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Sea ice: An extraordinary and unique, yet fragile, biome

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Sea ice – a unique and extraordinary biome in its nature and dynamics – is under threat. Ocean warming, sea-ice decline, and altered seasonality endanger the simple, vulnerable, and low resilient sea-ice and ice-associated food webs in both polar oceans.

Sea ice is one of the largest biomes on our planet, covering an area up to 14 million km^2 in the Arctic Ocean in March 2022 and up to 17 million km^2 in the Southern Ocean last September. While Arctic and Antarctic sea ice are similar in many facets, fundamental differences also affect the type of sea-ice biome they are associated with. The fact that the Arctic Ocean is surrounded by land makes the sea ice there more stationary, permanent, and deformed, and with more melt ponds due to a thinner snowpack (Fig. 1a). In contrast, the Southern Ocean surrounds an entire continent. It is affected by abundant precipitation with more snow-ice formation, more mobile sea ice prone to openings, and more young ice formation (Fig. 2a).

Since satellite records began providing reliable observations over 40 years ago, Arctic sea ice has steadily decreased annually in every season, reaching an annual minimum extent in summer, and first-year ice has replaced multiyear ice as the dominant ice type (Stroeve and Notz 2018). During the same period, Antarctic sea ice has shown strong regional and seasonal patterns of variability, with gradual increases in extent until a reversal of this trend in 2016. Since then, it has declined at a rate far exceeding that of Arctic sea ice (Parkinson 2019). Under a warming scenario of at least 2.0°C, the Arctic Ocean is expected to become ice-free throughout September regularly (Notz and Stroeve 2018). Sea ice in the Southern Ocean is also projected to decrease significantly in all seasons during this century in response to warming, with a larger spread of uncertainty in model estimates (Holmes et al. 2022).

The sea ice and ice-associated food webs

Sea ice is an extraordinary multiphase medium comprising a solid ice matrix, liquid salty brines, gas bubbles, and impurities. It is in the brines that a unique ecosystem develops. From viruses, fungi, bacteria, and microalgae to different forms of meio- and macrofauna, an entire food web inhabits sea ice (Figs. 1b, 2b). Compared to the Arctic, Antarctic sea ice is typically more snow-covered, insulated, and permeable, and contains more extensive brines, facilitating access by larger organisms. The most abundant group of organisms found in sea ice is usually tiny algae, which, together with their pelagic counterpart, phytoplankton, form the base of the entire polar marine food web.

In both hemispheres, and in both land-fast and pack ice alike, different algal species, often representing a single functional group, dominate; these include autotrophic flagellates in surface layers, mixed communities in the interior layers, and pennate diatoms in bottom layers (van Leeuwe et al. 2018; Figs. 1b, 2b). Among pennate diatoms, those of the genus *Nitzschia* are often dominant in both Arctic and Antarctic sea ice. Rotifers and nematodes are more commonly found in Arctic sea ice, while copepods are more commonly found in Antarctic sea ice (Bluhm et al. 2017; Figs. 1b, 2b). Crustaceans dominate under-ice communities. Copepods and amphipods are found in both under-ice environments; dominant taxa include euphausiids in the Southern Ocean and amphipods in the Arctic Ocean (Figs. 1b, 2b). Ice algae support key under-ice foraging species, i.e. Arctic cod (*Boreogadus saida*) in the Arctic Ocean (Fig. 1a, c) and Antarctic krill (*Euphausia superba*) in the Southern Ocean (Fig. 2). These species are dependent on the existence of stable sea ice and are key for transferring carbon from primary producers to higher trophic levels, from fish to marine mammals to humans (Figs. 1, 2).

Sea ice and terrestrial ecology

Strong linkages exist between Arctic marine and terrestrial ecology (Fig. 1c). Sea ice can act as an important ecological corridor, connecting land masses in the Arctic and thereby facilitating the exchange of individuals of some terrestrial species among populations. Moreover, sea ice is an important foraging and predator-escape platform for many species of marine pinnipeds, such as seals and walrus. As sea-ice extent diminishes and ice edges recede from shallow coastal waters, foraging conditions for species such as walrus shift from benthic (i.e. shallow water) to pelagic (i.e. deeper water), increasing foraging time and forcing animals ashore where crowding, trampling and disease transmission can increase (Post et al. 2013; Fig. 1c).

Recent studies have shown that sea-ice variations can modify the proximal abiotic environment on land adjacent to the ocean, influencing tundra vegetation productivity, phenology, and community composition; in some cases, these dynamics can alter the abundance of large herbivores such as caribou (Fauchald et al. 2017; Fig. 1c). Moreover, sea-ice dynamics can alter local abiotic conditions far inland, sometimes resulting in rain-on-snow events that encase reindeer pastures in ice, leading to massive reindeer die-offs (Forbes et al. 2016). The associations between tundra vegetation and Arctic sea-ice decline are complex and difficult to generalize, in some regions reducing shrub growth through local moisture limitation and in other regions promoting shrub growth through local warming and precipitation (Buchwal et al. 2020).

The threat of global warming on polar marine food webs

Ocean warming, sea-ice decline, and altered seasonality are major concerns for polar marine food webs (Figs. 1, 2), which are relatively simple and have low resilience, making them particularly vulnerable to perturbations

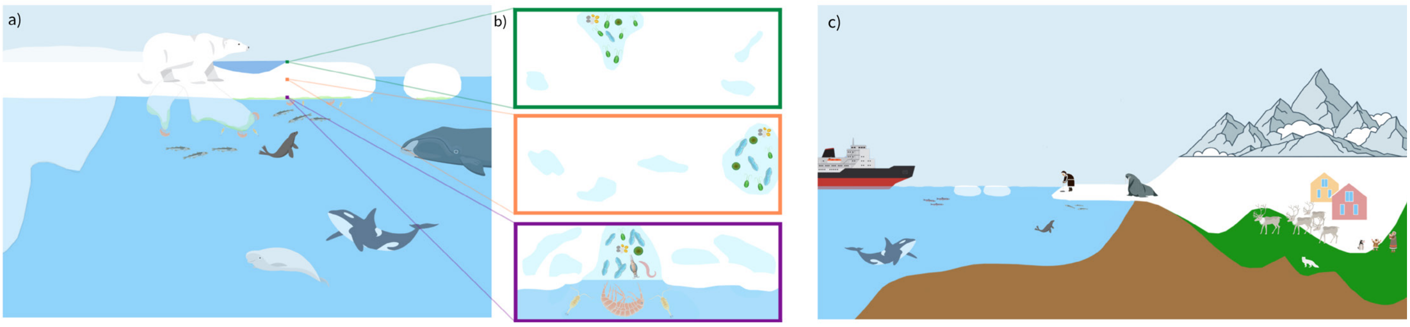

Figure 1: Schematic representation of the **(A)** Arctic ice types and ice-associated food web (partly adapted from Bluhm et al. 2017); **(B)** Arctic sea-ice food web in surface, interior, and bottom layers; and **(C)** Arctic terrestrial-marine ecological linkages (adapted from Meredith et al. 2022). See Figure 2 for legend keys.

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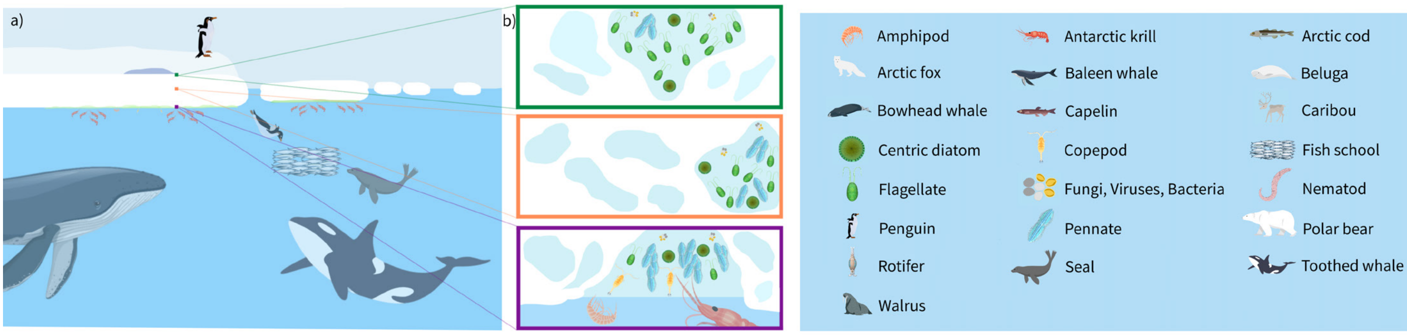

Figure 2: Schematic representation of the **(A)** Antarctic ice types and ice-associated food web (partly adapted from Bluhm et al. 2017); and **(B)** Antarctic sea-ice food web in surface, interior, and bottom layers.

at all trophic levels. The ongoing environmental changes exert a large stress at the base of the food web, with alterations in abundance, distribution, composition, and seasonality of the microbiota, which may result in major cascading effects.

Lannuzel et al. (2020) produced non-quantitative future expectations of how the changing sea-ice environment will likely impact the sea-ice biogeochemical dynamics and associated ecosystems in the Arctic Ocean. In the short term, sea-ice primary production is projected to generally increase due to the increased light availability after sea-ice and snow thinning, as long as nutrients are plentiful (Tedesco et al. 2019). However, as a consequence of earlier melt onset, the earlier timing of algal blooms is likely to have negative downstream effects on ice-dependent consumers such as copepods, amphipods, and Arctic cod, all of which are dependent on the availability of ice-algal food sources for their overwintering survival (Søreide et al. 2010). Consequently, a decline in conditions of those species feeding preferably on Arctic cod, such as ringed seals, belugas, and bowhead whales (Harwood et al. 2015; Fig. 1a), and the expansion northwards of sub-Arctic species such as capelins and killer whales, are expected (Fig. 1c).

The main population of Antarctic krill inhabiting the Southern Ocean has been found to have contracted significantly southward in response to rapid environmental changes (Atkinson et al. 2019). The changes in the distribution of krill populations directly impact fish, penguins, seals and whales dependent on krill for their survival, and indirectly impact the higher trophic level predators in the food web (Fig. 2a). A similar effort to that of Lannuzel et al. (2020), but focusing on the near-future changes of the Antarctic sea-ice ecosystem, is currently ongoing (Klaus Meiners, personal communication).

Hence, various consequences are to be expected for several ecosystem services. In a rigorous synthesis of the ecosystem services linked to the sea-ice ecosystem, Steiner et al. (2021) highlight that the sea-ice ecosystem supports all four ecosystem service categories: "supporting services" provided in the form of habitat, including feeding grounds and nurseries; "provisioning services" through harvesting, and medicinal and genetic resources; "cultural services" through Indigenous and local knowledge systems, cultural identity, and spirituality, and via cultural activities, tourism and research; and "regulating services" such as climate, through light regulation, the production of biogenic aerosols, halogen oxidation and the release/uptake of greenhouse gasses such as carbon dioxide.

Steiner et al. (2021) also emphasize that sea-ice ecosystems meet the criteria for ecologically or biologically significant marine areas and deserve specific attention in evaluating marine-protected area planning since conservation could help protect some species and functions. However, the paucity of sea-ice observations hinders our ability to understand, prepare for, and manage the changes. Due to their remote location and common extreme weather conditions, observations in the polar oceans are spatially and temporally sparse, satellite remote sensors have limited applicability, and the quality of sedimentary biological proxies is frequently disturbed.

Our inability to quantitatively predict the ecological changes associated with Arctic sea-ice decline during times of striking changes has led this research topic to be qualified as a "crisis discipline" in "conservation biology" (Macias-Fauria and Post 2018). Given the recent accelerating sea-ice changes in the Southern Ocean and the potential detrimental impacts on the associated ecosystems, we suggest that the ecological consequences of sea-ice changes should be qualified as a "crisis discipline" also in the Antarctic. Urgent knowledge and prompt decisions are needed in polar oceans facing significant uncertainties.

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