



Phytoplankton dynamics in a changing Arctic Ocean

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Changes in the Arctic atmosphere, cryosphere and Ocean are drastically altering the dynamics of phytoplankton, the base of marine ecosystems. This Review addresses four major complementary questions of ongoing Arctic Ocean changes and associated impacts on phytoplankton productivity, phenology and assemblage composition. We highlight trends in primary production over the last two decades while considering how multiple environmental drivers shape Arctic biogeography. Further, we consider changes to Arctic phenology by borealization and hidden under-ice blooms, and how the diversity of phytoplankton assemblages might evolve in a novel Arctic 'biogeochemical landscape'. It is critical to understand these aspects of changing Arctic phytoplankton dynamics as they exert pressure on marine Arctic ecosystems in addition to direct effects from rapid environmental changes.

The Arctic climate is in the process of irretrievably moving into a new state, forced by increases in atmospheric levels of carbon dioxide and other greenhouse gases^{1,2}. As a result, the years 2010 to 2015 were the warmest five years on record in the Arctic, with a dramatic 5 °C increase in January since 1900 (ref. ¹). This heat trapped by greenhouse gases triggers a cascade of feedbacks that collectively amplify Arctic warming¹. Over the next two decades, an additional 4–5 °C increase is predicted in the autumn and winter across the Arctic in conjunction with the projected increase in greenhouse gases concentrations¹. This expected temperature increase is more than twice that projected for the global average.

Associated with the increased temperatures, the Arctic Ocean is experiencing radical modifications in its hydrographic properties (that is, freshwater, salt and heat content) and in its overall circulation. Driven by increasing inputs from multiple freshwater sources (that is, river inflow, net precipitation and melting sea ice and glaciers), the volume of freshwater in Arctic surface waters has increased by 8,000 km³ (more than 11%) compared to the 1980–2000 period^{1,3}. Below the surface over much of the Arctic Ocean, a strong halocline layer acts as a barrier separating Atlantic water heat from the cold and fresh upper Arctic waters^{4,5}. Increased stability of the Arctic halocline, a potential consequence of climate change, would likely reduce both the vulnerability of sea ice to upward heat fluxes from the ocean interior and the vertical mixing of carbon and nutrients^{6,7}.

At the atmosphere–ocean interface, the traditional Arctic icescape is changing largely due to atmospheric forcing and, to a lesser extent, winter ocean heat flux, particularly in the Eurasian Arctic sector⁶. Since the 1970s, the extent of summer sea ice has decreased by >40% (Fig. 1a) and its thickness by 65%, with first-year ice largely replacing the thick multiyear pack ice (Fig. 1b,c)^{1,8}. In addition to the increased open-water area and duration that amplify ice albedo feedbacks, sea ice is becoming increasingly fragmented and dynamic, resulting in drastically altered under-ice light fields that significantly impact both pelagic and sympagic (that is, sea-ice-associated) ecosystem dynamics.

Together, these climate-driven changes within the atmosphere, cryosphere and ocean have wide-ranging consequences for Arctic

marine ecological dynamics, influencing productivity, species interactions, population mixing and pathogen and disease transmission^{9–11}. To advance knowledge of these unique ecosystems in an era of rapid change, here we have synthesized recent developments over the last decade to study phytoplankton dynamics (the base of marine ecosystems) by examining current changes in primary productivity, phenology and assemblage composition, and how these changes could alter the ecology and biogeochemistry of the Arctic Ocean.

Arctic primary production in a changing icescape

The reduction in sea-ice extent in the Arctic Ocean over the last few decades has resulted in both a longer phytoplankton growing season and increased open-water habitat for phytoplankton growth^{12–14}. Consequently, phytoplankton blooms now begin earlier^{13,15} and end later¹⁶ in the year, and annual net primary production (NPP) in open waters over the entire Arctic Ocean increased 30% between 1998 and 2012 (ref. ¹⁷), the year that summer sea-ice extent reached its historical minimum. This increase in NPP might have been even larger if it were not for a concomitant increase in cloudiness and decrease in light availability over the Arctic¹⁴. Over this period, the largest increases in annual NPP were restricted to the interior Arctic shelves (Laptev, Kara and Siberian), where NPP increased 70–112% over the 15-yr study and sea-ice loss was most severe (4.2–5.4% yr⁻¹). In contrast, NPP on the outflow shelves showed a much smaller increase (8%, Baffin) and even a decrease (–15%, East Greenland) in response to much smaller declines in sea-ice cover (0–0.9% yr⁻¹)¹⁷.

A more recent satellite-based study¹⁸ that was extensively validated using a large in situ database has shown that since reaching the minimum sea-ice extent in 2012, the rate of increase in open-water area in the Arctic Ocean has slowed considerably, decreasing from 88,000 km² yr⁻¹ between 1998 and 2012 to only 620 km² yr⁻¹ between 2012 and 2018 (Fig. 2a). In addition, the average ice-free period in the Arctic only increased from 147 to 152 open-water days (five days) between 2012 and 2018. Thus, neither the extent of open-water phytoplankton habitat nor the length of the growing season changed significantly during this time. Nevertheless, annual NPP in ice-free waters continued to increase at rate of 6.8 TgC yr⁻¹ between 1998 and 2018, peaking at 391 TgC yr⁻¹ in 2018

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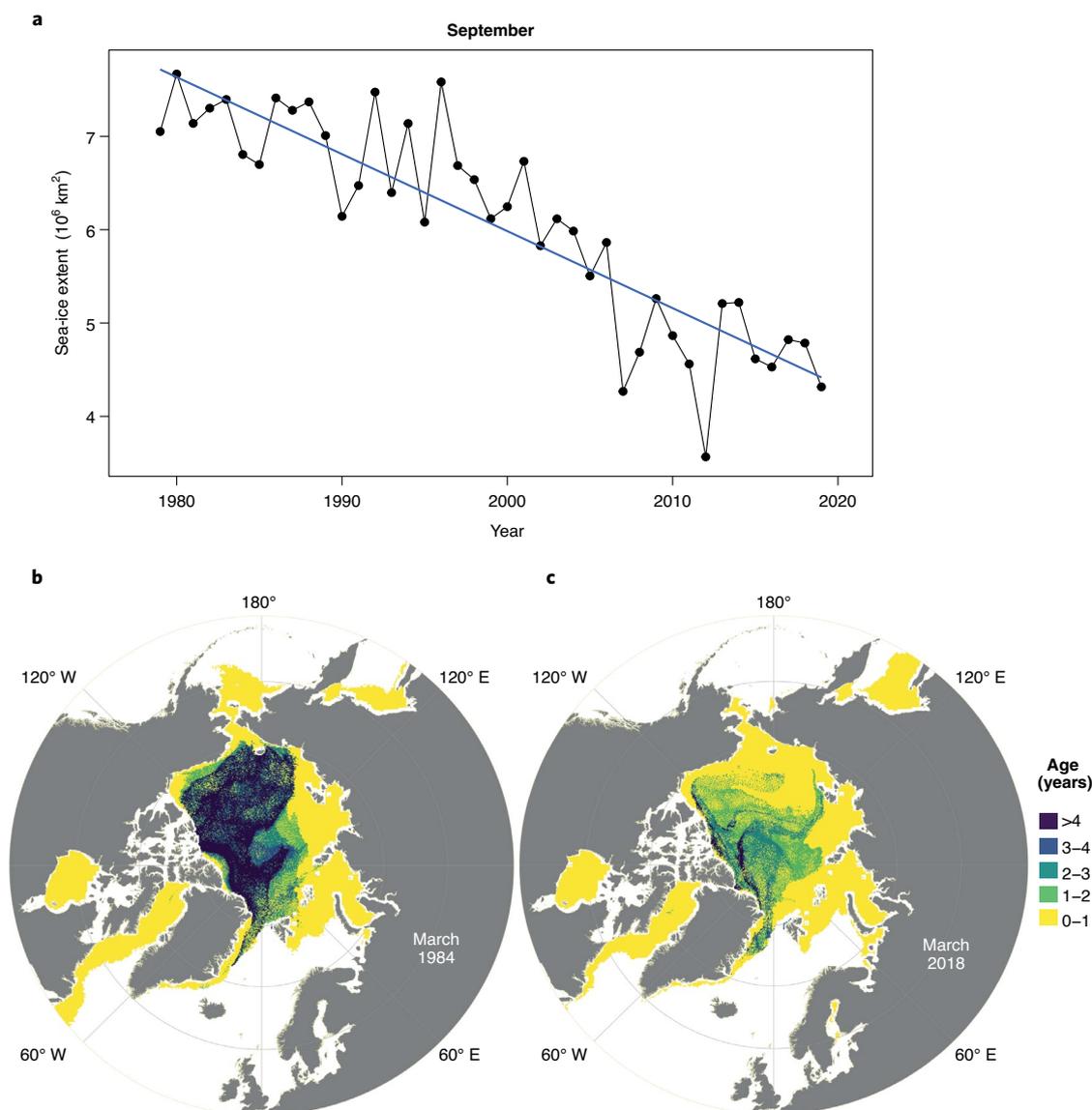


Fig. 1 | Changing sea-ice extent and age. **a**, Time series of the summer sea-ice extent (in 10^6 km^2) from 1979 to 2019. **b, c**, Maps comparing winter Arctic sea-ice age in 1984 (**b**) and 2018 (**c**). The satellite-derived sea-ice data are from the National Snow and Ice Data Center (NSIDC; Cavalieri et al.¹⁸⁵ and Tschudi et al.¹⁸⁶).

(Fig. 2c). Notably, despite the flattening in the trend in open-water area between 2012 and 2018, the increase rate in annual NPP over the Arctic during that time period (13.5 TgC yr^{-1}) was double that between 1998 and 2012 (6.4 TgC yr^{-1}). This suggests that the factors controlling annual net primary production changed between the early and late phases of the 1998–2018 time series.

Whereas the increase in annual NPP between 1998 and 2012 was highly correlated to the decline in sea ice and an increase on open-water phytoplankton habitat, the increase in annual NPP between 2012 and 2018 was associated with increased surface chlorophyll *a* (Chl *a*) concentrations (Fig. 2b,d). Prior to 2012, concentrations of Chl *a* across the Arctic Ocean were relatively constant, increasing by only $0.002 \text{ mg m}^{-3} \text{ yr}^{-1}$ (or 0.27%). However, between 2012 and 2018, mean Chl *a* concentration in Arctic Ocean surface waters increased at a rate of $4.3\% \text{ yr}^{-1}$, 16 times faster than the rate prior to 2012. The largest increases in Chl *a* between 1998 and 2018 were measured on the inflow shelves of the Chukchi Sea (26%) and Barents Sea (61%), and at

the recently exposed shelf break of the Laptev Sea (Fig. 2d). If we assume that increases in Chl *a* concentration are indicative of increases in phytoplankton biomass, the latter of which cannot increase without additional nutrients, these results suggest that increased nitrogen (N) supply from either increased vertical mixing near the shelf break or advection from lower latitude waters may be responsible for the NPP increase in ice-free Arctic waters since 2012 (ref. ¹⁸). However, we cannot eliminate the possibility that changes in grazing pressure also may have impacted phytoplankton populations, and hence NPP^{19–23}.

Biogeography shaped by changing environmental drivers

The complexity of Arctic biogeography makes it particularly challenging to fully comprehend the interplay of environmental drivers and their change and impacts on phytoplankton dynamics (Figs. 3 and 4). Here, we attempt to highlight at the regional scale (that is, between inflow, interior and outflow shelves and the central Arctic; following the terminology of Carmack et al.²⁴) how the

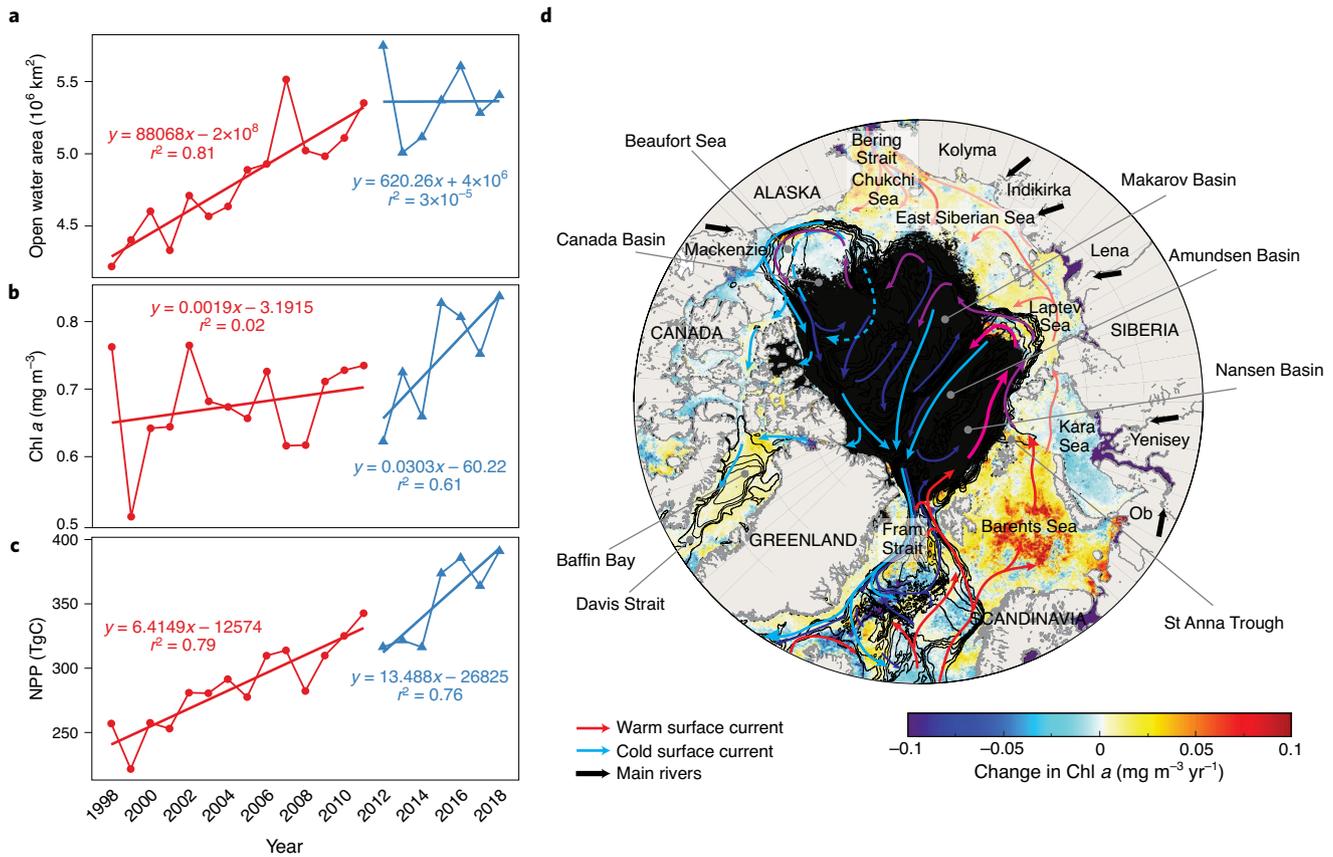


Fig. 2 | Global trends in Arctic primary production over the two last decades. a–c, Annual time series of Arctic Ocean mean open-water area (a), mean Chl a (b) and NPP (c). The time series is separated into two time periods because from 1998–2012, loss of sea ice was responsible for the increase in NPP for the Arctic Ocean. After that time, the loss of sea ice slowed considerably but NPP continued to increase. This increase from 2012–2018 was due primarily to an increase in phytoplankton biomass, likely because of increased nutrient supplies into Arctic surface water. **d,** Map showing the rate of change in Chl a ($\text{mg m}^{-3} \text{ yr}^{-1}$) between 1998 and 2018. Shown are the dominant Arctic Ocean currents with inflowing relatively warm surface currents (red arrows) and colder surface currents (light-blue arrows), together with intermediate and deep currents (burgundy and dark-blue arrows, respectively; currents modified from Anderson and Macdonald¹⁸⁷). Black arrows indicate the main river inputs and dashed light-blue arrows indicate the deep circulation of the Beaufort Gyre. Figure adapted from Lewis et al.¹⁸.

major environmental drivers will change and how new ones might emerge in a changing Arctic Ocean.

Nutrient supply and vertical mixing. Nutrient supply (primarily nitrate^{25,26} and, to a lesser extent, silicate^{27–29} and rarely iron³⁰) drives the biogeography and trophic status (that is, oligotrophic or eutrophic) of the Arctic Ocean, while light availability modulates the rate of NPP within each region^{29,31,32}. These key factors (that is, nutrients and light) are in turn regulated by a complex interplay of processes altering stratification and mixing as well as the presence of sea ice and snow cover superimposed on seasonal and latitudinal controls on light availability³³ (Fig. 3). Winter nutrient inventories show a strong linear relationship with annual NPP via their role in regulating phytoplankton biomass, except for areas where wind-driven and topographically enhanced mixing (that is, driving resuspension and upwelling events) resupply nutrients during the growing season³¹. Locally, depending on the interplay between atmospheric forcing (that is, intensity, duration and direction of the wind stress) and the strength of vertical stratification, the injection of nutrients into surface layers can easily vary by two orders of magnitude across the Arctic Ocean^{31,34,35}. Stratification is expected to increase in the Canada Basin³⁶ but decrease in other regions (for example, in the Eurasian sector^{6,37}; Fig. 4). On the other hand, the loss of sea ice is expected to increase winds and strong wind events by the end

of the century due to reduced atmospheric stability resulting from increased temperature and turbulent fluxes³⁸. These enhanced atmospheric forcings occur in all seasons but especially in autumn and winter (where they are expected to strengthen by up to 50% in the central Arctic and peripheral seas)³⁸. Changing the balance between vertical stratification and atmospheric forcing will be subject to antagonistic and region-specific environmental drivers (that is, advection, mesoscale activity, atmospheric forcing and related processes, such as upwelling) and will ultimately alter phytoplankton dynamics.

Advection at the Arctic gateways. The Arctic marine biome is tightly connected to lower latitudes through the northern Pacific and Atlantic oceans. In inflow shelves (Fig. 3), Atlantic and Pacific waters flow northward through the European Arctic Corridor and the Bering Strait, respectively, carrying heat, nutrients and planktonic organisms to the Arctic Ocean. A twofold increase in North Atlantic current velocities over the last 24 years was recently revealed, explaining decadal variations in the spatial distribution of the coccolithophorid *Gephyrocapsa huxleyi* (previously called *Emiliania huxleyi*)³⁹, a tracer for temperate ecosystems^{40–42}. Bio-advection, rather than the previously assumed water temperature, may be the major mechanism responsible for poleward intrusions of southern species like coccolithophores⁴⁰ (and potentially the picocyanobacteria

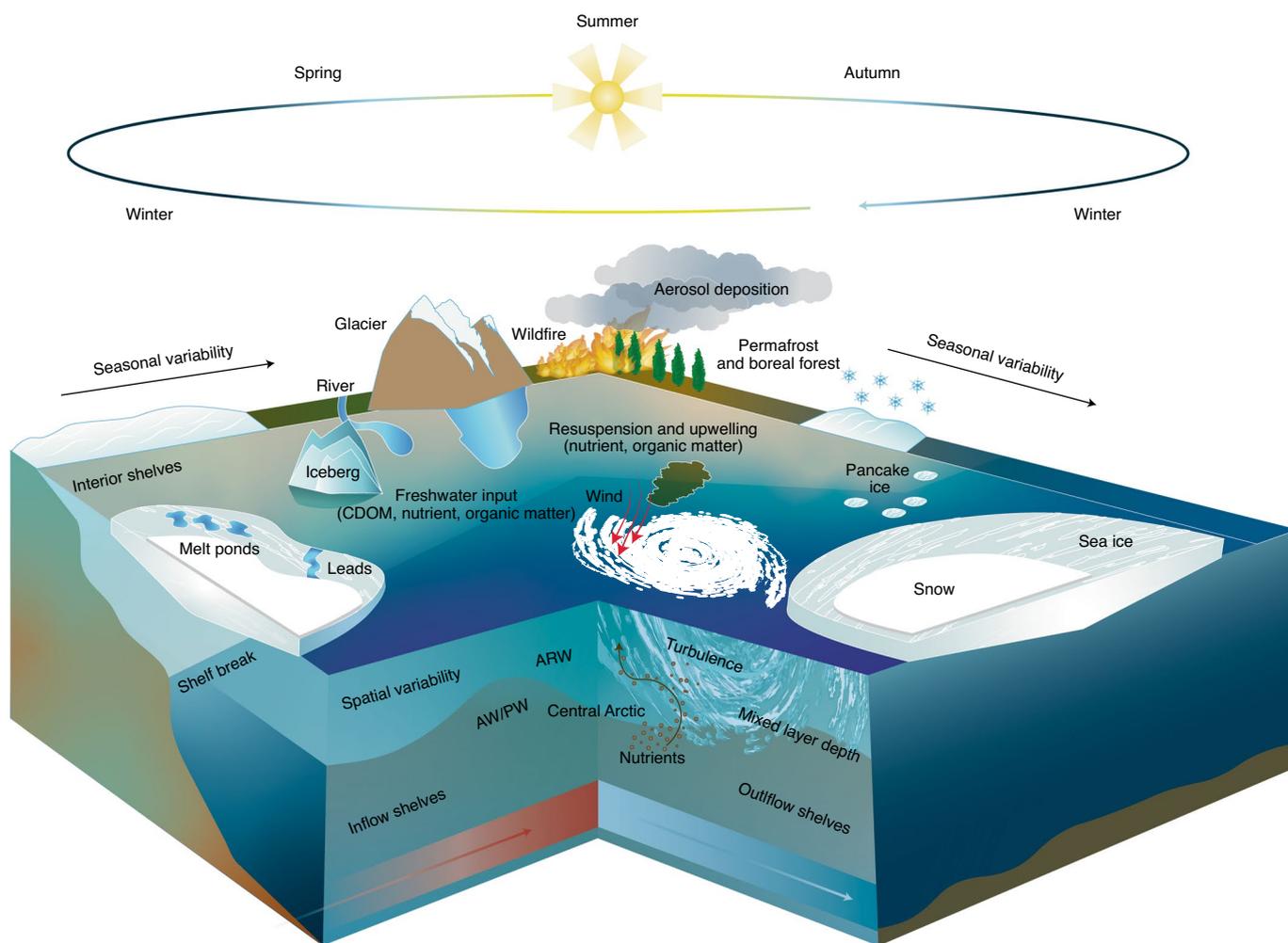


Fig. 3 | Environmental drivers shaping Arctic phytoplankton dynamics. The oceanic, terrestrial and atmospheric compartments are displayed over an annual cycle. The interconnectivity of the seasonal (that is, horizontal dimension) and the spatial (that is, vertical dimension) variability emerges as a framework to understand the mosaic of the environmental drivers shaping Arctic phytoplankton dynamics. Water masses are also indicated. ARW, Arctic waters; AW, Atlantic waters; PW, Pacific waters; CDOM, coloured dissolved organic matter.

*Synechococcus*⁴³). A similar increase in poleward advection of Pacific waters through the Bering Strait suggests that the shrinking Arctic domain may be prone to intrusions of temperate species at both of the Arctic gateways⁴⁴. However, as described previously, advective transport can result in a case of life or death in the Arctic Ocean depending on the ability of these invasive species to survive strong environmental gradients, low water temperature and long periods of darkness⁴⁵. Advective processes alter mostly lower trophic levels that have a limited capacity for mobility (for example, phytoplankton, zooplankton and some fish), and consequently can impact entire marine ecosystems by shifting species distributions and modifying interactions at higher trophic levels^{46–48}. Considering the role of bio-advection in ecological models (that is, trait-based and niche-based approaches) will be necessary to improve predictions of future ecosystem shifts in the context of climate change⁴⁹.

Not only are the inflow shelves shaped by advective processes, the outflow shelves (for example, the Canadian Arctic Archipelago–Baffin Bay complex and the East Greenland shelf) also respond strongly, and likely differently, to upstream changes in sea-ice dynamics and export, hydrographic structure and biogeochemical cycles^{33,50}. In both northern Baffin Bay and the East Greenland shelf, changes in stratification and sea-ice dynamics (that is, extent and export) shape spring bloom phenology and nutrient inventories

for the phytoplankton growing season^{51,52}. On the East Greenland shelf, the magnitude of sea-ice export can explain spatial shifts in the boundaries between stratification regimes (that is, haline- versus temperature-based stratification⁵³) and different phytoplankton dynamics (for example, more intense and early phytoplankton blooms in haline-based stratification). However, strong haline-based stratification reinforced by increasing freshwater input in the North Water Polynya within northern Baffin Bay, a biologically productive oasis for marine mammals and birds, resulted in a sharp decline in phytoplankton biomass (especially centric diatoms) and NPP during 1999–2011 (ref. ⁵⁴). In addition, early season nutrient consumption by phytoplankton blooms under the sea ice and/or at the sea-ice edge in waters that are advected into North Baffin Bay can contribute to this overall productivity decline along with a change in the algal community toward smaller cells⁵⁴. Assessing the impacts of climate change on the inflow and outflow shelves clearly requires proper consideration of the connectivity between the northern Pacific and Atlantic Oceans and the central Arctic Ocean.

Land–ocean continuum. Through the land–ocean continuum, peripheral environmental pressures play an increasing role in the functioning of Arctic marine biogeochemical cycles. In particular, increased inflow of glacial meltwater and freshwater from fjords

Environmental driver	Inflow shelves	Interior shelves	Outflow shelves	Central Arctic	Impact for phytoplankton dynamics
Sea-ice extent	+++	+++	+++	+++	Increasing light availability
Sea-ice thickness	++	++	++	+++	Increasing under-ice light availability
Temperature	+++	+	+	+	Increasing metabolism activity
Freshwater inputs (rivers, fjords, meltwater)	+	+++	++	+++	Increasing the vertical stratification, more lateral but less vertical nutrient inputs
Vertical stratification	++	+++	++	+++	Increasing (decreasing) the vertical stratification, less (more) vertical nutrient inputs
Wind speed and storminess	++	++	++	++	More storminess, more vertical nutrient inputs
Aerosol deposition	?	?	?	?	Nutrient fertilization of surface waters
Acidification	+++	++	+	+	Less calcification

Fig. 4 | Synthesis of selected observed regional environmental changes in the Arctic Ocean. For each region, environmental changes and impacts for Arctic phytoplankton are shown. For environmental changes, yellow and green colouring indicates an increase and decrease, respectively. The confidence level (+) refers to the confidence in attributing observed changes for phytoplankton dynamics. Question marks (?) indicate that the evaluation has not yet been assessed at the regional scale, or that there is insufficient evidence for the evaluation.

and river mouths (Fig. 3) will dramatically alter coastal biogeochemical cycles. Outflow from fjords impact near-shore nutrient inventories (phosphorus, silicate and iron)^{55–58} and can even fuel large summer phytoplankton blooms²¹. Interestingly, in the Greenlandic fjords, two types of glaciers (that is, marine- and land-terminating glaciers) have contrasting effects on phytoplankton productivity. Rising subsurface meltwater plumes originating from marine-terminating glaciers trigger upwelling of nutrient-rich deep water, which supports high summer phytoplankton productivity⁵⁹. On the other hand, fjords with land-terminating glaciers or anomalously strong freshening events lack such upwelling processes and result in increased stratification, which lowers productivity^{59,60}. As a result, future transitions from marine to terrestrial glaciers, and the associated increases in stratification intensity, will noticeably alter local productivity with potentially cascading effects on trophic levels.

The increase in pan-Arctic river inputs, driven by an intensifying Arctic water cycle, is also expected to affect marine coastal biogeochemical cycles. However, while nutrient supply by rivers can be locally important, it does not seem to support a significant fraction of Arctic NPP³¹. For example, field observations and modelling at the mouth of the Mackenzie River in the Beaufort Sea have shown that inorganic N from rivers was contained and entirely consumed within a few tens of kilometres of delta outlets^{61–64}, creating potential near-coastal biological hotspots. On the other hand, large river outflow will intensify the freshwater stratification and light-absorbing properties (that is, mainly via coloured dissolved organic matter and, to a lesser extent, particles^{65,66}). However, recent findings suggest that it does not appear to decrease phytoplankton productivity by limiting wind-driven shelf-break upwelling and decreasing light transmission¹⁸. Shelf-break waters have been shown to harbour massive phytoplankton blooms^{67,68} and are likely to form an ‘Arctic Green Belt’⁶⁴ as they become increasingly sea-ice-free and are exposed to atmospheric forcing⁵⁰.

Wildfire and Arctic aerosol deposition. In recent years, an unexpected increase in the frequency of wildfire events has been observed in summer in boreal forest⁶⁹ and tundra ecosystems at a pan-Arctic scale⁷⁰. Although wildfires are common in the northern hemisphere, they are becoming particularly unusual by their latitude, duration and intensity^{69,70}. Such extreme wildfire activity has been clearly correlated to high temperatures and dry conditions, and increased atmospheric disturbances (that is, thunderstorms)⁷¹. Increased wildfire activity in these areas can release large amounts of carbon (C) and N to the Arctic atmosphere^{72,73} and, by deposition, could alter sea-ice optical properties and, potentially, marine biogeochemical cycles (Fig. 3). Light-absorbing particles (including black C) is well recognized to be an efficient absorber of solar radiation⁷⁴, and its deposition onto, or incorporation into, snow and sea ice can decrease the surface reflectance and increase melt rates^{74–77}. More uncertain is whether wildfire-derived aerosols can be used as a new source of nutrients (mainly N species) in the summer, when N limits the Arctic phytoplankton NPP. Estimates of atmospheric nutrient deposition are scarce in the Arctic Ocean, but some global modelling budgets suggest that N and phosphorus inputs are low^{78–80}. Further evaluation is clearly needed to quantify and incorporate these intensifying climate-driven changes in Arctic biogeochemical models (Fig. 4).

Ocean acidification. Some of the fastest rates of ocean acidification have been recorded in the Arctic Ocean due primarily to the higher capacity of cold water to absorb CO₂, but also due to inputs from river run-off and ice melt and the inflow of naturally low pH waters from the Pacific⁸¹. However, the severity of acidification is not homogeneous across the Arctic Ocean, resulting in high temporal and spatial variability^{82–84} (Fig. 4). Overall, Arctic and sub-arctic phytoplankton communities seem to be relatively resilient to ocean acidification, with no significant change in productivity and little change in species assemblages under enriched scenarios up to

1,000 μatm pCO_2 (refs. ^{85–87}). Contrasting responses between species, however, seem to be characteristic of more acidic subarctic and Arctic waters⁸¹. For example, small picoeukaryotes seem to benefit from higher pCO_2 (refs. ^{88,89}), while prymnesiophytes (including coccolithophores) are generally negatively impacted^{90,91}, and varying responses are noted in diatoms^{85–87,92}. Predicting the complexity of the biological effects of ocean acidification—in particular, on Arctic phytoplankton dynamics (given varying species, life cycle stage, location and seasonal responses) as well as the phytoplankton–zooplankton interactions—remains poorly constrained and poorly understood⁶¹.

A new non-traditional Arctic phenology

The growth of phytoplankton at high latitudes is generally thought to begin in open waters of the marginal ice zone (MIZ) once the highly reflective sea ice^{93,94} retreats in spring, as solar elevation increases and surface waters become stratified by the addition of sea-ice melt water^{95–98}. In fact, virtually all recent large-scale estimates of NPP in the Arctic Ocean assume that phytoplankton NPP in the water column under sea ice is negligible^{14,17,26,99–101}. Accordingly, phytoplankton blooms in Arctic waters have been considered to be tightly coupled to the timing of sea-ice retreat^{15,17,96}.

Changing spring algal dynamics blooms. Recent observations contradict this paradigm that waters beneath the consolidated ice pack harbour little planktonic life. High concentrations of phytoplankton beneath Arctic sea ice have been reported in areas as widespread as Resolute Bay^{102–108}, north of Svalbard^{108,109}, Baffin Bay^{88,108}, the Greenland Sea¹¹⁰, the Barents Sea^{111,112}, the Laptev Sea^{97,113} and the Chukchi Sea^{67,68,108,114,115} (Fig. 5a–c). The largest and most well documented of these blooms was observed in the Chukchi Sea beneath fully consolidated sea ice^{67,68}. Physiological characteristics of the phytoplankton beneath the ice on the Chukchi shelf in early spring indicate that they were ‘primed’ to bloom once light levels became high enough to support net photosynthesis¹¹⁶. At their peak, these under-ice phytoplankton blooms (UIBs) reached Chl *a* concentrations in excess of 20 mg m^{-3} and extended from the ice–water interface to a depth of 25–70 m and from the ice edge to >100 km into the ice pack. The algal biomass associated with these features rivalled that of the most productive ocean ecosystems on Earth⁶⁷.

The observation of intense UIBs beneath fully consolidated sea ice has necessitated a re-examination of many aspects of Arctic marine ecology and biogeochemistry. Because these UIBs are invisible to satellite sensors, recent estimates of annual NPP in waters where UIBs develop may be at least an order of magnitude too low⁶⁷, indicating that seasonally ice-covered waters on Arctic continental shelves have the potential to support vastly higher rates of NPP than has been attributed to them in the past^{14,17,101}. In addition, the presence of UIBs shift maximum nutrient consumption and NPP to earlier in the season and farther into the ice pack relative to MIZ blooms. This is important because the timing and location of NPP and associated zooplankton grazing can directly influence the partitioning of organic C between the upper water column and benthic communities, and thus the efficiency of the biological pump and C sequestration¹¹⁷. Furthermore, in productive Arctic waters where diatoms dominate, food webs tend to be short and even small changes in NPP export pathways can have large cascading effects on higher trophic level organisms¹¹⁸. Therefore, it is important to determine how export rates of newly fixed C and the degree of benthic–pelagic coupling will respond to a shift in location and timing of peak rates of NPP from the MIZ^{119,120} to deeper within the ice pack.

‘Borealization’ of Arctic phytoplankton phenology. Given the ongoing changes in phytoplankton phenology, the ‘polar’ paradigm of a single annual phytoplankton bloom and subsequent sedimentation of organic matter needs to be revised. Not only has the start of

the growing season been profoundly accelerated, but the end of the growing season has been markedly delayed (Fig. 5)¹²¹. This finding supports an ongoing borealization of the Arctic Ocean and represents a paradigm shift with respect to Arctic Ocean NPP that is likely to impact both ecosystems and biogeochemical cycles in unpredictable ways. For example, a new phenological feature, a secondary (usually autumn) phytoplankton bloom, is developing in parts of the Arctic Ocean^{16,122–125}. Although secondary blooms were already prevalent in sea-ice-free regions of the Eurasian Arctic sector influenced by Atlantic waters^{42,126}, they are now developing in seasonally ice-covered regions of the Arctic Ocean due to concomitant delayed freeze-up (greater light availability) and increased exposure of the sea surface to wind stress (wind-driven mixing brings nutrients to the surface^{29,127}). However, these secondary blooms are necessarily restricted to low Arctic latitudes where stratification is not sufficient to inhibit wind-driven mixing (Fig. 5c), and the growing season is long enough to allow phytoplankton growth during any vertical mixing events (Fig. 5b,c). In a changing Arctic Ocean, the spring bloom will undoubtedly remain the major annual NPP event for C export to higher trophic levels and sequestration in the deep ocean and sediments^{121,127,128}. However, changes in phytoplankton phenology or additional pulses of phytoplankton NPP may alter the food web structure and lead to major ecosystem level changes in an environment where consumers must make the most of the short productive period before the long winter sets in¹⁶.

The borealization of the Arctic phytoplankton phenology will also be accompanied by a longer period of regenerated production and subsurface Chl *a* maxima (SCM), particularly in low productivity waters (for example, in the Western Arctic Ocean; Fig. 5). Widespread N deficiency in surface waters drives the seasonal persistence of SCM layers and phytoplankton C biomass in several regions^{29,64,129,130}. The contribution of these layers to NPP is possibly higher in the Arctic Ocean than in thermally stratified waters of the subtropical gyres due to a combination of extreme acclimation to low light and a shallow nitracline^{31,131}. Unsurprisingly, the deepening (related to the length of the growing season and the seasonal N consumption) and the steepness (associated to the intensity of the vertical stratification) of the nitracline determines the depth, biomass, productivity and assemblage composition of SCMs^{64,132,133}. For the deepest SCMs in late summer, even shifts from autotrophic to heterotrophic communities have been revealed due to severe light limitation¹³². In the context of current sea-ice loss, the potentially increased role of SCM layers on biogeochemical fluxes remain to be quantified directly, both regionally and at the pan-Arctic scale^{31,127}.

Arctic phytoplankton assemblage structure

Since the beginning of the nineteenth century, known Arctic and subarctic phytoplankton species have increased dramatically from 115 (ref. ¹³⁴) to 1,874 (ref. ¹³⁵) in 2011, and ultimately reaching 2,241 taxa in the latest updated pan-Arctic taxonomic inventory in 2017 (ref. ¹³⁶). Here, our goal is not to describe this expanded understanding of Arctic phytoplankton diversity but rather to delineate the ecological niches of phytoplankton ranging from bloom-forming to ultra-oligotrophic adapted species in the changing Arctic environment (Fig. 6).

The prevailing view of Arctic Ocean phytoplankton assemblages is usually based on large diatom blooms (centric or pennate forms) in nutrient-rich waters supporting a cascade of higher trophic levels. What is less recognized is that some Arctic regions (for example, the Canada Basin) are as oligotrophic and unproductive as subtropical gyres¹². The availability of N (mainly nitrate), which shapes the overall biogeography and regional trophic status of the Arctic, also drives large-scale shifts from diatom- to picoeukaryote (mostly flagellates)-dominated systems^{29,64,137,138} (Fig. 6). This does not mean, however, that in less productive areas no diatom-dominated spring blooms can develop (except probably in perennial stratified Arctic

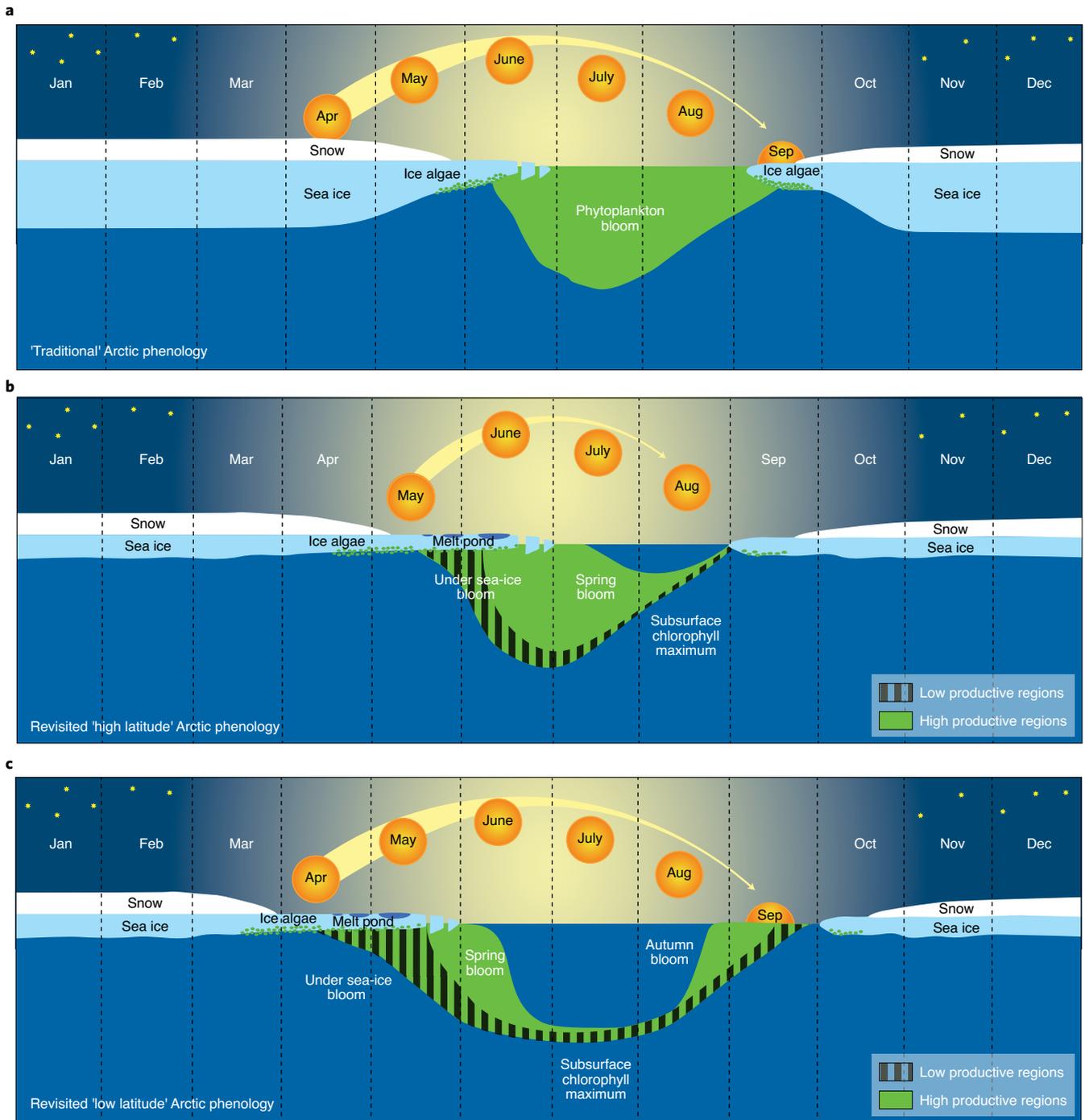


Fig. 5 | Changing Arctic sea-ice algae and phytoplankton phenology with the receding sea-ice cover. a, Traditional paradigm of seasonally ice-covered regions with the occurrence of a single annual phytoplankton bloom, and two blooms of sea-ice algae at the beginning and end of the productive season^{128,188}. **b, c**, Potential changes in production and duration of the spring bloom due to early productive season and the occurrence of under-ice phytoplankton blooms at low (**b**) and high (**c**) Arctic latitudes^{67,68,109,114,189}. In low (**b**) and high (**c**) Arctic latitudes, the presence and extent of sea-ice algae blooms could be affected by drastic changes in sea-ice dynamics^{103,107,90}. With a longer ice-free season, an increase in the importance of SCMs (in both low and high Arctic latitudes) and secondary/autumn blooms (only in low Arctic latitudes, when wind-driven mixing is strong enough to erode the vertical stratification and that replenishes sun-lit surface waters in nutrients) in the annual NPP estimates is expected¹⁶. Figure adapted from Wassmann and Reigstad¹²¹ under a Creative Commons License (<https://creativecommons.org/licenses/by/4.0/>).

waters), but only that these will be less intense and likely shorter (Fig. 5). In warmer, stratified and oligotrophic Arctic surface waters with a longer sea-ice-free season, the picoeukaryotic systems (in particular, the endemic prasinophyte *Micromonas polaris*)^{139–141} are strongly suspected to rely on mixotrophy; that is, via osmotrophic

and/or phagotrophic processes. Such an adaptive strategy of picoeukaryotes could increasingly be favoured over strictly phototrophic phytoplankton as sea ice continues to decline¹³⁸. In addition, such a scenario could considerably increase the risk of the proliferation of potentially bloom-forming, harmful or toxic species currently

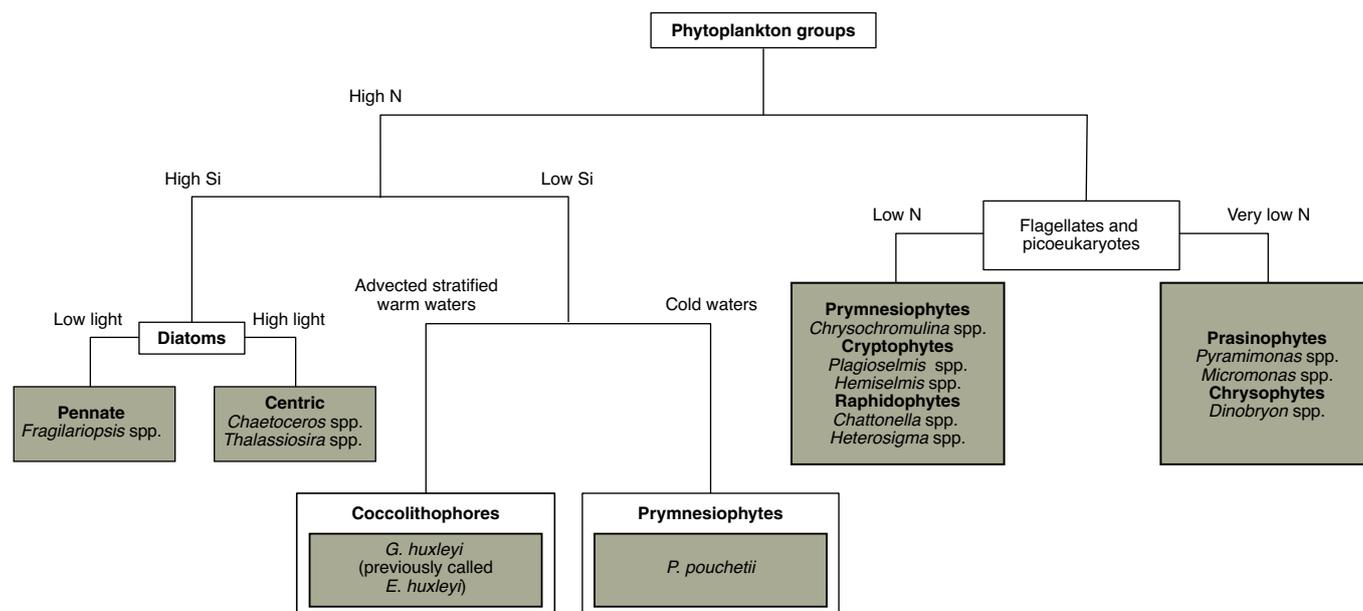


Fig. 6 | Major phytoplankton taxa and its environmental drivers in the Arctic Ocean. The schematic diagram delineates the main Arctic phytoplankton taxa driven by specific environmental drivers (that is, nutrient status, light and mixing regime, and water temperature). N and Si indicate nitrogen and silicate availability, respectively. Warm/stratified versus cold waters is related to hydrographic properties of the water masses. The different branches separate the phytoplankton taxa: the shift from diatom- to flagellates-based system (that is, high to low N)^{29,64,137,191}, the intra-specific taxa shift from pennate to centric diatoms (that is, low to high light)^{107,146,147,192,193}, the shift from diatoms to (1) colonial prymnesiophytes, namely *P. pouchetii* (that is, high-to-low Si, cold waters), and to (2) coccolithophores (that is, high-to-low Si, advected warm/stratified waters)^{28,40,108,150,194}, and the changes in phytoplankton taxa in the flagellates and picoeukaryotes^{64,138,142}. Note the species *E. huxleyi* have recently reassigned based on genomic analyses to the coccolithophorid *G. huxleyi*³⁹.

present in the Arctic Ocean (for example: diatom, *Pseudo-nitzschia*; dinoflagellate, *Alexandrium*, *Dinophysis* and *Karlodinium*; and prymnesiophyte, *Chrysochromulina* spp.)^{135,140,142–144}, potentially affecting already fragile marine Arctic ecosystems¹⁴⁵.

Diatoms, which commonly exhibit seasonal succession from pennate to centric species due to different light requirements^{146,147}, are not the only bloom-forming taxa observed in the Arctic Ocean (Fig. 6). Two other types of phytoplankton blooms have been reported, dominated either by the prymnesiophyte *Phaeocystis pouchetii* or by coccolithophores (Fig. 6). *P. pouchetii* blooms have long been observed in the Eurasian Arctic^{148,149} but are relatively recent phenomena in Labrador fjords^{150,151}, Baffin Bay¹⁰⁸ and under sea ice¹⁰⁹. Silicate limitation can likely explain more favourable growth conditions for *P. pouchetii* compared to diatoms^{108,152} and the co-occurrence or succession between diatoms and *P. pouchetii*¹⁵³. Since the early 1990s, silicate concentration has decreased by 20% (and nitrate by 7%) in inflowing Atlantic waters due to natural multi-decadal changes in surface circulation and decreased depth of winter convection at lower latitudes^{42,154,155}. Thus, as Atlantic Ocean silicate supplies continue to decline, *P. pouchetii* blooms may become more common in eastern Baffin Bay waters and perhaps at higher latitudes of the Eurasian Arctic sector, while diatom-dominated blooms will become less frequent. Coccolithophores, considered as new intruders to the Arctic Ocean and sentinel taxa in temperate waters, have already been discussed in detail in the previous subsection titled 'Advection at the Arctic gateways'.

Understanding overwintering strategies (including mixotrophy, dormancy and cyst or spore formation), dark survival and recovery among phytoplankton taxa are also urgent matters to resolve, particularly with ongoing environmental changes (for example, increasing water temperature and sea-ice loss). Cyst and spore production has been reported in polar phytoplankton taxa but remains limited to a few diatom and dinoflagellate species^{147,156}. Arctic diatoms have also been reported to survive long periods of darkness

and resume rapid growth as soon as light becomes available due to their ability to downregulate their metabolism and to maintain the main components of their photosynthetic machinery (PSII, pigments and Rubisco) at low light and temperature^{157,158}. On the other hand, mixotrophy seems to be a widespread strategy among dinoflagellates and other photosynthetic flagellate taxa, keeping them active throughout the polar night^{139,159–161}. With higher temperatures in the future, photosynthetic flagellate taxa that rely on heterotrophy could have an advantage over diatoms that exhaust stored metabolic resources more quickly^{140,162} during the polar night¹⁴⁰. The taxon-specific survival traits between diatoms and flagellates could shape their geographical distribution in high latitude regions and thus the community structure during the preconditioning period of the spring bloom, thereby impacting both the phenology and magnitude of the bloom¹⁶³.

Future Arctic Ocean and open questions

It is evident that the shift of the Arctic Ocean to a new atmospheric, cryospheric and oceanic state is resulting in profound and widespread changes in phytoplankton dynamics. Despite the many examples of the effects of this new Arctic 'biogeochemical landscape' on phytoplankton productivity, phenology and assemblage composition, foreseeing the consequences of intensifying climate change remains difficult. Model predictions can be particularly relevant to identify key climate change-mediated multi-stressors^{164,165} and to better portray the future Arctic Ocean^{166,167}. However, the taxonomic complexity of phytoplankton assemblages within diverse Arctic marine ecosystems remains difficult to model and parameterize correctly due to multiple little-known factors affecting growth¹⁶⁸. For example, no model has been able to reproduce the observed changes in phytoplankton phenology (for example, the occurrence of under-ice and secondary/autumn blooms) due to unique temperature- and light-dependent growth as well as metabolism of Arctic phytoplankton communities^{116,131,169,170}. This is best

exemplified by recent observations that have challenged the perception of the polar night, which has been shown to be a more active period for marine ecosystems and intense biogeochemical fluxes than previously recognized^{158,171–173}. Almost all recent winter expeditions have revealed unexpected scientific breakthroughs^{172,173}, and much remains to be done to document the key role of the polar night as a true continuum between the autumn and spring, and to better integrate it into the Arctic biogeochemical cycles.

Through the mosaic of environmental drivers influenced by climate change presented here, it is difficult to highlight particular ‘sentinel’ regions to be monitored in the near future: the interior shelves are mostly shaped by the land–ocean continuum, inflow and outflow shelves by advection, and the central Arctic by likely irreversible sea-ice loss. With the continued shrinking of the Arctic marine biome, however, multiple questions will need answers to better anticipate changes in the biogeochemical cycles of the central Arctic and predict its future. It is not yet possible to make definitive predictions about whether the central Arctic will become a new oasis or desert within the Arctic marine biome. However, we suspect that the shelf break, acting as a ‘green belt’, could effectively supply inorganic and organic matter to the strongly stratified, but soon-to-be sea-ice-free in summer, central Arctic Ocean^{64,174}. The key question is whether or not the disappearance of the summer sea-ice barrier will enhance atmospheric forcing and increase the efficiency of mixing on C cycling and nutrient exchanges.

As for the Arctic gateways, the importance of Pacific and Atlantic inflows that fundamentally shape Arctic biogeochemical cycles highlight the strong connectivity of the Arctic Ocean to the global ocean. In this Review, we mainly focused on the importance of potential changes in inflows from subarctic latitudes that carry heat, nutrients and planktonic organisms towards the Arctic Ocean. The reverse, also important but not addressed here, is the role of a changing Arctic Ocean on subarctic latitudes and the global circulation and climate. The initiation of industrial-era decline in subarctic Atlantic Ocean primary productivity, for example, seems to coincide with the onset of Arctic Ocean surface warming^{175,176}. More importantly, the increasing long-term influx of freshwater into northeastern subarctic Atlantic surface waters may be implicated in driving the industrial-era Atlantic Meridional Overturning Circulation (AMOC) decline and contributed to this primary productivity decline over the late nineteenth and twentieth centuries^{176–180}. Continued weakening of the AMOC, as projected for the twenty-first century^{181,182}, may therefore result in further productivity declines, with important ramifications for future atmospheric C drawdown¹⁸³ and northern Atlantic fisheries¹⁸⁴ in the subarctic Atlantic Ocean¹⁷⁶.

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M.A. and K.R.A. conceptualized and wrote the manuscript together.

Competing interests

The authors declare no competing interests.

Additional information

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