conditions based on snow cover.

Table 6. As in Table 4, testing the effects of light on the sea ice community during peak bloom phases in all three years. Wilcoxon Signed-Rank test calculated and P score with significant values (P<0.05) in bold.

Variable (unit)	Peak Bloom (High Light)		Peak bloom (Low Light)		Wilcoxon W
	mean	STD	mean	STD	W value Pr (>W)
Chlorophyll (µg L^{-1})	154.46	138.75	54.49	46.46	**0.047**
Diatom (mg C L^{-1})	5.36	4.64	1.22	1.19	**0.008**
Ratio of C:Chl	27.72	8.04	21.04	9.40	0.058
Pennate (mg C L^{-1})	5.03	4.60	1.05	0.98	**0.008**
Centric (mg C L^{-1})	0.32	0.17	0.16	0.22	**0.047**
Nitzschia (mg C L^{-1})	3.15	2.95	0.56	0.63	**0.008**
Navicula (mg C L^{-1})	0.55	0.52	0.13	0.07	**0.013**
Thalassiothrix (mg C L^{-1})	0.58	0.65	0.06	0.04	**0.001**
Fragilariopsis (mg C L^{-1})	0.38	0.35	0.15	0.27	0.215
Other Pennate (mg C L^{-1})	0.38	0.38	0.16	0.09	0.160
Diatom ratio (<5000 µm^3:>5000µm^3)	4.21	5.76	3.44	2.60	0.620
Diatom ratio (Pennate:Centric)	17.26	17.60	9.86	7.94	0.400
Diversity Index (H' by Abundance)	1.66	0.19	1.74	0.23	0.509
Diversity Index (H' by Biomass)	1.45	0.15	1.69	0.24	**0.026**
Nitzschia (Ratio of POC)	0.52	0.12	0.40	0.13	**0.039**
Navicula (Ratio of POC)	0.11	0.07	0.17	0.09	0.248
Thalassiothrix (Ratio of POC)	0.11	0.05	0.07	0.03	0.137
Fragilariopsis (Ratio of POC)	0.06	0.04	0.07	0.06	0.741

3.3.5 Inter-Annual Community Composition

Differences between sampling years in the sea ice communities were compared by combining the early, intermediate, and peak bloom phases of each year (Table 7). All variables tested showed significant difference between years except for the biomass of *Thalassiothrix* (Table 7). Differences were found using Dunn's multiple comparisons test however the differences found were not consistent between the same years (Table 8). Chlorophyll was significantly lower in 2012. Diatom biomass (including both pennate and centric) was significantly higher in 2013 (Fig. 7). The C:Chlorophyll ratio (15.61) was significantly lower in 2011. The "other" pennate category was significantly lower in 2012 than 2011 and 2013, whereas the *Nitzschia*, *Navicula*, and *Fragilariopsis* categories were significantly higher in 2013 compared to 2011 and 2012 (Fig. 7). The small:large size ($<5000\mu m^3$:$>5000\mu m^3$) ratio was significantly lower in 2013 and the ratio of pennate:centric diatoms was significantly lower in 2012 than 2011. H' (based on abundance of diatom taxa) was significantly lower in 2013, however H' (based on biomass) was significantly higher in 2011 compared to 2013.

Table 7. Mean values and standard deviations (STD) testing interannual differences in biomass and community composition between 2011, 2012, and 2013. Kruskal-Wallis test results with P-value <0.05 indicated in bold specify significant differences between years.

Variable (unit)	2011		2012		2013		Kruskal Wallis
	mean	STD	mean	STD	mean	STD	H value Pr (>H)
Chlorophyll (µg L^{-1})	112.18	122.57	34.41	16.15	152.96	107.03	**0.005**
Diatom (mg C L^{-1})	2.43	3.64	1.12	0.96	5.43	4.16	**0.001**
Ratio of C:Chl	15.61	9.64	35.69	24.09	43.91	31.16	**0.001**
Pennate (mg C L^{-1})	2.34	3.95	0.98	0.77	4.80	4.00	**0.001**
Centric (mg C L^{-1})	0.09	0.10	0.29	0.21	0.63	0.25	**0.000**
Nitzschia (mg C L^{-1})	1.31	2.51	0.59	0.64	3.48	3.55	**0.001**
Navicula (mg C L^{-1})	0.29	0.43	0.13	0.11	0.45	0.53	**0.015**
Thalassiothrix (mg C L^{-1})	0.30	0.54	0.11	0.08	0.17	0.13	0.454
Fragilariopsis (mg C L^{-1})	0.16	0.28	0.04	0.05	0.50	0.33	**0.000**
Other Pennate (mg C L^{-1})	0.28	0.28	0.04	0.05	0.50	0.33	**0.041**
Diatom ratio (<5000 μm^3:>5000μm^3)	3.43	1.40	5.95	5.70	0.86	0.44	**0.000**
Diatom ratio (Pennate:Centric)	20.66	17.31	7.08	7.67	7.77	4.59	**0.040**
Diversity Index (H' by Abundance)	1.85	0.14	1.71	0.19	1.38	0.14	**0.000**
Diversity Index (H' by Biomass)	1.74	0.25	1.53	0.15	1.29	0.25	**0.001**
Nitzschia (Ratio of POC)	0.38	0.15	0.42	0.11	0.58	0.14	**0.006**
Navicula (Ratio of POC)	0.19	0.09	0.12	0.07	0.07	0.02	**0.001**
Thalassiothrix (Ratio of POC)	0.11	0.05	0.09	0.05	0.03	0.02	**0.000**
Fragilariopsis (Ratio of POC)	0.06	0.03	0.03	0.02	0.12	0.08	**0.005**

Table 8. Post Hoc results using Dunn's multiple comparison test to determine differences between 2011, 2012 and 2013. Same letters indicate that no significant differences were found.

Variable (unit)	2011	2012	2013
Chlorophyll (µg L^{-1})	AB	A	B
Diatom (mg C L^{-1})	A	A	B
Ratio of C:Chl	A	B	B
Pennate (mg C L^{-1})	A	A	B
Centric (mg C L^{-1})	A	A	B
***Nitzschia* (mg C L^{-1})**	A	A	B
***Navicula* (mg C L^{-1})**	A	A	B
***Thalassiothrix* (mg C L^{-1})**	N/A	N/A	N/A
***Fragilariopsis* (mg C L^{-1})**	A	A	B
Other Pennate (mg C L^{-1})	A	B	A
Diatom ratio (<5000 μm^3:>5000μm^3)	A	A	B
Diatom ratio (Pennate:Centric)	A	B	AB
Diversity Index (H' by Abundance)	A	A	B
Diversity Index (H' by Biomass)	A	AB	B
***Nitzschia* (Ratio of POC)**	A	A	B
***Navicula* (Ratio of POC)**	A	AB	B
***Thalassiothrix* (Ratio of POC)**	A	A	B
***Fragilariopsis* (Ratio of POC)**	AB	A	B

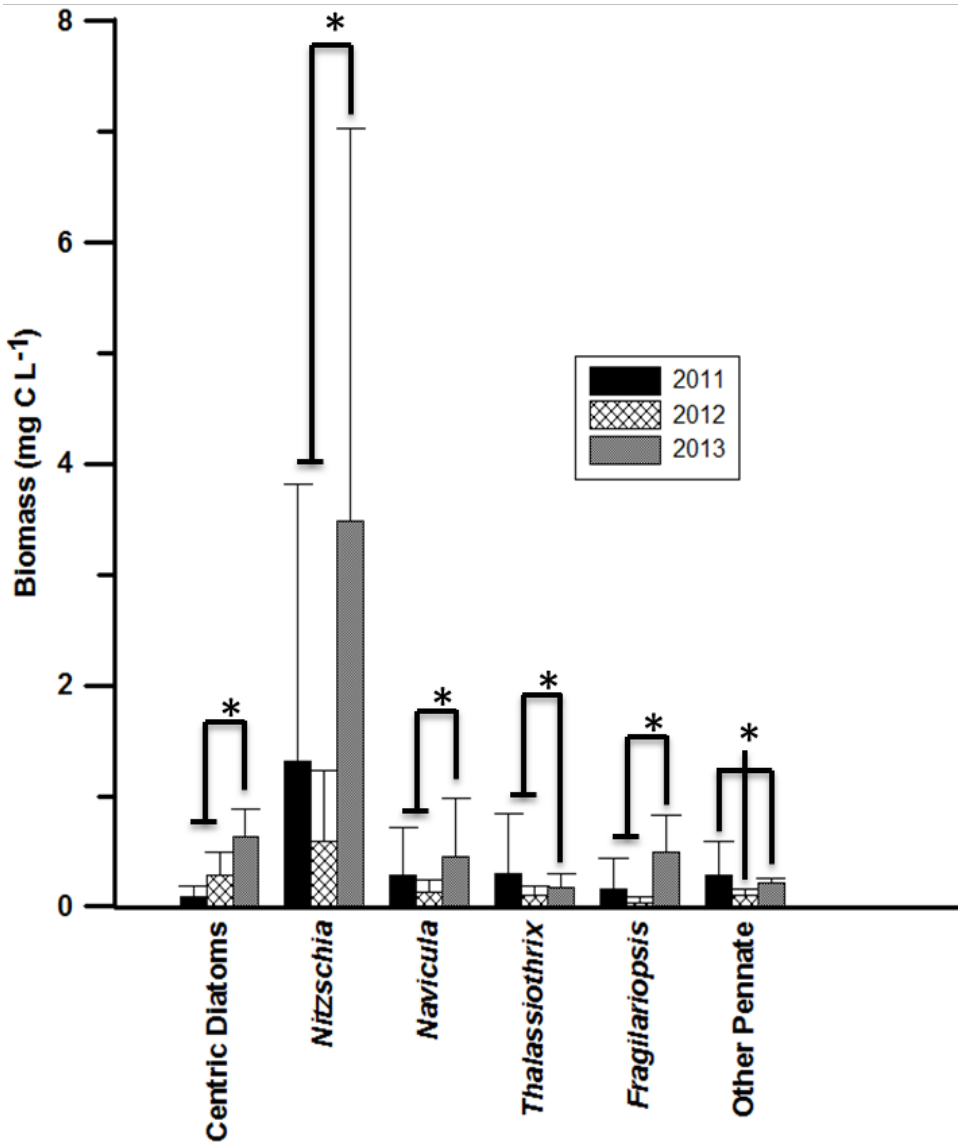

Fig. 7 Interannual comparison of diatom groups based on biomass. Significant differences (based on Dunn's multiple comparison) between years indicated by lines connecting the corresponding bars.

3.3.6 Heterotrophic Protists

Heterotrophic protist (Fig. 3) biomass and 'predator-prey' ratio (ratio of heterotrophic protist biomass: diatom biomass) were compared using the same phase determination and statistical tests as applied to the diatom communities. During 2011, no heterotrophic protists were quantified, thus the biomass of the heterotrophic protists is

only compared between 2012 and 2013 (Fig. 8). When comparing bloom development (early, peak, and decline), heterotrophic protist biomass decreased throughout all the phases but no significant differences were found using Kruskal-Wallis tests. Note that the results are consistent when abundance of the protists is compared. The 'predator –prey' ratio was lowest during the peak bloom phase however was not significantly different between any of the phase determinations (Fig. 8B). In 2012, when comparing peak and post export phases, heterotrophic protist biomass decreased while the predator:prey ratio increased after export, but again not significantly. Heterotrophic protist biomass was higher under high snow cover but not significantly (Wilcoxon-signed rank test) and the ratio of predator:prey was significantly higher during peak bloom phase under high snow compared to low snow ($P=0.014$). Finally, the comparison between years showed that heterotrophic protist biomass was higher in 2013 (thought not significantly) however the ratio of predator:prey was similar between 2012 and 2013.

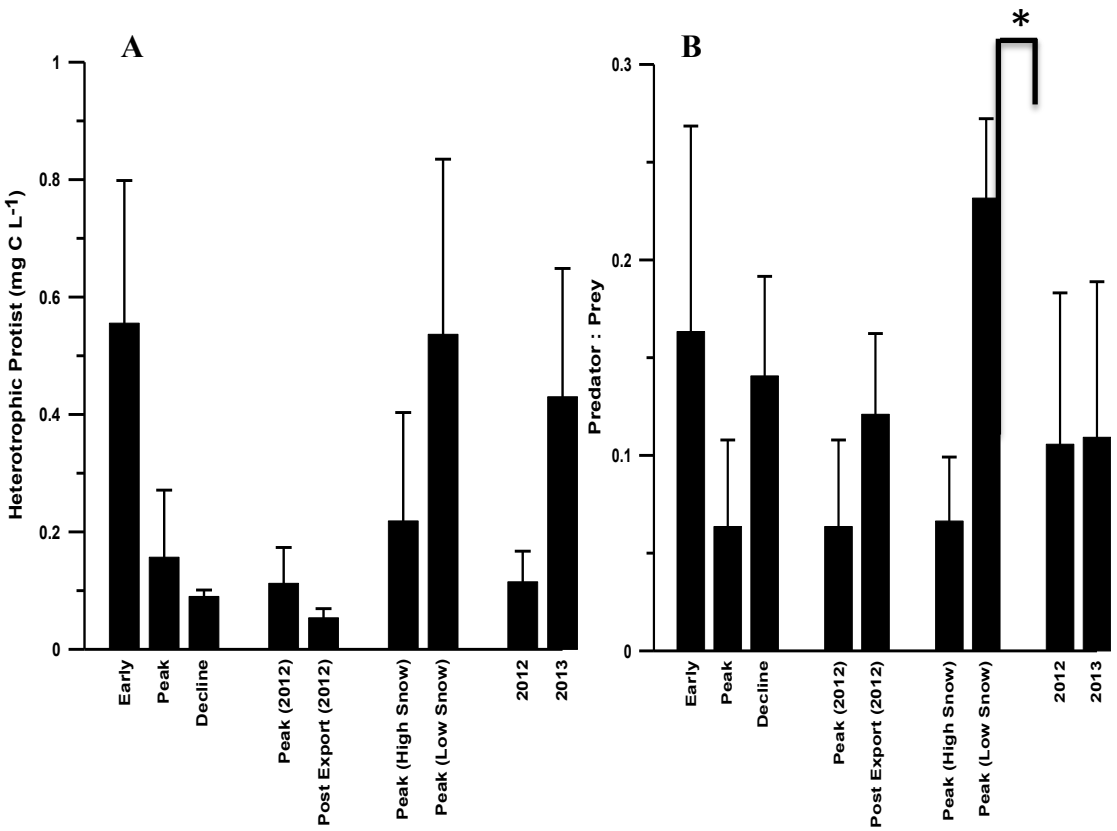

Fig. 8 A. Biomass of heterotrophic protists and B. Ratio of heterotrophic protist to diatom biomass ('Predator-Prey') in 2012 and 2013 compared between different bloom phases, light availability, as well as between sampling seasons in 2012 and 2013.

CHAPTER 4

DISCUSSION

I investigated bloom progression from pre-bloom to export in late spring in the land fast sea ice off the coast of northern Alaska in three years (2011 – 2013) at stations with varying overlying snow cover. The multi-year study allowed us to determine differences in bloom progression as a function of light availability and to compare differences in community composition between the three study years. I found that community composition was relatively similar (based on biomass ratios) across bloom progression and snow cover however large variability was found not only in biomass but the proportion of different taxonomic groups between the late bloom and export phase and between years.

To effectively compare Arctic sea ice communities, one must understand the sources of variability. Sea ice algal patchiness may partially be due to snow cover, brine channel salinity, and temperature (Cota & Horne 1989). Eicken et al. (1991) found that the brine channel size may vary, inducing differences in the chlorophyll concentration by an order of magnitude on small scales (0.25 – 20 m). Community distribution has been found to be quite patchy spatially and temporally within the same season in several other studies (Gosselin et al. 1986, Krembs et al. 2000, Rysgaard et al. 2001). Rysgaard et al. (2001) found patchiness of algal biomass in samples within 5 – 10 m of each other under similar snow depth. Gosselin et al. (1986) found that snow cover controlled the patchiness of sea ice algae on a smaller scale (20 – 90 m) whereas salinity controlled the patchiness of sea ice algae on a large scale (~30 km).

In my study I pooled data from bloom phases spanning multiple years with varying snow cover, to be able to reach statistically sound conclusions that integrate effects of small-scale patchiness. Similarly, in studying differences between years, I pooled data from all bloom phases and snow cover sites to be able to reach conclusions that might reveal interannual variability in community composition.

4.1. Phase Dependent Variability

Sea ice community composition in the Arctic has been studied ship-board (Gradinger et al. 1999, Brown & Belt 2012), which is not generally designed for repeat observations of a given site, and also from shore as in my study (Hsiao 1980, Horner & Schrader 1982 Cota & Horne 1989, Lund-Hansen et al. 2014). In my study, I focused exclusively on the bottom 10 cm of the ice where most of the biomass is found (Apollonio 1961, Horner & Schrader 1982, Cota & Horne 1989) and followed changes through time. I used a combination of chlorophyll measurements, inverted and epifluorescence microscopy to determine how the algal community changed throughout bloom phases in the land fast sea ice. The timing of the bloom was different each year and combining phases allowed for an interpretation across years (Fig. 5). Chlorophyll as a bulk parameter for photosynthetic biomass has been used to track bloom dynamics of sea-ice algal communities in the Arctic sea ice. Chlorophyll concentration increases towards a peak bloom phase, as more light becomes available, and declines once primary producers begin to melt out of the ice (Hsiao et al 1980, Horner 1982, Suzuki et al. 1997, Arrigo et al. 2008, Gradinger 2009, Juhl et al. 2011, Lee et al. 2012). I found the same trend; in the beginning of each field season chlorophyll was low (especially under higher

snow cover) then increased as the biomass peaked, followed by a decline in biomass. Light availability may delay the onset of the spring bloom (Horner & Schrader 1982) and is controlled by snow cover that in turn can be altered by precipitation and above-freezing temperatures (Juhl & Krembs 2010). Average temperatures in May of 2011, 2012, and 2013 temperatures were -5.3˚C, -5.75 ˚C, and -5.06 ˚C, respectively (Table 1). Temperature has less impact on the sea ice diatoms that experience much warmer temperatures near the ice-water interface, but impacts snow cover. Below freezing temperatures prevent snowmelt from occurring and in the spring, as the temperatures rise, the snow cover will begin to melt. Rapid changes in snow cover may accelerate export from the ice, which was found in the Canadian Arctic in 2011 (Galindo et al. 2014). Spring 2012 was on average the coolest of the three years sampled in this study, but showed the earliest snow melt which likely accelerated the development of the bloom and subsequent export.

When I followed the composition and biomass of diatoms during the early, peak, and declining phases in spring of 2011-2013, I found that the biomass of *Nitzschia*, *Navicula*, *Thalassiothrix* and *Fragilariopsis* increased until the peak bloom phase. During the declining phase, the biomass decreased for all groups as diatoms were presumably exporting out of the ice.

Overall the community composition was surprisingly similar between bloom phases, dominated by a few taxa of pennate diatoms, particularly *Nitzschia*. While the overall biomass, chlorophyll, and concentration of cells increased up to the peak bloom phase, the ratio of each taxon remained largely unchanged throughout bloom phases

including the declining phase. After export I saw large changes in community composition and my study is one of the first to show that the biomass of centric diatoms can become greater than that of pennate diatoms in the lower portion of the ice in the Chukchi Sea. Increased light availability (melting snow) or increased habitable space in the ice after export of pennate diatoms may explain why centric diatoms dominate after export. Lund-Hansen et al. (2014) found similar results in land-fast ice west of Greenland, where the centric diatoms *Melosira arctica* as well as *Porosira glacialis* increased in abundance as snow (~9.3 cm) was removed, while the pennate diatoms decreased in abundance. Along the southern shore of the Amundsen Gulf in the Canadian Arctic east of the Beaufort Sea, Mundy et al. (2011) found in late spring 2008, that centrics in the interior of the ice contributed almost 35% to total diatom abundance. In addition, a three year ship board based study conducted in the White Sea found that centric diatoms can dominate algal biomass in the bottom sections of the ice (Ratkova & Wassmann 2005) and Boetius et al. (2014) found during a cruise in 2012 in the high Arctic that *Melosira arctica* dominated ice algae in late summer sea ice. These studies confirm results of my study that centric diatoms can become a more substantial part of the sea ice community later in the spring and after export of the pennate diatom community.

My results indicate that a centric diatom dominated sea ice algal community in late spring after export may be due to export mechanisms that may favor centric diatom retention, or subsequent growth in the ice. Export is often controlled by temperature, which increases brine channel size and melts the snow and ice, as well as light which

may cause the diatoms to migrate closer to the ice-water interface to escape increasing solar radiations (Juhl et al. 2011, Aumack et al. 2014, Lund-Hansen et al. 2014). Eddie et al. (2010) found higher centric biovolume (relative to pennate diatoms) 50-60 cm below the top of the ice (Eddie et al. 2010). This location in the ice might provide a competitive advantage to centrics as they would receive more light and they would be protected from export compared to the cells in the bottom most section of the ice. A laboratory experiment studying a centric diatom (*Thalassiosira antarctica)* found increased growth with increased irradiance up to 57 μmol m^{-2} s^{-1} (Aletsee & Jahnke 1992), which is well above the light intensity found to initiate growth of diatoms in the ice off Barrow, AK (2.3 – 9.3μmol photons m^{-2} s^{-1}; Horner 1985). This light intensity is well within the range of light intensities experienced by the sea ice diatoms in the lower sections of the ice after snow melt (around 53 μmol photons m^{-2} s^{-1}, Aumack et al. 2014).

Diatoms in the ice contribute to the majority of the algal biomass, however, we also found heterotrophic protists, which are a common component of the sea ice ecosystem (Gradinger et al. 1999). The heterotrophic protist biomass was found to be highest during the pre-bloom phase which is consistent with observations by Rozanska et al. (2009) who found that flagellated cells (likely heterotrophic) dominated the bottom sea ice under high snow cover (>10 cm) during the early bloom phase, then decreased as the algal biomass peaked. During my study I did not find statistical differences in heterotrophic protist biomass between bloom phases however I did see a general decline through the sea ice bloom. During the spring bloom the ratio of heterotrophic protists to diatoms biomass ('predator:prey' ratio) decreased, however the ratio increased again as

diatoms exported out of the ice. This may be due to the ability of heterotrophic protists to remain in the ice during export, and may indicate that they can exert increased grazing pressure on diatoms as shown by the significant increase in the ratio of predator:prey after the peak bloom phase (Fig. 8B).

4.2. Light Dependent Variability

Lack of sunlight prevents growth of photosynthetic organisms in the northern latitudes during the winter and light availability continues to limit growth in the spring (Gosselin et al. 1990, Manes & Gradinger 2009). Other than light availability, the light reaching the ice algae is attenuated by algae themselves (self-shading), sediment entrapment, cloud cover, and snow cover (Horner 1985). During the spring periods of my study years (2011 - 2013) I compared the effect of snow cover on the sea ice algal community. I found that diatom biomass increased with decreased snow cover (almost three-fold compared to high snow cover sites). This has also been shown by Suzuki et al. (1997) at Resolute Passage in the Canadian Arctic (1997), Lee et al. (2008) off the coast of Barrow, AK and Lund-Hansen et al. (2014) in West Greenland. Lee et al. (2008) even attributed low primary productivity to light limitation during a study in 2003 compared to 2002 in the near shore land fast sea ice west of Barrow, AK. When comparing chlorophyll in the lower section of the ice, Campbell et al. (2014) found the highest values of chlorophyll (>30 mg m^{-2}) under low snow cover (<10 cm), however they showed the importance of high snow cover which causes a delay in the peak bloom. Even though the chlorophyll values are lower under high snow, the bloom season is extended and ice can be a habitat for sea ice algae later into the season after the low-snow sites

have experienced algae export (Campbell et al, 2014). Mundy et al. (2005) found that ice communities under low snow cover (<12 cm snow) had higher biomass (>40 mg Chlorophyll a m^{-2}) compared to high snow cover (>20 cm) where the peak biomass was much lower throughout the season (peaked at ~35 mg Chlorophyll a m^{-2}). Those authors found that even under high snow cover, sea ice algae are able to grow and are able to remain suspended in the ice longer as a result of the insulation from the snow cover above, thereby extending the growing season. In 2012, my highest snow cover site (30 cm) showed low chlorophyll values (15 μg L^{-1}) which increased as the snow melted (45 μg L^{-1}), reciprocating Mundy et al.'s (2005) findings that snow cover can regulate the growing season and that the algae may continue to grow later into the spring compared to those in sea ice covered by low snow.

Photosynthetic organisms can change the chlorophyll in their cell based on photoadaptation. Gradinger et al. (1991) found that chlorophyll values began to decrease while algal biomass increased when there was no snow covering the ice, indicating higher C:Chl ratios in high light environments (Gradinger et al. 1991). This is consistent with results in my study: Under high snow cover I found that the ratio of C:Chl was 24% lower than under low snow cover indicating light adaptation, however the difference was not statistically significant (Table 6). Studies on light requirements of Arctic diatoms have shown that diatoms found in the Arctic sea ice are well adapted to low light (Horner et al. 1982, Juhl et al. 2010, Aumack et al. 2014, Campbell et al. 2014). In addition, Aumack et al. (2014) suggested that pennate diatoms may be able to actively migrate in the ice as a response to environmental changes in snow thickness (Aumack et al. 2014).

Aumack et al. (2014) showed that if snow was removed from the ice, the diatoms migrated closer to the sea ice interface. This allows the pennate diatoms to actively control the light they receive by migrating closer to the light in low light or closer to the sea-ice interface in high light conditions (Aumack et al. 2014). Studies on the vertical distribution in sea ice have found that community composition is quite different between vertical horizons within the ice (Eddie et al. 2010). Eddie et al. (2010) found that in the upper sections (50-60 cm's from the snow-ice interface) of the ice, the biomass ratio of pennate:centric was lower compared to the lower-most section. I did not include the upper sections of the ice in this study but Eddie et al. (2010) concluded that centric diatoms might have a higher light requirement or tolerance if they are found in a section of the ice with higher light availability.

Studies on light-dependent growth rates of diatoms isolated from sea ice found that Arctic diatoms (including *Nitzschia)* grew faster with higher light availability (Gilstad & Sakshaug 1990 and Juhl & Krembs 2010). Gilstad & Sakshaug (1990) studied 10 Arctic Sea ice diatoms and found that there was little sign of photoinhibition even up to 500 µmol photons m^{-2} s^{-1} except for three of the *Nitzschia* strains which were inhibited by high irradiance and long exposure to high light (up to 24 hours). These authors also found that with constant but low light all of the diatoms were able to grow. Pennate diatoms grew fastest at 10 µmol photons m^{-2} $s^{-1,}$, however as irradiance increased (up to 500 µmol photons m^{-2} s^{-1}) the growth rate of the centric diatoms became higher than that of the pennate diatoms. Juhl et al. (2010) found that *Nitzschia frigida* when light adapted was able to respond positively to increasing irradiance up to 110 µmol photons m^{-2} s^{-1},

however unacclimated cultures when exposed to irradiances greater than 16 μmol photons m^{-2} s^{-1} responded with lower growth rates (Juhl et al. 2010). These two studies support the hypothesis that pennate diatoms are photoinhibited at higher light levels, especially if light levels increase rapidly, compared to the centric diatoms (Gilstad & Sakshaug 1990). This suggests that centric diatoms may be limited by light during the early spring bloom while snow cover and algal self-shading decrease irradiance; however, after export of the algae, when snow cover has decreased, the centric diatoms may have adequate light to grow. This is what I found in 2012 after the export event; once the snow had melted, the biomass of centric diatoms exceeded that of pennate diatoms. This shift in pennate:centric diatom biomass ratio coincided with the highest irradiance levels during the bloom season; irradiance in the bottom section of the ice without attenuating snow has been found to reach between 90-110 photons m^{-2} s^{-1} (McMurdo Sound, Antarctica, Grossi et al. 1987; Arctic; Juhl et al. 2011).

In my study the chlorophyll and diatom biomass (all categories except *Fragilariopsis* and the 'other' pennate category) were all significantly lower under high snow cover. These findings are consistent with a recent study in the West Greenland Arctic that compared sea ice community composition (dominated by *Fragilariopsis oceanica, Achnanthes taeniata, Navicula vanhoeffeni, N. directa, Melosira arctica* and *Porosira glacialis)* by removing snow (Lund-Hansen et al. 2014). These authors found that with moderate snow cover (9.3 ± 1.9 cm snow cover throughout the experiment), the algal community developed through the spring bloom showing increases of all diatom species identified in their study from beginning to end. In their snow removal plot (~9.3

cm initially), however, major pennate diatoms declined, specifically *Achnanthes* (which is a genus we do not find in the land-fast ice off Barrow), but the centric diatoms *Melosira arctica* and *Porosira glacialis* increased in abundance. In my study the biomass of diatom cells was four times greater under high snow compared to low snow, however, the ratio of each taxon to total POC was relatively similar, except for *Nitzschia,* which was significantly lower under high snow cover.

These results are especially relevant as the Arctic is warming due to climate change. Snow cover and ice thickness have been decreasing over the last two decades (Screen & Simmonds 2012, Comiso & Hall 2014, Webster et al. 2014) and are predicted to continue to decrease as a consequence of climate change, causing a shorter growing season for primary producers in the ice (Screen & Simmonds 2012, Overland et al. 2013, Webster et al. 2014). It is important to understand how the distribution of diatoms differs in response to environmental factors such as light, because consumers, for sustenance, depend on these organisms. My results and those of others referenced above show that with reduced snow cover ice algal biomass may reach higher levels, however the length of the growing season will be shortened. Also, rapid changes in snow cover may cause earlier export compared to intermediate snow depths.

4.3 Inter-Annual Variability

I compared the three different years in this study and found significant differences in almost all parameters (Table 7). However these differences were not consistent between sampling years (Table 8). This may be due to the history of the ice sheet or that

environmental differences were found between years. 2011 and 2013 were similar in many ways including temperature. The average air temperature above ground throughout May of 2011 and 2013 was -5.3°C and -5.06°C, respectively, and in 2012, the average temperature in May was lowest (-5.75°C). Air temperatures did not reach above-freezing levels in 2011 until 5/21/11, in 2012 until 5/17/12 and finally in 2013 until 5/19/13. This may have also influenced the shortened bloom season in 2012 as temperatures rose more quickly during that year. While this is not the temperature the diatoms experience in the lower-most section of the ice, it is however the temperature that controls precipitation changes and snow melt. Also, nutrient concentrations in the water column below the sea ice were different between the three years, which may affect the sea ice community because the ambient water supplies the nutrients for the diatoms in the lowermost sections of the ice. In 2012 I found the lowest biomass and chlorophyll in the ice, in addition to evidence for silicate limitation in the ambient sea water.

The year 2012 was the year of the lowest Arctic sea ice extent on record and this is attributed to changing sea ice conditions and also on cyclonic storm in August of that year (Parkinson & Comiso 2012, Simmonds & Rudeva 2012). These events do not impact the near shore ice, however; rapidly changing temperatures throughout the field season in 2012 did lead to melt-pond development and snow melt, shortening the growing season and allowed sampling after the majority of the diatoms had exported out of the ice.

In 2011 pennate diatoms were the dominant diatom category and centric diatoms only made up about 4% of total diatom biomass (Table 7). Diatom biomass was

significantly lower in 2012 compared to the other years. Diatom cells were smaller and the abundance of centric diatoms was higher in 2012 (the latter due to post-export sampling). I collected the fewest samples in 2013 however I still found that the 2013 field season had the greatest diatom biomass, made up mostly by large cells (cells >5000um^3 in biovolume, Table 7). This high diatom biomass may have also played a role in the decreased nutrients found in that year; silicate and nitrogen were both much lower in 2013 than in 2012 and these large-celled diatoms may have drawn down the nutrients in the ice during growth. *Nitzschia* was the dominant pennate diatom in all three years with *Navicula* being the second most abundant in all but 2013 when *Fragilariopsis* took this position. These results indicate that large differences are found between years, however the more dominant diatoms (especially *Nitzschia)* play the main role in the Arctic sea ice algal bloom independent of the year sampled. Heterotrophic protist biomass was higher in 2013, however the ratio of heterotrophic protist:diatoms was similar (Fig. 8A & B) in both years. This is not surprising as diatom biomass was also lower in 2012. I did however observe more examples of dinoflagellates actively grazing on the diatoms in 2012, which might have contributed to the low diatom biomass observed in that year (Fig. 3).

The interannual differences in the diatom community that I found might be due to interannual difference in ice conditions, light availability, temperature, grazing pressure, and the onset of the bloom in relation to the sampling time. I assume that history of sea ice formation and cell entrapment into the ice differs annually, as well.

CHAPTER 5

CONCLUSION

My three-year investigation of the vernal sea ice community in the land-fast ice off Barrow, AK, showed that the biomass of the sea ice community shifts throughout the growing season, but that the diatom community did not change significantly through the bloom phases until the termination of the bloom. When most of the pennate diatom community exported out of the ice, I found evidence that the export event left a niche for centric diatoms to occupy. Snow cover directly affects the diatom biomass; it was much higher under low snow cover, however the composition of diatoms remained again relatively unchanged. Finally, differences between years are much more pronounced than between phases or snow depths. This could be due to timing of the spring bloom, abiotic conditions in the ice, history and physical properties of the ice, or differences in grazing pressure. My approach of using time-series sampling and pooling data across several years resulted in a robust data set, and I found statistical differences in the composition and variability of sea ice communities in response to changes in environmental parameters despite the large variability between samples. I believe that this approach is an example for how sea ice community composition should be sampled and analyzed in the future. This time series study constitutes an important baseline for further studies of how the changing sea ice environment influences ice algal community development, which serves as the base of the Arctic food web. As the Arctic is continuing to warm, diminishing snow cover may be one of the most critical properties affecting these communities. My results show that as snow melts earlier and at accelerated rates, biomass levels in the ice may reach higher values but that the spring bloom may be

shortened in length. In the future, decreased snow cover may inhibit the algal bloom from reaching current levels of primary production within the ice. I predict that with export occurring earlier in the spring, the centric diatoms will play a more pivotal role in the sea ice algal community and more under ice and benthic algal blooms may occur, with consequences for higher trophic levels in the tightly coupled marine food web of the Arctic.

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