The Impact of Sea-ice Retreat on the Composition and Productivity of Phytoplankton Communities in the Arctic Ocean: a Perspective on Climate Change

Literature review as part of BIO458 - Primary Producers of the Sea

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Abstract

Sea ice in the Arctic Ocean dramatically declined during the last decades. A plethora of studies has shown that the rapidly changing icescape affects marine primary producers. However, evaluating the dynamics of ice-algae and phytoplankton communities necessitates further understanding of how ice losses shape community structure and productivity.

This study synergized the current state of knowledge in the context of climate change. I applied a reflexive thematic analysis (RTA) to identify thematic patterns in the literature that describe abiotic and biotic changes resulting from ice retreat.

The review highlights that seasonal and interannual ice losses shape the phytoplanktonic environment and community structure. Small mixotrophic species tend to become abundant as sea ice declines which likely impacts primary productivity. The findings appeal to future studies to consider both abiotic and biotic drivers in a multi-causal context to assess phytoplankton dynamics and primary production at high latitudes.

Introduction

Sea-ice dynamics in the Arctic Ocean in times of climate change

The decrease of sea ice in the Arctic Ocean is one of the most distinct signs of global warming. Ice extent and thickness have declined dramatically during the past decades (Brown et al., 2017), (Onarheim et al., 2018) (Fig. 1), and the predominance of multi-year ice (MYI) has shifted to first-year ice (FYI) (Brown et al., 2017). Summer sea-ice cover in the Arctic Ocean has shrunk by more than 40% since the 1970s, and average thickness by about 65% (Ardyna and Arrigo, 2020). Whereas MYI still accounted for two-thirds of the ice surface in 1984, the proportion was only about 30% in 2018 (Ardyna, Mundy, Mills, et al., 2020).

A reduced ice extent results in a lower surface albedo, causing the water to absorb more solar radiation (Arrigo et al., 2008). Higher surface temperatures and extended melting periods favor the premature formation and expansion of water ponds, and thus continue to drive melting (Markus et al., 2009). Exceptional high temperatures were measured in the years from 2010 to 2015 in comparison to the last two centuries (Ardyna and Arrigo, 2020).

Historically, sea-ice dynamics undergo distinct seasonal and regional fluctuations in the Arctic. Shelf seas as the Beaufort Sea, Canadian Archipelago, Central Arctic Sea, Chukchi Sea, and East Siberian Sea are ice-covered throughout winter, and change strongly between ice-covered and ice-free states in summer. In contrast, the icescape of southern seas as the Baffin Bay, Barents Sea, Greenland Sea, and Sea of Okhotsk are characterized by higher variation during winter (Onarheim et al., 2018). Ice-coverage shrinks during spring and summer with a minimum in September. In the open sea, around 50% of the winter ice coverage endures the summer season (Brown et al., 2017). However, those regional patterns tend to change, and climate models predict the Arctic Ocean to be ice-free in summer before the mid-century (Brown et al., 2017).

The progression of ice loss is likely to worsen re-

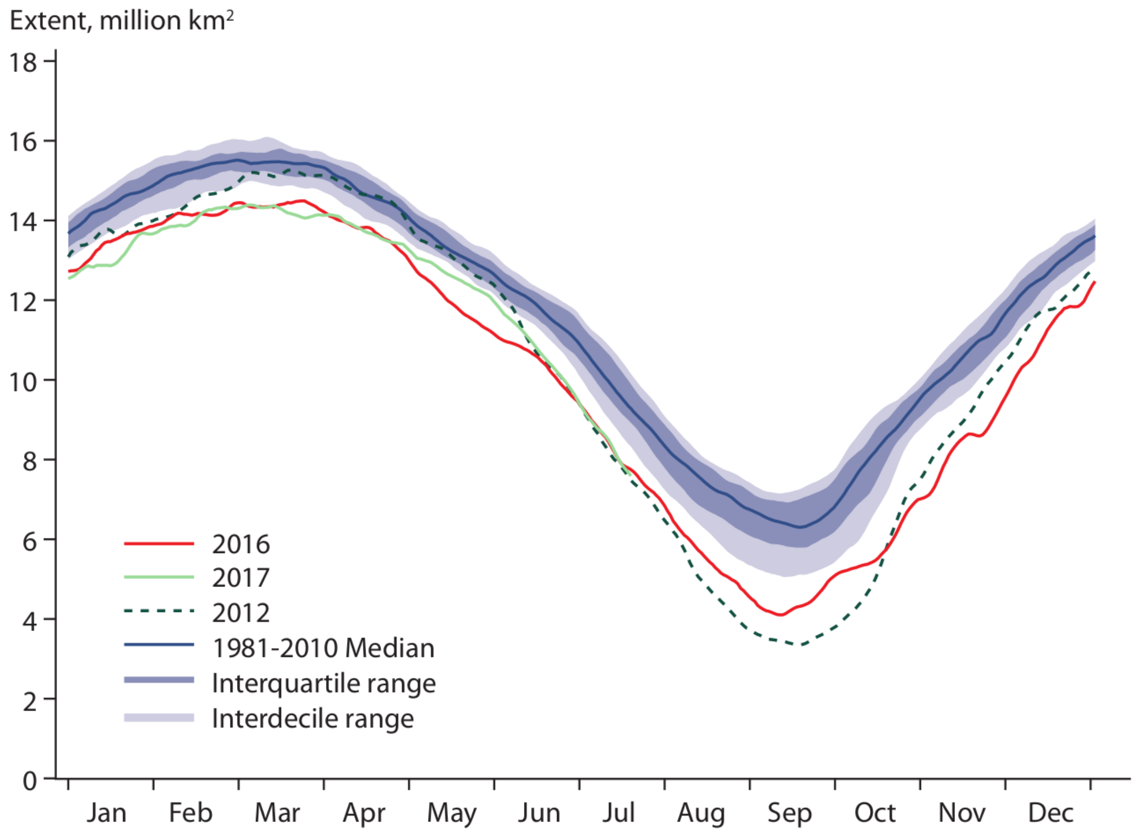

Figure 1: Average annual sea-ice extent in the Arctic Ocean between 1981 and 2017. *Note.* From "Snow, water, ice and permafrost in the Arctic (SWIPA) 2017" (ed. Simon, C., p. 106), by Brown, R., Vikhamar Schuler, D., Bulygina, O., Derksen, C., Luojus, K., Mudryk, L., Wang, L., and Yang, D., Oslo, Norway: Arctic Monitoring and Assessment Programme (AMAP). Copyright 2017 by Arctic Monitoring and Assessment Programme (AMAP).

gional stratification, as additional freshwater flows in from melting glaciers. At the same time, ice absence increases surface exposition to winds which alters mixing patterns. In constant exchange with atlantic and pacific waters, respectively via Fram Strait and Bering Strait, heat, nutrients, and microorganisms also enter the Arctic Ocean driven by advective processes (Ardyna and Arrigo, 2020). Rapid and enormous biophysical changes influence the arctic biodiversity and may alter primary productivity (Frey et al., 2021), (Gebruk et al., 2012).

Primary producers of the Arctic Ocean: bloom dynamics and taxonomic composition

Sea ice inhabiting algae and pelagic phytoplankton account mainly for the primary production in the Arctic Ocean (Frey et al., 2021). Nutrient (i.a., nitrate and silicate) and light availability shape the biogeography and the trophic structure of primary producers in the Arctic (Ardyna and Arrigo, 2020). Both nitrate and silicate decreased during the last decades as a result of altered circulation patterns (Ardyna and Arrigo, 2020).

In early spring, blooms start with ice-algae communities in liquid-filled cavities within the ice, with MYI showing a higher species diversity than FYI (Hop et al., 2020). The subsequent melt initiates the under-ice (UI) bloom (Ardyna and Arrigo, 2020), whereby released ice-algae may seed the emerging assemblage (Lin et al., 2018). As many species occur in both ice and pelagic communities, the extent of the ice algae's seeding effect on pelagic communities cannot be quantified based on observations (Selz et al., 2018). The snow layer on top and ice-algae assemblages in the ice determine light transmission, and thus the UI bloom formation (Ardyna, Mundy, Mills, et al., 2020). Thin ice and snow coverage increase the exposure of ice algae to light. Those may be harmed by over-irradiance in spring whereas under-ice phytoplankton growth may be promoted (Hop et al., 2020).

The UI bloom is followed by a bloom in late spring which extends into June or July, depending on latitude (Ardyna and Arrigo, 2020). Usually, the bloom shows a high abundance of large diatoms (e.g., *Fragilariopsis*, *Thalasiossila*, *Chaetoceros*) during that time (Fujiwara et al., 2014). After a decrease in biomass, a second bloom occurs in late summer (Ardyna and Arrigo, 2020), accompanied by a change in dominance from diatoms to dinoflagellates or picoeukaryotes (Fujiwara et al., 2014).

Extended ice-free periods open a larger temporal window for phytoplankton blooms, and the number of known phytoplankton taxa in the Arctic Ocean increased from 1,874 in 2011 to 2,241 in 2017 (Ardyna and Arrigo, 2020). Hence, assessing current and future dynamics of primary production in the Arctic Ocean necessitates the understanding of the effects of ice-loss-related changes in the phytoplanktonic environment on community structure and productivity.

Aim of the study

This study aimed to review scientific findings on the impact of sea-ice loss on the composition of Arctic phytoplankton communities. In a broader view, the review was intended to discuss the relationship between community composition and productivity of Arctic primary producers in the context of global warming. Three essential questions guided the review: (1) How do seasonal and interannual sea-ice losses change the phytoplanktonic environment? (2) How does the decline of sea ice alter the composition of phytoplankton communities in the Arctic Ocean? (3) What evidence does the literature provide on the relationship between sea-ice retreat, community composition, and productivity?

Methods

Literature search & selection criteria

I conducted the literature search on the literature databases JSTOR (on full-text level) and Scopus (on abstract level) using the search string: *((ice AND loss) OR (ice AND retreat) OR (ice AND decline)) AND (phytoplankton OR protist) AND (diversity OR composition OR (primary AND productivity)) AND (arctic AND sea OR arctic AND ocean)*. I scanned the significance of articles first on abstract level, and then on full-text level. The abstract had to contain all thematic components of the search string. In the systematic search, I included studies that directly addressed the relation between phytoplankton composition and relevant environmental variables.

Reflexive thematic analysis

According to Braun and Clarke's approach, the reflexive thematic analysis (RTA) aims at identifying and analyzing interpretative patterns of themes in a qualitative dataset (e.g., text information). The workflow consists of six iterative steps: familiarization with the data, generating initial codes, generating themes, reviewing initial themes, defining and naming themes, and producing the report (Byrne, 2021). In this study, I applied the RTA to reveal thematic patterns in the literature that describe sea-ice retreat related abiotic and biotic changes, and their effects on the composition and productivity of arctic phytoplankton communities.

I conducted the data visualization in R Studio (v. 4.0.4). R Scripts and data are available on: GitHub (github.com/codymoly/GU-student-projects).

Results

Search results & methodological homogeneity

The search yielded a total number of 111 papers on the two databases. I selected 33 articles based on title and abstract level. After critically reading the full text and removing duplicates, 14 articles remained. I considered seven additional articles from reference lists that met the selection criteria or were relevant in a broader sense.

All included articles studied either UI and/or epipelagic phytoplankton communities between March and November. Sampling locations within the Arctic Ocean and years varied among the studies (Fig. 2), and included stations at both coastal and open-sea areas. Taxonomic classification was performed differently by the authors, either by applying microscopic or molecular techniques. The majority of articles used a canonical correlation analysis to test for relationships between community composition and environmental variables. If examined, diversity estimations considered indices for richness, dominance, and in some cases evenness.

RTA: final themes

Sea-ice retreat and associated changes in the phytoplanktonic environment

Disaggregation and thinning of the ice cover increases the pelagic light availability which alters phytoplankton bloom initiation and modulation (Ardyna, Mundy, Mills, et al., 2020). Ice algae accumulating within the ice play also a major role in reducing the light available for UI phytoplankton (Ardyna, Mundy, Mills, et al., 2020). Some pelagic species show greater tolerance to light fluctuation, such as *Phaecocystis pouchetii*, and are affected differently (Ardyna, Mundy, Mills, et al., 2020).

Shrinking of the ice cover reduces the surface albedo (Arrigo et al., 2008). The increased exposure of water to solar radiation leads to elevated temperatures (Wang et al., 2018b). Accelerated ice-melting affects a stronger stratification of the water column (Flores et al., 2019) and a lower surface salinity (Wang et al., 2018b). Stratification further inhibits the vertical water exchange and nutrient upwelling (Flores et al., 2019), (Wang et al., 2018b).

Sea-ice can store nutrients that are gradually released during melting (Selz et al., 2018). For example, silicate is regenerated in pack ice over the winter to be released during melting in spring and summer (Neeley et al., 2018).

Topography shapes the community composition and response to sea-ice loss

Water column characteristics and sea-ice conditions vary along with the transition from the shallow shelf to the open sea within the Arctic Ocean (Lin et al., 2018), (Wang et al., 2018b), (Wang et al., 2018a).

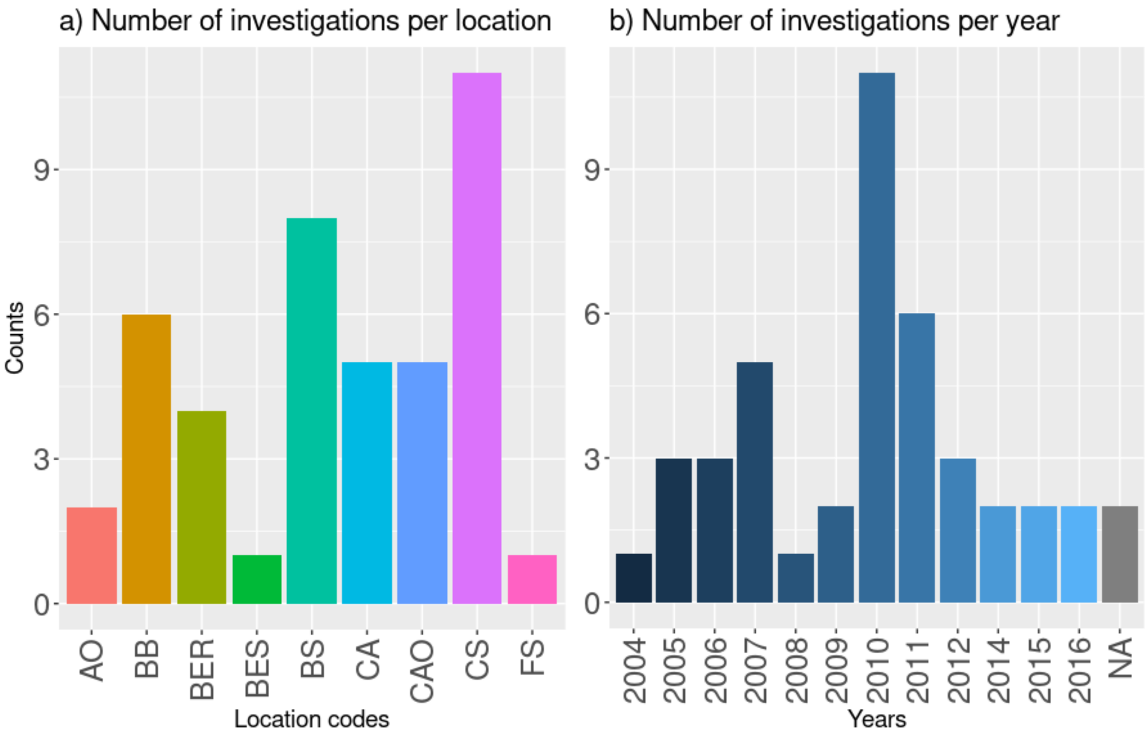

Figure 2: Distribution of investigations across a) locations and b) years in the reviewed studies. Some studies combined data from different expeditions. Hence, the figure does not show the number of articles but how often the location or year was represented. The reviews by Ardyna et al. (2011), and Ardyna and Arrigo (2020) addressed unspecific periods between the 1970s and 2018, and are therefore listed under *NA*. Location codes: *AO: Arctic Ocean (without further specification), BB: Baffin Bay, BER: Bering Sea, BES: Bering Strait, BS: Beaufort Sea, CA: Canadian Archipelago, CAO: Central Arctic Ocean, CS: Chukchi Sea, FS: Fram Strait.*

Compared to deep-sea areas, the euphotic zone in shelf zones is characterized by a fluctuating salinity, higher temperatures, and nutrient concentrations in summer, especially close to the Bering strait (Lin et al., 2018), (Wang et al., 2018a). Findings of Fujiwara et al. (2014) presented that those conditions are also present in late summer, and shape the phytoplankton composition (Fujiwara et al., 2014).

In the Chukchi Sea, summer sea-ice coverage and thickness increase from the shelf to the open sea (Lin et al., 2018). Subject to this, shelf assemblages of phytoplankton show a higher total abundance and species richness compared to deep-sea assemblages (Lin et al., 2018), (Wang et al., 2018a). Community composition also differs depending on the topographical location and related environmental traits (Fujiwara et al., 2014). Lin et al. (2018) revealed that sea-ice conditions are of greater importance for open-sea communities than for shelf communities in shaping the composition.

Ice-loss related shifts in relative abundances

Spring and early summer

Arctic phytoplankton communities are known to be dominated by centric and pennate diatoms with a seasonal shift from pennate species in spring to centric species in summer (Ardyna and Arrigo, 2020). Based on a long-term examination of UI blooms between 2004 and 2016, Ardyna et al. (2020b) defined two pan-arctic types of UI phytoplankton assemblages: diatom-dominated communities and those being dominated by *Phaecocystis pouchetii*. According to Neeley et al. (2018), *P. pouchetii* is known to be found in spring blooms in the Fram strait but showing low abundances. Especially at the ice edge, diatoms (e.g., *Nitzschia frigida*, *Melosira arctica*) are likely to be more abundant (Neeley et al., 2018). Evidence exists that nutrient depletion, particularly nitrate and silicate, may favour flagellate and *Phaecocystis sp.* species over diatoms (Ardyna, Mundy, Mills, et al., 2020). Stauffer et al. (2015) examined spring blooms in the shelf zone of the Bering sea. They observed a shift from *Phaecocystis sp.* in 2011 to large diatoms in 2012, where the ice cover was comparatively larger and thicker (Stauffer et al., 2015).

Summer and fall

Studying a phytoplankton bloom in later summer, Fujiwara et al. (2014) found that dinoflagellates and diatoms dominated shelf assemblages between 2008 and 2010 in the western Arctic Ocean. The occurrence of diatom-dominated accumulations correlated with high concentrations of silicate and inorganic nitrogen compounds (Fujiwara et al., 2014). In the basin area, prasinophytes and haptophytes were most abundant. Being adapted to cold temperatures and low light levels, prasinophytes tended to dominate assemblages. Particularly early ice-retreat led to a predominance of haptophytes which grow in oligotrophic and warmer waters, and tolerate light fluctuations (Fujiwara et al., 2014).

Nitrate-rich waters and higher temperatures up to 7 °C are conducive for the growth of diatoms (Ardyna and Arrigo, 2020), (Lasternas and Agustí, 2010). Depletion of nutrients may promote the trend towards flagellate-dominated communities but does not represent a sufficient criterion to predict abundance shifts (Ardyna and Arrigo, 2020). Investigations of the summer bloom in the Beaufort Sea and the East Siberian Sea in 2010 revealed diatoms to be dominant in relative abundance (around 94%) and species richness (around 61%). The authors suggest that those originated both from sea-ice and pelagic populations since nitrate and silicate concentrations were low (Wang et al., 2018b). During a massive melting event in the central Arctic basin in 2012, Flores et al. (2019) identified dinoflagellates as the most abundant taxonomic group (Flores et al., 2019). Contrary to this, Hardge et al. (2017) identified diatoms as the most abundant group, having a high proportion of species in common with the ice communities (e.g., *Melosira antarctica*). Overall phytoplankton diversity was lower in 2012 than in 2011, as the ice-cover showed a higher extent, concentration, and proportion of MYI (Hardge et al., 2017). The authors suggested that the composition of the pelagic phytoplankton was largely determined by the ice algae released during the melt (Hardge et al., 2017). Neeley et al. (2018) highlighted the dependence of diatom abundance on sea-ice conditions. Especially large taxa (i.a., *Bacteriosira*, *Nitzschia*, *Fragilariopsis*, and *Navicula*) depend on a large ice-cover resulting in a low surface water turbulence and a stable melt-water zone (Neeley et al., 2018).

Environmental forcing of the trophic community structure

Ardyna and Arrigo (2020) and Flores et al. (2019) singled out nutrient (NO_X, silicate, and iron) and light conditions as crucial drivers of the trophic structure in arctic phytoplankton communities. Changed ice-melt patterns and light conditions affect the growth of photo-autotrophs (Flores et al., 2019). This is supported by Fujiwara et al. (2014) who identified mixotrophic phytoplankton to be more abundant, when ice-melting starts early, and a low Albedo leads to heating of the water (Fujiwara et al., 2014). As the water column becomes more stratified and nutrients deplete, mixotrophic picocaryotes may be favored and outcompete exclusively phototrophic phytoplankton (e.g., diatoms) (Ardyna and Arrigo, 2020). In summer, particularly heterotrophs and mixotrophic protists like dinoflagellates tend to dominate as nutrient concentrations decline (Flores et al., 2019).

The link between ice-retreat and phytoplankton productivity

Average net primary production in the open Arctic Ocean increased by 30% between 1998 and 2012 (Ardyna and Arrigo, 2020). FYI which is thinner and less dense than MYI increases light availability for UI blooms, and elevates the productivity in spring (Ardyna, Mundy, Mills, et al., 2020). Extended melting periods and ice absence extend the growth phase of subsequent phytoplankton blooms (Ardyna and Arrigo, 2020). The relative increase of primary production varies regionally with the highest values in the Greenland Sea and the Barents Sea (Arrigo et al., 2008).

Contrary, Wang et al. (2018) argued that the inhibited nutrient exchange in a highly stratified water column may reduce the photosynthetic productivity in phytoplankton communities at surface levels. Oligotrophic conditions shape the community composition (i.e., more abundant flagellates) and consequently affect productivity (Ardyna, 2019). A high relative abundance of *Phaecocystis sp.* could inhibit the trophic transfer of carbon between pelagic and benthic layers since *Phaecocystis sp.* sediments in the surface. A dominance of *Phaecocystis sp.* may weaken the primary productivity compared to diatom-dominated communities (Ardyna, Mundy, Mills, et al., 2020). Also, Neeley et al. (2018) related reduced productivity to community composition. The interannual ice loss may favor diatom-poor taxonomic assemblages that are characterized by decreased chlorophyll *a* and carbon biomass (Neeley et al., 2018). Lasternas et al. (2010) attributed reduced productivity to changes in salinity and temperature as a result of exceptional ice melt. Particularly, the loss of MYI leads to the increased release of growth-inhibiting compounds that accumulated in the ice during industrialization (Lasternas and Agustí, 2010).

Discussion

How do seasonal and interannual sea-ice losses change the phytoplanktonic environment?

The decline of sea ice in the Arctic Ocean entails multiple consequences for marine primary producers. The interannual retreat of ice extent, thickness, and age alter the physical properties of the water column. Higher water temperatures result from a decreased surface albedo in the absence of ice (Arrigo et al., 2008), (Markus et al., 2009). Increasing freshwater supply strengthens the stratification of the water column and affects mixing dynamics (Wang et al., 2018b), (Wang et al., 2018a). Prolonged melting periods widen the temporal window for pelagic phytoplankton blooms (Ardyna et al., 2011). Considering the effect of the interannual ice-retreat on water-column stratification and thus, on the vertical nutrient transfer (Ardyna and Arrigo, 2020), (Wang et al., 2018b), ice-losses may be seen as a driver of trophic structures in phytoplankton communities. Gradual ice melting represents a source of nutrients (i.e., silicate) and trace elements through degrading sea-ice algae (Neeley et al., 2018), (Wang et al., 2018b). Consequently, the accelerated melting and the loss of ice during summer may even be considered as causes for oligotrophic conditions in the Arctic Ocean.

How does the decline of sea ice alter the composition of phytoplankton communities in the Arctic Ocean?

In view that MYI shows a higher diversity of ice-algae species than FYI (Hop et al., 2020), it can be assumed that the progressing loss of MYI results in a long-term depletion of ice-algae diversity. Since UI blooms are seeded by ice-algae and ice-embedded resting stages (Ardyna, Mundy, Mayot, et al., 2020), (Lin et al., 2018) pelagic communities may be affected by the loss of ice-algae species. As shown by Hardge et al. (2017) and Wang et al. (2018), pelagic communities can be significantly dominated by ice-algae species (e.g., *Melosira antarctica*, *Nitschia frigida*). It can be assumed that nutrient-poor conditions, increasing freshwater input, and a longer growth period will favor small phytoplankton over large (Wassmann, 2011), and mixotrophic taxa will gain in abundance (Flores et al., 2019), (Fujiwara et al., 2014). Accordingly, and presuming that nutrients will continue to deplete in marine arctic waters, the fate of large diatoms in the Arctic Ocean appears uncertain.

However, Lin et al. (2018) emphasized the temporal and regional variability of the community structure during summer. Biomass, total abundance, and taxonomic composition differ significantly between shelf and deep-sea regions in the Arctic Ocean, and follow biochemical and physical gradients (Lin et al., 2018), (Wang et al., 2018a). In this context, it is assumable that a spatial shift in species distribution could be more pronounced than a shift in local community composition, hypothesizing that spatial variability of phytoplankton communities modulates their responsiveness to environmental changes.

What evidence does the literature provide on the relationship between sea-ice retreat, community composition, and productivity?

Strong evidence exists that the retreat of arctic ice elevates primary production with some areas showing a higher increase in productivity than others (Arrigo et al., 2008). It seems reasonable that a premature bloom initiation and prolonged growth period increase annual productivity (Ardyna et al., 2011), (Ardyna and Arrigo, 2020). Although changes in community composition and persistent oligotrophic conditions may inhibit primary production (Wang et al., 2018b), (Wassmann, 2011), it remains unclear how altered circulation patterns will affect productivity as the ice-cover declines. While a strong stratification prevents nutrient upwelling (Flores et al., 2019), the contrary could result from higher surface turbulence of ice-free waters (Ardyna and Arrigo, 2020).

Until recently, as mentioned by Ardyna and Arrigo et al. (2020), the contribution of UI blooms to net primary production in the Arctic Ocean was considered insignificant. Past biomass-derived estimates of primary productivity in the Arctic Ocean may have led to misconceptions since UI blooms can hardly be detected by satellite imagery. As the ice extent decreases, study sites became more reachable over time resulting in a higher frequency of investigations (Ardyna and Arrigo, 2020). Moreover, as shown in this study, locations and years are examined unequally (Fig. 2). Accordingly, a temporally and regionally diverging data resolution could also bias findings.

Conclusion & outlook

The results highlighted a complex interconnection between environmental drivers and phytoplankton dynamics. The structure of phytoplankton communities reflects ice-retreat-related environmental patterns while being subject to strong seasonal and interannual variability. In the context of climate change, it can be expected that the taxonomic and trophic structure of phytoplankton communities changes as the arctic ice cover continues to degrade. Ambiguity prevails in terms of how varying environmental and biological variables affect primary productivity on a long-term scale.

Viewing the increasing number of marine phytoplankton species in the Arctic Ocean (Ardyna and Arrigo, 2020), it seems inevitable to consider interspecific interactions to evaluate the impact of certain environmental changes on phytoplankton communities. Hence, understanding the multi-causality behind changes in phytoplankton communities requires the consideration of both biotic and abiotic drivers.

Even though fragmentation and the overall decline of the ice cover favor the length and extent of phytoplankton blooms in the Arctic Ocean (Ardyna and Arrigo, 2020), it remains unclear how sea-ice loss, phytoplankton diversity, and community composition affect primary productivity. Measurements of phytoplankton biomass are often used to conclude about productivity (Vallina et al., 2014). However, given that the relative contribution to primary production differs among taxonomic groups (Ardyna, Mundy, Mills, et al., 2020), (Vallina et al., 2014), biomass may be insufficient to indicate productivity. Drawing the link between sea-ice retreat and primary productivity should therefore take diversity and taxonomy into account. In conclusion, leaning on Ardyna and Arrigo (2020), comparing estimations of productivity in the context of climate change should consider the influence of data resolution and potential underestimations in the past.

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