Seasonal patterns of primary production at the seafloor in the eastern Chukchi Sea based upon in-situ chlorophyll fluorescence measurements, 2010–2018

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# ABSTRACT

The Chukchi Sea consists of a broad, shallow (<45 m) shelf that is seasonally (November–July) covered by sea ice. In this study, we characterized the seasonal patterns of near-bottom primary production using moored instruments measuring chlorophyll fluorescence, oxygen, nitrate, and photosynthetically active radiation. Moorings were deployed at multiple sites each year from 2010 to 2017. Instruments were restricted to within 10 m of the seafloor, because of ice keels, which can reach 30 m below the surface. Near-bottom blooms were common at all mooring sites. The bloom onset followed directly on ice retreat whereas bloom end followed loss of light in September. The intensity of light at the seafloor (~40 m deep) was similar that was observed under ice floe (1–2 m thick) in the spring/early summer, which was sufficient for ice algae to continue to photosynthesize, utilizing nitrate and producing oxygen through summer. As a consequence of climate warming and earlier ice retreat, the bloom onset will occur earlier than currently, but bloom end timing will remain the same. The Chukchi Sea is highly productive even though the growing season is short. High production is promoted by a shallow seafloor, which allows multiple production layers (surface open water, bottom of the mixed layer, under-ice algae, and seafloor ice algae). We term this the Multiple Production Layers (MPL ‘maple’) hypothesis.

Key words: Chukchi Sea, sea ice, fluorescence, ice algae

# 1. Introduction

The Chukchi Sea consists of a broad shallow shelf, extending >800 km northward from the Bering Strait to the shelf break and the Arctic basin. It is characterized as an inflow shelf for the Arctic (Carmack and Wassmann, 2006), and is the sole source of Pacific water to the Arctic Ocean. The flow through Bering Strait provides heat, freshwater, and salt, including nutrients, to the Chukchi Sea and the Arctic Basin. The northward flow divides into two primary branches—the western branch flows into the basin through Herald Canyon and the eastern branch flows through Barrow Canyon (Coachman *et al.*, 1975).

Historically, the food web of the Chukchi ecosystem, with its extensive sea ice, has been based on primary production driven by under-ice algal communities. Nutrients are the primary limiting factor for ice algae production below the sea ice, with estimated production by ice algae during spring of 1–2 g C m-2 (Gradinger, 2009). Sea-ice algae are a major source of carbon to the benthic ecosystem (Grebmeier, 2012). The spring plankton bloom (initially ice algae) likely initiates under and within the sea ice. Seasonal ice retreat favors the export of aggregates of under-ice algae directly to the benthos, supporting the Chukchi’s rich, benthic-dominated ecosystem (Dunton *et al.*, 2014).

There has been a dramatic loss of sea ice in the Chukchi Sea during the last 15 years (Wood et al., 2015, 2018; Serreze *et al*., 2016; Frey *et al*., 2015), with earlier ice retreat in the spring and summer and later ice arrival in the fall. This loss of sea ice (including multi-year ice) has increased the heat-flux into the Chukchi Sea (Danielson *et al*., this issue). Earlier ice retreat also impacts the timing of export of ice algae to the bottom and the timing of open water phytoplankton production (Arrigo *et al*., 2008; Hill *et al*., 2017). Earlier sea-ice retreat also favors open water phytoplankton primary production that benefits a pelagic ecosystem (Grebmeier *et al*., 2006, 2015; Moore and Stabeno, 2015) and a longer open-water season is predicted to alter the composition and distribution of phytoplankton communities (Tremblay *et al*., 2009; Neeley *et al*., 2018).

It is unclear how earlier ice retreat might impact the vertical stratification of the Chukchi Sea. In the southern Bering Sea, the sea ice does not impact the vertical stratification during the following summer (Ladd and Stabeno, 2012). One possibility is that earlier warming and weak winds may lead to stronger stratification, which could result in a more stable mixed layer and reduced vertical infusion of nutrients into the surface layer from the nutrient rich bottom layer. Alternately, earlier ice retreat and stronger winds could allow stronger vertical mixing and, thus, reduce the salinity gradient. Regardless how stratification changes, a subsurface bloom supported by bottom nutrients and sufficient light could persist beneath the surface mixed layer. In fact, phytoplankton in the northeastern Chukchi are typically found below the pycnocline (subsurface; Martini *et al*., 2016; Lowry *et al*., 2015).

The focus in this paper is to examine the relationship among chlorophyll fluorescence, arrival and departure of sea ice, and photosynthetically active radiation (PAR). We utilize a variety of data sources, including hydrographic casts, pop-up buoys (a newly developed technology that measures properties underneath the ice), and a variety of time series collected on moorings. Chlorophyll fluorescence, PAR, oxygen and nitrate were measured near the seafloor at multiple mooring sites on the US Chukchi shelf over a 9-year period (Fig. 1). These instruments were all deployed within 10 m of the seafloor to avoid the deep ice keels.

Preliminary analysis (Berchok *et al*., 2015) indicated that the large export of ice algae to the seafloor coincides with ice retreat. In this earlier analysis, an increase in percent oxygen saturation and/or decrease in nitrate concentration are often associated with this export event, suggesting that net primary production continues at depth. Our objective was to test the multiple production layer or MPL ‘maple’ hypothesis of how the system works (Fig. 2). In this hypothesis, ice algae fall to the seafloor when ice retreats and continues to photosynthesize until light levels diminish in the fall. This layer of continued photosynthesis adds to other layers of primary production (phytoplankton in the upper water column in open water and beneath the surface mixed layer, and algae under the ice) that together account for the high primary productivity found on the Chukchi shelf.

# 2. Data and methods

## 2.1 Moorings

Moorings (Fig. 1) were deployed at 8 sites (C1–C8) on the Chukchi shelf during the late summer and recovered the following summer, when new moorings were deployed. The deployment years at each site, mooring locations and instrumentation are listed in Table 1. All moorings were short, taut wire moorings. During winter and spring, sea-ice keels can be as deep as 30 m below the surface (Stabeno *et al*., 2018a). To avoid these ice keels, each mooring was <10 m tall, keeping the upper float at least 30 m below the surface. This height limitation resulted in two moorings being deployed at each site, because of the limited amount of vertical wire space. The moorings contained instruments that measured temperature (SeaBird SBE-37, SBE-39 SeaCat), currents (Acoustic Doppler Profiler, RCM-9), salinity (SBE-37, SeaCat), chlorophyll fluorescence (Sea-Bird/WET Labs DLSB ECO Fluorometer), nitrate (Sea-Bird/Satlantic ISUS or SUNA), and PAR. All instruments were prepared according to manufacturers’ specifications and calibrated prior to deployment. Data were collected at hourly intervals.

The optical nitrate sensors (ISUS and SUNA; accuracy of ~2 µM) undergo a pre-deployment blank in distilled water and a calibration check using a nitrate standard of ~ 20 µM in distilled water. To reduce biofouling, the SUNA instruments have a wiper that is activated prior to each set of hourly measurements, and the ISUS instruments are plumbed into the outflow of a Sea-Bird Scientific SBE-16 with anti-fouling agents mounted on either side of the ISUS flow cell. Spectral plots were used to visually assess performance of each instrument and identify data dropouts. See Mordy *et al*. (this issue) for further details of data processing of nitrate sensors.

## 2.2 Hydrography

On 18 July 2015 aboard the USCGC Healy cruise HE1501, a GoPro camera was attached to the top of the conductivity-temperature-depth (CTD) frame. The instrument package consisted of a Sea-Bird 911plus with dual sensors measuring temperature and conductivity, pressure, oxygen, and chlorophyll fluorescence. During a down cast near C2 (Fig. 1), a movie was taken simultaneous with the CTD data collection (164.3°W, 71.2°N). Three frames were selected from this movie and presented herein.

## 2.3 Pop-up buoy

During the last four years, pop-up buoys have been developed at the Pacific Marine Environmental Laboratory (Langis *et al*., 2018). The purpose of this effort was to develop an inexpensive, expendable buoy to make under ice measurements, that could be deployed in summer or fall and rise to the surface in the following winter or spring on a prearranged day. When the ice melts the buoy will surface and transmit data back to the laboratory. The instruments collect data during three unique periods: (1) on the seafloor; (2) on the vertical profile as it rises to the surface; and (3) under the ice. The buoy presented in this manuscript is Generation 3 and collected temperature (±0.01 °C), depth (±0.21 m), fluorescence (±2%) and PAR (±3%).

## 2.4 Sea ice

The Advanced Microwave Scanning Radiometer for EOS (AMSR-E) data (available from the National Snow and ice Data Center, http://nsidc.org/data/amsre/) were used in this manuscript. AMSR is a data set of sea-ice extent and areal concentration consisting of daily ice concentration data at 12.5 km resolution. Time series of percent areal coverage were calculated in 50 km × 50 km boxes around each mooring site (C1–C8).

## 2.5 Data analysis

Time series of ice cover values were used to determine the timing and duration of the ice-free period in summer. These records were plotted, and the retreat and return dates were assigned (Fig. S1). Ice retreat was considered to have occurred when ice cover fell below 15% areal ice cover for the first time during each year. Ice return was considered to have occurred when areal ice cover increased above 15% for the last time during each year. The duration of the ice-free period was computed as the difference in days between ice retreat and ice return.

PAR values near the seafloor for each mooring and year were examined to determine the time and duration of the photic period in summer. These records were plotted and the onset, end and maximum value of PAR were assigned (Fig. S1). Onset and end of the PAR period were considered to have occurred when the PAR value crossed 0.1 μE m−2 s−1. PAR duration was computed as the difference in days between PAR end and PAR onset.

Chlorophyll values near the seafloor for each mooring and year were examined to determine the time and duration of the bloom in summer. These records were plotted and the onset, end and maximum value of the summer bloom were assigned (Fig. S1). Onset and end of the summer bloom were considered to have occurred when the concentration of chlorophyll crossed 1 μg l−1. Bloom duration was computed as the difference in days between bloom end and bloom onset.

Annual values of ice retreat, ice return, PAR onset, PAR end, bloom onset, and bloom end were plotted by year and mooring using box plots and the R package ‘ggplot2’. The relationships among values (e.g., between bloom onset and ice retreat) were plotted by year and mooring using scatter plots also using the R package ‘ggplot2’. Their relatedness was examined by computing correlation coefficients *r* (e.g., between bloom onset and ice retreat) and the statistical significance of the *r*-values were estimated using the R package ‘Hmisc’.

# 3. Results

## 3.1 Sea ice

Typically, ice cover was at or near 100% during winter for most mooring sites (Fig. 3a, Fig. S1). The exceptions were the three near coastal moorings—primarily C4 and C5 and to a lesser extent mooring C1. At these sites, winter and spring sea-ice cover was usually reduced when strong winds out of the east and/or northeast (referred to as a wind-driven polynya) or when warm Atlantic water surfaced (referred to as a sensible heat polynya) (Ladd *et al*., 2016, Hirano *et al*., 2016). Areal ice concentration during winter was smallest in 2013, 2014, and 2016 (Fig. 3a). The low areal concentrations were typically confined to the near coastal moorings. In 2013 and 2016, C2 also had reduced ice cover. The greatest variability in areal ice cover was at C4 and C5, the two moorings nearest the shelf break (Fig. 3b). At all the mooring sites discussed herein, sea ice eventually retreated in summer, returning in late summer or fall (Fig. S1).

The timing of sea-ice retreat varied greatly among years (Fig. 4a). The median day of ice retreat was approximately day 170 (mid-June) for 2010–2011, day 205 (late July) for 2012–2014, day 190 (early July) for 2015–2016, and day 135 (mid-May) for 2017. This pattern of two years of early retreat, three of late, two of mid-range, and finally one year of early ice retreat years largely occurred regardless of location with some exceptions. For example, consider C7 and C8; here while sea-ice retreat was clearly later for 2012–2014, ice retreat timing was similar for 2010–2011. Likewise, for two coastal moorings (C1 and C4), ice retreat was later in 2013–2014, but earlier in 2012. In this case, the early ice retreat in 2012 reflects a brief low ice period followed by higher ice cover for several weeks (Fig. S1).

Unlike the variability in the timing of sea-ice retreat, the variability of sea-ice return was less variable among years (Fig. 4d). In general, the range of sea-ice return was much narrower (~50 days, day 294–345) than the range of sea-ice retreat (~100 days, day 133–232) (Table 2). Thus, variability in the duration of the ice-free period was dictated more by ice retreat than ice return and ranged from 67 to 203 days. The median duration of the ice-free period was 127 days.

## 3.2 Ice Algae

Ice algae, which generally accumulate at the base of the sea ice in spring, are an important source of food during this period (Arrigo *et al*., 2008). With the retreat of sea ice, primary production shifts to open water phytoplankton blooms (Arrigo *et al*., 2012; Hill *et al*., 2017). Vertically, there can be multiple layers of significant chlorophyll fluorescence (Martini *et al*., 2016). This multilayer pattern was seen in a hydrographic cast done in 2015 (Fig. 5, left), when a camera was attached to the CTD frame (photos in Fig. 5, right). This CTD cast (164.3°W, 71.2°N on 18 July 2015) was done near C2, approximately 3 days after the ice retreated. Two increases in chlorophyll fluorescence are evident, a relatively small one at ~15 m and a larger one below 20 m. The photos show the different quality of the blooms. The one in the upper water column appears fairly clear (Fig. 5, photo A); the middle photo appears to have very small cells (Fig. 5, photo B), while the bottom photo (Fig. 5, photo C) has larger clumps of cells and extends over ~10 m depth (Fig. 5, left). There is no light once the CTD passes the halfway mark in the lower layer of fluorescence. This type of structure with two bands of increased chlorophyll fluorescence was discussed by Martini *et al*. (2016), and they hypothesized that the bloom just below the surface mixed layer was a subsurface phytoplankton bloom and the one near the bottom was sinking ice algae.

An under-ice bloom was observed in 2019 from a pop-up buoy that floated to the surface and came to rest at the bottom of the ice floe for approximately two months. In August 2018, the pop-up buoy mooring was deployed and anchored in the southern Chukchi Sea (71.2°N, 164.3°W). It included instruments measuring temperature, PAR, fluorescence and pressure. In addition, there was a camera that pointed horizontally, just below the ice bottom. On 30 April 2019, the pop-up buoy released from its anchor (as designed) and rose to the surface underneath a large (~20 km long) ice floe (Fig. 6a). This distinctive floe was traced via satellite images until 20 June, when the ice floe began to break apart. The floe traveled a distance of ~400 km over a period of 60 days (blue line, Fig. 6b). During this period, it successfully collected a suite of data. The top of the buoy rested immediately below the ice at a depth of ~1.5 m (an indication of ice thickness) during the first ~25 days and then began to shoal (Fig. 6c). Chlorophyll began to increase on ~14 May and the bloom continued through early June (Fig. 6d). This bloom occurred under low light conditions (max 2-3 μE m−2 s−1 prior to 27 May) and PAR increased reaching 4-8 μE m−2 s−1 in early June. In mid-June, the fluorescence disappeared and PAR increased to 20 μE m−2 s−1. It was unlikely that the disappearance of the bloom was related to photoinhibition, because Cota and Horne (1989) found that, even for algae adapted to low light, photo inhibition did not occur until ~40 μE m−2 s−1. While nutrient depletion cannot be discounted, the expectation is that the bloom sank toward the sea floor once the substrate began to erode.

The fate of a bloom falling to the seafloor can be seen in the time series collected at the moorings. For example, in 2018 at mooring C2, the ice retreated in mid-May (Fig. 7a), a very early date for ice retreat, and there was a sharp increase in chlorophyll fluorescence in the near-bottom water (30–40 m below the surface; Fig. 7b). Accompanying this increase in fluorescence was a sharp increase in the percent saturation of oxygen, from ~90% to > 120%, and at the same time a decrease in nitrate from ~15 μM to near 0 μM (Fig. 7d). Clearly, the chlorophyll, likely ice algae, continued to be productive in the bottom waters. Light (PAR) was very weak, but measurable through mid-May, decreasing to near zero during the period of high chlorophyll fluorescence and increasing markedly in early July with the disappearance of fluorescence. We suspect that the decrease in PAR to near zero in mid-May was a result of the algal bloom descending as a mass through the water column, and the resulting shading prevented most of the light from reaching the seafloor. Such a shading (sharp decrease in PAR) effect was evident in Fig. 5a, when the CTD entered the region with high chlorophyll. That the ice algae are exposed to sufficient light to continue production, is likely due to vertically mixing in the bottom ~10 m; that is, sometimes cells are at the top of layer and exposed to sufficient light and then mixed downward in this bottom mixed layer.

Chlorophyll fluorescence begins decreasing at the beginning of June perhaps because of the lack of nitrate (Fig. 7d), but more likely influenced by other mechanisms. First, advection is evident in the sharp increase in the nitrate in early June. In addition, sea ice arrives reducing light levels. In late June, PAR increases in the near bottom, when there is no ice algal bloom to shade it and areal ice concentration is <60%. When the ice retreated for the second time in early July, there was not an increase in fluorescence perhaps because there was insufficient nitrate to support a bloom or perhaps there no ice algae to seed the bottom layer. Finally, in mid-July a small bloom appeared and once again shaded the near-bottom and consuming nitrate.

This pattern of ice retreat, increased fluorescence, increased oxygen (by >20%) and/or decreased nitrate dominates at the mooring sites over the years (2010–2018), occurring 22 out of 23 times when there is sufficient data to detect it (Table 1). Each of these locations are shallow (<48 m) with light (PAR) reaching the bottom. The increased fluorescence was likely due to continued photosynthesis by ice algae near the seafloor, as evidenced by increasing percent oxygen saturation and/or decreasing nutrients. In the following sections, we explore the relationship among the timing and duration of the chlorophyll fluorescence bloom, ice retreat and duration and the magnitude of PAR.

## 3.3 PAR measured on the moorings

The PAR time series indicates the amount of light reaching the seafloor. The timing of PAR onset (>0.1 μE m−2 s−1) was earlier for 2011, missing for 2012, more variable and often later for 2013–2015, and earlier for 2016–2017 (Fig. 4b). The median of PAR onset was approximately days 80–120 for all years except in 2013, when the median was about day 170. Unlike the timing of PAR onset, the timing of PAR end was similar regardless of the year. In general, the range of PAR end (~80 days, day 224–305) was much narrower than the range of PAR onset (~150 days, day 86–233) (Table 2). Thus, the duration of the PAR period was dictated more by the timing of PAR onset than the timing of PAR end, ranging from 6 (C4 in 2014) to 200 days. The median duration of the PAR period was 151 days. The timing of PAR onset and ice retreat appeared unrelated (r = 0.32, p = 0.198; Fig. 8a) as were PAR end timing and ice return timing (r = 0.14, p = 0.546; Fig. 8d).

## 3.4 Bottom chlorophyll and its relationship to sea ice and PAR

The timing of bloom onset was earlier for 2011–2012, later for 2013–2014, and earlier for 2015–2017 (Fig. 4c). The median day of bloom onset was approximately day 160 for 2011–2012, 190 for 2013–2014, and 150 for 2015–2017. The timing of bloom end was later for 2011, missing for 2012 (no measurements), earlier for 2013–2015, and mid-range for 2016–2017 (Fig. 4f). The median day of bloom end was about day 320 for 2011, 280 for 2013–2015, and 300 for 2016–2017. The median duration of the bloom was 128 days and the range was 41–190 days (Table 2). One unusual observation was mooring C5 in 2014, which had a much earlier bloom onset (about day 130) than that year’s median (about day 190). This bloom began during a period of variable ice cover, but the ice was not so reduced that it reached the 15% threshold that defined ice retreat (Fig. S1).

Most, but not all, parameters were poorly correlated (Fig. 8). Only two sets (timing of bloom onset versus timing of ice retreat, and bloom duration versus duration when the water was ice free) were significantly correlated. The timing of bloom onset and ice retreat appeared related (r = 0.54, p = 0.007) whereas bloom end timing and ice return timing were not (r = 0.26, p = 0.199; Fig. 8c). Bloom duration was related to the duration of the ice-free period (r = 0.69, p = 0.001; Fig. 8i). The timing of bloom onset and PAR onset were weakly related (r = 0.51, p = 0.065; Fig. 8b), as were timing of bloom end and timing of ice return (r = 0.46, p = 0.098; Fig. 8e). Interestingly, bloom duration was unrelated to the duration of the PAR period (r = 0.27, p = 0.43; Fig. 8h). In Table 2, the maximum chlorophyll value was 37.4 g l-1, which occurred late in the growing season (~ day 237). Most chlorophyll values were much lower, with a median value of 7.5 g l-1 (Table 2). The median day for the bloom peak was day 212 and there was little variability in the timing of the bloom peak (middle quartiles day 200–218).

Chlorophyll increased early when ice cover was variable during late-winter and spring. Occasionally ice retreated early, partially returned and then retreated fully for the summer (e.g., mooring C1 in 2012; Fig. S1). In this case, a bloom began with the initial ice retreat and continued during the partial return. In some years, ice cover was variable during winter and spring (e.g., 2016), PAR increased early (April) and the spring bloom occurred after the early PAR increase (moorings C1 and C3).

# 4. Discussion

## 4.1 Annual fluorescence variation during summer

The growing season typically began with a sequence of ice retreat, a slight increase in PAR, followed by a reduction of PAR and increase in chlorophyll fluorescence at the moored instruments near the seafloor (e.g., Fig. 7). Starting in mid-spring, PAR remained low because of the shadowing effect of sea ice. As the ice melted, ice algae were released from the underside of the ice and dropped to the bottom. During the period of the bloom (high fluorescence) PAR was particularly low because of shadowing by the ice algae itself. In addition, any phytoplankton bloom in the surface layer or below the surface mixed layer contributed to shading of the water column. Such open-water blooms are common on the northern Chukchi shelf (Martini *et al*., 2016). Another good example of this sequence of events is mooring C2 in 2013 (Fig. S1), where ice cover reached 50% in early July and was quickly followed by increased chlorophyll concentration. PAR increased concomitant with declining chlorophyll.

Sea-ice retreat determined the start of the growing season near the seafloor. The timing of ice retreat dictated bloom onset, and, similarly, variations in bloom onset were synchronized with variations in ice retreat timing; bloom onset and ice retreat timing were significantly correlated. Sea-ice return, however, did not determine the end of the growing season. Instead the bloom was terminated by the seasonal reduction in light during early fall that preceded ice return during our sample years. The usual sequence at the end of the growing season was: PAR becoming undetectable around days 250–270; the bloom ending around days 270–300; and ice returning around days 300–320 (Fig. 4).

The growing season (bloom duration) was significantly related to the duration of the ice-free period. The relationship is supported by the significant correlation between bloom onset and ice retreat. This occurs despite the lack of a significant relationship among the ends of the bloom, PAR, and the length of the ice-free period. Instead the significant relationship likely occurred because the ends of the bloom, the ice-free period and PAR occupied a narrower window than their onsets and consequently, the durations of the bloom, PAR, and the ice-free periods were dictated by the timing of their onsets and not their ends. As a consequence, the significant relationship between bloom duration and the ice-free duration was an outcome of the significant relationship between ice retreat and bloom onset.

## 4.2 Spring chlorophyll spikes and ice cover variability

Areas of open water occurred during winter and spring in some years. Most often, this happened at mooring sites C1, C4, and C5 (2010, 2011, 2013, 2014, and 2016; Fig. 3). Each of these moorings are near the coast where the Chukchi Polynya occurs (Ladd *et al*., 2016). Intrusion of warmer, saltier Atlantic Water can contribute to or even cause this polynya (Ladd *et al*., 2016). Earlier blooms were more common in the Chukchi Polynya area (C1, C4, and C5) than outside this area. Using the median bloom onset day (day 154) as a threshold to separate “early” from “late” bloom onset, 8 of 12 bloom onsets were early in the Chukchi Polynya area and only 4 of 12 bloom onsets from this area were late.

Ice retreat is primarily a result of ice melt or advection forced by local winds and local currents, or more commonly a combination of melt and advection. The timing of ice retreat (defined here as the first occurrence of areal ice concentration < 15% for at least two days) varied among the five primary moorings (C1–C5 for period 2001–2016), with earliest retreat occurring at C1 followed by C4, C2, C3 and, finally, C5. The date of retreat among these five moorings was well correlated with the highest correlations (r = 0.86, p < 0.01) between the coastal moorings C1 and C4 and the weakest, but still significant, between C1 and C5 (r = 0.71, p <0.01). The expectation (Fig. 8c) would be that blooms occur earliest at C1 and latest at C3 and C5. Unfortunately, directly examining the timing of the blooms is more difficult, because of the limited number of the time series.

Bloom onset occurred earlier during years when ice retreated earlier or was episodic in nature (Fig. 8c). Occasionally ice retreated early, partially returned and then retreated fully for the summer (e.g., mooring C1 in 2012). In this case, a bloom began with the initial ice retreat and continued during the partial return. In other years (e.g., at C2 in 2018) the bloom began with ice retreat and stopped when ice returned (Fig. 7). In some years, ice cover was variable during winter and spring (e.g., 2016), PAR increased early (April) and the spring bloom occurred after the early PAR increase (moorings C1 and C3).

Even if early ice retreat occurred, an associated chlorophyll maximum was not guaranteed. The earliest observed chlorophyll maximums were during May. For example, a May bloom followed early ice retreat for mooring C5 in 2014 and 2015 (Fig. S1). Bloom occurrence was likely limited by light earlier in the year. For example, in 2016, ice cover was irregular in April at moorings C1, C2, and C4, yet substantial chlorophyll increases did not occur until May. There should be sufficient light and nutrients to support a bloom in May, so the lack of a bloom may be more indicative that either there were little ice algae present or the sea ice was advected away (taking its ice algae with it) as opposed to melted.

## 4.3 Primary production continues at the seafloor through summer

Virtually all the moorings that successfully measured chlorophyll fluorescence, and either oxygen or nitrate, showed the clear signal of continued production near the seafloor during the summer (Table 1). The magnitude of PAR at the seafloor was comparable to what was measured beneath the sea ice (Figs. 6d and 7c), so it is not surprising that the algal bloom could continue. In addition, the bottom layer (beneath the surface mixed layer) is rich in nutrients in spring before the export of ice algae to the bottom. After the nutrients are consumed by algae in the bottom layer, they can be replenished by advection of nutrient-rich Anadyr and Bering Water throughout the summer (Mordy *et al*., this issue). The concentration of nitrate, however, tends to be highly variable during the summer.

Ice algae at the seafloor contributes to the primary productivity of the Chukchi Sea, which together with the Chirikov Basin (region northern Bering Sea northeast of St. Lawrence Island) are the most productive regions in the Pacific Arctic (Hill *et al*., 2017). In most regions with seasonal sea ice, ice algae fall to a seafloor coming to rest below the photic zone, discontinuing the contribution of ice algae to primary production following ice melt. In contrast, much of the Chukchi Sea shelf is less than 45 m deep and lies within the photic zone. As mentioned before, in the Chukchi Sea, nitrate concentrations near the seafloor during summer are variable, but excepting the period when ice algae first falls to the bottom there is usually sufficient nitrate to support some production (see Figures 2 and 5 in Mordy *et al*., this issue). With both light and nutrients, the contribution of continued primary production on the seafloor can be substantial as indicated by the median value of the bloom peak is 8.2 μg l-1 (Table 2).

## 4.4 MPL hypothesis

Continued production of dissociated ice algae at the seafloor provides another source of primary production in addition to the spring phytoplankton bloom in the surface mixed layer, the subsurface phytoplankton blooms in the nutrient rich water beneath the surface mixed layer, and the under-ice algal bloom. There is also evidence of a late summer bloom, when summer/fall storms entrain water from the nutrient-rich lower layer (Hill *et al*., 2017; Ardyna *et al*., 2014). The bottom layer retains some nutrients throughout the summer, because of the advection of nutrient rich water through Bering Strait (Mordy *et al*., this issue). Together, the various blooms form Multiple Productive Layers that we term the MPL (maple) Hypothesis. The MPL hypothesis explains why the Chukchi Sea is so productive even though the growing season is short.

The Chukchi Sea is an inflow shelf (Carmack and Wassmann, 2006). The Arctic Marine Pulses Model describes the Chukchi Sea ecosystem as being dominated by various pulses out of the Bering Sea into the Chukchi and out of the Arctic basin onto the shelf (Moore et al., 2018). On monthly time scales, inflow through Bering Strait is typically weak in the winter, but in summer this changes with a strong increase (~1 × 106 m3 s-1) of relatively warm nutrient-rich water into the Chukchi Sea. With the melting of sea ice, a strong pulse of carbon (e.g., ice algae) is exported to the benthic community—an important pelagic-benthic coupling that supports the rich benthic community of the Chukchi Sea (Grebmeier, 2012). Herein, we add that while there is a sudden pulse of ice algae to the bottom, it continues to be productive throughout the summer.

## 4.5 Comparison of Chukchi and Bering Seas

The correlation of the onset of the growing season and ice retreat for the Chukchi Sea also occurred for the northern Bering Sea, but not for the southeastern Bering Sea (Sigler *et al*., 2014). In the southern Bering Sea, the timing of the spring bloom is dependent on ice and winds (Sigler *et al.*, 2014). If ice retreats early (prior to March 15) or does not arrive at all, storms continue to mix the upper water column, and the spring bloom commences only after surface waters are warmed enough to stratify and stabilize the vertical structure. If ice retreat is late, melt water stabilizes the water column and promotes an early spring under-ice algal bloom. The latter pattern is what occurs on the northern Bering Sea, at least until 2018 (Stabeno et al., 2018b; Stabeno 2019).  In 2018, the lack of sea ice at M8 resulted in late (June) open water bloom, similar to what occurs on the southern Bering Sea during years when there is no ice on the southern shelf after March 15. While the sub-surface blooms are uncommon on the southern Bering Sea, the northern is similar to the Chukchi Sea, with subsurface blooms being common.

The timing of the spring bloom in the southeastern Bering Sea affects the zooplankton species of the ecosystem, a phenomenon described as the Oscillating Control Hypothesis (OCH) (Hunt *et al*., 2002, 2011; Stabeno and Hunt, 2002). This control likely is spatially determined and related to the location of the ice edge (Siddon *et al*., 2013; Sigler *et al*., 2016). The region where the OCH is effective appears to be moving north as climate warms. For example, the entire eastern Bering Sea shelf was largely ice free during the winter of 2017–2018, a radical change that was not predicted to occur for at least a few decades (Stabeno *et al*., 2012; Stabeno and Bell, 2019). The lack of ice had widespread effects on the survival of large crustacean zooplankton and juvenile walleye pollock (Duffy-Anderson *et al*., 2017). Whether and when the OCH region will move into the Chukchi Sea remains to be examined.

Continued productivity of the ice algae that has sunk to the seafloor is much greater for the Chukchi Sea shelf than the eastern Bering Sea shelf, because the latter’s bottom depth is mostly below the photic zone. The eastern Bering Sea shelf deepens from east to west and the mid-shelf is ~70 m deep whereas the eastern Chukchi Sea shelf is predominantly shallower than 45 m. Thus, in the Bering Sea, primary production is limited to under-ice algal blooms, surface mixed layer phytoplankton blooms and subsurface phytoplankton blooms (in the Bering Sea), while in the Chukchi Sea, there is additional algal production on the seafloor.

## 4.6 As the ice season shortens on average one day per year, what are the consequences?

Sea ice in the Chukchi Sea has been arriving later and retreating earlier for ~30 years (Wood *et al*., 2015; Serreze *et al*., 2016; Stroeve *et al*., 2014) and this pattern is expected to continue (Wang *et al*., 2018). How changes in ice arrival and retreat will impact primary production in the Chukchi ecosystem is dependent upon how other parameters change. Consider two scenarios (from Berchok *et al*., 2015). As ice retreats earlier, there will be an earlier export of ice algae to the benthos, but the timing of the spring phytoplankton bloom is dependent upon wind conditions. If winds are strong, then the water column will be well mixed and the spring phytoplankton bloom will not set up until after winds weaken and water becomes stratified. In contrast, if winds are weak the water column will stratify with a warm, fresher (from ice melt) surface layer. This would support an earlier spring phytoplankton bloom. The first scenario will result in weaker stratification than the second scenario allowing more short summer blooms during wind events. The complexity of the system makes it difficult to predict how this ecosystem will react to changing ice conditions, but there is consensus on some changes.

With climate warming there will be a decrease in duration of sea-ice over the Chukchi Sea. Earlier ice retreat, will result in export of ice algae to seafloor, where there will be sufficient nutrients and light to support algal bloom. Production during the summer is limited by nutrient resupply (Lowry et al., 2015), which are advected northward in Bering Water (Mordy et al., this issue). The one caveat to this scenario is, can the sea ice retreat “too early”. Considering that there is insufficient light after the fall equinox to support algal production on the seafloor, it is likely that any ice algae dropping to the seafloor before the spring equinox also will be non-productive; this is unlikely to occur, since ice retreat is predicted to occur in June or later through 2050 (Wang *et al*., 2018). In contrast to earlier ice retreats, delayed ice return will have little impact on the bottom algal bloom, since they are largely controlled by the availability of light.

So, the magnitude of ice algal production could change with a reduction in under-ice production (shorter duration), and an increase in bottom production (longer duration). Ice algae, however, is only one component in primary production in the Chukchi Sea. Changes in phytoplankton blooms in spring (upper mixed layer), in the summer (sub-pycnocline) and fall (near surface) have been discussed by others. In open water, it has been suggested that phytoplankton production would increase, because of longer growing season (Arrigo and van Dijken, 2015; Arrigo *et al*., 2008; Brown *et al*., 2015), although nutrients could be limiting. Once nutrients are consumed in the surface layer, a bloom often forms below the surface mixed layer (e.g., Martini *et al*., 2016; Lowry *et al*., 2015). This bloom can be substantial, providing more than a third of primary productivity in the Beaufort Sea (Martinet al., 2013). Churnside *et al.* (this issue) suggest that with reduction in sea ice, the occurrence of these subsurface bloom could increase. This subsurface phytoplankton bloom would likely compete for nutrients with the bottom algal bloom and may reduce bottom algal production through shading.

# 5. Summary

The Chukchi Sea is highly productive even though the growing season is short. High production is promoted by a shallow seafloor, which allows multiple production layers (surface open water, bottom of the mixed layer, under ice algae, and dissociated ice algae on the seafloor; MPL hypothesis). High production occurs because the amount of light near the seafloor in mid-spring to early fall was similar to that measured beneath a 1.5-m thick ice floe. So, there was sufficient light at the seafloor (~40 m deep) for ice algae to continue to photosynthesize, utilizing nitrate and producing oxygen through summer; a unique feature that pertains to this shallow shelf.

Bloom onset occurred in summer following ice retreat, whereas bloom end occurred in September following loss of light. Even in a changing system with ice retreating later and arriving earlier, the primary change will be the timing of the export of ice algae to the bottom. Thus, the duration of benthic primary productivity will lengthen, because bloom onset occurs earlier.

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**Table 1.** List of moorings and instruments deployed since 2010. Deployments in 2018 are not included since these moorings have not been recovered yet. F indicates the fluorometer functioned correctly providing data for the entire deployment. Similarly, N is a nitrate sensor, O an oxygen sensor and P a PAR sensor. Bold indicates that the instrument data for only part of the deployment cycle. “*Yes*” indicates that there was production in the near bottom; “*No*” indicates that there was no production; and “-“ indicates that there was insufficient data to make a determination. In addition to the variables listed below, currents were measured at most sites.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Site**  **(depth)** | **Long.**  **Lat.** | **Aug**  **2010** | **Aug**  **2011** | **Aug**  **2012** | **Aug**  **2013** | **Sep**  **2014** | **Sep**  **2015** | **Aug**  **2016** | **Aug**  **2017** |
| C1  (45 m) | 70.835  163.119 | FNO**P**  Yes | F**O**P  - |  | **F**N**O**P  - | NP  - | FNOP*yes* | FNOP  yes | FNP  yes |
| C2  (44 m) | 71.222  164.250 | F**N**OP  Yes | FN**O**P  yes |  | FOP  yes | FN**O**P  yes | FN**O**P  yes | FNOP  yes | FNOP  yes |
| C3  (45 m) | 71.825  165.975 | OP  - | FN**O**P  yes | FOP  yes |  |  |  | NP  - | FNOP  yes |
| C4  (48 m) | 71.042  160.493 |  |  | OP  - | F**O**P  - | FNP  yes | FOP  yes | FP  - | FOP  yes |
| C5  (45 m) | 71.207  157.999 |  |  |  | FON  yes | FNOP  yes |  | FP  - | FP  - |
| C6  (43 m) | 71.777  161.875 |  |  |  | FNP  no | **F**NP  - |  |  |  |
| C7  (43 m) | 72.424  161.604 |  |  |  | FNP  yes | FNP  yes |  |  |  |
| C8  (46 m) | 72.586  161.215 |  |  |  |  | FOP  yes |  |  |  |

**Table 2.** Statistics from the mooring sites (C1-C8) for timing of ice retreat, timing of bloom, and timing of light. The units for timing of sea-ice retreat/return, bloom onset/end, and light onset/end is day of the year (DOY). For moorings and/or sensors that were not deployed each year, data for the onset or end may be missing.

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Moor.** | **Year** | **Sea Ice** | | **Bloom** | | | **Light** | | |
| **Retreat/**  **Return** | **Ice**  **Free** | **Onset/**  **end** | **Length** | **Max (day)** | **Onset/**  **end** | **Length** | **Max (day)** |
| C1 | 2010 | 140/304 | 164 | NA/NA | NA | NA | NA/274 | NA | NA |
| 2011 | 155/318 | 163 | 151/310 | 159 | 3.1 (164) | NA/NA | NA | NA |
| 2012 | 166/306 | 140 | 163/NA | NA | 13.4 (195) | NA/NA | NA | NA |
| 2013 | 195/322 | 127 | NA/NA | NA | NA | NA/278 | NA | NA |
| 2014 | 199/322 | 123 | NA/NA | NA | NA | 105/256 | 151 | 1.1 (210) |
| 2015 | 165/323 | 158 | NA/291 | NA | NA | 170/237 | 67 | 2.2 (205) |
| 2016 | 151/330 | 179 | 139/283 | 144 | 5.2 (157) | 87/287 | 200 | 1.1 (207) |
| 2017 | 133/336 | 203 | 132/321 | 189 | 9.3 (143) | 108/273 | 165 | 0.4 (269) |
| C2 | 2010 | 146/303 | 157 | NA/NA | NA | NA | NA/271 | NA | NA |
| 2011 | 160/319 | 159 | 155/318 | 163 | 37.4 (237) | 106/NA | NA | 1.5 (208) |
| 2012 | 202/305 | 103 | 162/NA | NA | 10.6 (210) | NA/263 | NA | NA |
| 2013 | 196/322 | 126 | 190/289 | 99 | 8.2 (204) | 107/277 | 170 | 1.4 (241) |
| 2014 | 199/328 | 129 | 200/288 | 88 | 5.0 (228) | 113/305 | 192 | 0.8 (210) |
| 2015 | 166/327 | 161 | 164/307 | 143 | 9.0 (205) | 183/242 | 59 | 1.2 (232) |
| 2016 | 194/343 | 149 | 142/301 | 159 | 3.0 (215) | 119/271 | 152 | 1.2 (226) |
| 2017 | 137/339 | 202 | 139/329 | 190 | 11.0 (173) | 110/271 | 161 | 1.4 (221) |
| C3 | 2010 | 169/334 | 165 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2011 | 172/325 | 153 | NA/318 | NA | NA | NA/NA | NA | NA |
| 2012 | 209/307 | 98 | 135/NA | NA | 13.6 (212) | NA/NA | NA | NA |
| 2013 | 200/321 | 121 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2014 | 195/322 | 127 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2015 | 181/316 | 135 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2016 | 194/345 | 151 | NA/NA | NA | NA | NA/263 | NA | NA |
| 2017 | 164/342 | 178 | NA/NA | NA | NA | 158/269 | 111 | 0.4 (160) |
| C4 | 2010 | 147/305 | 158 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2011 | 160/316 | 156 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2012 | 162/305 | 143 | NA/NA | NA | NA | 233/245 | 12 | 0.46(240) |
| 2013 | 196/316 | 120 | NA/262 | 95 | 7.2 (216) | 223/229 | 6 | 0.16(225) |
| 2014 | 203.303 | 100 | 193/288 | 122 | 9.0 (205) | 86/NA | NA | NA |
| 2015 | 182/316 | 134 | 164/264 | 163 | 5.3 (213) | 96/288 | 192 | 0.70(259) |
| 2016 | 151/325 | 174 | 139/139 | 134 | 10.1 (154) | 96/224 | 128 | 0.96(216) |
| 2017 | 133/332 | 199 | 139/139 | NA | NA | NA | NA | NA |

**Table 2 (continued)**

|  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Moor.** | **Year** | **Sea Ice** | | **Bloom** | | | **Light** | | |
| **Retreat/**  **Return** | **Ice**  **Free** | **Onset/**  **end** | **Length** | **Max (day)** | **Onset/**  **end** | **Length** | **Max (day)** |
| C5 | 2010 | 169/302 | 133 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2011 | 179/308 | 129 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2012 | 212/309 | 97 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2013 | 195/303 | 108 | NA/281 | NA | NA | NA/NA | NA | NA |
| 2014 | 209/302 | 93 | 132/274 | 142 | 4.5 (218) | NA/NA | NA | NA |
| 2015 | 189/314 | 125 | 141/252 | 111 | 8.1 (147) | 86/NA | NA | 1.2 (208) |
| 2016 | 151/317 | 166 | NA/307 | NA | NA | NA/253 | NA | NA |
| 2017 | 177/329 | 152 | 140/181 | 41 | 15.4 (150) | 98/224 | 126 | 2.5 (120) |
| C6 | 2010 | 174/304 | 130 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2011 | 179/316 | 137 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2012 | 220/304 | 84 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2013 | 210/296 | 86 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2014 | 203/303 | 100 | 179/255 | 76 | 6.4 (192) | NA/NA | NA | NA |
| 2015 | 185/312 | 127 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2016 | 212/298 | 86 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2017 | NA | NA | NA/NA | NA | NA | NA/NA | NA | NA |
| C7 | 2010 | 213/303 | 90 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2011 | 193/316 | 123 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2012 | 232/306 | 74 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2013 | 225/294 | 69 | NA/273 | NA | NA | NA/NA | NA | NA |
| 2014 | 227/301 | 74 | 207/280 | 73 | 9.1 (221) | NA/NA | NA | NA |
| 2015 | 196/310 | 114 | 160/258 | 98 | 7.5 (217) | NA/NA | NA | NA |
| 2016 | 196/298 | 102 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2017 | NA | NA | NA/NA | NA | NA | NA/NA | NA | NA |
| C8 | 2010 | 214/302 | 88 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2011 | 197/316 | 119 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2012 | 232/306 | 74 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2013 | 224/294 | 70 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2014 | 228/295 | 67 | NA/298 | NA | NA | NA/NA | NA | NA |
| 2015 | 196/308 | 112 | 154/257 | 103 | 6.2 (219) | NA/NA | NA | NA |
| 2016 | 196/298 | 102 | NA/NA | NA | NA | NA/NA | NA | NA |
| 2017 | NA | NA | NA/NA | NA | NA | NA/NA | NA | NA |

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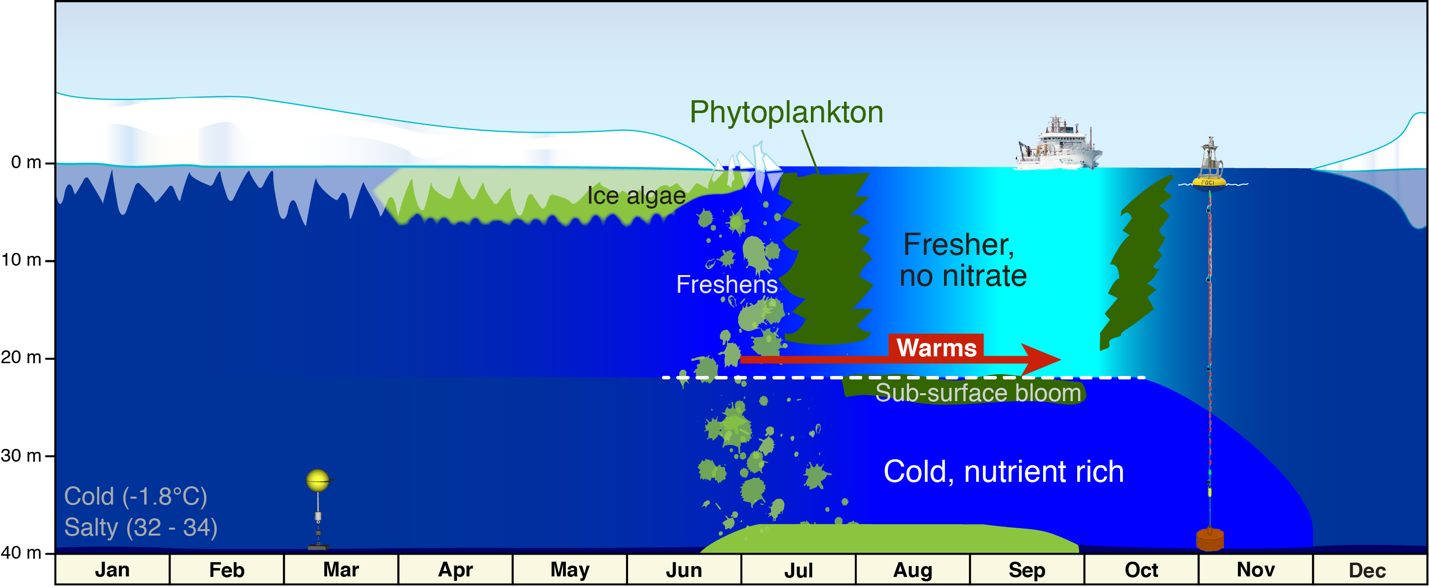
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# Figures



**Figure 1.** Map of the Chukchi Sea shelf with bathymetry and place names. The eight shelf mooring sites (C1–C8) are indicated in red. The periods of deployments are listed in Table 1.



**Figure 2.** Schematic of ecosystems and lower trophic level on the Chukchi shelf. Ice algae bloom occurs beneath the ice in spring, and with ice melt it is exported to the bottom, where there is sufficient light and nutrients to support further production. With ice retreat/melt the water stabilizes with a relatively warm, low salinity surface layer overlaying a cold more saline bottom layer. With this stabilization a surface phytoplankton bloom can occur consuming the remainder of the nutrients. With surface mixing in late summer a fall phytoplankton bloom may occur. (Adapted from Figure 136, Berchok *et al*., 2015)



**Figure 3.** (a) The mean winter (January–March) ice cover at each mooring site as a function of year. (b) The standard deviation of the mean winter ice cover shown in (a). The individual moorings are indicated by number, so “4” refers to the mooring site C4.

**Figure 4.** Box plots indicating (a) day of ice-retreat, (b) day on which the onset of PAR > 0.1 μE m−2 s−1, (c) day of bloom onset, (d) day of ice-return, (e) day on which PAR falls below >0.1 μE m−2 s−1, and (f) day of bloom end day, all versus year of mooring deployment. Moorings recovered in 2012 were not redeployed and so the bloom end day is at least day 230 in 2012.



**Figure 5.** (left) Hydrographic cast in 2015 near C2 showing multiple sub-surface chlorophyll maxima. A smaller subsurface maximum was observed just below the pycnocline, and a larger maximum was observed in the bottom layer. (right) Photos of the water column: the upper layer of relatively clear water; first chlorophyll maximum below the pycnocline; and at the top of the large maximum. The letters A, B, and C correspond to the appropriate depth shown on the left.



**Figure 6.** (a) Satellite image of sea ice on 30 April 2019 when the pop-up buoy surfaced. The red circle indicates the location of where the pop-up buoy was deployed. (b) The trajectory of the ice floe from April 30 to 28 June when it broke apart and the buoy began to transmit location and data (red dot). Selected dates are indicated in purple. The red box is the area shown in (a). (c) Time series of temperature beneath the sea ice and the depth of buoy. The depth of buoy is effectively the thickness of the sea ice at that point, since the buoy sits immediately beneath the ice. (d) Time series of chlorophyll fluorescence and PAR measured below the ice by instruments on the pop-up buoy. (e–g) Photos of water looking horizontal.



**Figure 7.** Time series of: (a) percent ice cover in 50 km × 50 km box centered on C2; (b) percent oxygen saturation (red) and chlorophyll fluorescence (green); (c) PAR and (d) nitrate. Except for (a), all time series were measured on mooring at C2 within 10 m of the bottom.

**Figure 8.** Scatter plots of the timing of (a) PAR onset versus ice retreat day, (b) bloom onset versus PAR onset, (c) bloom onset versus ice retreat, (d) PAR end versus ice return, (e) bloom onset versus PAR end, and (f) bloom end versus ice return. Scatter plots of duration of (g) measurable PAR versus period that was ice free, (h) bloom versus measurable PAR and (i) bloom and period that was ice free.

# Supplementary material

**Supplemental Figure S1.** Time series of average areal sea-ice extent (Ice) in a 50 km × 50 km box around the indicated mooring site (blue), PAR (red) and chlorophyll fluorescence measured at the mooring site. The figures are organized by year, starting with 2010 and ending with 2016.













