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Arctic spring awakening – Steering principles behind the phenology of vernal ice algal blooms

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ABSTRACT

Marine ecosystems at high latitudes are characterized by extreme seasonal changes in light conditions, as well as a limited period of high primary production during spring and early summer. As light returns at the end of winter to Arctic ice-covered seas, a first algal bloom takes place in the bottom layer of the sea ice. This bottom ice algae community develops through three distinct phases in the transition from winter to spring, starting with phase I, a predominantly net heterotroph community that has limited interaction with the pelagic or benthic realms. Phase II begins in the spring once light for photosynthesis becomes available at the ice bottom, although interaction with the water column and benthos remains limited. The transition to the final phase III is then mainly driven by a balance of atmospheric and oceanographic forcing that induce structural changes in the sea ice and ultimately the removal of algal biomass from the ice. Due to limited data availability an incomplete understanding exists of all the processes determining ice algal bloom phenology and the considerable geographic differences in sympagic algal standing stocks and primary production. We present here the first pan-Arctic compilation of available time-series data on vernal sea ice algal bloom development and identify the most important factors controlling its development and termination. Using data from the area surrounding Resolute Bay (Nunavut, Canada) as an example, we support previous investigations that snow cover on top of the ice influences sea ice algal phenology, with highest biomass development, but also earliest termination of blooms, under low snow cover. We also provide a pan-Arctic overview of sea ice algae standing stocks and primary production, and discuss the pertinent processes behind the geographic differences we observed. Finally, we assess potential future changes in vernal algal bloom phenology as a consequence of climate change, including their importance to different groups of grazers.

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1. Introduction

The extreme seasonal change in light availability experienced at high latitudes (Fig. 1) is the dominant control of high Arctic ecosystems. The presence of seasonal or permanent sea ice further reduces the amount of light available to microbial communities in and below sea ice, particularly when snow is present on the

ice due to its high albedo and capacity to attenuate incoming light. During the ice-free period, stratification of surface water masses often limits the supply of inorganic nutrients and leads to a termination of bloom events. The result is a rather short productive period that provides the entire annual biomass production available for higher trophic levels (Sakshaug, 2004). This production is most often partitioned between sympagic (ice-associated) and pelagic microalgae, while benthic microalgal communities play a minor role on large scales. However, benthic production can be of local or regional importance in shallow coastal areas (Gattuso et al., 2006; Glud et al., 2009).

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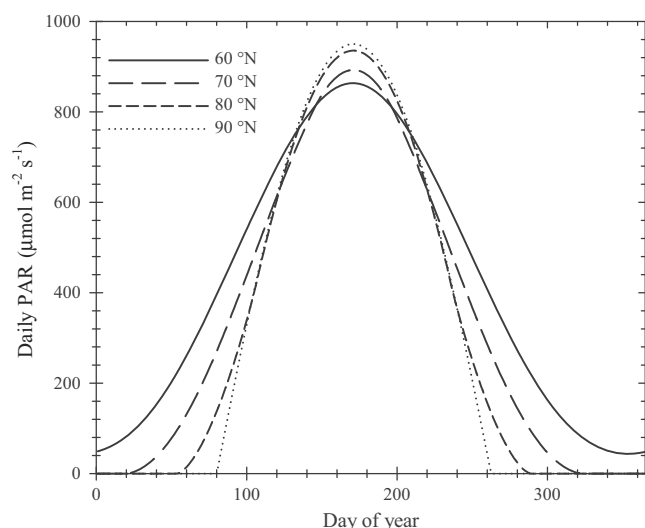


Fig. 1. Daily averaged solar irradiance at upper atmosphere (photosynthetically active radiation (PAR), 400–700 nm), calculated for different latitudes on the Northern Hemisphere (based upon sun–earth geometry and assumed solar constant).

During the winter months, no light (or very limited) is available for primary production (for a more extensive description of conditions in Arctic marine systems during the Polar night, see [Berge et al., this issue](#)). Despite the limited availability of light, sea ice is a unique habitat for microbial life, including the photosynthetic primary producers known as ice algae. With respect to the seasonal cycle of Arctic marine production, it is the ice algal blooms that marks the winter–spring transition in high latitude systems, as phytoplankton typically start blooming only after the sea ice has reached an advanced state of melt and disintegration ([Arrigo et al., 2012](#); [Fortier et al., 2002](#); [Mundy et al., 2014](#)). However, due to the poor data coverage, a reliable estimate of primary production taking place under the ice is still impossible. An indirect approach, measuring nitrate drawdown in surface waters over the entire ice algal bloom period, indicates much higher primary production activities than previously assumed ([Matrai and Apollonio, 2013](#)).

During the gradual change from dark winter conditions to the permanent light exposure of the midnight sun period, sea ice communities pass three distinct phases ([Fig. 2](#)). Phase I occurs while solar irradiance is not sufficient for bloom development of primary producers; thus the ice-associated community remains net heterotrophic. Phase II commences after ambient irradiances in the lowermost part of the ice (adjacent to the water) have passed a critical level where sea ice algae grow exponentially under favorable conditions, forming the first annual bloom event in ice-covered waters. This ice community sustains itself as long as there is sufficient access to inorganic nutrients from the water column underneath. Phase III starts after sea ice temperatures rise above a critical limit that leads to a widening of the brine channels and subsequent melting and mass drainage of brine, associated with a major loss of the previous in-ice communities (phase III). Over the course of phases I to III, which can span several weeks to months, the degree of interaction between the interstitial sea ice microbial community and the pelagic and benthic realm changes considerably. This change also affects the ecological significance of ice algal primary production. During phase I, there is hardly any interaction between life in the ice and life in the underlying water column. During the ice algal bloom phase (phase II), algal growth relies on inorganic nutrients from the water column either initially incorporated or through exchanges that are enhanced by

tidal currents and eddies created during brine drainage. During phase II, ice algae represent an important early food source for specialized pelagic key grazers, such as the copepod *Calanus glacialis* ([Runge and Ingram, 1988](#); [Søreide et al., 2010](#)), sea ice meiofauna ([McConnell et al., 2012](#); [Nozais et al., 2001](#)) as well as under-ice fauna specialists like amphipods ([Poltermann, 2001](#); [Werner, 1997](#)). During and after their release from the ice (phase III), ice particulate organic matter can be an important energy source for pelagic grazers ([Fortier et al., 2002](#); [Michel et al., 2006, 1996](#)), or sinks rapidly to the seafloor (due to the large aggregates and dominance of long-chained diatoms), where they represent an important food source for benthic grazers and filter feeders on shelves and even in the deep Arctic basins ([Boetius et al., 2013](#); [Renaud et al., 2007](#)).

In this article we summarize the current knowledge about the temporal development of ice algal blooms in the critical transition phase from winter to spring for the entire Arctic. We discuss the most important steering factors for the different regions, and their impact on bloom characteristics, exemplified by the extensive dataset from Resolute, Canada. We then give a comprehensive overview over the spatial variability of ice algal standing stocks, primary production, and species composition in Arctic first-year ice (FYI). We focus on interstitial bottom ice communities, as they are the most important of sea ice algal blooms in the Arctic. We define the (biologically relevant) winter–spring transition period to span from the return of the sun above horizon until the initialization of the first pelagic algal bloom ([Fig. 2](#)). Depending on latitude and ice conditions, this period may start between January and late March and last until April–August. At very high latitudes, the change from complete darkness to permanent daylight may take only a couple of days or weeks.

Knowledge about sea ice algae up to the 1980s was summarized by [Horner \(1985\)](#), and [Melnikov \(1997\)](#). This was followed up by very extensive reviews on sea ice algae by [Cota et al. \(1991\)](#), [Cota and Smith \(1991a,b\)](#), [Horner et al. \(1992\)](#), and [Legendre et al. \(1992\)](#), providing fundamental principles about the environmental control, the general ecology and comparative physiology of bottom sea ice algae. Some Arctic data on chlorophyll *a* (chl *a*) maxima, photosynthesis rates and primary production are compiled in the overview works by [Arrigo et al. \(2010\)](#), [Sakshaug \(2004\)](#), and [Smith and Sakshaug \(1990\)](#). In the current article, we focus mainly on the temporal development and dynamics of Arctic bottom ice algal blooms, together with their variability in biomass, productivity and species composition.

2. Seasonal succession of sea ice algae communities and their major steering factors

2.1. Phase I: pre-bloom

While the minimum daily solar irradiance is observed in mid December, the annual maximum of sea ice extent in the Arctic usually occurs in March. Growth conditions for sea ice algae within the brine channels vary with time and space ([Petrich and Eicken, 2010](#)). In winter, low ice temperatures coincide with high brine salinities, low brine volumes, and low algal biomass ([Gradinger and Ikävalko, 1998](#); [Werner et al., 2007](#)). Rather little is known about the protist communities inhabiting sea ice during stages of ice formation and growth in the dark winter period. However, it is understood that the incorporation of cells into the ice during formation is selective, where larger cells (mainly diatoms) are favored ([Gradinger and Ikävalko, 1998](#); [Riedel et al., 2007](#); [Róžańska et al., 2008](#)). After this, a protist community develops gradually distinct from the pelagic surface community. [Niemi et al. \(2011\)](#) described the taxonomic composition of protist assemblages in Arctic sea ice during the winter period (in the Beaufort Sea). Very low overall

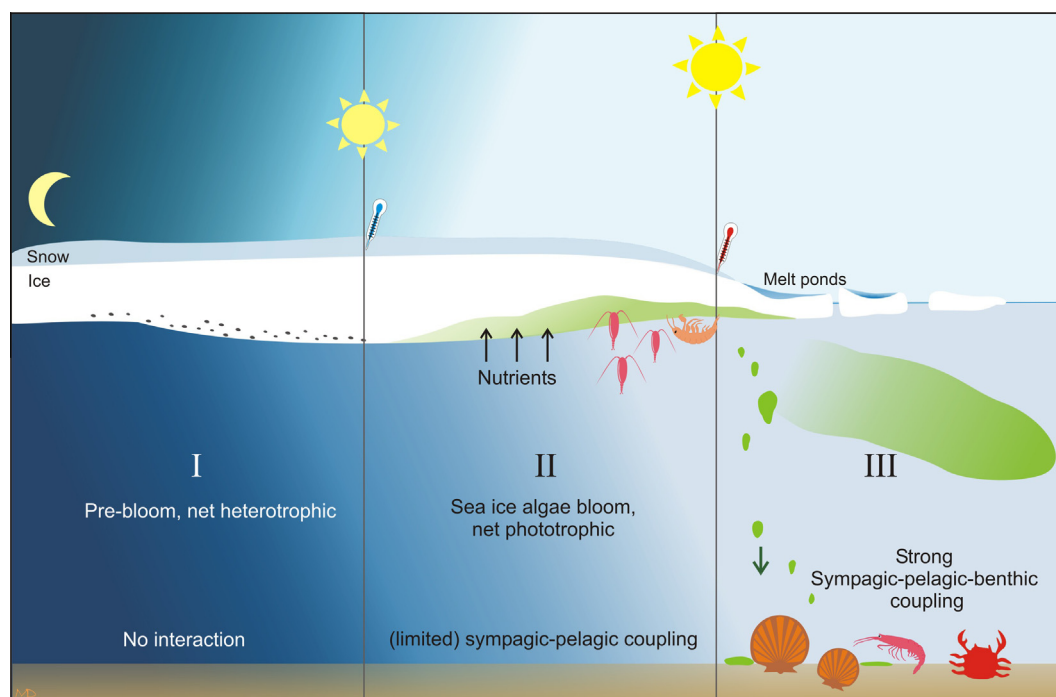


Fig. 2. The three major developmental phases of sympagic blooms during the winter–spring transition period. The change from phase I to II is steered by light, while temperature increase ultimately leads to the progression from phase II to III. For a more detailed explanation of the different phases, see text.

abundances (max. 4000 cells l^{-1}) indicated a limited retention of protists in the sea ice during this period. However, the diversity of the assemblages was similar to that found during spring, with pennate diatoms dominating the winter assemblage and *Nitzschia frigida* being the most abundant species. These authors also suggested that the timing of sea ice freeze-up may have a greater influence on the overall abundance than on the community structure of sea ice assemblages that are present at the initialization of the first spring bloom. The production of extracellular polymeric substances (EPS, e.g. [Krembs et al., 2011](#)), heterotrophy ([Horner and Alexander, 1972](#)) and physiological or morphologically defined resting stages ([Zhang et al., 1998](#)) are amongst the most important strategies for a successful winter survival in sea ice. The seasonal development in sea ice carbon cycling from winter to spring in FYI in the coastal Arctic Ocean on the Canadian shelf was studied by [Riedel et al. \(2008\)](#). During the early period of their investigation, they found a predominantly heterotrophic microbial food web in sea ice under high snow cover, accounting for almost 80% of the total sea ice carbon biomass during February and March.

2.2. Phase II: bloom

When the sun returns after the dark winter period, the phase of highest ice algal productivity starts as soon as there is enough light available. There are slightly different values for ice algal compensation light intensities reported in literature, ranging from 0.36 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ([Mock and Gradinger, 1999](#)), up to 2–9 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ ([Gosselin et al., 1986](#); [Horner and Schrader, 1982](#)). The lower estimate of [Mock and Gradinger \(1999\)](#) was recently suggested to be related to its retrieval from *in situ* incubations where multiple scattering in the sea ice environment can increase ice algal light absorption ([Ehn and Mundy, 2013](#)). In the transition period from winter to spring, ice algae experience highly dynamic environmental conditions that they are adapted to exploit for their (exponential) growth that is usually limited by light in the beginning and by nutrients during the peak and end phases of the bloom ([Cota and Smith, 1991a](#); [Gosselin et al., 1990](#); [Lavoie et al., 2005](#)).

Inorganic carbon also becomes potentially limiting for sea ice algal growth in dense assemblages, as indicated by exceptionally high ratios of ^{13}C to ^{12}C ([Gradinger et al., 2009](#); [Pineault et al., 2013](#)). At the end of the winter, rapidly increasing day length and solar angle together with melting snow gradually allows more light to penetrate through the sea ice ([Nicolaus et al., 2012](#)), where transmission of light is largely governed by snow depth, ice thickness, and sediment load of the ice (e.g., [Gradinger et al., 2009](#); [Light et al., 1998](#); [Perovich et al., 1998](#)). The first vernal algal bloom usually takes place in the bottommost centimeters of the sea ice, where shade-adapted algae start to grow within the brine network and spaces. Free movement of brine providing inorganic nutrients to the growing algae is essential and can occur when the percent brine volume fraction of sea ice exceeds 5%, which typically coincides with sea ice temperatures at or above -5°C and a bulk salinity of 5 ([Golden et al., 1998, 2007](#)). These conditions also provide substantial space for algal colonization and growth ([Mock et al., 2003](#)). In the bottom 1 cm of sea ice, the 5% threshold is permanently fulfilled and it is hence mostly light that limits sea ice algal growth there early in the season. The bulk of ice algal biomass in the Arctic usually occurs as bottom and sub-ice assemblages in the lowermost part of the ice close to and in the ice–water interface; therefore, a lot of data collection in the Arctic has focused on this community. Bottom ice algal blooms are dominated by pennate diatoms often accounting for >90% of the total algal cell abundance ([Róžańska et al., 2009](#); [Smith and Sakshaug, 1990](#); [von Quillfeldt, 2000](#)) and carbon biomass ([Gosselin et al., 1997](#); [Riedel et al., 2008](#)). While most algal species growing in sea ice can also be found in the water column, there are few, but highly abundant species that grow mostly within or attached to sea ice and are rarely found in significant abundances in the water column. The two most important representatives in the Arctic are the pennate diatom *Nitzschia frigida*, frequently dominating interstitial assemblages of bottom sea ice algal blooms in first-year ice (FYI), and *Melosira arctica*, a centric chain-forming diatom that has been described to produce extremely high biomass attached to the underside of multi-year ice (MYI) and FYI in the central Arctic

ocean (e.g., Gosselin et al., 1997; Gutt, 1995; Melnikov and Bondarchuk, 1987; Nansen, 1906). Despite their high local biomass accumulation, and their role in the ecosystem as important seasonal food source for sympagic, pelagic, and benthic herbivores in ice-covered areas (e.g., Renaud et al., 2007; Søreide et al., 2010; Werner, 1997), our knowledge about ice algal general ecology and physiology is still incomplete. Recent observations of massive sedimentation and utilization of *M. arctica* in the central Arctic ocean indicate the importance of this species to sympagic–benthic coupling, even in oceanic areas with water depths exceeding several thousands of meters (Boetius et al., 2013). *N. frigida* will also potentially increase its dispersal as FYI is increasing all over the Arctic. Another type of sub-ice communities can develop during the late summer as mucilaginous aggregates dominated by ice-associated pennate diatoms (Assmy et al., 2013; Fernández-Méndez et al., 2014; Glud et al., 2014).

2.3. Phase III: post-bloom

Towards summer, the solar angle continues to increase and the associated rise in air temperatures together with the net positive radiation balance of up to 100 W m^{-2} in June/July (Petrich and Eicken, 2010) start to warm the sea ice from the surface, causing subsequent changes in ice microstructure and brine salinity. Increased sea water temperatures in summer may also contribute to bottom melt of up to 0.1 m d^{-1} (Perovich, 2011), and affect the sea ice microstructure. In landfast ice zones, turbulent ocean–ice heat exchange associated with shear along the ice–ocean boundary layer has also been found to influence erosion of the ice bottom (Widell et al., 2006) and particularly during spring–tide conditions (Lavoie et al., 2005). Melting sea ice is considerably less salty than sea water, accumulating both on top of and at the ice bottom and forming extensive networks of ponds and puddles. The dynamics of ice growth and melt are heavily modified by the insulating layer of snow on top of the ice (Petrich and Eicken, 2010). As snow during the early part of the season reduces most of the incoming light through albedo and attenuation, it will inhibit algal growth through light limitation and will have a substantial control on the development of algal blooms. However, towards the end of the ice-covered period the snow layer thermally insulates the underlying ice and delays the melting process that terminates the ice-associated algal bloom (e.g., Fortier et al., 2002; Mundy et al., 2005; Campbell et al., 2015). Snow cover can thus extend the period of dominance of ice algal blooms over that of phytoplankton. Therefore, solar irradiance, snow cover, duration and extent of sea ice cover, physical forcing by underlying water masses (e.g. strong tidal currents), and ablation caused by a local inflow of warm water can all affect the ability of ice algae to form or maintain persistent blooms. During the late stage of the ice algal bloom, the dominance of diatoms decreases gradually, and flagellates become more abundant (Alou-Font et al., 2013; Horner and Schrader, 1982). Growth conditions deteriorate with decreasing availability of inorganic nutrients (e.g. Cota et al., 1990; Gosselin et al., 1990; Smith et al., 1997), and possibly local shortage of inorganic carbon within the brine channels (Gradinger, 2009; Pineault et al., 2013). Depending on the snow cover, sea ice algae might also be exposed to detrimentally high irradiance levels during this phase, with consequences for their physiology and biochemical composition (Gosselin et al., 1986; Leu et al., 2010).

3. Modeling sea ice algae dynamics

Contrary to the distribution and thickness of sea ice, abundance and distribution of sea ice algae cannot be monitored by remote sensing from space, making a comprehensive picture of their appearance and dispersal on large scales difficult to obtain.

Although under-ice remote sensing using transmitted spectral light composition shows promise to support future large-scale spatial observations (Mundy et al., 2007; Campbell et al., 2014). The relative importance of various environmental factors for the distribution and development of sea ice algal communities under rapidly changing conditions in the Arctic is hard to predict based upon the limited information gathered by scattered and rare data time series. Recent attempts in modeling try to bridge this gap. Tedesco and Vichi (2010) developed a sea ice addition to the Biogeochemical Flux Model (BFM-SI) and validated it against two time series from sub-Arctic studies. Originally, the first fast ice ecosystem model was developed by Arrigo et al. (1993), and tested in Antarctica. They later simplified the physics of the 1-D model of Arrigo et al. (1993) to produce a quasi 3-D model where productivity was prescribed in an interfacial layer of 0.02 m at the ice–snow interface and in a prescribed freeboard layer of 0.1 m (Arrigo et al., 1998, 1997). Lavoie et al. (2005) developed a simplified version of the ice algal model of Arrigo et al. (1993), assuming that algae grow in the bottom 0.02 m of sea ice. This model was validated against a time-series of ice algae collected near Resolute, Canada. Jin et al. (2006) developed a 1-D ice–ocean–ecosystem model to determine the factors controlling the bottom 0.02 m of the ice algal community of the landfast ice off Barrow, Alaska. Both of these landfast models described three stages of ice algal growth, starting with light limitation, followed by light and nutrient limitation and governance of melt related processes as stage 3. Application of the Barrow model to the Bering Sea demonstrated the importance of the ice melt stage for the initiation of the phytoplankton blooms (Jin et al., 2007). Ji et al. (2013) further investigated the correlation between sea ice phenology and the timing of primary production pulses in the Arctic (timing of sympagic and pelagic blooms and the time gap in between, including potential ecological consequences for grazers). Nishi and Tabeta (2005) developed an ice–ocean–ecosystem model and applied it to Saroma-ko Lagoon (Hokkaido, Japan), on the bottom 0.02 m of sea ice. First attempts to include ice algal components into regional 3D ocean modeling systems have been undertaken by Deal et al. (2011), Sibert et al. (2010), and Jin et al. (2012). Time series of sea ice biogeochemical properties generally show that ice bottom communities are highly variable in space and time and may not be well represented by a model assuming that biological assemblages live in a layer of constant thickness (Pogson et al., 2011; Tedesco et al., 2010). This has only recently been demonstrated by Vancoppenolle et al. (2010), who coupled a comprehensive 1D physical model of sea ice with an idealized sea ice biological component, and by Tedesco et al. (2010), who coupled a relatively simple sea ice thermodynamic model (Tedesco et al., 2009) with a new comprehensive biological model of sea ice algae. Tedesco et al. (2012) further tested different hypotheses concerning the potential coupling between sea ice algae and phytoplankton blooms. Modeling experiments by Tedesco and Vichi (2014) point at the potentially crucial role of sea ice cover duration for the magnitude of ice algal blooms. The recent 3D coupled biological–physical model of Sibert et al. (2011) simulates consistent seasonal cycles and spatial variability of ice algae and planktonic production in response to varying ice and ocean dynamics in the Hudson Bay system. For a recent review about the current status concerning modeling the role of sea ice in global biogeochemical cycles, see Vancoppenolle et al. (2013). However, common for all these studies and reviews was the relatively limited observational data basis they had to rely on.

4. Overview of available time series data – and modes of analyses

Even after the second International Polar Year, there are still very few data available on the seasonal development of Arctic

sea ice algal blooms, and those that exist were collected almost exclusively in landfast FYI (see Table 1). In a pan-Arctic perspective, the by far most extensive datasets are from the Canadian Arctic, in particular from the area around Resolute (Campbell et al., 2014; Fortier et al., 2002; Lavoie et al., 2005; Michel et al., 1996; Mundy et al., 2005, 2007; Smith et al., 1988, 1989, 1990, 1993, 1995; Welch and Bergmann, 1989). More recently, the two projects based on overwintering an icebreaker in the Beaufort Sea (Canadian Arctic Shelf Exchange Study (CASES) and Circumpolar Flaw Lead (CFL) System Study) provided valuable seasonal data, covering even the poorly studied winter months (Brown et al., 2011; Riedel et al., 2006; Róžańska et al., 2009; Mundy & Gosselin, unpubl. data). Within Alaskan waters, the best information comes from the seasonal landfast ice cover mainly sampled close to Barrow in recent years and also including other locations like Simpson lagoon in the past (Gradinger et al., 2009; Horner and Schrader, 1982; Juhl et al., 2011; Lee et al., 2008; Manes and Gradinger, 2009). In Greenland, studies on landfast FYI in fjord environments were carried out on both the east (Rysgaard et al., 2001; Glud et al., 2007), and the west coast (Mikkelsen et al., 2008; Søgaard et al., 2010, 2013). For the west coast of Greenland, data come from studies conducted near Nuuk, a sub-Arctic city near 64°N, as they represent the only studies from this region with good temporal resolution and coverage of sea ice algae development. In the Svalbard archipelago, seasonal studies of marine fjord ecosystems have been established only during more recent years (Leu et al., 2011, 2010; Søreide et al., 2010), and there is no continuous time series covering the entire winter–spring period. Available time series

data from the Russian shelf seas are scarce, and the only data that could be included in this overview were from the White Sea, covering several years, but only very short periods during spring in every single year (Krell et al., 2003; Rat'kova et al., 2004; Sazhin unpubl. data). Pack-ice studies during the winter months (November–February) are basically missing while spring/summer transition observations do exist from the North Water polynya study (NOW, (Nozais et al., 2001), Bering Sea (Gradinger unpubl. data), and Chukchi/Beaufort Sea region (e.g., Gradinger, 2009) as part of the Shelf Basin Interaction (SBI), and Bering Ecosystem Study (BEST). Furthermore, the Surface Heat Budget of the Arctic Ocean (SHEBA) drift study covered parts of the Beaufort/Chukchi Seas (Melnikov et al., 2002), and represents the only time series from drift ice we were able to obtain from the central Arctic multiyear ice pack.

Datasets of sea ice chlorophyll *a* concentration from both landfast and pack-ice sites were gathered from the existing literature and unpublished datasets (Table 1). We chose chl *a* as an indicator for algal biomass, as direct information on sea ice derived particulate and dissolved organic carbon is very scarce. When actual data was not directly accessible, DataThief (<http://datathief.org>) was used to extract data from figures presented in the literature.

To examine the timing of the different vernal ice algae blooms at each regional location (Fig. 3), data from different years were collated and then averaged for each day of the year (doy). It is noted that some ice algae blooms in the Arctic can exhibit more than one peak associated with mid-bloom sloughing events due to nutrient depletion followed by replenishment (e.g., Cota et al.,

Table 1
Overview of ice algae time series datasets analyzed in this article.

Site	Year	Core section (cm)	Chl <i>a</i> in sea ice	Ice thickness	Snow depth	Nutrients	Irradiance	Published by
Barrow	2002	Bottom 10	×	×	×		×	Gradinger et al. (2009)
Barrow	2003	Bottom 3–10	×	×	×	×		Lee et al. (2008)
Barrow	2003/04	Bottom 10	×	×	×			Juhl et al. (2011)
Barrow	2005/06	Bottom 10	×	×	×		×	Manes and Gradinger (2009)
Barrow Strait	1995	Bottom 10	×	×	×			Fortier et al. (2002)
Stefansson Sound	1978/79	n/a	×	×	×	×	×	Horner and Schrader (1982)
Narwhal Island	1980	n/a	×	×	×	×	×	Horner and Schrader (1982)
Bering Sea, pack ice	2008	Bottom 10	×	×	×		×	Gradinger, unpubl. data
Chukchi Sea, pack ice	2002	Bottom 10	×	×	×		×	Gradinger (2009)
Resolute passage	1985/86	Bottom 4	×	×	×			Welch and Bergmann (1989)
Resolute passage	1985	Bottom 4	×		×			Smith et al. (1988, 1989)
Resolute passage	1986/87	Bottom 4–6	×		×			Smith et al. (1990)
Resolute passage	1989	Bottom 5	×	×	×		×	Smith et al. (1993)
Resolute passage	1992	Bottom 4	×	×	×		×	Smith et al. (1995)
Resolute passage	1992	Bottom 4	×	×	×			Michel et al. (1996), Fortier et al. (2002)
Resolute passage	1994	Bottom 10	×	×	×			Fortier et al. (2002)
Resolute passage	2002	Bottom 2–4	×	(×)	(×)	×	×	Lavoie et al. (2005)
Resolute passage	2003	Bottom 5	×	×	×			Mundy et al. (2007)
Resolute passage	2011	Bottom 3	×	×	×			Campbell et al. (2014)
McDougall Sound	2002	Bottom 5	×					Mundy et al. (2005)
Franklin Bay	2004	Bottom 4	×	×	×	×	×	Riedel et al. (2006), Róžańska et al. (2009)
Amundsen Gulf	2003	Bottom 3	×	×	×	×	×	Brown et al. (2011), Mundy and Gosselin, unpubl. data
North Water Polynya	1998	Bottom 2–4	×	×	×			Nozais et al. (2001)
Canadian Basin	1997/98	Entire core	×	×	×	×		Melnikov et al. (2002)
Kobbefjorden	2005/06	Entire core	×	×	×	×	×	Mikkelsen et al. (2008)
Malene Bight	2008	Entire core	×	×	×	×	×	Søgaard et al. (2010)
Kapisigdlit Bight	2010	Entire core	×	×	×	×		Søgaard et al. (2013)
Young Sound	1999/2002	Entire core	×	×	×	×	×	Glud et al. (2007)
White Sea	2002/09/11	Entire core	×	×	(×)			Rat'kova et al. (2004), Krell et al. (2003), Sazhin unpubl. data
Rijpfjorden	2007	Bottom 6–10	×	×	×	×	×	Leu et al. (2010)
Billefjorden	2009, 2011	Bottom 3–10	×	×	×	×		Gabrielsen unpubl. data

* Asterisk indicates that those values were primarily POC values that are converted to Chl *a*.

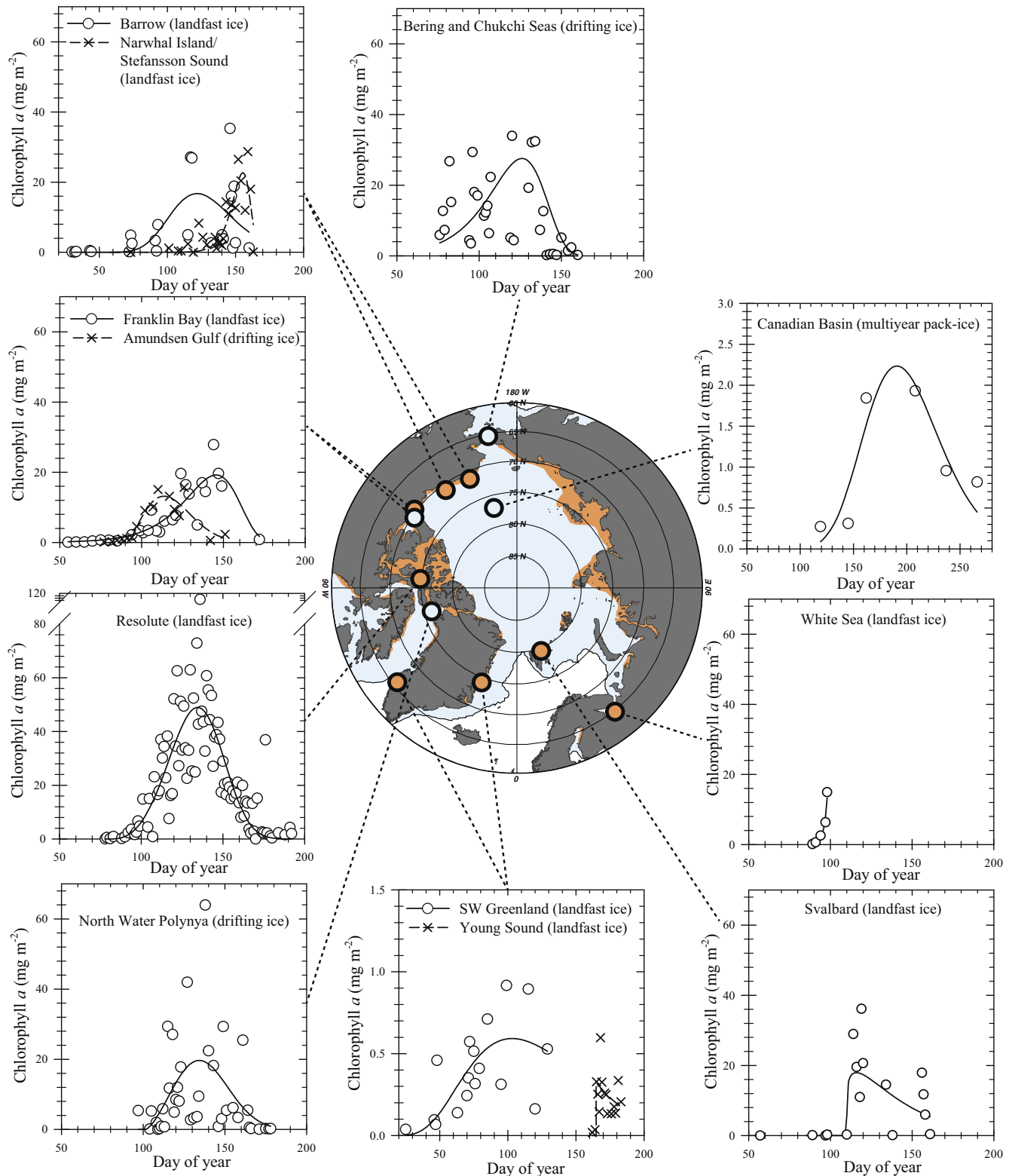


Fig. 3. Seasonal development of sympagic (ice-associated) chl *a* values in different regions of the Arctic. Where several years of measurements were available, the average of all measurements was calculated and plotted. Note different scales for chl *a*. The ice extent depicts the winter maximum, blue areas are pack ice, brown land-fast ice.

1987; Gosselin et al., 1990; Lavoie et al., 2005), bottom ice erosion (Mundy et al., 2007), or melt (Lee et al., 2008). However, to simplify the data analyses, we assumed a single peak and thus, Log-normal or Weibull peak distribution curves were statistically fit to the daily averages using Sigma Plot™. These curves fits were chosen

due to their ability to fit skewed distributions that were observed in the different regional datasets. Bloom start and end were defined as the date where bottom ice algal biomass increased above and decreased below 1 mg m^{-2} , respectively. The date of peak biomass was derived from the peak distribution curve.

5. A pan-Arctic overview of sea ice algal bloom phenology

The studied regions of the Arctic differ greatly with respect to virtually all environmental parameters that are relevant for algal bloom development, ranging in their location from 64° to >80°N, with corresponding differences in the duration of the polar night, and the level of solar elevation (Table 2). Solar angle is of great importance for the amount and spectral composition of light that is penetrating the ice cover and reaching the water column. Sea ice thickness and snow cover impose additional factors controlling light penetration to the water column. The duration of sea ice cover, ice thickness, and snow depth are therefore considered key parameters controlling the light regime in areas with seasonal or multiyear sea ice. Ice thickness varied greatly between the locations, ranging from 50 cm in Kobbefjord (Greenland) and White Sea (Russia) up to more than 150 cm in Barrow (Alaska), Young Sound (Greenland) and Resolute (Canada). The duration of ice cover ranged from 3.5 to 9 months (Table 2), depending on wind, water/air temperature, currents, and tides. In addition to their impact on ice cover, these factors may physically remove ice-associated biomass through periodic degradation of the ice from below. Winter surface nutrient concentrations reported in the analyzed studies ranged for nitrate from 8 to 13 μM , for silicic acid from 5 to 23 μM , and phosphate from 0.3 to 1.7 μM (Table 2).

This combination of physical and chemical factors ultimately controls the phenology and magnitude of sympagic and pelagic production during sea ice cover. Fig. 3 shows the peak distribution plots derived from the daily averaged datasets for each regional location. With the exception of Resolute Bay, the central Arctic (SHEBA), and Greenland locations, there was a relative consistency of distribution fit peak chl *a* concentrations near 20 mg m^{-2} across the different Arctic locations. The central Arctic Ocean dataset collected during SHEBA was the only time series available from multiyear sea ice the authors were able to locate. The chl *a* curve for the central Arctic Ocean location remained <2.5 mg m^{-2} throughout the bloom period and showed the latest start, peak, and end dates for the entire Arctic dataset. Interestingly, the Greenland fjords also revealed consistently low ice algal chl *a* concentrations that never increased above 1 mg m^{-2} . Therefore, start and end dates were not defined for these locations. The Resolute Bay curve fit—derived from the average of 14 different data time series from 10 different years spanning 1985–2011—showed a peak chl *a* concentration more than double any of the other locations across the Arctic.

A pairwise Pearson *r* correlation analysis of the start, peak, and end dates against latitude, freeze-up and break-up dates did not reveal any significant correlations ($p > 0.05$ for all cases). The degree of skewness in the different temporal distribution curves varied greatly between the datasets (Fig. 3). For example, the Svalbard datasets resulted in a curve that increased in chl *a* concentration rapidly to a peak followed by a long tail during the declining phase. Other locations such as the central Arctic, Barrow, Amundsen Gulf, North Water polynya, and Resolute Bay followed closer to a normal temporal distribution. The last curve type of a relatively slow increasing period, followed by a rapid bloom decline was typical for datasets from Narwhal Island/Stefansson Sound (Alaska), and Franklin Bay (Canada) locations. Indeed some of these results can be explained by low temporal resolution time series (e.g., Svalbard) versus many years of data that were averaged (e.g., Resolute Bay). We looked at the relation between snow depth and algal phenology in the most comprehensive multi-year data sets originating from Resolute (Canada) to examine why different types of temporal distribution curves were possible.

In addition to the temporal bloom development, also maximum chl *a* concentrations varied greatly between the different regions

(Table 3). Reported areal integrated values were lowest in the Greenland fjords at up to c. 2 mg m^{-2} . These values were followed closely by the central Arctic that reached a maximum of 7 mg m^{-2} . The European Arctic reached maximum concentrations of 53.8 mg m^{-2} . The Chukchi Sea, Beaufort Sea, and Canadian Arctic regions displayed the highest maximum concentrations that were up to 340 mg m^{-2} near Resolute in the centre of the Canadian archipelago. Most studies report the bulk biomass within the bottom centimeters of the sea ice while others have analyzed the entire core. It is worth to note that highly concentrated biomass at the bottom of the sea ice may be more susceptible to loss due to periodic melting and freezing of the sea ice from below.

6. The impact of snow cover on bloom phenology: a case study from Resolute Bay

To study the relevance of snow cover for the development of ice algal blooms, the multi-annual chl *a* dataset for Resolute was split into snow depth ranges of low (0–10 cm), medium (10–20 cm), and high (>20 cm). A relative estimate of the impact of those snow depths yields an approximate transmittance of surface penetrating irradiance (1 – albedo) through the snow cover of 50% for 5 cm, 10% for 15 cm, and 1% for 30 cm (calculations based upon an average attenuation coefficient of 15 m^{-1} ; Mundy et al., 2005). The highest chl *a* concentrations were observed under the low snow class (Fig. 4). Bloom start, peak, and decline occurred earlier with decreasing snow depth class with the exception of the high snow class that did not reach a peak. However, it is rare to have deep snow covers beyond the time series range of the high snow class (day 171; 21 June) due to snow melt. For example, the daily averaged snow depth time series for Resolute shows a rapid decrease following day 160 (9 June; Fig. 5), where snow covers rapidly melted on average for the dataset.

Due to the difference in bloom timing, chl *a* concentration was a negative function of snow depth class prior to day 151 (31 May) and a positive function thereafter (Fig. 4), driven by the associated differences in ice phase II and III (see intro sections). To examine this relationship in more detail, the original chl *a* and snow depth data were grouped based on time periods of before day 110, after day 160, and 10-day intervals between. Linear regressions were performed on natural logarithm transformed chl *a* versus snow depth. The examination of a log-linear relationship was assumed to highlight the exponential attenuation of light by increasing snow depths (Welch and Bergmann, 1989). All log-linear relationships were statistically significant, with most of them having a p -value < 0.0001, with the exception of groups <110 (p -value < 0.01) and 151–160 (p -value < 0.05). As the season progressed towards the peak biomass at the low snow class (Fig. 4), negative relationships became stronger (increasing r^2 ; Fig. 6). As peak biomass in the low and medium snow classes were surpassed (Fig. 4), the relationships weakened, until an abrupt switch to a positive relationship following day 151 (Fig. 5). Snow depth thus not only influences the transition from phase I to phase II with earlier transition under thinner snow cover, but also the transition from phase II to III with delayed transition under thicker snow cover. It should also be noted that snow depth is a critical variable in the sea ice system and that its influence on ice algae biomass may derive through its effect on other parameters rather than just light attenuation. For example, snow depth influences the ice freezing/warming rate (Lavoie et al., 2005) and therefore, brine volume and possibly nutrient availability at the ice bottom (Vancoppenolle et al., 2010). Furthermore, the attenuation coefficient of a snow cover is seasonally variable, largely dependent on grain size and water content (Mundy et al., 2005). Therefore, the above relationships should not necessarily be expected for every Arctic location.

Table 2

Characterization of the different study regions with respect to the most important abiotic factors in relation to sea ice algal blooms.

Area	Site	Latitude (°N)	Sun below the horizon	Max. solar elevation (°)		Ice covered period	Thickness (cm)	Snow depth (cm)	Nutrients: winter concentrations in surface water (µM)			Water depth (m)	Sampling year	References
				Spring equinox	Summer solstice				Nitrate	Silicic Acid	Phosphate			
Alaska	Narwhal Island	70	24.11–18.1	19.5	43	n/a	n/a	n/a	10.5	23	1.3	n/a	1978–80	Horner and Schrader (1982)
Alaska	Barrow	71	19.11–21.1	18.9	42.2	November/ December until mid July	75–180	2–27	8–9.8	≥ 15	1–1.5	6–10	Several	Lee et al. (2008) , Juhl et al. (2011) , Manes and Gradinger (2009)
Alaska	Bering and Chuckchi Seas	61	Never			November/ December until mid June	26–85	1–26				50–100		Gradinger, unpubl. data
Canada	Franklin Bay	70	25.11–16.1	20.1	43.4	October–July	132–201	3.8–15.6	3	10	1**	250	2004	Rózańska et al. (2009)
Canada	Amundsen Gulf	71	20.11–22.1	19.6	42.5	October–June	120–180	<5–>15	2.9– 10.0	7.8– 23.2	0.5–1.6	Variable	2008	Alou-Font et al. (2013)
Canada	Resolute	75	6.11–3.2	15.5	38.8	October–July	136–176	5–>30	4.3– 8.9	11.8– 28.6	1.1–1.7	>90	Several	Cota et al. (1990) , Michel et al. (2006) , Mundy et al. (2014) Tremblay et al. (2002)
Canada	North Water Polynya	77	30.10–11.2	13.1	36.4	October–June/July			10–11	12–22		Variable	1998	
Greenland	Kobbefjord	64	Never	25.9	49.3	December–May 2005–2006	58		13	3	0.3	100	2005/06	Mikkelsen et al. (2008)
Greenland	Young Sound	74	8.11–2.2	15.7	39.1	October–July	140–160	20–100				100 (mean)	Several	Glud et al. (2007)
Russia	White Sea	66		23.6	47.1	November/ January–April/June	50–60	3–30	8	15	1	60 (max)		Krell et al. (2003) , Sazhin, unpubl. data
Svalbard	Billefjorden	78	25.10–16.2	11.4	34.8	Until May/June	80–100	5–23	6.5	4	0.7	190	2009/11	Gabrielsen, unpublished
Svalbard	Rijpfjorden	80	19.10–23.2	9.5	32.9	1.2.–12.7.2007	100	3–27	9	5	0.7	160	2007/08	Leu et al. (2010)

Table 3
Depth-integrated carbon and chl *a* standing stocks of ice algae from different regions of the Arctic Ocean, with reference to source. Bold values indicate the range of reported values for a given geographical region.

Geographic area	Year	Season	Region	Ice type	Carbon standing stock (mg C m ⁻²)	Chl <i>a</i> standing stock (mg Chl <i>a</i> m ⁻²)	Dominant type of algae (in terms of biomass)	References
Pacific sector	1998	June	Chukchi Sea	Pack ice	–	0.3–123 mg m ⁻³	<i>Melosira arctica</i> and pennate diatoms (<i>Nitzschia frigida</i> , <i>N. promare</i> , <i>Synedropsis hyperborea</i> , <i>Fossula arctica</i>)	Ambrose et al. (2005)
	2002	May/June	Chukchi and Beaufort Sea	Pack ice	1100 ± 600	0.2–304 (mean 38)	No information	Gradinger (2009)
	1978–1980	March–June	Beaufort Sea	Pack ice	–	10–120	Pennate diatoms (<i>Nitzschia frigida</i> , <i>Fragilariopsis cylindrus</i> , <i>Navicula</i> spp., <i>Cylindrotheca closterium</i>) and small flagellates	Cota et al. (1991)
		April–June	Narwhal Island, Beaufort Sea	Landfast ice	–	1–26		Horner and Schrader (1982)
Canadian Arctic						0.2–304		
	1998	April–July	North Water Polynya	Pack ice	–	2–63	<i>Nitzschia frigida</i>	Tremblay et al. (2006)
	1997/1998	Whole year	Canada Basin	Pack ice	0–19.3 µg C L ⁻¹	0.1–1 mg m ⁻³	Pennate diatoms (<i>Nitzschia frigida</i> , <i>N. neofrigida</i> , <i>Navicula</i> spp., <i>Cylindrotheca closterium</i> and <i>Fragilariopsis cylindrus</i>)	Melnikov et al. (2002)
	1971–1977	Spring and fall	Canadian Arctic Archipelago	Landfast ice	–	0.02–8	Pennate diatoms (<i>Nitzschia frigida</i> , <i>Nitzschia polaris</i> , <i>Fragilariopsis cylindrus</i> , <i>Navicula septentrionalis</i>)	Hsiao (1980)
	1973–1975	February – May	Canadian Arctic Archipelago (Robeson Channel, Barrow Strait, Austin Channel, Hudson Bay and Gulf of St. Lawrence)	Landfast ice	–	0.01–25	Robeson Channel, Barrow Strait, Austin Channel and Hudson Bay: Pennate diatoms (<i>Amphiprora</i> spp., <i>Diploneis</i> spp., <i>Navicula</i> spp. and <i>Nitzschia</i> spp.), centric diatoms <5% Gulf of St. Lawrence: Pennate diatoms (<i>Navicula</i> spp. and <i>Nitzschia</i> spp.) and centric diatoms (43%; <i>Chaetoceros</i> spp., <i>Porosira glacialis</i> and <i>Thalassiosira</i> spp.)	Dunbar and Acreman (1980)
	1979–1986	Whole year	Canadian Arctic Archipelago, Frobisher Bay	Landfast ice	–	<4–>10	Pennate diatoms	Hsiao (1992)
	1983		Canadian Arctic Archipelago, Barrow Strait	Landfast ice	–	Max. 52 (mean 8)	Diatoms	Cota et al. (1987)
	1984		Canadian Arctic Archipelago, Barrow Strait	Landfast ice	–	Max. 80 (mean 18)	Diatoms	Cota et al. (1987)
	1985	May/June	Canadian Arctic Archipelago, Resolute Passage	Landfast ice	–	30–130	No information	Smith et al. (1987)
	1985	May	Canadian Arctic Archipelago	Landfast ice	–	<10–>100	No information	Cota and Horne (1989)
	1985/1986	March–June	Canadian Arctic Archipelago	Landfast ice	–	1.5–46	No information	Smith et al. (1988)
	1985/1986	April/May	Canadian Arctic Archipelago, Resolute Passage	Landfast ice	–	19–93	Pennate diatoms (<i>Nitzschia frigida</i> , <i>Fragilariopsis. oceanica</i>)	Smith et al. (1989)
	1986	May/June	Canadian Arctic Archipelago, Grise Fjord	Landfast ice	–	5–55	No information	Apollonio et al. (2002)
	1989	March–June	Canadian Arctic Archipelago, Resolute Passage	Landfast ice	85–1439	0.02–100	Pennate diatoms (<i>Nitzschia frigida</i> , <i>N. promare</i> , <i>Fragilariopsis cylindrus</i> , <i>F. oceanica</i> , <i>Pseudo-nitzschia delicatissima</i>)	Smith et al. (1993)
		March–June	Canadian Arctic Archipelago, Barrow Strait	Landfast ice	–	100–300	Diatoms	Cota et al. (1991)
		Spring	Canadian Arctic Archipelago	Landfast ice	–	10–145		Maranger et al. (1994)
	1992	April–June	Canadian Arctic Archipelago, Resolute Passage	Landfast ice	–	40–160	Pennate diatoms (<i>Nitzschia frigida</i> , <i>N. arctica</i> , <i>Synedra</i> sp., <i>Entomoneis paludosa</i>)	Michel et al. (1996)
	1992	April/May	Canadian Arctic Archipelago, Resolute Passage	Landfast ice	–	3–89	Pennate diatoms (<i>Nitzschia frigida</i> , <i>N. arctica</i> and <i>Navicula kariana</i>)	Suzuki et al. (1997)
	1992, 1994 and 1995	May–July	Canadian Arctic Archipelago, Barrow Strait	Landfast ice	–	<5–>80	Pennate diatoms (<i>Nitzschia</i> , <i>Navicula</i> , <i>Fragilariopsis</i>)	Fortier et al. (2002)

(continued on next page)

Table 3 (continued)

Geographic area	Year	Season	Region	Ice type	Carbon standing stock (mg C m ⁻²)	Chl <i>a</i> standing stock (mg Chl <i>a</i> m ⁻²)	Dominant type of algae (in terms of biomass)	References
	2002	May–July	Canadian Arctic Archipelago, Resolute Passage	Landfast ice	–	<1–80	No information	Lavoie et al. (2005)
	2002	May/June	Canadian Arctic Archipelago, McDougall Sound	Landfast ice	–	1–45	No information	Mundy et al. (2005)
	2004	February–June	Canadian Arctic Archipelago, Franklin Bay	Landfast ice	–	0.3–711 mg m ⁻³	Pennate diatoms (<i>Nitzschia</i> spp. and <i>Navicula</i> spp.)	Riedel et al. (2006)
	2008	June	Canadian Arctic Archipelago, Darnley Bay	Landfast ice	–	1.2–1.7	Pennate diatoms (<i>Cylindrotheca closterium</i> , <i>Nitzschia</i> spp., <i>Navicula</i> spp.), flagellates	Mundy et al. (2011)
Greenland						0.01–300		
	1994	July/August	Greenland Sea	Pack ice	25–150	0.1–3.3	Diatoms (60%) and flagellates	Gradinger et al. (1999)
	1994	June–August	Greenland Sea	Pack ice	13–230	0.13–2.9	72% pennate diatoms, 20% phytoflagellates	Gradinger (1999)
	1996	April/May	Greenland Sea, Disko Island	Pack ice	46–241 mg C m ⁻³	1.2–5.5 mg m ⁻³	Pennate diatoms	Buck et al. (1998)
Fram Strait	1999/2002	June	Young Sound, NE Greenland	Landfast ice	–	0.5–2.5	Diatoms (both pennate and centric species)	Glud et al. (2007)
						0.1–3.3		
	1999	September/October	Fram Strait and Greenland Sea	Pack ice	–	0.1–17.1 mg m ⁻³	Pennate diatoms	Meiners et al. (2003)
	2002/2003	September and March/April	Northern Fram Strait	Pack ice	–	0.1–2.3	No information	Schunemann and Werner (2005)
Svalbard	2010	June	Fram Strait	Pack ice	410	0.11–0.93	Pennate diatoms (<i>Navicula transitans</i> and <i>Nitzschia</i> spp.)	Glud et al. (2014)
	2010	June	Fram Strait	Floating ice-algal aggregates	–	2.97 ± 1.21 mg m ²	Pennate diatoms (<i>Navicula transitans</i> , <i>Navicula directa</i> , <i>Achnanthes taeniata</i> and <i>Nitzschia</i> spp.)	Glud et al. (2014)
						0.1–2.3		
	2007	April–June	Rijpfjorden, Svalbard	Landfast ice	54–450	1–48	<i>Nitzschia frigida</i> , <i>Navicula septentrionalis</i> , <i>Fragilariopsis cylindrus</i>	Leu et al. (2010)
Svalbard	2009	February–June	Billefjorden, Svalbard	Landfast ice	–	0.01–14	<i>Nitzschia</i> spp.	Gabrielsen unpublished
	2011	March–May	North-west Svalbard	Pack ice	–	0.3–9.8	Pennate diatoms (<i>Nitzschia frigida</i> , <i>Navicula</i> spp., <i>Entomoneis kjelmannii</i> , <i>Synedropsis hyperborea</i> , <i>Cylindrotheca closterium</i>)	Assmy unpublished
	2012	July	North-west Svalbard	Ice-algal aggregates	0.2–1.3	0.002–0.006	Pennate diatoms (<i>Navicula pelagica</i> , <i>Hantzschia weyprechtii</i> , <i>Entomoneis paludosa</i> and <i>Cylindrotheca closterium</i>)	Assmy et al. (2013)
						0.01–48		
Barents Sea	1993	August–October	Barents Sea	Pack ice	30–34	1	No information	Gradinger and Zhang (1997)
	2003–2005	May and July	Barents Sea	Pack ice	9–620	–	Pennate diatoms (<i>Nitzschia frigida</i> , <i>Synedropsis hyperborea</i> , <i>Fragilariopsis cylindrus</i> , <i>F. oceanica</i> and <i>Navicula pelagica</i>), the centric diatom <i>Chaetoceros socialis</i> , <i>Phaeocystis pouchetii</i> and <i>Dinobryon balticum</i>	Tamelander et al. (2009)
Russian Arctic	1993	August–October	Laptev Sea	Pack ice	4–45	0.1–1.5	No information	Gradinger and Zhang (1997)
Central Arctic	1991	August–October	Central Arctic	Pack ice	25–457	<0.01–7.1	72% pennate diatoms, 20% phytoflagellates	Gradinger (1999)

1994	July/August	Arctic Ocean section	Pack ice	3–27	0.1–14	<i>Melosira arctica</i> and <i>Nitzschia frigida</i>	Gosselin et al. (1997)
1994	July/August	Arctic Ocean 70°–86°N	Pack ice	–	0.1–3	No information	Wheeler et al. (1996)
2011/	August/	Arctic Ocean 81°6′–87°6′N; 31°7′–131°7′E	Pack ice	–	1.2–1.7	Pennate diatoms	Fernández-Méndez et al. (2014)
2012	September	Arctic Ocean 81°6′–87°6′N; 31°7′–	Ice-algal	–	0.1–3.7	Pennate diatoms (<i>Nitzschia</i> sp., <i>Navicula</i> sp., <i>Fragilariopsis</i> sp., and <i>Entomoneis</i> sp.)	Fernández-Méndez et al. (2014)
2012	September	131°7′E	aggregates	–	7.7	<i>Melosira arctica</i>	Fernández-Méndez et al. (2014)
2011/	August/	Arctic Ocean 81°6′–87°6′N; 31°7′–131°7′E	Pack ice	–	14–44	<i>Melosira arctica</i>	Fernández-Méndez et al. (2014)
2012	September	Arctic Ocean 81°6′–87°6′N; 31°7′–131°7′E	Ice-algal aggregates	–	0.01–44		Fernández-Méndez et al. (2014)

7. Underlying reasons for spatial and temporal variability of sea ice algal bloom phenology

The available time series on seasonal bloom development are for most regions incomplete, thus making it impossible to statistically deduce the effect of individual environmental steering factors. Most often, there are only single-year observations from one locality and, or the data series only cover a limited time period, making it very difficult to separate spatial from inter-annual variability, and to rule out artifacts caused by insufficient sampling that may have affected the seemingly different shapes of chl *a* development curves. Similar to previous studies, light emerges as the single most important factor for the initiation (phase I-phase II shift), and phenology of the first vernal algal bloom, and, hence the start of the important winter–spring transition period in our compilation and analyses of data. However, the actual light availability in a given environment in ice-covered seas is not only a function of latitude (despite the dependence of solar angle and day length on latitude). Instead, light is determined on a local scale by the prevailing ice conditions and particularly, the snow depth distribution. The influence of snow depth on spatial variability of ice algal chl *a* has been demonstrated in various studies from across the Arctic (e.g., [Campbell et al., 2015](#); [Juhl and Krembs, 2010](#); [Leu et al., 2010](#); [Mundy et al., 2005](#); [Rysgaard et al., 2001](#); [Welch and Bergmann, 1989](#)). However, to study the impact of snow on bloom phenology, multiple years of sampling under different snow conditions at one specific site are required. From the multi-year dataset compiled for Resolute in this article, a significant negative log-linear correlation was observed between chl *a* and snow depth throughout the light-limited phase of the ice algal bloom period. It switched rather abruptly towards a positive relationship at the end of the bloom period, as a function of too much light under shallower snow covers causing photo acclimation of algal biomass and potentially photoinhibition in extreme cases ([Campbell et al., 2015](#); [Juhl and Krembs, 2010](#)). Another reason for the positive relationship might be the insulating effect of the snow cover against melting under deeper snow covers ([Fig. 6](#)). Snow depth also affected the temporal development of bottom ice algal chl *a* concentrations ([Fig. 4](#)). Low snow covers allowed for a rapid increase of chl *a* concentrations during spring, a high peak chl *a* concentration, and ended with an early and steep decline. Intermediate snow covers resulted in a slower increase, a lower peak concentration and a later decrease, whereas the deepest snow covers kept algal production in a permanent light-limited state and resulted in the slowest increase of chl *a* concentrations that stopped abruptly as a consequence of snow melt without having reached a visible peak concentration. Light as the major limiting factor during the early bloom phase was identified by many previous studies (e.g., [Gosselin et al., 1985](#); [Horner and Schrader, 1982](#); [Mock and Gradinger, 1999](#); [Rysgaard et al., 2001](#)), whereas the direct negative impact of little snow and thus too much light (and potentially heat) during the late bloom phase has been emphasized by only a few studies so far ([Campbell et al., 2015](#); [Juhl and Krembs, 2010](#); [Welch and Bergmann, 1989](#)). The greater thermal insulation associated with a deeper snow cover slows the rate of brine release and melting towards the end of the sea ice algal growth season ([Mundy et al., 2005](#)).

In addition to snow cover, a study by [Welch and Bergmann \(1989\)](#) showed that ice thickness affects spatial variability of ice algal chl *a* concentrations. Significantly different ice thicknesses near Resolute Bay were found to be associated with a range of freeze-up dates and resulted in an offset of ice algal chl *a* concentrations yet similar accumulation rates overtime. It was thus concluded that colonization date affected chl *a* standing stocks; the thicker (older first-year ice) having a “head-start” over thinner

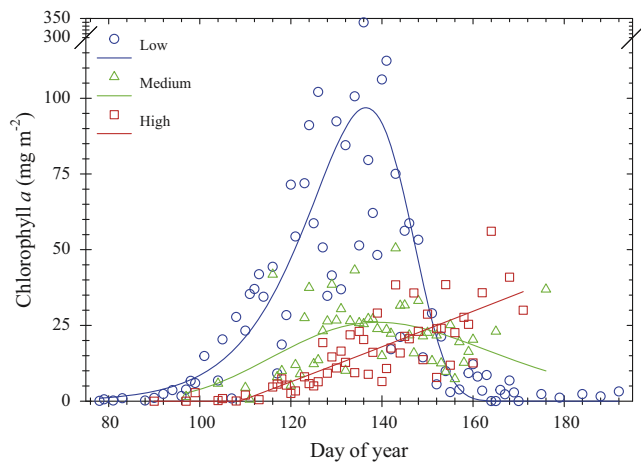


Fig. 4. Seasonal development of chl *a* concentrations in sea ice at Resolute Bay, measured at locations with low (0–10 cm), intermediate (10–20 cm) and high (>20 cm) snow cover. The dataset consists of 12 different data time series, and was collected between the years 1985–2011.

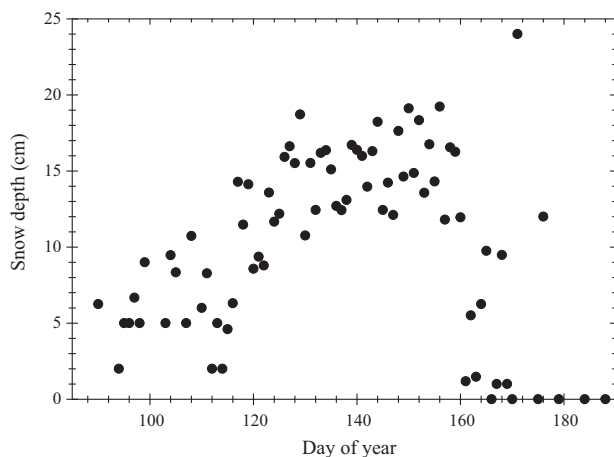


Fig. 5. Daily averaged snow depth time series for Resolute Bay (same dataset as used in Fig. 4).

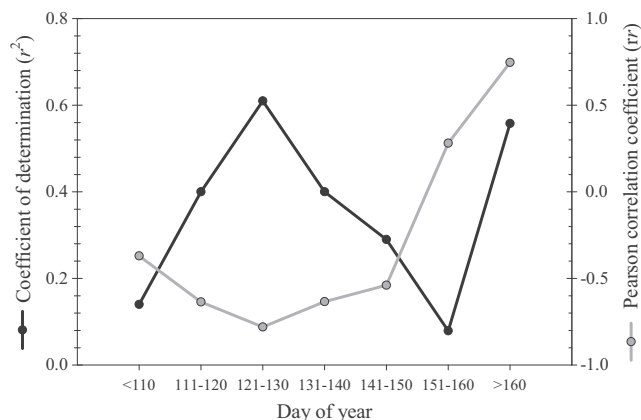


Fig. 6. Results of correlation analyses between $\ln(\text{chl } a)$ and snow depth during different time periods in the winter–spring transition period for the dataset from Resolute Bay (same dataset as in Figs. 4 and 5).

(younger) sea ice. Alternatively, Niemi et al. (2011) hypothesized that timing of ice formation directly impacts algal abundance in new ice, which is dependent on incorporation of algal cells from surface waters. That is, surface water algal abundance was observed to decrease during the seasonal transition from fall to winter. Therefore, assuming no net growth of ice-associated

diatoms during the light-limited winter period, the formation of ice later into the winter period would result in less ice algal abundance relative to ice formed in the fall, essentially delaying bloom development.

The importance of sufficient supply of inorganic nutrients and carbon for the initiation and termination of the bloom has been pointed out by, e.g., Cota et al. (1987), Gradinger (2009), and Søgaard et al. (2010), but could not be directly tested here due to the scarcity of respective data series. The impact of the amount of available nutrients for the magnitude of a sea ice algal bloom has been emphasized, amongst others, by Pineault et al. (2013), and Róžańska et al. (2009), and might well influence the potential maximum chl *a* concentrations that can be reached in a given area, as discussed in the proceeding section. Cota et al. (1987) were the first to convincingly demonstrate that ice algae nutrient demand greatly surpassed the supply available in sea ice brines alone, concluding that surface waters were the main nutrient source for ice algae. With ocean-ice nutrient re-supply during periods of turbulent exchange (Gosselin et al., 1985; Cota et al., 1987; Lavoie et al., 2005), an earlier bloom onset (e.g., under low snow depths) would result in a greater period for nutrient exchange with surface waters, thus allowing for a greater accumulation of biomass. However, increased biomass also increases nutrient demand for additional growth and therefore, nutrient limitation likely influences timing of bloom termination.

8. Spatial variability of sea ice algae chl *a* standing stocks and primary production

In addition to the few time series on sea ice algal bloom development, there are many more studies reporting standing stocks and daily primary production rates. Recordings over the last 40 years span four orders of magnitude from 0.01 to 340 mg chl *a* m^{-2} and 0.03–463 mg C $\text{m}^{-2} \text{d}^{-1}$, respectively (Tables 3 and 4) and are in a similar range as reported from a previous literature compilation (Arrigo et al., 2010, and references therein). Ice algal carbon standing stock estimates, derived from C:chl *a* (g:g) ratios, direct particulate organic carbon (POC) measurements or carbon conversion from microscopic cell counts, range from 3 to 1439 mg C m^{-2} (Table 3). In most studies, where both ice algal chl *a* and carbon stocks were recorded, the C:chl *a* ratio was between 20 and 45 but much higher ratios were also recorded for the winter months (heterotrophic phase I) where ratios can exceed 1000 (Table 3). Two-thirds of all studies reported in Table 3 were conducted on landfast ice, mainly between March and July and almost exclusively at various locations in the Canadian Arctic Archipelago. There are considerable variations in chl *a* standing stocks among and within sampling locations largely driven by environmental settings (e.g., Gradinger et al., 2009) and it is difficult to depict seasonal trends due to the relatively narrow time window covered by the different studies. However, within the Canadian Arctic archipelago certain locations like Resolute (including Barrow Strait) seem to support higher standing stocks. The remaining 16 studies were carried out on drifting pack-ice and covered a larger geographical area (including the central Arctic, the Canada Basin, the Siberian Shelf and the Atlantic and Pacific sectors of the Arctic) and wider seasonal scale (from March until October). The by far highest standing stocks were recorded from the Chukchi and Beaufort Sea while all other pack-ice areas exhibited one to two orders of magnitude lower standing stocks. The large decrease in ice algal biomass and production from the Chukchi/Beaufort Sea shelves into the deep basins were associated with decreasing surface water nutrient concentrations (Gradinger, 2009). Although maximum chl *a* standing stocks did not significantly differ between landfast and pack-ice, stocks were generally higher in landfast ice.

Table 4

Daily primary production of ice algae from different regions of the Arctic Ocean, with reference to source. Bold values indicate the range of values reported for the respective geographic area.

Geographic area	Year	Season	Region	Ice type	Incubation method and time	Primary production (mg C m ⁻² d ⁻¹)	Dominant type of algae (in terms of biomass)	Reference
Pacific sector	1980	April/May	Northern Beaufort Sea	Pack ice	¹⁴ C, 3–4 h	2–62	Pennate diatoms (<i>Nitzschia frigida</i> , <i>Fragilariopsis cylindrus</i> , <i>Navicula</i> spp., <i>Cylindrotheca closterium</i>) and small flagellates	Horner and Schrader (1982)
	2002	May/June	Chukchi and Beaufort Sea	Pack ice	¹³ C, 4–6 h	4–30	No information	Gradinger (2009)
Canadian Arctic						2–62		
	1978	April/May	Davis Strait	Pack ice	¹⁴ C, 4 h	0.03–2.4	Pennate diatoms (<i>Nitzschia</i> , <i>Navicula</i> and <i>Pleurosigma</i>)	Booth (1984)
	1984	March	Labrador Sea	Pack ice	¹⁴ C	58	Centric diatoms (<i>Coscinodiscus</i> spp. and <i>Thalassiosira</i> sp.) and pennate diatoms (<i>Navicula</i> sp., <i>Nitzschia</i> sp. and <i>Fragillaria</i> sp.)	Irwin (1990)
	1985/1986	March–June	Canadian Arctic Archipelago	Landfast ice	¹⁴ C, 1–24 h	21–463	No information	Smith et al. (1988)
		Spring	Canadian Arctic Archipelago	Landfast ice	¹⁴ C	20–157	No information	Smith and Herman (1991)
	1998	April/May	Canadian Arctic Archipelago, Baffin Bay	Landfast ice	¹⁴ C, 2–4 h	26–317	Diatoms	Nozais et al. (2001)
	1998	April–June	Canadian Arctic Archipelago, Baffin Bay, North Water Polynya	Landfast ice	¹⁴ C, 2–4 h	2–150	<i>Nitzschia frigida</i> dominated the bottom ice assemblage	Michel et al. (2002)
Greenland						0.03–463		
	1975/1976	March/April	Godhavn, West Greenland	Landfast ice	¹⁴ C	4–140	Pennate diatoms (<i>Navicula</i> -like species)	Andersen (1977)
	1999	June/July	Young Sound, NE Greenland	Landfast ice	¹⁴ C, 2 h	0.2	No information	Rysgaard et al. (2001)
	1999/2002	June	Young Sound, NE Greenland	Landfast ice	¹⁴ C, 2 h	1.6 (average)	Diatoms (both pennate and centric species)	Glud et al. (2007)
Barents Sea (including Svalbard, Fram Strait and Greenland Sea)						0.2–140		
	1996/1997	May–August	Northern Barents Sea	Pack ice	¹⁴ C, 6 h	0.2–52	Pennate diatoms (<i>Nitzschia frigida</i> , <i>N. promare</i> , <i>Fragilariopsis oceanica</i> , Hegseth (1998)	
						<i>Pseudogomphonema arctica</i> , <i>Fossula arctica</i> and <i>Synedropsis hyperborea</i>)		
	1997	May/June	Barents and Greenland Sea and Fram Strait	Pack ice	¹⁴ C, 8 h	0.8–9.7	No information	Mock and Gradinger (1999)
	2004	May	Northern Barents Sea	Pack ice	¹⁴ C, 6–7 h	4.9–55	<i>Nitzschia frigida</i>	McMinn and Hegseth (2007)
	2010	June	Fram Strait	Pack ice	¹⁴ C, 24 h	0.8–2	<i>Navicula transitans</i> and <i>Nitzschia</i> spp.	Glud et al. (2014)
	2012	July/August	North-west Svalbard	Floating ice-algal aggregates	¹⁴ C, 24 h	0.02–0.002	Pennate diatoms (<i>Navicula pelagica</i> , <i>Hantzschia weyprechti</i> , <i>Entomoneis paludosa</i> and <i>Cylindrotheca closterium</i>)	Assmy et al. (2013)
	2012	August	North-west Svalbard	Pack ice	¹⁴ C, 24 h	1–9.2	Pennate diatoms	Assmy et al. (2013)
						0.002–55		

(continued on next page)

Table 4 (continued)

Geographic area	Year	Season	Region	Ice type	Incubation method and time	Primary production (mg C m ⁻² d ⁻¹)	Dominant type of algae (in terms of biomass)	Reference
Central Arctic Ocean	1994	July/August	Arctic Ocean 70–86°N	Pack ice	¹⁴ C, 12 h	2–55	No information	Wheeler et al. (1996)
	1994	July/August	Arctic Ocean section	Pack ice	¹⁴ C, 4–12 h	0.5–310	<i>Melosira arctica</i>	Gosselin et al. (1997)
	2011/2012	August/September	Arctic Ocean 81°6′–87°6′N; 31°7′–131°7′E	Pack ice	¹⁴ C, 24 h	1–13	Pennate diatoms	Fernández-Méndez et al. (2014)
	2011/2012	August/September	Arctic Ocean 81°6′–87°6′N; 31°7′–131°7′E	Ice-algal aggregates	¹⁴ C, 24 h	0.4–9.7	Pennate diatoms (<i>Nitzschia</i> sp., <i>Navicula</i> sp., <i>Fragilariopsis</i> sp., and <i>Entomoneis</i> sp.)	Fernández-Méndez et al. (2014)
	2011/2012	August/September	Arctic Ocean 81°6′–87°6′N; 31°7′–131°7′E	Pack ice	¹⁴ C, 24 h	1.5	<i>Melosira arctica</i>	Fernández-Méndez et al. (2014)
	2011/2012	August/September	Arctic Ocean 81°6′–87°6′N; 31°7′–131°7′E	Ice-algal aggregates	¹⁴ C, 24 h	13–40	<i>Melosira arctica</i>	Fernández-Méndez et al. (2014)

0.4–310

A comparison between landfast and pack-ice carbon standing stocks is not possible because, with one exception, they have only been reported from pack-ice studies. Six out of the 15 estimates of primary production in sea ice are landfast ice studies from the Canadian Arctic archipelago and Greenland fjords conducted in spring and early summer (Table 4). Primary production rates were generally higher in the Canadian Arctic archipelago than in West and Northeast Greenland but a systematic comparison is difficult due to the limited number of measurements. Both minimum and maximum primary production rates in pack-ice were generally lower compared to landfast ice but high rates were recorded in the central Arctic associated with mats of the centric diatom *Melosira arctica*. Highest rates were recorded in spring at more southerly latitudes while the high rates associated with *M. arctica* in the central Arctic were recorded in late summer. These comparisons have to be judged with caution, however, as production was determined in different ways. Although all but one study used the ¹⁴C technique to measure primary production (Table 4), direct comparison of daily primary production rates is complicated due to the different incubation periods applied, ranging from 1 to 24 h, with the majority between 2 and 6 h. While the 24 h incubations represent net primary production (NPP), the shorter-term incubations are more likely to measure something between NPP and gross primary production (GPP), with the tendency towards NPP or GPP depending on the length of incubation (Williams et al., 2002). Furthermore, it has been shown that the incubation starting time can have a significant influence on the outcome of 24 h incubations (Mingelbier et al., 1994).

9. Dominating species patterns

The Arctic Ocean harbors a large diversity of marine pelagic and sea ice protists, rivaling that in lower latitude oceans. A total of 1027 sympagic protist taxa have been reported from four Pan-Arctic regions, with a strong dominance of pennate diatom species (Poulin et al., 2011; Syvertsen, 1991). Microscopic species identification in protists is biased towards mineral bearing and armored species, in particular towards the silica-walled diatoms. Recent advances in genomics have already revealed a previously unknown diversity of small and fragile taxa in the pico- and nanoplankton size range (Comeau et al., 2013). Nevertheless, despite high abundances of small photosynthetic flagellates, ice algal communities were almost exclusively dominated by pennate

diatoms in terms of biomass (Tables 3 and 4). Among the pennate diatoms, species of the genera *Nitzschia*, *Navicula* and *Fragilariopsis* occupy a particularly prominent role, with *Nitzschia frigida* as the single most important species in Arctic sea ice. *Nitzschia frigida* forms large, arborescent colonies while *F. cylindrus* grows in long, ribbon-like chains and both species usually dominate bottom ice communities (Horner et al., 1992; von Quillfeldt et al., 2009). In contrast to most other ice-associated diatoms, *F. cylindrus* can also significantly contribute to phytoplankton blooms in the marginal ice zone (see Barber et al., this issue). Although centric diatoms play a subordinate role in Arctic sea ice communities compared to pennate species, the centric, chain-forming diatom *Melosira arctica* can strongly dominate algal biomass of sub-ice communities (Poulin et al., 2014), both in the deep central Arctic and over the shallow shelves. This species forms long, strand-like aggregates that are attached to the underside of first and multi-year ice but grow in the sub-ice water column. The pennate *Synedropsis hyperborea* and the centric *Attheya septentrionalis* are two small, epiphytic diatoms that grow attached to colonies of *N. frigida* and *M. arctica* as well as to the sea ice itself (von Quillfeldt et al., 2009) and can be numerically important.

10. Physical forcing of geographic differences in ice-algal biomass and primary production

Large regional differences in maximum ice algal standing stocks can be used to make some inference about the proximate environmental factors that set an upper limit to ice algal biomass build-up at the regional scale. The by far highest chl *a* stocks were recorded in pack-ice from the Pacific sector and landfast ice from the Canadian Arctic archipelago. The high stocks in these regions can be explained in part by advection of high inventories of preformed nutrients into the Pacific sector from the adjacent High-Nutrient Low-Chlorophyll (HNLC) North Pacific through Bering Strait. As these waters enter the Arctic Ocean and penetrate westward into the Canadian Arctic, they flow below the nutrient deplete polar surface water layer, but can be mixed to the surface through wind induced coastal and ice-edge upwelling events (Carmack et al., 2004; Williams and Carmack, 2008; Mundy et al., 2009), where they have been shown to augment ice algae chl *a* standing stocks (Tremblay et al., 2011). Shallow points towards the centre of the Canadian Arctic archipelago near Barrow Strait also act to mix the Pacific origin waters into surface layers (Michel et al., 2006).

Additional mechanisms driving ocean-ice fluxes of water can further enhance nutrient supply within the sea ice matrix. For example, fortnightly tidal cycles have been correlated with bloom enhancement (both photosynthetic and biomass responses) in landfast ice regions in the Canadian Arctic (Gosselin et al., 1985; Cota et al., 1987; Cota and Horne, 1989). Enhanced ocean-ice tidal shear during spring tides can augment exchange of nutrient depleted brine in the ice with nutrient replete water from under the ice cover. This process was explained by Cota et al. (1987) and represented in an ice algal growth model for the first time in Lavoie et al. (2005).

On the other hand, areas influenced by Atlantic inflow, including Fram Strait, Svalbard, and the Barents Sea, exhibit much lower maximum chl *a* stocks. Despite the lower nutrient concentrations of Atlantic compared to Pacific water masses, the relatively warm Atlantic inflow might further facilitate bottom ice habitat ablation and constrain the ice algal growth season, thereby limiting ice algal bloom magnitude. Interestingly, the highest stocks falling within these three geographic areas were recorded from a cold, Arctic-influenced fjord on the northern shore of Svalbard (Rijpfjorden). The low stocks recorded from Greenland and the Russian Arctic could be attributed to the large volume of freshwater run-off from the massive glaciers in the former region and light limitation due to incorporation of riverine suspended particles into sea ice in the latter environment but this remains speculative due to the limited number of observations. Both light and nutrients limit ice algal biomass build-up in the perennial ice-covered, oligotrophic central Arctic Ocean. However, strands of the centric diatom *Melosira arctica* can build-up sizable stocks likely due to their unpalatable nature (Syvertsen, 1991) and ability to scavenge nutrients from the under-ice water column while being transported with the drifting pack-ice relative to the underlying Arctic surface layer (Boetius et al., 2013).

Our pan-Arctic data compilation points at several other major factors that might be just as important for the size of the actual standing stock of ice algal biomass: amongst others, it is conspicuous that all sea ice algal data reported from different Greenlandic fjords are much lower than the values found in either Svalbard, or Alaska, or – in particular – the Canadian Arctic. Winter values of silicic acid from Greenland are lower than those measured in Canada, Alaska, or the White Sea – but are within the range reported for Svalbard where considerably higher maximum chl *a* concentrations were reported (Table 2). The low sea ice algal biomass in Greenlandic fjords may be a result of strong tidal currents, which could affect the development of sympagic communities in the bottom sea ice layer. Periodic melting of the sea ice from below and subsequent re-growth has also been observed, which affect the algal biomass often concentrated in the bottom part of the ice profile (e.g., Mikkelsen et al., 2008; Søgaard et al., 2010, 2013). Freshwater from melting glacial and sea ice greatly affects the overall dynamics of many Greenlandic fjords. Hence, freshwater flooding of and discharge below landfast sea ice may occur locally during the ice season, which can substantially affect ice algal habitat space (Legendre et al., 1991). Furthermore, the Greenland fjords studied tend to be associated with considerable snowfall and thus homogeneous deep snow covers (e.g., 30 cm or greater), which have been demonstrated to limit ice algae growth until the snow starts to melt (Rysgaard et al., 2001). In fact, only in a Greenland fjord has an infiltration community associated with surface flooding been reported in the Arctic (Buck et al., 1998); a situation typically restricted to the Antarctic where thin ice and deep snow covers are common (Thomas and Dieckmann, 2010). McMinn and Hegseth (2004) also reported an infiltration community from the area around Svalbard; however, these assemblages were heavily dominated by *Phaeocystis* spp. occurring in a pelagic bloom at the same time, and possibly did not represent a specific ice algae community.

Although measurements of daily ice algal primary production (PP) for the five identified geographical areas are limited (Table 4), some patterns emerged. Highest ice algal PP rates were associated with landfast ice studies, particularly from the Canadian Arctic archipelago, while rates measured in pack-ice were generally lower. The higher rates recorded in the former environment could be partly explained by less disturbance of algal growth under the more stable landfast ice conditions as compared to the more dynamic conditions prevalent in pack-ice environments. Thus, differences in daily ice algal PP are more likely due to differences in ice type than geographic area. However, exceptions to these general patterns illustrate the need to take regional environmental conditions into account. The high PP rates measured for a pack-ice community from the central Arctic Ocean were associated with *Melosira arctica*, highlighting its ability to sustain high growth rates. On the other hand, PP rates measured in landfast ice from Young Sound, NE Greenland were amongst the lowest reported.

11. Challenges caused by climate change

The observed changes in Arctic sea ice cover during the last decades (Fig. 7), and in particular the decrease in MYI, has far-reaching implications for the primary production regime in the Arctic Ocean. Increasing temperatures have led in particular to an earlier ice break-up and increased transparency of Arctic sea ice due to decreasing thickness and an increasing melt pond coverage (Nicolaus et al., 2012), as well as later ice formation in fall. As a result of the changing ice cover, significant increasing trends in open water concentrations across the Arctic have been observed for every month of the year, with highly nonlinear increases during the fall period (Barber et al., this issue). FYI has become the dominant ice type in the Arctic and has replaced the rapidly disappearing MYI cover in most areas (Comiso, 2012). Generally, FYI is less thick and has a thinner snow cover (since it usually does not have as much time to accumulate as much snow as MYI), and has a greater areal melt pond coverage (due to less topographic relief; Polashenski et al., 2012) than MYI. As more light is absorbed in the water column in association with the ice-albedo feedback, the further increase in water temperature is anticipated to decrease seasonal sea ice growth (Perovich, 2011). Furthermore, regional differences have been observed in the icescape where changes in most of the Arctic appear to be predominantly atmospherically driven and associated with the spring period, while in the Barents and Kara seas, oceanographic forcing appears to play a more important role during the fall period (Barber et al., this issue). All of these factors will affect timing, duration, and magnitude of the different types of algal blooms usually found in seasonally ice-covered waters in Arctic marine ecosystems.

The ongoing earlier ice melt implies shorter bloom periods for ice algal production, and an increasing potential for pelagic primary production both underneath the (thinner and/or more transparent) sea ice cover (Nicolaus et al., 2012; Mundy et al., 2014) and in open water (Arrigo et al., 2008; Pabi et al., 2008). At the same time, a higher percentage of thinner FYI as opposed to previously prevailing MYI may offer better growth conditions for ice algae during the shorter ice-covered period due to higher initial nutrient load and brine volume. Snow cover on top of the ice is the most important factor controlling the amount of light transmitted into and through the sea ice in spring, and the fraction covered by ponds in summer. It is generally assumed that precipitation will increase in the future Arctic (IPCC report 2014); however, with respect to sea ice transparency, the timing and type of precipitation is of crucial importance: Precipitation as snow will decrease light transmittance, whereas precipitation as rain will enhance the amount of light penetrating through ice and speed up the melting process, thereby decreasing and increasing sea ice algal

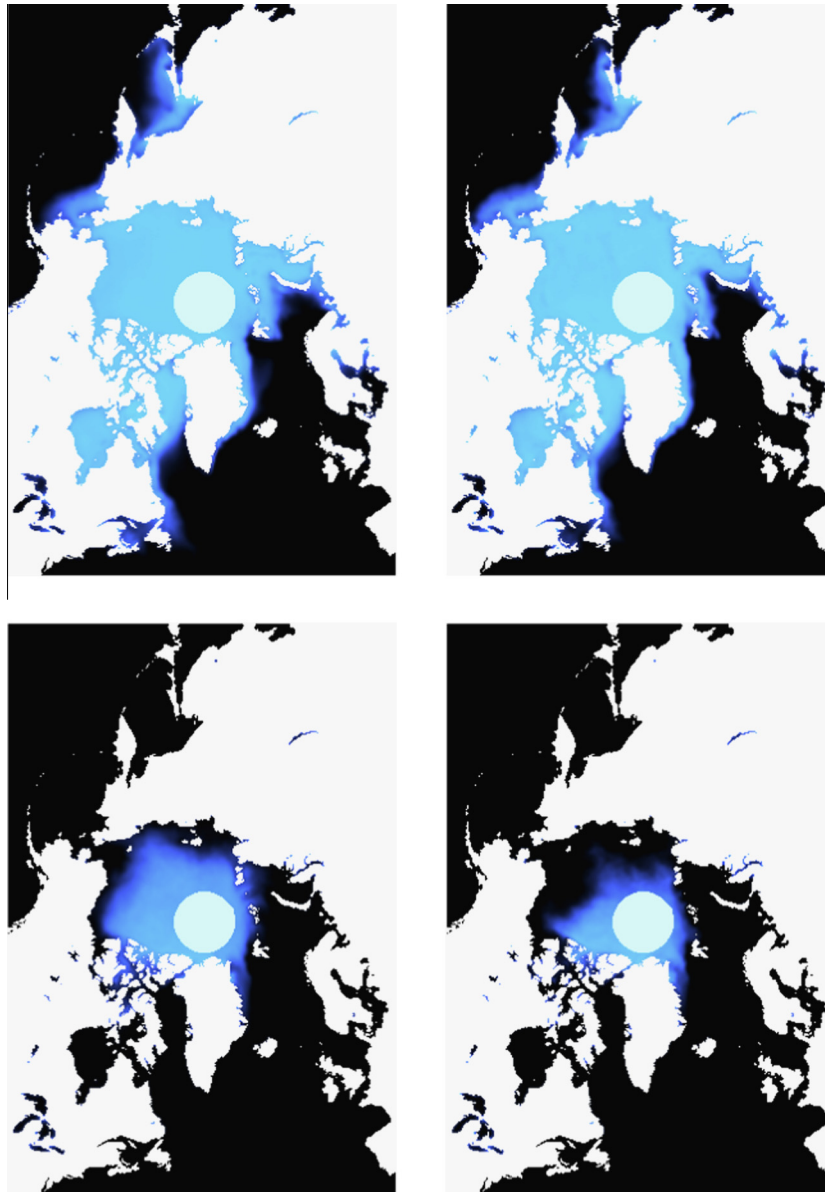


Fig. 7. Mean monthly sea ice concentration for March (top) and September (down) from the period 1979–2006 (left panel), and 2007–2012 (right panel). Original data were obtained through the calibrated sea ice concentration SMMR–SSM/I passive microwave dataset from the National Snow and Ice Data Center (Cavalieri et al., 1996, updated yearly).

productivity, respectively. In particular, the occurrence of rain events during late stages of sea ice melt may even drive early termination of the sea ice algal bloom (Campbell et al., 2014). The model of Hezel et al. (2012) showed that the loss of sea ice cover during autumn and winter reduces the platform to collect snowfall, and thereby overcompensates for increased winter snowfall, resulting in lower snow depths during spring. Contrary to the traditional perception that substantial primary production in the Arctic starts with an ice-edge bloom forming after the break-up of sea ice (e.g. (Engelsen et al., 2002; Sakshaug, 2004)), strong evidence indicates much earlier pelagic production starting underneath the ice in many regions (Fortier et al., 2002; Mundy et al., 2009; Arrigo et al., 2012; Mundy et al., 2014; Matrai and Apollonio, 2013). Considering the recent and ongoing changes in sea ice extent, thickness, and transparency, we anticipate that algal blooms within and underneath the ice will increase in the future. An example of an extraordinary dense pelagic bloom under rotten ice with numerous melt ponds was reported from the Chukchi Sea by Arrigo et al. (2012).

12. Implications for grazers, food web structure, and carbon flux

As the timing of key ecological processes such as the annual reproduction period of grazers and the life cycle of higher trophic levels is carefully adjusted to the prevailing sea ice regime, we can expect far-reaching consequences not only for the quantity and quality of annual ice algal primary production, but also its fate and, hence, ecological interactions, food web structure, and carbon fluxes. Several studies have proven the importance of ice algae as a food source for sympagic, pelagic, and benthic grazers (e.g. (Renaud et al., 2007; Søreide et al., 2010; Werner, 1997)). High densities of grazers were also found associated with the ice algal aggregates as described by Assmy et al. (2013). The efficiency of the respective pathways, however, is largely dependent on the appropriate timing of the bloom relative to other processes – and this is ultimately steered by the seasonal development of the sea ice cover and snow depth. McConnell et al. (2012) described the importance of sea ice algae as food source for the sympagic juve-

nile stages of the polychaete *Scolecopsis squamata* from the Chukchi Sea, and highlight that the growth and recruitment of this species will most likely be negatively affected by a shorter sea ice algae bloom period caused by an earlier ice break-up. Recent studies have pointed out the importance of appropriate timing of both ice-associated and pelagic algal blooms for the successful recruitment of key pelagic grazer species (Søreide et al., 2010; Leu et al., 2011; Wold et al., 2011), with potential mismatch scenarios decreasing markedly the reproductive success of pelagic secondary producers, and, hence, the efficiency of biomass transfer in this realm. However, a comparison of *Calanus glacialis* reproductive strategies also revealed a considerable ability to adjust successful reproduction to complete ice-free conditions by acting as a capital breeder (i.e. utilizing exclusively stored metabolic energy for fueling reproduction in the adult females; Daase et al., 2013). During the late phase of the annual ice algal bloom, when biomass starts being released from the ice, ice algae are also ingested by other pelagic grazers as was shown by analyzing the carbon budget for Resolute Passage (Michel et al., 1996). The ice-controlled timing of the pelagic bloom may also cause similar match/mismatch problems, as was illustrated by studies from Greenland where larger copepods in Disko Bay (West Greenland) ascend in time for the spring phytoplankton bloom. Earlier break-up of the sea ice, followed by an earlier spring phytoplankton bloom, resulted in a mismatch situation between phyto- and zooplankton and subsequent changes in the sinking export of organic material (Dunweber et al., 2010; Sejr et al., 2007). In the absence of pelagic grazers, most of the produced biomass sank down to the benthos. Cooper et al. (2013) found high biological activity in the shallow northern Bering Sea during March where sedimentation of ice algal production sustained a rich benthic fauna that again served as food for the spectacled eiders, representing an important part of the apex predators in this system. Strong indications for a relatively tight sympagic–benthic coupling by rapidly sinking sea ice algal aggregates were recently found in the central Arctic Ocean at greater than 4000 m, where substantial amounts of *Melosira arctica* were consumed by macrobenthic fauna (Boetius et al., 2013). Therefore, depending on the systems' structure and important players, a shift will happen from sympagic–pelagic to sympagic–benthic coupling – or the other way round (e.g., Carroll and Carroll, 2003; Hunt et al., 2011).

Due to the scarcity of seasonal data series from a range of high Arctic areas that are ice-covered for several months each year, it remains a challenge to generalize the factors driving the biological processes over the annual transition from the cold and dark winter towards the highly productive period in spring-early summer. A better understanding of these environmental factors is, however, vital to project future scenarios for Arctic marine ecosystem development in an era of climate change.

13. Outlook

Although considerable differences do exist in the timing and magnitude of the ice algal seasonal development between different Arctic regions, they all agreed in being characterized by the three suggested developmental stages which differ in their degree of heterotrophy and linkages to pelagic and benthic processes. Interestingly, the phenological differences between sites are not primarily a function of latitude, but depend greatly on the interplay of various environmental factors, of which light is likely the most obvious. The amount of light that penetrates to the lowermost part of the ice is regulated by solar angle, sea ice thickness, and –most dominantly– snow depth. Only after sufficient light reaches the lowermost part of the sea ice, sea ice moves from a net heterotrophic (phase I) to a net phototrophic stage (phase II), and accumulation of algal biomass occurs, initiating the spring bloom. While initially light limited, phase II can be extended by the insu-

lating effect of deeper snow covers due to reduced high-light stress and ice melt. The still limited number of seasonal field studies with a sufficient temporal resolution and duration, makes statistical comparisons between sites difficult, and impedes the distinct classification of the relative importance of single abiotic factors for the overall development of sympagic algal blooms. This compilation of pan-Arctic data on time series of sea ice algal bloom development points nevertheless at several factors that have a great impact on bloom development. They have the potential to explain the geographic differences in standing stocks and production and should be consistently included in sea ice sampling efforts across the Arctic. To improve our ability to predict future changes in the key processes during the crucial phase of winter–spring transition, we need to increase our knowledge about:

- Overwintering strategies of key species, and the origin of the seed population of sympagic blooms during phase I.
- The importance of sea ice algae as food source for various groups of organisms during phases I to III.
- The fate of biomass produced by sea ice algae during phase III.
- The relative importance of light vs. nutrients in phases II and III.

Furthermore, the need to develop consistent sea ice sampling protocols in order to obtain comparable datasets emerges as very urgent from this overview.

The timing, quantity and quality of sea ice algal production is important for sympagic, pelagic, and benthic grazers – and in most cases it is unknown today how a change in ice algal bloom phenology will affect higher trophic levels, including cascading consequences for ecosystem structure and functioning. Future research should be directed at unraveling the ecology, physiology and life history patterns of key sea ice algae species (in particular *Nitzschia frigida* and *Melosira arctica*), and should also include more time series and process studies. Furthermore, to be able to judge whether or not (or to which degree) grazers will be able to adapt to an altered future regime of Arctic primary production – with a shorter period of sea ice algal blooms, and an earlier start of pelagic primary production – the steering factors that control the seasonal development of important grazers need to be identified.

Author contributions

The two main authors, EL and CJM contributed evenly to this paper.

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