

REVIEW

Climate change impacts on sea-ice ecosystems and associated ecosystem services

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A rigorous synthesis of the sea-ice ecosystem and linked ecosystem services highlights that the sea-ice ecosystem supports all 4 ecosystem service categories, that sea-ice ecosystems meet the criteria for ecologically or biologically significant marine areas, that global emissions driving climate change are directly linked to the demise of sea-ice ecosystems and its ecosystem services, and that the sea-ice ecosystem deserves specific attention in the evaluation of marine protected area planning. The synthesis outlines (1) supporting services, provided in form of habitat, including feeding grounds and nurseries for microbes, meiofauna, fish, birds and mammals (particularly the key species Arctic cod, *Boreogadus saida*, and Antarctic krill, *Euphausia superba*, which are tightly linked to the sea-ice ecosystem and transfer carbon from sea-ice primary producers to higher trophic level fish, mammal species and humans); (2) provisioning services through harvesting and medicinal and genetic resources; (3) cultural services through Indigenous and local knowledge systems, cultural identity and spirituality, and via cultural activities, tourism and research; (4) (climate) regulating services through light regulation, the production of biogenic aerosols, halogen oxidation

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and the release or uptake of greenhouse gases, for example, carbon dioxide. The ongoing changes in the polar regions have strong impacts on sea-ice ecosystems and associated ecosystem services. While the response of sea-ice-associated primary production to environmental change is regionally variable, the effect on ice-associated mammals and birds is predominantly negative, subsequently impacting human harvesting and cultural services in both polar regions. Conservation can help protect some species and functions. However, the key mitigation measure that can slow the transition to a strictly seasonal ice cover in the Arctic Ocean, reduce the overall loss of sea-ice habitats from the ocean, and thus preserve the unique ecosystem services provided by sea ice and their contributions to human well-being is a reduction in carbon emissions.

Keywords: Sea-ice ecosystems, Ecosystem services, EBSA, Polar regions, Climate change, Marine Protected Area (MPA)

1. Introduction

The Intergovernmental Panel on Climate Change Special Report on the Ocean and Cryosphere in a Changing Climate (Pörtner et al., 2019) highlights the widespread impacts of climate change on the cryosphere over the recent and upcoming decades. These include accelerated warming of the polar regions, reductions in snow cover, sea-ice extent and thickness in the Arctic, and significant variability in the dynamics of snow-covered sea ice in the Southern Ocean. These changes have a strong impact on organisms associated with sea ice, including shifts in species composition, abundance and distribution, as well as altered trophic interactions with subsequent impacts on ecosystem structure and function, from the poles to the lower latitudes (e.g., Atkinson et al., 2004; Trivelpiece et al., 2011; Flores et al., 2012; Post et al., 2013; Moore et al., 2018; Atkinson et al., 2019; Huntington et al., 2020; Lannuzel et al., 2020). Resulting changes vary regionally and may have both positive and negative impacts on human well-being through, for instance, commercial fisheries, subsistence harvesting, Indigenous and local cultural activities and livelihoods, as well as tourism and recreation (e.g., CAFF, 2015). Pörtner et al. (2019) suggest that climate change impacts on polar ecosystems will have overall negative consequences for human health and well-being, especially for Arctic Indigenous Peoples and local communities that depend on these ecosystem services for subsistence.

As the rate and magnitude of environmental change in polar regions are projected to intensify in the second half of the 21st century, particularly under a high emissions scenario (Pörtner et al., 2019), the ecosystem services that sea ice provides are also likely to change. For instance, shifts in Antarctic sea-ice extent, seasonality, and duration are expected to influence krill recruitment (Meyer et al., 2017) with potential implications for higher trophic levels and the Southern Ocean krill fishery. In the Arctic, changes to key sea-ice physical, biogeochemical, and ecological properties and processes in response to environmental changes have recently been reviewed (Lannuzel et al., 2020) and can be used to assess potential impacts on sea-ice ecosystem services.

Definitions of ecosystem services (ES) revolve around the core principle of linking ecosystems to human well-being. Varying forms have been provided, for example, the

Millennium Ecosystem Assessment (MEA, 2005) defines ecosystem services as “the benefits people obtain from ecosystems,” and the Common International Classification of Ecosystem Services defines ES as the “contributions that ecosystems make to human well-being” (Haines-Young and Potschin, 2011). The concept of ES is widely used to assess the multiple ways by which ecosystems support human well-being, understand how biophysical changes can affect humans, and guide environmental decision-making (e.g., MEA, 2005; TEEB, 2010; Costanza et al., 2017). An ES-focused approach provides a common language to bridge information from multiple disciplines and types of knowledge on ecosystem contributions to human well-being (Granek et al., 2010) and fosters policy actions to act upon environmental pressures (e.g., Brondizio et al., 2019). ES are categorized into 4 main service types: (1) habitat, or supporting services, which highlight the importance of ecosystems to support functions essential to other ES, such as providing habitat (including nursery services) for migratory species, and maintaining genetic diversity; (2) provisioning services, represented by the products obtained from ecosystems such as food, fresh water, raw materials, genetic, medicinal, and ornamental resources; (3) regulating services, defined as the benefits obtained from the regulation of ecosystem processes such as climate regulation, natural hazard regulation, water purification and waste management, pollination or pest control; and (4) cultural services, which refer to non-material benefits that people obtain from ecosystems such as spiritual enrichment, inspiration and information for artistic and intellectual development, recreation, and aesthetic values.

In ecologically sensitive biomes, that is, the naturally occurring community of flora and fauna linked to a habitat, understanding implications of change to ES can guide and foster conservation and sustainable management (CAFF, 2015). Here, we aim to provide a first assessment of how climate-driven changes in sea-ice ecosystems are likely to impact ES in the polar oceans. Ultimately, our goal is to inform climate policy and ecosystem management in both polar regions.

Multiple linkages among the 4 types of ES and the impacts affecting them further highlight the importance of interdisciplinary (crossing disciplinary boundaries) and transdisciplinary (crossing disciplinary and academic

boundaries; Tress et al., 2005) research for monitoring the impacts of climate change on polar ES. For instance, climate models are essential to project how the sea ice-ocean system may change under different climate scenarios, while Indigenous and local knowledge provides key insights into past changes and the implications of these changes for food security (e.g., changes in the appearance, health, distribution and abundance of harvested species; Gadamus, 2013; Harwood et al., 2015; Loseto et al., 2018a; Ostertag et al., 2018; Waugh, 2018; Worden et al., 2020), health, livelihoods, and culture, such as the loss of important sea-ice travel routes (ICC-Canada, 2008; Wilson et al., 2020). Collaborations between tourism organizations and research organizations can provide valuable input into spatial planning, conservation, and management efforts. An example is the collaboration between the International Association of Antarctica Tour Operators (IAATO) and the Scientific Committee on Antarctic Research (SCAR; IAATO-SCAR, 2019). Transdisciplinary collaborations are key to help anticipate or even prevent unexpected or unwanted outcomes of climate change on ES and human well-being and lead to improved policy responses (Falardeau and Bennett, 2020).

Malinauskaite et al. (2019), in their systematic review of Arctic ES literature, conclude that although the ES concept is increasingly being applied in the Arctic, large knowledge gaps remain in the assessment of ES and more primary studies of Arctic ES are needed, as well as governance initiatives to move Arctic ES research from theory to practice. While the ES term is used by governing bodies like the Arctic Council (e.g., PAME, 2017), only few ES assessments for Arctic regions have been completed to date (including the Economics of Ecosystems and Biodiversity Scoping Study for the Arctic TEEB, 2010) and practical examples of direct ES study applications in management are scarce. Falardeau and Bennett (2020) analyzed climate change research across natural and social science disciplines, using an Arctic-adapted ES framework, and indicate that integrative research linking ecological to social changes (i.e., studies on the flow of impacts from ecosystem processes to ES and Inuit well-being) is still uncommon in the marine Arctic. For the Southern Hemisphere, Deininger et al. (2016) compiled a comprehensive analysis of core ES, including tourism, genetic diversity, and carbon sequestration for the Weddell Sea. They applied sea-ice coverage as a key factor for the analyses in their study and showed that the heterogeneity of the marine area of the Weddell Sea, especially related to variations in sea-ice cover, has a great impact on ecosystem services. Neumann et al. (2019) evaluated the ES supply for the western Antarctic Peninsula region and also included sea ice as a key service provider, and Rogers et al. (2020) and Cavanagh et al. (2021) in their review on ES of the Southern Ocean highlighted sea ice as an environmental factor with a high likelihood to change and medium to high impact on marine communities or species.

Eicken et al. (2009) first introduced the concept of sea-ice system services, which categorizes the way stakeholders and rights holders perceive, measure, and use sea

ice. Their approach focused on identifying information in each sea-ice system services category users need to track and forecast change. ES were introduced as one of several sea-ice system services, and here, we explicitly focus on these sea-ice ES. Although the evidence is mounting that sea ice is pivotal for many ES, the underlying biological and physical dynamics coupled to this biome are poorly constrained. For instance, many biogeochemical processes mediated in sea ice cannot currently be quantified at regional or pan-polar scales (Vancoppenolle et al., 2013). Significant knowledge gaps persist in determining the importance of sea ice for the population size and health of ecological key species, such as Antarctic krill (*Euphausia superba*; Flores et al., 2012; Meyer et al., 2017; Atkinson et al., 2019), and quantitative information is not sufficient to adequately summarize other key ecosystem components, such as mesopelagic fishes (Snoeijs-Leijonmalm et al., 2020), squid (Xavier et al., 2018), and bird and mammal populations (Constable et al., 2014; Fauchald et al., 2017). Finally, few studies have made the connection between changes in sea ice and cultural ES (Falardeau and Bennett, 2020).

Here, we summarize the state of knowledge of sea-ice ecosystems and the food webs linked to them, investigate how the sea-ice ecosystem might fulfil the criteria for ecologically or biologically significant marine areas (EBSAs; which strictly exclude human impacts), and evaluate the ES associated with sea ice (which has a key focus on human impacts). The designation of EBSAs is a fundamental step in the development and nomination of Marine Protected Areas (MPAs; CBD, 2008), while ES assessments can further guide environmental policy-making. Leenhardt et al. (2015) synthesized the role of MPAs for ES and highlight MPAs as key management tools to maintain biodiversity, ecosystem functions, and to secure the delivery of marine ES. The improvement in the quality of the natural environment provided by MPAs is expected to strengthen the capacity of coastal ecosystems to produce goods and services for local and global communities (TEEB, 2010). With respect to ES, we recognize 3 main components: (1) the lower trophic levels of the sea-ice ecosystems, which live within the sea ice and provide the base of the food chain for higher trophic level, harvested species, as well as contribute to carbon export and the cycling of essential nutrients; (2) sea ice as a floating habitat to support grazers and predators, that is, by providing a refuge and nursery for pelagic and benthic species, as well as a platform for breeding and resting for some higher trophic species; and (3) sea ice as a support and platform for human livelihoods, cultural practices, tourism, science, and other provisioning and cultural uses (**Figure 1**).

We have structured this article to first define EBSAs and ES in relation to sea-ice environments (Sections 2 and 3), followed by detailed scientific descriptions of these environments and how they support ES (Sections 4–7). We then outline implications of sea-ice ES for human well-being (Section 8) and describe trends and projections (Section 9). We conclude the paper with a discussion of conservation measures (Section 10) and a summary (Section 11).

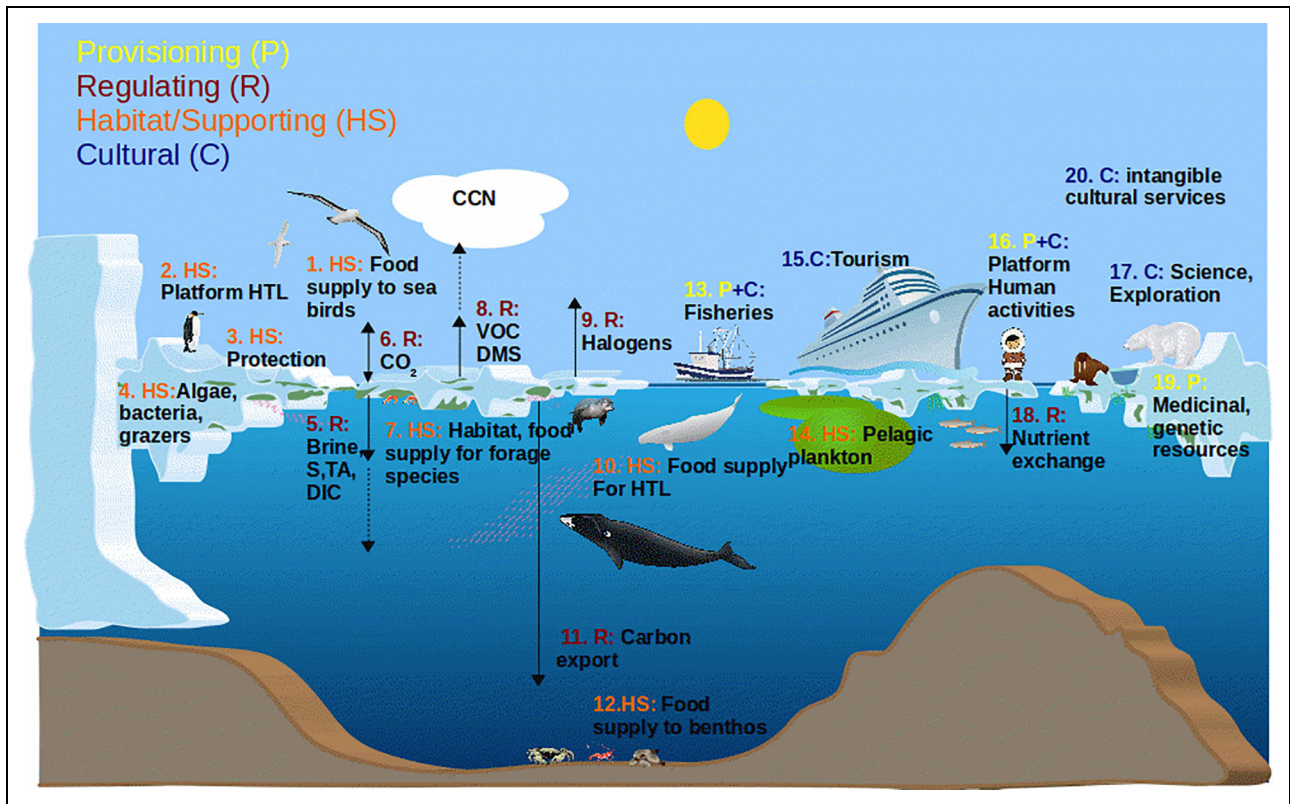


Figure 1. Key examples of sea-ice ecosystem services. Examples for provisioning (P, yellow), regulating (R, red) habitat/supporting (H, orange), and cultural (C, blue) ecosystem services provided by polar sea-ice ecosystems: (1) Food supply to higher trophic level species and sea birds; (2) Platform for birthing and neonatal care of higher trophic species; (3) Protection from predators for ice-adapted species; (4) Habitat for sympagic algae, bacteria, grazers (ice, melt pond, slush communities); (5) Brine drainage that exports salt (S), total alkalinity (TA), dissolved inorganic carbon (DIC); (6) CO₂ exchange; (7) Habitat and food supply for key foraging species (amphipods, Antarctic krill, Arctic cod); (8) Emission of aerosol precursors for cloud condensation nuclei (CCN), including volatile organic compounds (VOC) and dimethylsulfide (DMS); (9) Halogen oxidation via frost flowers and snow; (10) Food supply for higher trophic level species (fish, seals, whales); (11) Carbon export into the (deep) ocean; (12) Food supply to benthic species; (13) Fisheries and harvesting; (14) Nutrient supply to pelagic phytoplankton; (15) Tourism; (16) Platform for human transport and subsistence harvesting; (17) Spiritual connection and inspiration, science and exploration; (18) Nutrient exchange; (19) Medicinal and genetic resources; and (20) all of the intangible, cultural, services that connect coastal communities to the sea ice, such as spiritual experience and Indigenous and local knowledge (see **Table 1**). DOI: <https://doi.org/10.1525/elementa.2021.00007.f1>

2. EBSAs

The Convention on Biological Diversity (CBD, 2008) defines an EBSA as “a geographically or oceanographically discrete area that provides important services to one or more species/populations of an ecosystem or to the ecosystem as a whole, compared to other surrounding areas or areas of similar ecological characteristics.” Other EBSA definitions include “an area of especially high ecological or biological significance where greater risk aversion is required in the management of activities” (DFO, 2004). In addition, perturbations are expected to cause greater ecological consequences within EBSAs than in surrounding areas exposed to comparable pressures. Scientific criteria for identifying EBSAs in need of protection in open-ocean waters and deep-sea habitats have been established at international (CBD, 2008, Annex1), as well as national (e.g., within Canada, DFO, 2004, 2011) levels. While there are no universally agreed required scores for EBSA

designation, suggestions include medium to high scores on most criteria, and a high score on only one CBD criteria could be argued as sufficient for EBSA designation.

Table 2 summarizes the results for the assessment of the sea-ice ecosystem under the 7 criteria for designation of an EBSA (CBD, 2008). Justifications are provided in the supplementary material (Table S1) which synthesizes our evaluation of the sea-ice ecosystem under those criteria. Details supporting the justifications are provided in the sections below and are referenced in Table S1. Six of the criteria are ranked as high, while 1 criterion, biological productivity, was ranked as medium. For biodiversity and productivity, however, arguments for both medium and high rating could be made (see notes in **Table 2**). These rankings suggest that the sea-ice ecosystem should be recognized as an EBSA or, more specifically, that the sea-ice ecosystem represents an ecologically and biologically significant marine system, which is not necessarily fixed to

Table 1. Sea-ice ecosystem service categorization into provisioning, regulating,^a habitat/supporting and cultural services.^b DOI: <https://doi.org/10.1525/elementa.2021.00007.t1>

Ecosystem Service	Category	Description ^c
Habitat/ supporting	Life cycle maintenance	Essential habitat for sea-ice algae, habitat for bacteria, fungi, archaea and viruses (4.2.2), and ice fauna (4.2.3)
		Complete life cycle support for Arctic and Antarctic crustaceans and sympagic meiofauna (4.2.3)
		Habitat for critical life stages for some pelagic and benthic metazoan species (4.2.3)
		Ice algal carbon constitutes a key baseline item in polar food webs (4.3.1, 4.3.2); also regulating service, biological control.
		Key role for reproduction/survival/recruitment of juvenile stages of forage species (ice amphipods, copepods, Arctic cod, Antarctic krill; 4.2.3, 4.3.1, 4.3.2)
		Habitat for marine mammal and seabird species endemic to the sea-ice environment. (Sea ice is critical or important for one or more life stages; 4.3.3)
		Pack-ice zone and ice edge provide habitats for marine mammals and penguins in different periods of their annual life cycles (4.3.3).
		Ice edge/polynyas are important foraging grounds (4.3.3).
		Platform for a range of ice-based activities (7.1, 7.2)
		Gene pool protection
	Multiyear ice provides key support for sea-ice algal biodiversity (9.1.1).	
	Central Arctic under-ice habitat potential vector of genetic exchange and recruitment source for coastal Arctic cod populations (4.3.2)	
	Sea-ice barrier supports genetic distinction in species (4.3.3).	
Provisioning	Seafood	Key subsistence species for Arctic residents, especially Inuit, depend on sea ice and sea-ice algae (4.3.2, 4.3.3, 5.1.1).
		Limited commercial fisheries include sea-ice-associated species (Antarctic krill, Arctic cod) (5.1).
	Medicinal and genetic resources	Use of sea-ice algal and bacterial communities for potential pharmaceuticals, and health products (bioprospecting, 5.2)
	Pharmaceutical/aquaculture use are likely factors driving future growth in krill fishing industry (5.2).	
	Ornamental resources and raw materials	Sea-ice-associated species provide raw materials for the production of clothing and art (5.1.1, 7.1).
Regulating ^a	Air purification	Near-surface atmospheric cleansing via chemical interactions of halogens and sea ice (6.4)
	Climate regulation	Sea-ice and its biotic and abiotic contents regulate the surface albedo and radiative transfer, regulating light for pelagic primary production (6.1).
		Sea-ice carbon pump contributes to deep ocean carbon export (6.3).
		Ice-algal-produced DMSP supports the release of the climate active gas dimethylsulfide (DMS; 6.4).
		Supply of organic carbon and nutrients, including iron, to the ocean (6.5)
	Biological control	Released sea-ice algal carbon is either mineralized in the upper water column or exported to the deep ocean (6.2).
Sea-ice bacteria fulfill and mediate essential biogeochemical functions (decomposition of particulate organic matter, remineralization of nutrients; 4.2.2).		
Sea ice influences food web structure, energy flows among polar ecosystems, and indirectly population dynamics and ecosystem resilience (4.3.1, 4.3.2).		

(continued)

Table 1. (continued)

Ecosystem Service	Category	Description ^c
Cultural	Cultural heritage and identity	Sea ice is linked to culture and identity of Arctic coastal communities and provides a key transportation platform (7.1). Sea-ice-associated country foods are key components of culture and tradition for Arctic Indigenous Peoples with high spiritual, cultural, traditional and social values (7.1).
	Spiritual experience	Sea ice, sea-ice ecosystems, and sea-ice species contribute to spiritual experiences of Arctic coastal communities and visitors (7.1, 7.3).
	Inspiration for culture, art and design	Pristine landscapes, charismatic wildlife, and sea birds inspire Arctic residents, photographers, movie makers, writers, artists, and naturalists (7.2, 7.3).
	Recreation and leisure	Platform for recreational activities (walks, skidooring, fishing) of Arctic residents (7.1) Many marine-based recreational activities are linked to biological hotspots in the vicinity of sea ice (e.g., tourism in the Antarctic Peninsula area). Reduced sea-ice cover furthers the expansion of tourism operators into new regions (7.3).
	Aesthetic information	Inspiration of aesthetic power (7.2) including through habitat services for charismatic wildlife and sea birds (4.3.3)
	Information for cognitive development	Inspiration and support of Indigenous and local knowledge systems (7.1) Inspiration for scientific research and exploration, natural/remote/pristine laboratory (7.2) Unique proxy for extraterrestrial life (7.2)

^a Abiotic chemical transport processes impacted by sea ice are included into regulating ES; however, purely physical sea-ice system services (e.g., wave dampening, coastal erosion prevention, albedo effects, see Eicken et al., 2009) are not considered here.

^b Following TEEB (2010) and Böhnke-Henrichs et al. (2013).

^c Sections are referenced in parentheses.

Table 2. Criteria^a and ratings^b for designating sea ice as an ecologically or biologically significant area (ESBA) with links to associated ecosystem services.^c DOI: <https://doi.org/10.1525/elementa.2021.00007.t2>

Criteria and Description	Rating	Link to Ecosystem Service
Uniqueness or rarity	high	Habitat/supporting, cultural
Special importance for life-history stages of species	high	Habitat/supporting, provisioning
Importance for threatened, endangered, or declining species and/or habitat	high	Habitat/supporting, cultural
Vulnerability, fragility, sensitivity, or slow recovery	high	Habitat/supporting, cultural, regulating
Biological productivity	medium ^d	Habitat/supporting, provisioning, regulating
Biological diversity	high ^e	Provisioning, regulating
Naturalness	high	Cultural

^a Following CBD (2008).

^b The EBSA designation process usually follows a Delphi approach which consists of structured interactive discussions and estimates by a panel of subject matter experts. Here, the authors constitute subject matter experts, and rating is based on the outcomes of discussions among the authors; however, the table does not reflect results of a structured Delphi approach.

^c For details and justification, see Table S1.

^d A medium rating has been applied based on comparatively lower productivity in the sympagic system versus the pelagic system. However, given the highly concentrated productivity in sea ice, a high rating might also be defensible.

^e A high rating has been applied despite a comparatively lower biodiversity in the sympagic system versus the pelagic system, as the unique biodiversity in sea ice suggests that species lost with sea ice might be lost on a global scale and hence decrease global biodiversity.

a certain location. This distinction highlights a potential need for flexibility in the EBSA concept.

In 2014, the CBD convened a workshop to identify Arctic EBSAs with the goal to focus future conservation and management efforts. The CBD initiative built on earlier efforts identifying Arctic Marine Areas of Heightened Ecological and Cultural Significance (**Figure 2a**) as part of the Arctic Marine Shipping Assessment (Arctic Council, 2009). Several of the identified regions overlap with simulated areas of high sea-ice algal production. Canada's most recent MPA was created in part to protect an area which is suggested to be the last multiyear ice area (see Section 10 on MPA considerations below), indicating some recognition of areas containing sea-ice ecosystems for their biological or ecological significance. For the Southern Ocean, Hindell et al. (2020) put forward the concept of identifying areas of ecological significance to support mitigation efforts and conservation management. Their approach is based on assemblage-level tracking of marine predators, which integrates some of the criteria identified for EBSA designation, indicating a potentially comparable process.

3. Sea-ice ecosystem services

The sea-ice ecosystem and its contributions to each of the 4 service categories are summarized in **Table 1** and schematically displayed in **Figure 1**. **Table 1** is following the categorization per TEEB (2010) with typology for marine ES by Böhnke-Henrichs et al. (2013). Details are provided in the sections below. As ES include climate-regulating services, we include a discussion on abiotic chemical transport processes impacted by sea ice. Sea ice also contributes to the regulating services of disturbance prevention (e.g., through wave dampening), coastal erosion prevention, and radiation (e.g., albedo effects). The abiotic, physical processes of sea-ice formation and melt also contribute services to the adjacent marine ecosystem and global climate. Those services of the sea-ice system (i.e., not the sea-ice ecosystem) are discussed by Eicken et al. (2009), and we do not discuss them further here.

The majority of ES are similar in both polar oceans, with the exception that provisioning and cultural services to Indigenous Peoples are only relevant in the Arctic. Some sea-ice ES vary based on differences in, for example, the human groups shaping and benefiting from the supply of services, human habitation, pressures from industries (e.g., oil and gas exploration, fisheries, tourism), and existing treaties and moratoria (e.g., Antarctic Treaty System; Moratorium on fisheries in high Arctic Seas). Some differences are related to basin characteristics (e.g., the Arctic Ocean being surrounded by land versus the Southern Ocean surrounding a continent), oceanographic conditions, regional extent, and dynamics of sea-ice growth. With respect to sea ice, differences also arise due to ice types, for example, mobile pack ice versus stationary fast ice, multiyear ice versus first-year ice or marginal ice-zone sea-ice types, and sea-ice structure (e.g., snow-ice and platelet ice formation are typical for the Southern Ocean, while thick multiyear ice and melt ponds are more common in the Arctic).

4. Habitat and supporting services

4.1. The sea-ice ecosystem

Sea ice is a multiphase medium, containing concentrated salts in liquid brine and gas bubbles which are inclusions in the solid ice structure. The brine channels provide habitat space for microbial life from viruses, fungi, and bacteria to larger algae and grazing microorganisms, some of which are endemic to sea ice, while others also have benthic or pelagic life stages. The use of sea-ice habitat requires unique evolutionary adaptation (Sackett et al., 2013), and as a result, sea-ice habitats make a unique contribution to global biodiversity by supporting species that cannot be found elsewhere on the planet. As a dynamic interface, sea ice links rather than separates the global ocean from the atmosphere (e.g., Loose et al., 2011). With approximately 6–16 million km² (Arctic) and 4–19 million km² (Southern Ocean) covered by sea ice depending on season (Stroeve and Notz, 2018; Reid et al., 2020), sea ice represents one of the largest and most dynamic surface biomes on Earth (e.g., Arrigo, 2014).

4.2. Sympagic communities

4.2.1. Sea-ice algae

Sea ice provides a habitat for a variety of algae including diatoms, flagellates, and dinoflagellates. While some can thrive in both pelagic or benthic environments in addition to sea ice (e.g., the diatom *Cylindrotheca closterium*; Poulin et al., 2011), many ice-associated algal species have a clear preference for sea ice and can be considered unique to sea-ice habitats. Most notable is the widespread dominance of pennate diatoms of genus *Nitzschia*, in both Antarctic (Garrison, 1991) and Arctic sea ice (Poulin et al., 2011). This sea-ice preference is only possible due to unique morphological and physiological adaptations and life cycle strategies geared toward habitation of an ice substrate with extremes in light, salinity, and temperature conditions (e.g., Stoecker et al., 1997; Morgan-Kiss et al., 2006; Ligowski et al., 2012).

Primary productivity in sea ice plays important supporting and regulating roles in the ecosystem, fuelling the food web and driving the organic carbon pump, that is, ice-algal production is typically highest in early spring when stable sea-ice habitats are exposed to the light of the polar day (Leu et al., 2015) and provides an important carbon source to grazers before pelagic algae start blooming in the ocean (Wiedmann et al., 2020). In the Arctic, observations indicate strong regional variability in ice-algal versus pelagic primary production with most areas showing ice-algal primary production in the range of 3–25% of the pelagic production, but some areas with dense ice (>90%) showing 2–3 times as much ice algal primary production as pelagic primary production and uncertain contributions of under-ice primary production (Wiedmann et al., 2020). Models simulate sea-ice primary production to be 2–10% of the total primary production in the Arctic (Dupont, 2012; Jin et al., 2012; Hayashida et al., 2020). Similar to the Southern Ocean where the relative contribution of Antarctic sea-ice algal production to overall primary production in the sea-ice zone and the overall Southern Ocean is estimated to be about 10% and 1%,

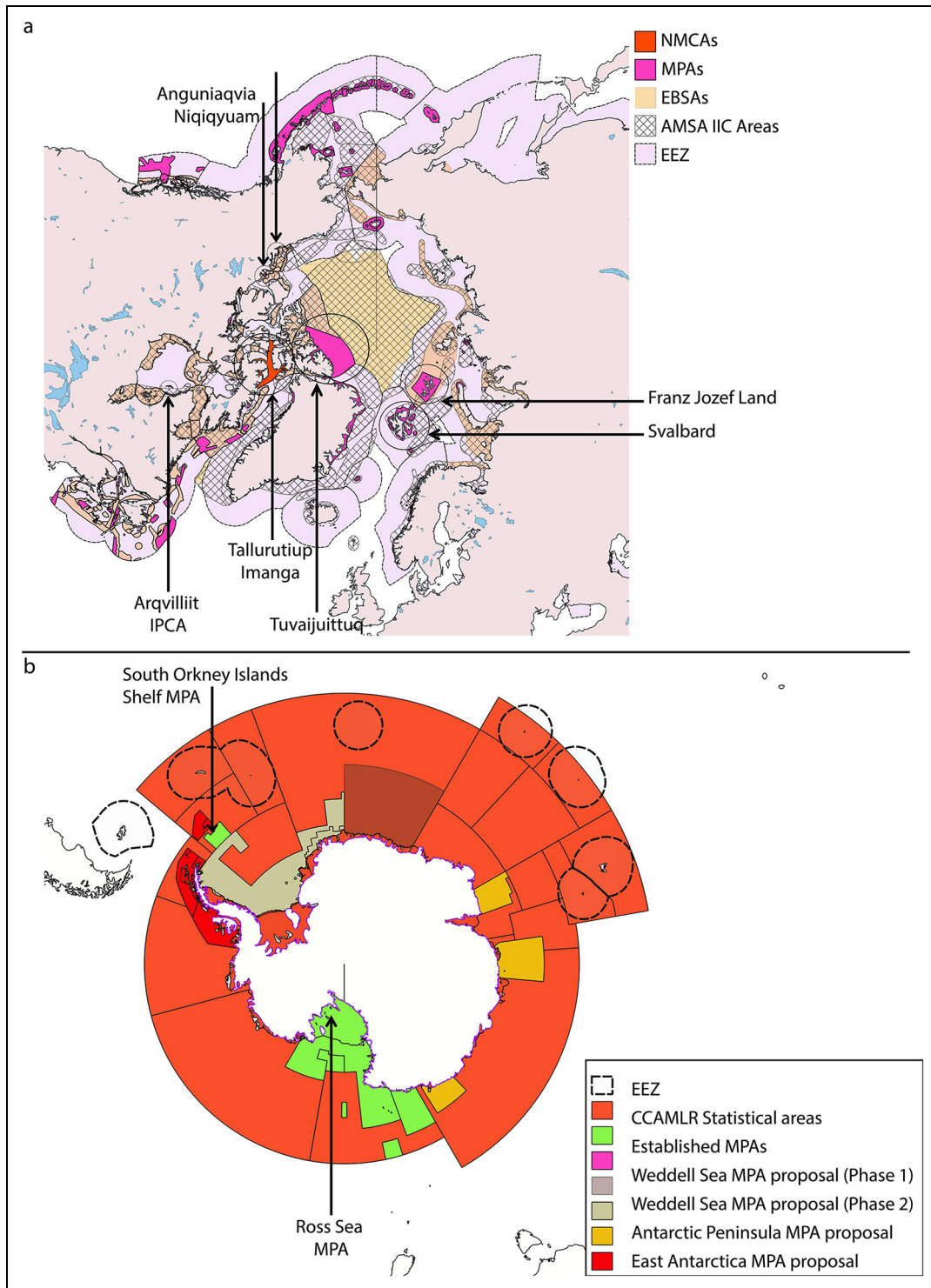


Figure 2. Maps of heightened ecological significance. (a) Map of the Arctic, indicating areas of heightened ecological and cultural significance (“Recommendation IIC areas”) as identified in the Arctic Marine Shipping Assessment (AMSA; CAFF, 2017), ecologically and biologically significant areas (EBSAs), marine protected areas (MPAs), including the new sea-ice-related Tuvaijuittuq MPA, as well as other conservation efforts with key Inuit involvement and leadership, for example, Tallurutiup Imanga National Marine Conservation Area (NMCA) and the Arqviiliit Indigenous Protected and Conserved Areas (IPCA). (b) Proposed and established MPAs, Conservation of Antarctic Marine Living Resources (CCAMLR) statistical areas and exclusive economic zones in the Southern Ocean. Exclusive economic zones (EEZ) relevant for national fisheries and conservation efforts are indicated in pink (a) or outlined in dashed lines (b). DOI: <https://doi.org/10.1525/elementa.2021.00007.f2>

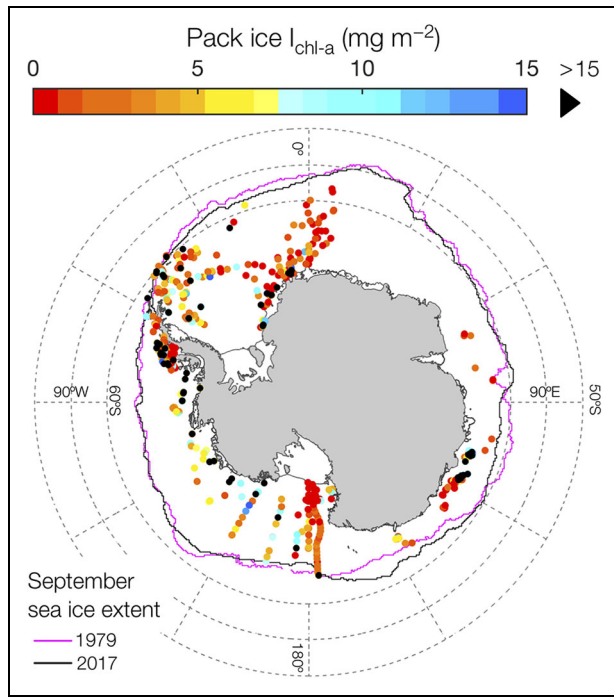


Figure 3. Southern Ocean ice-algal chlorophyll *a* distributions. Data points are color-coded by chlorophyll *a* concentration (mg m^{-2}) in pack ice cores around Antarctica. Pink and black lines indicate sea-ice extent in 1979 and 2017, respectively (updated from Meiners et al., 2012). DOI: <https://doi.org/10.1525/elementa.2021.00007.f3>

respectively (Saenz and Arrigo, 2014). This is despite a much smaller habitat volume compared to the surface ocean and corresponds to $3\text{--}73 \text{ Tg-C yr}^{-1}$ primary production in Arctic sea ice (Legendre et al., 1992; Watanabe et al., 2019) and $3\text{--}24 \text{ Tg-C yr}^{-1}$ in the Southern Ocean sea ice (Legendre et al., 1992; Saenz and Arrigo, 2014; Jeffery et al., 2020). **Figure 3** indicates sea-ice algal chlorophyll *a* as most abundant near the coastal zones of the Western Antarctic Peninsula and the Weddell and Ross seas. Biomass is overall highest in the bottom-ice layers with internal communities becoming more important in winter (Meiners et al., 2012; van Leeuwe et al., 2018).

Regionally, the relative contribution of ice algae to total marine primary production may be much higher. For example, ice-algal production in the central Arctic (order of 17 Tg C yr^{-1} ; Fernández-Méndez et al., 2015) can be significantly lower than ice-algal production of the central Canadian Archipelago (e.g., Lavoie et al., 2005), but have a far greater contribution to total production in the region (Gosselin et al., 1997; Wiedmann et al., 2020). In the Southern Ocean, the relative contribution of sea-ice primary production to total primary production is generally positively related to ice-cover duration. Values of up to 65% of daily ice-algal contribution to overall primary production have been reported for a coastal fast-ice location (McMinn et al., 2010). Ice-associated primary production is also amplified where platelet ice forms in the Antarctic (e.g., in proximity to ice shelves). There, sympagic algae can produce chlorophyll *a* concentrations up to $2400 \mu\text{g L}^{-1}$

(Van der Linden et al., 2020). Sympagic production adds a crucial, early pulse of energy to the system on which some grazers depend for their life cycle (e.g., *Calanus glacialis*; Soreide et al., 2010).

4.2.2. Sea-ice bacteria, archaea, fungi, and viruses

Sea-ice bacteria play a key supporting role in driving an active microbial loop, which recycles dissolved organic matter back to the upper trophic levels as bacterial biomass. They also fulfill essential biogeochemical functions such as decomposition of particulate organic matter and remineralization of nutrients. Sea-ice bacterial communities are regulated by both abiotic and biotic factors, such as salinity, temperature, nutrients, light, protozoan grazing, and viral lysis (Deming and Collins, 2017). They are entrained in new sea ice from seawater during freezing. The availability of dissolved organic matter can dramatically shorten the recovery time (Eronen-Rasimus et al., 2014) and the algal-derived organic matter from autumn blooms or other ice-associated carbon sources may sustain bacterial activity even during the cold winter months (Junge et al., 2004; Eronen-Rasimus et al., 2017). Usually, however, bacterial activity and abundance are at a minimum during the winter months (Delille et al., 1995; Collins et al., 2008) and remain low until the increasing solar radiation induces a mass growth of sea-ice algae providing substrate for bacterial growth (Thomas et al., 2001; Riedel et al., 2008; Deming and Collins, 2017). Hence, heterotrophic production is thought to lag primary production in the spring. The predominant classes of bacterial communities in the spring/summer at both poles are Gammaproteobacteria (e.g., genera *Glaciecola*, *Colwellia*, *Shewanella*), Bacteroidia (e.g., genera *Polaribacter* and *Flavobacterium*) and Alphaproteobacteria (e.g., genus *Octadecabacter*) as reviewed by Bowman (2015) and Deming and Collins (2017).

In addition to bacteria, archaea, fungi, and viruses are present in sea ice throughout the winter (Maranger et al., 1994; Wells and Deming, 2006; Collins et al., 2010; Collins and Deming, 2011; Cowie et al., 2011; Comeau et al., 2016; Hassett et al., 2019). Viruses are a major source of mortality for marine organisms ranging from bacteria to whales, thus shaping the community composition and biogeochemical cycles in marine systems (Suttle, 2005). However, the research to understand the ecological significance of archaea, fungi, and viruses in sea ice is ongoing.

4.2.3. Sea-ice meiofauna and under-ice fauna

Sea ice also serves as habitat for in-ice and under-ice fauna, which range in size from unicellular protists to large macrofauna, such as ice amphipods and Antarctic krill. Sympagic fauna constitutes a functional node in Arctic and Antarctic ecosystems, because it mediates cryopelagic-benthic coupling by channeling significant amounts of carbon from the sea ice to the pelagic food web (Budge et al., 2008; Kohlbach et al., 2016; Kohlbach et al., 2018; Ehrlich et al., 2021). Small forms known as “sea-ice meiofauna” inhabit brine channels and cavities within the sea-ice matrix. Sea-ice meiofauna comprises a diverse species community, covering many clades of the

taxonomic tree of marine life, including ciliates, foraminiferans, flatworms, rotifers, nematodes, copepods, cnidarians, and gastropods (Kiko et al., 2008; Piraino et al., 2008; Kramer et al., 2011; Bluhm et al., 2018; Ehrlich et al., 2020). Due to the complexity of the sea-ice habitat and logistical challenges to sample sea-ice meiofauna in a representative manner, the full diversity of this community, its abundance and biomass are poorly constrained. In the Arctic Ocean, observed sea-ice meiofauna abundances range from zero to 417,000 individuals m^{-2} , with highest abundances in coastal areas (Bluhm et al., 2018). In the Southern Ocean, abundances can reach a similar order of magnitude (Kramer et al., 2011).

The ice-water interface provides a habitat for numerous invertebrate macrofauna species. In the Arctic Ocean, amphipods are the dominant fauna at the underside of sea ice (e.g., *Gammarus wilkitzkii*, *Onisimus* spp., *Apherusa glacialis*; Gradinger and Bluhm, 2004; CAFF, 2017). In the Southern Ocean, sympagic amphipods are also present (e.g., *Eusirus laticarpus*), but the under-ice community is often heavily dominated by Antarctic krill (Krapp et al., 2008; Flores et al., 2011). The transition between sympagic fauna and pelagic under-ice fauna is gradual, impeding the estimation of distinct species numbers for sympagic under-ice fauna. Some species may only associate with sea ice for a part of their life cycle, such as Antarctic krill (Meyer et al., 2017) or the Arctic copepod *Calanus glacialis* (Søreide et al., 2010). Comparative studies with the same type of under-ice trawl indicate that taxonomic richness of under-ice fauna may be higher in the Southern Ocean (45–46 taxa per study) than in the Arctic Ocean (28–32 taxa per study), and local under-ice fauna abundances are highly variable, ranging from 0.1 ind. m^{-2} in Antarctic winter to nearly 7,000 ind. m^{-2} in Arctic spring (Flores et al., 2011; David et al., 2015; David et al., 2017; Ehrlich et al., 2020). The highest biomass is usually found in the Southern Ocean due to high abundances of Antarctic krill (Flores et al., 2011; David et al., 2021).

4.3. The links between sea ice and the food webs of the polar oceans

4.3.1. Sympagic inputs into polar food webs

Sympagic primary producers are an important source of energy, and they constitute a critical foundation for polar marine food webs. In both polar regions, strong direct reliance on sea-ice derived organic matter has been shown in all ecosystem compartments, that is, sympagic (Søreide et al., 2006; Budge et al., 2008; Kohlbach et al., 2016; Kohlbach et al., 2017b), pelagic (Wang et al., 2015; Jia et al., 2016; Kohlbach et al., 2018; Schmidt et al., 2018; Kohlbach et al., 2019b), and benthic (McMahon et al., 2006; Norkko et al., 2007; Søreide et al., 2013; Wing et al., 2018; Kohlbach et al., 2019a; Michel et al., 2019). Trophic linkages are not limited to primary consumers but extend to higher trophic levels (Bluhm and Gradinger, 2008; Kohlbach et al., 2017a; Brown et al., 2018; Choy et al., 2020) as indicated by the selection of ice-dependent species shown in **Figure 4**. In the Arctic Ocean, the under-ice fauna transfers the bulk of sympagic carbon to the pelagic system, and the contribution of the sea-ice

meiofauna is very small (Ehrlich et al., 2021). The strength of cryo-pelagic and/or cryo-benthic coupling also appears to be seasonally variable (Leu et al., 2015). Contributions of sea-ice material to the food web is vital in winter for the pelagic compartment (Kohlbach et al., 2018), while it appears to peak after spring/summer breakup for the benthic compartment (Calizza et al., 2018; Rossi et al., 2019).

Within the pelagic system, carbon derived from sea-ice algae is transferred through bacteria and small grazers, some of them predominantly associated with sea ice (Søreide et al., 2010; Brown et al., 2017; Ehrlich et al., 2020; Kunisch et al., 2020), to fish (Kohlbach et al., 2017b; McMullin et al., 2017), seabirds, including penguins (Goutte et al., 2013; Goutte et al., 2014), whales (Loseto et al., 2009; Brown et al., 2017), and polar bears (Brown et al., 2018). Through indirect carbon transfer, even abundant pelagic species such as the Antarctic euphausiid *Thysanoessa macrura* can derive a significant part of their carbon budget from ice algae (Kohlbach et al., 2019b). Hence, a multitude of polar species rely on sea-ice derived organic matter, emphasizing its importance as a major driver of food web structure in polar marine systems. This reliance suggests that multiscale variations in sea-ice dynamics could cause major modifications of the food web architecture (Michel et al., 2019; Rossi et al., 2019).

For forage species such as ice amphipods and copepods (e.g., Arndt and Swadling, 2006; Kohlbach et al., 2018), Arctic cod (e.g., Lønne and Gulliksen, 1989; Kohlbach et al., 2017b), and Antarctic krill (e.g., Meyer et al., 2017; Kohlbach et al., 2017a), the sympagic ecosystem is essential for reproduction, survival, and recruitment from juvenile stages. Juvenile Antarctic toothfish depend on Antarctic krill as a food source, and they possibly use the sea ice as a nursery habitat. Due to their parallel roles as a key energy conduit from sympagic algae to higher trophic level species, we highlight the roles and life cycles of Arctic cod in the Arctic Ocean and Antarctic krill in the Southern Ocean below (**Figure 5**). Some benthic consumers might prefer ice algae over other food items because of their high fatty acid content (McMahon et al., 2006).

4.3.2. Key carbon transmitters in ice-associated food webs

Arctic cod

Arctic cod (*Boreogadus saida*) is a critical carbon source for seabirds, fish, and marine mammals in high Arctic ecosystems (Bradstreet et al., 1986; Coad and Reist, 2004; Choy et al., 2020), many of which are key subsistence species harvested by northern communities (e.g., Inuvialuit communities; Harwood et al., 2015). Arctic cod has been reported as the most abundant fish species across a range of habitats (Rand and Logerwell, 2010; Hop and Gjosæter, 2013; Melnikov and Chernova, 2013; Walkusz et al., 2013; David et al., 2016; Majewski et al., 2017; Forster et al., 2020; Marsh et al., 2020). Arctic cod are optimized for a life under sea ice through a variety of factors: food conversion efficiency and maximum egg survival rate being highest at 0°C (declining at higher temperature) (Kunz et al., 2016; Dahlke et al., 2018), growth and metabolic performance declining at 8°C (Kunz et al., 2016;

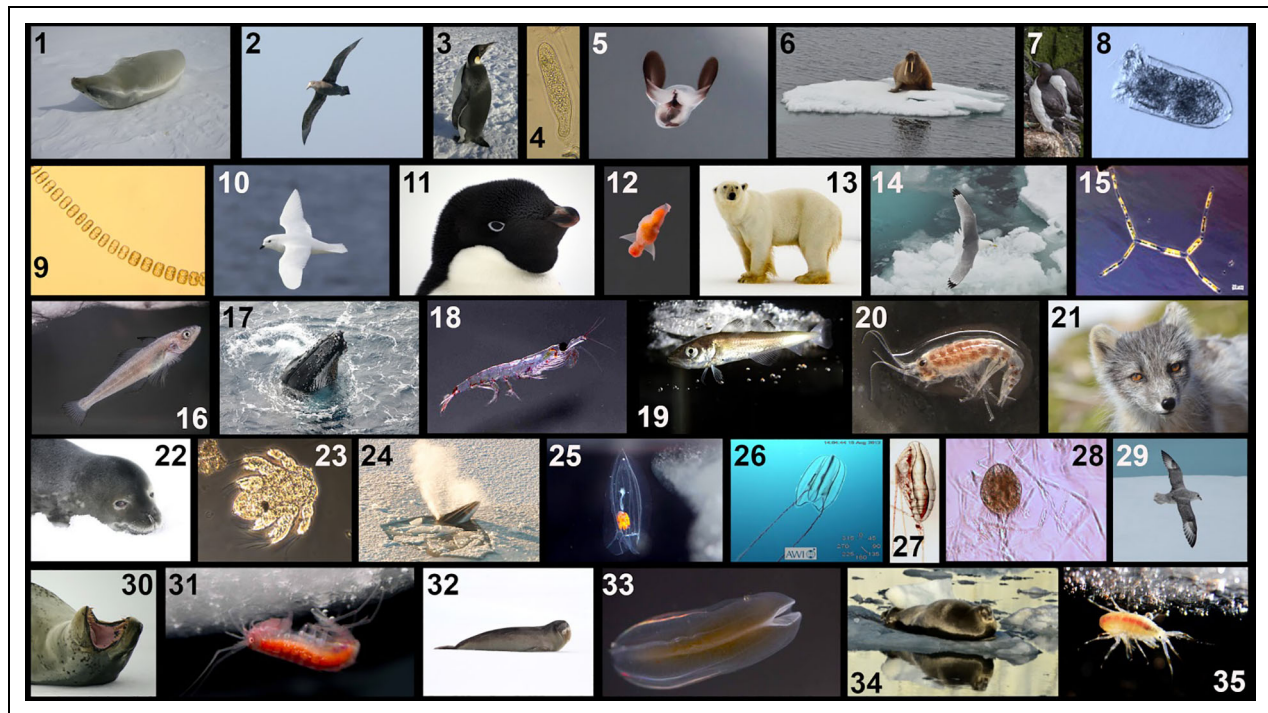


Figure 4. Selection of sea-ice-associated organisms. Nonexhaustive selection of sea-ice-associated organisms from the Southern Ocean (SO) and the Arctic Ocean (AO). Species from both hemispheres are shown together to stress the global importance of sea ice for ice-associated species. Species: (1) crabeater seal (*Lobodon carcinophaga*, SO); (2) giant petrel (*Macronectes giganteus*, SO); (3) emperor penguin (*Aptenodytes forsteri*, SO); (4) ciliate (Ciliophora, SO); (5) pteropod (*Limacina helicina*, SO); (6) walrus (*Odobenus rosmarus*, AO); (7) thick-billed murre (*Uria lomvia*, AO); (8) tintinnid (Tintinnidae, AO); (9) ice alga (*Thalassiosira* sp., SO); (10) snow petrel (*Pagodroma nivea*, SO); (11) Adélie penguin (*Pygoscelis adeliae*, SO); (12) sea angel (*Clione limacina*, SO); (13) polar bear (*Ursus maritimus*, AO); (14) Kittiwake (*Rissa tridactyla*, AO); (15) ice alga (*Nitzschia* sp., AO); (16) Antarctic fish (*Aethotaxis mitopteryx*, SO); (17) humpback whale (*Megaptera novaeangliae*, SO); (18) Antarctic krill (*Euphausia superba*, SO); (19) Arctic cod (*Boreogadus saida*, AO); (20) sea-ice amphipod (*Apherusa glacialis*, AO); (21) Arctic fox (*Vulpes lagopus*, AO); (22) Weddell seal (*Leptonychotes weddellii*, SO); (23) nauplius larva (Copepoda, SO); (24) Antarctic minke whale (*Balaenoptera bonaerensis*, SO); (25) siphonophore (*Diphyes antarctica*, SO); (26) comb jellyfish (*Mertensia* sp., AO); (27) copepod (*Calanus glacialis*, AO); (28) ciliate (*Didinium* sp., AO); (29) northern fulmar (*Fulmarus glacialis*, AO); (30) leopard seal (*Hydrurga leptonyx*, SO); (31) sea-ice amphipod (*Eusirus microps*, SO); (32) Ross seal (*Ommatophoca rossii*, SO); (33) comb jellyfish (*Beroe* sp., SO); (34) bearded seal (*Erignathus barbatus*, AO); (35) sea-ice amphipod (*Gammaris wilkitzkii*, AO). Photo credits: H.F. (1, 2, 3, 10, 11, 13, 17, 19, 22, 29, 30, 35); J.A.F. (5, 7, 12, 16, 18, 24, 25, 31, 32, 33); Julia Ehrlich (4, 8, 23, 28); Susanne Kühn (6, 14, 21, 34); J.S. (9); Clara Hoppe (15); Christian Katlein and Marcel Nicolaus (26); Carin Ashijan (27). DOI: <https://doi.org/10.1525/elementa.2021.00007.f4>

2018), the presence of antifreeze glycoproteins and specialized kidney function (Osuga and Feeney, 1978; Christiansen et al., 1996), and the ability to digest food at -1.4°C water temperature (Hop and Tonn, 1998). The Arctic cod life cycle is depicted in **Figure 5**.

Larval Arctic cod predominantly feed on copepod eggs and nauplii (Walkusz et al., 2011), but 26% of their stomach contents can consist of ice-algal cells (Gilbert et al., 1992), although Arctic cod eat bigger, pelagic prey as they grow (Mcnicholl et al., 2016; Kohlbach et al., 2017a; **Figure 5**). Amphipods and copepods channel ice algae-produced carbon to young Arctic cod, on which they critically depend (Budge et al., 2008; Kohlbach et al., 2016; Kohlbach et al., 2017b). Most adult Arctic cod populate deeper habitats (Rand and Logerwell, 2010; Walkusz et al., 2013; Majewski et al., 2017) and/or associate with the pack ice until the following year. David et al. (2016)

discovered that young Arctic cod were ubiquitous under sea ice throughout the Eurasian Basin. Assuming the observed Arctic cod followed the ice drift, their distribution in the Eurasian Basin was suggested to be dependent on the coastal populations on the Siberian shelf, where the sea ice originated. Thus, the central Arctic under-ice habitat may constitute a favorable environment for early survival and is a potential vector of genetic exchange and a recruitment source for coastal populations around the Arctic Ocean. Recent research in the Chukchi Sea hypothesizes that Arctic cod may track the springtime ice retreat and the wave of productivity that follows, performing a classical “migration triangle” between nursery grounds, feeding grounds, and spawning grounds (Forster et al., 2020). However, a recent synthesis on movement ecology of Arctic cod highlights the complex dynamics involved and points out a critical need for more direct research on

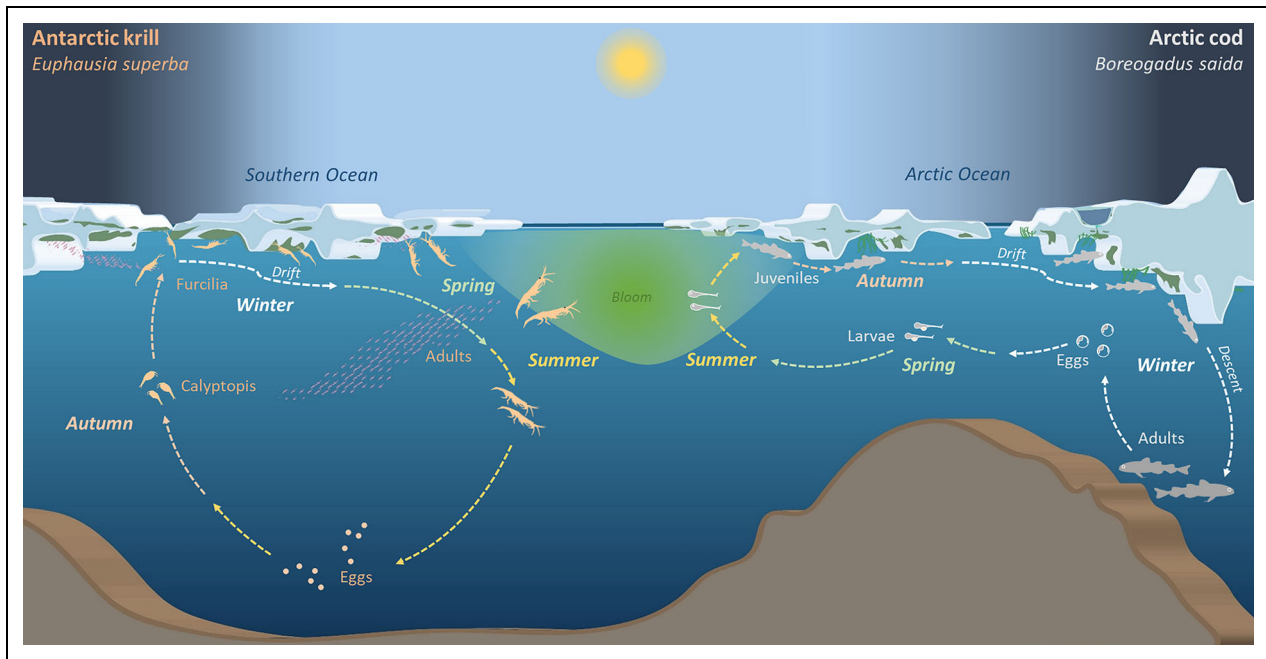


Figure 5. Life cycles of Arctic cod and Antarctic krill. Life cycles of Arctic cod (*Boreogadus saida*) and Antarctic krill (*Euphausia superba*), two ecologically key species associated with sea ice. For each life cycle stage, the season is indicated by coloured font and arrows: green (spring), yellow (summer), brown (autumn), and white (winter). Krill spawn during austral summer in the open ocean. The eggs sink to great depth (up to $\approx 1,000$ m), where the first larval stage hatches. From there, larvae slowly rise to the surface (developmental ascent, Marr, 1962) while they develop into the first feeding stages. In autumn, they feed on phytoplankton and ice algae, while they associate with the growing sea ice. They survive the winter in close association with the sea-ice underside, where they develop into juveniles. By spring, krill have passed through 12 distinct larval stages from hatching to juvenile. In summer, mature adults mate in deep waters following a complex behavioural pattern (Kawaguchi et al., 2011). Arctic cod spawning occurs in winter (Bouchard and Fortier, 2008, 2011), and the buoyant eggs are adapted to sub-zero temperatures under sea ice. Larvae develop from spring to late summer in largely ice-free waters (Bouchard and Fortier, 2008, 2011). Hatching is synchronized with the start of copepod production, which in turn depends on ice-algal bloom timing (Bouchard and Fortier, 2008). By October–November, Arctic cod that reach a threshold size of approximately 5.5 cm are assumed to join the adult populations in deeper habitats (Geoffroy et al., 2015). DOI: <https://doi.org/10.1525/elementa.2021.00007.f5>

circumpolar gadid movements to aid understanding of climate change impacts on Arctic ecosystems and fisheries (Pettitt-Wade et al., 2021). The current body of research on Arctic cod indicates that sea ice plays an important supporting role during each of their major life-history stages, thus suggesting a particular vulnerability to changes in the distribution and structure of sea-ice habitats and ocean warming (Steiner et al., 2019).

Antarctic krill

The crustacean Antarctic krill (*Euphausia superba*, often referred to as “krill”) is one of the most abundant multicellular animals on Earth. The life span of *Euphausia superba* is about 5–6 years, and individuals reach a maximum size of 65 mm (Cavan et al., 2019). Their circumpolar distribution pattern largely covers the average extent of the winter sea ice in the Southern Ocean (Siegel and Watkins, 2016). Krill form huge swarms extending over tens of square kilometers and constitute the staple food of many whales, seals, and seabirds in the Southern Ocean. Total biomass estimates of the entire Antarctic krill stock are associated with considerable

uncertainty, but the biomass is likely on the order of 400 million metric tonnes (Atkinson et al., 2009). In the western Atlantic sector of the Southern Ocean where Antarctic krill biomass is highest, krill abundance is positively related with the duration and extent of sea-ice coverage (Atkinson et al., 2004; Atkinson et al., 2019), highlighting a strong coupling between sea ice and krill abundance. Krill, and in particular larval krill, can concentrate at the sea-ice underside (O’Brien, 1987; Marschall, 1988; Stretch et al., 1988; Flores et al., 2012; Flores et al., 2014; David et al., 2017; Meyer et al., 2017). Due to their large bodies, high biomass, and dominant role in the food web, Antarctic krill constitute a key factor in elemental cycling and carbon flux in the whole Southern Ocean (Cavan et al., 2019).

Survival, reproduction, and life cycle (Figure 5) of Antarctic krill are closely coupled to sea ice, suggesting a strong susceptibility to sea-ice decline in the Southern Ocean. During winter, the survival of Antarctic krill larvae in the sea-ice habitat is considered a key mechanism ensuring the future health of krill populations (Flores et al., 2012). Unlike adult krill which can survive food scarcity

on lipid reserves, larval krill depend on continuous food supply (Quetin et al., 1994; Meyer et al., 2002; Meyer, 2012). Larval krill use highly deformed sea ice as a refuge during the day while drifting with the subsurface water during the night (Meyer et al., 2017). Krill larvae feed on ice algae, detritus, ice-associated copepods, and meiofauna (e.g., Schaafsma et al., 2017). Through these diverse food sources, krill larvae depend critically on ice algae-produced carbon during winter (Jia et al., 2016; Kohlbach et al., 2017a), and even after sea ice has melted in summer, krill can benefit from sea-ice derived production (Schmidt et al., 2018; Kohlbach et al., 2019a).

4.3.3. Marine birds and mammals

Several marine mammal and seabird species (flying and nonflying) are endemic to the sea-ice environment and are either ice-dependent or highly ice-associated, meaning sea ice is either critical or important for one or more stages of their life cycle (e.g., mating, breeding, calving) and/or for food provision. The fast ice is a breeding ground for ice-obligate breeders, while the dynamic ice edge is known as an important foraging ground. As a third component of the sea-ice ecosystem, polynyas, persistent open water areas in the pack ice, serve as oases, sustaining local ecosystems and providing access to food for many marine mammal and bird species (Labrousse et al., 2018).

Arctic Ocean

For Arctic seabirds (Billerman et al., 2020), important populations of many species depend on the Arctic sea-ice habitat for foraging for at least part of their annual cycle. Several alcid species, for example, Brünnich's guillemot (*Uria lomvia*), little auk (*Alle alle*), parakeet auklet (*Aethia psittacula*), and large numbers of black-legged kittiwake (*Rissa tridactyla*) and northern fulmar (*Fulmarus glacialis*), exploit the Arctic sea ice during the breeding season. They forage on fish and zooplankton that associate with the sea ice, such as Arctic cod and a range of amphipods. They are accompanied by scavenging species, such as ivory gull (*Pagophila eburnea*), or kleptoparasitic birds, like the pomarine skua (*Stercorarius pomarinus*). The major sea-ice areas over coastal shelf regions are of critical importance to, for example, Steller's eider (*Polysticta stelleri*), king eider (*Somateria spectabilis*), and spectacled eider (*S. fischeri*) populations. The coastal areas of the Arctic Ocean are of major importance to many geese, ducks, divers, waders, and skuas before and/or after the breeding season in high-arctic tundra and freshwater systems where the seasonal sea ice enriches their foraging habitat.

In the Arctic, there are only 11 species of marine mammals, 7 of which are endemic, that is, ringed (*Pusa hispida*) and bearded seals (*Erignathus barbatus*), walrus (*Odobenus rosmarus*), narwhal (*Monodon monoceros*), bowhead (*Balaena mysticetus*) and beluga whales (*Delphinapterus leucas*) and polar bear (*Ursus maritimus*; Laidre and Regehr, 2017). All 7 endemic species represent important subsistence resources for Indigenous Peoples in the Arctic. The cetaceans (beluga, narwhal, and bowhead whales) are not sea-ice obligates, unlike the seals, polar bears, and some walrus stocks that require sea ice for life history events

(e.g., breeding, hunting, rearing young; Kovacs et al., 2011; Laidre et al., 2015).

The only Arctic endemic baleen whale, the bowhead whale, is strongly ice-associated. It is physically well adapted to this environment as it has no dorsal fin and a very strong skull, enabling it to break through ice >1 m thick. Thus bowhead whales are able to thrive in heavy ice conditions (George et al., 1989; Burns et al., 1993). The species is exceptionally long lived (maximum > 200 years), slow to reproduce (3–4 year birthing interval with 13–14 month gestation) and primarily forages on macrozooplankton in the water column, as well as near bottom on epibenthic organisms (Koski et al., 1993; Lowry, 1993; George et al., 1999). Historically, there is evidence that bowhead whale movements spanned the Canadian Arctic archipelago (Alter et al., 2012). Currently, 4 management stocks recognized by the International Whaling Commission inhabit the Arctic year-round, moving from the high Arctic in summer to the low Arctic in winter (Burns et al., 1993; Kovacs et al., 2020; Givens and Heide-Jørgensen, 2021). Ice dynamics also largely determine the annual cycle of bowheads as they begin to move into summer areas with the formation of leads in the sea ice (e.g., Citta et al., 2015; Insley et al., 2021). Threats and stressors to the population include the increase of shipping activity associated with sea-ice loss (Logerwell and Skjoldal, 2019) and climate impacts on prey quality and quantity that remain difficult to predict (George et al., 2015; Moore, 2016).

The 2 toothed or odontocete whales that annually reside in the Arctic waters are the beluga and narwhal, both of which have evolved with no dorsal fin like the bowhead whale and have migrations associated with sea ice. Beluga whales are subdivided into 29 management populations distributed circum-Arctic, ranging from being entirely sub-Arctic, to mixed, to entirely Arctic (Jefferson et al., 2015; NAMMCO, 2018; Stafford et al., 2018). The influence of sea ice on beluga migration and distribution has been observed in several populations (e.g., Heide-Jørgensen et al., 2010; Hornby et al., 2016). However, the beluga-sea ice association is complex, showing variability across populations, as well as preference of ice concentration depending on size and sex demographics (e.g., Loseto et al., 2006; Hauser et al., 2017) and on season (e.g., Asselin et al., 2011; Hornby et al., 2016). The variability of sea-ice preference and/or avoidance reflects the indirect relationship between beluga and sea ice through sea-ice-associated prey (i.e., Arctic cod; Choy et al., 2020) or predator avoidance.

Narwhals have a more restricted distribution than beluga whales, with 12 populations occupying the Eastern Canadian waters and east and west Greenlandic waters and extending into the Russian-Siberian Seas (NAMMCO, 2018). Largely because of their more restricted distribution to areas associated with sea ice, narwhals are considered one of the most at-risk species in the Arctic (Laidre and Regehr, 2017). The narwhal has demonstrated sea-ice associations, such as seasonal migrations that are related to the retreat and advance of sea ice in Baffin Bay-Davis Strait (Laidre and Heide-Jørgensen, 2005). Threats and

stressors to both odontocete whales are either directly related or are associated with the impacts of sea-ice loss and climate change that include habitat loss, shifts in prey quality and quantity, exposure to shipping activity, increased predation (i.e., killer whales) and competitors, and exposure to contaminants from local sources (i.e., with increased industry) or distance sources with long range transport.

Of the pinnipeds, the ringed and bearded seals and some walrus populations are ice-associated year-round. All 3 pinniped species rely on the ice as a platform for birthing and moulting in the spring (although walrus are also known to moult on land). For ringed seals, however, the sea ice, particularly stable fast ice, is vital for building lairs of snow and ice to protect their newborn pups from weather and predators during a relatively long period of neonatal dependence. In addition, the sea ice is an important platform for bearded seals and walrus, allowing them access to rich benthic communities over shallow pelagic waters (Kovacs et al., 2011).

Finally, most aspects of polar bear ecology and life history depend on the sea ice (Wiig et al., 2015; Regehr et al., 2016; Brown et al., 2018). In particular, their ability to hunt their primary prey species, the ringed seal, whose rich fat allows them to survive in the Arctic, is entirely dependent on sea ice. In addition, their extensive home ranges are largely a function of sea ice facilitating their movement.

Southern Ocean

For seabirds in the Southern Ocean (Billerman et al., 2020), several penguin species largely or completely depend on the seasonal sea-ice areas. The emperor penguin (*Aptenodytes forsteri*) is fully dependent on sea ice, as virtually all of its colonies breed on the sea ice during winter with chicks ready to fledge once the sea ice breaks up, while adélie (*Pygoscelis adeliae*) and chinstrap penguins (*P. antarctica*) move between open ocean and sea-ice areas throughout the year. Gentoo penguins (*P. papua*) are more restricted to the coastal areas. Among tubenosed seabirds the sea ice is of critical importance to several of the endemic petrels, such as the Antarctic petrel (*Thalassoica antarctica*), snow petrel (*Pagodroma nivea*), southern fulmar (*Fulmarus glacialisoides*), southern giant petrel (*Macronectes giganteus*), and Wilson's storm-petrel (*Oceanites oceanicus*). They feed on Antarctic krill, other zooplankton, mesopelagic fishes, and squid that associate with the sea ice and icebergs. Throughout their range, they are followed by predatory and scavenging south polar skuas (*Catharacta maccormicki*) and Antarctic skuas (*C. lonnbergi*). Loss of sea ice will impact all of these species by loss of habitat and reduced populations of prey.

The solid fast-ice provides a stable substrate for 4 species of obligate ice-breeding pinnipeds: the crabeater seal (*Lobodon carcinophagus*), the Weddell seal (*Leptonychotes weddellii*), the leopard seal (*Hydrurga leptonyx*), and the Ross seal (*Ommatophoca rossii*; Bengtson et al., 2011; Bester et al., 2017; Southwell et al., 2008a; Southwell et al., 2008b; Southwell et al., 2008c). All 4 species breed in the austral spring (September–November; Schreer et al., 1996;

Laws et al., 2003) and fully depend on sea ice for their breeding success (Bester and Odendaal, 2000; EGS, 2008). Crabeater and Weddell seals inhabit the sea-ice covered areas year-round, foraging between the continent and the ice edge (Burns et al., 2004; Heerah et al., 2013; Boehme et al., 2016; Nachtsheim et al., 2017). Leopard seals are most commonly found in and around the outer fringes of the pack ice or close to the Antarctic Continent, following the expansion and contraction of the pack ice while foraging (Bester et al., 1995; Rogers et al., 2005). Ross seals have been tracked feeding in the pelagic area beyond the ice edge in austral winter but return to pack-ice regions for summer breeding (Blix and Nordøy, 2007). The southern elephant seal (*Mirounga leonina*) and the Antarctic fur seal (*Arctocephalus gazella*) breed almost exclusively on Antarctic and Subantarctic islands but seasonally migrate to the sea ice to forage. Adult male southern elephant seals have been shown to move into pack-ice areas during foraging trips, while females forage along the ice edge (Bailleul et al., 2007; Hindell et al., 2017). Post-breeding, Antarctic fur seals perform southward trips from sub-Antarctic islands to the ice edge during austral winter (Arthur et al., 2016).

The Antarctic minke whale (*Balaenoptera bonaerensis*) is strongly associated with sea-ice habitats, with highest densities occurring along the ice edge (Williams et al., 2014; Herr et al., 2019). They also feed under the ice at high rates (Friedlaender et al., 2014) and can be found up to 500 km into the pack-ice areas (Herr et al., 2019). During summer, the receding sea ice is a predictable foraging area for humpback whales (Cotté and Guinet, 2012; Andrews-Goff et al., 2018; Megaptera novaeangliae). Acoustic studies also demonstrate that the seasonal sea-ice zone acts as a main habitat for migrant and nonmigrant Antarctic blue whales (*Balaenoptera musculus intermedia*; Sirovi et al., 2004; Thomisch et al., 2016; Shabangu et al., 2017) which are listed as critically endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species. Despite no clear association with the ice, all other baleen whale species migrating to the Antarctic waters, that is, fin whales (*Balaenoptera physalus*), sei whales (*Balaenoptera borealis*), and Southern right whales (*Eubalaena australis*), depend on krill as their major prey resource in their summer feeding grounds. Populations still recovering from commercial whaling of the 20th century are starting to return to Antarctic feeding grounds, e.g. Southern Hemisphere fin whales (Herr et al., 2016). Replenishing their energy budgets for the remainder of the year during the austral summer feeding season is critical for breeding success of baleen whales (Bengtson-Nash et al., 2018).

Among the toothed whales, orcas (*Orcinus orca*), and some species of beaked whales (Ziphiidae) occur in the Antarctic sea-ice area. Four ecotypes of orcas, exhibiting different ecology and habitat preferences are distinguished in Antarctic waters (Pitman et al., 2007; Pitman and Ensor, 2003; Durban et al., 2017) with distributions varying from circumpolar to regional and open water to leads deep within heavy sea ice (e.g., around McMurdo Sound even in austral winter, Gill and Thiele, 1997), as

well as along the fast-ice edge (Eisert et al., 2014). Prey species also vary among those ecotypes. Some prey on Antarctic minke whales, ice-associated seal species or penguins, whereas others mainly feed on fish with specializations for Antarctic toothfish (Ainley et al., 2009; Ainley and Ballard, 2012; *Dissostichus mawsoni*; Pitman and Ennor, 2003), as well as smaller fish, such as Antarctic silverfish (*Pleuragramma antarcticum*) and other notothenids (Lauriano et al., 2007; Krahn et al., 2008). Of the beaked whales, only the Southern bottlenose whale (*Hyperoodon planifrons*) is known to occur in sea-ice covered waters year-round (MacLeod et al., 2006; Boyd, 2009). Arnoux' beaked whale (*Berardius arnouxii*) occurs in association with the ice edge and may penetrate into ice-covered waters in austral summer (Taylor, 1957; Balcomb, 1989; Hobson and Martin, 1996; Friedlaender et al., 2010).

5. Provisioning services

5.1. Harvesting

5.1.1. Arctic

About 4 million people live across the Arctic, with Indigenous populations representing 5–90% of the population, depending on the region (Bogoyavlenskiy and Siggner, 2004; Larsen and Fondahl, 2015; Statistics Canada, 2017). Inuit and their ancestors have harvested marine mammals, fish, and invertebrates for millennia for subsistence and cultural purposes (e.g., Friesen, 2002, 2004). Many of the species depending on ice algae as their energy source and on sea ice as part of their life cycle are key subsistence species for Inuit (e.g., Kuhnlein et al., 2001). Harvested marine mammal species include ice-associated species such as seals, beluga and bowhead whales, narwhal, walrus and polar bear, with regional variations in the importance of each species. Quantitative information on past Arctic harvesting and fishing records is sparse, patchy, and likely excludes much of the small-scale subsistence fisheries. Separating harvesting of sea-ice ecosystem-dependent species from pelagic ecosystem-driven species from these limited records is almost impossible. In many cases, the two are tightly linked, for example, through the energy transfer via Arctic cod and sea-ice amphipods (see Section 4).

Commercial harvesting of marine species started centuries ago in some areas of the Arctic such as the Barents Sea (Haug et al., 2017). Marine commercial finfish fisheries are quite variable across the Arctic and impacted by short fishing seasons, sea-ice cover, dangerous navigation routes, and the geographic separation from populated areas increasing operating cost (e.g., Zeller et al., 2011; Tai et al., 2019). Zeller et al. (2011) provided reconstructed small-scale fisheries (commercial and subsistence) catch estimates of over 950,000 t for Russia, United States, and Canada combined for the 1950–2006 time period. Their reconstructed catch declined from 24,100 t y⁻¹ in 1950 to 10,200 t y⁻¹ by the mid-2000s. The reasons for this trend vary by country and are in many cases uncertain. In Alaska, for instance, commercial catches have been in decline since the early 1980s, while subsistence catches have increased (Booth and Zeller, 2008). In Russia, a fisheries decline in the first half of the 1900s is attributed to

intense pollution but also linked to massive demographic changes, leaving mostly Indigenous Peoples and small-scale subsistence fisheries behind (Zeller et al., 2011). In Canada, commercial fisheries have grown in importance over the last decades, especially fisheries of turbot, shrimp, and Arctic Char (Government of Nunavut, 2016).

O'Garra (2017) estimated that commercial fisheries can yield an economic benefit of US\$1.26 billion per year across the Arctic and that the value of subsistence-based activities is much smaller than extractive industries, but given that these activities benefit a rather small human population, their value, per capita, is very high. Despite cumulative threats that likely reduce catch potential, fisheries in Arctic regions are expected to increase with the changing climate as access increases (Cheung et al., 2011; Tai et al., 2019). However, increased fisheries may also put the fragile Arctic marine ecosystems, including the declining sea-ice-based ecosystems at risk (Burgass et al., 2019) and needs to be approached cautiously. In a proactive and precautionary approach to future fishing activities in the high Arctic seas, an international agreement was drawn up and ratified by participating countries and Indigenous organizations in 2018/2019, preventing unregulated fisheries until adequate scientific information is available to inform management measures.

5.1.2. Southern Ocean

Exploratory and established commercial fisheries in the Southern Ocean are managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) following a precautionary ecosystem approach (CCAMLR, 1980). Fisheries target finfish and Antarctic krill. In 2018, the total fishery catch biomass in the Southern Ocean equalled about 25% of the Mediterranean Sea catch (FAO, 2020). Thus, the provisioning ES of Antarctic marine living resources is on the same order of magnitude as stocks harvested in densely populated areas. The fishery on Antarctic krill is by far the largest in the Southern Ocean and has significant economic value. Its mean annual gross value product has been estimated at about US\$ 70 million (Kawaguchi and Nicol, 2020). Krill is used for human consumption, aquaculture, chitin, enzymes, krill oil, and fishing bait. The development of products for pharmaceutical applications and aquaculture is a likely factor driving future growth in the krill fishing industry (Nicol and Foster, 2016). Hence, the fishery on Antarctic krill has intensified in the Southern Ocean over the past 2 decades and is expected to grow further. The Antarctic krill fishery of the Soviet Union was the largest in history, and after it collapsed in 1993, catches stabilized around 100,000 t y⁻¹, but in the past decade, they have been steadily rising (**Figure 6a**). The fishery today is concentrated in the Atlantic sector (CCAMLR area 48), where catch levels have recently surpassed levels of the Soviet fishery in the 1980s, reaching well over 400,000 t y⁻¹. Since 2013, Antarctic krill catches have regularly reached precautionary trigger levels in several subareas, leading to local closures of the fishery. This triggering is a sign that the limits for localized sustainable harvest set by CCAMLR are becoming more relevant.

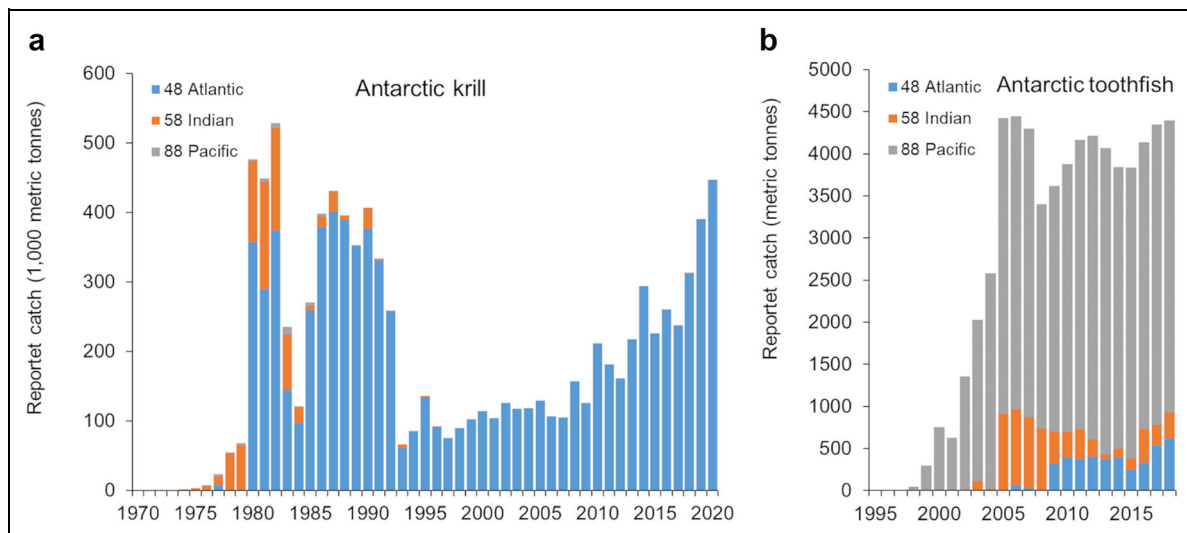


Figure 6. Commercial catches for Antarctic toothfish and krill. (a) Reported commercial catches in metric tonnes in different regions of the Conservation of Antarctic Marine Living Resources (CCAMLR) statistical area shown in **Figure 2b** for (a) Antarctic krill *Euphausia superba* between 1973 and 2020 (Catches in years 1973 and 1974 were very low), and (b) Antarctic toothfish (*Dissostichus mawsoni*) between 1998 and 2019 (CCAMLR, 2019; SC-CCAMLR, 2020). DOI: <https://doi.org/10.1525/elementa.2021.00007.f6>

Of the finfish harvested in the Southern Ocean, Antarctic toothfish (*Dissostichus mawsoni*) has received growing attention in recent decades. This slow-growing fish reaches a high market value which has been increasing at high rates (Grilly et al., 2015). Unlike its sub-Antarctic congener Patagonian toothfish (*Dissostichus eleginoides*), the distribution of Antarctic toothfish largely coincides with the Antarctic sea-ice zone. After initial growth in the early 2000s, the fishery has stabilized at a level of about $4,500 \text{ t y}^{-1}$ (**Figure 6b**), reflecting the precautionary catch quota set by CCAMLR. However, the high per-kilogram price of toothfish (Grilly et al., 2015) has attracted illegal, unreported, and unregulated fishing vessels to the Southern Ocean (primarily targeting *D. eleginoides*), adding uncertainty to the true amount of biomass harvested. Currently, the main catch area for Antarctic toothfish is the Ross Sea (CCAMLR area 88), and the majority of the Antarctic toothfish is taken by licensed vessels.

While CCAMLR is considered a pioneer in fisheries management, applying one of the most thorough ecosystem-based marine resource managements on the planet, the ability of CCAMLR to meet its precautionary goals has also been questioned by the scientific community. As stocks of Antarctic krill have been suggested to decrease in parallel with sea-ice decline (Atkinson et al., 2004; Atkinson et al., 2019), concerns have been raised whether current management procedures are able to adapt to the combined effects of the fishery and climate change (Schiermeier, 2010; Flores et al., 2012; Ainley and Pauly, 2014; Meyer et al., 2020; Watters et al., 2020). Regarding Antarctic toothfish, knowledge of both critical population parameters and its role in the ecosystem has been argued as too limited to justify CCAMLR's current catch limits (Abrams, 2014; Ainley and Pauly, 2014; Abrams et al., 2016), while CCAMLR attests that its adaptive management is well capable to address shortcomings

due to insufficient knowledge (Hanchet et al., 2015). These discussions have been taken up by fishing companies, nongovernmental organizations, and governments both in expert and public fora, raising significant media attention. This attention highlights the high societal importance of Antarctic marine living resources in spite of their globally limited economic value. Furthermore, it demonstrates the high relevance of both provisioning ES and cultural ES of the Antarctic sea-ice habitat and the constant need to balance between them.

5.2. Bioprospecting and other biological resources

Bioprospecting, the search for novel molecules for commercial use, from polar organisms is an active area of research. Diatoms, the dominant members of bottom-ice algal communities (Leu et al., 2015; van Leeuwe et al., 2018), and bacteria show relevant adaptations to cold environments, for example, the production of polyunsaturated fatty acids to maintain membrane fluidity and cold-adapted enzymes and antifreeze proteins which are of interest to the food-preservation industry (Morgan-Kiss et al., 2006; Christner, 2010; de Pascale et al., 2012). Phytoplankton, including diatoms, and polar microbes are already a source of potential pharmaceuticals and other compounds (de Pascale et al., 2012; Abida et al., 2013). A number of diatoms from the genus *Haslea* (e.g., *H. ostrearia*) increasingly have been found to produce blue marenine or marenine-like pigments, which are valuable to the food and beauty industries (Gastineau et al., 2014). Antarctic krill is also increasingly being used for pharmaceutical products.

6. Regulating services

6.1. Radiative transfer

While sea-ice loss strongly contributes to changes in albedo (Perovich et al., 2007) and amplified warming

(Arctic amplification; e.g., Koenigk et al., 2020), and sea ice and especially snow regulate light transmission and thus the light availability for phytoplankton (Light et al., 2008; Nicolaus et al., 2012), we regard these as sea-ice system services and will not discuss them in detail here. However, ice algae also absorb sunlight entering the sea ice and modify the spectral distribution and thus the quality of light reaching the ocean water below (e.g., Legendre and Gosselin, 1991; Perovich et al., 1998; Belzile et al., 2000; Mundy et al., 2007; Campbell et al., 2015; Kauko et al., 2017). Both field (Mundy et al., 2014) and modeling studies (Castellani et al., 2017) have indicated phytoplankton growth regulation due to ice-algal shading.

6.2. Organic carbon cycling (biological carbon pump)

With the onset of ice melt, sea-ice algae are released into the water column, where they are either consumed by grazers or their carbon biomass sinks to the deep ocean. The rate of export, and hence the amount of carbon reaching the seafloor, is determined by the algal composition and aggregation status (e.g., Tedesco et al., 2012; Rogers et al., 2020; Dybwad et al., 2021) and time of ice melt (Riebesell et al., 1991; Norkko et al., 2007; Tedesco et al., 2012; Wing et al., 2012; Lalande et al., 2019). In the Arctic and Southern oceans, the highest carbon fluxes are linked to bloom events along the marginal ice zone, including pelagic ice edge blooms (Ducklow et al., 2008; Cai et al., 2010a; Lalande et al., 2019).

In the Arctic, these events are best described for the shelf regions of the Kara ($6 \text{ mg C m}^{-2} \text{ d}^{-1}$), Laptev ($35 \text{ mg C m}^{-2} \text{ d}^{-1}$) and Barents Seas ($32 \text{ mg C m}^{-2} \text{ d}^{-1}$; Cai et al., 2010a, and references therein). Fluxes in the Central Basins are much lower, with rates of $2.4 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Cai et al., 2010a). In comparison, the Central Arctic Ocean is oligotrophic and considered a recycling system. Here, any organic carbon released from sea ice is efficiently remineralized in the upper water column and, as a result, it is unlikely to reach the seafloor. In the Arctic, carbon export also depends on episodic fluxes. In spring, rapid warming due to snow and ice melt may result in the sudden release of bottom-ice algal communities, like the ice diatom *Nitzschia frigida* (Campbell et al., 2015). These events often coincide with the formation of aggregates that eventually sink out of the euphotic zone and provide bursts of carbon export (Lalande et al., 2019). In addition, sympagic algae (e.g., centric diatoms *Melosira arctica* in the Arctic and *Berkeleya adeliensis* in the Antarctic) may form large colonies that can extend for several meters in the underlying seawater (van Leeuwe et al., 2018). The release of these colonies can result in locally significant pulses of carbon with an estimated deposit range of $1\text{--}156 \text{ g C m}^{-2}$ in one season (Boetius et al., 2013). Also, floating aggregates consisting of multiple species may form in the stratified waters under Arctic sea ice in late spring–summer. Following detachment from the ice or loss of buoyancy, sinking of these mats and aggregates represents an efficient pathway for carbon to the deep ocean and provision of a food resource to benthic consumers (Assmy et al., 2013; Boetius et al., 2013). This process can be

significantly enhanced by cryogenic gypsum (Wollenburg et al., 2018; 2020).

Southern Ocean sedimentation records in the vicinity of sea ice are more sporadic and show high regional and seasonal variability. During spring, export rates in the Weddell Sea averaged around $60\text{--}72 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Cai et al., 2010a), near the Ross Sea daily averages were $120 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Buesseler et al., 2003).

6.3. Sea-ice inorganic carbon pump

As seawater freezes, dissolved inorganic carbon (DIC, referring to the sum of carbonate and bicarbonate ions and dissolved CO_2) is expelled along with salts, releasing brine to the ocean and potentially contributing to global deep and intermediate water formation (Hoppema, 2004; Murakami et al., 2020). Initially, as seawater begins to freeze, DIC is released both to the atmosphere and the underlying water, but as the ice thickens, further DIC rejection is mainly downward, into the water (e.g., Rysgaard et al., 2007; Fransson et al., 2011; Fransson et al., 2013; Miller et al., 2011; König et al., 2018). Measurements of DIC and CO_2 under the ice have confirmed that concentrations increase during winter (e.g., Miller et al., 2011; Shadwick et al., 2011; Fransson et al., 2017). However, the importance of this vertical DIC transport on a global scale is uncertain. Modeling studies of carbon export with sea-ice brine formation (Grimm et al., 2016; Moreau et al., 2016) showed that 2–7% of the DIC mobilized by sea ice every year is exported to the deep ocean, which amounts to a few $\text{Tg C m}^{-2} \text{ y}^{-1}$, less than 1% of the global oceanic CO_2 uptake. However, deepwater formation is highly regional, and in areas of sustained sea-ice growth, such as coastal polynyas and the marginal ice zone, sea-ice brine rejection could result in substantial DIC export and alkalinity transport, contributing to local ocean acidification.

6.4. Impacts on the atmosphere

Extreme environmental conditions within the sea-ice habitat induce algal production of the osmolyte and cryoprotectant dimethylsulphoniopropionate (DMSP; Stefels et al., 2018). Sea ice hosts prolific DMSP producers (van Leeuwe et al., 2020). DMSP is the precursor of the climate-active gas dimethylsulfide (DMS). Upon sea-ice melt, DMS is released from the large pool of DMSP in sea-ice organisms. After emission to the atmosphere, the oxidation of DMS affects atmospheric chemistry, potentially promoting the formation of new aerosol particles and cloud condensation nuclei in the Arctic (Abbatt et al., 2019). Concentrations of both DMS and DMSP are 3 orders of magnitude higher in sea ice than in surface waters (Stefels et al., 2007; Tison et al., 2010), and sea-ice melt zones are without doubt the areas with highest DMS concentrations (Lana et al., 2011; Levasseur, 2013; Stefels et al., 2018; Webb et al., 2019). Recent modeling studies indicate a 20% contribution by ice algae to the total Arctic ocean DMS production and emissions; in late spring, sea-ice algae may even be the sole source of sea-to-air DMS flux (Abbatt et al., 2019; Hayashida et al., 2020).



Figure 7. Photographic selection of cultural services. (a) Polar bear hide hung up for drying, Ulukhaktok, NWT, Canada; (b) Inuit tapestry, Pangnirtung airport, Nunavut, Canada; (c) sea-ice sampling in the Southern Ocean, Antarctica; (d) expedition cruise tourism, vessel entering Lemaire Channel, Antarctic Peninsula. Photo credits: DL (a); NS (b, c); Finn Steiner, Quark Expeditions (d). DOI: <https://doi.org/10.1525/elementa.2021.00007.f7>

In addition, at the sea-ice surface, brine is suggested to trigger halogen oxidation. Reaction with sunlight leads to the formation of halogen radicals which can then cleanse the atmosphere of ground-level pollutants by reacting with ozone and a variety of organic and inorganic compounds, including SO_2 and mercury (Douglas et al., 2008; Shepson et al., 2012). Several events have been recorded where ground level ozone and mercury are depleted, probably linked to sea-ice emissions of bromine and iodine (Sturges et al., 1992; Saiz-Lopez et al., 2015).

6.5. Ocean fertilization

The Southern Ocean and central Arctic Ocean are remote from land masses, and therefore, the efficiency of the biological pump of carbon in these waters is constrained by the scarcity of iron, a key nutrient for algal growth. Work carried out at both poles over recent years has demonstrated that sea ice carries exceptionally high iron content compared to the ocean below, or the snow on top (Tovar-Sánchez et al., 2010; Kanna et al., 2014; Lannuzel et al., 2016). In spring, sea-ice melt stratifies the upper ocean and releases iron and organic ligands in the sea-ice zone (Lannuzel et al., 2016; Genovese et al., 2018), which can support highly productive phytoplankton blooms at retreating ice edges, particularly in the Southern Ocean (Strutton et al., 2000; Smith and Comiso, 2008). The effect

of these fertilization events are particularly striking in the marginal ice zone of the Southern Ocean, where Fitch and Moore (2007) estimated that sea-ice edge blooms occupied at least 17–24% of the marginal ice zone in summer in the Southern Ocean; such blooms have also been identified in the Arctic (Tovar-Sánchez et al., 2010). Seasonal sea ice therefore serves as a temporary reservoir of micro-nutrients, providing an ES to the ocean.

7. Cultural services

7.1. Intangible connections to sea ice and sea-ice – associated species

Provisioning and cultural services in the Arctic are tightly connected (Huntington et al., 2013). Indeed, country foods (also called “traditional foods” being all the plants and animals harvested from local environments) are a critical part of Inuit diet in the coastal regions of, for example, Greenland, Canada, Alaska, and Chukotka. These foods also hold high spiritual, cultural, traditional, and social values (ICC-Canada, 2008; ICC-Alaska, 2015; AMAP, 2017, 2018; **Figure 7a, 7b**). As stated by the Inuit Circumpolar Council of Alaska (2015), “Our traditional foods are much more than calories or nutrients; they are the lifeline throughout our culture and reflect the health of an entire ecosystem.” Inuit continue to actively use the ocean and sea ice as did their ancestors for thousands of years. The

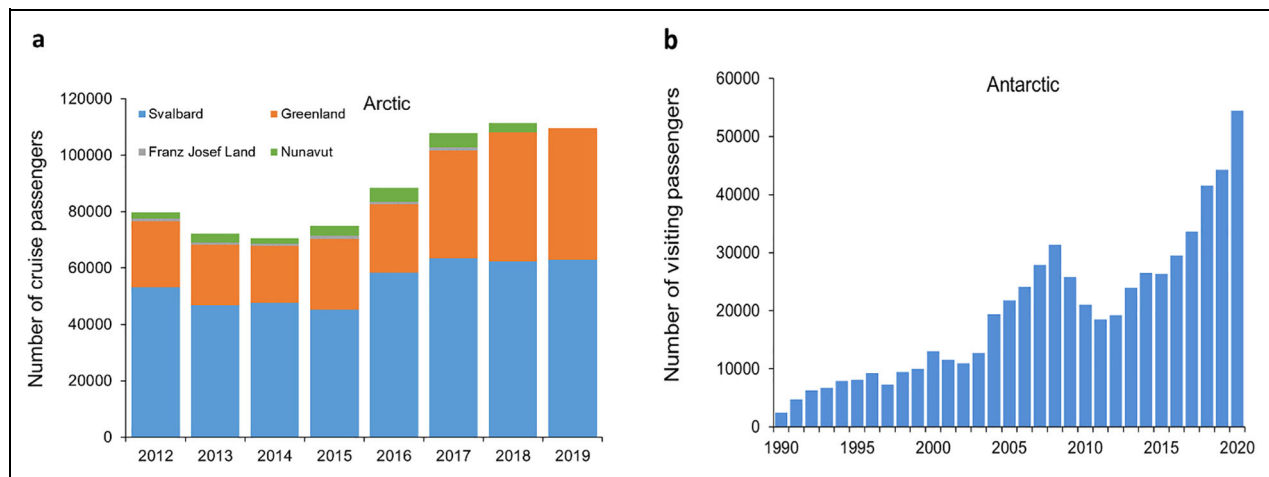


Figure 8. Tourism development in the Arctic and Antarctic. (a) Cruise passenger numbers from 2012 to 2019 for Svalbard, Greenland, Franz Josef Land, and Nunavut. These statistics were compiled by the Association of Arctic Expedition Cruise Operators (AECO) using the following sources: Visit Greenland, Statistics Greenland, Governor of Svalbard, Russian Arctic National Park Authorities, Government of Nunavut, Nunavut Tourism, and Bob Headland of Scott Polar Research Institute. Data were not included for Franz Josef Land in 2018 and 2019 or for Nunavut in 2019. (b) Number of passengers visiting the Antarctic Peninsula since the 1989–1990 austral summer season as recorded by the International Antarctic Tourism Organization (IAATO, 2021). DOI: <https://doi.org/10.1525/elementa.2021.00007.f8>

connection to the land and ice gives Inuit a great sense of pride, well-being, and connection to their cultural roots (ICC-Canada, 2008). Furthermore, Inuit life in the Arctic is dependent on movement. In winter, this movement (including recreational activities, such as taking walks, ski-dooing) takes place on the sea ice that surrounds and connects Inuit communities, as sea ice is their highway and key access to marine resources. In addition to food, hides, furs, and bones of harvested species are used for clothing, jewelry, carvings, and other art and utility items that contribute to cultural as well as provisioning services (AMAP, 2017, 2018).

Inuit around the Arctic have developed, over millennia, a deep understanding of sea ice and wildlife—often related to knowledge and skills for fishing and hunting—which is still passed on from Elders to younger generations (e.g., Krupnik and Jolly, 2002; ICC-Canada, 2008; Eicken, 2010; Huntington et al., 2016; AMAP, 2017, 2018). For instance, younger Inuit are trained to recognize a variety of ice types, each with their unique features, as well as the different risks associated with the seasons, such as being able to identify thin ice or ice edges that may break off (ICC-Canada, 2008). Inuit have also been witnessing changes in sea-ice dynamics over the past decades as related to climate change (Analok et al., 2001; Nickels et al., 2005). Inuit Qaujimagatuqangit (Inuit knowledge) provides a wealth of information to help understand ongoing and future changes, and the interweaving of Inuit knowledge with academic science can lead to more comprehensive assessments of climatic changes (Laidler, 2006). For example, Inuit Elders have observed extensive changes in sea ice, including a faster receding floe edge, thinner ice, and later ice formation in the fall, creating unsafe conditions (Analok et al., 2001; Huntington et al., 2016; Steiner et al., n.d.).

7.2. Art, scientific research, and exploration

The aesthetic value of landscapes perceived as pristine or unique is an important cultural service, inspiring art, photography and film, as well as naturalists, which in turn are key draws for tourism (see below). Both Arctic and Antarctic sea-ice scapes are remote, harsh, and difficult to access. They tend to be more pristine than other locations, as they are more isolated from the majority of human activities. This isolation is likely more so for the Antarctic, where permanent structures are limited to scientific research stations, while many of the Arctic coastal areas are inhabited by both Indigenous and non-Indigenous Peoples. The icy poles have been an inspiration for scientific research (Figure 7c) and exploration for centuries, ranging from the adventurous early explorations on foot, sled or ship, to fixed, permanently occupied research stations and sophisticated research and exploration vessels. In the Southern Ocean, the Antarctic Peninsula, rich in wildlife and human history, hosts a large number of research stations (e.g., Deininger et al., 2016). Due to the extreme conditions it represents, sea ice is also regarded as a unique proxy for extraterrestrial life (e.g., Deming and Eicken, 2007; Martin and McMinn, 2018).

7.3. Sea-ice-related tourism

7.3.1. Arctic tourism

Sea ice and ice-dependent wildlife, such as polar bears, walrus, and narwhals, contribute to the allure of the Arctic as a tourist destination, and there has been an increase in cruise tourism in the Arctic in recent years (Têtu et al., 2019). Figure 8a shows cruise passenger numbers for Svalbard, Greenland, Franz Josef Land, and Nunavut from 2012 to 2019. (As cruise passengers commonly travel in more than one region during the same voyage, these regional numbers cannot be totaled) Passenger numbers

for most of the Arctic regions are still relatively small, and for some locations, one or few larger cruise vessels may have a significant impact on the total numbers.

Sea ice can also pose a challenge for operations. This challenge is particularly true for expedition cruise vessels, which are typically smaller vessels (below 500 passengers) that travel to more isolated and remote regions. Expedition cruise operations are less reliant on ports and infrastructure compared to larger conventional cruise vessels, which allows for more flexibility in itineraries to adjust to any challenges arising from uncertain sea-ice conditions. Expedition cruising also typically includes excursions and shore landings with tender boats, which can be affected by the presence and movement of sea ice. Therefore, the planning of voyages is influenced by a combination of biological factors (e.g., presence of wildlife) and physical factors impacting hazards to tourism operations. To ensure responsible, and safe Arctic cruise tourism with mutual benefits for operators and destinations and minimal negative environmental impact, the Association of Arctic Expedition Cruise Operators (AECO) develops tools and guidelines that the members must follow, in addition to mandatory national and international regulations for cruise vessels. Regarding sea ice, AECO's operational guidelines (Arctic Expedition Cruise Operators, 2021) include information on conducting safe tender boat operations in drift and fast ice and prohibit expedition cruise vessels from breaking fjord ice during spring and summer in order to mitigate the negative impact on Arctic species depending on the sea ice for feeding and breeding.

7.3.2. Antarctic tourism

Antarctic tourism began in the late 1950s with a few hundred visitors on chartered ships and yachts. With 7 tour operators by 1990 active in Antarctica, the Antarctic Treaty Parties began seeking more information about tourism activities. IAATO was formed to help coordinate safety measures, environmental protection, and ship scheduling, coincidentally the same year (1991) that the Protocol on Environmental Protection to the Antarctic Treaty was signed. Today, nearly all visitors to the Antarctic do so under the auspices of IAATO with operations in accordance with the Antarctic Treaty System subscribing to the principle that their planned activities will have “no more than a minor or transitory impact on the Antarctic environment.” Data on IAATO activities are reported annually to the Antarctic Treaty Consultative Meeting.

IAATO growth periods (**Figure 8b**) were driven by improved technology and the availability for charter of ice-suitable vessels as a result of the breakup of the Soviet Union (1990s) and a period of expansion and increase in disposable income among the traveling public in major economic countries, such as the United States, coinciding with a series of high-profile publications and television documentaries (e.g., the British Broadcasting Company's “Life in the Freezer”; early 2000s). Following the 2007–2008 peak, numbers declined due to the world economic crisis and the International Maritime Organization ban on the use and carriage of heavy fuel oil in Antarctica. Since

2011, Antarctic tourism has been booming, reaching 74,400 visitors in the 2019–2020 austral summer season, with 99% on 70 different vessels, including yachts.

The vast majority (98%) of IAATO's Antarctic travelers visit the Antarctic Peninsula and its off-lying islands. The season depends on sea-ice extent and may begin as early as late October and can extend into early April. Apart from general advance scheduling to observe restrictions on time, passengers and daily visits to visitor sites in accordance with Antarctic Treaty System and IAATO requirements, ship itineraries remain flexible to respond to changes in ice and weather conditions. Areas with a tendency to become ice-free earlier in the season see increased traffic and landings. Vessels are concentrated in the areas of Lemaire and Neumayer channels (Bender et al., 2016; **Figure 7d**) which offer abundant wildlife and relatively safe, easy access to landing sites and water-based activities. These activities, being closer to the water and floating sea and glacier ice, offer expedition staff an opportunity to teach visitors about glaciology, sea-ice ecosystems, and ice-dependent wildlife.

Typically, less than 1% of visitors travel annually by vessel to visit the Ross Sea and East Antarctica. These areas have a shorter window of opportunity for operations because of heavier ice conditions and have a longer transit time, but the draws are the sea ice, visits to historic huts and penguin colonies. A further 1% of all visitors travel to Antarctica's deep field areas from where excursions to emperor penguin colonies are possible. To date, little discernible impact from tourism is evident, but the potential for change, including cumulative impacts of human activities on wildlife and the environment, has caused concern, particularly for the Antarctic Peninsula where tourism is growing and where climate change is most marked. The management of tourism is a priority within the Antarctic Treaty Multi-Year Strategic Work Plan, while IAATO supports collaborative research and monitoring (e.g., IAATO-SCAR, 2019; Happywhale, 2021; MAPPPD, 2021; Oceanites, 2021).

7.3.3. Sea-ice—related tourism in the Sea of Okhotsk

Sea ice is also present in nonpolar areas such as the Sea of Okhotsk. More than 110,000 people/year, mainly from Asian countries (Denyer et al., 2019), visit Abashiri, one of the major tourist attractions in Northern Hokkaido, Japan, which offers drift-ice cruises, observations of megafauna (e.g., eagles perched on the ice, seals, humpback, sperm whales, and orcas), a sea-ice tower and a permanent museum, as well as a drift-ice festival and sea-ice beer. Discussions on future developments with respect to tourism and sea ice include a variety of platforms (e.g., ships, towers), considerations of the impacts of climate change in combination with tourism impacts such as pollution, plastic waste, and noise, but also the potential of knowledge co-production by researchers, Indigenous Peoples and tourists (or tourism companies).

8. Implications for human well-being

Assessing the sociocultural and economic implications of changes in sea-ice ecosystems and ES is a challenging

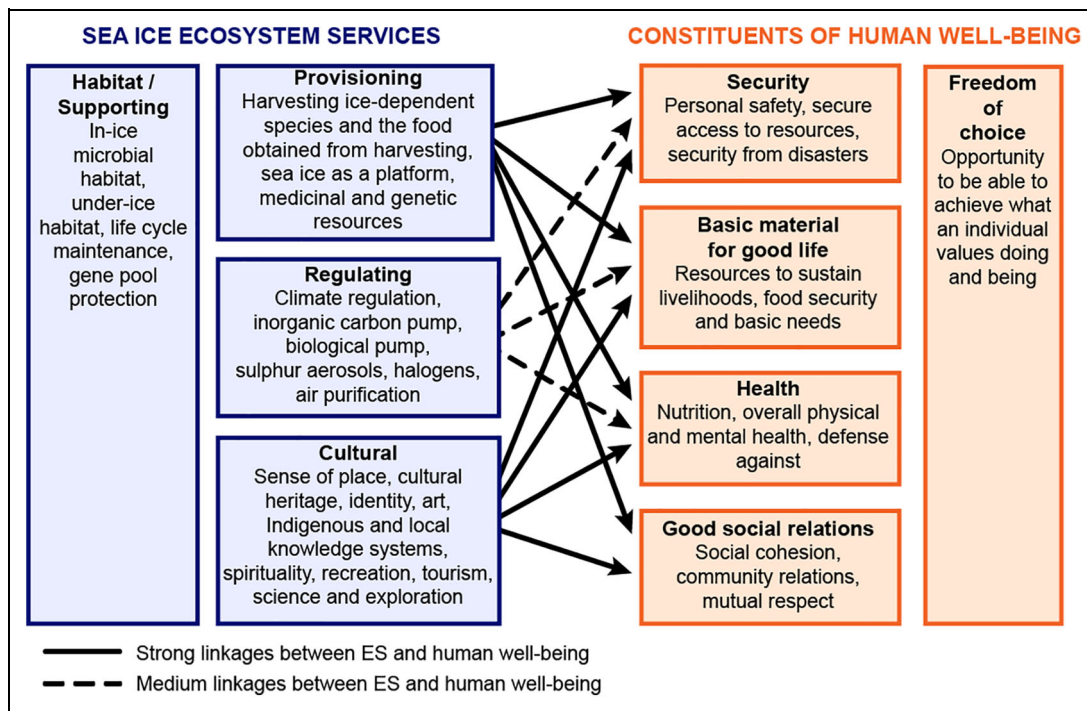


Figure 9. Link between sea-ice ecosystem services and constituents of human well-being. Link between sea-ice ecosystem services and constituents of human well-being (adapted from the Millennium Ecosystem Assessment; MEA, 2005). Habitat/Supporting services underlie other ecosystem services categories. Freedom of choice depends on, and influences, other constituents of human well-being and is not assessed here. DOI: <https://doi.org/10.1525/elementa.2021.00007.f9>

endeavour due to multiple linkages and feedbacks between ecosystem processes, services, and human well-being (Falardeau and Bennett, 2020). ES frameworks can help guide such assessments by providing a heuristic to assess social-ecological linkages (Tomich et al., 2010). The Millennium Ecosystem Assessment provides a foundational ES framework which can be adapted to explore how sea-ice ES support human well-being and assess the potential societal implications of changes in ES. The assessment decomposes human well-being into 5 dimensions: security, basic material for good life (including secure resources and income), health, good social relations, and freedom of choice (Figure 9; MEA, 2005; Scholes et al., 2010).

Habitat/supporting services underlie the supply of all of the other ES categories. Their contribution to human well-being is indirect but crucial for other services to be provided.

Regulating sea-ice ES contribute indirectly to human well-being, for instance, through carbon export to the deep ocean and atmospheric cleansing. Furthermore, regulating sea-ice services have a particularly wide breadth of beneficiaries, as the influence of the sea-ice ecosystem on inorganic and organic carbon and sulphur cycling will feed back to the global climate and thus have implications for the whole human population. The sea-ice decline changes the carbon system storage services (blue economy) provided in the region, which leads to both benefits and costs (Armstrong and Foley, 2018; Armstrong et al., 2019). One key example is that the increased inorganic carbon storage in the Arctic Ocean

and the continued ocean CO₂ uptake have resulted in a change of the ocean's carbonate chemistry, referred to as ocean acidification (AMAP, 2013, 2018), which can have detrimental effects on calcifying marine organisms but also stimulate primary production by some algal species (e.g., AMAP, 2018). Euskirchen et al. (2013) conducted a scoping study to determine the potential costs to society of losing global climate regulation services, especially the ice albedo effect that reflects solar energy back to space. They estimated that the annual cost of the thawing Arctic cryosphere alone could range between US\$19 and US\$448 billion by 2100 due to greater solar heat absorption from sea-ice loss, causing a positive feedback exacerbating climate change. While the present study focuses on the nonphysical impacts of sea ice, Euskirchen et al. (2013) provide an example for the monetary aspect associated with regulating services.

Provisioning sea-ice ES support human well-being in many tangible ways including through supporting food security, health, and income. In regions where food insecurity rates are at their highest, for instance, in 2017–2018 when food insecurity in Nunavut was up to 5 times higher than in other provinces of Canada (Tarasuk and Mitchell, 2020), country foods are vital to food security. Inuit consume a mix of market and traditional food products (Kuhnlein et al., 2004; Kenny et al., 2018), and there can be differences in the contribution of country foods to diets based on region, age, and sex (Kuhnlein et al., 2004; Lemire et al., 2015; Kenny et al., 2018). For instance, Kenny et al. (2018) found that in Nunavut in 2007–2008,

the contribution of country foods could range from 6.4% to 19.6% of total diet energy, depending on the region, and was at its highest among older adults (>40 years old). Even though the contribution of country foods to diet may seem rather small when averaged by region, their contribution to nutrient intakes is major (Kenny et al., 2018). Indeed, country foods are important sources of protein and micronutrients, including iron, niacin (vitamin B3), vitamin D, vitamin B6, vitamin B12, omega-3 polyunsaturated fatty acids, and selenium (an essential mineral that may offset the effects of methylmercury; Kuhnlein et al., 2004; Lemire et al., 2015; Kenny et al., 2018). However, some types of marine foods may also contain contaminants such as beluga meat that contained high methylmercury concentrations in Nunavik (Lemire et al., 2015). Improved knowledge of the health benefits of country foods and the specific sources of contaminants can help local/regional organizations formulate recommendations for country foods consumption. For instance, Nunavik Regional Board of Health and Social Services (2021) advises a balanced consumption of country food in the “Nunavik Food Guide,” given the critical importance of these foods for nutrition, as well as for identity and culture, while recommending that pregnant women and childbearing-age women limit their consumption of beluga meat specifically.

In addition to providing nutrition and health, provisioning services can support intangible aspects of human well-being, such as social cohesion and community relations, given that sharing systems related to fishing, hunting, and consuming country foods are a vital part of Inuit culture and a strong driver of food security (ICC-Alaska, 2015). Sharing can take different forms, including the sharing of fuel or equipment among community members to go harvesting, or sharing of country foods within and between communities (ICC-Alaska, 2015; Sheremata, 2018). Here, provisioning and cultural ES become closely intertwined.

Cultural sea-ice ES also support human well-being constituents in many different ways, including social relations, health, food security, physical security, and income. Some of the linkages between cultural services and human well-being are less tangible than others, such as how Inuit knowledge is important to safe travels on the sea ice (thus supporting security) or to track and harvest animals (thus supporting food security). Furthermore, the unique cultural and spiritual connections that Inuit have with sea ice and the ecosystem services associated with sea ice support mental well-being, so that sea-ice loss can have mental health impacts including anxiety and distress (Cunsolo Willow et al., 2013), particularly in communities that are already under pressure (e.g., from food insecurity and/or housing issues; Kanatami, 2018; Tarasuk and Mitchell, 2020). Other linkages between cultural services and human well-being are more tangible, including the income made by Inuit artists from selling their artworks and the economic benefits made by a variety of people involved in tourism activities in the Arctic, Antarctica, and some subpolar seas.

9. Trends, projections, and future social-ecological implications

Future climate projections consistently show that the thinning and decreasing spatial coverage of Arctic sea ice will continue throughout this century, although the pace of those declines will depend on the greenhouse gas emission rates (Pörtner et al., 2019; Tedesco et al., 2019). These changes include a significant decline in the amount of multiyear ice and potentially its complete loss in some regions (Kwok, 2018). Declines in Arctic sea-ice extent have been less dramatic in winter than in the summer, although the winter changes have accelerated and the timing of maximum ice cover is increasingly variable (Francis and Hunter, 2007; Brennan et al., 2020).

Long-term projections (e.g., up to 2100) of Antarctic sea-ice extent are much less confident due to the inability of many models to accurately reproduce observed seasonal cycles or multi-decadal trends. Confidence in sea-ice thickness and volume projections is even lower due, until recently, to the lack of large-scale snow and ice free-board observations (Fons and Kurtz, 2019). Currently available models from the Coupled Model Intercomparison Project v.6 show clear differences between forcing scenarios for predicted Antarctic sea-ice areas for the end of the 21st century, with projections of a decrease between 29% and 90% for austral summer (February) and 15% and 50% for winter (September; Roach et al., 2020).

Much work has been done to quantify uncertainty in terms of projecting changes in environmental conditions, including sea ice, ocean temperature, and primary production, through climate or Earth system model approaches and regional downscaling (e.g., Kirtman et al., 2013). These approaches revolve around performing multiple ensemble runs with one model, multiple models, and multiple emission or mitigation scenarios (e.g., Swart et al., 2015) and allow the projections to be constrained within a range of possible outcomes. However, a key uncertainty with respect to species impacts is the synergy of effects from multiple stressors related to environmental changes and anthropogenic activities (AMAP, 2018). Above, we reported on the direct and indirect dependencies of multiple trophic levels on the sea-ice ecosystem which highlights the complexity of the system, as well as the far-reaching impacts that a decline of the sea-ice ecosystem may have. Very little information exists on the ability of any species to adapt to those changes. While some species might be able to adapt, with the costs of adapting remaining unclear, others might not and may be driven to regional or global extinction.

9.1. Supporting and provisioning services

9.1.1. Arctic Ocean

The sea-ice habitat is highly sensitive to fragmentation, and ice retreat will lead to isolation of habitats and disruption of species mobility between habitats (e.g., Kramer et al., 2011; Hardge et al., 2017; Ehrlich et al., 2020). Lannuzel et al. (2020) anticipate that available sea-ice habitat will decrease as sea ice continues to retreat. Within the remaining sea ice, the habitable space may increase or decrease, depending on ice temperature and snow depth

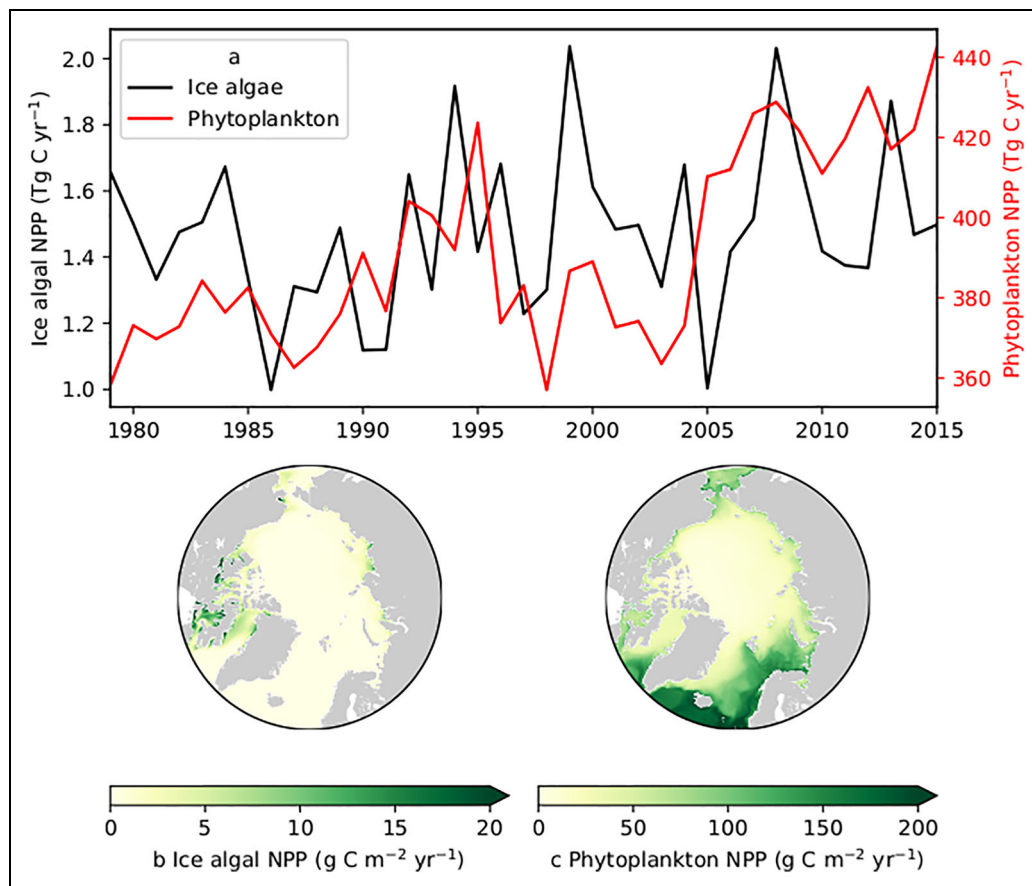


Figure 10. Simulated ice-algal and phytoplankton primary production in the Arctic. (a) Spatiotemporal variability in modeled ice-algal and phytoplankton primary production in the Arctic. (a) Time series of depth-integrated annual net primary production (NPP) by ice algae (bottom 3 cm of sea ice) and phytoplankton (upper 90 m of the water column) over the period of 1979–2015. Spatial distribution of NPP by (b) ice algae and (c) phytoplankton averaged over the period of 1979–2015. All results are based on numerical simulations using a pan-Arctic model (Hayashida et al., 2020). A comparable effort for the Southern Ocean is currently not available, but a coordinated effort to simulate ice-algal trends in both Arctic and Southern Ocean is underway within Phase 2 of the Ice Algae Model Intercomparison Project (IAMIP2; Hayashida et al., 2021). DOI: <https://doi.org/10.1525/elementa.2021.00007.f10>

and phenological changes. As a consequence, bacterially mediated processes may be altered, which can further affect the biogeochemical cycling and food webs of the ice-covered seas. For regions with increases in primary production, the heterotrophic microbial community will directly benefit from these increases, particularly the increased growth of pico-eukaryotic algae within ice (Campbell et al., 2018). In comparison, future changes in sea-ice dynamics and icescapes will probably have contrasting effects on polar herbivores, and the consequences are currently hard to predict (Lannuzel et al., 2020).

Results from the ice-algae model intercomparison project indicate large interannual variability in regional sea-ice algal production but no significant long-term trend (1980–2010) in most regions (Watanabe et al., 2019). **Figure 10** shows a model example from Hayashida et al. (2020), indicating no discernible trend for ice algae but an increase in oceanic primary production. The shrinking of Arctic sea-ice thickness has likely shifted the ice-algal bloom to earlier in the season, but the impacts on bloom intensity are highly variable. Potential increases in total ice

algal primary production are limited by the declining sea-ice area, especially in the Arctic below 74°N, while blooms in areas with expanding first-year ice can be limited by narrowed growth windows (Leu et al., 2015; Tedesco et al., 2019). Disruptions in the seasonality of the algal blooms can create mismatches with zooplankton life cycles, which in turn affect their key predators and higher trophic levels, leading to the possibility of phenological uncoupling between primary, secondary, and tertiary consumers (Post, 2017). Lewis et al. (2020) evaluate trends in pelagic phytoplankton biomass and production. They indicate that initial increases (from 1998) in primary productivity were due to increased light availability caused by reductions in sea-ice extent, but since about 2009, biomass increase is largely restricted to the inflow shelves of the Barents and Chukchi Sea and linked to increased nutrient inflow. These changes in nutrient inflow may also enhance sea-ice primary production.

The state of the Arctic marine biodiversity report (CAFF, 2017) indicates unknown or no trends so far for sea-ice biota for most species groups and regions, with the

exception of the Atlantic Arctic (decrease in under-ice macrofauna) and the central Arctic Basin (decrease in microalgae and other protists). Building on this study, Hop et al. (2020) highlighted that a decline in sea-ice protist diversity is anticipated with the decrease and potential disappearance of multiyear ice. Thick ice algal mats seem to be observed less frequently (e.g., in the Atlantic sector) and remaining species within first-year ice are likely to be more similar to the pelagic species. While incoming Atlantic and Pacific species might increase biodiversity, they will decrease uniqueness. Multiyear ice has been shown to contain more diatoms and other protist species than first-year ice (Hop et al., 2020), and a molecular study indicated more unique taxa than in the water column and melt pond habitats (Hardge et al., 2017). In areas where other seeding sources (such as bottom sediments) are unavailable, multiyear ice plays an important role as a repository and vector for the typical sea-ice algal communities (Olsen et al., 2017; Kauko et al., 2018) and meiofauna with poor swimming abilities (Kiko et al., 2017), which could seed newly formed ice from the adjacent multiyear ice. Hence, the observed and projected decline in multiyear ice extent has already (Hop et al., 2020) and will likely further result in a loss of ice-algal diversity and an increase in the relative importance of cryo-pelagic and pelagic species in biogeochemical cycling and Arctic food webs. Loss in algal diversity will affect the resilience of the ecosystem in general. For the Arctic Ocean, evidence is increasing that changing sea-ice drift and demise of multiyear ice have caused a change of species composition and a decline of diversity of sea-ice meiofauna. Overall, benthic-derived taxa such as flatworms and nematodes are disappearing, while pelagic-derived forms (e.g., ciliates) increase in relative abundance (Kiko et al., 2017; Ehrlich et al., 2020).

Arctic cod are projected to decline with increased warming and retreating sea ice, while sub-Arctic forage species (e.g., capelin) as well as harvestable fish species (e.g., various salmonids) are, and will increasingly be, more abundant in Arctic waters (Cheung et al., 2009; Cheung et al., 2016; Falardeau et al., 2017; Steiner et al., 2019; Tai et al., 2019), causing shifts in the higher trophic level food web (e.g., Harwood et al., 2015; Harwood et al., 2020; Brown et al., 2017; Choy et al., 2020).

Population trends of seabirds in the remote and inaccessible polar areas are not readily available and lack detail over the relatively short timescale of substantial reduction in Arctic sea-ice cover. Much of the data compiled by BirdLife (Billerman et al., 2020) concern historic changes observed during or even before the previous century and often relate to changes in breeding locations, hunting, fish stocks, bycatch, and so on. These data have little relevance to the assessment of the impacts of current rapid environmental change in the seasonal sea-ice areas of the high Arctic. As many seabird species do exploit the seasonal sea ice, they may be affected in different ways by seasonal change in sea-ice or snow cover. Probably the most recent and circumpolar information, for a restricted set of monitored species and locations, is provided by the Arctic Council working group on Conservation of Arctic Flora

and Fauna (CAFF, 2017). Ivory Gulls have suffered serious declines in most of the monitored colonies. Black-legged Kittiwake and Brünnich's Guillemots have undergone serious declines in the Atlantic Arctic where sea-ice changes are most rapid. Study plot details for Brünnich's Guillemots on Bear Island and Spitsbergen indicate annual population declines of 3% and 5%, respectively, over the past decade, but stability among the similarly ice-dependent Kittiwakes in these locations (Anker-Nilssen et al., 2020). Common Guillemots are declining but mostly depend on habitats south of the ice, and the observed change may relate more to changing fish stocks. Common Eiders show variable population trends, while Steller's, King, and Spectacled eider populations are listed as "decreasing and vulnerable," "least concern," and "near threatened," respectively, on the IUCN Red List. No adequate data appear to be available for other highly abundant high Arctic species like the Little Auk or Northern Fulmar. The global population of the Northern Fulmar is listed as a "least concern" species, but colonies on Bear Island (in the Barents Sea) in or near seasonally ice-covered areas have seen a 58% decline over about 25 years (Fauchald et al., 2015), and an alarming 87% decline has been observed in study colonies in the Canadian Arctic over the past 45 years (Mallory et al., 2020). In a general sense, species currently foraging by preference in sea-ice areas will meet problems when the ice disappears, and predicting their capacity to adapt is difficult.

An assessment of the abundance and trend in 78 recognized populations of Arctic marine mammals highlights large gaps in the data record. The assessment manages to establish trends only for 27 populations, of which 8 populations, including hooded seals (*Cystophora cristata*) and polar bears, are on the decline, and 10 populations, including walrus and some bowhead whale stocks, are increasing. Nine other populations are more or less stable (Laidre et al., 2015). Only poor population estimates exist for the pinnipeds, but Harwood et al. (2015; Harwood et al., 2020) have found a continual decrease in ringed seal condition over the past 20 years. Since 2018, elevated ice seal (ringed and bearded seal) strandings have occurred in the Bering and Chukchi seas and have been recognized as unusual mortality events (NOAA Fisheries, 2021).

The differences in the observed changes can be associated with different life history strategies, exploitation histories, biological productivity, and food web interactions. Several ice-dependent species are still recovering from human exploitation, and thus, their population increases most likely mask the consequences of habitat loss (Schweder et al., 2010; Niemi et al., 2019). Bowhead whales are the most heavily impacted by human exploitation, and of the 4 recognized stocks, only 2, the Bering-Chukchi-Beaufort and the Eastern Arctic-West Greenland populations, appear to be stable or increasing as compared to the Eastern Greenland-Spitsbergen populations which remain listed as Endangered (Givens and Heide-Jørgensen, 2021). Kovacs et al. (2020) highlight bowhead whale populations with extreme affiliation with cold, ice-filled waters as a group of concern with the potential to become critical in terms of habitat loss and thermal stress. Decreased sea

ice also removes barriers that isolate populations. In the case of bowhead whales, there is evidence that east–west contact between largely isolated populations is occurring (Heide-Jørgensen et al., 2011), as it has during past historically low ice periods (Alter et al., 2012). Mixing may in fact benefit the populations that are showing slow or no growth. Although decreasing sea ice is affecting the distribution patterns of western (i.e., Berig-Chukchi-Beaufort) populations of bowheads, the effect at the population level is not yet clear (Druckenmiller et al., 2018; Insley et al., 2021).

In addition to direct and somewhat predictable species impacts, the ongoing environmental change may even more seriously impact ecosystem processes in ways that are hard to predict. For example, several sources (CAFF, 2017) have reported that polar bears have changed their hunting strategy from sea ice to coastal areas. They are more frequently observed preying on nests of coastal waders, ducks, and geese and even climbing ledges in colonies of cliff-breeding seabirds, seriously affecting, for example, guillemots and kittiwake breeding success by predation and disturbance. Polar bears are particularly sensitive to sea-ice decline as most aspects of their ecology and life history depend on the sea ice (e.g., Wiig et al., 2015; Regehr et al., 2016; Brown et al., 2018). Large reductions in the mean global population size of polar bears are expected as sea-ice decline alters the species' habitat. Regehr et al. (2016) estimated a 71% median probability of a higher than 30% reduction over the next 3–4 decades but acknowledge high uncertainty in estimates of population trends. Furthermore, the loss of sea ice as a physical habitat supporting polar bears will likely be exacerbated by changes in the food web. New analytical techniques revealed that the carbon contribution of sympagic production to polar bear marine diet is on average 86% in the Baffin and Hudson Bay regions (Brown et al., 2018), suggesting that the replacement of sympagic prey by pelagic ones will have pronounced effects on polar bear diet. Molnár et al. (2020) assessed demographic impacts by estimating the threshold number of days that polar bears can fast before cub recruitment and/or adult survival decline. Using simulated numbers of ice-free days from Earth system models, they suggest that for some subpopulations, recruitment and survival impact thresholds may already be exceeded and that steeply declining reproduction and survival will jeopardize the persistence of most high-Arctic subpopulations by the end of the century for both high and moderate emission scenarios.

With wholesale ecosystem changes to ice and oceanographic conditions come fundamental shifts in predator and prey distributions. These shifts are exacerbated by human-caused noise and competition from increasing numbers of sub-Arctic species (Mueter et al., 2009; Grebmeier, 2012; Halliday et al., 2017; Ivanova et al., 2018; PAME, 2019). Species that forage on Arctic cod, such as ringed seals and beluga whales, may also move with cod or shift diets in response (Steiner et al., 2019; Insley et al., 2021). Current evidence indicates that ringed seal diets in the eastern Amundsen Gulf are becoming more diverse (Insley et al., 2021), and shifts have been observed in

beluga whale diet and distribution (Loseto et al., 2018a; Choy et al., 2020). Whether this diversification holds true for other species such as narwhal is unknown, but there is evidence of a decline in the condition of a number of higher trophic level species that have targeted primarily Arctic cod in the past (Harwood et al., 2015; Harwood et al., 2020).

Apart from changes within the sea-ice zone, warming leads to poleward expansion of temperate species with impact on the local ecosystem. Related biological invasions are expected to act synergistically as climate change enhances habitat disturbance and facilitates the establishment of invasive species, providing opportunities for hybridization and introgression at both poles. These effects influence local biodiversity that can be tracked through genetic and genomic approaches (Chown et al., 2015). In the Arctic, this expansion brings Atlantic and Pacific species into the Arctic Basin (Cheung et al., 2009; Lotze et al., 2019; Huntington et al., 2020) which might negatively affect its uniqueness. At the same time, the shift in the Arctic's apex predator from polar bears to orcas is resulting in marked shifts in distributions of now more vulnerable marine mammals such as narwhals, beluga, and bowhead whales (Breed et al., 2017; Matthews et al., 2020). Ice-adapted species no longer have the ice as a refuge from predators. Summaries of the vulnerabilities of different Arctic marine mammal species to changes in ice and oceanographic conditions indicate a multitude of contributing factors, with narwhals often suggested as the most vulnerable (Laidre et al., 2008; Laidre et al., 2015; Kovacs et al., 2012).

The impacts of increased storm activity and changing weather patterns on higher trophic level species remain unclear. However, the breakup and retreat of sea ice enhances the impacts of storms on wave activity, increases waves and ice hazards (Barber et al., 2014; Thomson and Rogers, 2014), and reduces the availability of sheltered areas available to mammals during a storm. For example, in the Arctic Beaufort Sea, high intensity and duration of storms in a coastal estuary led to increased water levels, flooding, and change in water temperature and resulted in belugas leaving their high aggregation area (Mackenzie Estuary) for 5 days (Scharffenberg et al., 2019). High water levels (caused by storms or flooding) may be to blame for upriver events where beluga may become disorientated with changing environmental patterns (Scharffenberg et al., 2021).

In addition, the increase in pathogens caused by warmer temperatures and increased vectors (e.g., invading species and waste and ballast water discharge from transiting vessels) may have catastrophic impacts on endemic species of marine mammals (in the Southern Ocean, the Antarctic Treaty System has ballast water exchange guidelines to help address this issue). Examples of large-scale mortality events caused by the phocine distemper virus have occurred on multiple occasions with pinnipeds at lower latitudes, and Arctic pinnipeds may be vulnerable to such events (Vanwormer et al., 2019). Several unusual mortality events with pinnipeds and gray whales have already occurred along the Alaskan North Slope in the

past decade (NOAA Fisheries, 2021). Whether increased and new pathogens result in direct population-level effects is possible, but more likely is their cumulative impact in combination with all of the other changing environmental and anthropogenic factors.

9.1.2. Southern Ocean

Chlorophyll *a* concentrations have appeared to increase in winter sea ice in the Weddell Sea over the last 3 decades in connection with increased snow load that has warmed the sea ice and increased the brine volume (Tison et al., 2017). These higher winter Chlorophyll *a* concentrations have been linked to higher bacterial production rates (Eronen-Rasmus et al., 2017) and suggest that warming of sea ice may lead to higher overall biological activity during the austral winter. Strong reductions in the seasonal sea-ice cover in the waters west of the Antarctic Peninsula have increased the annual pelagic primary productivity in the region (Moreau et al., 2015) and led to changes in phytoplankton communities (Montes-Hugo et al., 2008; Montes-Hugo et al., 2009). Enhanced production and shifts in species dominance are also projected for coastal zones and along the wider Antarctic marginal ice zone of the Western Antarctic Peninsula (van Leeuwe et al., 2020). Model projections indicate increased primary production in the Southern Ocean, associated with a shift in community structure towards smaller non-diatom species (Henson et al., 2016) and increased biological export production between 44 and 58°S (Hauck et al., 2015).

Over the past 50 years, decreases in total sea-ice cover and delays in winter sea-ice advance (Stammerjohn et al., 2008) have accompanied regional reductions in the standing biomass of krill (Loeb et al., 1997). In the Atlantic sector of the Southern Ocean, krill have suffered from sea-ice decline and climate change-related stressors (Atkinson et al., 2004; Atkinson et al., 2019; Flores et al., 2012). Using historical krill catch data, Atkinson et al. (2019) showed a southward contraction of Antarctic krill in the southwest Atlantic sector with sharp declines near the northern limit of the species over the past 90 years. A concomitant increase in mean body lengths reflects reduced recruitment of juveniles which showed sharp decreases in abundance since the 1970s. These decreases have been attributed to increases in temperatures and winds and a reduction in sea ice (Atkinson et al., 2019). Krill habitat is projected to continue to shift southwards due to ocean warming and changes in phytoplankton biomass (Veytia et al., 2020), and suitable spawning habitat will shrink by approximately 50% by the end of this century (Piñones and Fedorov, 2016). A shift in dominance from krill to salps in some regions has been correlated with higher concentrations in nitrogen and phosphorus and higher N:P ratios, indicating consequences for nutrient dynamics in the ocean (Plum et al., 2020).

Like in the Arctic, the inaccessible terrain and hostile climate in the Antarctic reduces the availability of data on species population sizes and trends in many regions. Exceptions are more accessible areas, where a majority of tourism and research operations take place, primarily the Antarctic Peninsula near longterm research stations (e.g.,

MAPPD, 2021). Clearly, loss of sea-ice habitat can be expected to affect the populations of species that depend on the sea ice for foraging or breeding. Almost all known emperor penguin colonies are situated on fast ice attached to the ice shelf, which breaks up only late in summer when chicks are able to leave the colonies. Changes in sea-ice conditions have been seen as potentially causing the loss of over a third of the global population of emperor penguins or even substantially more (Fretwell et al., 2014). On a regional scale, extremely fast climate changes and related changes in the sea ice in the Western Antarctic Peninsula have caused strong local declines in populations of the Adélie penguin, with chinstrap and gentoo penguins replacing Adélie penguins (Ducklow et al., 2007). However, on the full Antarctic scale, Adélie declines in the western Antarctic Peninsula were compensated by population increases in East Antarctica (Lynch and LaRue, 2014).

Population sizes and trends for tube-nosed seabirds such as Antarctic petrels, snow petrels, Wilson's storm petrel, and others are basically unknown. As with the polar bear example in the Arctic, ecosystem changes triggered by climate change are much more complex than explained by the size or quality of particular foraging habitats. For example, in a study colony of the Antarctic petrel in East Antarctica, rapid unexplained and increasing declines in breeding success were observed starting from the mid-1980s. While changes in the winter sea-ice habitat were speculated to have reduced the body condition of the birds at the start of the breeding season, observations in 1996 showed that increased winter snowfall created snowdrifts on the cliffs close to the colony that persisted into the first weeks of the breeding season. These snowdrifts provided southern giant petrels with access to previously inaccessible cliff sections allowing predation on nesting adult Antarctic petrels. In addition, crash landings by the giant petrels in the snow drifts caused major disturbances, driving the Antarctic petrels off their nests. Dramatic effects followed as south polar skuas preyed on virtually all eggs during colony disturbances leading to essentially zero breeding success (Franeker et al., 2001).

The seasonal and regional loss of Antarctic sea ice poses a major threat to Antarctic marine mammals. These obligate ice-breeding seal species, that is, the Weddell seal, the crabeater, the leopard seal, and the Ross seal, face a reduction of their breeding habitat. Particularly, the abundance and distribution of crabeater and Weddell seals are likely to be affected negatively by changes in the sea-ice extent (Siniff et al., 2008). Among the whales, Antarctic minke whales are especially vulnerable with regard to sea-ice loss, as the marginal ice zone represents a major part of their habitat (Friedlaender et al., 2014; Williams et al., 2014; Herr et al., 2019). Among the species of marine mammals of the Southern Ocean on the IUCN Red List of Threatened Species, the Antarctic blue whale is listed as "critically endangered," the sei whale as "endangered," the fin whale and the sperm whale (*Physeter macrocephalus*) as "vulnerable," and the Antarctic minke whale as "near threatened." However, assessing the impacts of climate change on whales in the Southern Ocean is difficult, as

commercial whaling of the 20th century has decimated most whale species, with some populations estimated to have been reduced by 99% of their pristine abundance (Clapham, 2016). Since the introduction of the moratorium on commercial whaling in 1986, some species and populations have been recovering well from exploitation, e.g. humpback whales, while others remain critically endangered, for example, the Antarctic blue whale. For populations in poor states of conservation, the effects of climate change are difficult to distinguish among a suite of cumulative effects potentially preventing a population recovery. Furthermore, as migratory species, baleen whales will also be affected by conditions in their low latitude breeding grounds, which may further complicate interpretation of potential impacts related to sea-ice changes.

As a key organism of the Antarctic food web, decreasing krill abundance linked to sea-ice loss likely poses the greatest threat to all Antarctic animals feeding on Antarctic krill, including all baleen whales and seals of the Southern Ocean. Reduced krill abundance may affect individual body condition, reproductive success, and, in the long term, population sizes of marine mammals (Nicol et al., 2008). Climate variables have been shown to affect pup survival in Antarctic fur seals and southern elephant seals (Forcada et al., 2005; McMahon and Burton, 2005). Fluctuations in humpback whale adiposity, as an indicator of their summer foraging success and therefore the productivity of their Antarctic feeding grounds, has been correlated with climate patterns (Bengtson-Nash et al., 2018). Also, a strong relationship between Southern right whale calving output and sea surface temperature deviations, or anomalies, at South Georgia has been observed (Leaper et al., 2006). Models that link krill and whale population dynamics with climate change drivers, including changes in ocean temperature, primary productivity, and sea ice, predict declines of whale populations under climate change (Tulloch et al., 2019).

Increasing intensity, diversity, and distribution of human activity and weakening ocean barriers enhance the connectivity of the Southern Ocean with the rest of the world, facilitating introduction of new organisms and threatening the region's pristine character. Interaction between non-native marine species and other anthropogenic stressors affecting Antarctic ecosystems, such as climate change (warming, ocean acidification) and pollution, may have irreversible ramifications for biodiversity and ecosystem services, with the Antarctic Peninsula, South Shetland Islands, and South Orkney Islands as the most invaded part of the Antarctic (McCarthy et al., 2019; Hughes et al., 2020).

9.2. Regulating services

As Arctic sea ice (and the overlying snow) becomes thinner and more ephemeral, more light will reach the ocean surface. The combined sympagic and pelagic primary productivity and associated CO₂ drawdown is thus estimated to increase in the future within the remaining sea ice, as well as in the ocean, on the condition that nutrients are plentiful (Lannuzel et al., 2020; Lewis et al., 2020). However, nutrient limitation due to increasing stratification

may severely restrict this increase in primary production. The combination of warmer ice and a shift toward smaller algae may lead to more grazing by smaller zooplankton and more microbial remineralization. This change in microalgal biodiversity will translate into a decrease in organic carbon export to the seafloor, as well as a change in the seasonality of this process. Overall, the Arctic system is expected to shift from exporting to recycling carbon, leading to a less efficient biological carbon pump (Lannuzel et al., 2020), despite the potential for more frequent under-ice blooms and associated episodic releases of large ice algal aggregates.

Outcomes are likely to be similar for the Southern Ocean, although large uncertainties remain with regard to future light and iron availability. The former largely depends on how much snow will be deposited on top of sea ice, which is a hot topic of debate. Light limitation also strongly depends on the depth of the upper mixed layer (e.g., Lloret et al., 2015), which is itself heavily influenced by ice growth and melt processes. Iron availability will vary regionally; more iron will become available on the coast as a consequence of ice sheet thinning (Gerringa et al., 2012; Hawkings et al., 2014; Herraiz-Borreguero et al., 2016; St-Laurent et al., 2017; Duprat et al., 2019; St-Laurent et al., 2019), while in the open ocean, the loss of iron-rich sea ice is likely to decrease the amount of iron seasonally delivered to the ocean surface (Lannuzel et al., 2016). Sea-ice loss is therefore likely to increase coastal but decrease open ocean primary productivity. Future projections suggest air-sea CO₂ fluxes will increase in the Southern Ocean due to more open ocean area and more leads over undersaturated waters due to thinner ice coupled with increased storm activity (e.g., Parmentier et al., 2013; Ito et al., 2015; Fransson et al., 2017). This increase in fluxes is confirmed by models from the Coupled Model Intercomparison Project (Phase 5) which suggest increased CO₂ uptake in the Southern Ocean sea-ice zone due to faster atmospheric CO₂ absorption by the surface ocean, indicated by a higher Revelle (buffer) factor (Hauck et al., 2015).

Moreover, a change from multiyear ice to young and first-year ice in the Arctic will result in higher rates of ice formation and brine export during the winter (Lannuzel et al., 2020), and inorganic carbon storage in the Arctic Ocean may increase in the future for the benefit of society (Armstrong et al., 2019). Some studies have projected increasing net carbon storage using different emission scenarios, where the increase is mostly explained by increased uptake of atmospheric CO₂ (Slagstad et al., 1999; AMAP, 2018; Armstrong et al., 2019). However, increasing stratification due to surface warming and increased meltwater may weaken deep-water formation and decrease deep CO₂ sequestration (Yamamoto et al., 2018), while the increasing CO₂ concentration in the upper ocean is reducing the ocean's capacity to absorb CO₂ (Cai et al., 2010b; Else et al., 2013). Hayashida et al. (2020) have suggested that DMS fluxes to the atmosphere have increased in spring and early summer over the last decade, partly due to slight increases in ice-algal production, but mostly due to increased under-ice and open ocean phytoplankton production with retreating and

thinning sea ice. Armstrong et al. (2019) investigated the effect of climate change and diminishing sea ice on blue carbon (the carbon stored in marine ecosystems), indicating increased storage.

9.3. Cultural services and society

Many of the connections between sea-ice ecosystem services and human well-being are, and will be, impacted by climate-driven changes in sea-ice systems and shifts from summer ice to open water. Foremost among those connections are any on-ice transportation activities and activities related to harvesting of impacted species, as well as shifts in species distribution and seasonality, including the appearance of new species. These changes and shifts might severely impact how traditional practices can be performed and traditional knowledge can be applied to, for example, hunting practices (boat and skidoo/dog-sled approaches), harvesting locations (use of traditional hunting and fishing camps), and seasonal timing of species appearance. Loss of sea-ice-related traditional ways of life and knowledge has been highlighted as a possible threshold of concern for Inuit in Greenland, Canada, Alaska, and Chukotka (AMAP, 2017, 2018). Inuit are resilient people with capacity for adaptation to climate change (Pearce et al., 2015), and some of these disrupted linkages may be overcome by adaptation strategies. Novel tools may help with adaptation, for example, mobile app and web platforms (SIKU, 2021) that bring together Inuit knowledge and technology (e.g., SmartICE, 2021) to support safe sea-ice travels in a period when sea-ice conditions are becoming more and more unpredictable. Some benefits from and connections to sea ice and sea-ice ecosystem services are hardly replaceable, such as unique cultural and spiritual connections that people have to sea-ice landscapes, ecosystems, and species. For instance, sea-ice-associated species support country foods which, although not necessarily representing the major part of people's diet, are a key part of culture and identity, given the multiple intangible, relational values of consuming and sharing country foods (Sheremata, 2018).

Marine mammal harvesting may be affected significantly by decreases in ice-associated mammals (Section 9.1.1) and accessibility, including increased sea state with retreating sea ice. Changing sea-ice conditions can alter marine mammal distributions and timing of migrations, as well as the transportation platform, affecting the travel time and safety of hunters who harvest these animals. For instance, hunters in the Bering Sea region are often ice-dependent as they follow the ice edge to find walrus and seals (Rosales and Chapman, 2015). Hence, walrus harvests in the Bering Sea have started to occur earlier in the spring due to the earlier melt (Fidel et al., 2014). Some hunters also reported having to travel longer distances than before to find sea ice and ice-associated marine mammals, in conditions that they believe are less safe than they used to be (Rosales and Chapman, 2015). Beluga hunting in the Inuvialuit Settlement Region has experienced significant interannual variability, with a general tendency for arrivals earlier in the season, but also appearances in areas previously not known for beluga harvest

(Loseto et al., 2018b). In addition, climate change mediated local weather change (i.e., wind direction/intensity/duration) including increased storm activity has impacted beluga hunting by changing predictability of weather and travel safety (i.e., rough and dangerous waters; Waugh, 2018) and was shown to reduce beluga presence in the Mackenzie Estuary (Scharffenberg et al., 2019). Climate change influences on environmental features, specifically water levels, may be to blame for recent beluga upriver events, which serve to change harvesting accessibility (Scharffenberg et al., 2021). Investigation of the declining beluga hunting from the community of Aklavik revealed multiple drivers, including the impacts of climate change. For example, earlier ice breakup dates have resulted in belugas moving offshore earlier in the season and, compounded with rougher waters, has challenged hunter accessibility to belugas. Additionally, shifting socioeconomics, cultural practices, and loss of Elders has impacted beluga hunting practices (Worden et al., 2020).

Deininger et al. (2016) found that Antarctic tourism was inversely related to sea-ice coverage and speculated that the tourism industry would probably benefit from further sea-ice decline. Cavanagh et al. (2021) in their recent evaluation of Southern Ocean ecosystem services highlight sea ice as an intermediate risk to tourism but indicate that while there is confidence in the impact on wildlife, there is no confidence assessment on tourism and recreation overall. In subpolar seas, changes could be detrimental to sea-ice-associated tourism. For example, sea-ice production in the Okhotsk Northwestern polynya, the highest in the northern hemisphere, has been declining for decades (Ohshima et al., 2016). In Northern Hokkaido's Shiretoko National Park and UNESCO World Heritage Site, sea ice drives a vital tourism industry, but the drift ice extent has retreated poleward from the Shiretoko peninsula over the last 100 years and could vanish entirely from northern Hokkaido by the end of this century (Denyer et al., 2019).

While much of the uncertainty in future projections is linked to climate model projections and species responses, additional uncertainties apply when trying to assign a cost to sea-ice ES or ES in general. For example, in the estimates provided by Euskirchen et al. (2013), high uncertainties are linked to uncertainties in future climate feedbacks, as well as economic uncertainties. With respect to economics, price tags attached to fisheries are likely the most tenable, as they refer to landed values of specific species which are recorded for many fisheries across the globe (e.g., Tai et al., 2019). The Commonwealth of Nations promotes the emerging concept of a "Blue Economy" which encourages better stewardship of our ocean or "blue" resources. The World Bank refers to the term as the "sustainable use of ocean resources for economic growth, improved livelihoods, and jobs while preserving the health of ocean ecosystems." Within the blue economy framework, a system to estimate values and values at risk may be established (Shaw et al., 2020). Another example is the use of the social cost of carbon and carbon market values to estimate a monetary value of the Arctic Ocean's carbon storage and its future changes (Armstrong et al.,

2019). Assigning a value to any of the intangible cultural services is even less straight forward.

10. Conservation and ecosystem services

An ecologically or biologically significant marine area designation does not have any associated management measures, but it represents one step in the formal designation of marine protected areas. MPAs include a variety of types of protected areas in the marine environment, some of which are known by other terms (International Union for Conservation of Nature, 2021). As defined by the International Union in the Conservation of Nature/World Commission on Protected Areas, an MPA is “a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated ecosystem services and cultural values” (International Union for Conservation of Nature, 2008).

While the sea-ice system cannot be considered as a “clearly defined geographical space,” designating the sea-ice ecosystem as an ecologically or biologically significant marine system suggests that the sea-ice ecosystem or the presence of sea-ice ecosystems could be considered explicitly in the designation of MPAs. One example is Canada’s Tuvaijuittuq MPA which is the only MPA specifically designated due to its sea-ice ecosystem (**Figure 2a**). The Inuktitut word Tuvaijuittuq means “the place where the ice never melts,” and the region is considered globally, nationally, and regionally unique due to the presence of multi-year pack ice.

Leenhardt et al. (2015) highlight that the goals of MPAs are expanding increasingly beyond the protection and restoration of a few species to the restoration of ecosystem functions and services, as well as the maintenance of long-term ecosystem health to sustain multiple ecosystem functions and services within the context of changing environmental conditions. Leenhardt’s synthesis indicates that empirical evidence for positive effects of MPAs on ecosystem service provision by coastal marine ecosystems is accumulating. Leenhardt et al. (2015) suggest that though species and functional diversity are generally correlated, functional diversity is more likely to respond positively to protection, and measuring species diversity alone may lead to failure to detect adverse effects on functional diversity. In this context, Leenhardt et al. (2015) propose that quantifying and monitoring the functional trait distributions of species and the functional diversity of species assemblages are promising approaches for assessing the effects of MPAs on ecosystem functioning and services.

Within the Aichi biodiversity targets defined by the CBD, target 14 states that “ecosystems that provide essential services, including services related to water, and contribute to health, livelihoods and well-being, are restored and safeguarded, taking into account the needs of women, Indigenous and local communities, and the poor and vulnerable” (CBD, 2021). More specifically, goal 14.5 calls for 10% of marine areas to be protected by 2020, and in 2016 the members of International Union for the Conservation of Nature approved a 30% goal by 2030. While this target is nonbinding, efforts to achieve Aichi target 14.5 suggest that such percentage-based targets help motivate

governments to designate MPAs. However, despite major conservation progress over the past 2 decades, only 7.4% of ocean area is currently protected, and only 5.3% is protected with fully implemented MPAs (Duarte et al., 2020).

In the Southern Ocean, CCAMLR is responsible for designating and regulating MPAs. Currently, 5% of the Southern Ocean is protected (**Figure 2b** indicates established and proposed MPAs around Antarctica). The South Orkney Islands Shelf MPA was established in 2009 and the Ross Sea region MPA in 2016. Three more proposals for MPAs are being considered for (1) East Antarctica, (2) the Weddell Sea and Dronning Maud Land, and (3) the Antarctic Peninsula. To move MPA proposals to the designation state, proposals are put forward by member countries and are considered by the Scientific Committee. Once consensus is reached that the proposal is based on the best available science, the proposal goes to the Commission where all members must agree to establish the MPA. The indicated proposals have so far failed to achieve the consensus needed to pass (most recently in 2020). Using the Peninsula example, Sylvester and Brooks (2019) highlight that a highly collaborative, transparent, and science-based process exemplifying best practices for actionable science and coproduction may not be sufficient to drive consensus; MPA designation in the Southern Ocean ultimately requires the political will to make the decision. The Ross Sea MPA (the world’s largest MPA) covers one of the most productive areas of the Southern Ocean including a highly productive sea-ice ecosystem, with key habitat and breeding areas for about 25%–30% of the world’s Adélie and emperor penguins and Weddell seals. The majority of the Ross Sea MPA is fully protected under a General Protection Zone and also includes a Special Research Zone and a Krill Research Zone that allow limited fishing for krill and toothfish for scientific research. The duration for the MPA is set to 35 years (fishing restrictions to expire after 30 years) with assessments on scientific progress every 5 years and evaluation of objectives every 10 years through CCAMLR (Convention for the Conservation of Antarctic Marine Living Resources, 2021).

Unlike for the Southern Ocean, no single governance mechanism pertains to the Arctic as a whole, and the question of which legal instruments could be used to create and implement MPAs encompassing waters and ice-covered areas beyond national jurisdiction is unresolved (Hossain and Czarski, 2018). In the interim, the draft Agreement to Prevent Unregulated High Seas Fisheries in the Central Arctic Ocean (USDS, 2017) adopts a precautionary approach to potential future commercial fisheries and commits Parties to establish a Joint Program of Scientific Research and Monitoring. Regionally, all Arctic States have legal and policy tools for designating and managing MPAs in the Arctic that offer flexibility with respect to the level of protection and management regime. The Arctic Council has adopted a Framework for a Pan-Arctic Network of Marine Protected Areas aiming to develop networks of MPAs within national jurisdictions of Arctic States, as well as other area-based conservation measures, in order to improve resilience to climate change

and other hazards (PAME, 2015, 2017). Hossain and Czarski (2018) summarize that by 2018, 13 EBSAs covering 22.7% of the Arctic marine area had been identified, with only 1% of EBSAs being protected by MPAs. Under the Arctic Council's framework of the Arctic Marine Shipping Assessment (AMSA), 98 separately designated areas, totaling 76% of the Arctic Ocean, have been designated as areas of heightened ecological and cultural significance ("Recommendation IIC areas") with only 5% of these IIC areas within currently recognized MPAs. Visual comparison between the IIC areas (**Figure 2a**) and the areas with expected key ice algae production (**Figure 9b**) suggests that the ecological consequences supported by the sea-ice ecosystem are reflected to a limited extent with the AMSA effort.

In addition to Tuvaijuittuq MPA, a culturally and historically significant marine area long used by Inuit for travel and harvesting and which has been identified as a potentially important future summer habitat for ice-dependent species, other MPAs in the Canadian Arctic include the Anguniaqvia Niqiqyuam (established 2016) and Tarium Niryutait (established 2010, **Figure 2a**). The latter is an important summer habitat for the Eastern Beaufort Sea beluga and a diverse range of fish species; both MPAs have the conservation objective to maintain habitat and support populations of key species such as beluga whales, Arctic char, and ringed and bearded seals, all of which are strongly ice-associated through habitat or provisional sea-ice ES (Fisheries and Oceans Canada, 2021). In addition, the Government of Canada and the Qikiqtani Inuit Association recently signed an Inuit Impact and Benefit Agreement required for the establishment of Tallurutiup Imanga National Marine Conservation Area (NMCA, **Figure 2a**). Tallurutiup Imanga is an area that has been used since time immemorial by the Inuit. The agreement states that "Inuit Qauijimajatuqangit (traditional knowledge) will inform future decision making for the management and protection of the NMCA and the NMCA will protect Inuit harvesting rights guaranteed under the Nunavut Land Claims Agreement while also ensuring the protection of species at risk and their habitat." Specifically mentioned are bowhead and beluga whales, narwhal, walrus, and polar bear (Parks Canada, 2021). In Norway, the Svalbard protected area complex comprises a combination of national parks, nature reserves, bird sanctuaries, and 1 geotope protected area. Conservation goals include habitat for polar bear as well as other ice-associated mammal and bird species (NEA, 2009). Svalbard also has restrictions for vessels on breaking fjord ice, where the breaking of ice is considered a deterioration of the natural environment (Governor of Svalbard, 2021). The Russian Arctic National Park (established 2009, expanded in 2016 to include Franz-Josef-Land; The Arctic, 2021) aims at conserving pristine ecosystems and threatened species, including walrus, bowhead whales, polar bears, and narwhals. The national park is also important for the preservation of cultural heritage related to the history of Arctic discovery and colonization. The park does not restrict resource extraction and hence is not designated as an MPA.

In addition to Inuit co-development and co-management of MPAs and NMCAs, there is mounting

international recognition of the significant role Indigenous Protected and Conserved Areas (IPCA), and Indigenous Peoples' and Community Conservation Areas can play in biodiversity conservation and the protection of cultural heritage. An example for the Arctic is the Arqviilit, an island chain in the northeastern Hudson Bay designated to become the first IPCA in Arctic waters. Arqviilit IPCA conservation goals include preserving the Nunavik Inuit's cultural connection to the land and protecting habitat for species at risk, including the culturally significant polar bear and other sea-ice-associated species (e.g., Atlantic walrus, common eider; Radio Canada International, 2021).

In addition to these local conservation measures, international regulations on conservation, shipping, and fisheries can be relevant to the sea-ice ecosystem. In the Northern hemisphere, the Arctic Council is the "leading intergovernmental forum promoting cooperation, coordination and interaction among the Arctic States, Arctic Indigenous Peoples and other Arctic inhabitants on common Arctic issues, in particular on issues of sustainable development and environmental protection in the Arctic" (Arctic Council, 2021). The Arctic Council supports extensive monitoring and assessment and derives policy recommendations based on those assessments. Including the sea-ice ecosystem into these assessments is essential. Fisheries, exploration, science, tourism, and environmental protection within a country's exclusive economic zone are generally within the jurisdiction of the respective country; they may be co-managed by federal and Indigenous agencies and can play a key role in conservation measures for sea-ice ecosystems, while fisheries in the high seas are addressed via the International Agreement to Prevent Unregulated High Seas Fisheries in the Central Arctic Ocean.

All direct human activities in the Southern Ocean (including science, tourism and fishing) are managed, to varying degrees, through the Antarctic Treaty System and its related agreements. The Protocol on Environmental Protection to the Antarctic Treaty (the Protocol) designates Antarctica as a "natural reserve, devoted to peace and science," setting forth basic principles applicable to human activities, including science and tourism in Antarctica (Secretariat of the Antarctic Treaty, 2021a). Any activities are required to be made publicly available (e.g., through the Electronic Information Exchange System EIES; Secretariat of the Antarctic Treaty, 2021b). Ship traffic in the Antarctic is predominantly due to tourism, research (including research station supply), and fisheries (legal and illegal fishing; e.g., Weimerskirch et al., 2020), with a large component of human activity concentrated around the Antarctic Peninsula (Deininger et al., 2016; IAATO, 2021).

At the time of writing, access restrictions related to the COVID-19 pandemic are significantly reducing research and tourism activities in both the Arctic and Antarctic. However, this reduction is expected to be temporary. In the meantime, these restrictions have led to an enhancement of Inuit participation in community-based research projects in the Arctic, further highlighting the need for community and Inuit leadership in research projects within their respective regions or territories.

11. Concluding remarks

Our assessment highlights the need to sustain the provision of sea-ice ES in the future. It indicates that the sea-ice ecosystem fulfills the criteria for ecologically or biologically significant marine areas, which provides a reference to identify conservation needs and can guide the designation of marine protected areas in polar regions. MPA designation helps to protect ecosystems from additional, mostly localized human-induced stressors. Such protection may help individual species and ecosystems to cope or adapt, but it does not address the global issue of climate change itself. In the case of sea-ice ecosystems, climate warming threatens the base substance of the ecosystem and as such associated conservation objectives. The disappearance of sea ice is a direct consequence of global warming and can only be addressed by international efforts to reduce greenhouse gas emissions. Therefore, local and regional conservation objectives and management strategies must be combined with international efforts on emission reduction.

If the conservation objectives of existing and proposed MPAs were to directly identify the linkage to global warming as the human stressor impeding the MPA's ability to conserve, then, collectively, MPAs could advance international regulations on emissions and climate change. In this context, the fact that governance in the Arctic and Antarctic is very different (i.e., national jurisdictions vs. a general treaty system) is relevant. Some climate intervention approaches have been proposed to retain or recover sea-ice cover. However, such approaches can have significant impacts on biological production and gas and material exchanges, that is, they might not be favorable for the sea-ice ecosystem (Miller et al., 2020).

The sea-ice ecosystem supports all 4 key ecosystem services. Supporting services are provided in the form of habitat, including feeding grounds and nurseries for microbes, meiofauna, fish, birds, and mammals, as well as life-cycle maintenance. The key species Arctic cod (*Boreogadus saida*) and Antarctic krill (*Euphausia superba*) are tightly linked to the sea-ice ecosystem and transfer carbon from sea-ice primary producers to higher trophic level fish, mammal species and humans. Through harvesting and the supply of potential medicinal products and genetic resources, the system also contributes to provisioning services. The sea-icescape and its biology provide a multitude of cultural services, such as inspiration and attraction for cultural activities, tourism, and research and provide the base for Indigenous and local knowledge systems, cultural identity, and spirituality. In addition, the sea-ice ecosystem contributes to climate regulating services through radiative transfer, the production of biogenic aerosols, halogen oxidation, and the release or uptake of climate-relevant gases such as carbon dioxide and dimethylsulfide.

The ongoing changes in the polar regions have large impacts on sea-ice ecosystems and the ecosystem services sea ice provides to society. Multi-scale variations in sea-ice dynamics could cause major modifications of the food web architecture. Even though the response of sea-ice-associated primary production to environmental change is regionally

variable, the effect on ice-associated mammals and birds is predominantly negative, subsequently impacting human harvesting and cultural services in both polar regions. The understanding of past trends and future projections for populations and species are made exceedingly complicated by the interactions among all the possible abiotic, biotic, and human factors and their direct and indirect impacts. Many changes might interact synergistically. Ongoing and future changes in sympagic communities can magnify the pressure on polar ecosystems caused by ocean warming, ocean acidification and sea-ice decline. Additional anthropogenic activities such as exploration and development, tourism, commercial harvesting, and shipping are rapidly increasing as access opens opportunities. Impacts to all species from microbial communities to marine mammals may be affected by related noise, ship strikes, pollution, and the introduction of pathogens (Arctic Council, 2009; Logerwell and Skjoldal, 2019) and might be complicated in that they can cause direct and indirect impacts through multiple pathways.

The EBSA designation highlights that the sea-ice ecosystem deserves specific attention in the evaluation of marine protected area planning. On the other hand, the ecosystem services discussion highlights the widespread implications a loss, decrease or disturbance in this system may have for human well-being. Conservation can help preserve important species. However, the key mitigation measure that can slow the transition to a strictly seasonal ice cover with climate change, reduce the overall loss of sea-ice habitats from the ocean, and thus preserve the unique ecosystem services provided by sea ice and their contributions to human well-being is a reduction in carbon emissions.

Data accessibility statement

No new data sets were generated for this publication. Shapefiles to create **Figure 2** (MPA graphs) were obtained from various sources: <https://www.marinerregions.org/> (EEZ shape files), Arctic: http://geo.abds.is/geonetwork/srv/eng/catalog.search#/search?resultType=details&from=1&to=20&sortBy=relevance&fast=index&_content_type=json&_cat=Protected%20Area, <https://open.canada.ca/data/en/dataset/a1e18963-25dd-4219-a33f-1a38c4971250>, <https://www.dfo-mpo.gc.ca/oceans/maps-cartes/conservation-eng.html>, <https://www.natureearthdata.com/downloads/>, <https://www.canada.ca/en/environment-climate-change/services/national-wildlife-areas/protected-conserved-areas-database.html>; Southern Ocean: <https://data.ccamlr.org/search/type/dataset>, <https://data.ccamlr.org/dataset/marine-protected-areas>, <https://data.ccamlr.org/dataset/statistical-areas-subareas-and-divisions>. Data for Tourism graphs are accessible through IAATO (<https://iaato.org/information-resources/data-statistics/>) and AECO (<https://www.aeco.no/resources-and-tools/>). Data on toothfish and krill fisheries are available through CCAMLR in annually published reports: <https://www.ccamlr.org/en/system/files/e-sc-39-prelim-v2.pdf>. Detailed accessibility information to model code and output for **Figure 9** is provided in Hayashida et al. (2020). Free clipart was used to create **Figure 1**.

Supplemental files

The supplemental files for this article can be found as follows:

Table S1. Criteria^a for designation of an ecologically or biologically significant area (EBSA).

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Competing interests

No competing interests were identified.

Author contributions

Contributed to the conception and design: All authors.

Contributed to figure creation and photographs: NS, SM, HF, JvF, MF, AL, MN, DL, PW.

Contributed to the writing of the manuscript (core contributions by sections): JB, EER, KB, MvL (microbial sections), KM, LT, NS, KC, HK (ice algae and Chlorophyll *a* sections), AL, MN, NS, PW (tourism sections), AM, NS, HF, LM, LNM, KM, SM, MF (Arctic cod, Antarctic krill, meiofauna, and food web sections), SM, DN, LM, NS, AF,

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