

## Query Details

[Back to Main Page](#)

### 1. Please confirm that all affiliation details are correct.

all affiliation details are now correct

### 2. Please add the following details to affiliations: 1) A city location for affiliation 1; 2) A department name for affiliation 3, if a p appropriate; 3) A city location for affiliation 4; 4) A city location for affiliation 5; 5) A city location for affiliation 6; 6) A department name for affiliation 12, if a p appropriate, and a city location for affiliation 12; 7) A city location for affiliation 17; 8) A city location for affiliation 22.

The details for affiliations have been corrected

### 3. Please check your article carefully, coordinate with any co-authors and enter all final edits clearly in the eproof, remembering to save frequently. Once corrections are submitted, we cannot routinely make further changes to the article.

I have checked the article carefully

### 4. Note that the eproof should be amended in only one browser window at any one time; otherwise changes will be overwritten.

understood

### 5. Author surnames have been highlighted. Please check these carefully and adjust if the first name or surname is marked up incorrectly. Note that changes here will affect indexing of your article in public repositories such as PubMed. Also, carefully check the spelling and numbering of all author names and affiliations, and the corresponding email address(es).

Surnames are correct, and the spelling ok.

### 6. You cannot alter accepted Supplementary Information files except for critical changes to scientific content. If you do resupply any files, please also provide a brief (but complete) list of changes. If these are not considered scientific changes, any altered Supplementary files will not be used, only the originally accepted version will be published.

understood

### 7. Please confirm that edits to the sentence beginning "Sea-ice algal biomass flourishes..." have retained their intended meaning.

Yes, the intended meaning is retained. Please remove the coma after the word "upwards".

### 8. Please confirm that edits to the sentence beginning "On the shelves, ..." have retained the intended meaning of the sentence.

Remove the words "or" so that the meaning of the sentence is retained.

### 9. Please confirm that the expansion of the abbreviation 'pCO<sub>2</sub>' to 'partial pressure of CO<sub>2</sub>' is

correct.

this is correct

**10. Please confirm that the phrase ‘export to depth of CO<sub>2</sub>-rich brines’ is correct, or suggest alternative wording.**

this phrase is correct

**11. Please confirm that the title of Box 2 is correct.**

this is correct

**12. Please provide the publisher details for ref. 22 and details of the editor(s), if possible.**

Perovich, D.K. in *Sea Ice* (Ed. Thomas, D. N.) 110–137 (John Wiley & Sons, Ltd, 2017).

**13. For ref. 70, please state the journal name, volume number and page range/article number.**

Replace with the following reference:

Darnis, G. & Fortier, L. Zooplankton respiration and the export of carbon at depth in the Amundsen Gulf (Arctic Ocean). *J. Geophys. Res.* 117, C04013 (2012)

**14. Please confirm the details in ref. 84 are correct.**

this is correct

## Perspective

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

Delphine Lannuzel, <sup>1</sup>✉

Email [delphine.lannuzel@utas.edu.au](mailto:delphine.lannuzel@utas.edu.au)

Letizia Tedesco, <sup>2</sup>

Maria van Leeuwe, <sup>3</sup>

Karley Campbell, <sup>4</sup>

Hauke Flores, <sup>5</sup>

Bruno Delille, <sup>6</sup>

Lisa Miller, <sup>7</sup>

Jacqueline Stefels, <sup>3</sup>

Philipp Assmy, <sup>8</sup>

Jeff Bowman, <sup>9</sup>

Kristina Brown, <sup>7</sup>

Giulia Castellani, <sup>5</sup>

Melissa Chierici, <sup>10,11</sup>

Odile Crabeck, <sup>12</sup>

Ellen Damm, <sup>5</sup>

Brent Else, <sup>13</sup>

Agneta Fransson, <sup>8</sup>

François Fripiat, <sup>14</sup>

Nicolas-Xavier Geilfus, <sup>15</sup>

Caroline Jacques, <sup>16</sup>

Elizabeth Jones, <sup>10</sup>

Hermann Kaartokallio, <sup>2</sup>

Marie Kotovitch, <sup>6,16</sup>

Klaus Meiners, <sup>17</sup>

Sébastien Moreau, <sup>8</sup>

Daiki Nomura, <sup>18</sup>

Ilka Peeken, <sup>5</sup>

Janne-Markus Rintala, <sup>19</sup>

Nadja Steiner, <sup>7</sup>

Jean-Louis Tison, <sup>16</sup>

Martin Vancoppenolle, 20

Fanny Van der Linden, 6,16

Marcello Vichi, 21

Pat Wongpan, 22

<sup>1</sup> Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Australia

<sup>2</sup> Finnish Environment Institute, Marine Research Centre, Helsinki, Finland

<sup>3</sup> Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

<sup>4</sup> Department of Arctic and Marine Biology, The Arctic University of Norway, Tromsø, Norway

<sup>5</sup> Helmholtz Centre for Polar and Marine Research, Alfred Wegener Institute, Bremerhaven, Germany

<sup>6</sup> Unité d'océanographie chimique, FOCUS, Université de Liège, Liège, Belgium

<sup>7</sup> Institute of Ocean Sciences, Fisheries and Oceans Canada, Sidney, British Columbia, Canada

<sup>8</sup> Norwegian Polar Institute, Fram Centre, Tromsø, Norway

<sup>9</sup> Scripps Institution of Oceanography, University of California, San Diego, CA, USA

<sup>10</sup> Institute of Marine Research, Fram Centre, Tromsø, Norway

<sup>11</sup> University Centre in Svalbard, Longyearbyen, Svalbard, Norway

<sup>12</sup> Centre for Ocean and Atmospheric Sciences, University of East Anglia, Norwich, UK

<sup>13</sup> Department of Geography, University of Calgary, Calgary, Alberta, Canada

<sup>14</sup> Department of Geosciences, Environment and Society, Université Libre de Bruxelles, Brussels, Belgium

- 15 Centre for Earth Observation Science, University of Manitoba, Winnipeg, Canada
- 16 Laboratoire de Glaciologie, DGES, Université Libre de Bruxelles, Brussels, Belgium
- 17 Australian Antarctic Division, Hobart, Australia
- 18 Hokkaido University, Hakodate, Hokkaido, Japan
- 19 Institute for Atmospheric and Earth System Research (INAR), Faculty of Science, University of Helsinki, Helsinki, Finland
- 20 Laboratoire d'Océanographie et du Climat, Institut Pierre-Simon Laplace, Paris, France
- 21 Department of Oceanography, University of Cape Town, Cape Town, South Africa
- 22 Australian Antarctic Program Partnership, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, Australia

Received: 7 March 2019 / Accepted: 24 September 2020

---

## Abstract

The Arctic sea-ice-scape is rapidly transforming. Increasing light penetration will initiate earlier seasonal primary production. This earlier growing season may be accompanied by an increase in ice algae and phytoplankton biomass, augmenting the emission of dimethylsulfide and capture of climate-active dimethyl sulfide 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.

---

Editor's Summary

The Arctic is warming and undergoing rapid ice loss. This Perspective considers how changes in sea ice will impact the biogeochemistry and associated ecosystems of the region while calling for more observations to improve our understanding of this complex system.

---

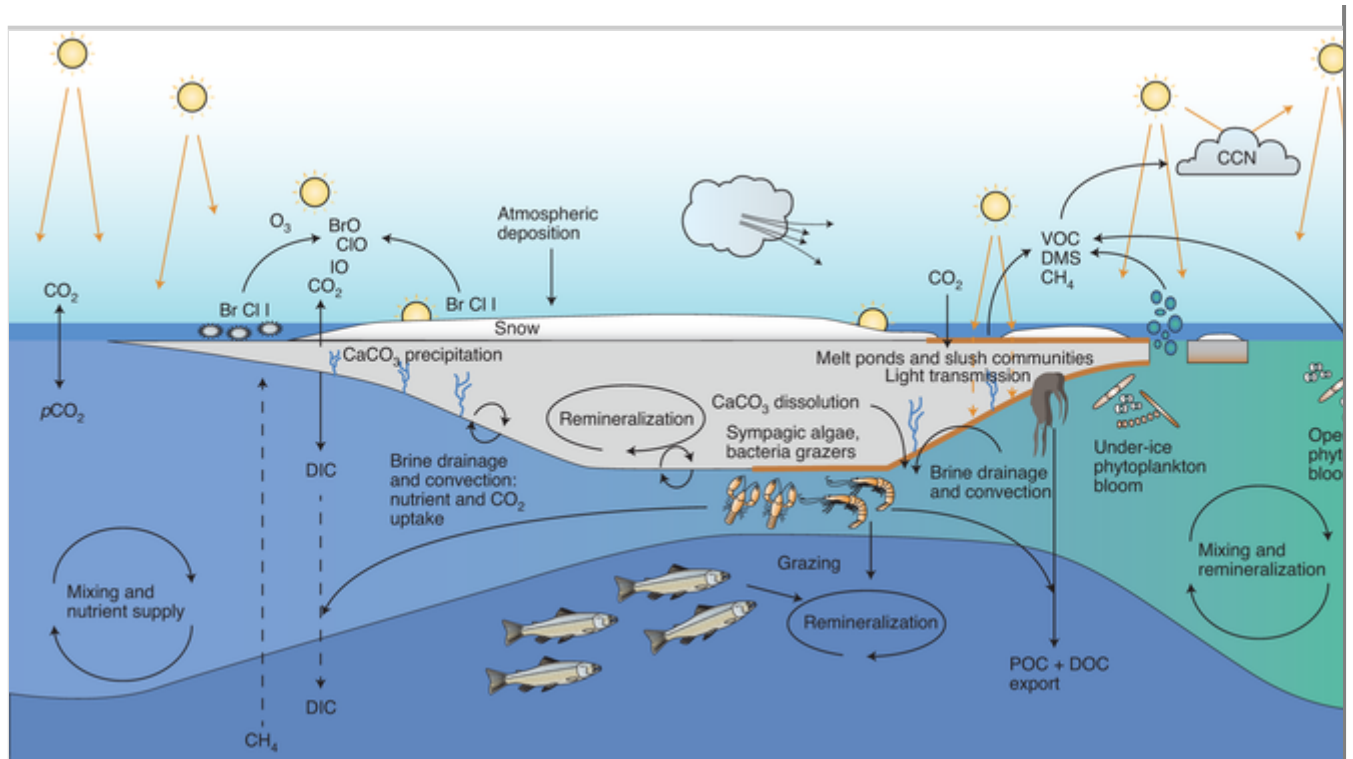
## Main

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 (for example, fluid, gas and solutes) are regulated. These fluxes contribute to physical and biogeochemical processes (Fig. 1) that influence the climate system, provide food and support businesses.

### Fig. 1

Schematic of seasonal sea-ice biogeochemical processes in the Arctic Ocean.

Black arrows represent the directionality of biogeochemical exchanges; for example, across an interface (such as [carbon dioxide \(CO<sub>2</sub>\)](#), [efflux](#) the parenthesis in the text here should be as follows: (CO<sub>2</sub>), and below: (CH<sub>4</sub>). I could not fix it with the online editing. ... from the ocean to the atmosphere and release of reactive halogen species from the ice surface) or throughout an interval (such as brine drainage and convection along the ice–water interface, and 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 \(CH<sub>4</sub>\)](#) as well as volatile organic compounds (VOC), which can contribute to the formation of cloud condensation nuclei (CCN). Figure adapted from [ref.](#) [109].



AQ1

AQ2

AQ3

AQ4

AQ5

AQ6

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 whales[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 ( $\text{CO}_2$ ), and the Arctic Ocean is currently a sink for atmospheric  $\text{CO}_2$  (~~refs-~~[6, 7]). Sea ice also regulates the uptake and emission of other climate-relevant gases such as methane ( $\text{CH}_4$ ) and dimethyl sulfide replace with "dimethylsulfide" (DMS), providing positive and negative climate feedbacks, respectively (Fig. 1). The ecosystem services provided by sea ice are however under threat in the

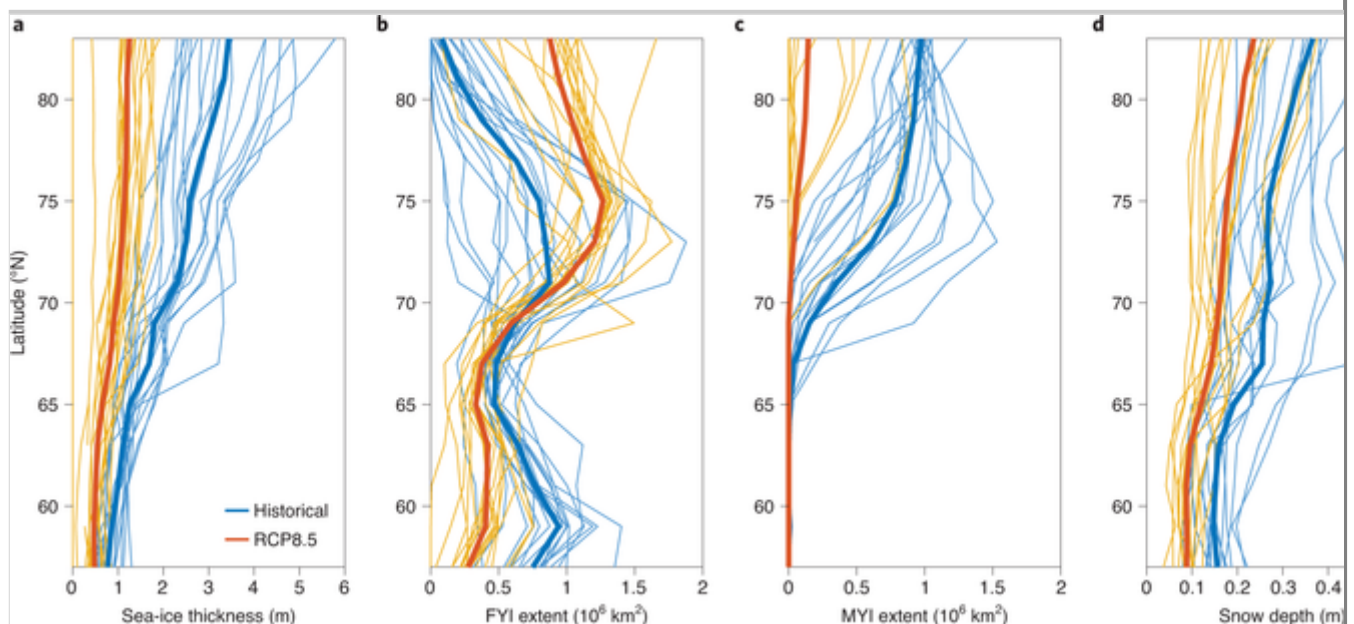
Arctic due to its rapid retreat (Fig. 2) at a pace dictated by cumulative CO<sub>2</sub> emissions[8] as well as other anthropogenic stressors (Box 1).

## 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 sea-ice thickness (a), first-year ice extent (b), multi-year ice extent (c) and snow depth (d).

Source data



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 Representative Concentration Pathway 8.5 (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 as well as 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.

## Box 1 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 (for example, salinity and albedo) and marine life[112]. Given the small size of the particles (<50  $\mu\text{m}$ ), 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  $\text{CO}_2$ -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 [the 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, [changes in sea-ice coverage](#) will probably promote ocean acidification overall.

## Framework

We consider the following aspects of change in the region.

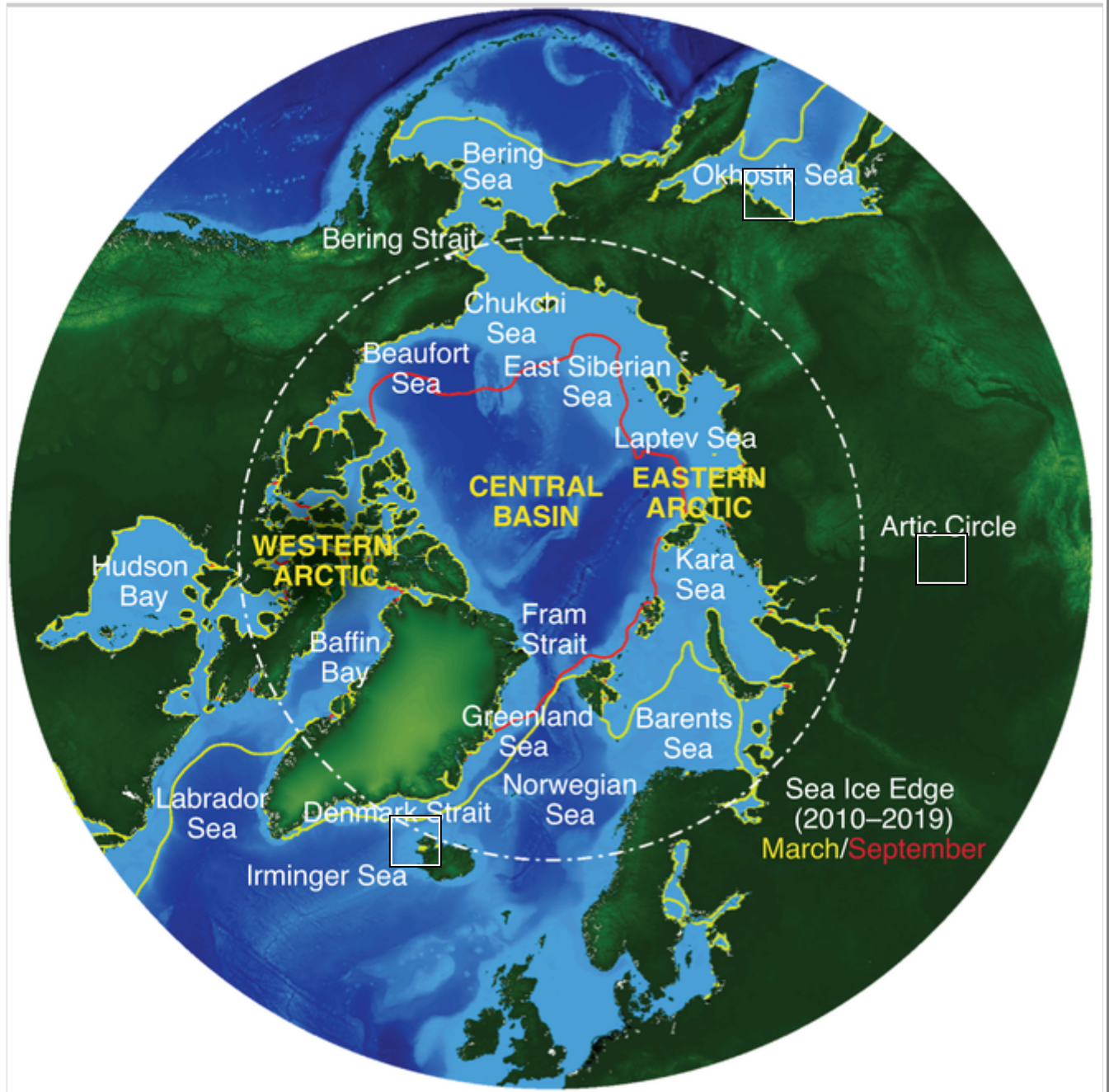
### Arctic sea-ice regions

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.

### **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) shown. Red and yellow lines represent the 2010–2019 averaged minimum (September) and maximum (March) sea-ice extents, respectively.



## Forcing categories

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

- (1) Changes in sea-ice coverage (that is, 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 (that is, vertical changes): younger and thinner sea ice, and 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 (ref. [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 ultraviolet (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 (for example, snow, ice and other algae) likely makes UV 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 colour[30]. Earth system model simulations reproduce this increase as long as nutrients are sufficient[18].

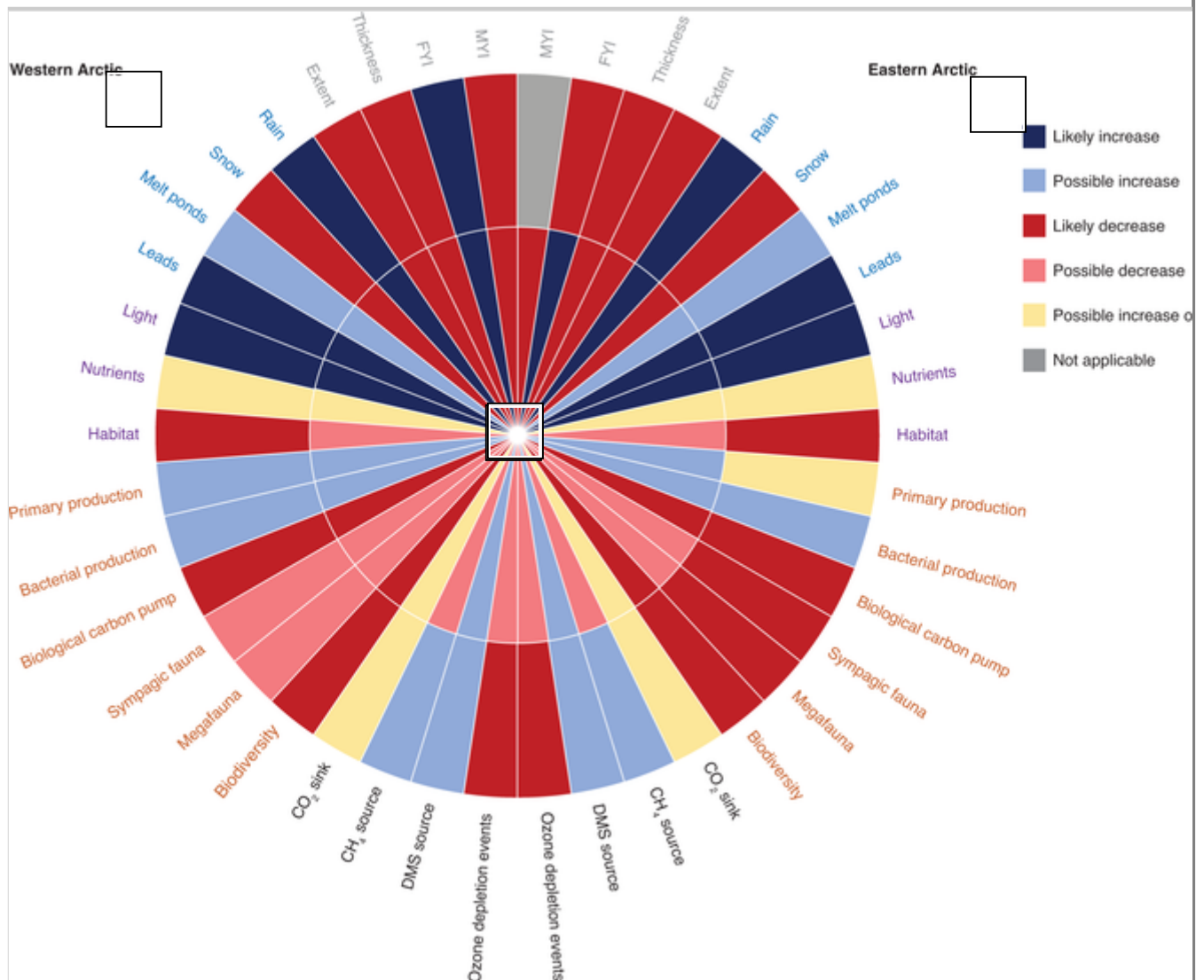
### Future expectations

Likely increase in light availability (Fig. 4).

### 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.



## 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 remineralization[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 (that is, 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 (for example, brine dynamics and 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 (Fig. 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 (Fig. 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: that is, 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.

AQ7

### Sea-ice coverage

In the most extreme case, the total disappearance of sea ice in some regions **will have** ~~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 (that is, 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 compared to 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 cylindrus*. 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 ~~of~~ sympagic consumers by sub-polar ~~of~~ pelagic consumers will predominantly result in a replacement of large, lipid-rich zooplankton by more numerous but smaller, and comparatively lipid-poor, species; for example, *Pseudocalanus* spp., *Metridia* spp. and *Cyanea* spp. Furthermore, these changes will negatively affect higher levels of the food chain; for instance, 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.

AQ8

### Future expectations

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 (for example, kelp[64]), and through increased planktonic primary production may 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 faecal 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 faecal pellets[74]. As a result, the shift towards organisms that produce smaller faecal pellets (for example, *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.

### Future expectations

The expected increase in primary productivity, shift towards smaller algae and warmer ice will lead to more grazing by smaller zooplankton and higher microbial remineralization. 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 (for example, CO<sub>2</sub>, CH<sub>4</sub> and 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<sub>2</sub>

During autumn and winter, sea ice acts as a source of CO<sub>2</sub> (ref. [76]) due to high brine partial pressure of CO<sub>2</sub> ( $p\text{CO}_2$ ) and precipitation of calcium carbonate (Fig. 1)[77]. However, during spring and summer, sea ice acts as a sink of CO<sub>2</sub> 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.

AQ9

### Sea-ice coverage

In the Central Basin, the formation of more new ice will result in an increased CO<sub>2</sub> efflux to the atmosphere in winter[79]. However, sea-ice formation will also increase the rejection of CO<sub>2</sub>-rich brines to the ocean[80]. Model simulations indicate that this rejection to the ocean and export to depth of CO<sub>2</sub>-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].

AQ10

The increase in ice-free ocean area and consequent carbon drawdown may have enhanced the CO<sub>2</sub> sink by as much as 1.4 TgC yr<sup>-1</sup> between 1996 and 2007 (ref. [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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> uptake from the atmosphere. The prediction of higher primary production at the bottom of Arctic FYI should enhance CO<sub>2</sub> uptake from the water[93] in spring and summer.

A change from MYI to FYI will increase brine drainage and, therefore, increase brine CO<sub>2</sub> export from the ice to underlying water this sentence should be part of the paragraph above, not a new paragraph. ....

### Future expectations

Increased air–sea fluxes, due to more open-ocean area and more leads over undersaturated waters, and increases in CO<sub>2</sub>-rich brine export may lead to an increase in the Arctic Ocean CO<sub>2</sub> sink (Fig. 4). This additional sink would be offset by increased stratification (capping CO<sub>2</sub> uptake) and outgassing in some regions due to enhanced vertical mixing with deep CO<sub>2</sub>-rich waters, and to our prognosis that the Arctic Ocean will transfer from a carbon export system to a carbon retention system.

### CH<sub>4</sub>

The impact of sea ice on ocean–atmosphere fluxes of CH<sub>4</sub> is still unclear. Recent studies highlighted a CH<sub>4</sub> super-saturation in sea-ice-influenced waters of the Central Basin[94] and an enhanced CH<sub>4</sub> efflux to the atmosphere above areas with fractional sea-ice cover[95]. An impermeable sea-ice cover likely enhances CH<sub>4</sub> exposure to microbial oxidation[96]. This process would have the potential to reduce CH<sub>4</sub> sea–air fluxes, particularly above continental shelves whose sediments represent the main source of CH<sub>4</sub> to the Arctic Ocean[97].

### Sea-ice coverage

More open water will facilitate the efflux of excess CH<sub>4</sub> to the atmosphere. A shorter sea-ice season and warmer temperatures will also result in an increase of sea-ice permeability, allowing CH<sub>4</sub> 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<sub>4</sub> storage in sea ice[98].

### Sea-ice properties

The shift from MYI to FYI will accelerate CH<sub>4</sub> cycling and likely increase the transfer of CH<sub>4</sub> from sea ice to the atmosphere.

### Future expectations

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

## Halogens and ozone interactions

Reactive halogen species are responsible for atmospheric cleansing and ozone depletion events (ODEs) as well as 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 and 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.

### Future expectations

Decrease in ODEs (Fig. 4).



## Challenges and future directions

The Intergovernmental Panel on Climate Change (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 parameterizations of: (i) light transmission through snow and ice; (ii) controls on primary production and diversities in sea ice, as well as ice algal incorporation and release; and (iii) 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. 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.

### Box 2 Uncertainties in these prognoses

#### AQ11

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; the 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; the effect of shorter but more intense sea-ice algal blooms on biogases, consumers and carbon export; the 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.

### Supplementary information

is available for this paper at <https://doi.org/10.1038/s41558-020-00940-4>.

**Peer review information** *Nature Climate Change* thanks Jørgen Berge, Suhas Shetye and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

## Acknowledgements

This Perspective is a product of the Biogeochemical Exchange Processes at Sea-Ice Interfaces (BEPSII) research community. This manuscript was first conceived at the Arctic Sea-Ice Change foresight workshop held in Davos, Switzerland, in June 2018 and is supported by the Euromarine Network.

### 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** The authors declare no competing interests.

# Source data

## Source Data Fig. 2

Historical and ‘worst-case’ RCP8.5 scenario source data.

## References

1. Arrigo, K. R. in *Sea Ice* (Ed. Thomas, D. N.) 352–369 (John Wiley & Sons, Ltd, 2017).
2. Steiner, N. S. et al. Impacts of the changing ocean-sea ice system on the key forage fish Arctic cod (*Boreogadus saida*) and subsistence fisheries in the western Canadian Arctic—evaluating linked climate, ecosystem and economic (CEE) models. *Front. Mar. Sci.* **6**, 179 (2019).
3. Kohlbach, D. et al. The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: food web relationships revealed by lipid and stable isotope analyses. *Limnol. Oceanogr.* **61**, 2027–2044 (2016).
4. Boetius, A. et al. Export of algal biomass from the melting Arctic sea ice. *Science* **339**, 1430–1432 (2013).
5. Riebesell, U., Schloss, I. & Smetacek, V. Aggregation of algae released from melting sea ice: implications for seeding and sedimentation. *Polar Biol.* **11**, 239–248 (1991).
6. MacGilchrist, G. A. et al. The Arctic Ocean carbon sink. *Deep. Res. Part I Oceanogr. Res. Pap.* **86**, 39–55 (2014).
7. Bates, N. R. & Mathis, J. T. The Arctic Ocean marine carbon cycle: evaluation of air-sea CO<sub>2</sub> exchanges, ocean acidification impacts and potential feedbacks. *Biogeosciences* **6**, 2433–2459 (2009).
8. Notz, D. & Stroeve, J. Observed Arctic sea-ice loss directly follows anthropogenic CO<sub>2</sub> emission. *Science* **354**, 747–750 (2016).
9. Meier, W. N. et al. Arctic sea ice in transformation: a review of recent observed changes and impacts on biology and human activity. *Rev. Geophys.* **52**, 185–217 (2014).

10. Kwok, R. Arctic sea ice thickness, volume, and multiyear ice coverage: losses and coupled variability (1958–2018). *Environ. Res. Lett.* **13**, 105005 (2018).
11. Maslanik, J., Stroeve, J., Fowler, C. & Emery, W. Distribution and trends in Arctic sea ice age through spring 2011. *Geophys. Res. Lett.* **38**, L13502 (2011).
12. Stroeve, J. C., Crawford, A. D. & Stammerjohn, S. Using timing of ice retreat to predict timing of fall freeze-up in the Arctic. *Geophys. Res. Lett.* **43**, 6332–6340 (2016).
13. Webster, M. A. et al. Interdecadal changes in snow depth on Arctic sea ice. *J. Geophys. Res. Ocean.* **119**, 5395–5406 (2014).
14. Strong, C. & Rigor, I. G. Arctic marginal ice zone trending wider in summer and narrower in winter. *Geophys. Res. Lett.* **40**, 4864–4868 (2013).
15. IPCC *Climate Change 2013: The Physical Science Basis* (eds Stocker, T. F. et al.) 1029–1136 (Cambridge Univ. Press, 2013).
16. Overland, J. E. & Wang, M. When will the summer Arctic be nearly sea ice free? *Geophys. Res. Lett.* **40**, 2097–2101 (2013).
17. Bintanja, R. & Andry, O. Towards a rain-dominated Arctic. *Nat. Clim. Change* **7**, 263 (2017).
18. Vancoppenolle, M. et al. Role of sea ice in global biogeochemical cycles: emerging views and challenges. *Quat. Sci. Rev.* **79**, 207–230 (2013).
19. Berge, J. et al. In the dark: a review of ecosystem processes during the Arctic polar night. *Prog. Oceanogr.* **139**, 258–271 (2015).
20. Leu, E. et al. Arctic spring awakening — steering principles behind the phenology of vernal ice algal blooms. *Prog. Oceanogr.* **139**, 151–170 (2015).
21. Assmy, P. et al. Leads in Arctic pack ice enable early phytoplankton blooms below snow-covered sea ice. *Sci. Rep.* **7**, 40850 (2017).
22. Perovich, D. K. *Sea Ice* 110–137 (2017).

AQ12

23. Nicolaus, M., Katlein, C., Maslanik, J. A. & Hendricks, S. *Solar Radiation Over and Under Sea Ice During the POLARSTERN Cruise ARK-XXVI/3 (TransArc) in Summer 2011* (PANGAEA, 2011); <https://doi.pangaea.de/10.1594/PANGAEA.786717>
24. Arrigo, K. R. et al. Massive phytoplankton blooms under Arctic sea ice. *Science* **336**, 1408 (2012).
25. Pistone, K., Eisenman, I. & Ramanathan, V. Observational determination of albedo decrease caused by vanishing Arctic sea ice. *Proc. Natl Acad. Sci. USA* **111**, 3322–3326 (2014).
26. Horvat, C. et al. The frequency and extent of sub-ice phytoplankton blooms in the Arctic Ocean. *Sci. Adv.* **3**, e1601191 (2017).
27. El-Sayed, S. Z., Van Dijken, G. L. & Gonzalez-Rodas, G. Effects of ultraviolet radiation on marine ecosystems. *Int. J. Environ. Stud.* **51**, 199–216 (1996).
28. Elliott, A. et al. Spring production of mycosporine-like amino acids and other UV-absorbing compounds in sea ice-associated algae communities in the Canadian Arctic. *Mar. Ecol. Prog. Ser.* **541**, 91–104 (2015).
29. Ryan, K. G., McMinn, A., Hegseth, E. N. & Davy, S. K. The effects of ultraviolet-b radiation on antarctic sea-ice algae. *J. Phycol.* **48**, 74–84 (2012).
30. Arrigo, K. R. & van Dijken, G. L. Continued increases in Arctic Ocean primary production. *Prog. Oceanogr.* **136**, 60–70 (2015).
31. Gradinger, R. Sea-ice algae: major contributors to primary production and algal biomass in the Chukchi and Beaufort Seas during May/June 2002. *Deep. Res. Part II Top. Stud. Oceanogr.* **56**, 1201–1212 (2009).
32. Tremblay, J.-E. & Gagnon, J. in *Influence of Climate Change on the Changing Arctic and Sub-Arctic Conditions* (eds Nihoul, J. C. J. & Kostianoy, A. G.) 73–93 (Springer, 2009).
33. Nomura, D. et al. Nutrient distributions associated with snow and sediment-laden layers in sea ice of the southern Sea of Okhotsk. *Mar. Chem.* **119**, 1–8 (2010).

34. Meiners, K. M. & Michel, C. in *Sea Ice* (Ed. Thomas, D. N.) 415–432 (John Wiley & Sons, Ltd, 2017).
35. Fripiat, F. et al. Macro-nutrient concentrations in Antarctic pack ice: overall patterns and overlooked processes. *Elem. Sci. Anth.* **5**, p13 (2017).
36. Tremblay, J. É. et al. Global and regional drivers of nutrient supply, primary production and CO<sub>2</sub> drawdown in the changing Arctic Ocean. *Prog. Oceanogr.* **139**, 171–196 (2015).
37. Miller, J. R. & Russell, G. L. Projected impact of climate change on the freshwater and salt budgets of the Arctic Ocean by a global climate model. *Geophys. Res. Lett.* **27**, 1183–1186 (2000).
38. Peterson, B. J. et al. Increasing river discharge to the Arctic Ocean. *Science* **298**, 2171–2173 (2002).
39. Rainville, L., M. Lee, C. & Woodgate, A. R. Impact of wind-driven mixing in the Arctic Ocean. *Oceanography* **24**, 136–145 (2011).
40. Lamarque, J. F. et al. Multi-model mean nitrogen and sulfur deposition from the atmospheric chemistry and climate model intercomparison project (ACCMIP): evaluation of historical and projected future changes. *Atmos. Chem. Phys.* **13**, 7997–8018 (2013).
41. Stroeve, J. C., Markus, T., Boisvert, L., Miller, J. & Barrett, A. Changes in Arctic melt season and implications for sea ice loss. *Geophys. Res. Lett.* **41**, 1216–1225 (2014).
42. Tedesco, L., Vichi, M. & Scoccimarro, E. Sea-ice algal phenology in a warmer Arctic. *Sci. Adv.* **5**, eaav4830 (2019).
43. van Leeuwe, M. A. et al. Microalgal community structure and primary production in Arctic and Antarctic sea ice: a synthesis. *Elem. Sci. Anth.* <https://doi.org/10.1525/elementa.267> (2018).
44. Hardge, K. et al. Sea ice origin and sea ice retreat as possible drivers of variability in Arctic marine protist composition. *Mar. Ecol. Prog. Ser.* **571**, 43–57 (2017).
45. Campbell, K., Mundy, C. J., Belzile, C., Delaforge, A. & Rysgaard, S. Seasonal dynamics of algal and bacterial communities in Arctic sea ice under

variable snow cover. *Polar Biol.* **41**, 41–58 (2018).

46. Leu, E., Søreide, J. E., Hessen, D. O., Falk-Petersen, S. & Berge, J. Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. *Prog. Oceanogr.* **90**, 18–32 (2011).

47. Fernández-Méndez, M. et al. Composition, buoyancy regulation and fate of ice algal aggregates in the Central Arctic Ocean. *PLoS ONE* **9**, e107452 (2014).

48. Ardyna, M. et al. Recent Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms. *Geophys. Res. Lett.* **41**, 6207–6212 (2014).

49. Wassmann, P. & Reigstad, M. Future Arctic Ocean seasonal ice zones and implications for pelagic-benthic coupling. **24**, 220–231 (2011).

50. Dalman, L. et al. Enhanced bottom-ice algal biomass across a tidal strait in the Kitikmeot Sea of the Canadian Arctic. *Elem. Sci. Anth.* **7**, p22 (2019).

51. Williams, W. et al. Joint effects of wind and ice motion in forcing upwelling in Mackenzie Trough, Beaufort Sea. *Cont. Shelf Res.* **26**, 2352–2366 (2006).

52. Ardyna, M. et al. Environmental drivers of under-ice phytoplankton bloom dynamics in the Arctic Ocean. *Elem. Sci. Anth.* **8**, 30 (2020).

53. Eronen-Rasimus, E. et al. Ice formation and growth shape bacterial community structure in Baltic Sea drift ice. *FEMS Microbiol. Ecol.* **91**, 1–13 (2015).

54. Bowman, J. S. The relationship between sea ice bacterial community structure and biogeochemistry: a synthesis of current knowledge and known unknowns. *Elem. Sci. Anthr.* **3**, 000072 (2015).

55. Eronen-Rasimus, E. et al. An active bacterial community linked to high chl-a concentrations in Antarctic winter-pack ice and evidence for the development of an anaerobic sea-ice bacterial community. *ISME J.* **11**, 2345–2355 (2017).

56. Kohlbach, D. et al. The importance of ice algae-produced carbon in the central Arctic Ocean ecosystem: food web relationships revealed by lipid and

stable isotope analyses. *Limnol. Oceanogr.* **61**, 2027–2044 (2016).

57. Fossheim, M. et al. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nat. Clim. Change* **5**, 673–677 (2015).

58. Søreide, J. E., Leu, E. V. A., Berge, J., Graeve, M. & Falk-Petersen, S. Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. *Glob. Chang. Biol.* **16**, 3154–3163 (2010).

59. Eriksen, E., Skjoldal, H. R., Gjørseter, H. & Primicerio, R. Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. *Prog. Oceanogr.* **151**, 206–226 (2017).

60. David, C., Lange, B., Rabe, B. & Flores, H. Community structure of under-ice fauna in the Eurasian central Arctic Ocean in relation to environmental properties of sea-ice habitats. *Mar. Ecol. Prog. Ser.* **522**, 15–32 (2015).

61. Melnikov, I. Recent Arctic sea-ice ecosystem: dynamics and forecast. *Dokl. Earth Sci.* **423**, 1516–1519 (2008).

62. Haug, T. et al. Future harvest of living resources in the Arctic Ocean north of the Nordic and Barents Seas: a review of possibilities and constraints. *Fish. Res.* **188**, 38–57 (2017).

63. Kędra, M. et al. Status and trends in the structure of Arctic benthic food webs. *Polar Res.* **34**, 23775 (2015).

64. Filbee-Dexter, K., Wernberg, T., Fredriksen, S., Norderhaug, K. M. & Pedersen, M. F. Arctic kelp forests: diversity, resilience and future. *Glob. Planet. Change* **172**, 1–14 (2019).

65. Murillo, F. J. et al. Sponge assemblages and predicted archetypes in the eastern Canadian Arctic. *Mar. Ecol. Prog. Ser.* **597**, 115–135 (2018).

66. Hamilton, C. D., Lydersen, C., Ims, R. A. & Kovacs, K. M. Predictions replaced by facts: a keystone species' behavioural responses to declining arctic sea-ice. *Biol. Lett.* **11**, 1–6 (2015).

67. O'Corry-Crowe, G. et al. Genetic profiling links changing sea-ice to shifting beluga whale migration patterns. *Biol. Lett.* **12**, 20160404 (2016).



68. Descamps, S. et al. Climate change impacts on wildlife in a High Arctic archipelago — Svalbard, Norway. *Glob. Chang. Biol.* **23**, 490–502 (2017).
69. Wollenburg, J. E. et al. Ballasting by cryogenic gypsum enhances carbon export in a *Phaeocystis* under-ice bloom. *Sci. Rep.* **8**, 7703 (2018).
70. Priou, P. et al. Vertical distribution of pelagic fish and zooplankton under the European Arctic pack ice. <https://doi.org/10.13140/RG.2.2.16920.29449> (2017).
- AQ13
71. Darnis, G. et al. From polar night to midnight sun: diel vertical migration, metabolism and biogeochemical role of zooplankton in a high Arctic fjord (Kongsfjorden, Svalbard). *Limnol. Oceanogr.* **62**, 1586–1605 (2017).
72. Wiedmann, I., Reigstad, M., Sundfjord, A. & Basedow, S. Potential drivers of sinking particle's size spectra and vertical flux of particulate organic carbon (POC): turbulence, phytoplankton, and zooplankton. *J. Geophys. Res. Ocean.* **119**, 6900–6917 (2014).
73. Flores, H. et al. Sea-ice properties and nutrient concentration as drivers of the taxonomic and trophic structure of high-Arctic protist and metazoan communities. *Polar Biol.* **42**, 1377–1395 (2019).
74. Belcher, A. et al. The potential role of Antarctic krill faecal pellets in efficient carbon export at the marginal ice zone of the South Orkney Islands in spring. *Polar Biol.* **40**, 2001–2013 (2017).
75. Lalande, C. et al. Variability in under-ice export fluxes of biogenic matter in the Arctic Ocean. *Global Biogeochem. Cycles* **28**, 571–583 (2014).
76. Miller, L. A., Carnat, G., Else, B. G. T., Sutherland, N. & Papakyriakou, T. N. Carbonate system evolution at the Arctic Ocean surface during autumn freeze-up. *J. Geophys. Res. Ocean.* **116**, C00G04 (2011).
77. Dieckmann, G. S. et al. Brief Communication: ikaite ( $\text{CaCO}_3 \cdot 6\text{H}_2\text{O}$ ) discovered in Arctic sea ice. *Cryosphere* **4**, 227–230 (2010).
78. Rysgaard, S. et al. Ikaite crystals in melting sea ice — implications for  $p\text{CO}_2$  and pH levels in Arctic surface waters. *Cryosph. Discuss.* **6**, 1015–1035 (2012).

79. Nomura, D. et al. CO<sub>2</sub> flux over young and snow-covered Arctic pack ice in winter and spring. *Biogeosciences* **15**, 3331–3343 (2018).
80. König, D., Miller, L. A., Simpson, K. G. & Vagle, S. Carbon dynamics during the formation of sea ice at different growth rates. *Front. Earth Sci.* **6**, 234 (2018).
81. Grimm, R., Notz, D., Glud, R. N., Rysgaard, S. & Six, K. D. Assessment of the sea-ice carbon pump: insights from a three-dimensional ocean-sea-ice-biogeochemical model (MPIOM/HAMOCC). *Elem. Sci. Anthr.* **4**, 000136 (2016).
82. Rysgaard, S., Glud, R. N., Sejr, M. K., Bendtsen, J. & Christensen, P. B. Inorganic carbon transport during sea ice growth and decay: a carbon pump in polar seas. *J. Geophys. Res.* **112**, C03016 (2007).
83. Manizza, M. et al. Changes in the Arctic Ocean CO<sub>2</sub> sink (1996–2007): a regional model analysis. *Global Biogeochem. Cycles* **27**, 1108–1118 (2013).
84. Mortenson, E. *Modelling carbon exchange in the air, sea, and ice of the Arctic Ocean*. PhD thesis, Univ. of Victoria (2019).

## AQ14

85. Fransson, A. et al. Effects of sea-ice and biogeochemical processes and storms on under-ice water fCO<sub>2</sub> during the winter-spring transition in the high Arctic Ocean: implications for sea-air CO<sub>2</sub> fluxes. *J. Geophys. Res. Ocean.* **122**, 5566–5587 (2017).
86. Mathis, J. T. et al. Storm-induced upwelling of high pCO<sub>2</sub> waters onto the continental shelf of the western Arctic Ocean and implications for carbonate mineral saturation states. *Geophys. Res. Lett.* **39**, L07606 (2012).
87. Pipko, I. I., Semiletov, I. P., Pugach, S. P., Wählström, I. & Anderson, L. G. Interannual variability of air-sea CO<sub>2</sub> fluxes and carbon system in the East Siberian Sea. *Biogeosciences* **8**, 1987–2007 (2011).
88. Steiner, N. et al. What sea-ice biogeochemical modellers need from observers. *Elementa* **4**, 000084 (2016).
89. Cai, W.-J. et al. Decrease in the CO<sub>2</sub> uptake capacity in an ice-free Arctic Ocean Basin. *Science* **329**, 556–559 (2010).

90. Else, B. et al. Further observations of a decreasing atmospheric CO<sub>2</sub> uptake capacity in the Canada Basin (Arctic Ocean) due to sea ice loss. *Geophys. Res. Lett.* **40**, 1132–1137 (2013).
91. Fransson, A. et al. CO<sub>2</sub>-system development in young sea ice and CO<sub>2</sub> gas exchange at the ice/air interface mediated by brine and frost flowers in Kongsfjorden, Spitsbergen. *Ann. Glaciol.* **56**, 245–257 (2015).
92. Geilfus, N. X. et al. First estimates of the contribution of CaCO<sub>3</sub> precipitation to the release of CO<sub>2</sub> to the atmosphere during young sea ice growth. *J. Geophys. Res. Ocean.* **118**, 244–255 (2013).
93. Brown, K. A. et al. Inorganic carbon system dynamics in landfast Arctic sea ice during the early-melt period. *J. Geophys. Res. Ocean.* **120**, 3542–3566 (2015).
94. Damm, E., Rudels, B., Schauer, U., Mau, S. & Dieckmann, G. Methane excess in Arctic surface water- triggered by sea ice formation and melting. *Sci. Rep.* **5**, 16179 (2015).
95. Kort, E. A. et al. Atmospheric observations of Arctic Ocean methane emissions up to 82° north. *Nat. Geosci.* **5**, 318 (2012).
96. Tison, J.-L. Biogeochemical impact of snow cover and cyclonic intrusions on the winter weddell sea ice pack. *J. Geophys. Res. Ocean.* **122**, 7291–7311 (2017).
97. *AMAP Assessment 2015: Methane as an Arctic Climate Forcer* (AMAP, 2015).
98. Zhou, J. et al. Physical and biogeochemical properties in landfast sea ice (Barrow, Alaska): insights on brine and gas dynamics across seasons. *J. Geophys. Res. Ocean.* **118**, 3172–3189 (2013).
99. Levasseur, M. Impact of Arctic meltdown on the microbial cycling of sulphur. *Nat. Geosci.* **6**, 691 (2013).
100. Hayashida, H. et al. Implications of sea-ice biogeochemistry for oceanic production and emissions of dimethyl sulfide in the Arctic. *Biogeosciences* **14**, 3129–3155 (2017).

101. Abbatt, J. P. D. et al. Overview paper: new insights into aerosol and climate in the Arctic. *Atmos. Chem. Phys.* **19**, 2527–2560 (2019).
102. Galindo, V. et al. Biological and physical processes influencing sea ice, under-ice algae, and dimethylsulfoniopropionate during spring in the Canadian Arctic Archipelago. *J. Geophys. Res. Ocean.* **119**, 3746–3766 (2014).
103. Simpson, W. R. et al. Halogens and their role in polar boundary-layer ozone depletion. *Atmos. Chem. Phys.* **7**, 4375–4418 (2007).
104. Jacobi, H.-W., Morin, S. & Bottenheim, J. W. Observation of widespread depletion of ozone in the springtime boundary layer of the central Arctic linked to mesoscale synoptic conditions. *J. Geophys. Res. Atmos.* **115**, 17302 (2010).
105. Abbatt, J. P. D. et al. Halogen activation via interactions with environmental ice and snow in the polar lower troposphere and other regions. *Atmos. Chem. Phys.* **12**, 6237–6271 (2012).
106. Frey, M. M. et al. First direct observation of sea salt aerosol production from blowing snow above sea ice. *Atmos. Chem. Phys. Discuss.* **20**, 2549–2578 (2019).
107. Tarasick, D. W. & Bottenheim, J. W. Surface ozone depletion episodes in the Arctic and Antarctic from historical ozonesonde records. *Atmos. Chem. Phys.* **2**, 197–205 (2002).
108. Kiko, R., Kern, S., Kramer, M. & Mütze, H. Colonization of newly forming Arctic sea ice by meiofauna: a case study for the future Arctic? *Polar Biol.* **40**, 1277–1288 (2017).
109. Steiner, N. & Stefels, J. Commentary on the outputs and future of Biogeochemical Exchange Processes at Sea-Ice Interfaces (BEPSII). *Elem. Sci. Anth.* **5**, 81 (2017).
110. Echeveste, P., Agustí, S. & Dachs, J. Cell size dependent toxicity thresholds of polycyclic aromatic hydrocarbons to natural and cultured phytoplankton populations. *Environ. Pollut.* **158**, 299–307 (2010).
111. Peeken, I. et al. Arctic sea ice is an important temporal sink and means of transport for microplastic. *Nat. Commun.* **9**, 1505 (2018).

112. Obbard, R. W. et al. Global warming releases microplastic legacy frozen in Arctic Sea ice. *Earth's Futur.* **2**, 315–320 (2014).
113. Steiner, N. S., Christian, J. R., Six, K. D., Yamamoto, A. & Yamamoto-Kawai, M. Future ocean acidification in the Canada Basin and surrounding Arctic Ocean from CMIP5 earth system models. *J. Geophys. Res. Ocean.* **119**, 332–347 (2014).
114. Fransson, A. et al. Impact of sea-ice processes on the carbonate system and ocean acidification at the ice-water interface of the Amundsen Gulf, Arctic Ocean. *J. Geophys. Res. Ocean.* **118**, 7001–7023 (2013).
115. Geilfus, N.-X. et al. Estimates of ikaite export from sea ice to the underlying seawater in a sea ice–seawater mesocosm. *Cryosph.* **10**, 2173–2189 (2016).
116. Moreau, S. et al. Assessment of the sea-ice carbon pump: Insights from a three-dimensional ocean-sea-ice biogeochemical model (NEMO-LIM-PISCES). *Elementa* **4**, 000122 (2016).