The future of Arctic sea-ice biogeochemistry and ice-associated ecosystems

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Abstract

The Arctic sea-ice-scape is rapidly transforming. Increasing light penetration initiates earlier seasonal primary production. This earlier growing season may be accompanied by an increase in ice algae and phytoplankton biomass, augmenting emission or capture of climate-active dimethylsulphide and carbon dioxide. Secondary production may also increase on the shelves, although the loss of sea ice exacerbates the demise of sea-ice fauna, endemic fish and megafauna. Sea-ice loss may also deliver more methane to the atmosphere, but warmer ice may release fewer halogens, resulting in fewer ozone depletion events. The net changes in carbon drawdown are still highly uncertain. Despite large uncertainties in these assessments, we expect disruptive changes that warrant intensified long-term observations and modelling efforts.

Keywords: Arctic, sea ice, biogeochemistry, ecosystems, climate change

MAIN

The reduction in Arctic sea ice is one of the most prominent manifestations of global climate change, with implications for the planetary albedo and ocean stratification, accelerating global warming and possibly affecting the global overturning circulation and northern hemisphere weather patterns. At the interface between the ocean and atmosphere, sea ice is a thin, ephemeral and active environment through which heat, momentum and mass (e.g., fluid, gas, solutes) are regulated. These fluxes contribute to physical and biogeochemical processes (Fig. 1) that influence the climate system, provide food and support businesses.

Primary producers within the ice (ice algae, sympagic) and in the underlying ocean (phytoplankton, pelagic) rely on light and nutrients to grow. When conditions are optimal, sea ice harbours dense communities of algae, with sea-ice chlorophyll-*a* concentrations among the highest ever recorded for any aquatic environment[1]. Ice algae and phytoplankton form the base of the food-web, supporting key foraging species such as Arctic cod (*Boreogadus saida*), which sustain subsistence species like ringed seals and beluga[2,3]. Primary producers also control the production and export of particulate organic carbon (POC) to the deep ocean, the so-called "biological carbon pump" [4,5]. This biological pump can be particularly efficient in sea-ice covered areas because ice algae often form fast sinking aggregates [4,5].

The sea-ice zone is also chemically active. The distribution, timing and properties of the sea-ice cover control the air-sea exchange of carbon dioxide (CO_2), and the Arctic Ocean is currently a sink for atmospheric CO_2 [6,7]. Sea ice also regulates the uptake and emission of other climate relevant gases such as methane (CH_4) and dimethyl-sulphide (DMS), providing positive and negative climate feedbacks, respectively (Fig. 1). The ecosystem services provided by sea ice are however under threat in the Arctic, due to its rapid retreat

(Fig. 2) at a pace dictated by cumulative CO_2 emissions[8], as well as other anthropogenic stressors (Box 1).

The decrease in Arctic sea-ice extent spans all seasons and culminates in summer[9]. Arctic sea ice has also thinned over the last four decades[10] in response to warming. Older ice that has survived multiple summers (multi-year ice - MYI) is rapidly shrinking and being replaced by first-year ice (FYI) that melts completely during the spring and summer each year [9,11]. Freeze-up also starts later and melt onset is earlier than in the recent past, leading to a longer ice-free period[12]. The snow cover is becoming thinner[13], while the extent of highly biologically productive marginal ice zones (MIZ) is on the rise in summer, mostly advancing poleward towards regions where sea ice is increasingly younger and thinner[14]. These trends are projected to continue (Fig. 2), with their amplitude depending on the carbon emission scenario considered[15]. Several models predict a nearly ice-free summer Arctic Ocean by the end of the century or earlier under the RCP8.5 "worst-case" emission scenario[16] (Fig. 2c). Rain, rather than snow, may become the dominant form of precipitation by the end of the century[17] and ocean stratification is projected to increase[18]. As a consequence of these changes, sea ice is expected to generally become thinner, younger, and more ephemeral than before (Fig. 2). This perspective assesses potential changes for key sea-ice climatic, biogeochemical and biological properties and processes in response to environmental changes, and highlights crucial uncertainties in the understanding of the Arctic sea-ice system. With this assessment, we aim to motivate future scientific efforts, raise public awareness, and facilitate policy making.

FRAMEWORK

We consider the following aspects of change in the region.

Arctic sea-ice regions The interplay between ocean circulation, continental influences, riverine input and complex bathymetry lead to vastly different sea-ice conditions across the Arctic. For example, the Canadian Arctic Archipelago (CAA) exhibits a large fraction of perennial land-fast sea ice. The Central Basin contains both seasonal and perennial pack ice, whereas the Eastern Arctic sector is mostly covered by seasonal drift ice[9] (Fig. 3). This contrast across icescapes leads to regional differences in biogeochemical processes and associated ecosystems. Ice-covered regions located north of the Arctic circle are discussed in this paper, and when possible, our future expectations reflect regional differences.

Forcing categories The near-future (i.e., middle of this century) expectations address the potential response of key variables in two categories of physical forcings:

(1) *Changes in sea-ice* ***coverage (i.e., horizontal changes)***: reduced overall sea-ice concentrations and reduced duration of the sea-ice season (later freeze-up and earlier break-up);

(2) *Changes in sea-ice* ***properties (i.e., vertical changes)***: younger and thinner sea ice, decreasing snow accumulation (and increasing rain).

CHANGES IN ENVIRONMENTAL CONDITIONS

Changes in the properties and coverage of sea ice directly impact the light, nutrients and space available for primary producers to grow, with cascading effects on the entire Arctic marine ecosystem.

Light Light is a primary driver of algal growth in the sea-ice zone. At high latitudes, a strong seasonality in light cycle[19] dictates the timing and magnitude of ice algal and phytoplankton blooms[20,21]. Downwelling solar radiation is largely reflected back to space due to much higher albedos for sea ice and snow than for seawater. Albedo is higher for deep snow-covered and thick ice and lower when moisture is present within the snow, accumulated at the surface as melt ponds or as open water between ice floes[22]. The fraction of light available within sea ice decreases exponentially with depth; absorption is larger for snow than for sea ice and scattering depends on the presence of brine pockets, air bubbles and impurities. Thus, depending on sea-ice and snow conditions, anywhere from less than 1% to ~20% of the incoming sunlight is transmitted to the ocean underneath [23]. Ice algae and phytoplankton directly respond to changes in available light stemming from variations in ice thickness, snow depth[20], lead opening[21] and/or melt pond formation[24].

Changes in both *sea-ice coverage* and *sea-ice properties* have similar effects on light availability. There is little doubt that because of snow and ice thinning, as well as longer surface melt and open water seasons, the Arctic planetary albedo has decreased by 4-6% between 1979 and 2011[25]. Thus, the light supply to ice algae and phytoplankton has likely increased over the same period, as indicated by model simulations[26]. Increased transmission of light includes greater exposure to potentially damaging UV radiation[27]. However, sympagic algae have shown capacity for UV photoprotection[28] and the positioning of a majority of cells beneath UV-absorbing materials (e.g. snow, ice and other algae) likely makes its impact minimal[29]. More light at the ocean surface contributes to initial increases in overall pelagic Arctic primary production, which has been captured by ocean color[30]. Earth system model simulations reproduce this increase, as long as nutrients are sufficient[18].

Future expectations: Likely increase in light availability (Fig. 4).

Nutrients Nutrients are also key for algal growth. Both in sea ice[20, 31] and in the water column[32], nutrients are thought to regulate the bloom magnitude and termination. However, compared to light, large uncertainties remain in the understanding of nutrient dynamics in sea ice. The ultimate source of nutrients in sea ice is seawater, with a possible atmospheric contribution[33], depending on the season. Nutrient concentrations in sea ice are controlled by brine circulation and exchange with underlying seawater, as well as biogeochemical processes such as assimilation and remineralisation[34]. Adsorption to brine channel walls and biofilm processes likely affect sea-ice nutrient availability and mobility [35]. Nutrients in the underlying seawater are controlled by stratification and the origin of water masses (i.e., nutrient-rich Pacific versus nutrient-poor Atlantic waters), river and glacial runoff, and advection[36].

Sea-ice coverage – Increased meltwater and riverine input[37,38] enhance surface water stratification, whereas thinner ice with larger open water fraction increases exposure of the surface ocean to wind and waves[39] promoting mixing. These processes have competing and uncertain effects on the supply of sub-surface nutrient-rich waters to phytoplankton and ice algae and therefore on primary production. Earth system model simulations and theoretical arguments suggest that increasing stratification and decreasing nutrients will dominate in the pelagic environment[18]. Other models predict an increase in atmospheric deposition, which may overcome the nutrient limitation induced by the increasing stratification[40].

Sea-ice properties – Changes in nutrient concentrations in sea ice are mainly affected by vertical processes (e.g., brine dynamics, ice-ocean fluxes), and future brine dynamics depend on ice temperature and salinity. Ice temperatures may increase because of a warmer atmosphere, but could also decrease due to less snow accumulation. Sea-ice salinity is expected to increase in autumn and winter, because FYI is more saline than MYI, but would become lower in summer, due to increased flushing associated with earlier melt onset[41]. If seawater nutrient concentrations remain unchanged, more saline brine in winter would imply higher nutrients in sea ice in spring and possibly increase sympagic productivity. However, the nutrients gained from dynamics within sea ice would be counterbalanced if seawater nutrient concentrations decrease[18].

Future expectations: High uncertainties on future nutrient stocks in open waters and on nutrient dynamics in sea ice (Fig. 4).

Habitat Sympagic algae depend on sea ice as a substrate to grow. Since a large fraction of Arctic sea ice is FYI, and more FYI is projected to replace MYI in the future (Figure 2), sea ice may be considered a limiting resource and controlling factor of algal growth. Sea-ice algal biomass flourishes in brines mostly close to the underlying seawater (Figure 1), where nutrients are easily accessible, and extends as far upwards as brine permeability allows fluid transport and nutrient supply[34]. The permeable space within sea ice therefore sets a boundary for algal biomass accumulation. Sea-ice permeability is determined by brine temperature and salinity, i.e., the colder and saltier the ice, the lower the brine volume and permeability. We anticipate that ongoing climate warming will result in two possible categories of change in terms of sea-ice permeability and consequently space for colonization inside the ice.

Sea-ice coverage – In the most extreme case, the total disappearance of sea ice in some regions has the obvious consequence of a disruption of sea-ice sympagic productivity in these areas. The delayed formation and earlier melt onset of seasonal sea ice will further reduce the space available for colonization. The loss of sea ice as a physical habitat for organisms may become a primary factor limiting ice-associated organisms and biodiversity in some Arctic regions[42].

Sea-ice properties – During the melting period, the current and future increase in temperatures at the interface between the lower atmosphere and the surface snow, ice or ocean (the so-called “skin temperature”) would lead to warmer and more permeable sea ice, thus to more habitable space. In winter, however, snow insulation, sea-ice temperature and permeability would decrease with thinner snow (Fig. 2d), contracting brine volume and reducing the space available for colonization.

Future expectations: Overall, the sea-ice habitat will likely decrease as sea ice continues to shrink (Fig. 4). Within the remaining sea ice, the space available for colonization may increase with warmer ice temperatures in spring-summer allowing for higher local biomass build-up in ice, while in autumn-winter the reverse will occur.

CHANGES IN BIOTA

Changes in the light, nutrient and habitat conditions discussed above affect the timing, composition and abundance of primary producers, and more specifically, the relative contribution of ice algae versus phytoplankton. Changes in primary production may then subsequently impact secondary production (microbial and metazoan consumers), higher trophic levels and ocean carbon sequestration.

Microalgal communities Shifts in ice algae and phytoplankton communities will have cascading consequences for the Arctic marine ecosystem. For example, the efficiency of carbon export and role of organisms in the food web are dependent on the size and shape of algal cells. Furthermore, production of secondary aerosol precursors (i.e., volatile organics, including DMS) varies between algae species.

Sea-ice coverage – The transition from MYI to FYI will reduce the availability of overwintering habitat and will possibly result in a decrease in diversity of the ice algae community[43,44]. Intrusion of sub-Arctic phytoplankton species like *Phaeocystis* into the high Arctic[21] will result in a more uniform latitudinal distribution of species. In particular, the abiotic changes described above will favour phytoplankton with greater capacity for growth under higher light conditions, and possibly lower nutrients and salinities than present communities[45]. This may include a greater presence of flagellate species within communities that at present are overwhelmingly dominated by diatoms[46]. We also anticipate a decrease in abundance of sea ice-specialists, such as *Nitzschia frigida,* in favour of cryo-pelagic species like *Fragilariopsis cylindru*s. Melt ponds might become an increasingly dominant feature of spring sea ice, and they may favour the development of dense algal colonies like the centric diatom *Melosira arctica*[47], which presently drives episodic pulses of carbon export to the benthos[4]. Under-ice pelagic diatom species (*Chaetoceros, Thalassiosira* and *Fragilariopsis*) are also likely to increase in prevalence with melt pond coverage[1].

Both open ocean and under-ice phytoplankton production are expected to increase in magnitude and aerial extent, as well as commence earlier in the spring due to earlier melt onset and increased light availability. However, the overall increase in phytoplankton production will be constrained by the finite availability of nutrients in the water column. Autumn phytoplankton blooms are likely to become a regular feature as a result of later freeze-up, particularly at the periphery of the Arctic Ocean[48].

Sea-ice properties – The predicted increase in light availability from a thinning ice and snow cover will increase the potential for ice algal primary production across the Arctic. The substantial thinning of the snow cover is expected to have the greatest effect south of 66°N, where light availability will significantly extend the length of the sympagic growing season[42]. From 66 to 74°N the decrease in duration of ice cover into spring and summer will set an upper limit to the total accumulation of ice algal biomass[42]. In the Eurasian shelf areas and the CAA, the bloom of sea-ice bottom micro-algal communities may start and end earlier in the spring[49]. We expect the largest relative increase in algal primary production in the high Arctic, due to the more productive FYI largely replacing the less productive MYI[42]. Whereas an increase in stratification of the upper water column would decrease the availability of surface water nutrients for bottom-ice communities, some regions will experience enhanced vertical mixing due to new open-water areas exposed to winds and storms[39], enhanced tidal currents[50], or increased upwelling[51], which would benefit ice algal production.

The presence of under-ice phytoplankton blooms will become more frequent as the Arctic ice cover becomes thinner and more transparent, with possibly greater coverage of melt ponds[52] and leads[21] that act as windows into the underlying ocean. However, the blooms may also become smaller in magnitude and shorter in duration, if nutrients become more limited.

Future expectations: Overall, increasing open ocean conditions are expected to favour phytoplankton growth and an overall shift towards cryo-pelagic and pelagic species. As light availability and surface stratification increase, nutrients will become increasingly limiting for both sympagic and pelagic production. The sign and magnitude of changes in primary production will vary regionally, with the largest relative increase expected in the Central Basin (Fig. 4). In the Western Arctic, where FYI is expected to largely replace MYI, a general increase in primary productivity is expected (Fig. 4) alongside a likely loss in ice-algal biodiversity. In the Eastern Arctic, where a large fraction of FYI is shrinking, the potential increase in primary productivity will be constrained not only by uncertain future nutrient inventories, but also by the potential loss of habitat (Fig. 4).

Microbial loop Although growth temperatures in sea ice are well below optimal, bacterial production in sea ice can exceed rates measured in the productive waters of temperate regions[53]. Carbon used to support this heterotrophic production is largely sourced from primary producers[54]. As a result, primary and secondary microbial production in the sympagic realm are expected to exhibit similar changes with climate warming.

Sea-ice coverage – As MYI has a low brine volume fraction compared to FYI, a shift from MYI to FYI will promote heterotrophic activity.

Sea-ice properties – The thinner and warmer sea ice in summer will support a greater degree of heterotrophic activity[55]. Because the brine channels in warmer ice are more connected, with larger pore spaces that may facilitate the grazing of bacteria by bacterivorous protists, there is the potential for a strengthened carbon transfer from microbial compartments to upper trophic levels. Following the trends in primary productivity, pelagic microbial heterotrophic activity is most likely to increase following spatial and seasonal changes in primary production.

Future expectations: Changes in the Arctic will result in increased heterotrophic activity (Fig. 4). The heterotrophic microbial community will directly benefit from increases in primary productivity. Secondly, heterotrophic activity will increase with warmer sea-ice temperatures.

Metazoan consumers The continuing transformation of sea-ice habitats will profoundly change the biodiversity of Arctic metazoan consumer communities that depend significantly on ice algae as a carbon source[56]. On the Arctic shelves, a warmer ocean with a shorter seasonal ice coverage will promote the replacement of polar communities by sub-polar communities, causing a retreat of cold-adapted and sympagic species towards the Central Basin[2,57].

Sea-ice coverage – Changes in the areal coverage and timing of sea ice may disrupt the life-cycles of sympagic consumers, especially those not adapted to survive in the water column[58]. Shorter ice-algae bloom seasons in the Eastern Arctic[59] will reduce sympagic food availability for ecologically important species, such as *Calanus*[58], ice amphipods and polar cod. Emerging mismatches of the timing of ice algae and phytoplankton blooms with grazer reproductive cycles could reduce reproductive success[44,58]. In some regions, an increase in total production of the Arctic Ocean, with a shift from sympagic to pelagic producers, would promote growth of herbivorous consumers[59]. Omnivores and predators (*Themisto* spp., euphausiids, jellyfish) may regionally increase in biomass too[59].

Sea-ice properties – The change to thinner, younger, and more dynamic sea ice will alter the distribution patterns of sympagic consumers, including under-ice amphipods, in-ice meiofauna and forage fish. Species-specific habitat requirements cause variations in consumer community structure in response to variations in sea-ice properties[60]. On the shelves, the anticipated replacement of polar/sympagic consumers by sub-polar/pelagic consumers will predominantly result in a replacement of large, lipid-rich zooplankton by more numerous but smaller, and comparatively lipid-poor species, e.g., *Pseudocalanus* spp., *Metridia* spp., *Cyanea* spp.. Furthermore, these changes will negatively affect higher levels of the food chain, for instance with the replacement of polar cod with capelin and sand lance species of lower energetic contents[2]. In the future seasonally ice-covered Central Basin, a potential relative increase in primary production is unlikely to support large stocks of consumers if they cannot adapt their life cycles to the altered algal phenology[46,52]. Furthermore, declining taxonomic diversity[61] could cause a decline of functional diversity, reducing resilience to environmental stress.

<u>Future expectations:</u> We expect an overall decrease in biomass and diversity of sympagic consumers (Fig. 4) due to altered algal phenology and lower algal food quality. On the shelves, pelagic secondary productivity will mostly increase, but a shift to small and gelatinous zooplankton will profoundly affect food web structure. In the Central Basin,

secondary productivity will remain low, but loss of biodiversity will negatively affect the resilience of the ecosystem to environmental perturbations and anthropogenic stress.

Higher trophic levels and marine living resources As sub-polar and Atlantic fish expand their ranges north, the biomass of polar cod and other cold-adapted fish resident to the Arctic Ocean[2,57] will continue to decline across many of the Arctic shelf regions[59,62]. These species have shifted their distribution range towards the northern shelf slope[57]. Benthic secondary production will generally decline due to reduced sympago-benthic coupling and a lack of ice-algae downfalls, in spite of locally enhanced food availability due to increasing pelagic productivity[63]. In shallow regions, increased light and ice-scouring due to sea-ice retreat might positively impact macroalgal growth (e.g. kelp[64]) and through increased planktonic primary production also locally favour benthic animal communities including sponges[65]. Continued declines in key prey fish, such as polar cod, will likely intensify the loss of sympagic predators, including ringed seals, beluga whales and polar bears[2,66,67], which is already being observed. Consequently, these mammals may face local- to regional-scale extinctions in the Arctic shelf domains. In contrast, the presence of generalist predators like baleen whales, orcas, and certain seabird species is expected to increasingly expand into Arctic shelf seas[68].

Future expectations: The abundance of species endemic or common to the Arctic like beluga whales, polar bears and polar cod will decline (Fig. 4) as sub-polar species become increasingly abundant in Arctic waters. Iconic Arctic fauna face the risk of local to regional extinction.

Biological carbon pump A small fraction of the POC produced at the surface of the Arctic Ocean by sea-ice algae and under-ice phytoplankton can be directly exported to the seafloor. More specifically, events of massive downward flux of *Melosira* can cause episodic maxima of carbon export[4] in the Central Basin. The export of this POC can be significantly enhanced by minerals released by sea ice that ballast sinking algae aggregates and by zooplankton[69,70]. Primary producers also serve as a vital source of food for sympagic and (meso-)pelagic consumers. Through respiration, feeding and excretion during vertical migrations[71], as well as through fecal pellet production[72], (meso-)pelagic and sympagic consumers play an important role in the POC export and carbon burial at the seafloor.

Changing sea-ice habitats and nutrient limitation will promote a more heterotrophic food web[73]. The predicted shifts in food web structure will result in greater recycling and retention of carbon in the pelagic food web[63], which will directly compete with the intensifying biological carbon pump to determine the net flux of carbon in the Arctic Ocean. The most abundant sympagic and cryo-pelagic consumers (ice amphipods and *Calanus* spp. copepods) produce large and fast sinking fecal pellets[74]. As a result, the shift towards organisms that produce smaller fecal pellets (e.g., *Pseudocalanus* spp.) will decrease the contribution of consumers to POC export on the Arctic shelves. In the Central Basin, future POC export by consumers is expected to remain low[75], but it has the potential to further decrease when populations of sympagic fauna decline.

<u>Future expectations:</u> The expected increase in primary productivity, shift towards smaller algae and warmer ice will lead to more grazing by smaller zooplankton and higher microbial remineralisation. So, except for potentially periodic *Melosira* blooms and subsequent export pulses, all processes point towards a less efficient biological carbon pump (Fig. 4), as we expect a shift from an export system to a retention system.

CHANGES IN CLIMATE-ACTIVE GASES

Gas dynamics and fluxes in sea ice strongly depend on ice temperature, salinity and texture. In addition, most climatically-active gases (e.g., CO_2, CH_4, DMS) are produced and/or consumed by organisms living in or under the ice and are taken up or released during the natural cycle of sea-ice formation and melt. The cycles of these "biogases" are therefore closely linked to biological processes. Ice algae, phytoplankton and bacterial communities will adapt to changes in sea ice, with direct consequences for the uptake and release of climate active gases.

CO_2 During autumn and winter, sea ice acts as a source of CO_2[76], due to high brine pCO_2 and precipitation of calcium carbonate (Fig. 1)[77]. However, during spring and summer, sea ice acts as a sink of CO_2 due to brine dilution, calcium carbonate dissolution, and the biological carbon pump, driven by algal productivity[78]. The balance may be a net sink, due to the net export of brine to underlying waters.

Sea-ice coverage – In the Central Basin, the formation of more new ice will result in an increased CO_2 efflux to the atmosphere in winter[79]. However, sea-ice formation will also increase the rejection of CO_2-rich brines to the ocean[80]. Model simulations indicate that this rejection to the ocean and export to depth of CO_2-rich brines combined with precipitation and transport of calcium carbonate during sea-ice growth and melt processes (sea-ice carbon pump) has a minor effect on the global oceanic carbon uptake, but can have larger regional effects[81,82].

The increase in ice-free ocean area and consequent carbon drawdown may have enhanced the CO_2 sink by as much as 1.4 TgC y^{-1} between 1996 and 2007[83], and including the ice algal system may have added another 2% per decade to the pan-Arctic ocean carbon uptake[84]. In winter, storms and openings in the ice cover, such as leads and cracks, will allow for increased ocean CO_2 uptake in undersaturated areas[85]. Outgassing will increase in open waters that become supersaturated (from excess respiration over photosynthesis), particularly in upwelling areas and coastal regions influenced by large rivers[86,87]. Model results indicate that enhanced fluxes due to continuing sea-ice retreat extend the maximum uptake in fall and reduce the uptake in summer[88], and the projected increase in ocean stratification will further limit the ocean's capacity to absorb CO_2 and possibly lead to widespread outgassing in summer[36,89,90].

Sea-ice properties – The shift from MYI to FYI will promote the formation of frost flowers and upwards brine rejection, which mediates ice-to-atmosphere CO_2 transfer in winter[91,92] . The general increase in ice temperature and permeability will favour air-sea ice gas exchange. However, with warmer and more rainy conditions, snow will tend to melt and refreeze (superimposed ice formation), decreasing air-sea ice gas exchange[79]. In spring, precipitation (snow and rain) may promote melt pond formation, leading to greater CO_2 uptake from the atmosphere. The prediction of higher primary production at the bottom of Arctic FYI should enhance CO_2 uptake from the water[93] in spring and summer. A change from MYI to FYI will increase brine drainage and, therefore, increase brine CO_2 export from the ice to underlying water.

<u>Future expectations:</u> Increased air-sea fluxes, due to more open ocean area and more leads over undersaturated waters, and increases in CO_2-rich brine export may lead to an increase in the Arctic Ocean CO_2 sink (Fig. 4). This additional sink would be offset by increased stratification (capping CO_2 uptake) and outgassing in some regions due to enhanced vertical mixing with deep CO_2-rich waters and to our prognosis that the Arctic Ocean will transfer from a carbon export system to a carbon retention system.

<u>CH_4</u> The impact of sea ice on ocean-atmosphere fluxes of CH_4 is still unclear. Recent studies highlighted a CH_4 super-saturation in sea ice-influenced waters of the Central

Basin[94] and an enhanced CH_4 efflux to the atmosphere above areas with fractional sea ice cover[95]. An impermeable sea-ice cover likely enhances CH_4 exposure to microbial oxidation[96]. This process would have the potential to reduce CH_4 sea-air fluxes, particularly above continental shelves whose sediments represent the main source of CH_4 to the Arctic Ocean[97].

Sea-ice coverage – More open water will facilitate the efflux of excess CH_4 to the atmosphere. A shorter sea-ice season and warmer temperatures will also result in an increase of sea-ice permeability, allowing CH_4 in under-ice seawater or in the sea ice itself to escape more readily. Indeed, seasonality directly influences ice permeability which is one of the major physical processes controlling CH_4 storage in sea ice[98].

Sea-ice properties – The shift from MYI to FYI will accelerate CH_4 cycling and likely increase the transfer of CH_4 from sea ice to the atmosphere.

Future expectations: Significant uncertainties are still associated with the current and future CH_4 cycle in the Arctic Ocean. Nevertheless, sources of CH_4 are expected to increase. A decreasing sea-ice cover, enhanced sea-ice permeability, and a shift from MYI to FYI will facilitate the CH_4 flux from the seawater to the atmosphere, likely resulting in an overall increase of the oceanic source of CH_4 in the Arctic (Fig. 4).

DMS DMS is a precursor of sulfate aerosols in the atmosphere, limiting the exchange of both short- and long-wave radiation between Earth’s atmosphere and space. Mainly derived from dimethylsulfoniopropionate (DMSP) produced by macro- and microalgae in response to stress (freezing, high salinity), DMS occurs at high concentrations in sea ice[99]. DMSP is either converted to DMS in the ice by bacterial activity and then released to the atmosphere, or released to the underlying water where it is partly converted to DMS. The fraction of DMSP resulting in DMS emissions is strongly related to the abundance and taxonomy of microalgae, bacterial activity and environmental conditions. Model simulations highlight that the sea-ice sulfur cycle particularly affects DMS emissions in spring when the accumulation of DMS under ice can sporadically escape and cause spikes in atmospheric concentrations high enough to initiate cloud nucleation[100,101] (Fig. 1).

Sea-ice coverage – Given that sea ice acts as a source of DMS to the atmosphere, sea-ice loss should weaken this source. However, an anticipated increase in under-ice and pelagic blooms - especially when consisting of *Phaeocystis* sp. - may increase the pelagic DMS source. Reduced ice extent may therefore have an insignificant impact on net, basin-scale DMS fluxes. However, regional changes in total primary production, microplankton assemblages and gas transfer velocity may result in very large regional variations in DMS fluxes.

Sea-ice properties – The shift from MYI to FYI, in association with less snow accumulation and ensuing shifts towards more *Phaeocystis* sp. and increased primary production, will promote DMS release to the atmosphere. The impact of increasing sea-ice mobility and related turbulence can potentially increase the fluxes, while increasing rain would promote flushing and release of DMS into the water column[102].

Future expectations: Since DMS pulses are associated with ice types of the MIZ, an increased aerial coverage of the MIZ is anticipated to result in increased DMS production.

Halogens and ozone interactions Reactive halogen species are responsible for atmospheric cleansing and ozone depletion events (ODEs), and associated mercury deposition, in the polar tropospheric boundary layer[103]. Young sea ice is strongly associated with ODEs[104], which have been ascribed to the release of reactive halogen species (bromine and iodine compounds)[105] (Fig. 1). Sea ice, frost flowers and saline snow are potential sources of atmospheric halogens[105], and blowing snow above sea ice has been confirmed as a halogen source in the Southern Ocean[106].

Sea-ice coverage – A shift from sea-ice covered seas to open waters will decrease ODEs.

Sea-ice properties – Younger and more permeable ice will likely promote salty ice/snow surfaces by brine wicking and related halogen activation. However, warmer sea-ice conditions may impede active bromine species release and ODEs requiring low surface temperatures[107]. In parallel, more rain and less snow accumulation are likely to reduce the specific surface area for halogen activation, as well as the blowing-snow vector of halogen mobilization.

<u>Future expectations:</u> Decrease in ODEs (Fig. 4).

CHALLENGES AND FUTURE DIRECTIONS

The IPCC specifically calls for improvement in the fundamental understanding of sea ice to advance its representation in global climate models. Reducing uncertainties is currently the main challenge (Box 2). Ice algae production and biogeochemical exchange processes are now included in some Arctic ocean modelling efforts, but model intercomparisons reveal significant differences between models. Particularly important gaps include understanding and parameterisations of: a) light transmission through snow and ice; b) controls on primary production and diversities in sea ice, as well as ice algal incorporation and release; and c) fluxes, deposition and emission of climatically active gases and aerosols.

In the short term, primary productivity is predicted to generally increase in both sea ice and seawater in the Arctic, as long as nutrients are plentiful[18,42]. The timing of the blooms is however likely to change, with negative downstream effects on ice-dependant consumers[58,108]. A number of studies[2,66,67] are reporting declines in condition, health and population sizes of high-Arctic top predators, which must be seen as a warning sign that ecosystem changes could be more disruptive than expected. Understanding the consequences of ecological changes in sea-ice habitats for resource conservation and management is fundamental to the development of marine governance schemes that consider both socio-economic and ecological changes.

There is an urgent need for the establishment of long-term observing platforms in climate sensitive sea-ice regions (for example: the CAA, East Siberian Shelf and the Central Basin) to collect benchmark data and to record seasonal and decadal trends, as well as to anticipate thresholds and tipping points for the full suite of variables discussed in this perspective paper. Sea ice is still considered biogeochemically inert in most large-scale Arctic models and, in particular, Earth System Models. As computer resources continue to become more affordable and available, we advocate for new modelling studies that can address the role of sea-ice biogeochemistry in the Earth system. This holistic approach will allow the science community to deliver firmer predictions on how the Arctic system is (and we, as a community, are) responding to the Great Arctic Thaw.

Box1: Other anthropogenic stressors

Reduced sea-ice extent will result in an increase in human pressure on wildlife in the Arctic through shipping, oil and gas exploration, fisheries and tourism. In addition to direct pressure on stocks by fishing activities, general disturbance by an increasing human presence will have negative effects on the life-cycles of many megafauna species. Smaller species seem to be more sensitive to pollution, due to their higher surface area-to-volume ratios[110]. Concentrations of microplastics in sea ice are several orders of magnitude higher than in the underlying water[111], with potential to affect both sea-ice properties (e.g., salinity, albedo) and marine life[112]. Given the small size of the particles (<50 µm), which are in the same range as sea-ice algae, it is likely that they are incorporated into the food web, with yet unknown consequences.

Models suggest sea-ice retreat will promote ocean acidification due to increased air-sea exchange and meltwater input[113]. However these models do not account for the rejection of CO_2-rich brines that further promote ocean acidification[114] nor for the dissolution of calcium carbonate in sea ice during melt, which can act to potentially decrease the effect of ocean acidification at the most critical time of the year in ice-covered areas[115] or remove alkalinity from the Arctic Basin via sea-ice drift and exit through Fram Strait[116]. Mortenson[84] found that summer calcium carbonate saturation states are overestimated when the sea-ice carbon pump is excluded from models. Nonetheless, while the impact of changes in *sea-ice properties* is uncertain, change in *sea-ice cover* will probably promote ocean acidification, overall.

Box2: Uncertainties in this prognoses

Our group of sea-ice experts has generated future expectations of how the changing sea-ice environment is likely to impact biogeochemical systems, based on the current knowledge of the Arctic (Fig. 4). These attempts are not quantitative. New and sustained field data and improved models are crucially needed to improve predictive capabilities. The most pertinent knowledge gaps include:

- sustained snow observations;
- relative importance of freshwater inputs and storm events on Arctic ocean stratification and nutrient budgets;
- contributions of the Pacific and Atlantic water masses to the nutrient reservoirs in the Arctic ocean;
- effect of shorter but more intense sea-ice algal blooms on biogases, consumers and carbon export;
- composition of current sympagic algal communities and the potential shifts in speciation as a consequence of environmental changes;
- long-term trends in under-ice phytoplankton blooms;
- the life-cycles of sympagic flora and fauna, and their resilience to habitat change or loss;
- the diversity, distribution and standing stocks of pelagic macrofauna, especially fish, in the Central Basin;
- partitioning between pathways of carbon transmission and nutrient cycling in the ecosystem, and their effect on the biological carbon pump;
- air-ice-water gas fluxes over the annual cycle, particularly in winter;
- the impact of shifts in phytoplankton phenology on pelagic DMS production; and

the impact of ocean acidification on ice-associated species.

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Author Contributions

D.L., L.T., M. v.L., K. C., H. F., B. D., L. M. and J. S. led the design and the writing of the paper. G. C., F. F., N. S., M. V. and M. V. significantly contributed to the "Environmental conditions" section. P. A., J. B., H. K., K. M., I. P., J.-M. R. and P. W. significantly contributed to the "Biota" section. K. B., M. C., O. C., E. D., B. E., A. F., N.-X. G., C. J., E. J., M. K., S. M., D. N., N. S., J.-L. T. and F. v.d.L. significantly contributed to the "Gases" section.

Competing Interests statement

The authors declare no competing interests.

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Figure Legends

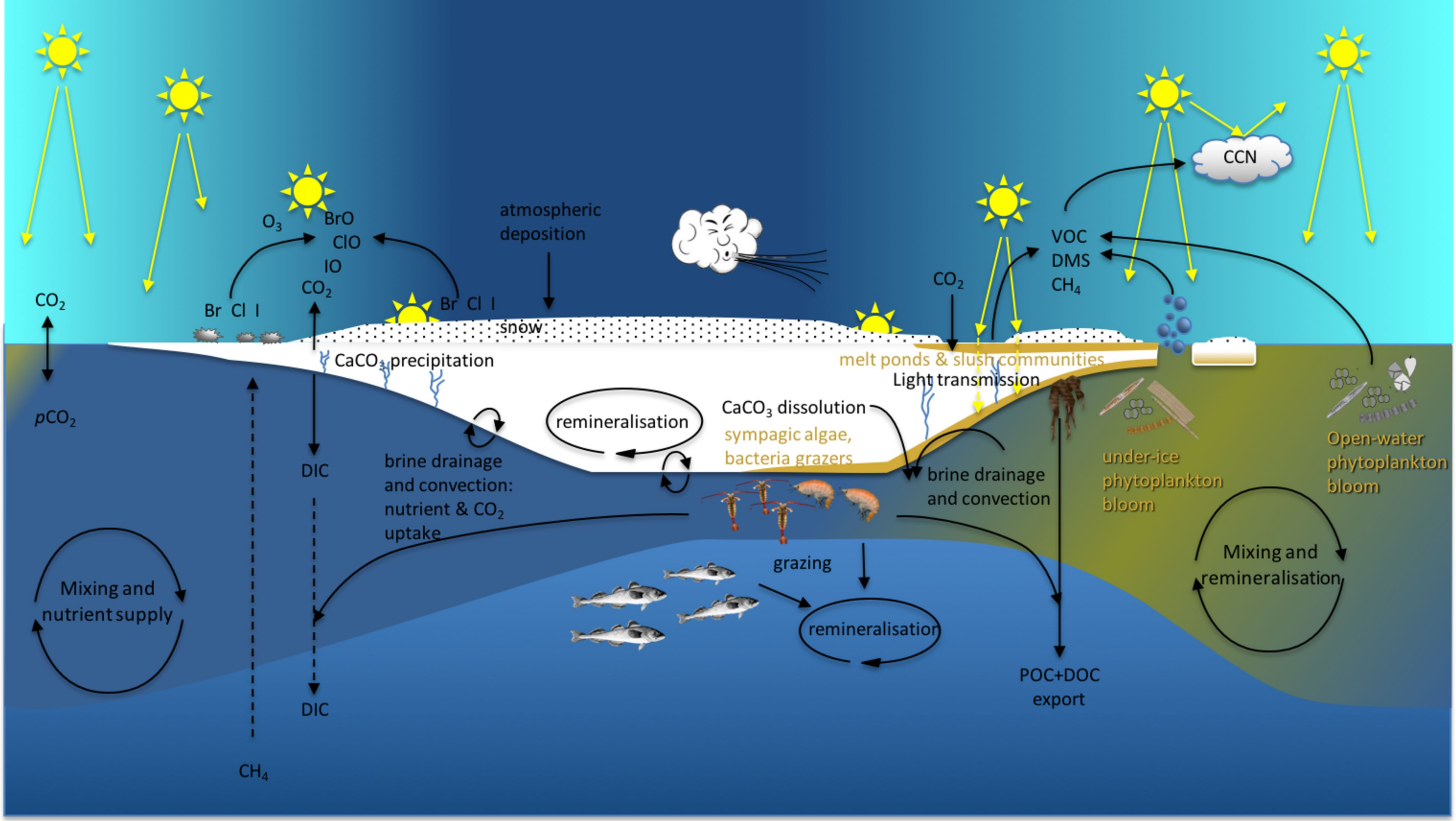
Fig. 1: Schematic of seasonal sea-ice biogeochemical processes in the Arctic Ocean, modified from[109]. Black arrows represent the directionality of biogeochemical exchanges, for example, across an interface (e.g., CO_2 efflux from the ocean to the atmosphere, release of reactive halogen species from the ice surface) or throughout an interval (e.g., brine drainage and convection along the ice-water interface, heterotrophic remineralization of organic material throughout the brine network). Dashed lines illustrate diffusive gradients, such as that of Dissolved Inorganic Carbon (DIC). Yellow arrows indicate solar radiation. Ice associated and pelagic microalgal communities and their grazers are represented by orange shading and symbols. The biological carbon pump links carbon exchange processes in the surface to sequestration at depth through particulate organic carbon (POC) and dissolved organic carbon (DOC) export, illustrated by arrows penetrating below the mixed layer (darker shading). Surface processes further impact climate active gases, such as dimethylsulfide (DMS) and methane (CH_4), as well as volatile organic compounds (VOC), which can contribute to the formation of cloud condensation nuclei (CCN).

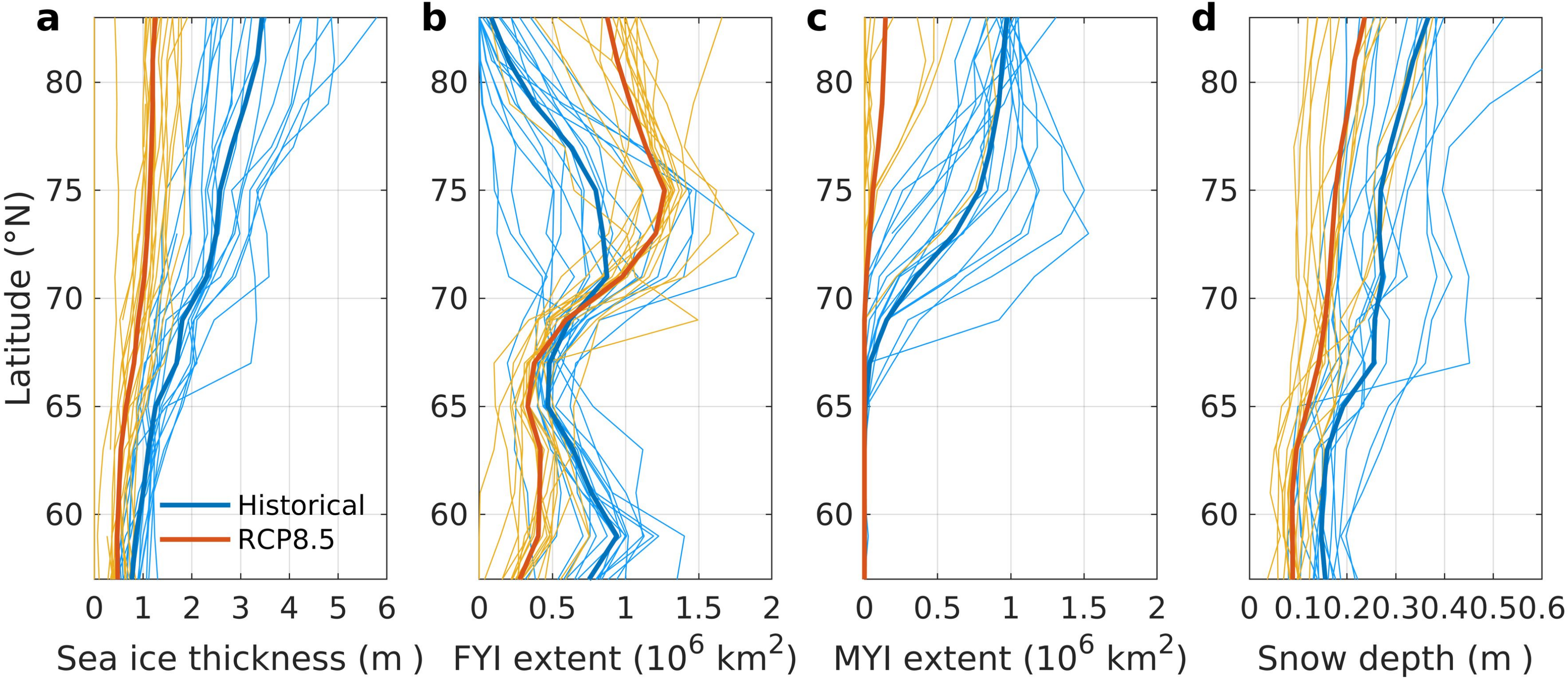
Fig. 2: Past and predicted changes in sea-ice physical characteristics along latitudes. Comparison between the historical (1961–2005, blue lines) and the “worst-case” RCP8.5 scenario (2061–2100, orange lines). Medians of the empirical probability density functions from each of 18 CMIP5 climate models[42] (thin lines) and their ensemble mean (thick lines) for **a**, sea-ice thickness. **b**, first-year ice extent. **c**, multi-year ice extent. **d**, snow depth.

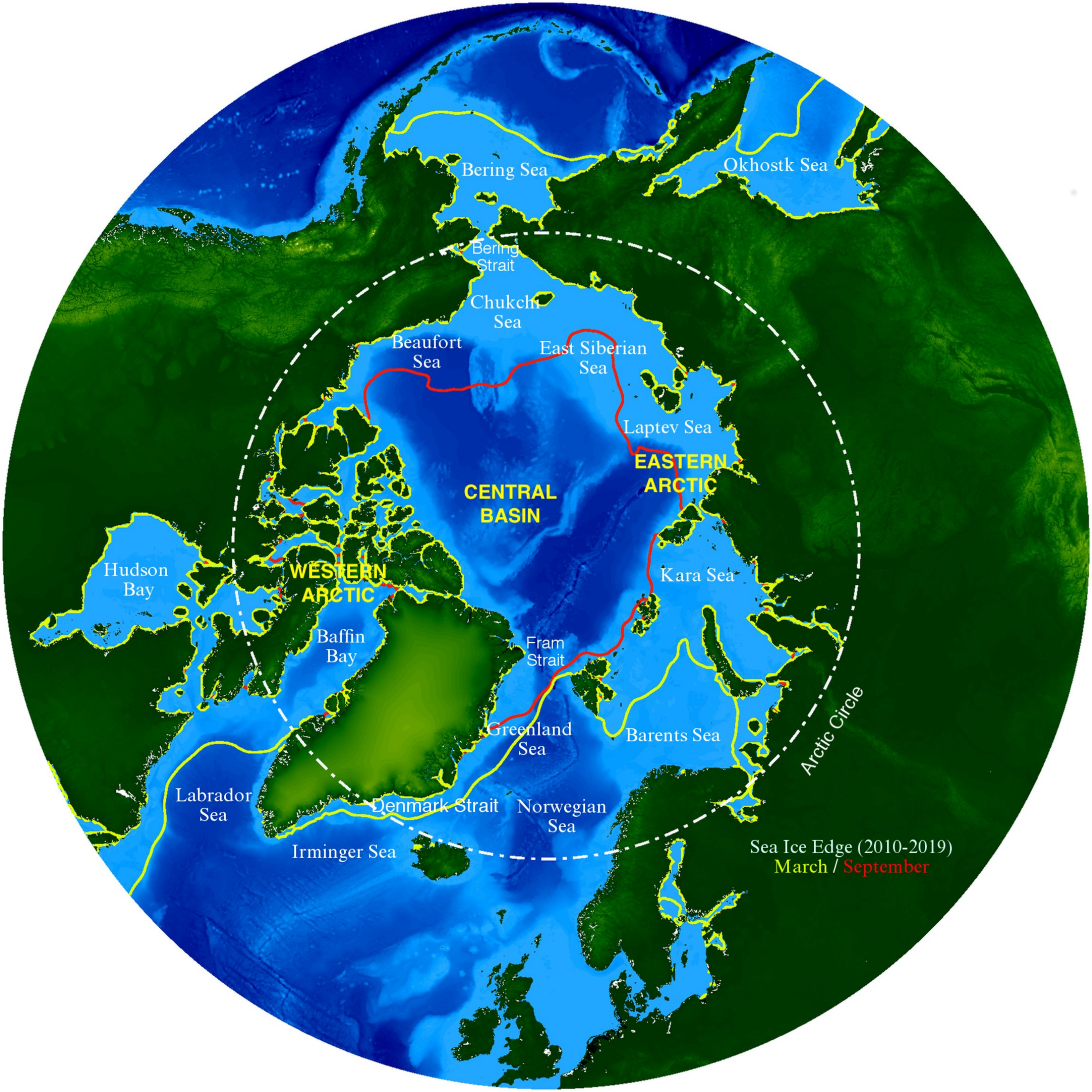
Fig. 3: Map of the Arctic Ocean. The Western Arctic, Central Basin, and Eastern Arctic regions discussed in the text are indicated in yellow, with bathymetry (blue shading) and

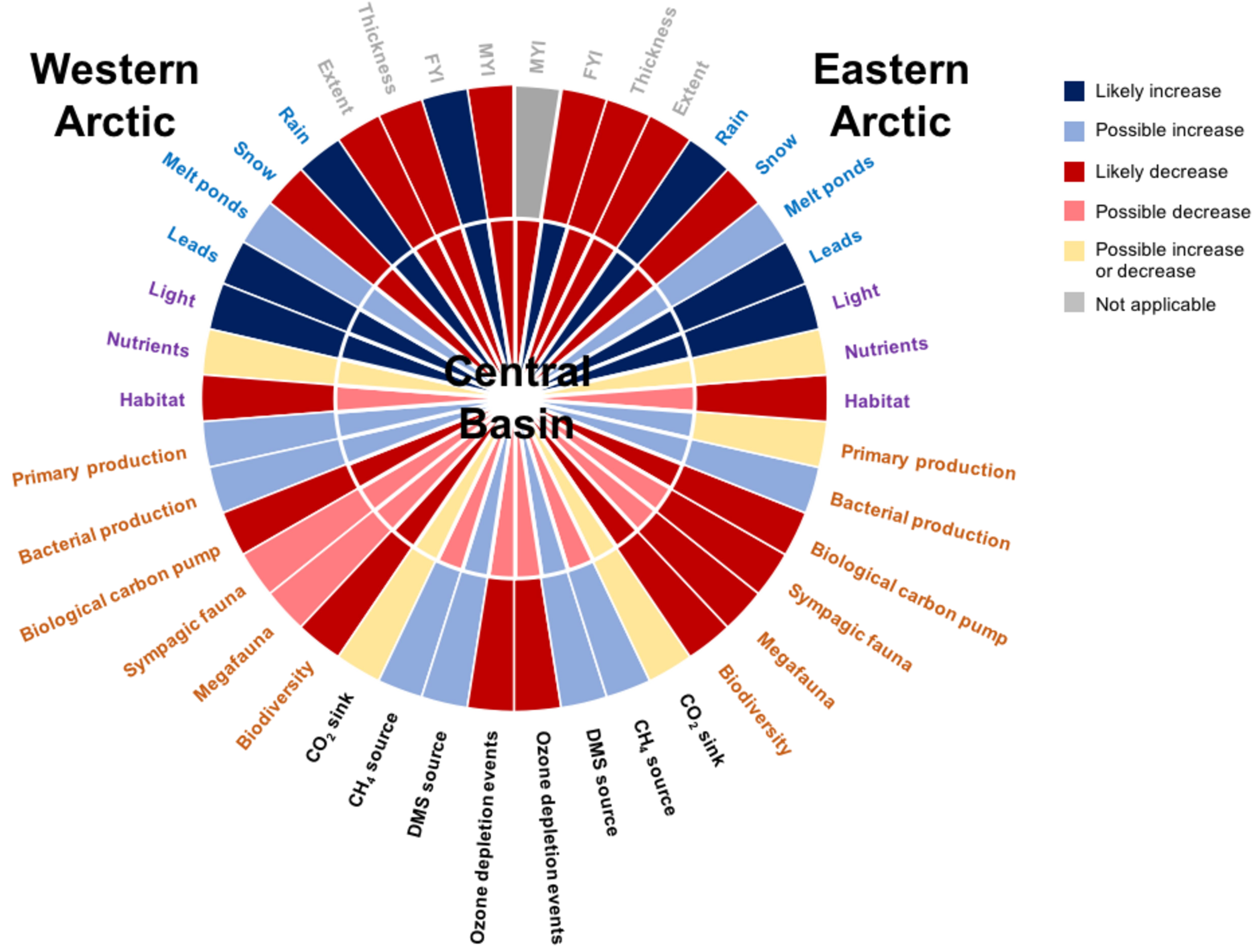
land elevation (green shading). Red and yellow lines represent the 2010-2019 averaged minimum (September) and maximum (March) sea-ice extents, respectively.

Fig. 4: Future expectations of changes in the sea-ice biogeochemical system in the Arctic. The Western Arctic includes the Chukchi, Beaufort and Canadian Archipelago shelves, and the Eastern Arctic includes the shelves from the Barents to East Siberian Seas (as in Fig. 3). The categories of changes are repeated opposite to each other in the schematic hemispheres of the Western Arctic Ocean and the Eastern Arctic Ocean of the circular diagram. Their colours indicate sea-ice changes (grey), icescape changes (blue), abiotic drivers (purple), biological changes (brown), and changing gas fluxes (black). For further details see Box 2.


CO_2
pCO_2
O_3
BrO
ClO
IO
CO_2
Br Cl I
atmospheric deposition
Br Cl I
snow
CCN
CO_2
VOC
DMS
CH_4
$CaCO_3$ precipitation
melt ponds & slush communities
Light transmission
remineralisation
$CaCO_3$ dissolution
sympagic algae, bacteria grazers
DIC
brine drainage and convection: nutrient & CO_2 uptake
brine drainage and convection
under-ice phytoplankton bloom
Open-water phytoplankton bloom
Mixing and nutrient supply
grazing
Mixing and remineralisation
remineralisation
POC+DOC export
DIC
CH_4


a
b
c
d
Latitude (°N)
80
75
70
65
60
Historical
RCP8.5
0 1 2 3 4 5 6
Sea ice thickness (m)
0 0.5 1 1.5 2
FYI extent (10^6 km^2)
0 0.5 1 1.5 2
MYI extent (10^6 km^2)
0 0.1 0.2 0.3 0.4 0.5 0.6
Snow depth (m)


Bering Sea
Okhostk Sea
Bering Strait
Chukchi Sea
Beaufort Sea
East Siberian Sea
Laptev Sea
EASTERN ARCTIC
CENTRAL BASIN
WESTERN ARCTIC
Hudson Bay
Kara Sea
Baffin Bay
Fram Strait
Greenland Sea
Barents Sea
Arctic Circle
Labrador Sea
Denmark Strait
Norwegian Sea
Irminger Sea
Sea Ice Edge (2010-2019)
March / September


Western Arctic
Eastern Arctic
Central Basin
Extent
Thickness
FYI
MYI
MYI
FYI
Thickness
Extent
Rain
Snow
Melt ponds
Leads
Light
Nutrients
Habitat
Primary production
Bacterial production
Biological carbon pump
Sympagic fauna
Megafauna
Biodiversity
CO_2 sink
CH_4 source
DMS source
Ozone depletion events
Ozone depletion events
DMS source
CH_4 source
CO_2 sink
Biodiversity
Megafauna
Sympagic fauna
Biological carbon pump
Bacterial production
Primary production
Habitat
Nutrients
Light
Leads
Melt ponds
Snow
Rain
Likely increase
Possible increase
Likely decrease
Possible decrease
Possible increase or decrease
Not applicable