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REVIEW

Microalgal community structure and primary production in Arctic and Antarctic sea ice: A synthesis

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Sea ice is one the largest biomes on earth, yet it is poorly described by biogeochemical and climate models. In this paper, published and unpublished data on sympagic (ice-associated) algal biodiversity and productivity have been compiled from more than 300 sea-ice cores and organized into a systematic framework. Significant patterns in microalgal community structure emerged from this framework. Autotrophic flagellates characterize surface communities, interior communities consist of mixed microalgal populations and pennate diatoms dominate bottom communities. There is overlap between landfast and pack-ice communities, which supports the hypothesis that sympagic microalgae originate from the pelagic environment. Distribution in the Arctic is sometimes quite different compared to the Antarctic. This difference may be related to the time of sampling or lack of dedicated studies. Seasonality has a significant impact on species distribution, with a potentially greater role for flagellates and centric diatoms in early spring. The role of sea-ice algae in seeding pelagic blooms remains uncertain. Photosynthesis in sea ice is mainly controlled by environmental factors on a small scale and therefore cannot be linked to specific ice types. Overall, sea-ice communities show a high capacity for photoacclimation but low maximum productivity compared to pelagic phytoplankton. Low carbon assimilation rates probably result from adaptation to extreme conditions of reduced light and temperature in winter. We hypothesize that in the near future, bottom communities will develop earlier in the season and develop more biomass over a shorter period of time as light penetration increases due to the thinning of sea ice. The Arctic is already witnessing changes. The shift forward in time of the algal bloom can result in a mismatch in trophic relations, but the biogeochemical consequences are still hard to predict. With this paper we provide a number of parameters required to improve the reliability of sea-ice biogeochemical models.

Keywords: biogeochemical models; functional groups; microalgae; production; sea ice

1. Introduction

Sea ice is one of the largest biomes on earth. The area covered by Arctic (15.6×10^6 km^2) and Antarctic (18.8×10^6 km^2) sea ice is roughly 4 and 5% of the global ocean surface (361.9×10^6 km^2) at their respective maximum extents (Meier, 2017; Stammerjohn and Maksym, 2017). Sea ice is a very diverse and potentially very productive habitat, with primary production estimated to amount to 2–24% of total production in sea-ice covered marine areas (Arrigo, 2017). Sea ice is especially productive in spring and summer when, locally, carbon biomass can be ten times higher in the bottom ice than in the seawater, with values greater than 3 mg chlorophyll a L^{-1} (Chl a L^{-1}) in bottom layers (e.g., Corneau et al., 2013). On some occasions, ice algae may contribute up to 50–60% of total primary production (Gosselin et al., 1997; McMinn et al., 2010; Fernandez-Mendez et al., 2015). Sympagic (ice-associated) microalgae (see Horner et al., 1992, for terminology) are

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relevant for global biogeochemical cycles (Vancoppenolle et al., 2013a), especially through their uptake of carbon dioxide (CO_2) and role as food source for specialized sympagic and pelagic zooplankton (Søreide et al., 2010; Bluhm et al., 2017; Thomas, 2017). Their contribution to a food chain that supports seabirds (Ramirez et al., 2017) and seals and whales (see Thomas, 2017, and references therein) is especially important due to ice-algal growth prior to any significant phytoplankton blooms. Algal carbon that is not consumed in the ice, water column, or by the benthos, is remineralized or permanently buried at the seafloor. Large export fluxes of carbon biomass from the sea ice into the deep ocean, up to 6.5 g Cm^{-2} $year^{-1}$, have been recorded in the Arctic (Boetius et al., 2013). Ice algae released from the sea ice may also form the seeding population for sub-ice algal and ice-edge blooms (Arrigo, 2014).

The contribution of sympagic communities to polar marine biogeochemical cycles is still poorly described, despite its general importance (Vancoppenolle and Tedesco, 2017). This shortcoming is partly due to the fact that when studied in detail the production and composition of microalgae in sea ice range widely and are thus hard to quantify. Algal cell concentrations in sea ice vary by up to six orders of magnitude and algal production rates show similar variation (Arrigo, 2017). Biomass accumulation and production depend on the vertical position of sea-ice algae in the ice cover, and are controlled by various environmental parameters like light, nutrients, temperature and salinity that change with the season (e.g., Cota et al., 1991). Here we summarize available data on sea-ice microalgal biodiversity and production to derive parameters that may serve to improve the functional diversity aspect of sea-ice biogeochemical models. Although this approach may sometimes result in only rough averages, model improvement requires further parameterization. First the various habitats for microalgae in the sea ice are described briefly and modeling aspects discussed, after which a synthesis of over 55 studies on algal community structure and primary production is presented and the strength of the derived parameters is evaluated.

1.1. Sea ice as a habitat for microalgae

Sea ice is a complex habitat that is highly heterogeneous over space and time. The structure of sea ice has been described extensively in a number of reviews (Horner et al., 1992; Ackley and Sullivan, 1994; Arrigo, 2014; Petrich and Eicken, 2017). Several distinct layers in terms of both biochemical and physical properties can be defined. Each layer forms a specific habitat for a variety of microalgal communities with different physiological characteristics and production capacities.

At the ice surface, two different types of communities may evolve. So-called *infiltration layers* or *gap layers* can develop following the flooding of surface sea ice with seawater (Haas et al., 2001; Kattner et al., 2004). Flooding occurs when the ice is suppressed below sea level due to snow accumulation. Alternatively, ice floes may be pushed downwards by the pressure of overriding ice floes. The infiltration layer provides a good habitat for microalgae, as the inflowing seawater provides fresh nutrients, and light conditions near the surface are generally not limiting. Production in these layers may be high, and reach more than 2 g C m^{-2} day^{-1} (Lizotte and Sullivan, 1991). Whereas infiltration layers are quite common in the Antarctic, *melt ponds* are more characteristic for the Arctic. Their role in biogeochemical cycles is not well defined. Melt ponds are estimated to contribute less than 5% of the total annual production in the Arctic (Lee et al., 2012). Yet, occasionally they can host large aggregates of diatoms that may form an important carbon source for pelagic and benthic systems (Fernandez-Mendez et al., 2014).

Within the sea ice, dense *interior communities* may develop, with Chl *a* concentrations higher than 300 mg m^{-2} (Archer et al., 1996). Interior ice is structurally different between landfast and pack ice. Landfast ice is formed predominantly from columnar growth that creates a denser structure as it grows under more quiet conditions (Ackley and Sullivan, 1994). Pack ice has a more heterogeneous structure, due to the deformation of sea ice by mechanical stress of wave action. Algal biomass in the interior of Antarctic pack ice may contribute ca. 25% of the depth-integrated ice-algal standing stock within the ice column (Meiners et al., 2012). Turbulent conditions during ice formation result in *frazil ice*. The loose structure and high brine volume of frazil ice forms a suitable, well-protected habitat for sympagic communities. More biomass accumulates within frazil ice compared to columnar ice (Horner et al., 1992; Ackley and Sullivan, 1994).

Ice-algal production in the interior layers is controlled by a number of stressors that include extreme conditions of light, nutrients, temperature, salinity, and pH (Arrigo, 2014, and references therein). During the freezing process, brine pockets are formed that make a sometimes hostile habitat for sympagic algae. With the extraction of fresh water from the seawater during the freezing process, salinities in the brine pockets in upper ice may increase to more than 200 and temperatures can drop below –20°C (Thomas and Dieckmann, 2002; Petrich and Eicken, 2017). If microalgae can sustain these conditions and biological activity continues, the pH will slowly increase and can reach extreme values higher than 10 (Thomas and Dieckmann, 2002). Some algal species can survive these conditions but production in the sea-ice interior is generally low and concentrated at the seawater interface (Kottmeier and Sullivan, 1987; Lizotte, 2001).

Dense *bottom communities* may develop in the bottom layers of sea ice. Values higher than 50 g C m^{-2} have been recorded (Hsiao, 1980; Arrigo and Sullivan, 1992; Arrigo, 2017). Some of the most favorable habitats are found beneath landfast ice in Antarctica, where advection of ocean currents underneath ice sheets depresses the freezing point, resulting in the production of supercooled water and the formation of *platelet ice* (Smetacek et al., 1992; Arrigo, 2014). The sheltered, yet permeable conditions allow free exchange of nutrients. Platelet ice may support communities of more than 6 g Chl *a* m^{-2}, which is an order of magnitude higher than concentrations in columnar ice (Arrigo et al., 1995).

Biological production in the bottom communities can be high. The bottom layer is strongly influenced by seawater conditions, and temperature and salinity are moderate. Bottom communities are well adapted to the ambient light climate. Early in the season, irradiance levels below sea ice are low, due to the low angle of incoming solar radiation and as snow cover may attenuate irradiance (Palmisano et al., 1987). Microalgae can acclimate to low irradiance levels by expansion of the light-harvesting complexes and adjustment of the pigment composition (Van Leeuwe et al., 2005; Van Leeuwe and Stefels, 2007; Alou-Font et al., 2013). Changes in the structure of the photosynthetic units may be accompanied by a decrease in their numbers (Barlow et al., 1988; Thomas et al., 1992). In addition, sympagic algae not only acclimate well to changes in light quantity, but also show chromatic acclimation to changes in the light spectrum with strong attenuation in the red, as light penetrates through the ice (Robinson et al., 1995).

The structure of sea ice is dynamic and shows strong vertical gradients in its physical and chemical properties. It is shaped by processes of ice melt and ice formation that altogether govern the biological processes in sea ice. In addition, nutrient supply (e.g., Gradinger, 2009; Fripiat et al., 2017) and snow cover (e.g., Gosselin et al., 1986; Mundy et al., 2007) exert external control on microalgal growth. The algal communities that inhabit sea ice are subsequently subject to seasonal changes in composition, as will be discussed in this paper, as well as biomass accumulation, as has been reviewed in Meiners et al. (2012) for Antarctic sea ice and in Leu et al. (2015) for the Arctic.

1.2. Organizing data for modeling purposes

Sea-ice biogeochemical models are composed of i) state variables, measurable quantities that vary in time and space, such as bulk microalgal biomass, and ii) biophysical parameters, constant values such as algal maximum growth rate and the light utilization coefficient (Vancoppenolle and Tedesco, 2017). However, biophysical parameters can vary in space and time and between different species or taxonomic groups (e.g., Cota and Sullivan, 1990; Campbell et al., 2016). This variability limits the development and general applicability of current sea-ice biogeochemical models across different systems. Simple biogeochemical models require lower levels of detail and thus fewer parameters than more complex biogeochemical models. Most of the existing sea-ice biogeochemical models feature only one group of algae resembling mostly diatoms (see Vancoppenolle and Tedesco, 2017, for a complete review of models). However, the sea-ice ecosystem is diverse and may not be represented realistically by a single group of algae. There have been few attempts to introduce biological diversity into sea-ice biogeochemical models, all by Tedesco et al. (2010, 2012, 2010). Their models include only two functional groups, distinguished by specific growth characteristics. The complexity of sea-ice models is further constrained by parameterization of biogeochemical processes. The major processes that can be defined in sea-ice algae models are nutrient uptake, primary production, respiration, lysis, exudation and predation (Tedesco and Vichi, 2014). Each process can be parameterized with a different level of complexity, from a simple linear equation to a complex set of equations that require numerical methods to solve.

There is an urgent need to improve biogeochemical sea-ice models, as our ability to predict ecological responses upon climate change is still limited: a comparison of models predicting change in Arctic primary production during the 21st century did not even agree on the sign of change (Vancoppenolle et al., 2013b). We need to find a proper balance between the level of detail required and the level of simplicity that is eventually adopted in these models. Finding this balance requires constraining the specific scientific question we want to answer with the computational resources that are available. If we want to consider the bulk properties of sea-ice Chl *a* on a scale that includes both poles, such as with a global biogeochemical model, the use of one generic group of sea-ice algae representing mostly fast-growing and high nutrient-demanding diatoms, might be a valid or useful approximation. If instead, we want to look at the regional carbon fluxes from sea ice, their fate and the sea ice–pelagic–benthic coupling, then more diversity in the composition of the biological community is desirable.

One major shortcoming to the possibility of increasing diversity in models is the limited data available for model calibration and validation. To fill this gap, in this paper we review and combine data on biodiversity and photosynthetic activity of sea-ice microalgae into a systematic framework. This paper does not contain an exhaustive list of the more than 1000 species of single-celled eukaryotes that have been reported in sea ice (Poulin et al., 2011); for a more detailed description of the composition of sea-ice algal communities, we refer the reader to the available extensive reviews (e.g., Garrison, 1991; Poulin et al., 2011). Likewise, reviews containing long lists of studies have been published on primary production and photosynthesis-irradiance relationships in polar regions (Cota and Smith, 1991; Legendre et al., 1992; Lizotte, 2001; Arrigo et al., 2010, 2014). In this paper, variables and parameters are summarized to expand the potential for increased model complexity. The aim is to update the available studies, to provide a more comprehensive overview of the composition and photosynthetic capacity of microalgae in sea ice, and to derive generic parameters that may facilitate the inclusion of further complexity in sea-ice biogeochemical models (Tedesco and Vichi, 2014; Steiner et al., 2016).

2. Data collection and analysis

In this work, we reviewed and combined published and unpublished data collected over 40 years in both the Arctic and Antarctic sea-ice regions (**Table 1**). Data from the sub-Arctic (e.g., Sea of Okhotsk and Baltic Sea) have not been included, as they comprise their own unique system.

2.1. Microalgal community structure

The dataset on algal species composition consists of data that were collected from 32 regions in 280 ice cores, divided into 626 sea-ice sections (**Figure 1**; **Table 1**).

Table 1: Information on sea-ice data compiled for this review, with sampling location, date, ice type, and literature references. DOI: https://doi.org/10.1525/elementa.267.t1

Type of data	Location	Month	Year	Ice type[b]	Reference
Community composition	East Antarctica	11	1993	L	Archer et al., 1996
	McMurdo Sound	10	1989	L	Arrigo et al., 1995
	Svalbard	5	2011	P	Assmy, unpubl
	McMurdo Sound	11	2011	L	Carnat et al., 2014
	Arctic Archipelago	5	2014	L	Campbell et al., 2017
	Canadian Arctic	3	2008	P	Comeau et al., 2013
	East Antarctica	10	2003	P	Dumont et al., 2009
	Terre Adelie, Antarctica	5	1998	L	Fiala et al., 2006
	Weddell Sea	11	1983	P	Garrison and Buck, 1989
	Weddell Sea	2	1992	P	Gleitz and Thomas, 1993
	Arctic Ocean	7	1994	P	Gosselin et al., 1997
	Greenland Sea	5	1994	P	Gradinger et al., 1999
	Canadian Archipelago	5	1972	L	Hsiao, 1980
	Canadian Arctic	4	1998	L	Michel et al., 2002
	Kobbefjord, Greenland Sea	11	2005	L	Mikkelsen et al., 2008
	Canadian Arctic	6	2008	L	Mundy et al., 2011
	Beaufort Sea	1	2008	L	Niemi et al., 2011
	Arctic Ocean	7	2001	P	Ratkova and Wassmann, 2005
	McMurdo Sound	1	2003	L	Remy et al., 2008
	Terre Adelie, Antarctica	5	1995	L	Riaux-Gobin et al., 2003
	Beaufort Sea	2	2004	L	Rozanska et al., 2009
	Ross Sea	11	2003	P	Ryan et al., 2006
	West Antarctic Peninsula	11	2014	P	Selz and Arrigo, unpubl
	Arctic Ocean	6	2010	P	Selz and Arrigo, unpubl
	Resolute Passage	4	1992	L	Sime-Ngando et al., 1997
	McMurdo Sound	11	1995	L	Stoecker et al., 1998
	Arctic Ocean	7	2003	P	Tamelander et al., 2009
	East Antarctica	11	1996	L	Thomson et al., 2006
	Marguerite Bay	12	2014	L	Van Leeuwe, unpubl
	Weddell Sea	11	2004	P	Tison et al., 2010
	Arctic Ocean	12	2003	P	Werner et al., 2007
Photosynthetic parameters[a]	McMurdo Sound	11	1988	L	Arrigo and Sullivan, 1992
	Hudson Bay	4	1985	L	Barlow et al., 1988
	Canadian Arctic	5	1986	L	Bergmann et al., 1991
	Northwest Passage	4	1985	L	Cota and Horne, 1989
	McMurdo Sound	11	1985	L	Cota and Sullivan, 1990
	Arctic Ocean	8	2012	P	Fernandez-Mendez et al., 2015
	Weddell Sea	10	1988	P	Gleitz and Kirst, 1991[c]
	Hudson Bay	5	1983	L	Gosselin et al., 1986
	Barents Sea	5	1988	P	Johnsen and Hegseth, 1991
	Terra Nova Bay	11	1999	P	Lazzaro et al., 2007
	Weddell Sea & Peninsula	3	1987	L	Lizotte and Sullivan, 1991
	Terra Nova Bay	11	1997	P	Mangoni et al., 2009
	Greenland Sea	5	1997	P	Mock and Gradinger, 1999[d]
	McMurdo Sound	12	1983	L	Palmisano et al., 1985
	McMurdo Sound	11	1987	L	Palmisano et al., 1987
	McMurdo Sound	11	1988	L	Robinson et al., 1995
	McMurdo Sound	8	1989	L	Robinson et al., 1998
	West Antarctic Peninsula	11	2014	P	Selz and Arrigo, unpubl
	Arctic Ocean	6	2010	P	Selz and Arrigo, unpubl
	Resolute Bay	5	1988	L	Smith and Herman, 1991
	Resolute Bay	5	1985	L	Smith et al., 1988
	McMurdo Sound	11	1995	L	Stoecker et al., 2000
	Resolute Passage	4	1992	L	Suzuki et al., 1997
	East Antarctica	9	2015	P	Ugalde et al., 2016

[a] All photosynthetic parameter values are based on the photosynthesis-irradiance relationship established by Platt et al. (1980), except in two cases; the alternative relationship applied in those cases did not significantly affect the derived values.

[b] Landfast ice (L) or pack ice (P).

[c] Calculated according to Tilzer et al. (1986).

[d] Calculated according to Strickland and Parsons (1972).

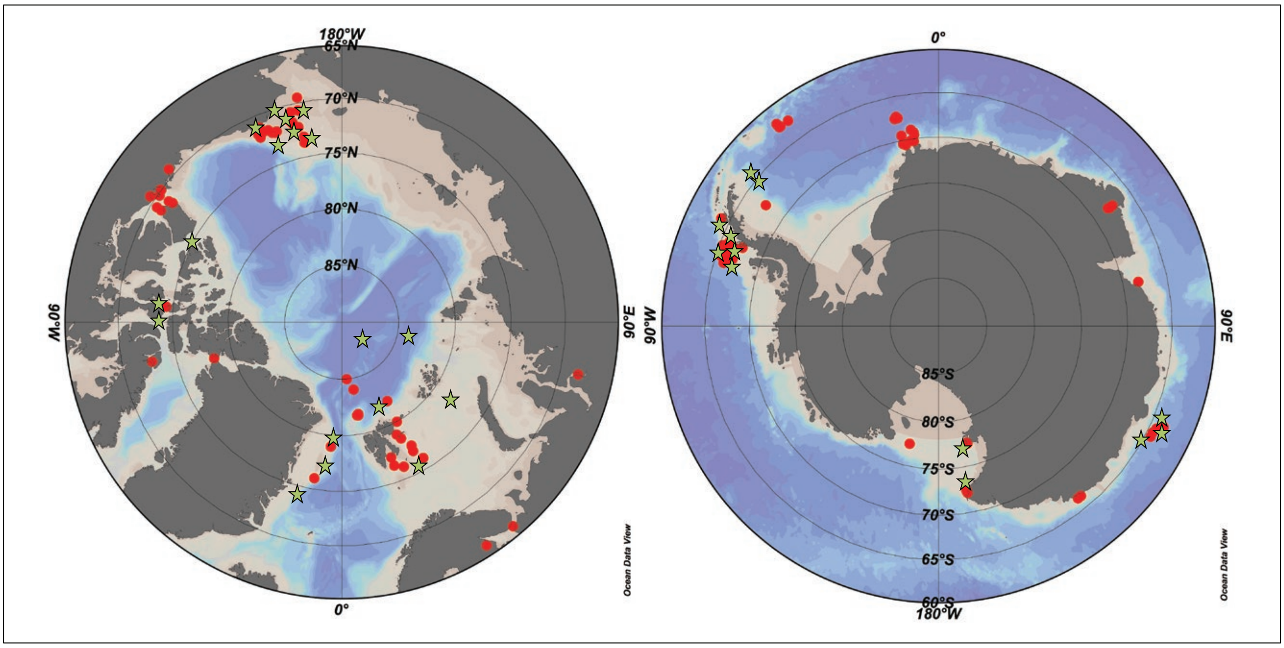

Figure 1: Maps showing the sampling locations of ice cores included in this study. Samples on microalgal species composition are denoted as red circles, and photosynthetic parameters are denoted as green stars. DOI: https://doi.org/10.1525/elementa.267.f1

We included only data that were based on a quantitative assessment of microalgae through microscopy, flow cytometry, FlowCam or Imaging Flow Cytobot.

A limited number of functional algal groups was defined according to their perceived importance related to an explicit role in biogeochemical cycles. The number of groups was constrained by their quantitative role in biogeochemical cycles and by the limited availability of data. The four following functional groups of algae were distinguished:

i. pennate diatoms: often dominating algal biomass and therefore playing a major role in carbon fluxes;
ii. centric diatoms: typically less abundant, but often rich in carbon and relevant for carbon fluxes;
iii. autotrophic flagellates, including autotrophic dinoflagellates: occasionally highly abundant (e.g., in surface blooms) and important for their specific role in biogeochemical cycles (e.g., as producers of dimethylsulphide); and
iv. heterotrophic protists: specifically functioning as demineralizers that are important during periods of low light levels. This group includes heterotrophic (dino-) flagellates and ciliates. This group was not always defined in the literature, and therefore may be underestimated in this study.

In the analyses presented here, we have included only quantitative data based on cell counts, and thus some algal species may be underestimated. The progress made in molecular techniques has introduced new information on species abundance in sea ice (e.g., Bachy et al., 2011; Piwosz et al., 2013; Torstensson et al., 2015; Hardge et al., 2017). These new approaches are a major strength in studying smaller eukaryotic groups. As studies using these approaches are limited in number and generate a different type of data, we have not incorporated them into our analyses.

We did not discriminate between collection and processing techniques (e.g., method of fixation, type of microscope, cell retrieval; for discussion of melting techniques, see Rintala et al., 2014, and Miller et al., 2015). The data retrieved from the literature are expressed as cell numbers, or units of carbon or Chl *a*. In the Arctic, 95% of the data for landfast ice and 69% for pack ice are based on cell counts. In the Antarctic, these percentages are 72% for landfast ice and 30% for pack ice. The functional groups in this study are presented as percentages of the provided unit. Normalization to carbon biomass was not possible, as the majority of studies on community composition do not report carbon content and cell size. We note that presenting the functional groups as percentages makes generalizations, and that the various groups likely contribute differently to the total carbon inventory of sea ice.

Sub-ice colonial centric diatoms like *Melosira arctica* and *Berkeleya adeliensis* form strands and comprise a specific group of sea-ice algae. *M. arctica* is omnipresent in the Arctic Ocean (e.g, Poulin et al., 2014), while *B. adelienesis* is mainly associated with landfast ice in Antarctica (Riaux-Gobin et al., 2003; Belt et al., 2016). Both species may be of local importance in late spring when long strands of > 8m can be formed. *Melosira* strands can contribute over 85% of carbon export to the sea floor (Boetius et al., 2013). Because of the heterogeneous distribution and the limited amount of data available, strand-forming sea-ice diatoms were not included in our study.

2.2. Photosynthetic parameters

The photosynthetic parameter dataset consists of data collected from 23 regions in 90 ice cores, divided into 137 sea-ice sections (**Figure 1**; **Table 1**). Parameters were derived from photosynthesis-irradiance relationships as defined by Platt et al. (1980):

i. the maximum photosynthetic capacity, P_{max} (μg C μg Chl a^{-1} h^{-1});
ii. the slope of photosynthesis versus light, α (μg C μg Chl a^{-1} h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$); and
iii. the index for photoadaptation, I_k (μmol photons^{-1} m^{-2} s^{-1}),

where α is conventionally used as an indication for light affinity and I_k as an index for light saturation. Data were taken only from studies that established photosynthesis-irradiance relationships by means of ^{14}C-incorporation in an effort to minimize variability associated with methodology. We did not discriminate among experimental conditions (e.g., extraction of samples from the ice, time of incubation). By combining all data, a certain measure of variability was introduced to the dataset. The choice of incubation technique (e.g., *in situ* versus *in vivo*) can have a strong effect on photosynthetic performance. Due to alterations in light and nutrient availability and variations in temperature, differences in photosynthetic parameters up to an order of magnitude may occur (Smith and Herman, 1991). Adequate tracer diffusion is another requirement for accurate analyses (Mock and Gradinger, 1999) and was not guaranteed in all studies. Furthermore, differences in the timing of incubations can potentially affect the results, as many microalgae have a diurnal rhythm. Diurnal cycles may affect microalgal photophysiology; however, various studies have shown that the diurnal signal in polar regions is of secondary importance relative to other driving parameters, given the reduced daily dynamics in polar algae that experience extended periods of daylight during spring and summer (e.g., Palmisano et al., 1987; Johnsen and Hegseth, 1991).

2.3. Data analysis

Three layers were distinguished for their different physical and biochemical properties:

i. the infiltration/gap layer at the surface;
ii. the interior layer; and
iii. the bottom layer, varying in thickness from 0.01 to 0.10 m, depending on the method of sample collection.

These layers are partly isolated from each other, but also influence each other over the seasons. Each layer is affected in different ways by the various environmental parameters that shape sea-ice communities (Tedesco et al., 2012; Duarte et al., 2015). Consequently, each layer has its own characteristics, with a specific algal composition and specific photosynthetic capacities (Grossi and Sullivan, 1985; Manes and Gradinger, 2009).

Melt ponds form a separate habitat at the sea-ice surface. As very few quantitative data are available to allow for accurate parameterization, this habitat has not been distinguished from infiltration communities in our analyses. Given the potential importance of melt ponds, however, we have discussed the role of melt ponds specifically in the discussion. Pressure ridges, which may have the potential for large biomass accumulations (Horner et al., 1992), were also not incorporated. As these features are quite unique in their character, we chose not to merge the limited available data with the other communities.

Land fast ice was distinguished from pack ice because of differences in structure and hence habitat (as briefly discussed in Section 1.1). For similar reasons, the Arctic was separated from the Antarctic. A distinction can also be made between first year ice (FYI) and multi-year ice (MYI). MYI can reach a thickness of several meters, and tends to be more ridged. Several layers of microalgae may be incorporated (e.g., Lange et al., 2015; Werner et al, 2007). We did not distinguish FYI from multiyear ice MYI, however, because the limited dataset did not allow for proper statistical analyses.

Data were categorized per ice layer for statistical testing. To establish significant effects of hemisphere, ice type and season (analyzed as month-of-year for each hemisphere separately) on the microalgal community structure and photosynthetic parameters, and to establish interactions, data were analyzed by linear modeling in R (RStudio, 0.99.902). Within the datasets (**Figures 2–6**), significant differences were established by one-way ANOVA on ranks (Kruskal-Wallis), followed by Dunn's Multiple Comparison test, assuming non-Gaussian distribution. Seasonality effects on community structure and photosynthesis were tested by Spearman rank correlation. A significance level of $p < 0.05$ was applied. Data are presented as mean ± standard error (SE), which best indicates the accuracy of a parameter as an estimate of the population mean.

3. Results and Discussion

Although sea ice is a very complex biome with many different micro-habitats subject to extreme variations over the seasons, the general patterns of algal distribution were found to be remarkably consistent, with clear patterns for the different layers (Section 3.1.). The succession of functional groups over time had a strong impact on community composition, especially as recorded in the bottom layer, and is discussed separately (Section 3.1.2.). Patterns for photosynthetic parameters were more difficult to structure than community composition (Section 3.2.), most likely because these parameters are subject to short-term environmental perturbations and therefore exhibit more variance (Section 3.2.1.). Overall, the data analysis presented in this paper confirm general concepts of distribution of functional groups and photosynthetic activity that previously had not been quantified.

3.1. General patterns in microalgal community structure

Different sympagic communities were observed to characterize each sea-ice layer. The most significant effects on the distribution of algal groups over the ice column were by the ice type (landfast or pack ice) and hemisphere (**Table 2**). Diatoms were the most susceptible to interactions of the various factors (**Table 2**).

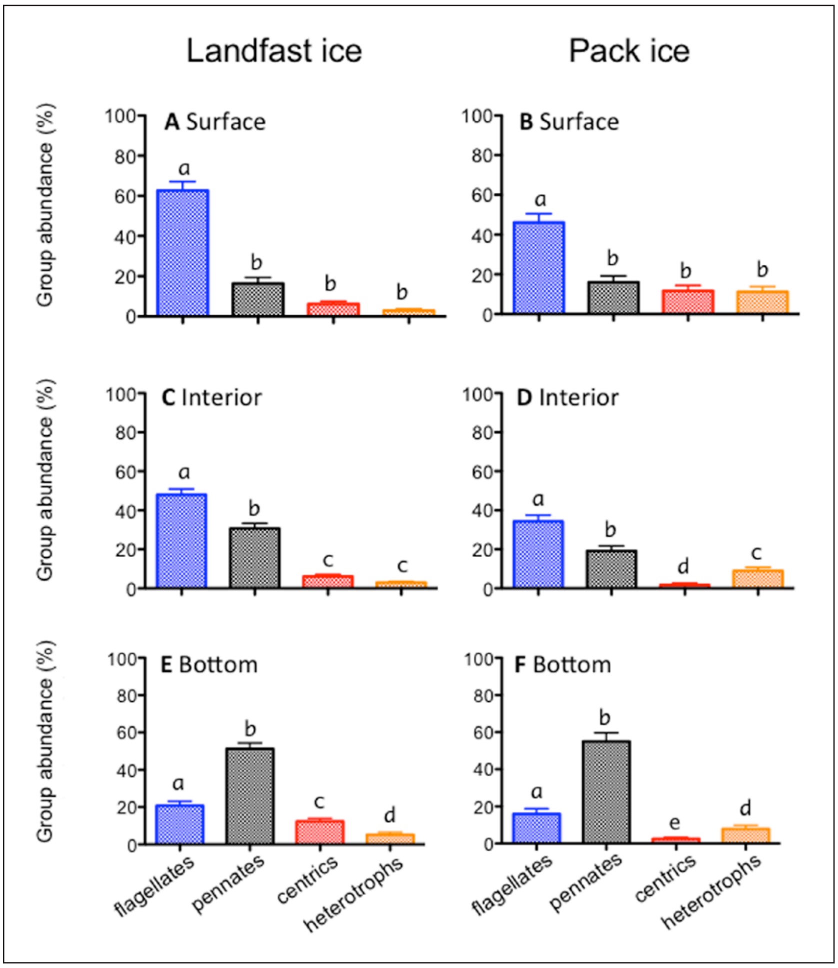

Figure 2: Vertical distribution of algal groups in sea ice. Distribution of each algal group is presented for landfast **(A, C, E)** and pack ice **(B, D, F)** as a percentage of abundance over three layers of the ice column: surface layer (A, B), interior layer (C, D), and bottom layer (E, F). Average values for combined Arctic and Antarctic data are plotted; error bars indicate standard error. Significance was tested within each layer by Kruskal-Wallis test. Different letters (a–f) indicate significant differences; same letters indicate no significant difference (t-test, $p < 0.05$). Pennates and centrics refer to diatoms. DOI: https://doi.org/10.1525/elementa.267.f2

Table 2: The significance levels derived by linear modeling for impact of hemisphere (Arctic/Antarctic), ice type (landfast/pack) and season (month-of-year) on the relative abundance of functional algal groups determined in three layers of the ice column. DOI: https://doi.org/10.1525/elementa.267.t2

Algal group	Ice layer	Hemisphere (H)	Ice type (T)	H*T	Month (M)		M*T	
		Combined	Combined	Combined	Arctic	Antarctic	Arctic	Antarctic
Flagellates	Surface	n.s.[a]	$p < 0.005$	$p < 0.05$	n.s.	$p < 0.0005$	n.s.	$p < 0.0005$
	Interior	$p < 0.0005$	n.s.	n.s.	n.s.	n.s.	$p < 0.0005$	n.s.
	Bottom	$p < 0.05$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Pennate diatoms	Surface	n.s.	n.s.	$p < 0.0005$	n.s.	$p < 0.0005$	$p < 0.05$	$p < 0.0005$
	Interior	$p < 0.0005$	$p < 0.0005$	$p < 0.05$	$p < 0.005$	$p < 0.005$	$p < 0.0005$	$p < 0.0005$
	Bottom	$p < 0.05$	n.s.	n.s.	n.s.	n.s.	n.s.	$p < 0.0005$
Centric diatoms	Surface	n.s.	$p < 0.05$	$p < 0.0005$	n.s.	$p < 0.0005$	$p < 0.05$	$p < 0.0005$
	Interior	$p < 0.0005$	$p < 0.0005$	$p < 0.05$	n.s.	n.s.	$p < 0.0005$	n.s.
	Bottom	$p < 0.005$	$p < 0.0005$	n.s.	n.s.	n.s.	$p < 0.0005$	n.s.
Heterotrophs	Surface	n.s.	$p < 0.005$	n.s.	n.s.	n.s.	n.s.	n.s.
	Interior	n.s.	$p < 0.005$	n.s.	n.s.	$p < 0.05$	$p < 0.0005$	$p < 0.05$
	Bottom	$p < 0.05$	n.s.	n.s.	n.s.	n.s.	$p < 0.05$	n.s.

[a] Not significant ($p > 0.05$).

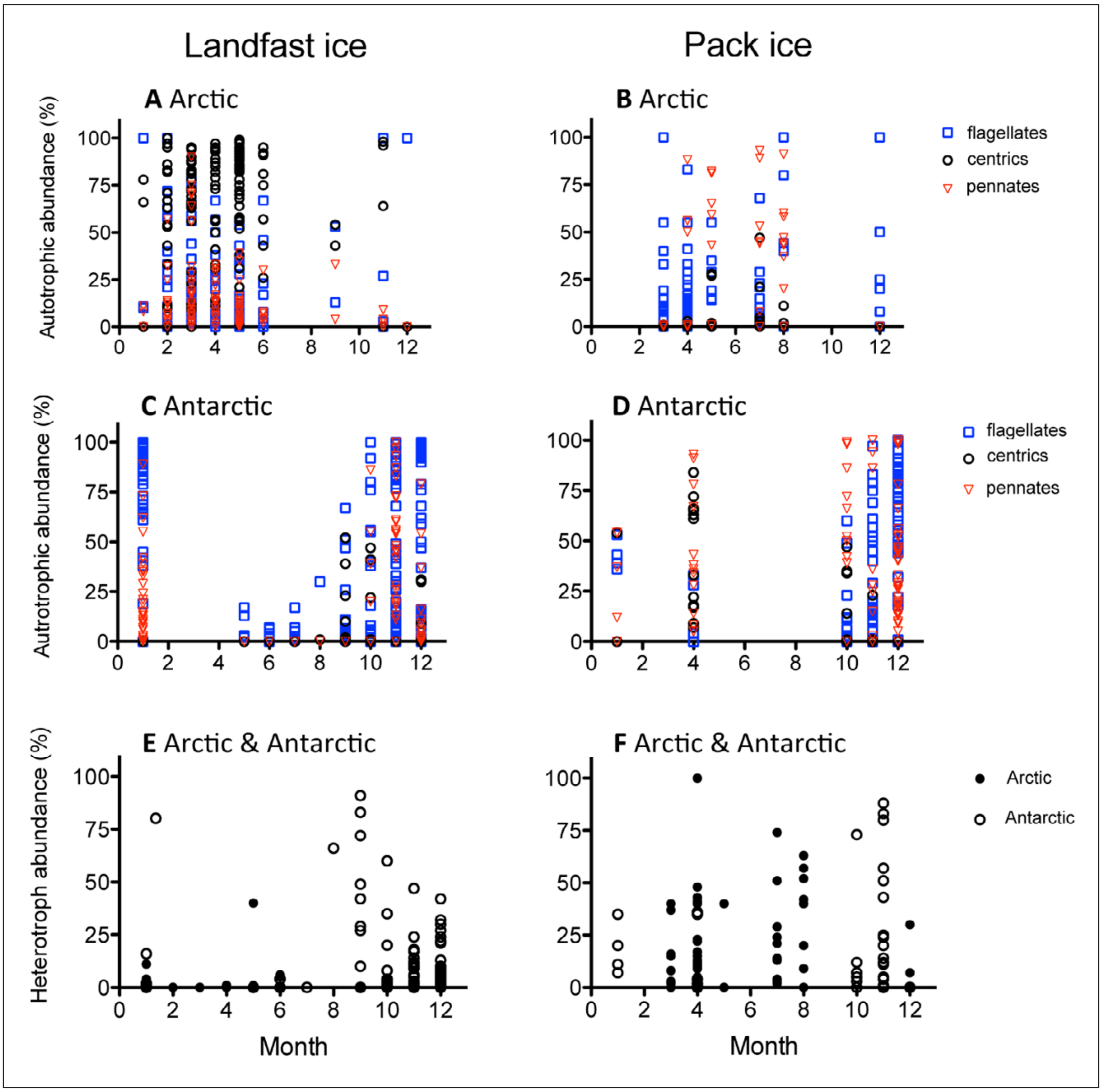

Figure 3: Seasonal distribution of algal groups in sea ice. Monthly distribution of autotrophic algal groups (flagellates, and pennate and centric diatoms) is shown for all layers combined in landfast **(A, C, E)** and pack ice **(B, D, F)**, separately for the Arctic (A, B) and Antarctic (C, D). Monthly distribution for heterotrophic protists is shown for landfast (E) and pack ice (F), with Arctic and Antarctic data on the same panel. Note that in several communities (e.g., in Antarctic landfast), diatoms were not distinguished in different groups in the winter months (May–July); this mixed group of diatoms was not plotted, but they make up the majority to 100%. DOI: https://doi.org/10.1525/elementa.267.f3

The surface layer is dominated by flagellate species in both the landfast (about 60% of the whole community) and pack ice (about 45% of the whole community) datasets (**Figure 2a, b**). Light conditions can be extreme at the ice surface, and especially in spring UV-levels can be quite high (UVA > 5 Wm^{-2} and UVB > 0.35 Wm^{-2}; Mundy et al., 2011). The surface dataset contains data collected largely from infiltration layers; only three of the included sites were referred to as having true surface melt ponds. These infiltration layers, which thus determine the signature of the surface layer, contain communities that are generally mixed (e.g., Garrison and Buck, 1989; Horner et al., 1992), though sometimes dominated by a single species, like the flagellate *Phaeocystis antarctica* (Garrison et al., 2005; Dumont et al., 2009). The interaction between hemisphere and ice type had a significant effect on the surface community structure (**Table 2**), which we attribute to snow-loading on pack ice in Antarctica, mostly characterized by infiltration communities, versus melt pond communities more frequently observed in the Arctic.

The limited dedicated (Arctic) studies on melt ponds show that the species distribution in ponds is more homogeneous than in infiltration layers, especially early in the melt-pond season, with observations of the freshwater

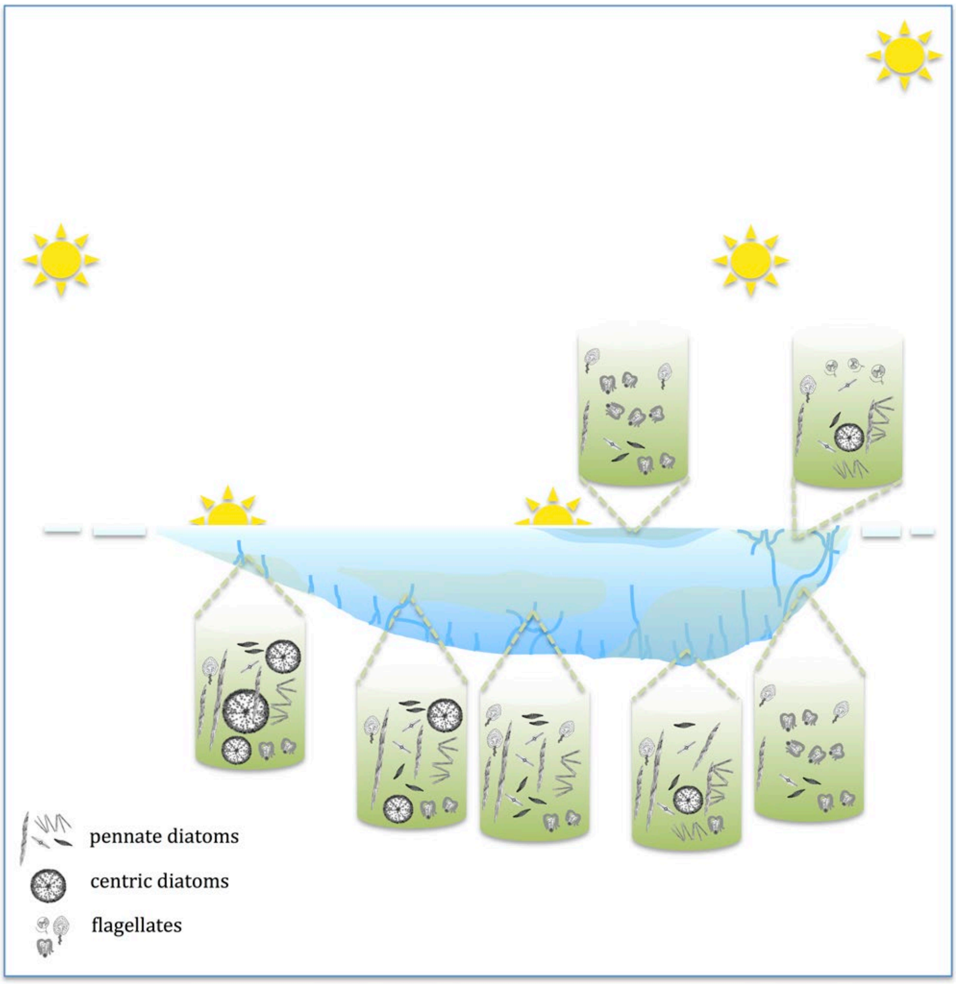

Figure 4: Schematic representation of the evolution of sympagic algal communities during sea-ice development. In autumn, a mixture of algal species is incorporated into sea ice during ice formation. Over winter, selection occurs during which the larger (centric) diatoms disappear. The spring community consists of a mixed community in bottom and infiltration layers. Towards summer, conglomerates of pennate diatoms are lost from the bottom ice, leaving mainly flagellate species. Isolated surface melt pond communities mainly consist of flagellates. Connection with the ice interior or bottom during melt can result in more mixed communities. DOI: https://doi.org/10.1525/elementa.267.f4

alga, *Chlamydomonas nivalis* (Melnikov et al., 2002; Lee et al., 2011), and of *Pyramimonas* sp. (e.g., Mundy et al., 2011). The absence of regular intrusions of fresh seawater supply might well promote the dominance of a single species (Stoecker et al., 1992). The relatively strong contribution of flagellates in the ponds is noteworthy, as it contrasts with the pelagic system, where the paradigm is that diatoms can better tolerate high levels of irradiance than flagellates (Richardson et al., 1983). Melt ponds change in character later in the season, when brine channels gradually open up during melt (Mundy et al., 2011). Mixed communities may develop then, benefitting from a renewed nutrient supply from below. Strong melt may open the connection between surface melt ponds and seawater below the ice, creating open saline ponds. Communities in these ponds are similar to those in seawater (Lee et al., 2012).

The interior layer consists of more mixed communities, with a slight prevalence of flagellates and pennate diatoms in both landfast and pack ice (**Figure 2c, d**), with various taxa including *Nitzschia sp., Navicula sp., Pyramimonas* sp. and *Gymnodinium sp.* (e.g., Mikkelsen et al., 2008). These communities can originate from algae trapped in the sea ice during ice formation that continue growing. The interior layer shows the most significant difference between the Arctic and Antarctic and between ice type (**Table 2**). In the ice interior, the distribution of pennate diatoms is quite different for pack ice versus landfast ice (**Table 3**). In the Arctic, pennate diatoms dominate with a 63% relative abundance in interior communities in landfast ice; in pack ice they make up only 7% (**Table 3**). This pattern is reversed for Antarctic interior layers, with 10% pennate diatoms in landfast ice versus 36% in pack ice (**Table 3**). The interaction of ice type and time of year had a strong impact on the community structure in the ice interior (Month * Ice type; **Table 2**; Section 3.1.2.), which may partly explain this hemispheric difference.

Pennate diatoms are observed to dominate the bottom layers (**Figure 2e, f**). The most ubiquitous species are *Fragilariopsis cylindrus* (formerly *Nitzschia cylindrus*) and *N. frigida (*Horner and Schrader, 1982; Rozanska et al., 2009; Leu et al., 2015). Pennate diatoms are fast-growing

Table 3: Distribution of algal groups in landfast and pack ice in the Arctic and Antarctic, expressed as average abundance (bold) in percentage. DOI: https://doi.org/10.1525/elementa.267.t3

Type of ice	Ice layer	Hemisphere	Flagellates	Pennate diatoms	Centric diatoms	Heterotrophs
Landfast ice	Surface	Arctic	**40** (*6, 0, 100*)[a]	**39** (*6, 0, 91*)	**15** (*2, 0, 57*)	**3** (*2, 0, 40*)
		Antarctic	**76** (*5, 0, 100*)	**3** (*1, 0, 47*)	**1** (*1, 0, 41*)	**3** (*1, 0, 47*)
		Combined	**63** (*4*)[b]	**16** (*3*)	**6** (*1*)	**3** (*1*)
	Interior	Arctic	**22** (*3, 0, 100*)	**63** (*4, 0, 100*)	**14** (*2, 0, 90*)	**1** (*1, 0, 5*)
		Antarctic	**65** (*4, 1, 100*)	**10** (*2, 0, 73*)	**1** (*1, 0, 47*)	**5** (*1, 0, 60*)
		Combined	**48** (*3*)	**31** (*3*)	**6** (*1*)	**3** (*1*)
	Bottom	Arctic	**15** (*2, 0, 100*)	**65** (*3, 0, 100*)	**18** (*2, 0, 72*)	**2** (*1, 0, 40*)
		Antarctic	**31** (*5, 0, 98*)	**28** (*5, 0, 100*)	**4** (*2, 0, 52*)	**10** (*3, 0, 91*)
		Combined	**21** (*2*)	**51** (*3*)	**12** (*1*)	**5** (*1*)
Pack ice	Surface	Arctic	**66** (*12, 0, 100*)	**1** (*1, 0, 1*)	**1** (*1, 0, 1*)	**15** (*6, 0, 40*)
		Antarctic	**43** (*5, 0, 97*)	**19** (*4, 0, 98*)	**14** (*3, 0, 84*)	**11** (*3, 0, 88*)
		Combined	**46** (*4*)	**16** (*3*)	**12** (*3*)	**11** (*3*)
	Interior	Arctic	**20** (*3, 0, 100*)	**7** (*3, 0, 91*)	**1** (*1, 0, 11*)	**15** (*3, 0, 100*)
		Antarctic	**54** (*4, 0, 100*)	**36** (*4, 0, 86*)	**4** (*2, 0, 47*)	**1** (*1, 0, 20*)
		Combined	**34** (*3*)	**20** (*3*)	**2** (*1*)	**9** (*2*)
	Bottom	Arctic	**21** (*3, 0, 68*)	**32** (*6, 0, 93*)	**5** (*2, 0, 47*)	**16** (*4, 0, 74*)
		Antarctic	**16** (*7, 0, 99*)	**83** (*7, 4, 100*)	**1** (*1, 0, 14*)	**6** (*4, 0, 73*)
		Combined	**16** (*3*)	**55** (*5*)	**3** (*1*)	**8** (*2*)

[a] Parenthetic numbers indicate the standard error of the mean followed by minimum and maximum percentages.

[b] A single number given parenthetically is the standard error of the mean.

and probably the most efficient at nutrient utilization under low light levels (Hegseth, 1992; Gradinger et al., 1999; Lizotte, 2001). The Arctic and Antarctic bottom communities again are quite different in landfast ice, with significant differences in the relative abundance of flagellates in the Antarctic (31%) compared to the Arctic (15%) (**Table 3**).

Heterotrophic protists (or protozoa) do not appear as a dominant group in our datasets (**Figure 2**; **Table 3**). The relative abundance of heterotrophic protists is greatest in early spring (**Figure 3e**), when light availability is still low and autotrophs are at low abundances (see also Rozanska et al., 2009). Numbers of protozoa are likely often underestimated in field studies. They may be overlooked in microscopic analyses because they are small and do not show up brightly as they often lack chlorophyll. In fact, phylogenetic analysis has revealed the dominance of a heterotrophic dinoflagellate (SL163 A10 clade) in summer interior sea ice in the Amundsen and Ross seas (Torstensson et al., 2015). Heterotrophic protists as clustered in this review represent a mixed group of species. Many of the protozoa (flagellates as well as ciliates) do not necessarily have a fully heterotrophic lifestyle. Some species are autotrophic or mixotrophic (Torstensson et al., 2015; Caron et al., 2017, and references therein). Phylogenic analysis of protists in sea ice has revealed a wide variety of mixotrophic taxa at the end of the Arctic winter (Bachy et al., 2011; Paterson and Laybourn-Parry, 2017). These protists feed mainly on organic detritus or bacteria, rather than other microalgae (Michel et al., 2002). As such, they contribute to the remineralization of nutrients, specifically nitrate and phosphate (Arrigo et al., 1995). The remineralization of silicate is much slower (Cota et al., 1991). As nutrient concentrations in the semi-enclosed ice interior drop with algal consumption, remineralization activity by heterotrophic flagellates plays an important role locally (e.g., Tamelander et al., 2009). In pack ice, heterotrophic protists are more abundant in the Arctic than the Antarctic (e.g., Sime-Ngando et al., 1997; **Table 3**). This comparatively high abundance is possibly related to the more extended period of darkness at high Arctic latitudes, and may also be linked to greater concentrations of dissolved organic matter that support active microbial foodwebs (Meiners and Michel, 2017).

Defining the importance of sea ice in seeding the pelagic community is difficult, and very few dedicated studies are available. Species identified in sea ice have often been found to be the same as the ones in the water column (e.g., Horner and Schrader 1982; Mundy et al., 2011), yet the opposite has also been observed (e.g., Riaux-Gobin et al., 2003; Barber et al., 2015). Even if species in the pelagic system are similar to the sympagic community, the seeding capacity of sympagic microalgae is hard to demonstrate. A microscopic study in the Beaufort Sea by Horner and Schrader (1982) showed that many of the cells released from ice were unhealthy. A brief pulse in pelagic production was recorded, but the bloom did not last long. The fate of sympagic algae might depend on the timing and size of the pulse released (Tedesco et al., 2012; Selz et al., 2017). In two consecutive seasons in the high Arctic, an early and rapid release of sympagic algae initiated a pelagic bloom, yet in another season when the release of sympagic microalgae occurred only towards summer, no such effect was recorded (Galindo et al., 2014). This difference in fate may be related to the physiological state of the cells when they are released from the sea ice. Export of sympagic algae into deeper waters has been related to aggregation of cells and the production of extracellular

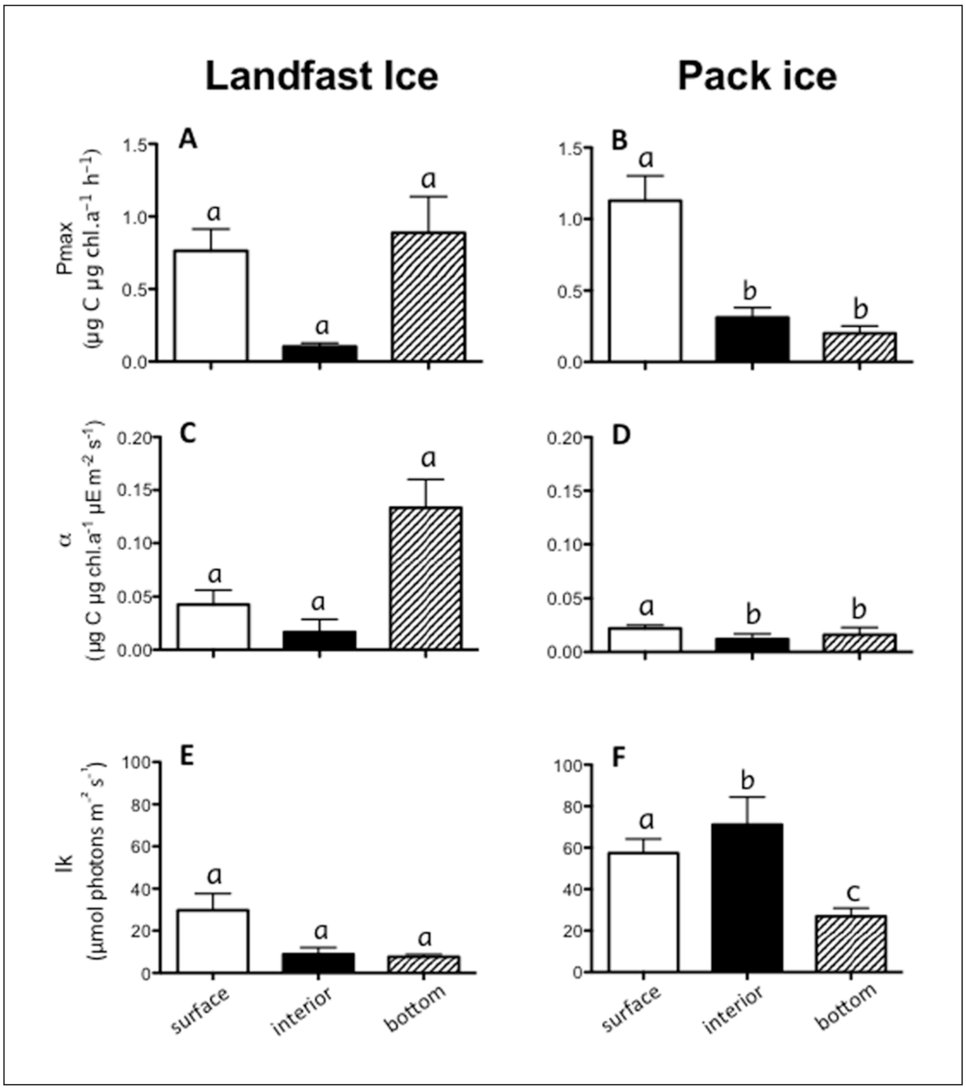

Figure 5: Vertical distribution of photosynthetic parameters in the sea ice. Distribution of each parameter is presented for landfast **(A, C, E)** and pack ice **(B, D, E)** over three layers of the ice column: surface, interior and bottom. Average values for combined Arctic and Antarctic data are plotted for maximum photosynthetic capacity, P_{max} (A, B), α (C, D), and I_k **(E, F)**; error bars indicate standard error. Significance was tested within each layer by Kruskal-Wallis test. Different letters (a–f) indicate significant differences; same letters indicate no significant difference (t-test, $p < 0.05$). DOI: https://doi.org/10.1525/elementa.267.f5

polysaccharide substances (EPS; Riebesell et al., 1991). The importance of sea-ice algae in seeding the water column requires more dedicated studies that focus on early spring.

3.1.1. (Dis)similarities in the biodiversity of microalgae in various ice types

Sympagic microalgae show a high degree of biodiversity. Pennate diatoms are the most diverse group: 446 pennate versus 122 centric species have been recorded (Arrigo, 2014). Maximum biodiversity is observed in pack-ice interior layers (Stoecker et al., 1992; von Quillfeldt et al., 2003). The relatively porous structure of pack ice is influenced by infiltration of seawater, occasionally bringing in new species (Syvertsen and Kristiansen, 1993). This layer is also the layer with the most variable and extreme conditions, which hints at an evolutionary adaptation to the various niches in sea ice. In the Canadian Arctic, only 27 diatom species were recorded in FYI versus 55 diatom species in MYI (Melnikov et al., 2002), the latter providing a potentially more stressful habitat due to lower levels of nutrients. Likewise, a phylogenetic study in the central Arctic Ocean revealed the highest biodiversity in MYI (Hardge et al., 2017). Successful survival of microalgae in the heterogeneous sea-ice habitat is apparently based on evolutionary adaptation and high plasticity (Sackett et al., 2013).

Although sympagic communities show a high biodiversity, there is also overlap between species found in landfast and pack ice. Some species, like *Polarella glacialis* (Montresor et al., 2003; Thomson et al., 2006) and *Fragilariopsis cyclindrus* (Roberts et al., 2007, and references therein; Poulin et al., 2011), are distributed in both polar regions, which supports the hypothesis that many ice-algal species living in sea ice are in fact pelagic phytoplankton species (see **Table 2** in Garrison, 1991, for an extensive species list). A similar correspondence in

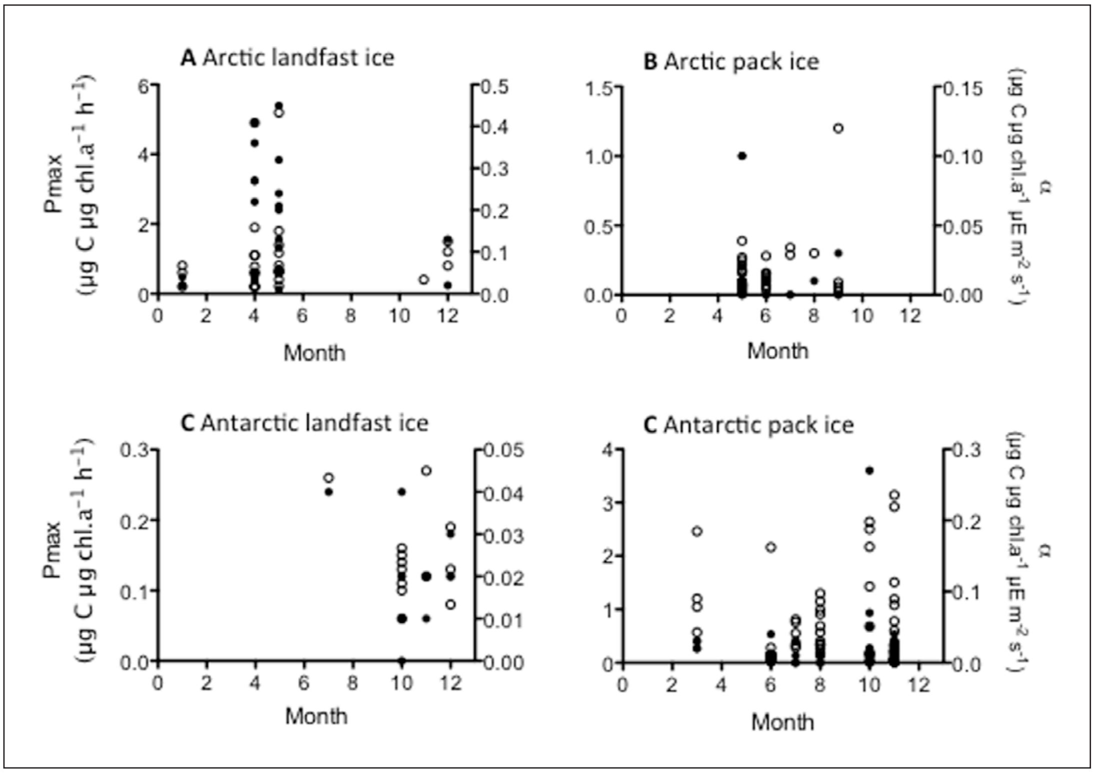

Figure 6: Seasonal distribution of photosynthetic parameters in sea ice. Data for maximum photosynthetic capacity ($P_{max,}$ open symbols), and for light affinity (indicated by α, closed symbols) were combined from all three layers of the ice column, then presented separated for Arctic **(A, B)** and Antarctic **(C, D)** landfast (A, C) and pack ice (B, D). DOI: https://doi.org/10.1525/elementa.267.f6

species composition at the genus level has been observed between pack ice in the Arctic and the Antarctic, with the genera *Fragilariopsis*, *Nitzschia* and *Navicula* illustrating the cosmopolitan characteristics of many microalgal genera (McMinn and Hegseth, 2003). Similarities were also found when comparing FYI with MYI (e.g., Melnikov et al., 2002).

Comparing landfast and pack-ice surface communities, the composition of heterotrophic protists also appears remarkably similar in two separate and remote sites in Antarctica (Archer et al., 1996). Whereas commonly observed choanoflagellates were considered less abundant, the heterotrophic nanoflagellate *Cryothecomonas sp.* appears to be a ubiquitous species in the Antarctic (see Archer et al., 1996, and references therein).

3.1.2. Seasonal variation

The data presented in **Figure 2** and **Table 3** are average values, without discrimination over time. However, significant correlations were established between microalgal functional groups and time of year, especially in Antarctica (**Table 4**; **Figure 3a–f**). The interior layer appears as the most susceptible to seasonal variation, dictated by changes in the physicochemical environment related to ice formation. The phenology of sea-ice communities has been described in only a few papers (Rozanska et al., 2009; Leu et al., 2015; Campbell et al., 2017a). In our datasets, the patterns are hard to retrieve (**Figure 3**). The data are too scattered in time and space, and seasonal patterns can be related to specific phenomena in ice formation. A schematic depiction of seasonal fluxes is presented in **Figure 4**.

Previous studies have suggested that in early spring, the sea-ice community consists mainly of pennate diatoms (e.g., Leu et al., 2015). This pattern is indeed shown for the Arctic data compiled here, with high pennate diatom abundance in May (**Figure 3a, b**). The dominance of pennate diatoms in the Antarctic is more pronounced in pack ice than in landfast ice (**Figure 3c, d**). In the Arctic (e.g., Mikkelsen et al., 2008) and Antarctic (e.g., Stoecker et al., 1998), flagellates can also be present, although seasonal patterns of flagellates are less clear (**Figure 3a–d**). High abundance of centric diatoms in spring is most obvious in Arctic landfast ice, and less so in the Antarctic and in pack ice (**Figure 3a–d**). Notably, early spring may witness a succession of diatom species; in the Arctic, centric diatoms can become more abundant than pennate diatoms with the progressive increase of light availability (Melnikov et al., 2002; Campbell et al., 2017a, and references therein). This phenomenon may be related to high resistance to UV-radiation (Karentz et al., 1991) and high nutrient affinity (Campbell et al., 2017a) in centric species.

The composition of the spring community is largely determined by species that survive the winter (Tedesco et al., 2010), often in the ice interior. The winter algal community originates in autumn, when algae are trapped during ice formation. They may continue to grow, encapsulated in the grazer-protected ice environment (Garrison et al., 1983), despite the fact that over winter temperature drops and salinity increases. Newly formed sea ice may

Table 4: Significance of the correlation between season (analyzed as month-of-year) and the abundance of algal groups and photosynthetic parameters, tested for Arctic and Antarctic landfast and pack ice by Spearman's rank correlation. DOI: https://doi.org/10.1525/elementa.267.t4

Type of data		Arctic landfast ice	Arctic pack ice	Antarctic landfast ice	Antarctic pack ice
Algal groups	Flagellates	$p < 0.05$	n.s.[a]	$p < 0.05$	$p < 0.05$
	Pennate diatoms	n.s.	n.s.	$p < 0.05$	$p < 0.05$
	Centric diatoms	$p < 0.05$	$p < 0.05$	$p < 0.05$	n.s.
	Heterotrophs	n.s.	n.s.	n.s.	$p < 0.05$
Photosynthetic parameters	P_{max}	n.s.	$p < 0.05$	n.s.	n.s.
	α	n.s.	n.s.	n.s.	n.s.
	I_k	n.s.	n.s.	n.s.	n.s.

[a] Not significant ($p > 0.05$).

contain an algal community with high biodiversity (Gleitz and Thomas, 1993). Larger cells, especially EPS-producing species, are likely the most easily scavenged by the rising ice crystals that lead to ice formation and therefore tend to dominate in young sea-ice communities (Syvertsen, 1991; **Figure 4**). Larger pennate diatoms are scavenged preferentially (Garrison et al., 2005; Rozanska et al., 2008), forming occasional autumn sea-ice blooms (Fiala et al., 2006). Besides pennate diatoms, centric diatoms (Hsiao, 1980; Gleitz et al., 1998; Garrison et al., 2005) and flagellates (Gradinger and Ikävalko, 1998; Rozanska et al., 2008) have also been observed in newly formed sea ice.

When the ice column thickens, due to ice growing at the bottom or to ice rafting, interior layers are formed (Grossi and Sullivan, 1985; Ackley and Sullivan, 1994). The zonation of microalgae within the ice column is partly the result of a passive process, as algae are simply trapped in position even as the ice continues to grow. Pennate diatoms, however, are also known to be motile and can migrate within the ice column along favorable physicochemical gradients (Grossi and Sullivan, 1985; Aumack et al., 2014). The confined conditions within the ice may involve morphological adaptation (Ratkova and Wassmann, 2006) and stimulate selection for smaller species (Gleitz and Thomas, 1993; Krembs et al., 2000). Naviculoid diatoms like *Navicula glaciei,* observed to be the most motile (Grossi and Sullivan, 1985), and are also the most likely species to occur in interior layers (**Figure 4**).

Over winter, acclimation and natural selection occurs. The few winter data that were available to include in our dataset (Arctic: November, December; Antarctic: May–August) show high abundances of flagellates as well as mixed diatom communities (**Figure 3a–d**). Various adaptations are required to endure the extreme temperature, light and salinity conditions characteristic of the winter season. Energy storage, mixotrophy and heterotrophy may be the most important traits when photosynthetic activity is reduced (Zhang et al., 1998). Secondarily, the production of EPS, particularly by pennate diatoms, can aid their incorporation into the ice and subsequent persistence by altering the physical structure of sea ice (Rozanska et al., 2008; Krembs et al., 2011). Ice-binding proteins and cryo-osmolytes such as dimethylsulphonioproprionate (DMSP) produced by a number of psychrophilic microalgae may also offer protection against low temperatures and high salinity (Stefels, 2000; Krell et al., 2008). Finally, resting spore and cyst formation are often mentioned as important traits that enable microalgae to survive the winter. Microalgae may survive the dark period by formation of resting cells or spores that can be used for short-term dormancy in the case of diatoms or of cysts that often require a dormancy period before the germination in the case of dinoflagellates. Such spore or cyst formation, however, remains a poorly characterized trait of sea-ice algae. Various microalgal species have been suggested to form resting stages, but not all of them are prominent ice-algal species (see Appendix in Quillfeldt et al., 2003). Further investigation into resting stages may reveal not only more about survival strategies, but also the link between the sea-ice and pelagic biomes (Rintala et al., 2007).

The community composition in winter can be quite diverse, with up to 140 taxa reported (Werner et al., 2007; Niemi et al., 2011). Pennate diatoms are the most adapted to conditions in winter, specifically the more specialized species, like *Nitzschia frigida* (Syvertsen, 1991; Gradinger et al., 1999; Leu et al., 2015). An increasing number of observations, however, has made clear that besides pennate diatoms, flagellates also subsist through the winter (Ikävalko and Gradinger, 1997; Stoecker et al., 1998). Fewer observations are available for centric diatoms. They may survive only in the bottom layers (Kottmeier and Sullivan, 1987), where relatively high abundances have been observed in early spring in Arctic landfast ice (**Figure 3a**). In the ice interior, however, centric diatoms observed in high abundance in young pack ice (**Figure 3d**) apparently disappear from the ice column over time (Gleitz et al., 1998; Ratkova and Wassmann, 2006; Olsen et al., 2017). Heterotrophic protists are present throughout the year in pack ice (**Figure 3f**). In landfast ice, highest abundances have been recorded in early spring in the Antarctic. The relative abundance of protozoa declines when brine channels open up and fresh nutrients are provided, initiating the ice-algal spring bloom (Archer et al., 1996).

When ice-melt starts in spring, the sub-ice community of diatoms is the first to be sloughed off the bottom of the sea ice (**Figure 4**). Generally, flagellate species (autotrophic and heterotrophic) persist longer in sea-ice bottom communities (e.g., Tamelander et al., 2009; Torstensson et al., 2015). Nutrient limitation towards the end of sympagic blooms can also explain a dominance of flagellates later in the year (**Figure 3d**). Whereas nitrate gets depleted before silicate in the sea-ice interior (Fripiat et al., 2017), in bottom layers silicate often becomes the first limiting nutrient (Riaux-Gobin et al., 2003). In the final phases of the sea-ice cover, flagellates may thus contribute significantly to carbon fluxes (Tamelander et al., 2009).

3.2. Primary production

The photosynthetic parameters compiled in this study are highly variable (see Section 3.2.1.), and fewer statistically significant differences were detected (**Figure 5**) than for community composition. Hemisphere had slightly more significant impact on photosynthesis than did ice type (**Table 5**). Only bottom layers in the Arctic were susceptible to the interaction of ice type and time-of-year (**Table 5**).

Surface communities showed high photosynthetic capacity, P_{max} (**Figure 5a, b**), with highest average values recorded in Arctic pack ice (**Table 6**). At the same time, maximum values for light saturation, I_k, were measured at the surface, with average values of almost 100 μmol photons m^{-2} s^{-1} recorded in Arctic pack ice (**Figure 5e, f**; **Table 6**). These high values for I_k confirm that the communities were adapted to high light. Only one study provided

Table 5: Significance levels derived by linear modeling for impacta of hemisphere (Arctic/Antarctic), ice type (landfast/pack) and season (month-of-year) on photosynthetic parameters, determined in two layersb of the ice column. DOI: https://doi.org/10.1525/elementa.267.t5

Parameter	Ice layer	Hemisphere (H)	Ice Type (T)	Month (M)	M*T	
		Combined	Combined	(Ant)arctic	Arctic	Antarctic
P_{max}	Surface	n.s.[c]	n.s.	n.s.	n.s.	n.s.
	Interior	n.d.[d]	n.d.	n.d.	n.d.	n.d.
	Bottom	n.s.	$p < 0.005$	n.s.	$p < 0.005$	n.s.
α	Surface	$p < 0.05$	n.s.	n.s.	n.s.	n.s.
	Interior	n.d.	n.d.	n.d.	n.d.	n.d.
	Bottom	n.s.	$p < 0.0005$	n.s.	$p < 0.0005$	n.s.
I_k	Surface	$p < 0.05$	$p < 0.05$	n.s.	n.s.	n.s.
	Interior	n.d.	n.d.	n.d.	n.d.	n.d.
	Bottom	n.s.	n.s.	n.s.	n.s.	n.s.

[a] The interaction between the factors hemisphere and ice type was also tested but never found to be significant ($p > 0.05$).

[b] The interior layer could not be included in the analyses due to the limited number of data.

[c] Not significant ($p > 0.05$).

[d] Not determined.

Table 6: Average photosynthetic parameters in landfast and pack ice in the Arctic and Antarctic. DOI: https://doi.org/10.1525/elementa.267.t6

Type of ice	Ice layer	Hemisphere	P_{max}	α	I_k
Landfast ice	Surface	Arctic	**0.83** (*0.15, 0.2, 1.5*)[a]	**0.048** (*0.015, 0.018, 0.134*)	**32.4** (*8.6, 11, 75*)
		Antarctic	0.13[b]	0.011	10.4
		Combined	**0.76** (*0.15*)[c]	**0.044** (*0.014*)	**29.0** (*8.2*)
	Interior	Arctic[d]			
		Antarctic	**0.10** (*0.02, 0.06, 0.14*)	**0.018** (*0.010, 0.004, 0.038*)	**8.9** (*3.2, 2.8, 13.5*)
		Combined	**0.10** (*0.02*)	**0.018** (*0.010*)	**8.9** (*3.2*)
	Bottom	Arctic	**1.25** (*0.35, 0.19, 5.20*)	**0.189** (*0.033, 0.014, 0.45*)	**7.4** (*1.7, 1.4, 21.9*)
		Antarctic	**0.16** (*0.02, 0.08, 0.27*)	**0.021** (*0.003, 0.007, 0.037*)	**7.9** (*1.1, 4.2, 13.4*)
		Combined	**0.89** (*0.25*)	**0.133** (*0.027*)	**7.6** (*1.1*)
Pack Ice	Surface	Arctic	**2.00** (*0.80, 1.20, 2.80*)	**0.040** (*0.010, 0.030, 0.050*)	**98.5** (*40.5, 58, 139*)
		Antarctic	**1.12** (*0.18, 0.04, 3.14*)	**0.021** (*0.003, 0.005, 0.074*)	**57.4** (*7.1, 3, 134*)
		Combined	**1.28** (*0.17*)	**0.022** (*0.003*)	**57.4** (*6.8*)
	Interior	Arctic	**0. 07** (*0.03, 0.01, 0.16*)	**0.037** (*0.032, 0.005, 0.100*)	
		Antarctic	**0.37** (*0.08, 0.03, 1.20*)	**0.007** (*0.002, 0.001, 0.030*)	**71.1** (*13.2, 14, 274*)
		Combined	**0.31** (*0.07*)	**0.012** (*0.004*)	**71.1** (*13.2*)
	Bottom	Arctic	**0.15** (*0.02, 0.02, 0.39*)	**0.011** (*0.003, 0.002, 0.100*)	**27.8** (*5.0, 6.7, 111.5*)
		Antarctic	**0.32** (*0.17, 0.02, 2.17*)	**0.031** (*0.022, 0.001, 0.268*)	**25.5** (*6.3, 7, 91*)
		Combined	**0.20** (*0.05*)	**0.016** (*0.007*)	**27.0** (*3.9*)

[a] Parenthetic numbers indicate the standard error of the mean followed by minimum and maximum percentages.

[b] Only a single dataset available.

[c] A single number given parenthetically is the standard error of the mean.

[d] No data available.

quantitative data on photosynthesis-irradiance relationships in melt ponds. The P_{max} of 2.8 μg C μg Chl a^{-1} h^{-1}, an α of 0.05 μg C μg Chl a^{-1} h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$ and I_k of 139 μmol photons m^{-2} s^{-1} are worthwhile mentioning (Fernandez-Mendez et al., 2015), as the I_k is the highest in our dataset. Melt-pond communities appear well adapted to high light. Production, however, may be inhibited by depletion of nitrate and phosphate (Stoecker et al., 2000). An increase in nutrient limitation can be reflected in a seasonal decline in P_{max} and α (Stoecker et al., 2000; Fernandez-Mendez et al., 2014). Later in the season, when melt ponds can become connected to the ice interior and even to underlying seawater, a fresh supply of nutrients may be provided (e.g., Mundy et al., 2011). Production in infiltration layers is seldom inhibited by nutrients, as they are regularly supplied by flooding seawater (Fripiat et al., 2017). Melting and freezing processes in sea ice, however, can affect nutrient supply (Fripiat et al., 2017). In MYI, surface drainage through brine channels and subsequent refreezing results in nutrient depletion in surface layers. Alternatively, nutrients that are captured in organic material will be retained upon refreezing (Fripiat et al., 2017). Altogether, melting and freezing processes make it difficult to link nutrient availability to any specific ice condition (Vancoppenolle et al., 2013a; Meiners and Michel, 2017).

Surface blooms are often terminated by the deleterious effects of decreasing salinity and increasing irradiance in the course of spring (e.g., Campbell et al., 2014). Various adaptive mechanisms towards exposure to high irradiance and UV have been recorded, including adjusting pigment composition or the production of mycosporine-like amino acids (Mundy et al., 2011; Kauko et al., 2016). However, it is the low salinity shock in combination with high irradiance levels that especially suppresses algal growth (Cota and Smith, 1991; Ralph et al., 2007; Ryan et al., 2011). Conditions appear more severe for landfast than for pack-ice communities (**Figure 5e, f**). For instance, a relatively low I_k of < 30 μmol photons m^{-2} s^{-1} was determined for landfast ice at McMurdo Sound, which probably related to overexposure to high irradiance and ensuing strong downregulation of photosynthesis (see also Palmisano et al., 1987). The difference between the two ice types may be related to differences in snow cover, but not enough data are available to confirm this relationship.

Very few data exist on production by interior communities. For landfast ice, only one dataset was available, with P_{max} values of < 0.1 μg C μg Chl a^{-1} h^{-1} recorded at McMurdo Sound (Palmisano et al., 1987). This maximum photosynthetic capacity is less than 10% of the average production rates in surface and bottom sea ice (**Figure 5a, b**). Interior communities are subject to extreme conditions of salinity and temperature, which suppress photosynthetic activity (Palmisano et al., 1987; Gleitz and Kirst, 1991; Arrigo and Sullivan, 1992). These communities are also the most subject to temporal changes in sea-ice structure and biogeochemistry. In FYI, production may also be controlled by nutrient limitation, but this limitation is less likely to occur in the ice interior where nutrients are recycled rapidly and therefore in ample supply (Gleitz et al., 1995; Fripiat et al., 2017; Roukaerts et al., 2016). Algal biomass in the ice interior can build to concentrations of 193 μg C L^{-1}, accounting for 50% of total biomass (Archer et al., 1996). Production to such levels, however, ultimately leads to nutrient depletion, as recorded in the Canadian Arctic where silicate and phosphate values in both FYI and MYI did not exceed 0.1 μmol l^{-1} (Melnikov et al., 2002). Production rates in MYI have been recorded as lower than in FYI, but other factors contribute to this difference, particularly light, salinity and space limitations (Mock and Gradinger, 1999). Lower production in older ice will result in a shift of the system towards heterotrophy, as observed in comparative bottom ice communities of McMurdo Sound (Remy et al., 2008). Though production rates may be low, integrated over the ice column, production may be a factor of significance, especially in Antarctic pack ice (**Table 6**) but also in the Arctic (Mock and Gradinger, 1999), and therefore should not be ignored in biogeochemical models.

The highest value for P_{max} of 5.2 μg C μg Chl a^{-1} h^{-1} was recorded in a bottom community in Arctic landfast ice (Gosselin et al., 1986). The high P_{max} values in the bottom layer of our complied datasets (**Figure 5a**) indicate optimal photoacclimation. Shade adaptation by the bottom communities is also reflected by very low I_k values, with lowest values just over 1 μmol photons m^{-2} s^{-1} recorded in early spring in Arctic landfast bottom communities (Suzuki et al., 1997). Overall a 60–70% reduction in I_k was recorded for the bottom layers versus the surface (**Figure 5e, f**). Shade adaptation will also shape α, the index of light affinity; however, data were highly variable and significant differences between the various layers could not always be detected (**Figure 5c, d**). A minimum α of 0.0012 μg C μg Chl a^{-1} h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$ was recorded in bottom pack-ice communities in East Antarctica (Ugalde et al., 2016). Low values for α are the result of high Chl *a*/carbon ratios that are typical under shade adaptation (see Johnsen and Hegseth, 1991, and references therein). Light affinity α is ten times lower in pack-ice bottom communities compared to landfast communities (**Figure 5a–d**). This difference can be attributed to relatively low light levels under pack ice, as a result of various factors such as snow cover and ice thickness (Lazzara et al., 2007; Ugalde et al., 2016; Arndt et al., 2017) as well as self-shading (Johnsen and Hegseth, 1991).

The average value for α of 0.13 μg C μg Chl a^{-1} h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$, as established for landfast bottom communities (**Figure 5c**), is near the proposed theoretical maximum (see Cota and Smith, 1991, and references therein). This average indicates relatively high growth efficiency under the ambient light conditions. It is an order of magnitude higher than values for α generally observed in natural communities of polar phytoplankton (see also Cota and Smith, 1991, for comparison), which confirms the high capacity of photoacclimation in sympagic microalgae.

The relatively high P_{max} of communities in the bottom layer of landfast ice is most likely linked to differences in nutrient availability. Landfast ice forms in coastal and shelf areas, where current regimes are often more dynamic

(Cota et al., 1991) and nutrient concentrations in the water are often higher than in open ocean areas (see also Gradinger, 2009, and references therein). A tight relationship between increased production and enhanced nutrient availability as provided by tidal currents was recorded in the Arctic Archipelago (Cota and Horne, 1989). In the Antarctic, platelet-ice systems appear especially productive, partly because their porous structure facilitates high rates of nutrient exchange (Grossi et al., 1987; Arrigo et al., 1995). In contrast, pack ice in the Arctic often forms over open ocean areas that are generally low in nutrients (e.g., Lee et al., 2010; Fernandez-Mendez et al., 2015). In addition, stagnation of currents underneath pack ice can result in stratification that inhibits the nutrient exchange between deeper layers and surface waters (Cota et al., 1991; Barber et al., 2015). Especially in the Arctic, a strong halocline is persistent (Cottier et al., 2017), which results more often in nutrient limitation within the sea ice.

Comparing landfast bottom communities in the Arctic and Antarctic confirms that conditions other than ice type control production capacity. Photosynthesis rates in the Arctic are on average ten times higher than in the Antarctic (**Table 6**). These differences can be linked directly to the local light climate, as studied closely in the Antarctic by Lizotte and Sullivan (1991). They compared pack-ice with landfast ice communities, observing higher values for P_{max} in the pack ice, and related this difference to higher irradiance levels under the pack ice. Additional research on Antarctic pack ice led to the same conclusion: light availability more so than structure of the sea ice made the difference between low and high production rates (Ugalde et al., 2016).

3.2.1. Acclimation to variations in light and temperature

Whereas significant patterns can be established for the microalgal community composition, identifying similar common regularities for photosynthetic parameters is difficult (**Table 6**). The only significant effect recorded for time of year, for example, was on P_{max} in Arctic pack ice (**Table 4**). Photosynthetic parameters are highly variable, and variations of an order of magnitude within one dataset are not exceptional (e.g., Lizotte and Sullivan, 1991). Values for P_{max} can vary by >200%, variations that are larger than the average estimates presented in **Figure 5**. In sea ice, small-scale differences in structure are associated with large variations in environmental factors like temperature, salinity and light, accounting for the heterogeneity of the habitat. These small-scale variations in space and time are the features that control algal physiology and biomass (e.g. Lizotte and Sullivan, 1991), more than general characteristics that define sea ice as either landfast or pack ice.

The most dominant factor that governs photosynthesis is light. The light climate in sea ice is controlled to a large extent by ice thickness and snow (Mundy et al., 2005, 2007; Arndt et al., 2017; Perovich, 2017). A thick snow cover prevents light penetration into the sea ice, which can result in light limitation of sympagic microalgal communities (Arrigo, 2014, 2017). Seasonal changes in photosynthetic activity due to changes in irradiance are in fact observed (e.g., Gosselin et al., 1986; Hawes et al., 2012; Campbell et al., 2017b), but they are difficult to grasp in meta-analyses. Environmental conditions that determine the onset of the spring bloom are too site-specific.

Photoacclimation and associated changes in photosynthetic parameters may occur on a time scale of days, i.e., the generation time of a community, to weeks (Grossi et al., 1987; Cota and Horne, 1989; Cota and Smith, 1991; Juhl and Krembs, 2010). Fluorescence analyses have clearly shown how local photosynthetic activity can be triggered in spring by increasing temperature (Hawes et al., 2012) and improvement of the light climate (Manes and Gradinger, 2009; Campbell et al., 2017b). Similarly, a 3–5-fold increase in P_{max} and α was recorded in response to gradual snow thinning over the course of two months (Gosselin et al., 1986; Barlow et al., 1988). Gradients can be observed not only in time but also in space. In the ice column, vertical gradients in photosynthetic activity were recorded by fluorescence analyses at Point Barrow, Alaska (Manes and Gradinger, 2009). The highest activity was measured in bottom communities. Vertical patterns became stronger with increasing photosynthetic activity over the course of time.

Snow clearing that improves light penetration into sea ice does not always stimulate microalgal growth. Differences in light history and site-specific variations in the light climate introduce further scatter in a meta-analyses as presented here. For instance, sudden exposure to increased light intensities can trigger migratory movement away from the light (Aumack et al., 2014; Lund-Hansen et al., 2014). Rapid removal of snow can also have more deleterious effects. In a number of experiments, snow clearance resulted in a decline in photosynthetic activity and a decrease in biomass as the change in light climate was apparently too abrupt for an adequate response (McMinn et al., 1999; Juhl and Krembs, 2010). A sudden change in photosynthetic parameters in bottom layers can also be due to mechanical damage and losses associated with a rapid deterioration of the sea ice habitat induced by snow melt and increased temperatures (Smith et al., 1988; Mundy et al., 2005; Campbell et al., 2014, 2015). Recent studies on Arctic landfast ice have shown a seasonally changing influence of snow cover on ice-algal bottom communities (Mundy et al., 2005; Campbell et al., 2014, 2015; Leu et al., 2015) and demonstrated how snow dynamics can alter the timing, duration and magnitude of ice-algal spring blooms. Similar concepts have recently been postulated for Antarctic pack ice (Meiners et al., 2017), but a comparable snow-driven ice-algal phenology is currently lacking for Antarctic fast ice.

In sea ice, both light and temperature influence algal growth. The strong ability of photoacclimation in sympagic algae does not necessarily imply that growth is efficient. Sympagic microalgae perform rather poorly in terms of biomass-specific production. P_{max} in sympagic algae rarely exceeds 1 μg C μg Chl a^{-1} h^{-1}. Phytoplankton may produce more than 5 μg C μg Chl a^{-1} h^{-1} (Cota and Smith, 1991). Sympagic microalgae appear specifically adapted for growth at low temperatures (Kottmeier and Sullivan, 1988). Sympagic algae from polar sea ice have growth optima between –0.5°C and 4°C (Rochet et al., 1985; Palmisano et al., 1987; Cota and Smith, 1991), which implies that sympagic microalgae often grow under suboptimal (colder) conditions, as confirmed by fluorescence and oxygen-based production studies. In studies at Cape Evans (Antarctica), low production efficiency was observed, which according to the authors indicated that the landfast sea-ice algae were not functioning at maximum capacity (Robinson et al., 1998; McMinn et al., 2003).

Despite these apparent shortcomings, sympagic algae in the sea-ice interior survive under conditions that temperate species could not endure. The polar winter allows only for very low photosynthetic rates (Lizotte, 2001; Berge et al., 2015). Growth can be maintained because respiration rates are equally low due to the low temperatures. With increasing temperatures, respiration rates increase faster than photosynthetic rates (Tilzer and Dubinsky, 1987; Thomas et al., 1992; Regaudie-de-Gioux and Duarte, 2012). When metabolic costs increase with the rise in temperature in spring, a positive growth balance can still be maintained because carbon assimilation increases even more as a consequence of the simultaneous extension of daytime (Tilzer and Dubinsky, 1987). It is because of this relative high temperature sensitivity that sympagic microalgae can survive the polar winter.

4. A future perspective on climate change and sea-ice algae

In the past three decades, the summer minimum sea-ice extent in the Arctic has decreased by 45% (Arrigo, 2014; Thomas, 2017, and references therein). In 1991, the sea ice cover in the Arctic would range from 8.5 × 10^6 km^2 in September to a maximum of 15 × 10^6 km^2 in March (Cota et al., 1991). In 2014, the ice cover in the Arctic varied between 5 × 10^6 and 15 × 10^6 km^2 (Arrigo, 2014). Associated with this decrease in ice cover, the sea ice is thinning, and a marked shift has already occurred with FYI replacing MYI (Meier, 2017; Stammerjohn and Maksym, 2017). The Arctic is also likely to witness a reduction of landfast sea ice (Tamelander et al., 2009). Changes in the Antarctic are more variable. The Western Antarctic Peninsula has shown a 41% decline relative to the mean sea-ice extent over the period 1979–2007 (Ducklow et al., 2012). On the other hand, sea-ice extent in East Antarctica has not changed over the last several decades. Overall the Antarctic sea-ice extent has slightly increased over the satellite observing period, but this trend is masking strong regional changes in extent and duration of the sea-ice cover (Stammerjohn and Maksym, 2017).

Changes in the extent and structure of the sea ice will have consequences for sympagic communities. So far, the data have been too sparse geographically to record broadly significant changes, but a number of papers have summarized the potential effects of climate change (e.g., Post et al., 2013; Barber et al., 2015). In the Arctic, thinning of the sea ice is a factor that can already be recognized as affecting sympagic algae. Bottom communities develop earlier in the season because light penetration increases with decreasing ice thickness (Lazzara et al., 2007; Barber et al., 2015). In addition, snow cover is thinner on FYI compared to MYI as there is less time for snow accumulation, which results in more irradiance penetrating the sea ice. Larger surface areas are covered by melt ponds on FYI compared to MYI, which also makes FYI more transparent (Nicolaus et al., 2012). Because of enhanced light availability bottom sea-ice communities may reach higher biomass, though more condensed in time, as nutrients will be consumed more rapidly (Leu et al., 2015). An increase in the frequency of storms is predicted to result in the formation of more leads (open water between ice floes), which upon refreezing support high algal growth rates, though overall refrozen leads are less productive than thicker ice floes (Duarte et al., 2017).

The ecological consequences of the changes in ice structure and algal biomass are enigmatic. Current distribution patterns show that flagellates characterize surface communities, mixed communities inhabit interior ice, and pennate diatoms dominate bottom communities. Changes in sea-ice conditions, as established and predicted for specific regions of the Antarctic sea-ice zone, may alter the vertical distribution of ice-algal communities in pack-ice floes (Meiners et al., 2012). Productivity of sympagic communities will be affected by the foreseen changes in community structure (Campbell et al., 2017a). In addition, climate change can be expected to impact primary production directly, as the physiology and photosynthesis of microalgae are very responsive to environmental perturbations. Production may in fact increase with changes in the light climate. This increase may not necessarily be beneficial for biogeochemical fluxes, as the expected shift forward in time of the algal bloom can result in a mismatch in trophic relations. Pelagic herbivores feeding on sea-ice algae may not be able to synchronize with the algal bloom, with negative consequences for their reproduction (Leu et al., 2011; Søreide et al., 2010). The coupling between primary and secondary producers becomes more important as sympagic blooms may become shorter. Arctic sea-ice thinning and consequent ablation of bottom communities is likely to happen earlier in the season (Barber et al., 2015). As a result, fluxes of carbon into the deep ocean upon ice melt may increase (Tamelander et al., 2009), with positive consequences for benthic communities that feed on them (Boetius et al., 2013). The consequences of sea ice seeding the pelagic community are hard to predict, as not enough is known about the current relevance of this process let alone future changes.

Over the last two decades, the occurrence and extent of melt ponds in the Arctic has increased (Lee et al., 2011). At the same time, the nature of these ponds has changed. With the thinning of sea ice, more ponds become connected with the ice interior and the seawater below the ice, turning closed pond-systems into open ponds (Lee et al., 2011). Consequently, melt ponds lose their unique character and become more like seawater communities. Predicting how much the contribution of melt ponds to carbon fluxes will change is difficult. Melt ponds currently contribute less than 5% to total annual production in the Arctic. However, locally they can contribute to more than 30% of annual production, thus an increasingly important role of melt ponds in biogeochemical cycles can be anticipated (Fernandez-Mendez et al., 2015). Closed ponds will likely be prone to nutrient limitation (Lee et al., 2012). With a limited nutrient supply, the composition of algal communities will shift towards species of smaller size, which generally contribute less to carbon export than larger species. The role of smaller species in biogeochemical cycles may be more significant as potential producers of DMSP and halocarbons (e.g., Stefels et al., 2007). The importance of sea ice as a link with the atmosphere may thus increase. Model studies show that especially the Arctic foodweb is sensitive to species loss that may result from climate change (Carscallen and Romanuk, 2012), implying negative consequences of sea-ice habitat loss for connected biomes.

Our analysis has made clear that state-of-the-art sea-ice biogeochemical models require more complexity than currently adopted. At least a 3-layer model featuring bottom, internal and surface communities would be needed to reproduce both Arctic and Antarctic habitats, and both landfast and pack-ice conditions (**Figures 2** and **3**). Besides diatoms, our analysis shows that at least one more group of algae, namely autotrophic flagellates, deserve consideration both spatially, in both hemispheres, and temporally, for playing an important role in community succession. Regionally, both centric diatoms and heterotrophic/mixotrophic populations may need to be considered. The analysed photosynthetic parameters (**Figures 5** and **6**) further show the large range of photoacclimation that characterizes sea-ice algae, which stresses the importance of considering mechanisms of photoacclimation in sea-ice algal models. The inclusion of such mechanisms is still rarely done, but with the analysis presented here, sea-ice algal models can now be greatly and soundly improved.

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Competing interests

The authors have no competing interests to declare.

Author contributions

- MAvL wrote the first draft and revised the article. LT and JS contributed significantly to the design. MAvL and LT produced Figure 4.
- MAvL, KRA, PA, KC, KMM, J-MR, VS and DNT contributed mostly to the acquisition of data. MAvL analyzed and synthesized the data.
- All authors contributed significantly to the interpretation of the data.
- All authors approved the submitted version for publication.

References

Ackley, SF and **Sullivan, CW** 1994 Physical controls on the development and characteristics of Antarctic sea ice biological communities – a review and synthesis. *Deep Sea Res I* **41**: 1583–1604. DOI: https://doi.org/10.1016/0967-0637(94)90062-0

Alou-Font, A, Mundy, C-J, Roy, S, Gosselin, M and **Agusti, S** 2013 Snow cover affects ice algal pigment composition in the coastal Arctic Ocean. *Mar Ecol Prog Ser* **474**: 89–104. DOI: https://doi.org/10.3354/meps10107

Archer, SD, Leakey, RJC, Burkill, PH, Sleigh, MA and **Appleby, CJ** 1996 Microbial ecology of sea ice at a coastal Antarctic site: community composition, biomass and temporal change. *Mar Ecol Prog Ser* **135**: 179–195. DOI: https://doi.org/10.3354/meps135179

Arndt, S, Meiners, KM, Ricker, R, Krumpen, T, Katlein, C and **Nicolaus, M** 2017 Influence of snow depth and surface flooding on light transmission through Antarctic pack ice. *J Geophys Res Oceans* **122**. DOI: https://doi.org/10.1002/2016JC012325

Arrigo, KR 2014 Sea ice ecosystems. *Annu Rev Mar Sci* **6**: 439–467. DOI: https://doi.org/10.1146/annurev-marine-010213-135103

Arrigo, KR 2017 Sea ice as a habitat for primary producers., In: Thomas, DN (ed.), *Sea Ice*, 3rd Edition, 352–369. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch14

Arrigo, KR, Dieckmann, G, Gosselin, M, Robinson, DH, Fritsen, CH and **Sullivan, CW** 1995 High resolution study of the platelet ice ecosystem in McMurdo Sound, Antarctica: biomass, nutrient, and production profiles within a dense microalgal bloom. *Mar Ecol Prog Ser* **127**: 255–268. DOI: https://doi.org/10.3354/meps127255

Arrigo, KR, Lizotte, MP and **Mock, T** 2010 Primary producers and sea ice. In: Thomas, DN and Dieckmann, GS (eds.), *Sea Ice* 2nd Edition, 283–326. Oxford, UK: Wiley-Blackwell.

Arrigo, KR and **Sullivan, CW** 1992 The influence of salinity and temperature covariation on the photophysiological characteristics of Antarctic sea ice microalgae. *J Phycol* **28**: 746–756. DOI: https://doi.org/10.1111/j.0022-3646.1992.00746.x

Aumack, CF, Juhl, AR and **Krembs, C** 2014 Diatom vertical migration within land-fast Arctic sea ice. *J Mar Syst* **139**: 496–504. DOI: https://doi.org/10.1016/j.jmarsys.2014.08.013

Bachy, C, Lopez-Garcia, P, Vereshchaka, A and **Moreira, D** 2011 Diversity and vertical distribution of microbial eukaryotes in the snow, sea ice and seawater near the North Pole at the end of the polar night.

Front Microbiol **2**. DOI: https://doi.org/10.3389/fmicb.2011.00106

Barber, DG, Hop, H, Mundy, CJ, Else, B, Dmitrenko, IA, et al. 2015 Selected physical, biological and biogeochemical implications of a rapidly changing Arctic Marginal Ice Zone. *Prog Oceanogr* **139**: 122–150. DOI: https://doi.org/10.1016/j.pocean.2015.09.003

Barlow, R, Gosselin, M, Legendre, L, Therriault, J-C, Demers, S, et al. 1988 Photoadaptive strategies in sea-ice microalgae. *Mar Ecol Prog Ser* **45**: 145–152. DOI: https://doi.org/10.3354/meps045145

Belt, ST, Smik, L, Brown, TA, Kim, J-H, Rowland, SJ, et al. 2016 Source identification and distribution reveals the potential of the geochemical Antarctic sea ice proxy IPSO25. *Nature Comm* **7**: 12655. DOI: https://doi.org/10.1038/ncomms12655

Berge, J, Daase, M, Renaud, PE, Ambrose Jr, WG, Darnis, G, et al. 2015 Unexpected levels of biological activity during the polar night offer new perspectives on a warming Arctic. *Current Biol* **25**: 2555–2561. DOI: https://doi.org/10.1016/j.cub.2015.08.024

Bergmann, MA, Welch, HE, Butler-Walker, JE and **Siferd, TD** 1991 Ice algal photosynthesis at Resolute and Saqvaqjuac in the Canadian Arctic. *J Mar Syst* **2**: 43–52. DOI: https://doi.org/10.1016/0924-7963(91)90012-J

Bluhm, BA, Swadling, KM and **Gradinger, R** 2017 Sea ice as a habitat for macrograzers. In: Thomas, DN (ed.), *Sea Ice* 3rd Edition, 394–414. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch16

Boetius, A, Albrecht, S, Bakker, K, Bienhold, C, Felden, J, et al. 2013 Export of algal biomass from the melting Arctic sea ice. *Science* **339**(6126): 1430–1432. DOI: https://doi.org/10.1126/science.1231346

Campbell, K, Mundy, CJ, Barber, DG and **Gosselin, M** 2014 Remote estimates of ice algae biomass and their response to environmental conditions during spring melt. *Arctic* **67**(3): 375–387. DOI: https://doi.org/10.14430/arctic4409

Campbell, K, Mundy, CJ, Barber, DG and **Gosselin, M** 2015 Characterizing the sea ice algae chlorophyll *a*–snow depth relationship over Arctic spring melt using transmitted irradiance. *J Mar Syst* **147**: 76–84. DOI: https://doi.org/10.1016/j.jmarsys.2014.01.008

Campbell, K, Mundy, CJ, Belzile, C, Delaforge, A and **Rysgaard, S** 2017a Seasonal dynamics of algal and bacterial communities in Arctic sea ice under variable snow cover. *Polar Biol.* DOI: https://doi.org/10.1007/s00300-017-2168-2

Campbell, K, Mundy, CJ, Gosselin, M, Landy, JC, Belzile, C, et al. 2017b Net community production in the bottom of first-year sea ice over the Arctic spring bloom. *Geophys Res Let* **44**. DOI: https://doi.org/10.1002/2017GL074602

Campbell, K, Mundy, CJ, Landy, JC, Delaforge, A, Michel, C and **Rysgaard, S** 2016 Community dynamics of bottom-ice algae in Dease Strait of the Canadian Arctic. *Prog Oceanogr* **149**: 27–39. DOI: https://doi.org/10.1016/j.pocean.2016.10.005

Caron, DA, Gast, RJ and **Garneau, M-E** 2017 Sea ice as a habitat for micrograzers., In: Thomas, DN (ed.), *Sea Ice* 3rd Edition, 370–393. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch15

Carscallen, WMA and **Romanuk, TN** 2012 Structure and robustness to species loss in Arctic and Antarctic ice-shelf meta-ecosystem webs. *Ecol Model* **245**: 208–218. DOI: https://doi.org/10.1016/j.ecolmodel.2012.03.027

Comeau, AM, Philippe, B, Thaler, M, Gosselin, M, Poulin, M and **Lovejoy, C** 2013 Protists in Arctic drift and land-fast sea ice. *J Phycol* **49**: 229–240. DOI: https://doi.org/10.1111/jpy.12026

Cota, GF and **Horne, EPW** 1989 Physical control of arctic ice algal production. *Mar Ecol Prog Ser* **52**: 111–121. DOI: https://doi.org/10.3354/meps052111

Cota, GF, Legendre, L, Gosselin, M and **Ingram, RG** 1991 Ecology of bottom ice algae: I. Environmental controls and variability. *J Mar Syst* **2**: 257–277. DOI: https://doi.org/10.1016/0924-7963(91)90036-T

Cota, GF and **Smith, REH** 1991 Ecology of bottom ice algae: III. Comparative physiology. *J Mar Syst* **2**: 297–315. DOI: https://doi.org/10.1016/0924-7963(91)90038-V

Cota, GF and **Sullivan, CW** 1990 Photoadaptation, growth and production of bottom ice algae in the Antarctic. *J Phycol* **26**: 399–411. DOI: https://doi.org/10.1111/j.0022-3646.1990.00399.x

Cottier, F, Steele, M and **Nilsen, F** 2017 Sea ice and Arctic Ocean oceanography. In: Thomas, DN (ed.), *Sea Ice* 3rd Edition, 197–215. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch7

Duarte, P, Assmy, P, Hop, H, Spreen, G, Gerland, S and **Hudson, SR** 2015 The importance of vertical resolution in sea ice algae production models. *J Mar Syst* **145**: 69–90. DOI: https://doi.org/10.1016/j.jmarsys.2014.12.004

Duarte, P, Meyer, A, Olsen, LM, Kauko, HM, Assmy, P, et al. 2017 Sea ice thermohaline dynamics and biogeochemistry in the Arctic Ocean: Empirical and model results. *J Geophys Res Biogeosci* **122**: 1632–1654. DOI: https://doi.org/10.1002/2016JG003660

Dumont, I, Schoemann, V, Lannuzel, D, Chou, L, Tison, J-L and **Becqquevort, S** 2009 Distribution and characterization of dissolved and particulate organic matter in Antarctic pack ice. *Polar Biol* **32**: 733–750. DOI: https://doi.org/10.1007/s00300-008-0577-y

Fernandez-Mendez, M, Katlein, C, Rabe, B, Nicolaus, M, Peeken, I, et al. 2015 Photosynthetic production in the central Arctic Ocean during the record sea-ice minimum in 2012. *Biogeoscience* **12**: 3525–3549. DOI: https://doi.org/10.5194/bg-12-3525-2015

Fernandez-Mendez, M, Wenzhofer, F, Peeken, I, Sørensen, HL, Glud, RN and **Boetius, A** 2014 Composition, buoyancy regulation and fate of ice algal aggregates in the Central Arctic Ocean. *PLoS ONE* **9**(9): e107452. DOI: https://doi.org/10.1371/journal.pone.0107452

Fiala, M, Kuosa, H, Kopczynska, EE, Oriol, L and **Delille, D** 2006 Spatial and seasonal heterogeneity of sea ice microbial communities in the first-year ice of Terre Adélie area (Antarctica). *Aquat Microb Ecol* **43**: 95–106. DOI: https://doi.org/10.3354/ame043095

Fripiat, F, Meiners, KM, Vancoppenolle, M, Papadimitriou, S, Thomas, DN, et al. 2017 Macronutrient concentrations in Antarctic pack ice: Overall patterns and overlooked processes. *Elem Sci Anth* **5**: 13. DOI: https://doi.org/10.1525/elementa.217

Galindo, V, Levasseur, M, Mundy, CJ, Gosselin, M, Tremblay, J-E, et al. 2014 Biological and physical processes influencing sea ice, under-ice algae, and dimethylsulfoniopropionate during spring in the Canadian Arctic Archipelago. *J Geophys Res Oceans* **119**. DOI: https://doi.org/10.1002/2013JC009497

Garrison, DL 1991 Antarctic sea ice biota. *Amer Zool* **31**: 17–33. DOI: https://doi.org/10.1093/icb/31.1.17

Garrison, DL, Ackley, SF and **Buck, KR** 1983 A physical mechanism for establishing algal populations in frazil ice. *Nature* **306**: 363–365. DOI: https://doi.org/10.1038/306363a0

Garrison, DL and **Buck, KR** 1989 The Biota of Antarctic Pack Ice in the Weddell Sea and Antarctic Peninsula Regions. *Polar Biol* **10**: 211–219. DOI: https://doi.org/10.1007/BF00238497

Garrison, DL, Gibson, A, Coale, SL, Gowing, MM, Okolodkov, YB, Fritsen, CH and **Jeffries, MO** 2005 Sea-ice microbial communities in the Ross Sea: autumn and summer biota. *Mar Ecol Prog Ser* **300**: 39–52. DOI: https://doi.org/10.3354/meps300039

Gleitz, M, Bartsch, A, Dieckmann, GS and **Eicken, H** 1998 Composition and succession of sea ice diatom assemblages in the eastern and southern Weddell Sea, Antarctica, In: Lizotte, MP, Arrigo, KR (eds.), *Antarctic Sea Ice: Biological processes, interactions and variability.* Washington DC: American Geophysical Union, 107–120. DOI: https://doi.org/10.1029/AR073p0107

Gleitz, M and **Kirst, GO** 1991 Photosynthesis-irradiance relationships and carbon metabolism of different ice algal assemblages collected from Weddell Sea pack ice during austral spring (EPOS 1). *Polar Biol* **11**: 385–392. DOI: https://doi.org/10.1007/BF00239691

Gleitz, M, Rutgers, vd, Loeff, M, Thomas, DN, Dieckmann, GS and **Millero, FJ** 1995 Comparison of summer and winter inorganic carbon, oxygen and nutrient concentrations in Antarctic sea ice brine. *Mar Chem* **51**: 81–91. DOI: https://doi.org/10.1016/0304-4203(95)00053-T

Gleitz, M and **Thomas, DN** 1993 Variation in phytoplankton standing stock, chemical composition and physiology during sea-ice formation in the southeastern Weddell Sea, Antarctica. *J Exp Mar Biol Ecol* **173**: 211–230. DOI: https://doi.org/10.1016/0022-0981(93)90054-R

Gosselin, M, Legendre, L, Therriault, J-C, Demers, S and **Rochet, M** 1986 Physical control of the horizontal patchiness of sea-ice microalgae. *Mar Ecol Prog Ser* **29**: 289–298. DOI: https://doi.org/10.3354/meps029289

Gosselin, M, Levasseur, M, Wheeler, PA, Horner, RA and **Booth, BC** 1997 New measurements of phytoplankton and ice algal production in the Arctic Ocean. *Deep Sea Res II* **44**: 1623–1644. DOI: https://doi.org/10.1016/S0967-0645(97)00054-4

Gradinger, R 2009 Sea-ice algae: Major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. *Deep Sea Res II* **56**: 1201–1212. DOI: https://doi.org/10.1016/j.dsr2.2008.10.016

Gradinger, R, Friedrich, D and **Spindler, M** 1999 Abundance, biomass and composition of the sea ice biota of the Greenland Sea pack ice. *Deep Sea Res II* **46**: 1457–1472. DOI: https://doi.org/10.1016/S0967-0645(99)00030-2

Gradinger, R and **Ikävalko, J** 1998 Organism incorporation into newly forming Arctic sea ice in the Greenland Sea. *J Plankton Res* **20**: 871–886. DOI: https://doi.org/10.1093/plankt/20.5.871

Grossi, SM, Kottmeier, ST, Moe, RL, Taylor, GT and **Sullivan, CW** 1987 Sea ice microbial communities. 6. Growth and primary production in bottom ice under graded snow cover. *Mar Ecol Prog Ser* **35**: 153–64. DOI: https://doi.org/10.3354/meps035153

Grossi, SM and **Sullivan, CW** 1985 Sea ice microbial communities. V. The vertical zonation of diatoms in an Antarctic fast ice community. *J Phycol* **21**: 401–409. DOI: https://doi.org/10.1111/j.0022-3646.1985.00401.x

Haas, C, Thomas, DN and **Bareiss, J** 2001 Surface properties and processes of perennial Antarctic sea ice in summer. *J Glaciol* **47**: 613–625. DOI: https://doi.org/10.3189/172756501781831864

Hardge, K, Peeken, I, Neuhaus, S, Lange, BA, Stock, A, et al. 2017 The importance of sea ice for exchange of habitat-specific protist communities in the Central Arctic Ocean. *J Mar Syst* **165**: 124–138. DOI: https://doi.org/10.1016/j.jmarsys.2016.10.004

Hawes, I, Lund-Hansen, LC, Sorrell, BK, Nielsen, MH, Borzak, R and **Buss, I** 2012 Photobiology of sea ice algae during initial spring growth in Kangerlussuaq, West Greenland: insight from imaging variable chlorophyll fluorescence of ice cores. *Photosynth Res* **112**: 103–115. DOI: https://doi.org/10.1007/s11120-012-9736-7

Hegseth, EN 1992 Sub-ice algal assemblages of the Barents Sea – species composition, chemical composition, and growth rates. *Polar Biol* **12**: 485–496. DOI: https://doi.org/10.1007/BF00238187

Horner, R, Ackley, SF, Dieckmann, GS, Gulliksen, B, Hoshiai, T, et al. 1992 Ecology of sea ice biota. I. Habitat, terminology, and methodology. *Polar Biol* **12**: 417–427. DOI: https://doi.org/10.1007/BF00243113

Horner, R and **Schrader, GC** 1982 Relative contribution of ice algae, phytoplankton, and benthic microalgae to primary production in nearshore regions of the Beaufort Sea. *Arctic* **35**: 485–503. DOI: https://doi.org/10.14430/arctic2356

Hsiao, SIC 1980 Quantitative Composition, Distribution, Community Structure and Standing Stock of Sea Ice Microalgae in the Canadian Arctic. *Arctic* **33**: 768–793. DOI: https://doi.org/10.14430/arctic2595

Ikävalko, J and **Gradinger, R** 1997 Flagellates and heliozoans in the Greenland Sea ice studied alive using light microscopy. *Polar Biol* **17**: 473–481. DOI: https://doi.org/10.1007/s003000050145

Johnsen, G and **Hegseth, EN** 1991 Photoadaptation of sea-ice microalgae in the Barents Sea. *Polar Biol* **11**: 179–184. DOI: https://doi.org/10.1007/BF00240206

Juhl, AR and **Krembs, C** 2010 Effects of snow removal and algal photoacclimation on growth and export of ice algae. *Polar Biol* **33**: 1057–1065. DOI: https://doi.org/10.1007/s00300-010-0784-1

Karentz, D, Cleaver, JE and **Mitchell, DL** 1991 Cell survival characteristics and molecular responses of Antarctic phytoplankton to ultraviolet-B radiation. *J Phycol* **27**: 326–341. DOI: https://doi.org/10.1111/j.0022-3646.1991.00326.x

Kattner, G, Thomas, DN, Haas, C, Kennedy, H and **Dieckmann, GS** 2004 Surface ice and gap layers in Antarctic sea ice: highly productive habitats. *Mar Ecol Prog Ser* **277**: 1–12. DOI: https://doi.org/10.3354/meps277001

Kauko, HM, Taskjelle, T, Assmy, P, Pavlov, AK, Mundy, C, et al. 2016 Windows in Arctic sea ice: light transmission and ice algae in a refrozen lead. *J Geophys Res – Biogeosc*. DOI: https://doi.org/10.1002/2016JG003626

Kottmeier, ST and **Sullivan, CW** 1987 Late winter primary production and bacterial production in sea ice and seawater west of the Antarctic Peninsula. *Mar Ecol Prog Ser* **36**: 287–298. DOI: https://doi.org/10.3354/meps036287

Kottmeier, ST and **Sullivan, CW** 1988 Sea ice microbial communities (SIMCO). 9. Effects of temperature and salinity on rates of metabolism and growth of autotrophs and heterotrophs. *Polar Biol* **8**: 293–304. DOI: https://doi.org/10.1007/BF00263178

Krell, A, Beszteri, B, Dieckmann, G, Glockner, G, Valentin, K and **Mock, T** 2008 A new class of ice-binding proteins discovered in a salt-stress-induced cDNA library of the psychrophilic diatom *Fragilariopsis cylindrus* (Bacillariophyceae). *Eur J Phycol* **43**: 423–433. DOI: https://doi.org/10.1080/09670260802348615

Krembs, C, Eicken, H and **Deming, J** 2011 Exopolymer alteration of physical properties of sea ice and implications for ice habitability and biogeochemistry in a warmer Arctic. *Proc Natl Acad Sci USA* **108**: 3653–3658. DOI: https://doi.org/10.1073/pnas.1100701108

Krembs, C, Gradinger, R and **Spindler, M** 2000 Implications of brine channel geometry and surface area for the interaction of sympagic organisms in Arctic sea ice. *J Exp Mar Biol Ecol* **243**: 55–80. DOI: https://doi.org/10.1016/S0022-0981(99)00111-2

Lange, BA, Michel, C, Beckers, JF, Casey, JA, Flores, H, et al. 2015 Comparing springtime ice-algal chlorophyll *a* and physical properties of multi-year and first-year sea ice from the Lincoln Sea. *PLoS ONE* **10**: e0122418. DOI: https://doi.org/10.1371/journal.pone.0122418

Lazzara, L, Nardello, I, Ermanni, C, Mangoni, O and **Saggiomo, V** 2007 Light environment and seasonal dynamics of microalgae in the annual sea ice at Terra Nova Bay, Ross Sea, Antarctica. *Antarctic Sc* **19**: 83–92. DOI: https://doi.org/10.1017/S0954102007000119

Lee, SH, Jin, M and **Whitledge, TE** 2010 Comparison of bottom sea-ice algal characteristics from coastal and offshore regions in the Arctic Ocean. *Polar Biol* **33**: 1331–1337. DOI: https://doi.org/10.1007/s00300-010-0820-1

Lee, SH, McRoy, CP, Joo, HM, Gradinger, R, Cui, X, et al. 2011 Holes in progressively thinning Arctic sea ice lead to new ice algae habitat. *Oceanography* **24**: 302–308. DOI: https://doi.org/10.5670/oceanog.2011.81

Lee, SH, Stockwell, DA, Joo, H-M, Son, YB, Kang, C-K and **Whitledge, TE** 2012 Phytoplankton production from melting ponds on Arctic sea ice. *J Geophys Res* **117**(C04): 030. DOI: https://doi.org/10.1029/2011JC007717

Legendre, L, Ackley, SF, Dieckmann, GS, Gulliksen, B, Horner, R, et al. 1992 Ecology of sea ice biota. 2. Global significance. *Polar Biol* **12**: 429–444. DOI: https://doi.org/10.1007/BF00243114

Leu, E, Mundy, CJ, Assmy, P, Campbell, K, Gabrielsen, TM, et al. 2015 Arctic spring awakening – Steering principles behind the phenology of vernal ice algal blooms. *Prog Oceanogr* **139**: 161–170. DOI: https://doi.org/10.1016/j.pocean.2015.07.012

Leu, E, Søreide, JE, Hessen, DO, Falk-Petersen, S and **Berge, J** 2011 Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: Timing, quantity, and quality. *Prog Oceanogr* **90**: 18–32. DOI: https://doi.org/10.1016/j.pocean.2011.02.004

Lizotte, MP 2001 The contributions of Sea Ice Algae to Antarctic marine primary production. *Amer Zool* **41**: 57–73. DOI: https://doi.org/10.1093/icb/41.1.57

Lizotte, MP and **Sullivan, CW** 1991 Photosynthesis-irradiance relationships in microalgae associated with Antarctic pack ice: evidence for in situ activity. *Mar Ecol Prog Ser* **71**: 175–184. DOI: https://doi.org/10.3354/meps071175

Lund-Hansen, LC, Hawes, I, Sorrell, BK and **Nielsen, MH** 2014 Removal of snow cover inhibits spring growth of Arctic ice algae through physiological and behavioral effects. *Polar Biol* **37**: 471–481. DOI: https://doi.org/10.1007/s00300-013-1444-z

Manes, SS and **Gradinger, R** 2009 Small scale vertical gradients of Arctic ice algal photophysiological properties. *Photosynth Res* **102**: 53–66. DOI: https://doi.org/10.1007/s11120-009-9489-0

Mangoni, O, Carrada, GC, Modigh, M, Catalano, G and **Saggiomo, V** 2009 Photoacclimation in Antarctic bottom ice algae: an experimental approach. *Polar*

Biol **32**: 325–335. DOI: https://doi.org/10.1007/s00300-008-0517-x

McMinn, A, Ashworth, C and **Ryan, K** 1999 Growth and productivity of Antarctic sea ice algae under PAR and UV Irradiances. *Bot Mar* **42**: 401–407.

McMinn, A and **Hegseth, EN** 2003 Early spring pack ice algae from the Arctic and Antarctic: how different are they? In: Huiskes, AHL, Gieskes, WWC, Rozema, J, Schorno, RML, van der Vies, SM and Wolff, WJ (eds.), *Antarctic biology in a global context*, 182–186. Leiden: Backhuys publishers.

McMinn, A, Pankowskii, A, Ashworth, C, Bhagooli, R, Ralph, P and **Ryan, K** 2010 In situ net primary productivity and photosynthesis of Antarctic sea ice algal, phytoplankton and benthic algal communities. *Mar Biol* **157**: 1345–1356. DOI: https://doi.org/10.1007/s00227-010-1414-8

McMinn, A, Ryan, K and **Gademann, R** 2003 Diurnal changes in photosynthesis of Antarctic fast ice algal communities determined by pulse amplitude modulation fluorometry. *Mar Biol* **143**: 359–367. DOI: https://doi.org/10.1007/s00227-003-1052-5

Meier, WN 2017 Losing Arctic sea ice: observations of the recent decline and the long-term context. In: Thomas, DN (ed.), *Sea Ice* 3rd Edition, 290–303. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch11

Meiners, KM, Arndt, S, Bestley, S, Krumpen, T, Ricker, R, et al. 2017 Antarctic pack ice algal distribution: Floe-scale spatial variability and predictability from physical parameters. *Geophys Res Lett* **44**. DOI: https://doi.org/10.1002/2017GL074346

Meiners, KM and **Michel, C** 2017 Dynamics of nutrients, dissolved organic matter and exopolymers in sea ice. In: Thomas, DN (ed.), *Sea Ice* 3rd Edition, 415–432. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch17

Meiners, KM, Vancoppenolle, M, Thanassekos, S, Dieckmann, GS, Thomas, DN, et al. 2012 Chlorophyll *a* in Antarctic sea ice from historical ice core data. *Geophys Res Lett* **39**(L2): 1602. DOI: https://doi.org/10.1029/2012GL053478

Melnikov, IA, Kolosova, EG, Welch, HE and **Zhitina, LS** 2002 Sea ice biological communities and nutrients dynamics in the Canada Basin of the Arctic Ocean. *Deep Sea Res I* **49**: 1623–1649. DOI: https://doi.org/10.1016/S0967-0637(02)00042-0

Michel, C, Nielsen, TG, Nozais, C and **Gosselin, M** 2002 Significance of sedimentation and grazing by ice micro- and meiofauna for carbon cycling in annual sea ice (northern Baffin Bay). *Aquat Microb Ecol* **30**: 57–68. DOI: https://doi.org/10.3354/ame030057

Mikkelsen, DM, Rysgaard, S and **Glud, RN** 2008 Microalgal composition and primary production in Arctic sea ice: a seasonal study from Kobbefjord (Kangerluarsunnguaq), West Greenland. *Mar Ecol Prog Ser* **368**: 65–74. DOI: https://doi.org/10.3354/meps07627

Miller, L, Fripiat, F, Else, BGT, Bowman, JS, Brown, KA, et al. 2015 Methods for biogeochemical studies of sea ice: The state of the art, caveats, and recommendations. *Elem Sci Anth* **3**: 000038 DOI: https://doi.org/10.12952/journal.elementa.000038

Mock, T and **Gradinger, R** 1999 Determination of Arctic ice algal production with a new *in situ* incubation technique. *Mar Ecol Prog Ser* **177**: 15–26. DOI: https://doi.org/10.3354/meps177015

Montresor, M, Loveloy, C, Orsini, L, Procaccini, G and **Roy, S** 2003 Bipolar distribution of the cyst-forming dinoflagellate *Polarella glacialis. Polar Biol* **26**: 186–194.

Mundy, CJ, Barber, DG and **Michel, C** 2005 Variability of snow and ice thermal, physical and optical properties pertinent to sea ice algal biomass during spring. *J Mar Syst* **58**: 107–120. DOI: https://doi.org/10.1016/j.jmarsys.2005.07.003

Mundy, CJ, Ehn, JK, Barber, DG and **Michel, C** 2007 Influence of snow cover and algae on the spectral dependence of transmitted irradiance through Arctic landfast first-year sea ice*. J Geophys Res* **112**(C03): 007. DOI: https://doi.org/10.1029/2006JC003683

Mundy, CJ, Gosselin, M, Ehn, JK, Belzile, C, Poulin, M, et al. 2011 Characteristics of two distinct high-light acclimated algal communities during advanced stages of sea ice melt. *Polar Biol* **34**: 1869–1886. DOI: https://doi.org/10.1007/s00300-011-0998-x

Nicolaus, M, Katlein, C, Maslanik, J and **Hendricks, S** 2012 Changes in Arctic sea ice result in increasing light transmittance and absorption. *Geophys Res Lett* **39**(L2): 4501. DOI: https://doi.org/10.1029/2012GL053738

Niemi, A, Michel, C, Hille, K and **Poulin, M** 2011 Protist assemblages in winter sea ice: setting the stage for the spring ice algal bloom. *Polar Biol* **34**: 1803–1817. DOI: https://doi.org/10.1007/s00300-011-1059-1

Olsen, LM, Laney, SR, Duarte, P, Kauko, HM, Fernandez-Mendez, M, et al. 2017 The role of multiyear ice in seeding ice algae blooms in the Arctic pack ice. *J Geophys Res – Biogeosci* **122**. DOI: https://doi.org/10.1002/2016JG003660

Palmisano, AC, Beeler Soohoo, J and **Sullivan, CW** 1987 Effects of four environmental variables on photosynthesis-irradiance relationships in Antarctic sea-ice microalgae. *Mar Biol* **94**: 299–306. DOI: https://doi.org/10.1007/BF00392944

Paterson, H and **Laybourn-Parry, J** 2012 Sea ice microbial dynamics over an annual cycle in Prydz Bay, Antarctica. *Polar Biol* **35**: 993–1002. DOI: https://doi.org/10.1007/s00300-011-1146-3

Perovich, DK 2017 Sea ice and sunlight., In: Thomas, DN (ed.), *Sea Ice* 3rd Edition, 110–137. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch4

Petrich, C and **Eicken, H** 2017 Overview of sea ice growth and properties. In: Thomas, DN (ed.), *Sea Ice* 3rd Edition, 1–41. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch1

Piwosz, K, Wiktor, JM, Niemi, A, Tatarek, A and **Michel, C** 2013 Mesoscale distribution and functional diversity of picoeukaryotes in the first-year sea ice of the

Canadian Arctic. *ISME Journal* **7**: 1461–1471. DOI: https://doi.org/10.1038/ismej.2013.39

Platt, T, Gallegos, CL and **Harrison, WG** 1980 Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J Mar Res* **38**: 687–701.

Post, E, Bhatt, US, Bitz, CM, Brodie, JF, Fulton, TL, et al. 2013 Ecological consequences of sea-ice decline. *Science* **341**(6145): 519–524.

Poulin, M, Duagbjerg, N, Gradinger, R, Ilyash, L, Ratkova, T and **von Quillfeldt, C** 2011 The pan-Arctic biodiversity of marine pelagic and sea-ice unicellular eukaryotes: a first-attempt assessment. *Mar Biodiv* **41**: 13–28. DOI: https://doi.org/10.1007/s12526-010-0058-8

Poulin, M, Underwood, GJC and **Michel, C** 2014 Sub-ice colonial *Melosira arctica* in Arctic first-year ice. *Diatom Res* **29**: 213–221. DOI: https://doi.org/10.1080/0269249X.2013.877085

Ralph, PJ, Ryan, KG, Martin, A and **Fenton, G** 2007 Melting out of sea ice causes greater photosynthetic stress in algae than freezing in. *J Phycol* **43**: 948–956. DOI: https://doi.org/10.1111/j.1529-8817.2007.00382.x

Ramirez, F, Tarroux, A, Hovinen, J, Navarro, J, Afan, I, et al. 2017 Sea ice phenology and primary productivity pulses shape breeding success in Arctic seabirds. *Sci Rep* **7**: 4500. DOI: https://doi.org/10.1038/s41598-017-04775-6

Ratkova, TN and **Wassmann, P** 2005 Sea ice algae in the White and Barents seas: composition and origin. *Polar Res* **24**: 95–110. DOI: https://doi.org/10.3402/polar.v24i1.6256

Regaudie-de-Gioux, A and **Duarte, CM** 2012 Temperature dependence of planktonic metabolism in the ocean. *Glob Biogeochem Cy* **26**(GB1): 015. DOI: https://doi.org/10.1029/2010GB003907

Remy, J-P, Becquevort, S, Haskell, TG and **Tison, J-L** 2008 Impact of the B-15 iceberg "stranding event" on the physical and biological properties of sea ice in McMurdo Sound, Ross Sea, Antarctica. *Antarctic Sci* **20**: 593–604. DOI: https://doi.org/10.1017/S0954102008001284

Riaux-Gobin, C, Poulin, M, Prodon, R and **Treguer, P** 2003 Land-fast ice microalgal and phytoplanktonic communities (Adélie Land, Antarctica) in relation to environmental factors during ice break-up. *Antarctic Sci* **15**: 353–364. DOI: https://doi.org/10.1017/S0954102003001378

Richardson, K, Beardall, J and **Raven, JA** 1983 Adaptation of uni-cellular algae to irradiance: an analysis of strategies. *New Phytol* **93**: 157–191. DOI: https://doi.org/10.1111/j.1469-8137.1983.tb03422.x

Riebesell, U, Schloss, I and **Smetacek, V** 1991 Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. *Polar Biol* **11**: 239–248. DOI: https://doi.org/10.1007/BF00238457

Rintala, J-M, Piiparinen, J, Blomster, J, Majaneva, M, Muuler, S, et al. 2014 *Polar Biol* **37**(12): 1811–1822. DOI: https://doi.org/10.1007/s00300-014-1563-1

Rintala, J-M, Spiling, K and **Blomster, J** 2007 Temporary cyst enables long-term dark survival of Scrippsiella hangoei (Dinophyceae). *Mar Biol* **152**: 57–62. DOI: https://doi.org/10.1007/s00227-007-0652-x

Roberts, D, Craven, M, Cai, M, Allison, I and **Nash, G** 2007 Protists in the marine ice of the Amery Ice Shelf, East Antarctica. *Polar Biol* **30**: 143–153. DOI: https://doi.org/10.1007/s00300-006-0169-7

Robinson, DH, Arrigo, KR, Iturriaga, R and **Sullivan, CW** 1995 Microalgal light-harvesting in extreme low-light environments in McMurdo sound, Antarctica. *J Phycol* **31**: 508–520. DOI: https://doi.org/10.1111/j.1529-8817.1995.tb02544.x

Robinson, DH, Arrigo, KR, Kolber, Z, Gosselin, M and **Sullivan, CW** 1998 Photophysiological evidence of nutrient limitation of platelet ice in McMurdo sound, Antarctica. *J Phycol* **34**: 788–797. DOI: https://doi.org/10.1046/j.1529-8817.1998.340788.x

Rochet, M, Legendre, L and **Demers, D** 1985 Acclimation of sea-ice microalgae to freezing temperature. *Mar Ecol Prog Ser* **24**: 187–191. DOI: https://doi.org/10.3354/meps024187

Roukaerts, A, Cavagna, A-J, Fripiat, F, Lannuzal, D, Meiners, KM and **Dehairs, F** 2016 Sea-ice algal primary production and nitrogen uptake rates off East Antarctica. *Deep Sea Res II* **131**: 140–149. DOI: https://doi.org/10.1016/j.dsr2.2015.08.007

Rozanska, M, Gosselin, M, Poulin, M, Wiktor, JM and **Michel, C** 2009 Influence of environmental factors on the development of bottom ice protist communities during the winter-spring transition. *Mar Ecol Prog Ser* **386**: 43–59. DOI: https://doi.org/10.3354/meps08092

Rozanska, M, Poulin, M and **Gosselin, M** 2008 Protist entrapment in newly formed sea ice in the Coastal Arctic Ocean. *J Mar Syst* **74**: 887–901. DOI: https://doi.org/10.1016/j.jmarsys.2007.11.009

Ryan, KG, Tay, ML, Martin, A, McMinn, A and **Davy, SK** 2011 Chlorophyll fluorescence imaging analysis of the responses of Antarctic bottom-ice algae to light and salinity during melting. *J Exp Mar Biol Ecol* **399**: 156–161. DOI: https://doi.org/10.1016/j.jembe.2011.01.006

Sackett, O, Petrou, K, Reedy, B, De Grazia, A, Hill, R, et al. 2013 Phenotypic plasticity of Southern Ocean diatoms: Key to success in the sea ice habitat? *PLoS ONE* **8**(e8): 1185. DOI: https://doi.org/10.1371/journal.pone.0081185

Selz, V, Lowry, K, Lewis, K, Joy-Warren, H, Van de Poll, W, et al. 2017 Distribution of *Phaeocystis antarctica*-dominated sea ice algal communities and their potential to seed phytoplankton across the west Antarctic Peninsula in spring. *Mar Ecol Prog Ser.* DOI: https://doi.org/10.3354/meps12367

Sime-Ngando, T, Gosselin, M, Juniper, SK and **Levasseur, M** 1997 Changes in sea-ice phagotrophic microprotists (20–200-μm) during the spring algal bloom, Canadian Arctic Archipelago. *J Mar Syst* **11**: 163–172. DOI: https://doi.org/10.1016/S0924-7963(96)00036-X

Smetacek, V, Scharek, R, Gordon, LI, Eicken, H, Fahrbach, E, et al. 1992 Early spring phytoplankton blooms in ice platelet layers of the southern Weddell

Sea, Antarctica. *Deep Sea Res* **39**(2A): 153–168. DOI: https://doi.org/10.1016/0198-0149(92)90102-Y

Smith, REH, Anning, J, Clement, P and **Cota, G** 1988 Abundance and production of ice algae in Resolute Passage, Canadian Arctic. *Mar Ecol Prog Ser* **48**: 251–263. DOI: https://doi.org/10.3354/meps048251

Smith, REH and **Herman, AW** 1991 Productivity of sea ice algae: In situ vs. incubator methods. *J Mar Syst* **2**: 97–110. DOI: https://doi.org/10.1016/0924-7963(91)90016-N

Søreide, JE, Leu, E, Berge, J, Graeve, M, Falk-Petersen, S, et al. 2010 Timing in blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Global Change Biol.* DOI: https://doi.org/10.1111/j.1365-2486.2010.02175.x

Stammerjohn, S and **Maksym, T** 2017 Gaining (and losing) Antarctic sea ice: variability, trends and mechanisms. In: Thomas, DN (ed.), *Sea Ice*, 3rd Edition, 261–289. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch10

Stefels, J 2000 Physiological aspects of the production and conversion of DMSP in marine algae and higher plants. *J Sea Res* **43**: 183–197. DOI: https://doi.org/10.1016/S1385-1101(00)00030-7

Stefels, J, Steinke, M, Turner, S, Malin, G and **Belviso, S** 2007 Environmental constraints on the production and removal of the climatically active gas dimethylsulphide (DMS) and implications for ecosystem modelling. *Biogeochem* **83**: 245–275. DOI: https://doi.org/10.1007/s10533-007-9091-5

Steiner, N, Deal, C, Lannuzel, D, Lavoie, D, Massonnet, F, et al. 2016 What sea-ice biogeochemical modellers need from observational scientists. *Elem Sci Anth* **4**: 000084. DOI: https://doi.org/10.12952/journal.elementa.000084

Stoecker, DK, Buck, R and **Putt, M** 1992 Changes in the sea-ice brine community during the spring-summer transition, McMurdo Sound, Antarctica. I. Photosynthetic protists. *Mar Ecol Prog Ser* **84**: 265–278. DOI: https://doi.org/10.3354/meps084265

Stoecker, DK, Gustafson, DE, Baier, CT and **Black, MMD** 2000 Primary production in the upper sea ice. *Aq Microb Ecol* **21**: 275–287. DOI: https://doi.org/10.3354/ame021275

Stoecker, DK, Gustafson, DE, Black, MMD and **Baier, CT** 1998 Population dynamics of microalgae in the upper land-fast sea ice at a snow-free location. *J Phycol* **34**: 60–69. DOI: https://doi.org/10.1046/j.1529-8817.1998.340060.x

Strickland, JDH and **Parsons, TR** 1972 A practical handbook of seawater analysis. *Bull Fish Res Bd Can* **167**.

Suzuki, Y, Kudoh, S and **Takahashi, M** 1997 Photosynthetic and respiratory characteristics of an Arctic ice algal community living in low light and low temperature conditions. *J Mar Syst* **11**: 11–121. DOI: https://doi.org/10.1016/S0924-7963(96)00032-2

Syvertsen, EE 1991 Ice algae in the Barents Sea: types of assemblages, origin, fate and role in the ice-edge phytoplankton bloom. *Polar Res* **10**: 277–287. DOI: https://doi.org/10.3402/polar.v10i1.6746

Syvertsen, EE and **Kristiansen, S** 1993 Ice algae during EPOS, leg 1: assemblages, biomass, origin and nutrients. *Polar Biol* **13**: 61–65. DOI: https://doi.org/10.1007/BF00236584

Tamelander, T, Reigstad, M, Hop, H and **Ratkova, T** 2009 Ice algal assemblages and vertical export of organic matter from sea ice in the Barents Sea and Nansen Basin (Arctic Ocean). *Polar Biol* **32**: 1261–1273. DOI: https://doi.org/10.1007/s00300-009-0622-5

Tedesco, L and **Vichi, M** 2010 BFM-SI: a new implementation of the Biogeochemical Flux Model in Sea Ice. *CMCC Research Papers*, RP0081, www.earthprints.org/bitstream/2122/5956/6/rp0081.pdf.

Tedesco, L and **Vichi, M** 2014 Sea Ice Biogeochemistry: A Guide for Modellers. *PLoS ONE* **9**: e89217. DOI: https://doi.org/10.1371/journal.pone.0089217

Tedesco, L, Vichi, M, Haapala, J and **Stipa, T** 2010 A dynamic Biologically-Active Layer for numerical studies of the sea ice ecosystem. *Ocean Modelling* **35**: 89–104. DOI: https://doi.org/10.1016/j.ocemod.2010.06.008

Tedesco, L, Vichi, M and **Thomas, DN** 2012 Process studies on the ecological coupling between sea ice algae and phytoplankton. *Ecol Model* **226**: 120–138. DOI: https://doi.org/10.1016/j.ecolmodel.2011.11.011

Thomas, DN (ed.) 2017 *Sea Ice*, 3rd Edition, 652. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371

Thomas, DN, Baumann, MEM and **Gleitz, M** 1992 Efficiency of carbon assimilation and photoacclimation in a small unicellular *Chaetoceros* species from the Weddell Sea (Antarctica): Influence of temperature and irradiance. *J Exp Mar Biol Ecol* **157**: 195–209. DOI: https://doi.org/10.1016/0022-0981(92)90162-4

Thomas, DN and **Dieckmann, GS** 2002 Antarctic Sea Ice—a Habitat for Extremophiles. *Science* **295**: 641–644. DOI: https://doi.org/10.1126/science.1063391

Thomson, PG, McMinn, A, Kiessling, I, Watson, M and **Goldsworthy, PM** 2006 Composition and succession of dinoflagellates and chrysophytes in the upper fast ice of Davis Station, east Antarctica. *Polar Biol* **29**: 337–345. DOI: https://doi.org/10.1007/s00300-005-0060-y

Tilzer, MM and **Dubinsky, Z** 1987 Effects of temperature and day length on the mass balance of Antarctic phytoplankton. *Polar Biol* **7**: 35–42. DOI: https://doi.org/10.1007/BF00286822

Tilzer, MM, Elbrachter, M, Gieskes, WWC and **Beese, B** 1986 Light-temperature interactions in the control of photosynthesis in Antarctic phytoplankton. *Polar Biol* **5**: 105–111. DOI: https://doi.org/10.1007/BF00443382

Tison, J-L, Brabant, F, Dumont, I and **Stefels, J** 2010 High-resolution dimethylsulfide and dimethylsulfoniopropionate time series profiles in decaying summer first-year sea ice at Ice Station Polarstern, western Weddell Sea, Antarctica. *J Geophys Res* **115**(G04): 044. DOI: https://doi.org/10.1029/2010JG001427

Torstensson, A, Dinasquet, J, Chierci, M, Fransson, A, Riemann, L and **Wulff, A** 2015 Physicochemical control of bacterial and protist community composition and diversity in Antarctic sea ice. *Environ Microbiol* **17**(10): 3869–3881. DOI: https://doi.org/10.1111/1462-2920.12865

Ugalde, SC, Westwood, KJ, van den Enden, R, McMinn, A and **Meiners, KM** 2016 Characteristics and primary productivity of East Antarctic pack ice during the winter-spring transition. *Deep Sea Res II* **131**: 123–139. DOI: https://doi.org/10.1016/j.dsr2.2015.12.013

Vancoppenolle, M, Bopp, L, Madec, G, Dunne, J, Ilyina, T, Halloran, PR and **Steiner, N** 2013b Future Arctic Ocean primary productivity from CMIP5 simulations: Uncertain outcome, but consistent mechanisms, *Global Biogeochem Cy* **27**: 605–619. DOI: https://doi.org/10.1002/gbc.20055

Vancoppenolle, M, Meiners, KM, Michel, C, Bopp, L, Brabant, F, et al. 2013a Role of sea ice in global biogeochemical cycles: emerging views and challenges. *Quaternary Sci Rev* **79**: 207–230. DOI: https://doi.org/10.1016/j.quascirev.2013.04.011

Vancoppenolle, M and **Tedesco, L** 2017 Numerical models of sea ice biogeochemistry., In: Thomas, DN (ed.), *Sea Ice*, 3rd Edition, 492–515. Oxford, UK: Wiley-Blackwell. DOI: https://doi.org/10.1002/9781118778371.ch20

Van Leeuwe, MA, van Sikkelerus, B, Gieskes, WWC and **Stefels, J** 2005 Photoacclimation to fluctuating irradiance in two Antarctic algal species: taxon-specific differences in *Chaetoceros brevis* (Bacillariophyceae) and *Pyramimonas* sp. (Prasinophyceae). *Mar Ecol Prog Ser* **288**: 9–19. DOI: https://doi.org/10.3354/meps288009

Van Leeuwe, MA and **Stefels, J** 2007 Photosynthetic responses in *Phaeocystis antarctica* towards varying light and iron conditions. *Biogeochem*, 83: 61–70. DOI: https://doi.org/10.1007/s10533-007-9083-5

Von Quillfeldt, CH, Ambrose, WG, Jr. and **Clough, LM** 2003 High number of diatom species in first-year ice from the Chukchi Sea. *Polar Biol* **26**: 806–818. DOI: https://doi.org/10.1007/s00300-003-0549-1

Werner, I, Ikavalko, J and **Schunemann, H** 2007 Sea-ice algae in Arctic pack ice during late winter. *Polar Biol* **30**: 1493–1504. DOI: https://doi.org/10.1007/s00300-007-0310-2

Zhang, Q, Gradinger, R and **Spindler, M** 1998 Dark survival of marine microalgae in the high Arctic (Greenland Sea). *Polarforschung* **75**: 111–116.

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