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S. Renault, E. Devred, M. Babin. Northward Expansion and Intensification of Phytoplankton Growth During the Early Ice-Free Season in Arctic. *Geophysical Research Letters*, 2018, 45 (19), pp.10,590-10,598. 10.1029/2018GL078995 . hal-02415146

HAL Id: hal-02415146

<https://hal.science/hal-02415146>

Submitted on 10 Apr 2022

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RESEARCH LETTER

10.1029/2018GL078995

Key Points:

- We report on the temporal and spatial variability of phytoplankton spring blooms between 2003 and 2013 in the Arctic Ocean
- Primary productivity of phytoplankton spring blooms is increasing in several areas of the Arctic Ocean between 2003 and 2013
- Satellite observations revealed a northward expansion of these blooms at a rate of 1° per decade

Supporting Information:

- Supporting Information S1

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Citation:

Renaut, S., Devred, E., & Babin, M. (2018). Northward expansion and intensification of phytoplankton growth during the early ice-free season in Arctic. *Geophysical Research Letters*, 45, 10,590–10,598. <https://doi.org/10.1029/2018GL078995>

Received 31 MAY 2018

Accepted 23 AUG 2018

Published online 15 OCT 2018

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Northward Expansion and Intensification of Phytoplankton Growth During the Early Ice-Free Season in Arctic

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Abstract In the last decades, reduction of the ice cover has been documented to affect the structure and the functioning of Arctic marine ecosystems. One direct consequence is earlier phytoplankton spring blooms and larger annual primary production compared with previous decades. However, the impact of changes in the dynamics of sea ice specifically on phytoplankton spring blooms, a major contributor of the annual primary production in the Arctic Ocean, remains poorly known. Here we report on their temporal and spatial variabilities in open waters between 2003 and 2013 using satellite ocean color data. We observed a significant increase in primary productivity of phytoplankton spring blooms in different sectors of the Arctic Ocean, especially in the Barents and Kara Seas. Satellite observations also revealed a northward expansion of these blooms at a rate of 1° per decade driven by the Barents and the Kara regions.

Plain Language Summary The declining of the ice cover in the Arctic Ocean has a strong impact on the dynamics of the marine ecosystem. The phytoplankton spring bloom, which can contribute to more than half of the annual primary production in open waters in some regions of the Arctic Ocean and which is tightly linked to the ice cover, is undergoing drastic changes. This key feature represents also a significant food source for higher trophic levels. Our study reveals rapid changes in the magnitude of primary productivity and the spatial distribution of these blooms. We observed a significant increase in primary productivity of phytoplankton spring blooms in different areas of the Arctic Ocean. A northward expansion of these blooms was also observed. Their occurrence at very high latitudes in the central basin, where they were nonexistent and where a low productivity usually prevails, is also a significant finding.

1. Introduction

The shrinking of the summer ice pack in the Arctic Ocean (Stroeve et al., 2012) is reshaping marine ecosystems (Post et al., 2013; Serreze et al., 2007). Annual and summer monthly maximum pan-Arctic net primary production have increased by approximately 47% between 1998 and 2015 in the spring and summer months, as a result of the increase in surface area of open waters during summer and a longer phytoplankton growth season (Kahru et al., 2016). In spring, the growth of primary producers in open waters greatly depends on sea ice dynamics (Sakshaug & Skjoldal, 1989). Following the ice breakup, favorable light and nutrient conditions generally support phytoplankton blooms along the ice edge at moderate polar latitudes (Tremblay & Gagon, 2009). A recent study showed that the length of the productive period has increased by about 17 days between 1998 and 2015 in open waters of the Arctic Ocean due to an earlier ice retreat and a later freezing (Kahru et al., 2016). Additionally, the phytoplankton bloom may start, and even end, more frequently under sea ice before breakup (Arrigo et al., 2012; Lowry et al., 2014; Mundy et al., 2009, 2014), since the ice pack may increasingly allow light to penetrate the ocean during spring due to a decrease in snow precipitation, thinner ice (Haas et al., 2008), and more abundant leads and melt ponds (Assmy et al., 2017). The frequency of fall blooms, a common trait at temperate latitudes, is also increasing at high latitudes (>70°N) (Ardyna et al., 2014). Overall, the phytoplankton phenology of this polar ecosystem has undergone drastic changes in recent decades and is likely to keep evolving in the future.

Despite the short duration of the phytoplankton spring bloom (PSB; i.e., a few weeks), it can contribute more than half of the annual primary production in some regions of the Arctic Ocean (Perrette et al., 2011; Sakshaug, 2004) and represents a significant food source for higher trophic levels (Wassmann et al., 2008). Until recently, at very high latitudes (i.e., central basin, >80°N), PSBs were nonexistent, and productivity was low due to the presence of the perennial sea ice and the late breakup of first-year sea ice in September while low solar

radiation prevails (Kröncke et al., 2000). Several studies using ocean color remote sensing have investigated recent multiyear changes in annual primary production with satellite observations in the Arctic Ocean (Arrigo et al., 2008; Arrigo & van Dijken, 2011, 2015; Babin et al., 2015; Bélanger et al., 2013; Matrai et al., 2013; Pabi et al., 2008; Petrenko et al., 2013). Also, Kahru et al. (2011) showed that chlorophyll *a* (chl *a*) concentration is increasingly peaking earlier in the year in several regions of the Arctic Ocean. More recently, Kahru et al. (2016) documented a 47% increase in the summer monthly maximum pan-Arctic primary production. But the impact of ongoing changes in Arctic sea ice specifically on the PSB has not yet been addressed with a dedicated regional approach. Understanding the dynamics of PSBs, a key feature of the open water season in the Arctic, is critical given its preponderant role in sustaining the entire marine ecosystem. In this study, we used satellite observations of ocean color, which provide estimates of phytoplankton biomass and primary productivity (PP), to assess the dynamics of PSBs between 2003 and 2013 in the Arctic Ocean. Our approach was inspired by the study of Perrette et al. (2011) who showed, using ocean color data from year 2007, that the PSB contributes a significant fraction of annual primary production in the Arctic Ocean.

2. Methods

2.1. Satellite Data

Daily binned Level-3 (4.64 km spatial resolution) chl *a* concentrations, an index of phytoplankton biomass, from the Moderate-Resolution Imaging Spectroradiometer Sensor (MODIS, 2003–2013) were downloaded from NASA's ocean color website (<http://oceandata.sci.gsfc.nasa.gov>). The GSM01 semianalytical bio-optical algorithm was used to retrieve chl *a* concentration from remote sensing reflectance (R_{rs} ; Maritorena & Siegel, 2005). This algorithm was selected because it was found to perform better than standard empirical algorithms, such as the standard 3-band OC3 MODIS ocean color algorithm, in Arctic waters dominated by colored dissolved organic matter (Ben Mustapha et al., 2012). Also, satellite observations of surface chl *a* may not correlate well with the depth-integrated biomass when a subsurface chlorophyll maximum is present, which can happen in some regions of the Arctic Ocean, close to the nitracline, when surface nutrients become depleted (Martin et al., 2010). However, previous sensitivity analyses that used large data sets of in situ vertical chl *a* profiles suggest a limited impact of subsurface chlorophyll maximums on large-scale estimates of depth-integrated PP in the Arctic Ocean (Ardyna et al., 2013; Arrigo et al., 2011).

Daily sea ice cover and concentrations, downloaded from the National Snow and Ice Data Center (<http://nsidc.org>) and derived from the Special Sensor Microwave/Imager (2003–2007) and from the Special Sensor Microwave Imager/Sounder (2008–2013) at a 25-km spatial resolution, were projected on the MODIS grid (4.64 km) using a nearest neighbor approach for consistency with the chl *a* concentration grid. Pixels with a chl *a* concentration that exhibited sea ice concentration greater than 10% were discarded to limit the contamination of the ocean color signal by the presence of sea ice. *Ice-adjacency effect* and subpixel ice floes can introduce bias in the remote sensing open-ocean reflectance collected in the vicinity of the ice edge, leading to an underestimation or an overestimation of the chl *a* concentration (Bélanger et al., 2007). However, the use of median instead of arithmetic mean when computing the average chl *a* concentration at a given pixel during the PSB minimizes these effects by removing possible outliers from the analysis.

In addition to chl *a*, PP rates (see below), and sea ice concentrations, daily photosynthetically available radiation (PAR) just beneath the sea surface was computed using MODIS atmospheric products, that is, ozone concentration, cloud optical thickness, and the sun zenith angle, which were used as inputs to lookup tables generated using the Santa Barbara DISORT Atmospheric Radiative Transfer (SBDART) model of Ricchiuzzi et al. (1998; see Laliberté et al., 2016, and Ayyala Somayajula et al., 2018, for details on the method and the performance of the PAR model).

2.2. Definition of a PSB Using Ocean Color Data

According to in situ observations, PSBs usually last from 1 to 3 weeks without an extra supply of nutrients resulting, for instance, from an upwelling event (Niebauer et al., 1990; Niebauer & Alexander, 1985). Two criteria used in previous studies (Pabi et al., 2008; Perrette et al., 2011), based on sea ice and chl *a* concentrations thresholds, were used in the current study to operationally set the occurrence of a PSB in a given location in a given year: (1) it takes place during the earliest 20 consecutive days when sea ice concentration is always below 10%, and (2) within this 3-week period, there must be at least one chl *a* concentration observation

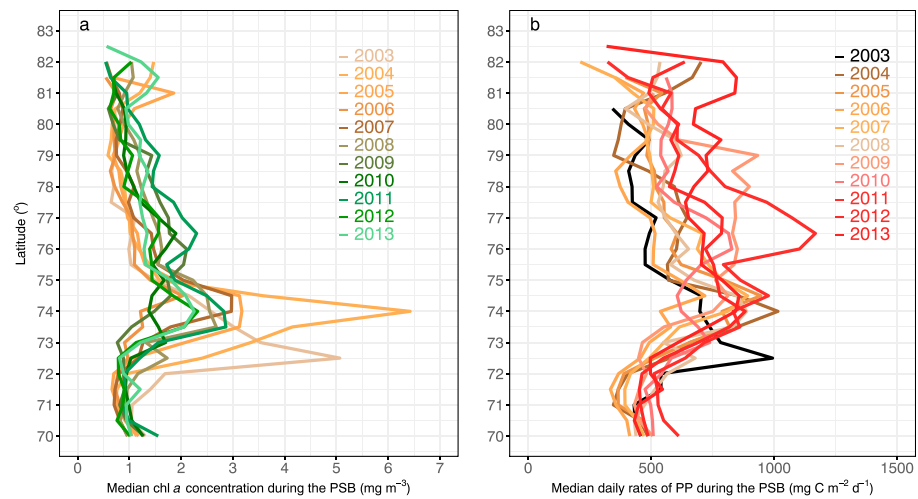


Figure 1. Latitudinal distribution in phytoplankton spring blooms (PSBs) of median chlorophyll *a* (chl *a*) concentration (a) and median daily rates of primary productivity (PP) (b) in the open water of the Arctic Ocean between 2003 and 2013.

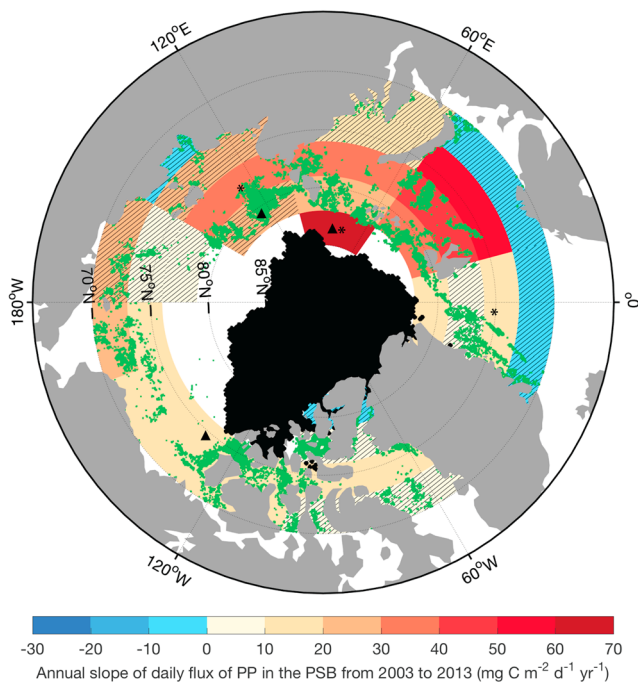


Figure 2. Estimates of annual trends in daily flux of primary productivity (PP; in $\text{mg C m}^{-2} \text{ day}^{-1} \text{ year}^{-1}$) during the phytoplankton spring bloom (PSB) determined from satellite ocean color data from 2003 to 2013 for 40 geographic subsectors of the Arctic Ocean. Solid colored areas correspond to slopes with $p \text{ value} \leq 0.05$, and black stars on solid colored areas correspond to slopes with $0.05 < p \text{ value} \leq 0.1$. Striped colored areas denote slopes with a lack of statistical significance ($p \text{ value} > 0.1$). Black triangles correspond to subsectors located in the central basin (see the supporting information, Table S1). Green pixels correspond to new PSBs observed only since 2010. Black indicates pixels that had sea ice concentration always $> 10\%$ during the 2003–2013 time period. White areas below 70°N are not included in the analysis as our study is performed between 70° and 90°N . White areas above 70°N correspond to subsectors with not enough observations (i.e., 4 years) to perform the trend analysis.

greater or equal to 0.5 mg/m^3 . The above criteria discarded cases where sea ice concentration re-increased because of growth of new sea ice or the occurrence of drifting of ice by currents and winds. It is also important to keep in mind that using these criteria, blooms that started under sea ice or even blooms in the declining phase are included in our analysis only if the 0.5 mg/m^3 chl *a* threshold is met during the open-water 3-week bloom period. Such situations are likely to happen more often at lower latitudes. Our analysis was also conducted for sea ice concentration thresholds of 25% and 50% to determine the beginning of the PSB with no significant changes to the final results.

2.3. Satellite Data Binning and Time Series Analysis

We performed our analyses on all pixels located between 70° and 90°N . First, we calculated the median chl *a* concentrations observed during the PSB and defined according to the above criteria for each pixel. Second, daily rates of PP observed during the PSB were computed using the PP model of Bélanger et al. (2013) as implemented in Benoit-Gagné et al. (2017). Evaluation of the model showed consistent results when compared to in situ measurements (Lee et al., 2015). Because the currency of our model is carbon, the reported PP values may not fully reflect variations in actual growth, which is highly constrained by nutrients. We also calculated the medians of the daily rates of PP and PAR observed during the PSB for each pixel. The day of ice breakup was also recorded for each pixel, according to the above criteria (see section 2.2).

To study the latitudinal progression of the PSB, the medians of all the available median chl *a* concentrations (Figure 1a) and median daily rates of PP (Figure 1b) computed for each pixel were retrieved across all longitudes (between 180°W and 180°E) for 0.5° latitudinal bins from 70° to 90°N . The median was selected over the mean to decrease the influence of possible outliers, as suspicious very high chl *a* concentrations ($> 200 \text{ mg/m}^3$) can be found close to the sea ice edge.

We also computed the annual trends of median daily rates of PP observed during the PSB for eight different sectors of the Arctic Ocean (Figure 2; see the supporting information, Figure S1) as described in Pabi et al. (2008):

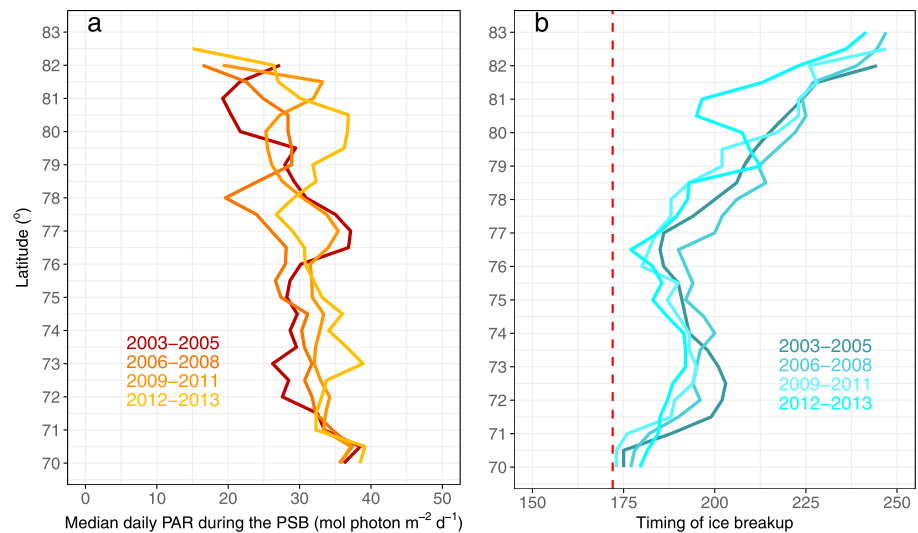


Figure 3. Daily rates of photosynthetically available radiation (PAR) observed during the phytoplankton spring bloom (PSB) (a) and timing of ice breakup (b). Daily rates of PAR and timing of ice breakup were retrieved over all longitudes between 2003 and 2013 for the Arctic Ocean and combined over a 2- or 3-year time period (2003–2005, 2006–2008, 2009–2011, and 2012–2013). The dashed red line represents the day of the summer solstice (the 172th day of the year, 21 June).

the Chukchi (180 to 160°W), Beaufort (160 to 100°W), Barents (15 to 55°E), Kara (55 to 105°E), Laptev (105 to 150°E), Siberia (150° to 180°E), Baffin (100° to 45°W), and Greenland (45°W to 15°E) sectors (see the supporting information, Figure S2). These eight sectors were further divided in 3° latitudinal bins (i.e., 70–73°N, 73–76°N, 76–79°N, 79–82°N, and 82–85°N) to produce a total of 40 subsectors. This approach was chosen to separate the time series analysis between cases of new areas of open waters at the highest latitudes and areas where seasonal ice-free water always existed between 2003 and 2013. In addition, it allowed us also to discriminate the subsectors located in the central basin from other subsectors (see the supporting information, Table S1). We proceeded by calculating the median of all the available pixels of median daily rates of PP observed during the PSB for all subsectors and for each year between 2003 and 2013. Only subsectors with at least 4 years of observations of PSBs were used in the analysis, and 28 out of the 40 subsectors met this criterion. We computed the trends as the slope of the linear regression of the annual median versus year. The linear regression was weighed by the number of pixels (i.e., PSBs) available in each subsector for each year. The number of observations for each subsector is presented in Figure S3 (see the supporting information).

We also computed for each pixel the median daily rates of PAR observed during the PSB (Figure 3a) and day of ice breakup (Figure 3b). To minimize some of the interannual variations without aliasing trends, we calculated the median of median daily rates of PAR and timing of ice breakup over a 2- or 3-year time period (2003–2005, 2006–2008, 2009–2011, and 2012–2013).

The annual northernmost latitude, Lat_{max} , reached by the PSB, was derived using only pixels with at least four observations of chl *a* concentrations that matched the criteria defined above. A linear regression of Lat_{max} versus year was performed to detect any trend in the annual maximum latitude of the PSB. The same analysis was performed without the criteria of chl *a* (i.e., chl *a* concentration > 0.5 mg/m³) to obtain information on new ice-free area that did not develop a bloom.

3. Results and Discussion

3.1. Spatial and Temporal Variabilities of Biomass and Daily Rates of PP of PSBs

Chl *a* concentrations and daily rates of PP during the PSB increased at latitudes greater than 75°N from 2003 to 2013 in the Arctic Ocean (Figures 1a and 1b). Reduction in chl *a* concentration observed around 72° to 75°N is likely due to a reduction in nutrients either explained by the occurrence of under-ice blooms or an increase in stratification at these latitudes. We also observed low chl *a* concentrations and daily rates of PP during the

PSB above 81°N in the Arctic basin where daily PAR is low (Figure 3a), and low concentrations of nutrients prevail all year long (Codispoti et al., 2013). Regarding the spatial distribution of PSBs, there was a strong variability in the total number of annual PSBs observed in the Arctic Ocean over the 2003–2013 time period (see the supporting information, Figure S4). A small number of annual PSBs are recorded in northern areas of the Arctic Ocean (>75°N), which were more covered by sea ice early in the time series. Moreover, at pan-Arctic scale, there was a strong variability in the number of observations (i.e., chl *a* concentrations) for a given pixel during the PSB (see the supporting information, Figure S5). The frequent occurrence of clouds or low-lying fog just after ice melt, especially during late summer and early fall, limited the number of available chl *a* data and made the ocean color observations patchy (Perrette et al., 2011).

We observed a strong regional variability of the PP trends in the PSB within the eight different sectors of the Arctic Ocean. Positive and significant annual trends in PP during the PSB were found in 11 (p value ≤ 0.05) and 3 ($0.05 < p$ value ≤ 0.1) out of the 28 subsectors with sufficient observations from 2003 to 2013. The highest increase in PP was observed in the Barents ($53.54 \text{ mg C m}^{-2} \text{ day}^{-1} \text{ year}^{-1}$ between 73° and 76°N) and Kara ($75.70 \text{ mg C m}^{-2} \text{ day}^{-1} \text{ year}^{-1}$ between 82° and 85°N) subsectors (Figure 2). The Chukchi, Beaufort, Baffin, and Greenland sectors showed the lowest trends of annual PP of about $15 \text{ mg C m}^{-2} \text{ day}^{-1} \text{ year}^{-1}$ over the 2003–2013 time period and for different ranges of latitudes between 70° and 82°N (Figure 2). Overall in the Arctic Ocean, we observed a significant increase in PP during the PSB of about 31% between 2003 and 2013 (an annual increasing trend of $21.43 \text{ mg C m}^{-2} \text{ day}^{-1} \text{ year}^{-1}$, p value < 0.01 , $R^2 = 0.65$; see the supporting information, Figure S1). Moreover, the spatial distribution of chl *a* concentration shows that high values occur mostly on the shelves compared to the central basin where the waters are considered as oligotrophic (Ardyna et al., 2011; Coupel et al., 2011, 2015; see the supporting information, Figure S6).

The sea ice breakup was observed later in the season at latitudes above 80°N in the Arctic Ocean (day of the year 195–250 on average, i.e., mid-July to early September) compared to lower latitudes (day of the year 170–210 on average, i.e., mid-June to late July). We found positive and significant annual trends in daily PAR beneath the sea surface during the PSB in four out of the 28 defined subsectors of the Arctic Ocean with sufficient observations from 2003 to 2013, such as the Barents, Kara, and Laptev sectors (see the supporting information, Figure S7). This can be explained by the fact that the breakup happened earlier in the season and closer to the summer solstice (Figure 3b; i.e., at the maximum of daily solar radiation, 21 June), resulting in a longer photoperiod and in an increase of PAR at these latitudes.

Our results suggest that for some subsectors located in the Barents, Kara, and Laptev sectors, an increase in daily PAR due to an earlier ice breakup contributes (i) to an increase in the accumulation of phytoplankton biomass due to favorable bloom dynamics (Behrenfeld et al., 2016) and (ii) to an increase in the daily rates of PP during the open-water PSB observed between 2003 and 2013. This observation is also in accordance with the study of Zhang et al. (2010) who showed concomitant increases in PAR and marine PP in the Arctic Ocean between 1988 and 2007 with a coupled 3-D pan-Arctic model. The ongoing shift in the timing of ice breakup has therefore important consequences for PSB PP in the Arctic. However, other factors than PAR that could affect the phytoplankton bloom, such as nutrient availability and its potential replenishment in the water column, could explain the increase in daily rates of PP during the open-water PSB for other subsectors and should be examined in the future (Popova et al., 2010; Rainville et al., 2011; Tremblay et al., 2015; Tremblay & Gagon, 2009). The observed spatially heterogeneous responses of the annual trends of PP suggest a dependence of PP on multiple confounding factors driving the Arctic ecosystem dynamics that needs to be better understood and characterized.

A mismatch between the spring bloom burst of phytoplankton and the activity of zooplankton grazers resuming winter diapause could also explain this increase in the daily rates of PP during the open-water PSB, since the life cycles of phytoplankton and zooplankton grazers are tightly linked to the timing of the blooms (Behrenfeld et al., 2016; Ji et al., 2013; Leu et al., 2011; Søreide et al., 2010). The PSB is usually followed by a long-delayed peak in zooplankton biomass, dominated by large copepods of the genus *Calanus* that overwinters at depth (Ashjian et al., 2003; Campbell et al., 2009). Because of a low grazer biomass and activity at the onset of the PSB, much of the PP may not be consumed in the water column, as it has been documented, for example, in the Chukchi and Beaufort Seas where more than half of the PP may not be consumed by the zooplankton (Campbell et al., 2009; Sherr et al., 2009).

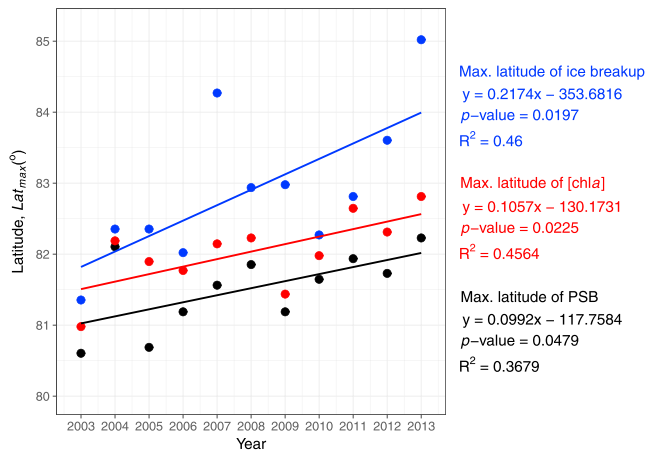


Figure 4. Highest latitude reached by phytoplankton spring blooms (PSBs) in the open water of the Arctic Ocean from 2003 to 2013. The red dots and red regression line refer to the analysis with the pixels where chl *a* concentration (at least four observations, any concentration) was observed within the 20 consecutive days of ice breakup. The black dots and black regression line show the same, but only when at least 1 value of chl *a* concentration went beyond the threshold of 0.5 mg/m³ and defined the beginning of the PSB. The blue dots and blue regression line refer to the maximum latitude where at least one ice-free pixel (i.e., sea ice concentration below 10% during 20 consecutive days) was observed. Trends computed as the slope of the linear regression of highest latitude versus year are weighed by the number of available observations (i.e., pixels) between 2003 and 2013 (slopes of the linear regression, *p* values, and coefficients of determination *R*²).

The increasing PP in PSBs might have contributed to a significant fraction of increased open ocean PP that has notably been observed in recent Arctic studies (Arrigo & van Dijken, 2015; Bélanger et al., 2013; Pabi et al., 2008). It is also important to note that these observations do not account for PP that could occur within or beneath sea ice cover or for PP located at the subsurface chlorophyll maximum. Major phytoplankton under-ice blooms have recently been observed in different regions of the Arctic Ocean (Arrigo et al., 2012; Fortier et al., 2002; Mundy et al., 2009). The occurrence of such under-ice blooms, invisible to satellite remote sensing, may increase in the future in an Arctic Ocean dominated by thinner first year ice (Lowry et al., 2014; Mundy et al., 2009).

3.2. Northward Expansion of PSB Estimates

*Lat*_{max} reached by the PSB between 2003 and 2013 was recorded for each year. The most northern PSB in the Arctic Ocean was recorded in 2013 at a latitude of 82.23°N compared to the maximum latitude of 80.60°N reached by the PSB in 2003 (Figure 4). The slope of the linear regression of the annual maximum latitude reached by the PSB on time (in year) corresponds to a northward progression of the PSB by about 1° per decade for the Arctic Ocean (*p* value < 0.05, *R*² = 0.37). This result is mostly driven by the Barents and Kara sectors where a clear northward progression of these blooms is observed since 2003 at a rate of about 1.1° (*p* value < 0.05, *R*² = 0.42) and 1.2° (*p* value < 0.05, *R*² = 0.54) per decade, respectively (see the supporting information, Table S2). In addition, most of the recorded PSBs since 2010 occurred above 80°N and were located in the Barents, Kara, and Laptev sectors (Figure 2). Trends in other sectors of the Arctic Ocean were not found to be statistically significant (*p* value > 0.05; see

the supporting information, Table S2). Interestingly, we observed a negative trend of about 2.4° per decade (*p* value = 0.03, *R*² = 0.42), a southward progression of PSBs, in the Greenland sector (see the supporting information, Table S2) where the pixels recorded for the analysis were mostly located in the Fram Strait.

At the highest latitude (i.e., >80°N), the PSB develops around early September (on average the 250th day of year, result not shown). It is noteworthy that the positive trend of the linear regression of the annual maximum latitude reached by the open water is twice as fast as the northward progression of the PSB with a value of 2.1° per decade (*p* value < 0.05, *R*² = 0.46, Figure 4, and see the supporting information, Table S2). This may suggest, if nutrients are not the limiting factor, that the ice breakup takes place too late in the year in the most northern regions of the Arctic Ocean, when sun elevation is too low to provide the required energy for phytoplankton to bloom. If ice breakup occurs earlier in the future, the minimum light requirement could be met and PSBs could eventually happen and spread over 82°N.

The northward progression of the PSB observed in the Barents and Kara sectors likely results from an earlier retreat of the ice cover driven by the increased input of warm Atlantic waters through Fram Strait (Årthun et al., 2012; Oziel et al., 2016; Spielhagen et al., 2011). The southward progression of the PSB observed in the Greenland sector could likely be related to the increasing export of sea ice from the Arctic Ocean through Fram Strait preventing northward expansion of PSBs in this area (Halvorsen et al., 2015; Smedsrud et al., 2017). The occurrence of PSBs in the central Arctic basin is also a significant finding given that these remote waters are defined as oligotrophic (Ardyna et al., 2011; Coupel et al., 2011, 2015). Low nutrient concentrations limiting the PP in spring and summer and resulting from the strong stratification of the water column all year long have been documented in this region even in wintertime (Codispoti et al., 2013).

Important and significant changes in annual PSB PP and northward progression of PSBs were observed in the Arctic Ocean, especially in the Barents and Kara sectors. The increasing PP of PSBs and their occurrence in the central basin challenge our understanding of the dynamics of the marine ecosystem in this region and the future role of the Arctic Ocean as a source or a sink of carbon for the global climate. With the decline of the ice cover, competition for light and nutrients could happen between under-ice blooms and PSBs and impact the dynamics of the marine ecosystem. Moreover, in a possibly future Arctic ice-free summer, our

results suggest that PSBs could extend in the central basin, but the PP may likely remain low due to an increased sea ice melting and a subsequent intensified stratification of the water column, preventing nutrient-rich deep waters to be mixed with surface waters (Coupel et al., 2015; Slagstad et al., 2011). On the contrary, storms and associated high winds could trigger strong vertical mixing in an ice-free ocean, increase the nutrient supply in the upper water column, and favor the occurrence of PSBs (Ardyna et al., 2014; Mundy et al., 2009). The impact of PSBs on higher trophic levels (Leu et al., 2011; Post, 2017; Richardson, 2008) and the subsequent export fluxes of organic matter (Wassmann & Reigstad, 2011) remain also to be determined (Yool et al., 2015).

Acknowledgments

MODIS data were made available by the NASA's Ocean Color Processing Group at <http://oceandata.sci.gsfc.nasa.gov>. Sea ice concentration data were provided by the National Snow and Ice Data Center from their website <http://nsidc.org>. We gratefully thank M. Benoît-Gagné, P. Massicotte, L. Oziel, and E. Rehm for programming assistance and helpful comments on the manuscript, and D. Christiansen-Stowe for language support. We also thank two anonymous reviewers for constructive and insightful reviews. S. R. received a postgraduate scholarship from the Canada Excellence Research Chair (CERC) in Remote Sensing of Canada's New Arctic Frontier and stipends from Québec-Océan and ArcticNet. This is a contribution to the research programs of the CERC in Remote Sensing of Canada's New Arctic Frontier, Takuvik Joint International Laboratory, ArcticNet, and Québec-Océan.

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