

Contrasting interannual changes in phytoplankton productivity and community structure in the coastal Canadian Arctic Ocean

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Abstract

The rapid physical changes affecting the Arctic Ocean alter the growth conditions of primary producers. In this context, a crucial question is whether these changes will affect the composition of phytoplankton communities, augment their productivity, and eventually enhance food webs. We combined satellite and model products with in situ datasets collected during fall and provide new insights into the response of phytoplankton biomass and production in the Canadian Arctic by comparing an interior shelf (Beaufort Sea) and an outflow shelf (Baffin Bay). Correlation analysis was used to distinguish between seasonal and interannual variability and revealed that most biological variables are responding to the interannual pressures of climate change. In southeast Beaufort Sea, a change in phytoplankton community composition occurred, with a significant increase in diatoms from 2% (2002) to 37% (2010–2011) of the total protist abundance. In 2011, photosynthetic picoeukaryotes were twice as abundant as in 2002. For these two phytoplankton groups, abundance was correlated with the duration of the open-water period, which also increased and affected vertical stratification and sea-surface temperature. In contrast, there was a sharp decline in centric diatom abundance as well as in phytoplankton biomass and production in northern Baffin Bay over the years considered. These decreases were linked to changes in seasonal progression and sea-ice dynamics through their impacts on vertical stratification and freshwater input. Overall, our results highlight the importance of stratification and the duration of the open-water period in shaping phytoplankton regimes—either oligotrophic or eutrophic—in marine waters of the Canadian Arctic.

In the Arctic Ocean, it is generally accepted that phytoplankton are limited by light prior to the onset of vernal blooms and become limited by nutrients, mainly dissolved inorganic nitrogen, later during the productive season (Tremblay and Gagnon 2009). However, as the sea-ice cover shrinks and freshwater runoff to the Arctic Ocean increases, changes in stratification are drastically altering the balance between light and nutrient availability (Peterson et al. 2006; Kwok et al. 2009). These changes could affect the whole

marine ecosystem from the bottom up by triggering drastic changes in the productivity, biomass, and assemblage composition of phytoplankton. In this context, one of the most crucial questions is whether or not these changes will translate into enhanced phytoplankton production and, eventually, higher ecosystem productivity (Tremblay et al. 2015). The Arctic Ocean receives inflows from the Atlantic and Pacific oceans as well as a large input of freshwater from large rivers and less saline water from the Pacific. The Arctic domain has been divided into inflow, interior, and outflow shelves based on water mass properties (Carmack et al. 2006; Williams and Carmack 2015). Due to this spatial heterogeneity, the response of phytoplankton communities will likely not be the same throughout the Arctic Ocean (Carmack et al. 2006). Numerous factors, including the assemblage

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composition and the size structure of phytoplankton communities in specific regions of the Arctic Ocean, must be taken into account when predicting future scenarios.

Several studies have sought to track possible synoptic changes in Arctic primary production with different methodological approaches, sometimes obtaining contrasting results (see Babin et al. 2015). Using a worldwide dataset of chlorophyll *a* (Chl *a*) concentrations and water transparency measurements (from Secchi disk), Boyce et al. (2010) showed an overall decrease of phytoplankton biomass in the global ocean over the last century. However, three out of four global coupled carbon cycle climate models showed a reverse situation for the upcoming century, with an expected rise in primary production for the Arctic Ocean (Steinacher et al. 2010). The primary production rise was mostly explained by the deepening of the mixed layer depth, while the model associated with a decrease in primary production showed a reduction of the mixed layer depth. These models mostly agree with both Arrigo and van Dijken (2015), who showed a global 30% increase in primary production from 1998 to 2012 in the Arctic Ocean using remote sensing, and with the satellite-based model of Bélanger et al. (2013). However, this latter study reported that some of the most productive Arctic regions, such as the North Water Polynya (NOW, northern Baffin Bay), have seen their productivity decrease dramatically over the last decade. More recently, Marchese et al. (2017) showed a decrease in phytoplankton bloom amplitude over the 1998–2014 period. Numerical models of the Arctic Ocean still lack validation with in situ time series and rely mainly on the assimilation of satellite observations (Forest et al. 2011; Dupont 2012; Babin et al. 2015). While allowing for a broad spatial and temporal coverage of the Arctic Ocean, satellite observations provide much less detail than field studies at the local scale, especially in the ice-covered Arctic. Satellite-derived observations are limited to the surface and do not include the contribution of under-ice algae (Mundy et al. 2009; Arrigo et al. 2012) or the subsurface chlorophyll maximum (SCM), a common feature in the Arctic Ocean (Martin et al. 2010). These limitations result in a variable and sometimes large underestimation of primary production at different stages of seasonal development (spring bloom for under-ice algae and post-bloom for the SCM in late summer – early fall; see Arrigo and van Dijken 2011; Ardyna et al. 2013). Moreover, the identification of phytoplankton functional types (PFTs) by satellites is still under development and has not been validated in polar seas (Stuart et al. 2000; Nair et al. 2008; Devred et al. 2011; IOCCG 2014, 2015; Rousseaux and Gregg 2015). Information on PFTs is essential to assess the ecological role of phytoplankton communities in biogeochemical cycles and the potential transfer of carbon toward the food chain or export to the deep sea. In this context, field studies are thus essential to support model and remote sensing studies, and to corroborate large temporal trends.

To our knowledge, very few field studies have investigated interannual trends in phytoplankton biomass, productivity, and community composition in specific sectors of the Arctic Ocean, especially during fall (Wassmann et al. 2011; Gallinat et al. 2015), when satellite data are no longer available or valid due to low solar elevation (see details in IOCCG 2015). The recent study of Bergeron and Tremblay (2014) used changes in nutrient inventories to document shifts in net community production for the southeast Beaufort Sea and Baffin Bay but did not address associated changes in total primary production or phytoplankton community composition. These authors found a 1.6-fold increase in nitrate consumption in Beaufort Sea and a 65% decrease of nitrate consumption in Baffin Bay, reflecting the different physical and biological settings highlighted more than a decade ago during the International North Water Polynya Study (NOW; Deming et al. 2002) and the Canadian Arctic Shelf Exchange Study (CASES; Vincent and Pedrós-Alió 2008). The long-held view for these two regions is one of a highly stratified, low-nutrient, oligotrophic system characterized by low productivity and flagellate dominance on the Canadian Beaufort Shelf, and a highly mixed, high-nutrient eutrophic system based mostly on large-sized algal cells, namely diatoms, in northern Baffin Bay (Booth et al. 2002; Carmack and Macdonald 2002; Klein et al. 2002; Tremblay et al. 2002; Ardyna et al. 2011). This view needs to be re-assessed in light of ongoing climate change and the results of Bergeron and Tremblay (2014).

In combination with the NOW (1999) and CASES (2002–2003) datasets, we used data from the ArcticNet field program (2006–2011) to investigate interannual changes in the production, biomass, size structure, abundance, and taxonomic composition of the phytoplankton community in these two contrasting regions during fall in order to assess the influence of environmental factors on phytoplankton communities in the context of current climate change. Furthermore, we aimed to provide a better understanding of phytoplankton dynamics and trends that can be expected across the Arctic by comparing two different environments: an interior shelf and an outflow shelf of the Arctic Ocean.

Methods

Study area and sampling design

Sampling was performed at recurrent stations in the southeast Beaufort Sea and northern Baffin Bay during six fall campaigns between 2006 and 2011 onboard the CCGS *Amundsen* as part of the ArcticNet program. To augment the dataset, we used data collected during the NOW project in fall 1999 in northern Baffin Bay (Mostajir et al. 2001; Booth et al. 2002; Klein et al. 2002) and during the CASES project in fall 2002 and 2003 in southeast Beaufort Sea (Brugel et al. 2009). During these early expeditions, water column sampling of environmental and biological variables was very similar to the sampling done during the ArcticNet program (see Klein et al. 2002; Brugel et al. 2009 for details). Sampling

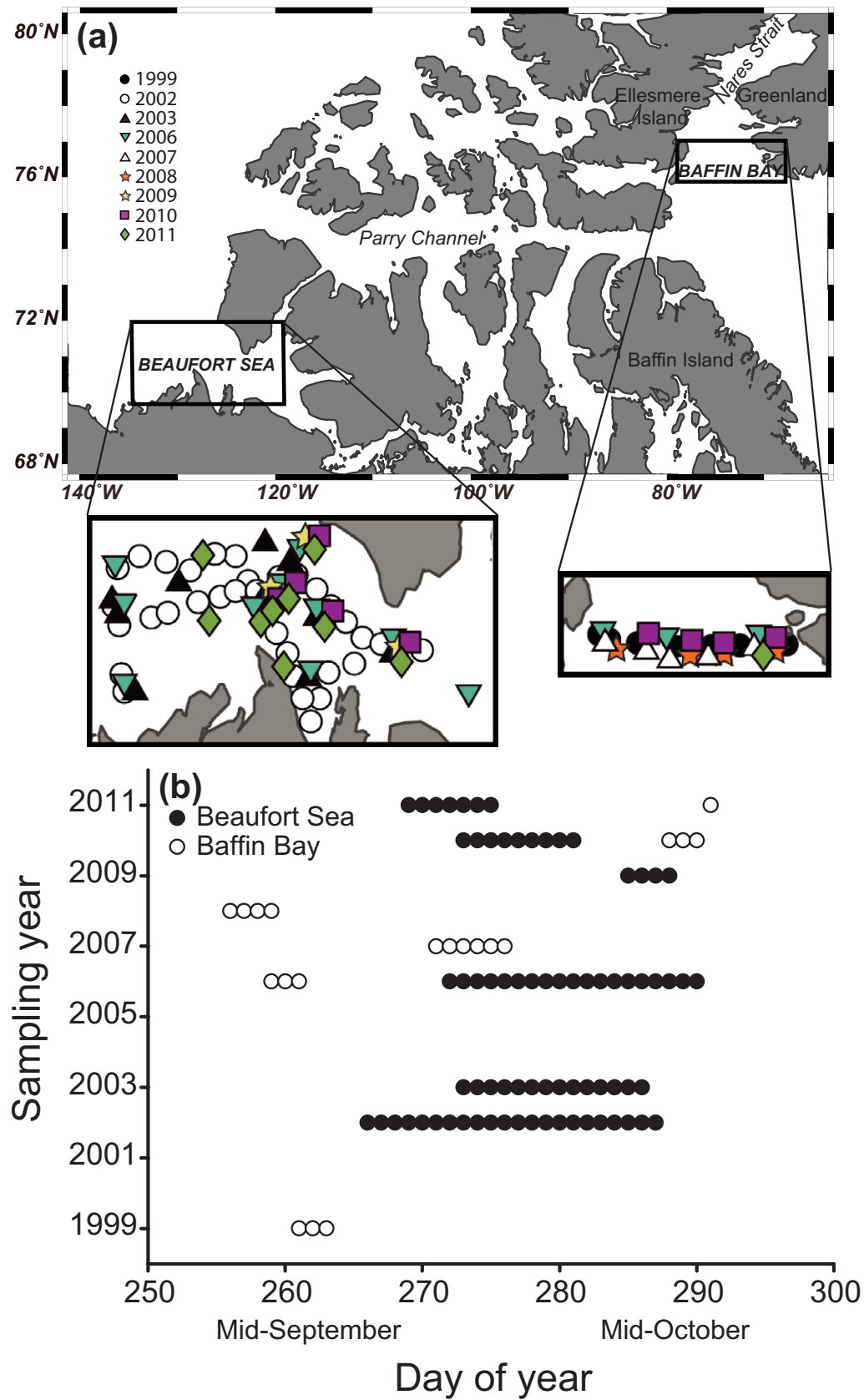


Fig. 1. (a) Location of stations sampled and (b) the sampling periods during fall from 1999 to 2011 in southeastern Beaufort Sea and northern Baffin Bay, Canadian Arctic Ocean.

Table 1. Overview of chemical and biological variables collected during the study in Beaufort Sea (upper rows) and Baffin Bay (lower rows). Samples were collected at optical depths when a light profile was done prior to water collection; otherwise, samples were collected at fixed depths.

Optical depth (%): Fixed Depth (m):		95	50	30	15	5	1	0.2			
		2	5	10	20	30	40	50	Z_{scm}	75	100
Year	Sampling date										
Beaufort Sea											
2002	23 Sep–14 Oct	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2003	30 Sep–13 Oct	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2006	29 Sep–09 Oct	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2009	12 Oct–15 Oct	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2010	30 Sep–08 Oct	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2011	26 Sep–02 Oct	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
Baffin Bay											
1999	18 Sep–20 Sep	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2006	16 Sep–18 Sep	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2007	29 Sep–03 Oct	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2008	12 Sep–15 Sep	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2010	15 Oct–17 Oct	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B
2011	18 Oct	N, P, B	N, P, B, A, T	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, P, B	N, B	N, B

N, nutrients; P, primary production; B, chlorophyll *a* biomass; A, cell abundance; T, taxonomy.

station locations and dates from 1999 to 2011 are shown in Fig. 1.

At most stations, a vertical profile of the downwelling photosynthetically active radiation (PAR, 400–700 nm) was performed with a PNF-300 radiometer (Biospherical Instruments) to determine the diffuse attenuation coefficient (K_d) and the depth of the euphotic zone (Z_{eu} : 0.2% of surface irradiance, as in Tremblay et al. 2009). When meteorological conditions did not allow deployment of the radiometer, a Secchi disk was used to estimate K_d and Z_{eu} values. Incident downwelling PAR was measured at 10 min intervals from the beginning to the end of each expedition with a LI-COR LI-190 SA cosine-corrected flat sensor placed on the ship's fore-deck and protected from shading.

At each station, water samples were collected with a rosette sampler equipped with 24 12 L Niskin-type bottles (OceanTest Equipment). A Sea-Bird 911plus recorded profiles of conductivity, temperature, and depth (CTD), and was equipped with a nitrate sensor (ISUS V2, Satlantic), a chlorophyll fluorometer (SeaPoint), and a PAR sensor (QSP-2300, Biospherical Instruments). At most stations, water was collected at seven optical depths (ca. 95%, 50%, 30%, 15%, 5%, 1%, and 0.2% of surface water irradiance), at the depth of the SCM (Z_{scm}), and at two depths in the aphotic zone (75 m and 100 m). When light profiles or Secchi disk depth were not available prior to water sampling, optical depths were replaced by fixed depths (2 m, 5 m, 10 m, 20 m, 30 m, 40 m, 50 m), and K_d and Z_{eu} were determined afterwards from the CTD's PAR sensor. Water subsamples for the determination of nutrient

concentrations and the measurement of biological variables were transferred into dark acid-washed bottles and processed immediately after collection. See Table 1 for an overview of sample collection. Nitrate plus nitrite ($\text{NO}_3 + \text{NO}_2$), phosphate (PO_4), and silicic acid ($\text{Si}(\text{OH})_4$) concentrations were measured immediately after sampling using a Bran-Luebbe 3 autoanalyzer (adapted from Grasshoff et al. 1999).

Phytoplankton productivity, biomass, and community

At selected stations, primary production was estimated using the ^{14}C -uptake method and 24 h simulated in situ deck incubations (Knap et al. 1996; Ardyna et al. 2011). Subsamples were filtered onto Whatman GF/F glass-fiber filters (total particulate primary production, $\geq 0.7 \mu\text{m}$, P_T) and 5 μm Nuclepore polycarbonate membrane filters (primary production by large cells, $\geq 5 \mu\text{m}$, P_L). As an index of phytoplankton biomass, Chl *a* concentrations were measured. Subsamples of water collected at every depth were size-fractionated onto Whatman GF/F filters (total phytoplankton biomass, $\geq 0.7 \mu\text{m}$, B_T) and 5 μm Nuclepore polycarbonate membrane filters (biomass of large cells, $\geq 5 \mu\text{m}$, B_L). Subsamples were also filtered onto 20 μm silk mesh to determine the presence of aggregates or colonial cells. Fluorometric measurements of Chl *a* concentrations were performed using a Turner Designs fluorometer 10-AU following the acidification method of Parsons et al. (1984). Biomass and production due to phytoplankton cells $< 5 \mu\text{m}$ are referred to as B_S and P_S , respectively.

Pico- ($\leq 2 \mu\text{m}$) and nanophytoplankton (2–20 μm) cell abundances were determined at each station in the surface

waters. Duplicate subsamples were fixed with Grade I glutaraldehyde (Sigma) to a final concentration of 0.1%, quick-frozen in liquid nitrogen, and stored at -80°C until analysis. Cell counts were performed using an EPICS ALTRA flow cytometer (Beckman Coulter) equipped with a 488 nm laser (15 mW output). Microspheres (1 μm or 2 μm , Fluoresbrite plain YG, Polysciences) were added to each sample as an internal standard. Picocyanobacteria and photosynthetic eukaryotes were distinguished by their difference in orange fluorescence from chlorophyll (675 ± 10 nm). Pico- and nanophytoplankton were discriminated based on forward scatter calibration with known-sized microspheres (Tremblay et al. 2009). Samples for the identification and enumeration of protists > 2 μm in the surface waters were preserved in acidic Lugol's solution (final concentration of 0.4%; Parsons et al. 1984) and stored in the dark at 4°C until analysis. Cell identification was carried out to the lowest possible taxonomic rank using an inverted microscope (Wild Herbrugg or Zeiss Axiovert 10) in accordance with Lund et al. (1958). The main taxonomic references used to identify the protist cells were Tomas (1997) and Bérard-Therriault et al. (1999).

Satellite and model products

To complement and/or validate our in situ measurements, we also used a wide array of satellite and model products. Daily incident downwelling irradiance data 3 d prior to the sampling day were estimated and averaged (E_{3d}) in Beaufort Sea and Baffin Bay using the model described in Laliberté et al. (2016). Briefly, the model employs a precomputed Look-Up-Table (LUT) generated using radiative transfer simulations. The LUT associates spectral irradiance reaching the surface with a given set of input parameters derived from satellite observations (passive microwaves and optical remote sensing), namely solar zenith angle, cloud optical thickness, cloud fraction, and ozone concentration. Estimates of PAR from the LUT were computed with respect to station position at a 3 h time interval corresponding to the atmospheric data time resolution of the International Satellite Cloud Climatology Project (ISCCP). Atmospheric inputs from ISCCP available for the 1999–2009 period have a 280 km grid resolution and were bi-linearly interpolated at station locations. For 2010 and 2011, a cloud climatology computed from the ISCCP time series (1984–2009) was used as input to the PAR model. This model has been recently validated with in situ PAR measurements collected onboard during various field campaigns in the Canadian Arctic (with an accuracy of 30%; see Laliberté et al. 2016). Finally, irradiance was averaged over 3 d (E_{3d}) prior to sampling.

Subsurface PAR and surface Chl *a* estimates for the whole year were obtained with a 4 km resolution from the European Space Agency's GlobColour project (<http://www.globcolour.info>) to confirm observed trends in northern Baffin Bay. Daily composite Chl *a* concentrations using standard Case 1 water algorithms (O'Reilly et al. 2000; Maritorena

et al. 2010) were averaged over the productive period (i.e., from the end of May to early September).

Surface wind velocities were obtained from the NCEP–NARR Reanalysis 1 (National Center for Environmental Prediction/North American Regional Reanalysis) gridded dataset (<http://www.esrl.noaa.gov/psd/data/gridded/data.narr.html>) and were used to calculate the along-shelf component of wind velocity in Beaufort Sea. Data at 10 m were squared as an index of wind stress, noted *u*-wind as in Tremblay et al. (2011), and averaged from mid-September to mid-October.

Daily sea-ice cover extents were obtained from the Special Sensor Microwave Imager (SSM/I) and the Special Sensor Microwave Imager Sounder (SSMIS) (Cavalieri et al. 1996; Maslanik and Stroeve 1999). All valid pixels within a radius of 16–40 km around each station location were averaged daily for each sampling year. The dates (day of year, DOY) of the beginning (OWS) and end (OWE) of the open-water season (defined as five consecutive days with ice cover $< 20\%$ and $> 20\%$ respectively, as in Ferland et al. 2011), as well as its duration (OWD), were determined. The 20% threshold allows the removal of most atmospheric interferences with the microwave signal that erroneously suggest a small amount of ice (Parkinson and Cavalieri 2008). The presence or absence of the ice bridge in Nares Strait was determined from a visual analysis of ice charts produced by the Canadian Ice Service (CIS) and the Danmarks Meteorologiske Institut (DMI). In these charts, ice properties such as concentration, stage of development, and form of ice are used to define regions or polygons of homogeneous characteristics (Environment Canada 2005). The ice bridge, when present, appears clearly as a concave line joining Ellesmere Island and Greenland near the constriction point between the two land masses.

Calculation and statistical analyses

The surface mixed layer depth (Z_m) was estimated as the depth at which the gradient in density (σ_t) between two successive depths was > 0.03 kg m^{-3} (threshold gradient method: Thomson and Fine 2003; Tremblay et al. 2009). The strength of water column stratification was determined using a stratification index ($\Delta\sigma_t$), which was defined as the difference in σ_t between 80 m and 5 m, as in Tremblay et al. (2009). As another indicator of water column stratification, the highest Brunt–Väisälä frequency (N^2) in the upper 100 m of the water column was also recorded. Temperature (T_m), salinity (S_m), and $\text{NO}_3 + \text{NO}_2$, PO_4 , and Si(OH)_4 concentrations were averaged over Z_m . The freshwater inventory in Z_{eu} (FWI_{eu}) was defined as the integrated salinity fraction below a reference salinity of 34.8 (S_{ref} ; McPhee et al. 2009) from the equation:

$$\text{FWI}(m) = \int_0^{Z_{eu}} [(S_{ref} - S_{Z_{eu}})/S_{ref}] dz \quad (1)$$

as previously used in Lapoussière et al. (2013).

Spearman's rank correlations (r_s) were used to detect monotonic trends over time (i.e., gradual increase or decrease during fall and over the entire sampling period) in environmental and biological variables. This test was also used to assess relationships between two variables. When no trend over years was detected, one-way analysis of variance by ranks (Kruskal–Wallis test; Zar 1999) was performed to seek year-to-year variability in some environmental and biological variables. ANOVAs were completed by a multiple comparison test using rank sums (Dunn's test). Pearson's linear regressions (r) were used to determine temporal trends in satellite-derived PAR and Chl *a*. Statistical tests were performed with the R-3.2.3 and JMP Pro 12.0.1 software packages.

Results and discussion

Interannual changes in southeast Beaufort Sea

In southeast Beaufort Sea, there were significant increases in the salinity and temperature of the surface mixed layer from 2002 to 2011 (Tables 2, 3). The significant decreases of the stratification index ($\Delta\sigma_t$) from 6.5 kg m^{-3} to 2.7 kg m^{-3} and of the Brunt–Väisälä frequency (N^2) from 0.011 s^{-2} to 0.003 s^{-2} over the last decade were better correlated with changes in salinity than with water temperature (Tables 2, 3). Peralta-Ferriz and Woodgate (2015) confirmed a general increase in the salinity of the surface mixed layer in Beaufort Sea from 1979 to 2012. This rise in salinity was not expected, considering the general backdrop of increased freshwater discharge from rivers and glacier melt (Peterson et al. 2002, 2006), and is likely due to deep-water intrusion into the surface layers. In 2010–2011, the open-water season lasted about four times longer than in 2002–2003 due to a combination of earlier ice break up and later ice growth (Table 4). In addition, the along-shelf component of wind stress on the sea surface increased with time (Fig. 2). A change was also observed in the average wind direction, which shifted from westerly in 2002 and 2003 to easterly thereafter, thereby increasing the transport of sea ice away from the sampling region (Figs. 1, 2). Easterly winds along the coast of Beaufort Sea, such as those observed in 2010–2011 (Fig. 2), favor upwelling events (Williams et al. 2006; Williams and Carmack 2008), especially considering the delayed onset of fast-ice cover during these 2 yr (Table 4).

Over the same period, B_T generally varied between $17 \text{ mg Chl } a \text{ m}^{-2}$ and $28 \text{ mg Chl } a \text{ m}^{-2}$, but it increased to $53 \text{ mg Chl } a \text{ m}^{-2}$ in 2010 (Fig. 3a). Variability in Chl *a* biomass between years was mostly due to the SCM since Chl *a* concentration stayed quite stable in surface waters (Fig. 4a). Similarly, P_T showed great variability between years, being lowest in 2009 ($28 \text{ mg C m}^{-2} \text{ d}^{-1}$) and highest in 2010 ($164 \text{ mg C m}^{-2} \text{ d}^{-1}$; Fig. 3c). Using satellite imagery, Arrigo and van Dijken (2015) observed an increase of ca. $5\% \text{ yr}^{-1}$ in the annual net primary production of Beaufort Sea from

Table 2. Environmental variables (mean and SE in parentheses) in Beaufort Sea (upper panel) and Baffin Bay (lower panel) during fall from 2002 or 1999 to 2011. Nutrients are averaged over Z_m .

Year	n	Z_{eu} (m)	Z_m (m)	Z_{scm} (m)	S_m (psu)	T_m (°C)	$\Delta\sigma_t$ (kg m^{-3})	N^2 (s^{-2})	FWI _{eu} (m)	E_{3d} ($\text{mol quanta m}^{-2} \text{ d}^{-1}$)	$(\text{NO}_3 + \text{NO}_2)_m$ ($\mu\text{mol L}^{-1}$)	$(\text{Si(OH)}_4)_m$ ($\mu\text{mol L}^{-1}$)	$(\text{PO}_4)_m$ ($\mu\text{mol L}^{-1}$)
<i>Beaufort Sea</i>													
2002	37	54.8 (3.7)	8.9 (0.7)	10.4 (3.3)	23.9 (0.4)	−0.7 (0.1)	6.5 (0.3)	0.0110 (0.0008)	8.6 (0.4)	6.1 (0.4)	0.54 (0.08)	6.48 (0.52)	0.43 (0.03)
2003	10	66.2 (6.5)	8.6 (2.1)	13.0 (3.3)	25.3 (0.6)	−1.0 (0.1)	5.3 (0.3)	0.0076 (0.0007)	9.9 (0.9)	4.4 (0.5)	0.25 (0.04)	5.10 (0.86)	0.55 (0.05)
2006	10	58.9 (6.5)	11.8 (1.5)	24.6 (6.9)	28.3 (0.7)	1.2 (0.5)	3.5 (0.6)	0.0043 (0.0008)	7.2 (1.0)	4.9 (0.4)	0.77 (0.46)	5.40 (1.52)	0.67 (0.10)
2009	3	71.0 (6.8)	19.3 (4.8)	24.0 (8.6)	28.7 (0.4)	0.1 (0.1)	3.0 (0.2)	0.0037 (0.0006)	8.6 (1.3)	3.4 (0.1)	0.33 (0.09)	3.14 (0.67)	0.55 (0.08)
2010	5	68.7 (5.1)	22.6 (3.0)	41.6 (4.6)	30.1 (0.1)	3.1 (0.2)	2.1 (0.1)	0.0024 (0.0004)	7.2 (0.7)	6.5 (0.4)	0.40 (0.11)	1.80 (0.13)	0.70 (0.02)
2011	9	60.9 (6.6)	9.7 (1.8)	22.2 (3.8)	29.3 (0.4)	2.8 (0.5)	2.7 (0.3)	0.0028 (0.0003)	6.7 (1.0)	8.0 (0.2)	0.61 (0.15)	2.63 (0.42)	0.63 (0.03)
<i>Baffin Bay</i>													
1999	7	47.0 (2.2)	21.1 (3.0)	21.0 (2.9)	31.5 (0.4)	0.0 (0.4)	1.4 (0.2)	0.0014 (0.0001)	3.8 (0.5)	6.6 (0.2)	0.77 (0.19)	1.67 (0.16)	0.34 (0.09)
2006	3	55.9 (7.5)	27.0 (11.6)	17.0 (5.7)	32.1 (0.4)	0.9 (0.7)	1.0 (0.1)	0.0011 (0.0006)	3.8 (1.0)	8.6 (0.1)	1.06 (0.63)	2.20 (0.89)	0.44 (0.09)
2007	5	62.3 (9.1)	20.0 (4.8)	23.8 (10.4)	31.7 (0.6)	−1.0 (0.3)	1.0 (0.1)	0.0010 (0.0002)	4.9 (1.5)	3.1 (0.1)	2.86 (1.10)	3.56 (1.17)	0.95 (0.20)
2008	4	62.9 (7.9)	17.8 (3.0)	21.3 (5.5)	30.7 (0.6)	2.0 (1.0)	2.2 (0.2)	0.0019 (0.0006)	5.2 (0.6)	7.9 (0.4)	0.70 (0.23)	0.69 (0.22)	0.31 (0.11)
2010	4	78.2 (7.0)	16.3 (4.6)	27.5 (11.1)	31.1 (0.7)	−1.4 (0.2)	1.6 (0.3)	0.0011 (0.0003)	5.8 (1.6)	0.8 (0.1)	3.65 (0.93)	5.18 (0.95)	0.76 (0.06)
2011	1	60.4	12.0	7.0	32.6	−1.8	0.8	0.0006	3.0	0.7	4.18	4.20	0.57

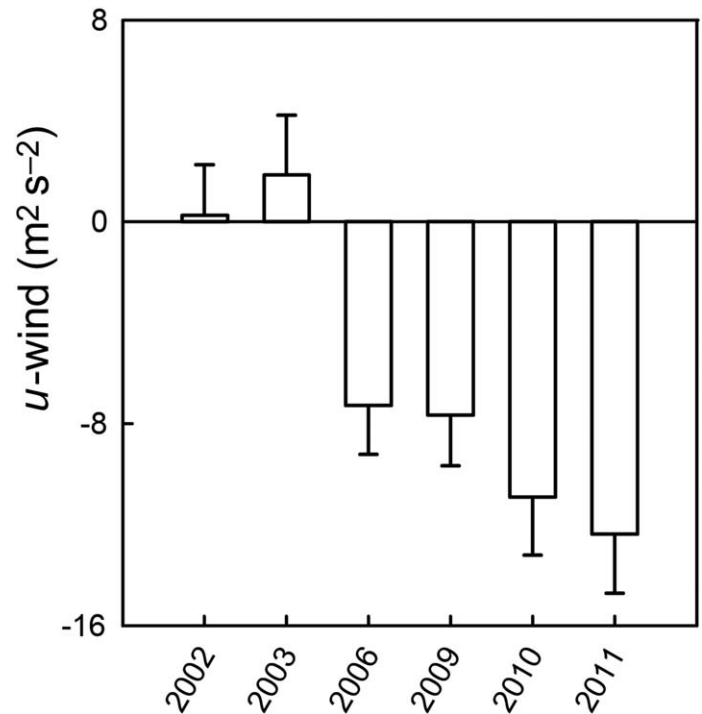
Table 3. Spearman's rank correlation coefficients between environmental variables measured in Beaufort Sea (lower half-panel) and in Baffin Bay (shaded upper half-panel). Bold indicates significance at the $p < 0.05$ level.

	Year	DOY	S_m	T_m	$\Delta\sigma_t$	N^2	FWI_{eu}	E_{3d}	$(NO_3 + NO_2)_m$	$(Si(OH)_4)_m$	$(PO_4)_m$	OWS	OWE	OWD
Year		0.39	-0.10	-0.39	0.15	-0.17	0.25	-0.45	0.46	0.27	0.40	-0.16	0.56	0.41
DOY	0.01		0.16	-0.76	-0.33	-0.34	-0.06	-0.92	0.58	0.75	0.61	0.25	0.34	-0.08
S_m	0.78	0.13		0.31	-0.85	-0.38	-0.90	-0.00	0.28	0.22	-0.27	-0.01	0.32	0.27
T_m	0.63	-0.43	0.36		-0.06	0.19	-0.42	0.85	-0.36	-0.56	-0.81	-0.25	0.03	0.36
$\Delta\sigma_t$	-0.76	-0.05	-0.96	-0.35		0.62	0.68	0.15	-0.27	-0.38	0.07	-0.10	-0.12	-0.05
N^2	-0.78	-0.11	-0.81	-0.40	0.79		0.15	0.25	-0.34	-0.47	-0.20	0.19	-0.05	-0.20
FWI_{eu}	-0.22	-0.07	-0.35	-0.15	0.35	0.15		-0.09	-0.03	-0.05	0.40	-0.02	-0.26	-0.23
E_{3d}	0.04	-0.95	-0.04	0.44	-0.04	-0.01	0.00		-0.51	-0.65	-0.74	-0.17	-0.26	0.10
$(NO_3 + NO_2)_m$	0.40	-0.15	0.46	-0.07	-0.47	-0.36	-0.49	0.26		0.56	0.46	0.05	0.36	0.14
$(Si(OH)_4)_m$	-0.42	0.25	-0.08	-0.72	0.06	0.10	-0.25	-0.24	0.07		0.51	-0.11	0.22	0.14
$(PO_4)_m$	0.47	-0.17	0.81	0.00	-0.85	-0.48	-0.62	0.27	0.42	-0.09		-0.02	0.19	-0.01
OWS	-0.73	-0.04	-0.57	-0.55	0.59	0.55	0.32	0.00	-0.36	0.45	-0.35		-0.15	-0.78
OWE	0.81	0.22	0.71	0.61	-0.67	-0.64	-0.38	-0.15	-0.17	-0.51	0.18	-0.75		0.68
OWD	0.81	0.13	0.68	0.66	-0.65	-0.65	-0.42	-0.04	0.26	-0.55	0.34	-0.88	0.94	

Table 4. Sea-ice conditions in Beaufort Sea (upper panel) and Baffin Bay (lower panel) for each sampling year. In 2009, no data were available after 24 October; OWE could not be determined, but it was > 297 and OWD was > 101 d.

Year	OWS (DOY)	OWE (DOY)	OWD (days)
<i>Beaufort Sea</i>			
2002	241 (5)	281 (1)	32 (3)
2003	191 (11)	284 (4)	55 (12)
2006	215 (6)	305 (2)	90 (8)
2009	196 (1)	n/a	n/a
2010	163 (2)	319 (1)	156 (1)
2011	162 (7)	304 (0)	139 (7)
<i>Baffin Bay</i>			
1999	175 (4)	282 (5)	107 (5)
2006	154 (12)	293 (13)	139 (10)
2007	174 (15)	294 (7)	118 (21)
2008	152 (8)	293 (6)	142 (10)
2010	166 (4)	307 (1)	137 (1)
2011	188	291	103

1998 to 2012. The model of Forest et al. (2011) and Tremblay et al. (2011) also showed an 80% increase in gross primary production in 2008 compared to 2004 that they attributed to a reduction in ice cover. A similar trend is not evident from our field data. Only fall 2010, when the longest open-water season and among the strongest upwelling-favorable winds were recorded (Table 4; Fig. 2), appears to be unusual, with high Chl *a* biomass and productivity (Fig. 3a,c). B_L accounted for $< 45\%$ of the biomass except in 2006 and 2010, when it accounted for 52% and 66% of B_T , respectively (Fig. 3a). Small cells dominated primary production

**Fig. 2.** Along-shelf wind velocity squared (u -wind) as an index of surface stress (negative values indicate upwelling-favorable winds) averaged from mid-August to mid-October over our study area in Beaufort Sea for each sampling year. Error bars represent SE.

every year during fall (Fig. 3c). The abundance of photosynthetic picoeukaryotes in surface waters increased nearly two-fold over the last decade (Table 5; Fig. 5a) and could be explained by the extended open-water season (Table 4) and the relatively high temperature of the surface mixed layer

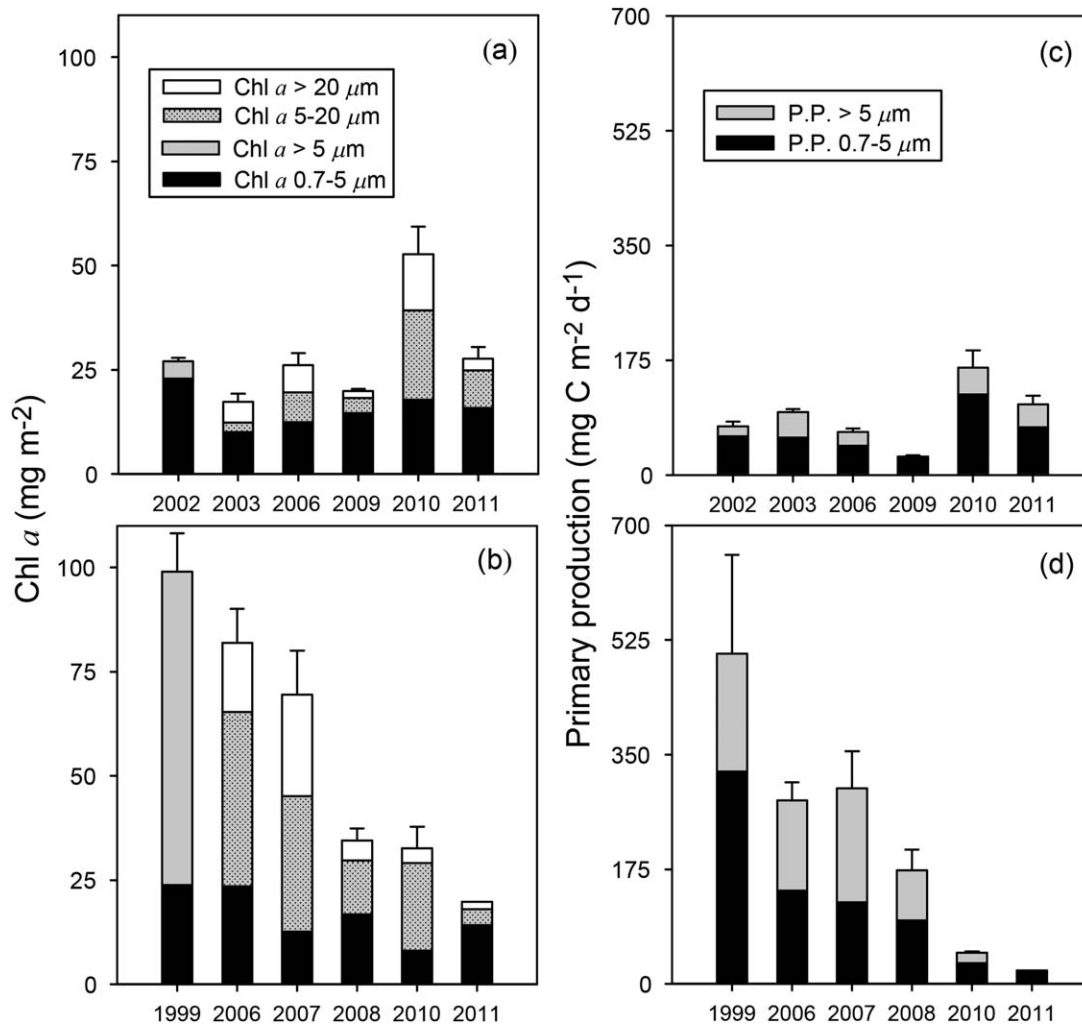


Fig. 3. Variations in size-fractionated Chl *a* biomass (left panels) and primary production (P.P.) (right panels) over years during fall in (a, c) Beaufort Sea and (b, d) Baffin Bay. Data were integrated over the euphotic zone (down to 0.2% surface irradiance). In 1999 and 2002, only two size fractions were measured. Values are mean + 0.5 SE. In (d), the production by large cells is 3.2 mg C m⁻² d⁻¹ for fall 2011.

(Table 2; Li et al. 2009; Tremblay et al. 2009; Morán et al. 2010; Terrado et al. 2012).

Overall, the most striking difference between the beginning and end of the last decade is the change in the phytoplankton community composition. Autotrophic flagellates were the numerically dominant protists (> 2 μm) in 2002, 2003, and 2006 whereas the protist community was more diversified afterwards, with a higher proportion of diatoms (Fig. 5c). In 2010, the community was numerically dominated by centric diatoms (mostly *Leptocylindrus minimus* Gran), which accounted for the large increase in total Chl *a* observed that year (Figs. 3a, 5c). In 2011, the diatom community was mainly composed of the centric diatoms *Leptocylindrus minimus*; *Arcocellulus cornucervus* Hasle, von Stosch and Syvertsen; and *Skeletonema* cf. *costatum* (Greville) Cleve. In 2002, diatoms made up only 2% of the total protist abundance (Fig. 5c), and there was a significant increase in

centric diatom abundance over the years (Table 5). Diatom abundance was positively correlated with S_m , T_m , and duration of the open-water season, and negatively correlated with $\Delta\sigma_t$ and N^2 ; thus it was clearly associated with the importance of stratification (Table 5). The negative correlation of diatom abundance with Si(OH)_4 concentrations, its low concentration in 2010 and 2011, and the fourfold decrease in the molar ratio Si(OH)_4 to $\text{NO}_3 + \text{NO}_2$ in Z_m (Table 2) can be attributed to higher Si consumption by diatoms (Brzezinski 1985).

The high Chl *a* biomass and productivity measured in fall 2010 were mostly due to centric diatoms. Even though they were not highly productive at the time of sampling, as estimated from the contribution of large cells (> 5 μm) to total primary production, their high abundance in early October suggests the occurrence of a fall bloom, prior to our sampling. Enhanced nutrient consumption by phytoplankton

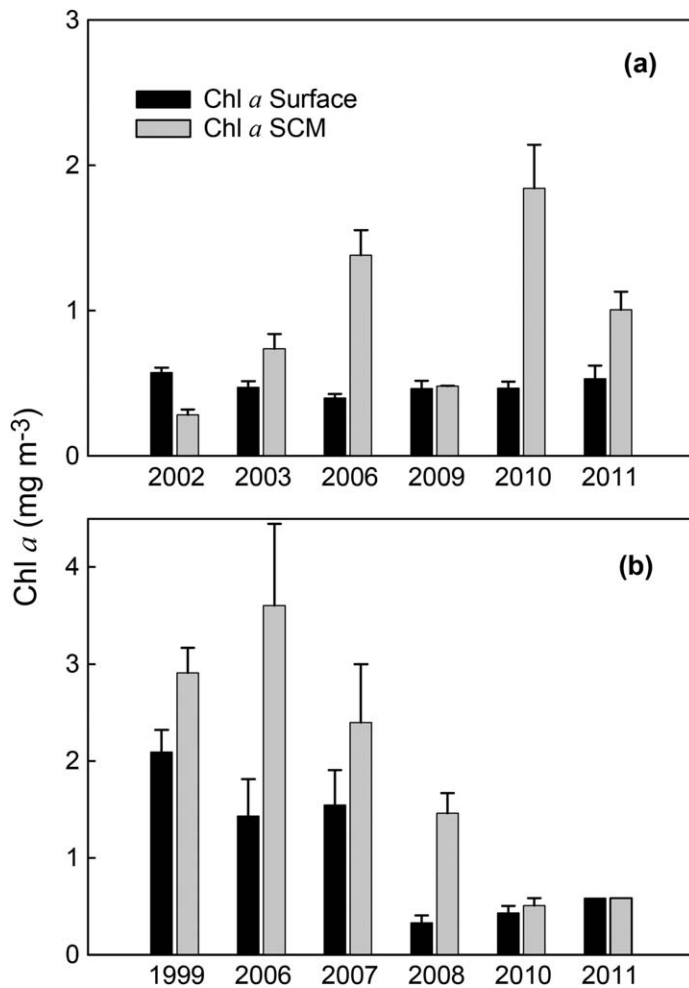


Fig. 4. Comparison of the year-to-year variability in Chl *a* concentration in surface waters and at the depth of the subsurface chlorophyll maximum (SCM) in (a) Beaufort Sea and (b) Baffin Bay. Vertical bars are mean + 0.5 SE.

following upwellings, as shown by Ardyna et al. (2017), likely occurred prior to our field sampling in 2010 and explains the relatively low nutrient concentrations in Z_m measured at our sampling stations (Table 2). Indeed, if sufficient light is available for primary production when surface waters are replenished with nutrients, a fall bloom can occur; this was likely the case in 2010 and 2011 (Fig. 5a,c). This interpretation seems consistent with the 15% increase in the frequency of fall blooms on the Canadian Beaufort Shelf between 1998–2001 and 2007–2012 (Ardyna et al. 2014).

Interannual changes in northern Baffin Bay

In northern Baffin Bay, the duration of the open-water season increased over the years, but durations were similar in 1999 and 2011 due to a late ice breakup and early ice formation during these 2 yr (Table 4). Satellite images and aerial surveys have shown that an ice bridge has historically formed in Nares Strait around 78.6°N between Ellesmere

Island and Greenland (Fig. 6), with the date of formation being highly variable. Prior to 1994, the ice bridge broke up during week 29.9 ± 3.5 (mid- to late July; Fig. 7). Since 1994, the ice bridge has broken up on average during week 26.3 ± 3.5 (end of June), but there have been some years when the southern Nares Strait ice bridge did not form at all (2007, 2009, and 2010). In 2008, it had broken up by mid-May (week 22), 4–5 weeks earlier than the long-term average (Table 4; Fig. 7).

Without the ice bridge, sea ice drifts southward, thus decreasing the overall ice concentration in southern Nares Strait (mainly in Kennedy Channel, Kane Basin, and Smith Sound) while increasing it in northern Baffin Bay along the coast of Ellesmere Island compared to years when the ice bridge is present (Fig. 6b,c; see also Kwok et al. 2010). This allows light to penetrate much earlier into the water column at these high latitudes and triggers nutrient consumption in the upper ocean before currents carry these waters to our sampling stations at 76°N. The occurrence of an under-ice phytoplankton bloom in the thinner and ponded sea ice would also reduce the quantity of nutrients available for primary production down-current in late spring – early summer (Mundy et al. 2009; Arrigo et al. 2012; Palmer et al. 2014). However, $\text{NO}_3 + \text{NO}_2$ in Z_m increased over the years in late fall in northern Baffin Bay (Table 3). Ice floes moving south might also result in intermittent shading of the water column, as observed at our sampling latitude (Fig. 6c), and could amplify the significant decrease of E_{3d} observed over the years (Table 3) that was attributed mostly to seasonality (see next section). Interestingly, 2007–2008 and 2010 were associated with the highest FWI_{eu} measured during our study (Table 2). In the absence of an ice bridge, the increased occurrence of ice floes transiting through northern Baffin Bay suggests accrued sea-ice melting and stratification in northern Baffin Bay. Moreover, glacial meltwater from the Greenland Ice Sheet and the flux of fresher water from the Arctic Ocean through Nares Strait (Haine et al. 2015) may further increase freshwater content and stratification. Sea-ice melt could also explain why the temperature was colder by about 2°C in 2010–2011 compared to 1999 (Table 2).

In northern Baffin Bay, B_T diminished drastically and significantly over the years (Table 5), being as high as 99 mg Chl *a* m⁻² in 1999 and as low as 20 mg Chl *a* m⁻² in 2011 (Fig. 3b). The significant decrease in phytoplankton biomass during fall was mostly due to decreased numbers of large cells. B_L dominated the Chl *a* biomass every year until 2011, when it accounted for only 28% of B_T (Fig. 3b). Changes in the B_L contribution to B_T were observed at both the surface and SCM (Fig. 4b). Between 1999 and 2010–2011, a 25-fold decrease was observed for P_T , which dropped from 500 mg C m⁻² d⁻¹ to 20 mg C m⁻² d⁻¹ (Fig. 3d). The decrease in production of both small and large phytoplankton cells over the sampled years was also large and significant. The contribution of P_L to P_T ranged between 33% and 58% except in

Table 5. Spearman's rank correlation coefficients between environmental and biological variables measured in Beaufort Sea (upper panel) and in Baffin Bay (lower panel). Bold indicates significance at the $p < 0.05$ level.

	Year	DOY	S_m	T_m	$\Delta\sigma_t$	N^2	FWI_{eu}	E_{3d}	$(NO_3 + NO_2)_m$	$(Si(OH)_4)_m$	$(PO_4)_m$	OWS	OWE	OWD
<i>Beaufort Sea</i>														
B_T	0.00	0.06	0.10	0.23	-0.03	-0.10	0.14	-0.02	0.00	-0.48	0.14	0.01	0.21	0.18
$B_L : B_T$	0.70	0.35	0.64	0.34	-0.59	-0.59	-0.34	-0.33	0.22	-0.06	0.45	-0.62	0.72	0.68
P_T	0.17	-0.27	0.05	0.22	0.10	0.01	0.12	0.21	0.25	-0.40	0.34	-0.22	0.19	0.21
$P_L : P_T$	0.00	0.15	0.24	0.07	-0.12	-0.15	-0.08	-0.16	-0.10	-0.08	0.02	-0.06	0.34	0.11
Total Euk	0.36	-0.10	0.14	0.40	-0.12	-0.11	-0.28	0.13	0.09	-0.21	0.01	-0.30	0.30	0.40
Pico-Euk	0.40	-0.15	0.15	0.44	-0.13	-0.16	-0.23	0.17	0.05	-0.23	-0.05	-0.32	0.31	0.40
Nano-Euk	-0.11	0.16	-0.09	-0.12	0.13	0.20	-0.34	-0.17	0.41	0.57	0.29	0.10	0.03	0.04
C. diatoms	0.76	0.01	0.71	0.60	-0.66	-0.68	-0.37	0.13	0.14	-0.47	0.43	-0.64	0.71	0.80
A. flagellates	-0.36	0.07	-0.32	-0.11	0.31	0.19	0.05	-0.13	-0.45	0.38	-0.13	0.37	-0.18	-0.35
<i>Baffin Bay</i>														
B_T	-0.69	-0.14	0.44	0.30	-0.42	-0.08	-0.55	0.24	-0.29	0.10	-0.24	-0.21	-0.12	0.14
$B_L : B_T$	-0.42	0.28	0.17	-0.12	-0.15	-0.06	-0.29	-0.25	-0.03	0.38	0.18	-0.07	0.08	0.04
P_T	-0.81	-0.47	0.16	0.65	0.04	0.20	-0.40	0.56	-0.29	-0.37	-0.44	-0.20	-0.18	0.12
$P_L : P_T$	-0.32	-0.22	-0.03	0.17	0.13	0.13	-0.15	0.17	-0.31	-0.07	0.19	-0.43	0.04	0.53
Total Euk	0.10	-0.13	0.74	0.47	-0.37	-0.02	-0.74	0.18	0.06	-0.03	-0.39	-0.24	0.41	0.49
Pico-Euk	0.34	-0.02	0.64	0.33	-0.31	-0.07	-0.58	0.09	0.10	0.01	-0.25	-0.22	0.59	0.56
Nano-Euk	-0.53	-0.19	0.61	0.42	-0.52	-0.22	-0.76	0.24	-0.16	-0.03	-0.35	-0.28	-0.19	0.21
C. diatoms	-0.65	-0.47	0.61	0.84	-0.42	-0.17	-0.69	0.56	-0.24	-0.13	-0.46	-0.54	0.08	0.56
A. flagellates	-0.19	-0.44	0.32	0.60	0.10	0.50	-0.49	0.30	-0.33	-0.49	-0.29	0.02	0.37	0.13

2011, when it was 15% (Fig. 3d). Satellite studies have also shown a strong decrease in productivity in Baffin Bay over the last decade throughout the productive period (Arrigo and van Dijken 2011, 2015; Bélanger et al. 2013).

The total abundance of eukaryotic cells $< 20 \mu m$ did not change significantly over years, but there was a major change in the community size structure (Table 5; Fig. 5b,d). Indeed, there was a significant decrease of photosynthetic nanoeukaryote abundance in the surface waters over the study period (Table 5), and their lowest abundance was recorded in 2010 (Fig. 5b). This decrease seems to be balanced by a general (but not significant) increase in photosynthetic picoeukaryotes over the same period (Table 5; Fig. 5b). Total protist abundance ($> 2 \mu m$) exhibited a significant decline, with values being nearly fivefold higher in 2006 than in 2011 (Fig. 5d). Early in the study period, centric diatoms accounted for $> 50\%$ of the total protist abundance but represented only 10% of total abundance in 2011. The other major group in 1999 was flagellated cells (mostly prymnesiophytes, dinoflagellates, and dictyochophytes; Mostajir et al. 2001; Booth et al. 2002). In 1999, the centric diatom *Chaetoceros gelidus* Chamnansinp, Li, Lundholm and Moestrup, which had been previously misidentified as *Chaetoceros socialis* Lauder (see Chamnansinp et al. 2013; Balzano et al. 2017), was the most common species in northern Baffin Bay, with abundances ranging from 1.4 to 4.3×10^6 cells L^{-1} (Booth et al. 2002). In 2006 and 2007, the protist community

was still dominated by centric diatom taxa, mostly *Chaetoceros* spp. ($\leq 20 \mu m$), *Leptocylindrus danicus* Cleve, and *C. gelidus*. The decrease in centric diatoms from 2006 to 2011 was significant (Table 5). In 1999, the phytoplankton community was similar to the southeast Beaufort Sea community of recent years in terms of dominant taxonomic groups (Fig. 5c,d). In 2010–2011, however, the phytoplankton community $> 2 \mu m$ in northern Baffin Bay was numerically dominated by flagellated cells (mostly unidentified flagellates, dinoflagellates, and prymnesiophytes) and a relatively high abundance of photosynthetic picoeukaryotes (presumably the prasinophyte *Micromonas* Manton and Parke; Lovejoy et al. 2007). This type of community is usually typical of a light-limited system in late fall (Simo-Matchim et al. 2016). The community composition, the abundance of nutrients, and the lack of SCM (Table 2; Fig. 4b) suggest that an early fall bloom did not occur prior to our sampling. Increased stratification due to freshwater accumulation likely dampened the occurrence of diatom-dominated fall blooms in recent years, as has been widely observed in the Arctic Ocean (Ardyna et al. 2014).

Centric diatom and photosynthetic nanoeukaryote abundances were negatively correlated with FWI_{eu} and positively correlated with S_m (Table 5); these observations point to ice changes and related alterations in stratification as major players in shaping the fall phytoplankton assemblage in northern Baffin Bay. Consequently, the variability in biomass and production as well as the change in the taxonomic

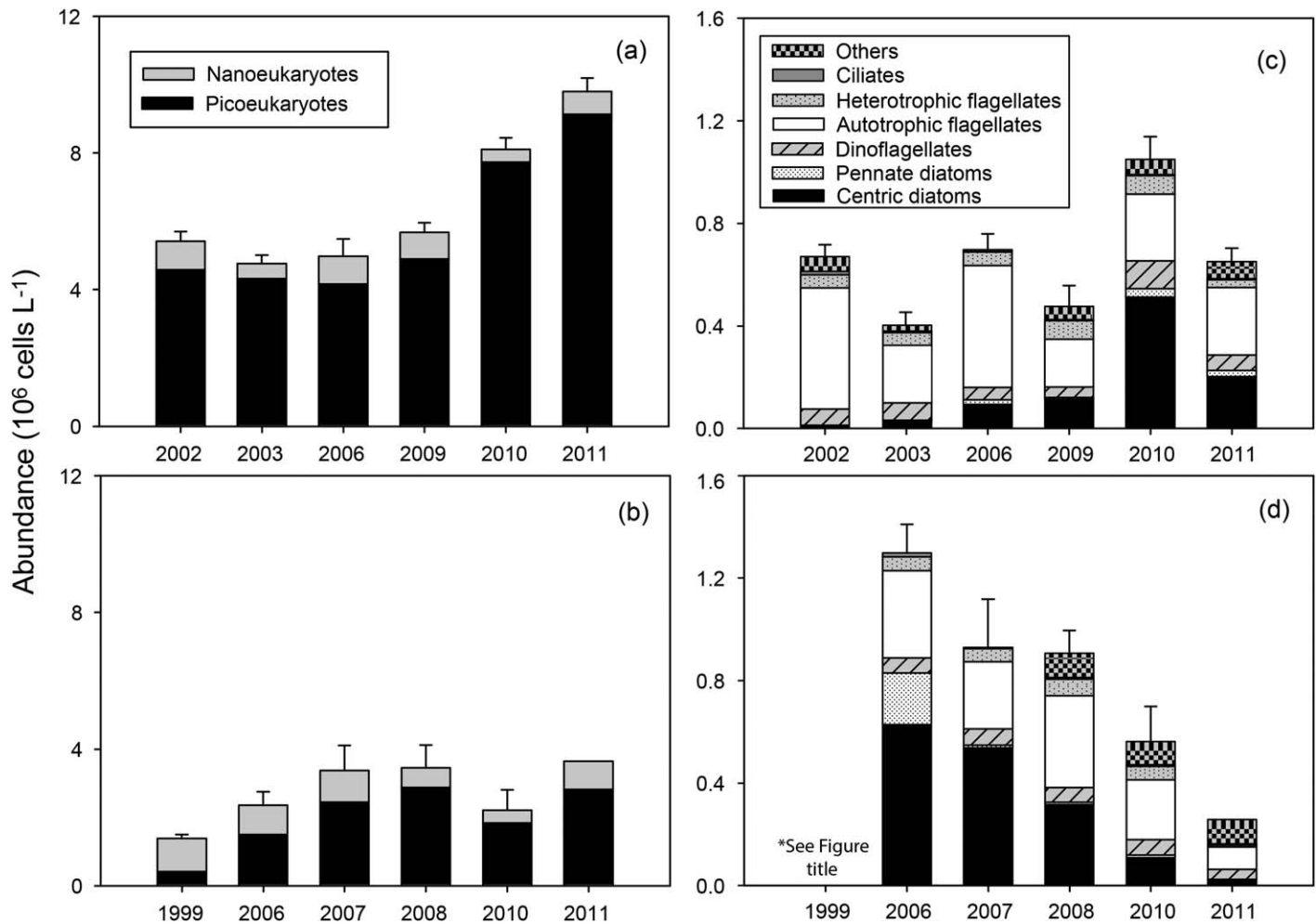


Fig. 5. Variations in the abundance of photosynthetic pico- and nanoeukaryotes (left panels) and of different protist groups (right panels) during fall in the surface waters of (a, c) Beaufort Sea and (b, d) Baffin Bay. Bars and vertical lines represent mean and 0.5 SE of total protist cell abundance. The autotrophic flagellate group includes chrysophytes, cryptophytes, dictyochophytes, euglenophytes, prasinophytes, prymnesiophytes, raphidophytes, and unidentified flagellates. The heterotrophic flagellate group comprises taxa such as *Telonema* spp., *Leucocryptos marina* (Braarud) Butcher, and *Meringosphaera mediterranea* Lohmann, along with choanoflagellates. "Others" are unidentified cells. *: Total protist abundance is not available for Baffin Bay in 1999. However, the abundance of the dominant centric diatom *Chaetoceros gelidus* in the euphotic zone ranged from 1.4 to 4.3×10^6 cells L⁻¹ at our sampling site (Booth et al. 2002). Some pico- and nanophytoplankton abundance data in Baffin Bay in fall 1999 are from Mostajir et al. (2001). Note that *C. gelidus* was misidentified as *Chaetoceros socialis* Lauder in Mostajir et al. (2001) and Booth et al. (2002).

composition of the phytoplankton community reported here for the fall period can be attributed mostly to a decrease in irradiance (discussed in the next section) that was amplified by increased ice transport and to stronger vertical stratification. The decrease in irradiance was likely high enough that it hampered nutrient consumption, and this explains why relatively high nutrient concentrations were measured at the time of sampling. Moreover, these low-light and stratified conditions apparently favor the development of small phytoplankton cells and increase the importance of the microbial food web (Cushing 1989; Li et al. 2009; Yamamoto-Kawai et al. 2009; McLaughlin and Carmack 2010), which relies on recycled nitrogen sources rather than NO₃.

Seasonal variability in southeast Beaufort Sea and northern Baffin Bay

Given the logistical constraints inherent to oceanographic work in remote Arctic regions, sampling did not systematically occur at the exact same period every year. The sampling period consistently occurred during fall (Fig. 1b) and within a 3-week window for the southeast Beaufort Sea (23 September–15 October; 2002–2011) and a 5-week window for northern Baffin Bay (12 September–18 October; 1999–2011). This methodological limitation might create spurious interannual trends or conceal real ones if seasonality was the dominant factor controlling biological variables. We therefore attempted to highlight the influence of variable sampling dates on our results, and this task was further

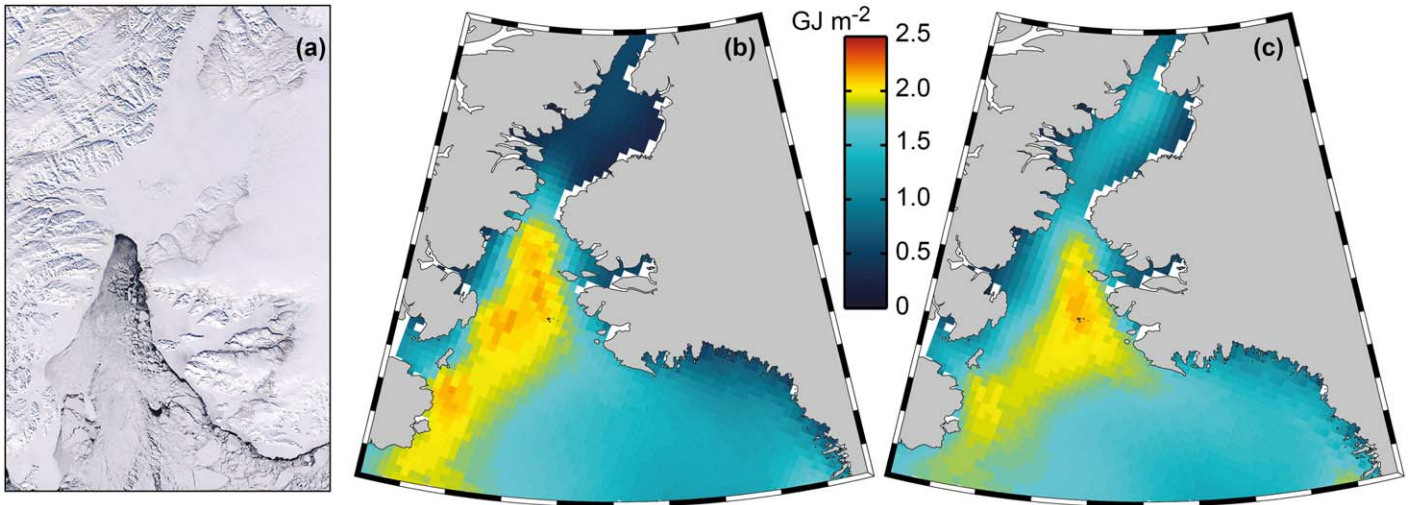


Fig. 6. (a) MODIS image of the North Water Polynya on 23 April 2002, when the ice bridge was present. (b, c) Measurements of solar radiative energy ($\times 10^9 \text{ J m}^{-2}$) incident at the ocean's surface, below the ice and assuming the ice is opaque, that were collected from 01 January to 30 September. These values were averaged over years during which (b) the ice bridge in southern Nares Strait formed and (c) it did not form (1990, 1993, 1995, 2007, and 2009) over the 1979–2009 period. Sea-ice concentration data were taken from the EUMETSAT Ocean and Sea Ice Satellite Application Facility (OSI-SAF) Global sea-ice concentration reprocessing dataset 1978–2009 and are available at <http://osisaf.met.no>. In (b, c), the lowest values are associated with persistent and recurrent landfast ice regions.

complicated by the short time series that does not encompass a pre-industrial baseline. Irradiance, temperature, stratification, and nutrient supply would all covary with sampling date (DOY) if seasonality was the dominant factor shaping the ecosystem every fall. In order to test if differences in sampling time could be associated with different stages of the seasonal progression, we computed rank correlations between DOY and all environmental and biological variables collected during the study (Tables 3, 5).

In Beaufort Sea, there was no directional shift in sampling DOY with the years, implying that the time of sampling did not create spurious interannual trends in the data but might conceal real trends (Table 3). E_{3d} and T_m were the only physical variables that significantly correlated with sampling date, and the contribution of phytoplankton $> 5 \mu\text{m}$ to total Chl *a* biomass ($B_L : B_T$) was the only biological variable correlated with E_{3d} (Tables 3, 5). These relationships reflect the decrease in incident irradiance and water temperature as well as the increase in the contribution of large cells to the total Chl *a* biomass as the season progressed. The year 2010 had the highest $B_L : B_T$ ratio, but not the highest E_{3d} (Table 2), meaning that other environmental variables that are not subordinated to seasonal transitions, such as upwellings, played an important role in driving the observed differences in physical and biological variables between years.

For Baffin Bay, sampling occurred over a larger seasonal window than in Beaufort Sea (Fig. 1b), and sampling DOY possibly had a greater influence on the results. In 2010 and 2011, sampling occurred later than in the previous years and drove a positive but not significant correlation ($p = 0.06$)

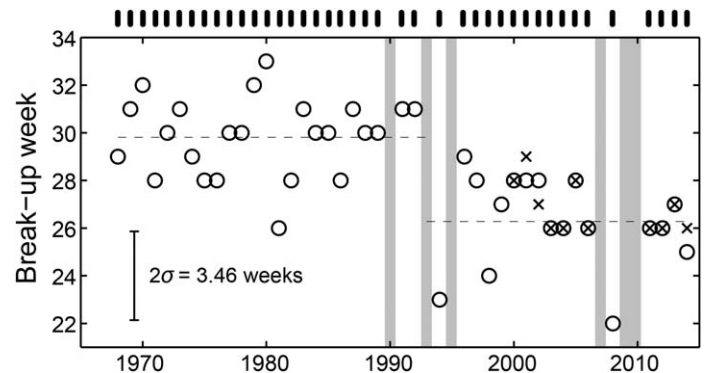


Fig. 7. Break-up date of the ice bridge in Nares Strait over the 1968–2014 period as assessed by the Canadian Ice Service (CIS, circles) and the Danmarks Meteorologiske Institut (DMI, crosses). The black tick marks on top of the graph correspond to years during which an ice bridge formed while gray zones indicate years during which it did not. The vertical bar indicates variability of the de-trended signal ($2\sigma = 3.46$ weeks).

between DOY and sampling year (Fig. 1b; Table 3). E_{3d} and T_m decreased while the availability of nutrients, mostly $\text{NO}_3 + \text{NO}_2$, increased with DOY and over the years (Tables 2, 3). The decrease in incident irradiance and water temperature along with the increase in nutrient concentrations reveal the seasonal progression. However, most biological variables were not significantly correlated with DOY and were presumably affected by environmental forcing that superseded seasonality (Table 5). Interannual changes in the phytoplankton community cannot be detected using a

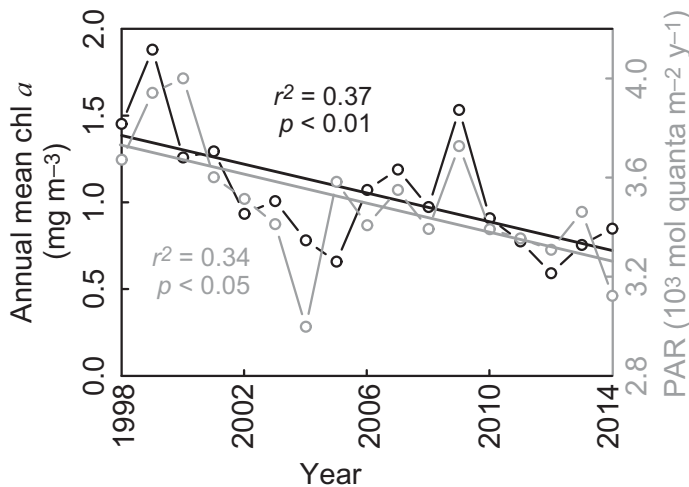


Fig. 8. Annual changes in average surface Chl *a* (black) and integrated subsurface photosynthetically active radiation (PAR) (light gray) in Baffin Bay from 1998 to 2014. Data are derived from satellite observations (GlobColour) for the period between the end of May and early September.

biological variable that responds primarily to changes in irradiance, temperature, or nutrient availability. This was the case for P_T , but all other biological variables were rather correlated with other variables such as salinity, freshwater inventory, or open-water duration (Table 5), confirming that changes in ice dynamics and the vertical stability of the water column were also responsible for the observed changes in phytoplankton community structure.

Even so, it is tempting to relate the large decrease in phytoplankton biomass and production during fall uniquely to the large decrease of near-surface PAR over the years in northern Baffin Bay. Irradiance is a key factor shaping the size structure of phytoplankton communities, with large cells performing better than small ones at high light intensities (Pesant et al. 1996). Since nutrients were quite abundant in the surface waters during fall 2010–2011 (Table 2), irradiance was likely the limiting factor. Seasonal variations in incident PAR certainly explain some of the reported biological variability (Table 5). However, the decrease in phytoplankton biomass and production for a 5-week time difference seems fairly large to be only due to seasonality in irradiance (Fig. 3b,d). Based on satellite observations, surface Chl *a* biomass and near-surface PAR data averaged or integrated for our specific study area over the whole productive period (i.e., from the end of May to early September) independently confirmed that major and significant declines in biomass and PAR occurred during the last 15 yr in northern Baffin Bay (Fig. 8). In addition, seasonal variations in incident PAR could not explain the continuous drop in biomass and production between 1999, 2006, and 2008, which were all measured in mid-September.

Despite the limitation in our study due to the sampling time lag, these correlations suggest that the production and structure of Arctic phytoplankton in two different environments—an interior shelf (Beaufort Sea) and an outflow shelf (Baffin Bay)—are responding to the interannual pressures of climate change. In addition to seasonal variability, altered ice dynamics—mostly a reduction in the duration of sea-ice cover—induced modifications in water column stratification. It is the phytoplankton assemblage, in terms of size-structure and taxonomic composition, that is mostly impacted by these changes in both regions. This suggests that stratification does not only control the timing of the spring bloom (Janout et al. 2016), but also the fall phytoplankton assemblage. We now evaluate how ongoing changes may affect the overall functioning of Arctic marine ecosystems and assess the pan-Arctic relevance of our regional study.

Food-web implications of an altered phytoplankton assemblage in the Canadian Arctic Ocean

Previous studies have shown the important role of stratification in controlling trophic status in marine Arctic environments (Ardyna et al. 2011, 2014), and the two regions studied responded differently to environmental changes. In southeast Beaufort Sea, this study has shown that, besides stimulating primary production, upwelling events lead to the modification of phytoplankton assemblages. With the ongoing climate change, these events are likely to become more common during fall, when ice cover formation is delayed (Ardyna et al. 2011; Forest et al. 2011; Tremblay et al. 2011; Uchimiya et al. 2016). The resulting phytoplankton community that is dominated by large cells could enhance carbon export toward higher trophic levels (Søreide et al. 2010; Bergeron and Tremblay 2014). We hypothesize that changes in the phytoplankton size structure and taxonomic composition could partly explain the high occurrence of bowhead whales in our sampling area at the end of August – early September 2010, when the bloom likely peaked, compared to 2006–2009 (Citta et al. 2015). Walkusz et al. (2012) showed that upwelled waters around Cape Bathurst in Beaufort Sea consistently provided zooplankton to the foraging bowhead whales during late summer 2008. However, data on the interannual variability in zooplankton abundance in this coastal region are still lacking to corroborate this hypothesis.

In northern Baffin Bay, sea-surface warming and sea-ice changes altered spring bloom phenology (Marchese et al. 2017) and likely the nutrient distribution for the entire productive period. Our study showed that these changes combined with reduced near-surface irradiance and increased stratification did not allow the diatom-dominated assemblages to persist throughout fall, and the fall bloom did not occur in 2010–2011. Food export to higher trophic levels during fall will likely be greatly limited due to the small size of the phytoplankton species present (Pesant et al. 1996).

Small cells have low sinking velocities and are normally recycled within the euphotic zone, feeding the microbial food web (Legendre and Rassoulzadegan 1995). These changes are thus likely to hamper the pelagic food web. However, the absence of the ice bridge in Nares Strait (Fig. 2) would lead to more sea ice transiting southwards across Baffin Bay, and there could be an increase in ice-algal aggregates being exported to the sea floor during spring-summer that could feed the benthic food web (Assmy et al. 2013; Brown et al. 2014; Roy et al. 2015).

Overall, at the end of the last decade, water column stratification and phytoplankton size structure and community composition in southeast Beaufort Sea were becoming more like those of northern Baffin Bay in the mid-2000s, when this latter was still considered a eutrophic system (Ardyna et al. 2011). Conversely, northern Baffin Bay has become more of a mesotrophic region in recent years. This will certainly alter the food web in different ways in both regions, but it might not alter the overall productivity of the Canadian Arctic Ocean in the near future.

Expected interannual variability in phytoplankton communities of the Arctic Ocean

The southeast Beaufort Sea and other interior shelves of the Arctic Ocean (Kara, Laptev, and East Siberian seas) receive high inputs of freshwater, about 80% of the total freshwater input to the Arctic Ocean (Williams and Carmack 2015). Consequently, the high turbidity and haline stratification, which limit surface light availability and nutrient inputs, are responsible for the overall low biological activity in these regions (Sakshaug 2004; Ardyna et al. 2017). Upwellings are thus essential for stimulating phytoplankton productivity in interior shelves, where nutrient-rich Pacific waters subduct below low-nutrient river waters (Williams and Carmack 2015). An analysis of annual time series of surface stress due to wind and ice motion from 1979 to 2011 showed a general increase in upwelling-favorable annual surface-water stress along the interior shelves (Williams and Carmack 2015). Thus, we can hypothesize that the change toward larger cells and increased diatom contribution to total phytoplankton abundance and biomass observed here for the Canadian Beaufort Shelf is likely to occur elsewhere along interior shelves.

Waters coming from the Pacific Ocean circulate through the Arctic Ocean and finally reach the North Atlantic Ocean through the outflow shelves, including Baffin Bay (Michel et al. 2015). The initial physical and chemical properties of incoming Pacific waters are modified across the Arctic Ocean (Tremblay et al. 2015), and the freshwater content of the surface mixed layer increases with sea ice melt as it flows toward the North Atlantic Ocean. With this increase in stratification, Arctic outflow shelves, like the East Greenland Shelf and the Canadian Arctic Archipelago, could experience a decrease in their overall productivity along with a change

in their algal community toward smaller cells, similar to what was observed here. This scenario emphasizes the need to consider inter-regional connectivity when attempting to predict changes in phytoplankton productivity, biomass, and size structure in a specific area.

Summary and concluding remarks

This study presents a unique in situ dataset collected during fall, a season that is generally neglected in climate change studies (Gallinat et al. 2015) and for which few satellite observations are available. At high latitudes, satellite observations are limited to the period spanning early spring to late summer and provide little information on fall blooms, highlighting the importance of the present data set and in situ studies in general. In this study, the interannual changes in phytoplankton communities were characterized with a level of detail not attainable with remote sensing or numerical approaches. This multi-year dataset is an invaluable tool to verify assumptions and validate the predictions of current numerical models (Forest et al. 2011; Dupont 2012; Babin et al. 2015).

While the time series presented here is among the longest field time series published on Arctic phytoplankton, it is nevertheless relatively short and does not include a pre-industrial baseline (Wassmann et al. 2011), making it difficult to distinguish between long-term effects, year-to-year variability, and cyclic events (Kahru et al. 2010). We thus stress the view that sustained in situ monitoring (at least for several decades) is essential to better assess the ecological and socioeconomic consequences of climate change. More details on the phenology and taxonomic composition of spring and fall phytoplankton blooms in diverse regions of the Arctic will also be necessary to fully understand the consequences of ongoing changes. The contrasting responses described here underscore the diversity, complexity, and connectivity of Arctic marine ecosystems, and emphasize that additional regional studies are necessary to develop a truly pan-Arctic perspective on the sensitivity or resilience of phytoplankton production, biomass, and community composition. Such a perspective is required to understand how environmental changes will affect food webs, potential harvest of living resources, and carbon storage in the Arctic Ocean.

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Conflict of Interest

None declared.

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