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EDITED BY
Torben Røjle Christensen,
Aarhus University, Denmark

REVIEWED BY
Jan Kavan,
Masaryk University, Czechia
Oran Young,
University of California, Santa Barbara,
United States

*CORRESPONDENCE
Bérengère Husson,
✉ berengere.husson@hi.no

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Borealization impacts shelf ecosystems across the Arctic

Bérengère Husson[1]*, Bodil A. Bluhm[2], Frédéric Cyr[3], Seth L. Danielson[4], Elena Eriksen[1], Maria Fossheim[5], Maxime Geoffroy[2,6], Russell R. Hopcroft[7], Randi B. Ingvaldsen[8], Lis L. Jørgensen[9], Connie Lovejoy[10,11], Lorenz Meire[12,13], Franz Mueter[4], Raul Primicerio[9,14] and Mie Winding[13]

[1]Ecosystem processes , Institute of Marine Research, Bergen, Norway, [2]Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø, Norway, [3]Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, St. John's, NL, Canada, [4]College of Fisheries and Ocean Sciences, University of Alaska, Fairbanks, AK, United States, [5]Barents Sea and Arctic Ocean Program Direction, Institute of Marine Research, Tromsø, Norway, [6]Centre for Fisheries Ecosystems Research, Fisheries and Marine Institute of Memorial University of Newfoundland and Labrador, St. John's, NL, Canada, [7]Institute of Marine Science, University of Alaska, Fairbanks, AK, United States, [8]Oceanography and Climate, Institute of Marine Research, Bergen, Norway, [9]Ecosystem Processes, Institute of Marine Research, Tromsø, Norway, [10]Département de Biologie, Université Laval, Québec City, QC, Canada, [11]Takuvik International Research Laboratory, Université Laval, Québec City, QC, Canada, [12]Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta Systems, Yerseke, Netherlands, [13]Greenland Climate Research Centre, Greenland Institute of Natural Resources, Nuuk, Greenland, [14]Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway

Climate change is rapidly modifying biodiversity across the Arctic, driving a shift from Arctic to more boreal ecosystem characteristics. This phenomenon, known as borealization, is mainly described for certain functional groups along sub-Arctic inflow shelves (Barents and Chukchi Seas). In this review, we evaluate the spatial extent of such alterations across the Arctic, as well as their effects on ecosystem-level processes and risks. Along the inflow shelves, borealization is driven by long-term strengthened inflow of increasingly warm waters from the south and punctuated by advection and low sea ice extreme events. A growing body of literature also points to an emerging borealization of the other Arctic shelf ecosystems, through a "spillover" effect, as local changes in environmental conditions enable movement or transport of new species from inflow shelves. These modifications are leading to changes across functional groups, although many uncertainties remain regarding under-sampled groups, such as microbes, and technical challenges of consistent, regular monitoring across regions. There is also clear consensus that borealization is affecting phenology, species composition, community traits, population structure and essential habitats, species interactions, and ecosystem resilience. Non-dynamic environmental factors, such as depth and photoperiod, are thought to limit the complete borealization of the system, and may lead to intermediate, "hybrid" ecosystems in the future. We expect current borders of Arctic and boreal ecosystems to progress further northward and ultimately reach an equilibrium state with seasonal borealization. Risks to the system are difficult to estimate, as adaptive capacities of species are poorly understood. However, ice-associated species are clearly most at risk, although some might find temporary refuge in areas with a slower rate of change. We discuss the likely character of future Arctic ecosystems and highlight the uncertainties. Those changes have implications for local communities and the potential to support Blue Growth in the Arctic. Addressing these issues is necessary to assess the full scale of Arctic climate impacts and support human mitigation and adaptation strategies.

KEYWORDS

Climate change, Arctic, biodiversity, ecosystem functioning, species distribution, Blue Growth

1 Introduction

Global redistributions of marine species under climate change are leading to unprecedented changes in biodiversity worldwide (Pinsky et al., 2013; Poloczanska et al., 2016). These redistributions are largely driven by populations following their thermal preferences (Burrows et al., 2019), leading to long-term poleward or depth displacements of species with lower thermal affinities. At mid-latitudes, poleward shifts of fish species have led to the progressive declines of cold-affinity boreal species in favour of warm-affinity Lusitanian species (Dulvy et al., 2008; Hofstede et al., 2010; Engelhard et al., 2011). At higher latitudes, regions that border the Arctic and receive the inflows from lower latitude Atlantic- and Pacific-influenced waters are the ultimate gateways of the poleward displacements of boreal species to the Arctic. Beyond these frontiers is the Arctic, with its strong seasonal light variability, and harsh environmental and living conditions, to which resident communities are well-adapted.

Climate change and Arctic amplification are responsible for warming rates in this region nearly 4 times faster than the rest of the world (Rantanen et al., 2022), and are causing structural changes across the Arctic ecosystems. Global projections suggest increasing biomass of commercial species coming from lower latitudes and thriving in increasingly productive, warmer, and ice-free ecosystems (Lam et al., 2016; Lotze et al., 2019; Tai et al., 2019). However, these projections vary strongly both in magnitude and direction among models (Bryndum-Buchholz et al., 2019). In addition, the strong seasonality in solar radiation will remain in the north due to the Earth inclination on its axis that could limit boreal species' northward progress and survival (Kaartvedt, 2008). A large body of literature reports evidence of such northward shifts into the Arctic by boreal species of many functional groups, driven by local habitat modifications and advection of warm water and associated species from lower latitudes (Polyakov et al., 2020a; Brandt et al., 2023), a phenomenon called "borealization" (Fossheim et al., 2015). Arctic shelves and basins vary strongly with regard to hydrological, geochemical and biological functioning (Carmack and Wassmann, 2006). However, they are also strongly connected through large scale atmospheric, sympagic and oceanic circulation patterns (Carmack and Wassmann, 2006; Wassmann et al., 2020). Understanding the possible temporal and geographical extent of this borealization initially observed at inflow shelves, the risk posed to Arctic species and ecosystem functioning, and the consequences for the dependent local human inhabitants, are essential to facilitate planning for an adaptive, equitable management of Arctic and sub-Arctic ecosystems, and for the conservation of biodiversity.

Borealization of Arctic and sub-Arctic regions can be defined as a process by which ecosystems that were historically characterised as Arctic are progressively or transitively acquiring features typical of more southern, boreal ecosystems (Polyakov et al., 2020a). Sea surface temperatures in Arctic marine ecosystems are typically near or at the freezing point year-round (in the central Arctic Ocean) or seasonally (mostly on the shelves). In the central Arctic Ocean, the stratification is strong throughout the year with a cold, fresh Arctic water mass laying on top of the warmer and saltier Atlantic water mass. The overlaying fresher Arctic water mass contributes to high local sea-ice production.

Arctic and sub-Arctic ecosystems display very distinct communities and functions tuned to local conditions. In first-year ice areas, at the edge of the central Arctic Ocean and in seasonally ice-covered shelf regions, remineralized and recycled nutrients are used by ice-algae that can lead to a strong under-ice bloom (Arrigo et al., 2012; Assmy et al., 2017), followed by a stronger pelagic bloom dominated by diatoms when the ice is melting (Ardyna and Arrigo, 2020). There is greater diatom diversity in the sea-ice compared to the water column, where diversity differs by region with intermediate levels in the Canadian Arctic Archipelago and Pacific Arctic, and lower diversity in the Russian inner shelf seas, Hudson Bay and the Central Arctic Basin (CAFF, 2017). Microbial diversity (about ~2000 taxa for pelagic and sympagic eukaryotes, Poulin et al., 2011) includes endemic microbial populations that have evolved to thrive under the extreme ice-influenced local conditions (Lovejoy et al., 2006; Lovejoy et al., 2007; Verde et al., 2016; van Leeuwe et al., 2018; Dorrell et al., 2023). Phytoplankton especially are able to survive prolonged dark periods that limit photosynthesis (Kvernvik et al., 2018; Lacour et al., 2019; van de Poll et al., 2020), using flexible strategies such as mixotrophy or overwintering as metabolically quiescent cells or as cysts (Stoecker and Lavrentyev, 2018). Some Arctic bacteria also use normally recalcitrant sources of organic carbon, including terrestrial organic matter from the large rivers that continue to flow into the Arctic even during winter (Colatriano et al., 2018).

Zooplankton are the primary link between the primary producers and higher trophic levels in Arctic and sub-Arctic marine food-webs. Some 300–400 zooplankton species occur in the Arctic water column (Kosobokova et al., 2011). Hyperiid amphipods and large, lipid-rich mesozooplankton, such as *Calanus glacialis* and *Calanus hyperboreus* play a crucial trophic role in the Arctic ecosystem (Søreide et al., 2010; Kohlbach et al., 2016; Brown et al., 2017). Gelatinous zooplankton, including hydrozoans (e.g., *Aglanta digitale*), are also ubiquitous in the Arctic pelagic niche (Kosobokova et al., 2011), and in the central Arctic basins, the gelatinous zooplankton appears to be more abundant than pelagic fishes (Ingvaldsen et al., 2023). The pan-Arctic hosts over 5,000 metazoan species, including 229 fish species (Bluhm et al., 2011b; Mecklenburg et al., 2011). Benthic communities sometimes rely strongly on the sympagic-benthic coupling driven by sinking sea ice algae to the bottom after they bloom and at ice breakup (Koch et al., 2020; Cautain et al., 2022). Arctic demersal and benthic fish communities are mainly composed of species such as sculpins (Cottidae), snailfish (Liparidae), eelpouts (Zoarcidae) and eelblennies (Lumpenidae), but the benthos is typically dominated by invertebrates including many benthic polychaetes and other worms, molluscs, arthropods and echinoderms. In contrast, the pelagic compartment is less diverse. Polar cod (*Boreogadus saida*) sometimes represents more than 95% of the fish species abundance (Geoffroy et al., 2023), while ice cod (*Arctogadus glacialis*), saffron cod (*Eleginus gracilis*), capelin (*Mallotus villosus*) and Arctic sand lance (*Ammodytes hexapterus*) are less abundant. Mesopelagic species are scarce in the deep basins. Glacier lanternfish (*Benthosema glaciale*), armhook squid (*Gonatus fabricii*), and even single individuals of Atlantic cod (*Gadus morhua*) are also present in the pelagic, but in low densities (Snoeijs-Leijonmalm et al., 2022; Ingvaldsen et al., 2023).

Typically, offshore boreal ecosystems exhibit contrasting characteristics, with warmer, saltier, and less stratified waters, higher phytoplanktonic primary production, smaller mesozooplankton species and abundant krill and pelagic amphipods in the North Atlantic compared to Arctic ecosystems (e.g., Dalpadado et al., 2003; Dalpadado et al., 2014; Weydmann et al., 2014). Similar gradients exist in the Pacific-Arctic but zooplankton communities on the extensive shallow inflow shelves are dominated by neritic species (Questel et al., 2013; Hunt et al., 2014; Ershova et al., 2015). The boreal pelagic niche is more diverse than the Arctic one, including a more prominent mesopelagic compartment in deeper water hosting, among the fishes, abundant myctophidae and stomiidae (Sameoto, 1989; Byrkjedal et al., 2004). Boreal and Arctic communities of demersal fish and benthic invertebrates differ in terms of traits such as temperature tolerance windows (Aune et al., 2018; Jørgensen et al., 2022; Logerwell et al., 2022), longevity (Ravelo et al., 2017), and age-at-maturity. Boreal fish include many mobile generalists of large size, such as Atlantic cod (*Gadus morhua*), Pacific cod (*G. macrocephalus*) and walleye pollock (*G. chalcogrammus*). This higher generalism implies a higher trophic redundancy, but also connectivity (i.e., feeding link richness) in the trophic network (Livingston and Tjelmeland, 2000; Kortsch et al., 2019). One of the key questions posed by the occurring process of borealization is whether this process can ultimately lead to a complete transformation of Arctic shelf ecosystems into boreal ones (replacement scenario), or to a hybrid version of both ecosystems (hybridization scenario, “cocktail”), and what the consequences for overall ecosystem functioning may be.

We review the existing knowledge on the mechanisms driving borealization and compile the evidence of borealization across ecosystem compartments in the marine Arctic. Our objectives are 1) to explore the spatial and temporal extent of borealization across the Arctic shelves, 2) to explore its extent across functional groups and consequences for ecosystem functioning, 3) to discuss the degree of transformation of Arctic ecosystems into boreal ones, now and in the future, 4) to discuss consequences for societies and management.

2 The environmental context of borealization across the pan-Arctic

The Arctic climate is driven by large scale processes within, and interactions between, the atmosphere, the cryosphere and the ocean (Timmermans and Marshall, 2020). Powerful local feedback processes associated with the air-sea-ice system amplify warming and sea-ice loss (Serreze and Barry, 2011; Ivanov et al., 2016; Polyakov et al., 2020b; Previdi et al., 2021). The recent decades have shown accelerated atmospheric and oceanic warming caused by a combination of global, regional and local drivers (Polyakov et al., 2020a; Shu et al., 2021; Isaksen et al., 2022; Smedsrud et al., 2022). Numerous studies have reported the many transformations of the entire Arctic system, including the intensification of hydrological cycles (increased precipitation and river discharge), glacier and sea ice melting and thinning, and modal shifts in atmosphere altering ocean circulation patterns (Greene et al., 2008; Wood et al., 2015; Box et al., 2019; Huntington et al., 2020; Polyakov et al., 2023). Extreme seasonal ice or temperature conditions have become more frequent (Hinzman et al., 2005; Dörr et al., 2021, Pécuchet et al., 2024). The current warming appears to have peaked between 2012 and 2018 for most of the Arctic (Danielson et al., 2020; Ingvaldsen et al., 2021), accompanied by record low sea ice cover (Stabeno and Bell, 2019). Nevertheless, the years post 2018 are a temporary reprieve, and the Arctic climate is projected to continue to warm as a result of increasing levels of atmospheric carbon dioxide (Pörtner et al., 2019).

Regional differences in climate change footprint across the Arctic can mostly be explained by the different hydrologic and geographic contexts of the sub-Arctic areas (Figure 1). These can be separated into four categories: the *inflow shelves* (Bering and Chukchi seas on the Pacific side, Barents Sea on the Atlantic side, west Greenland shelf), the *outflow shelves* (Canadian Arctic Archipelago, Western Baffin Bay, Eastern Greenland Shelf), the *interior shelves* (Kara, Laptev and Siberian Seas) and the *Arctic basins* (Carmack and Wassmann, 2006; Wassmann et al., 2020). Sea ice loss in the Barents and Bering inflow shelves are strongest during winter (Figure 2). This is a direct effect of warmer or stronger advection of sub-Arctic waters into the Arctic (Onarheim et al., 2018; Woodgate, 2018), and causes an increase in the extent of thermal habitat associated with boreal ecosystems throughout the year. Year-long suitable conditions favours the gradual borealization of the inflow shelf ecosystems, which can occur due to advection from the sub-Arctic seas and along the flow into the basins (Polyakov et al., 2020a). The Chukchi Sea and interior shelves, as well as the Canadian Arctic Archipelago, on the other hand, show strong sea ice loss during summer (Figure 2), but are strongly connected to neighbouring shelves through currents (Figure 1). Progressing borealization on to the interior shelves could occur through planktonic species advected through lateral basin-shelf or inter-shelf exchanges when sea ice loss and warming is sufficient (Nelson et al., 2014), and through mobile boreal shelf species reaching their northernmost depth habitat at the inflow shelves, thereby expanding their distribution to nearby shelves.

We used Sea Surface Temperature (SST) data to support our general comparison of the upper ocean warming experienced by Arctic shelves in the past century. We note that as these data are based on surface waters, they are interlinked with the loss of sea ice

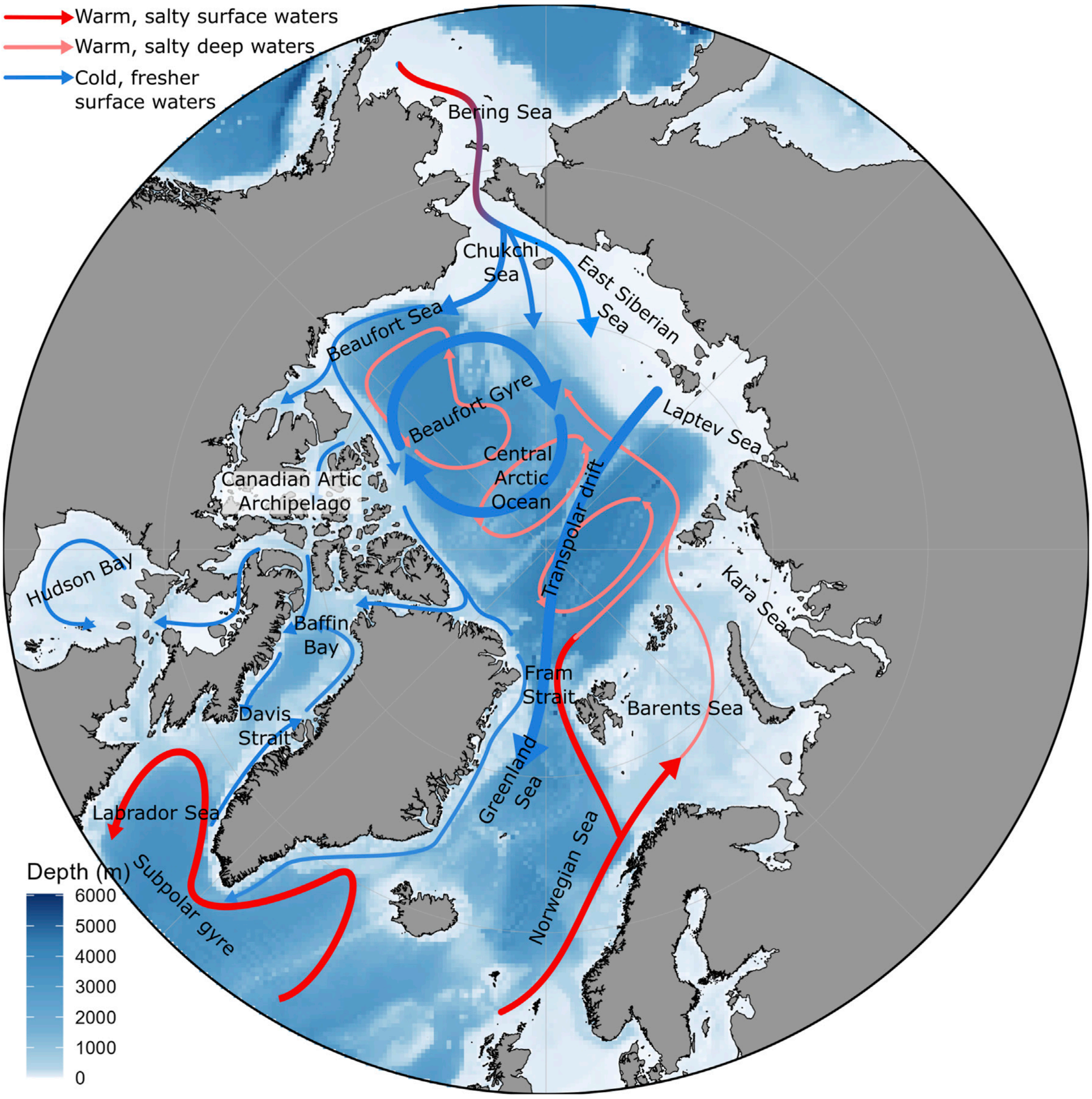

FIGURE 1
Main arctic and sub-arctic oceanic currents. Adapted from Anderson and Macdonald (2015), Armitage et al. (2017), and Constantin and Johnson (2023).

and may not be representative of changes at depth. The NOAA Extended Reconstructed SST V5 (ERSSTv5; Huang et al., 2017) is a global monthly SST analysis from 1854 to the present derived from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS) data with missing data filled in by statistical methods. The data are available on a 2° × 2° (latitude-longitude) grid globally, but here were restricted to latitudes north of 50°N (see coverage in Figure 3). Several analyses were performed with this dataset. To illustrate the regional differences in warming rates, linear trends were calculated on the annual summer (July-September) temperatures for each pixel of the dataset for the period 1950–2023 (Figure 3) and averaged by regions (Table 1). Regions were defined following the Arctic Ocean and Adjacent Seas (AOAS) from the Conservation of Arctic Flora and Fauna (CAFF). Monthly SSTs averaged over the same regions for each year also highlight the warming trends and the increasing length of the open water season over time (Figure 4). Finally, decadal anomalies of summer SSTs (in °C) were calculated. For this analysis, the annual time series of summer mean SST for each region was built by averaging monthly values between July and September for a given year. Anomalies were calculated for each year by subtracting the long-term summer average over 1900–2000, before computing averages of the annual anomalies for each 10-year periods (1955–1964, 1965–1974, until 2015–2024). Decadal anomalies are illustrated per region (Figure 5), and values are provided for the last decade (Table 1).

Summer surface waters of the Arctic Ocean have been warming unevenly over the last seven decades (Figure 3). The warming trends are in relatively close correspondence with the sea ice loss trends (Figure 2). When averaged by region, greatest warming trends are

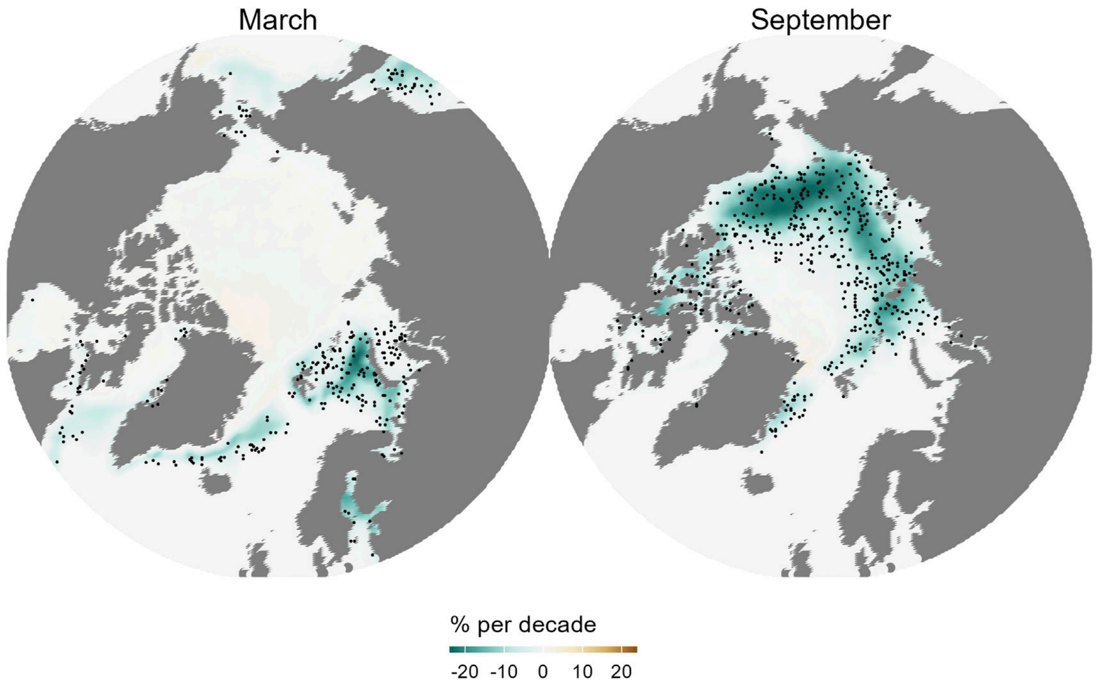

FIGURE 2
From copernicus climate indicators for sea-ice (https://climate.copernicus.eu/climate-indicators/sea-ice). Linear trends in sea ice concentration during 1979–2023 (% per decade) for March and September. Dots indicate areas where the trends are statistically significant. Credit: ECMWF, copernicus climate change service (C3S) C3S/ECMWF/EUMETSAT/MET Norway.

found in the northernmost regions of the Russian (Kara, Laptev and Siberian seas), Alaskan (Chukchi Sea) and Canadian Arctic coasts (Beaufort Sea and the Canadian Arctic Archipelago, Table 1). Those regions are mainly outflow shelves and interior shelves. Outflow shelves such as the East Greenland and the Canadian Arctic Archipelago also show signs of significant decrease in multi-year ice and relocation of different ice types (Sou and Flato, 2009; Michel et al., 2015). In contrast, interior shelves experience the effects of changing Arctic coasts, such as massive erosion in non-lithified coasts, and of run-off of freshwater and organic and inorganic materials contained in it (e.g., Williams and Carmack, 2015; Irrgang et al., 2022). The central Arctic basin north of Greenland and the Canadian Arctic Archipelago did not show large trends in SST due the quasi-permanent sea ice cover.

These warming trends in surface waters are, in some regions, associated with both warming and a longer ice-free summer season (deeper tones of yellow and widening of the white lines towards the top of the panels, Figure 4). The regions with the more moderate surface warming trends are generally those not exhibiting full sea ice cover for any month of the year (regions without white lines in Figure 4). Longer-term trends in summer SST anomalies (Figure 5) confirm earlier studies revealing that the warming of the Arctic started in most of the region in the second half of the 20th century, with an overall acceleration in the last three decades (Bengtsson et al., 2004; Matishov et al., 2012; Shu et al., 2021; Isaksen et al., 2022). The Canadian Arctic (Beaufort Sea, Canadian Arctic Archipelago and the Hudson Bay Complex) as well as the Greenland and Kara seas exhibited the largest SST increases in the last decade (2015–2024) compared to the long-term average (Table 1).

Compared to other regions, inflow shelves experienced slower warming trends in the summer (Figure 3; Table 1). However, this observation changes when studying other seasons. The Chukchi Sea, in autumn, and the Barents Sea, in winter, displayed the largest warming rates of air temperature in the Arctic since the 1980’s (Koenigk et al., 2020). Arctic waters cool to the freezing point prior to ice formation in autumn; warmer waters thus transfer more heat from the ocean to the atmosphere during the fall process of oceanic heat loss (Danielson et al., 2020). The Chukchi and Barents Seas are under the dual influence of the Arctic and the lower latitude systems that drive very strong inter- and intra-annual variability, with seasonal sea-ice cover, changes in temperature and important contrasts in seasonal light regime. These seas are the main gateways to borealization (Polyakov et al., 2020a). In the hydrosphere, their systems have evolved toward something less Arctic, and more similar to lower latitudes in the northern Pacific and the Atlantic, two phenomena referred as “Pacification” and “Atlantification”, respectively (Polyakov et al., 2017; Danielson et al., 2020; Ingvaldsen et al., 2021). Both are driven by anomalous advection of warmer Pacific and Atlantic water (Woodgate et al., 2010; Woodgate, 2018; Ingvaldsen et al., 2021; Smedsrud et al., 2022), leading to higher ocean heat transport into the shelf ecosystems and the Arctic (Xu et al., 2024). Consequently, average temperatures in both systems are increasing, at a rate of +0.04°C/year since 1980 in the Bering Strait and on the Chukchi Sea shelf (Danielson et al., 2020), and +0.05°C/year since 2000 in the Barents Sea (Ingvaldsen et al., 2021). The inflow shelf changes are also characterised by the loss of sea ice extent, increased open water season duration and faster transitions (Frey et al., 2015; Danielson et al., 2017; Onarheim et al., 2018; Dalpadado et al., 2020).

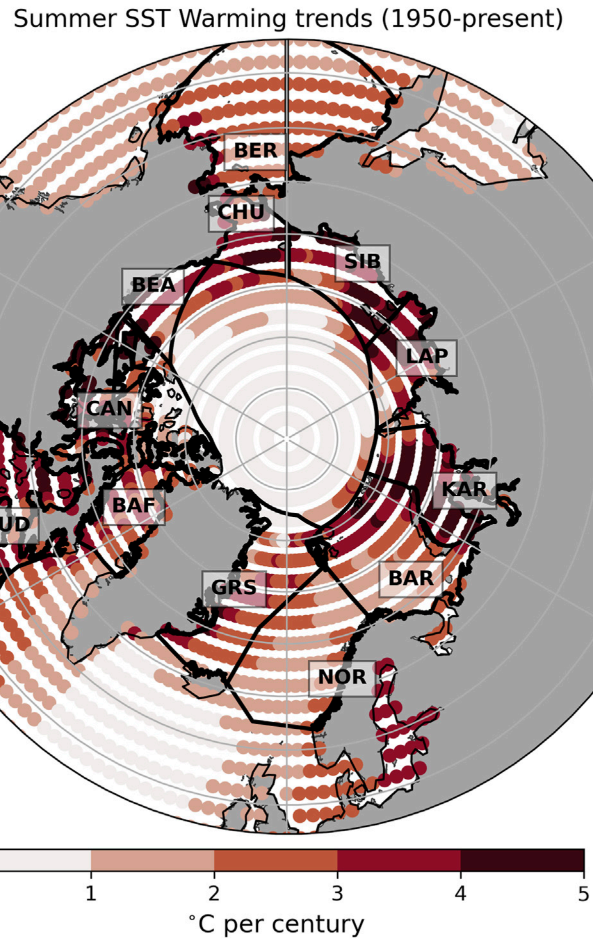

FIGURE 3
Map of summer (July-September average) SST warming trends (in °C per century) between 1950 and 2024 for each pixel (2° × 2° latitude-longitude) derived from ERSSTv5. The Arctic Ocean and adjacent Arctic seas (AOAS) regions, drawn here in black, were used for further regional analyses. These regions are (counterclockwise from top): Bering Sea (BER), Chukchi Sea (CHU), Beaufort Sea (BEA), Canadian Arctic Archipelago (CAN), Hudson Bay Complex (HUD), Baffin Bay (BAF), Greenland Sea (GRS), Norwegian Sea (NOR), Barents Sea (BAR), Kara Sea (KAR), Laptev Sea (LAP) and Siberian Sea (SIB).

3 Evidence of borealization across the Arctic and impact on the functioning of ecosystems

3.1 Changes in the environment affect Arctic biogeochemistry and microbial communities

Climate driven changes in atmospheric, ice and oceanic conditions are likely resulting in shifts in the biogeochemical processes and microbial communities at pan-Arctic scales. However, a comprehensive understanding of regional trends and potential disparities among regions is hampered by the scarcity of long-term datasets of observed or modelled conditions (CAFF, 2017; Juranek, 2022). A set of studies describing the different hydrographic functioning and ecosystem production have revealed a wide variety of properties and pathways in the carbon cycle across the Arctic (Dunton et al., 2006; Grebmeier et al., 2006; Hirche et al., 2006; Hop et al., 2006; Michel et al., 2006; Rysgaard and Nielsen, 2006; Schmid et al., 2006; Tremblay et al., 2006; Wassmann et al., 2006a). These carbon cycles vary in efficiency depending on the processes transforming organic matter into nutrients (carbon mineralisation), and nutrients into organic matter (primary productivity). Productivity on the Arctic shelves is generally considered to be limited by the concentrations of available nitrogen compounds, especially in the Pacific Arctic (Mills et al., 2018; Ko et al., 2020), rather than by irradiance limitation from sea-ice and photoperiod (Tremblay and Gagnon, 2009; Tremblay et al., 2015). Most of the nutrient supply is advected through inflow shelves (Le Fouest et al., 2013b; Torres-Valdés et al., 2013; Tremblay et al., 2015). River inputs into sub-Arctic inner shelves may also be an important local source of nutrients and organic matter from land (Dittmar and Kattner, 2003; Dunton et al., 2006; Carmack et al., 2016), and estimates suggest terrestrial sources with coastal erosion, contribute to 28%–51% of net primary productivity in the Arctic Ocean via the Transpolar Drift (Le Fouest et al., 2013a; Terhaar et al., 2021), but see contrasting results in Le Fouest et al. (2013a).

At the pan-Arctic scale, rising temperatures and prolonged open water seasons have driven substantial increases (>50% over two

TABLE 1 SST mean trends (in °C per century) averaged over 1950–2023 for each of the Arctic Ocean and Adjacent Seas (AOAS) regions defined in Figure 3. The 6 regions with trends larger than 3°C per century are in bold. For SST anomalies during the last decade (2015–2024) compared to the 1900–2000 period, the 5 regions with anomalies larger than +2°C are in bold.

AOAS region	Mean trend (°C per century)	2015–2024 anomaly (°C)
Bering Sea	+2.3	+1.6
Chukchi Sea	**+3.7**	+1.8
Beaufort Sea	**+3.2**	**+2.6**
Canadian Arctic Archipelago	+2.3	**+2.5**
Hudson Bay Complex	**+3.4**	**+2.6**
Baffin Bay	+2.7	+1.9
Greenland Sea	+2.3	**+2.6**
Norwegian Sea	+1.9	+1.9
Barents Sea	+2.9	+1.3
Kara Sea	**+4.0**	**+2.3**
Laptev Sea	**+3.2**	+1.2
Siberian Sea	**+3.8**	+1.3

decades) in sub-Arctic primary productivity, with earlier and extended blooms of pelagic phytoplankton (Arrigo et al., 2008; Kahru et al., 2011; Kahru et al., 2016; Hill et al., 2013; Hill et al., 2018; Ardyna et al., 2014; Arrigo and van Dijken, 2015). In addition, the decrease in multi-year ice and increase in first-year ice extent are driving a temporary increase in ice-algae habitat (Lim et al., 2022). Production increased in most regions but with varying magnitude (Arrigo and van Dijken, 2015). The Barents Sea was the area that experienced the highest increase in primary production over the last two decades (Dalpadado et al., 2020; Lewis et al., 2020). Primary production has also increased in spatial extent in the Bering Sea during warm years (Nielsen et al., 2024). The Canadian Arctic Archipelago, Baffin Bay and the eastern Greenland shelf display an altered functioning, with changes in productivity spatial-temporal patterns (Michel et al., 2015; Blais et al., 2017; Mayot et al., 2020). Data are scarce for other shelves, but short term studies also revealed interannual variation in production and particulate organic carbon export between years with varying sea ice cover (Lalande et al., 2009; Bienhold et al., 2022).

In recent years, ice dynamics and water temperature no longer suffice to explain increases in primary production on inflow shelves (Lewis et al., 2020). It has been hypothesised that the increased transport of deep Atlantic waters into the Arctic might have increased dissolved inorganic nitrogen (DIN) supply, favouring higher primary production in downstream regions (Henley et al., 2020; Lewis et al., 2020). However, despite increasingly northward Atlantic water flow and subsequent increased vertical mixing, multiple studies point to a long-term decrease in nutrients across most of the pan-Arctic, with the exception of the pan-Arctic slope (Oziel et al., 2022). Oxygen and nutrients seem to have decreased within the halocline of the Eastern and Western Eurasian Basin (Polyakov et al., 2020a). Similarly, there has been a decline in nitrate concentrations in the Atlantic water inflow into the Barents Sea between 1990–2010 (Oziel et al., 2017), and no long-term (35 years) trend in nutrients from Atlantic water flowing into the Arctic north of Svalbard (Duarte et al., 2021). In the Chukchi and Beaufort seas, only oxygen concentration has increased (Polyakov et al., 2020a), while nitrate and phosphate concentrations have decreased by 79% and 29% respectively (Zhuang et al., 2021). This was hypothesised to result from the joint effect of decreased vertical mixing following the strengthened stratification due to the loss of multi-year sea ice, and the increased consumption by primary producers (Zhuang et al., 2021). At interior and outflow shelves, nitrogen discharge from river outputs is usually quickly utilised, for example, through efficient denitrification in the Laptev Sea (Sanders et al., 2022; Tuerena et al., 2022), and nitrate and other dissolved inorganic nutrient fluxes from land seem to have declined (Tank et al., 2023). Lack of observations currently greatly limits our understanding of nutrient transport and budgets (Torres-Valdés et al., 2016).

Changes in primary production can also be linked to changes in phytoplankton communities. Phytoplankton communities affect carbon flux attenuation and production regimes (Ardyna et al., 2011; Wiedmann et al., 2020), and vary with environmental conditions across all Arctic shelves and basins (Ardyna et al., 2011; Min Joo et al., 2012; Lee et al., 2019; Ibarbalz et al., 2023). For example, small algae, more efficient at assimilating nutrients and thus potentially more competitive compared to local larger species, have been observed in higher quantities in the Canada Basin and coastal Canadian Arctic Ocean (Li et al., 2009; Blais et al., 2017), and in the Atlantic water masses west of Svalbard (Lalande et al., 2013). In the Beaufort Sea, microbial communities have transitioned towards taxa characteristic of oligotrophic environments (Comeau et al., 2011). In addition, strong advection at inflow shelves has driven the northward shift of temperate species of coccolithophores (Winter et al., 2014; Neukermans et al., 2018; Oziel et al., 2020). In contrast, there is no evidence of temporal changes in microbial community composition or biomass in the North Water (northern Baffin Bay) or the Laptev Sea (Freyria et al., 2021; Bienhold et al., 2022). In the rest of the Arctic, time series are scarcer, but microbial communities, including phytoplankton, have

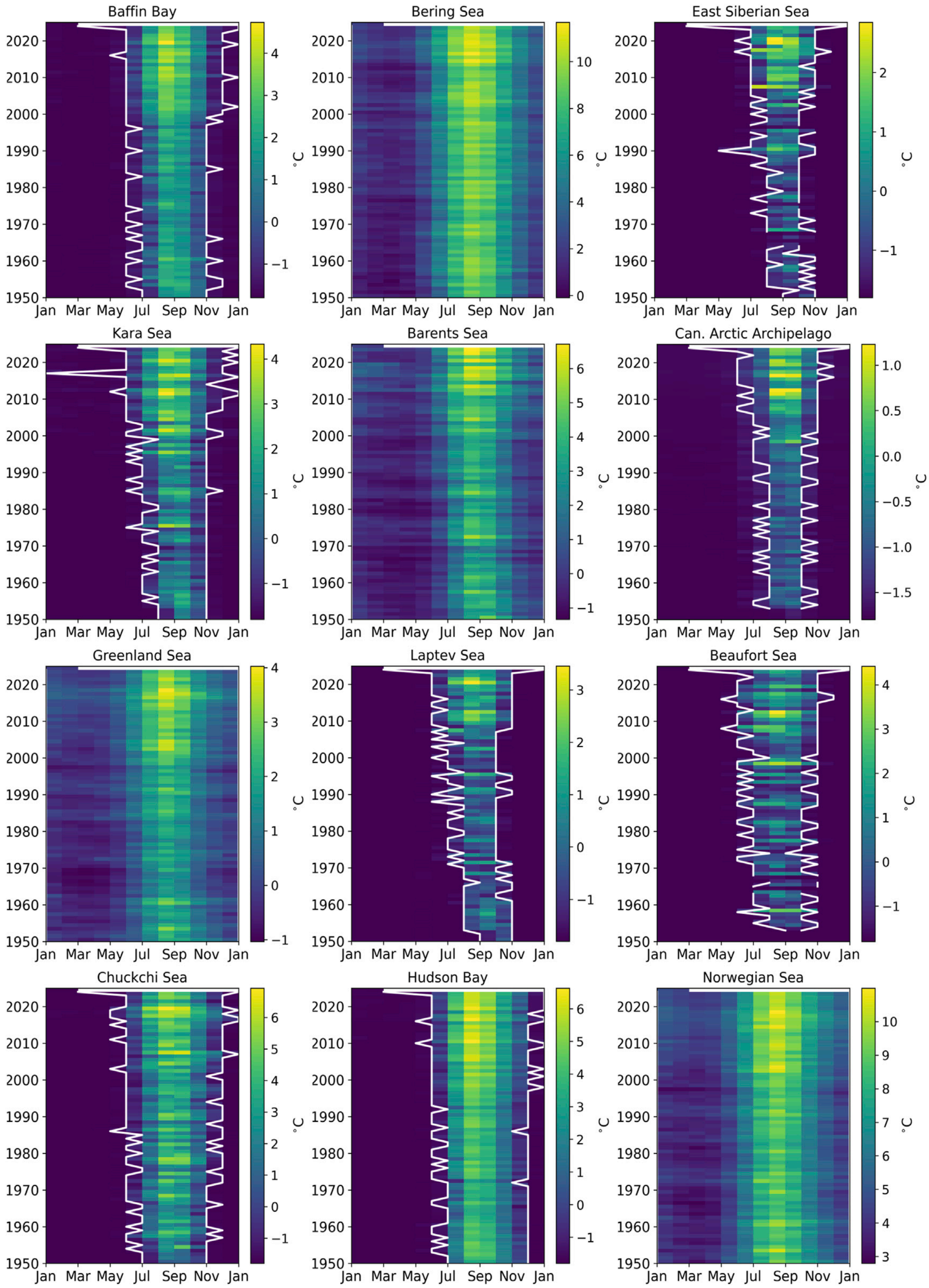

FIGURE 4
SST annual cycles between 1950 and present for each of the regions of the arctic identified in Figure 3. For each year (vertical axis), the averaged SST is plotted for each month on the horizontal axis. Months with a 100% ice cover are at a fixed value of −1.8°C (dark blue). This allows us to plot the opening and closure of the open water period defined here as the first and last month with average temperatures above −1.8°C (white lines). Note that the colour bar scale is different for each subplot.

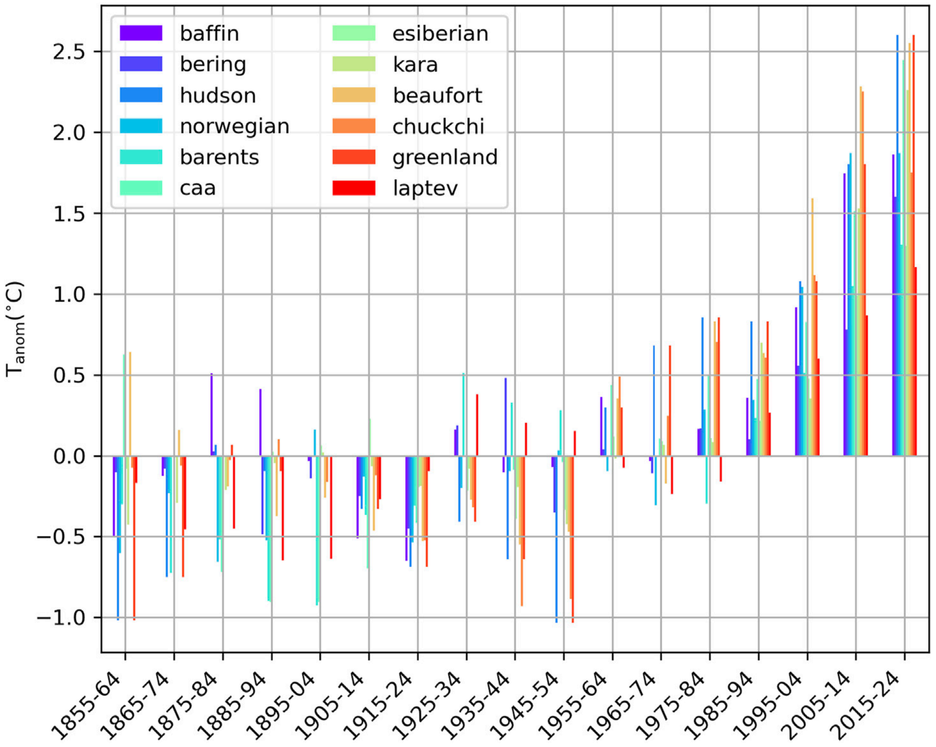

FIGURE 5
Decadal summer (July-September) SST anomalies referenced to the period 1900–2000 for each of the regions in Figure 3.

been characterised by recent studies, setting baselines for the investigation of climate impacts (Demidov et al., 2021; Polyakova et al., 2021; Sukhanova et al., 2021; Liu et al., 2023; Bezzubova et al., 2024). Shifts in microbial communities are likely to drive changes in trophic functioning, affecting the diets, phenology and development of grazing species (Søreide et al., 2010; Daase et al., 2011). Changes in planktonic communities and new environmental conditions can cause harmful algal blooms (HAB), which have direct impacts on the food-webs and human consumption (Okolodkov, 2005; Bruhn et al., 2021). Cases of HAB have been noticeably increasing northward in recent years, with many reports from the Pacific Arctic in particular (Anderson et al., 2021; Anderson et al., 2022; Einarsson et al., 2022; Fachon et al., 2024), with important impacts on top predators, including humans (Hendrix et al., 2021; Lefebvre et al., 2022; Van Hemert et al., 2022).

3.2 Altered habitats and feeding conditions affect pelagic systems

Changes in the environment and in primary productivity (species composition, spatial and temporal patterns) are propagating through the food web, driving the borealization of the pelagic compartments. Indeed, environmental changes trigger contrasting responses of the boreal and Arctic pelagic communities, due to their strong differences in biogeography, life history strategies and functions. For example, many zooplankton communities dominate successively across seasons and regions, varying in their ecological niches and functional traits (Questel et al., 2013; Balazy et al., 2018; Kimmel et al., 2018; Kimmel et al., 2023; Mańko et al., 2020; Mańko et al., 2022; Hop et al., 2021; Darnis et al., 2022; Mazanowski et al., 2023; Van Engeland et al., 2023; Wold et al., 2023). Large, lipid-rich Arctic copepod species such as *C. glacialis* and *C. hyperboreus* can utilise allochthonous production, and survive low productivity periods owing to their large lipid reserves (Hunt et al., 2014; Hirche et al., 2024). Arctic species thus tend to dominate the biomass in late summer/autumn during years with low advection and late sea ice retreat (Kimmel et al., 2018; Spear et al., 2020). However, Arctic zooplankton have a slower increase in respiration rate with rising temperatures compared to their Atlantic counterparts, which implies that, although they might be resilient to warming, Atlantic zooplankton may become more competitive under such conditions (Kaiser et al., 2022). In contrast, boreal species typically consist of smaller zooplankton with less reserves. Along the continental slope of the Atlantic Water inflow, high concentrations of *C. finmarchicus* prevail (Bluhm et al., 2020). Differing traits of Arctic and boreal zooplankton might be adaptative of their respective environment (Renaud et al., 2018), and a shift from lipid-rich Arctic to more boreal communities might not have strong impacts on plankton-feeders as boreal zooplankton occur in larger numbers, over a longer period of time, and have a faster life cycle. However, reduced abundances of lipid-rich *C. glacialis* on the Bering Sea shelf have been associated with poor energetic condition and reduced survival of young walleye pollock (Heintz et al., 2013).

Warm water advection and sea-ice retreat are major determinant of zooplankton community dominance across the Arctic (Ershova et al., 2015; Kimmel et al., 2018; Kimmel et al., 2023; Spear et al., 2019; Abe et al., 2020; Dalpadado et al., 2020; Drits et al., 2023; Ramondenc et al., 2023). Krill, gelatinous zooplankton, ichthyoplankton and young-of-the-year pelagic fish also display different life history strategies and habitat preferences and respond strongly to varying advection regimes (Eriksen and Dalpadado, 2011; Eriksen et al., 2015; Eriksen et al., 2020; Oviatt et al., 2015; Benkort et al., 2019; Deary et al., 2021; Skjoldal et al., 2022). Adult pelagic fish are often less directly affected by variations in environmental conditions. Boreal mobile pelagic fish can relocate to follow the production and expand into newly suitable habitats, thus propagating the borealization of the lower trophic levels up the food chain, although other important factors such as recruitment and availability of suitable spawning habitat also have a strong impact on population spatial-temporal dynamics (Hollowed et al., 2013b; Eriksen et al., 2017). In contrast, some Arctic species such as polar cod are very dependent on ice to complete their life cycle, and loss of sea-ice thus drives a loss of essential habitats for those species (David et al., 2016; Huserbråten et al., 2019; Gjøsæter et al., 2020; Marsh and Mueter, 2020; Deary et al., 2021; Geoffroy et al., 2023).

Long-term borealization has thus been reported on for many pelagic compartments. Shifts from lipid-rich Arctic zooplankton to communities of smaller individuals are of concern in western Greenland (Møller and Nielsen, 2020), the Bering sea (Kimmel et al., 2018; Kimmel et al., 2023), the Chukchi Sea (Abe et al., 2020; Spear et al., 2020; Ershova et al., 2021; Mueter et al., 2021a), Labrador, eastern Greenland and the Barents Sea (Trudnowska et al., 2012; Weydmann et al., 2014; Eriksen, 2016; Eriksen et al., 2017; Freer et al., 2022), and the Fram Strait, main gateway of Atlantic inflow into the Arctic (Gluchowska et al., 2017). Subtle changes in species composition may also be underway within neritic species complexes (Ershova et al., 2015). Krill is also shifting in species composition from Arctic to temperate in the Barents Sea (Eriksen and Dalpadado, 2011; Orlova et al., 2015; Eriksen, 2016), Svalbard, and Bering Sea (Hunt et al., 2016). Lack of long time series hampers our ability to detect changes in zooplankton community composition on the other shelves. Similarly, boreal gelatinous species are thought to also extend northward on the inflow shelves (Brodeur et al., 2002; Brodeur et al., 2008; Eisner et al., 2014; Eriksen et al., 2017; Geoffroy et al., 2018). But drivers of their abundance may be complex (Decker et al., 2023) and historical data and from other shelves are limited, making temporal and regional comparisons difficult.

Further up in the food web, the geographical retreat of polar cod due to the loss of sea-ice is often concomitant with the northward expansion of more southern species, such as capelin, saffron cod or walleye pollock in the Atlantic or Pacific Arctic (Hop and Gjøsæter, 2013; Stige et al., 2019; Wildes et al., 2022; Levine et al., 2023; von Biela et al., 2023). Increased abundance of more southern fish species, such as capelin and Pacific sand lance, are also observed at interior and outflow shelves: in the Canadian Arctic Archipelago (Falardeau et al., 2017), in the Hudson Bay (Gaston et al., 2003), and northern Baffin Bay (Ulrich and Tallman, 2021). While mesopelagic fish have been suggested to be limited in their northward expansion because of the light conditions (Ljungström et al., 2021; Langbehn et al., 2022) or a combination of both light and temperature (Chawarski et al., 2022), studies based on observations rather than modelling have partially challenged the light hypothesis by reporting mesopelagic sound scattering layers partly formed of boreal fish species (e.g., glacier lanternfish *Benthosema glaciale* and juvenile redfish) in the high Arctic (Knutsen et al., 2017; Geoffroy et al., 2019; Snoeijs-Leijonmalm et al., 2022; Ingvaldsen et al., 2023). Moreover, studies looking at both temperature and latitude (a proxy for irradiance) have concluded that temperature fronts might also contribute to hindering the northward range expansion of mesopelagic fish (Chawarski et al., 2022). Data are more limited for the inner shelves of the Kara, Laptev and East Siberian seas, but those ecosystems are often relatively poor in pelagic fish (Hirche et al., 2006; Schmid et al., 2006).

Pelagic borealization is affecting populations and ecosystem functioning. Changes in zooplankton development and community succession along the seasons have been linked to pelagic fish diet and biomass trends (Orlova et al., 2010; Dalpadado et al., 2024), propagating climate effects to upper trophic levels. They also affect first year juvenile fish survival, mainly walleye pollock and polar cod, as lipid-rich species associated with autumn blooms during cold years are a critical source of reserve for the juvenile fish before the winter (Kimmel et al., 2018; Kimmel et al., 2023; Bouchard and Fortier, 2020; Dupont et al., 2020), and as prey size impacts that of its visual predators, as shown by bioenergetic and behavioural modelling studies (Ljungström et al., 2020). In contrast, the sustained advection of krill in the Barents, Chukchi and western Beaufort seas is altering trophic controls and stabilising predator populations (Berline et al., 2008; Eriksen and Dalpadado, 2011; Orlova et al., 2013; Ashjian et al., 2021). Increasing co-occurrence of polar cod with other species such as capelin or Pacific sand lance would lead to more competition for food at inflow and interior shelves, with negative consequences for both species (Orlova et al., 2010; Falardeau et al., 2014; McNicholl et al., 2016; McNicholl et al., 2018; Pedro et al., 2020). Changes in dominant forage fish and zooplankton prey have altered marine mammals' and seabirds' migration patterns and diet across the pan-Arctic, sometimes leading to lower growth rate for chicks or altered demography (Provencher et al., 2012; Chambellant et al., 2013; Gaston and Elliott, 2014; Falardeau et al., 2017; Gall et al., 2017; Balazy et al., 2018; Kuletz et al., 2020; de la Vega et al., 2021; Merkel et al., 2021; Ulrich and Tallman, 2021; Descamps et al., 2022; Moore et al., 2022).

3.3 Changes in benthic demersal systems

Many studies have reported changes in benthic (mostly invertebrates) and demersal (mostly fish) ecosystems across Arctic and sub-Arctic shelves. Signals of borealization are stronger on inflow shelves, where shifts in demersal fish communities have been widely reported, such as in the Barents Sea (Fossheim et al., 2015; Bergstad et al., 2018; Spotowitz et al., 2022), in western Greenland (Post et al., 2021), as well as the northern Bering Sea and, to a lesser extent, the Chukchi Sea (Mueter et al., 2021a; Zhang et al., 2022). An emerging pattern from recent studies is that borealization of inflow regions seems to impact neighbouring areas by spillover effect. In eastern Greenland (Emblemsvåg et al., 2022a; Emblemsvåg et al., 2022b), demersal communities across depths have rapidly reorganised in response to climate change, in particular between 350 and 1000m depth. Specifically, studies have found that Atlantic cod, beaked redfish and deep-sea shrimps (*Pandalus borealis*) observed on the northeast Greenland shelf originated from the Barents Sea populations (Christiansen et al., 2016; Andrews et al., 2019). In addition, across the Siberian Arctic (Kara Sea, Laptev Sea, East Siberian Sea), North Atlantic species have expanded eastward while North Pacific species have expanded westward (Orlov and Volvenko, 2024).

Borealization in inflow shelves has also been documented for benthic communities, although responses are lagged with regard to climatic signals (Grebmeier, 2012; Jørgensen et al., 2019; Waga et al., 2020; Zakharov et al., 2020; Calvet et al., 2024). Interestingly, the borealization of benthic communities does not necessarily lead to an increase in productivity or biomass (Zakharov et al., 2020 for the Barents Sea; but see Krause-Jensen et al., 2020, for pan-Arctic increases in seaweeds). In contrast, unchanged community biogeography could suggest resilient communities in the Laptev Sea (Kokarev et al., 2017), and to some degree in the Bering and Chukchi Seas, over several decades (Grebmeier et al., 2015a but see Grebmeier et al., 2006; Huntington et al., 2020, for biomass declines). The lack of repeated surveys hinders our ability to evaluate the degree of borealization of benthic communities, especially on interior and outflow shelves, but bycatch data from commercial or scientific bottom trawls can serve as a baseline for future assessments (Jørgensen et al., 2022), and the Distributed Biological Observatory in the Pacific Arctic provides time series for macro- and megabenthic fauna (Grebmeier et al., 2015b; Grebmeier et al., 2018).

At smaller scales, some studies have revealed the borealization of some coastal zones across the Arctic, as suggested by an increase in boreal fish species in lagoons on the Beaufort Sea (von Biela et al., 2023), and by increased macroalgal cover (Krause-Jensen et al., 2020), abundance of boreal species and coincident shifts in benthic invertebrate communities in Svalbard fjords and near Franz Josef Land (Kortsch et al., 2012; Węsławski et al., 2018; Al-Habahbeh et al., 2020; Dvoretsky and Dvoretsky, 2024). However, the degree of borealization of benthic communities in Atlantic Arctic fjords might depend on the bathymetric features of the coastline, such as fjord sills and the interannual strength of the Atlantic Water inflow (Beuchel et al., 2006; Renaud et al., 2007; Jordà-Molina et al., 2023). A more important driver of major changes in Arctic coastal ecosystems and landscapes could instead be the melting marine terminating glaciers (Lydersen et al., 2014; Meire et al., 2017; Williams et al., 2021; Kavan and Strzelecki, 2023). Some sub-Arctic coastal regions do not display any particular response to climate change. For example, western Greenland intertidal ecosystems do not vary with latitude, which would suggest resilience to climate change, based on space-for-time substitution (Thyrring et al., 2021), and in the Baydaratskaya Bay, Kara Sea, benthic communities were unchanged until 2013, and only seemingly impacted by other local anthropogenic impacts since then (Azovsky and Kokarev, 2019).

As in the pelagic systems, demersal and benthic borealization appears to be mainly driven by changes in suitable habitats and prey distribution induced by climate change. Rates of response to environmental changes are often lagged and species-specific (Alabia et al., 2018). At the inflow shelves, the main drivers are the fluctuating extent of colder and warmer water masses and timing of ice retreat. This has been shown in the northern Bering Sea and Chukchi Sea, for both demersal and benthic communities (Grebmeier, 2012; Nishio et al., 2020; Zhang et al., 2022), and in the Barents Sea (Ingvaldsen et al., 2021; Nascimento et al., 2023). In addition to expanding suitable warmer habitats, advected waters transport demersal and benthic early life stages. Variations in water mass extent across interannual to decadal scales have been linked to the varying abundance of advected ichthyoplankton species, leading to variation in dominance regime of fish larvae in the Eastern Chukchi Sea (Randall et al., 2019; Axler et al., 2023), and in the Barents Sea (Eriksen et al., 2015; Eriksen et al., 2017). These fluctuations in water mass inflows are linked to large-scale circulation patterns, such as the sub-polar gyre in the northern Atlantic in western Greenland (Post et al., 2021), or the Arctic dipole in other inflow shelves (Polyakov et al., 2023). While warm conditions are maintained at inflow shelves and neighbouring regions are gradually warming due to local changes in the environment, mobile populations such as fish are likely able to further expand beyond inflow shelves (Andrews et al., 2019; Orlov and Volvenko, 2024), but demersal Arctic fish species living on the edge of the shelves cannot move north as they run out of shelf (Wassmann et al., 2006b; Fossheim et al., 2015). The northward expansion of less mobile boreal benthos is likely more dependent on the dispersion of the larval phase (Ershova et al., 2019; Meyer-Kaiser et al., 2022), although those will may not settle successfully (Wassmann et al., 2015; Ershova et al., 2019; Descôteaux et al., 2022).

Shifts in species distribution can drive changes in both pelagic and benthic-demersal life cycles, oceanic seascapes, population structures and interspecific interactions. In the Chukchi Sea, increasing number of boreal pre-spawning, spawning and post-spawning walleye pollock have been observed in recent years (Emelin et al., 2022). This could indicate an expansion of their spawning location or range but does not necessarily correlate with juvenile survival. Survival of the early life stages depends on species capacity to take advantage of available food and to resist harsh winter conditions. Polar cod, adapted to Arctic conditions, have a unique fat storage strategy, from diatoms and *Calanus* origin, that enables it to thrive in cold ice-covered region (Copeman et al., 2022). In contrast, juvenile walleye pollock have better condition in the southern than in the northern Chukchi Sea (Copeman et al., 2022), which suggests that they are not yet adapted to colder northern conditions. In the Barents Sea, climate induced changes in temperature and food availability also drive trends in 0-group fish lengths (Skjoldal et al., 2022) and distribution (Eriksen et al., 2017). Apart from their lipid storage strategy, differences in spawning timing between species is likely a key driver of their successful survival during the Polar Night. Indeed, winter surveys around Svalbard show that the spring spawning strategy of boreal fish, which contrasts with winter-spawning Arctic and arcto-boreal species, might lead to a temporal mismatch between their planktonophagous larvae and zooplanktonic blooms (Berge et al., 2015; Geoffroy and Priou, 2020). Large incoming boreal fish are often generalists which are thus able to feed on boreal as well as Arctic prey. This was shown by the diet composition of walleye pollock in the northern Chukchi Sea, where Arctic copepods, euphausids and polar cod were observed in their stomach content (Benzik et al., 2022). Walleye pollock also consume other incoming species, such as Pacific sand lance, whose abundance has been increasing with the decline of sea-ice (Baker et al., 2022). Similarly, in the Barents Sea, ctenophore species, which might benefit from warmer conditions in the region, and snow crab (*Chionoectes opilio*), which overlaps increasingly with Northeast Arctic cod as these expand north-eastward, increased in frequency in Northeast Arctic cod diets (Eriksen et al., 2018; Holt et al., 2021). However, there is no sign that polar cod are increasing in Northeast Arctic cod's diets (Holt et al., 2019).

3.4 Ecosystem-level impacts of borealization

3.4.1 Biological and functional diversity across compartments

Understanding the degree of borealization of Arctic ecosystems necessitates knowledge on biological diversity of native and incoming communities. Efforts to catalogue species across the pan-Arctic are still ongoing (Renaud et al., 2006; Bluhm et al., 2011b; Bluhm et al., 2011a; Kosobokova et al., 2011; Poulin et al., 2011; Lin et al., 2014; Jørgensen et al., 2022). The Central Arctic Ocean can be divided in two main regions with distinct biodiversity: the Eurasian and American regions (Alfaro-Lucas et al., 2023). There is relatively little difference in species composition between the central Arctic Ocean basins (Bluhm et al., 2015; Alfaro-Lucas et al., 2023), yet substantial variation among benthic habitats within the basins (Ramirez-Llodra et al., 2023). However, some ecological compartments and regions are still largely under studied (CAFF, 2017; Alfaro-Lucas et al., 2023). Where long time series are available, studies highlight the strong impact of borealization on biodiversity. Species distribution ensemble models applied to 69 apex- and mesopredators revealed varying trends in species richness across the pan-Arctic over the last two decades (Alabia et al., 2023). The authors suggested that species richness has been increasing overall in the Arctic, in line with large range shifts, especially from large mobile apex predators, but more strongly in interior and outflow shelves than inflow shelves. In the Barents Sea, an 8-year study showed a steady increase in species richness and biodiversity indices, especially within the advected waters (Prokopchuk and Trofimov, 2019). A study on shorter time scales in the Chukchi Sea revealed contrasting responses of functional group diversity between warm and cooler years: during a warm year, diversity increased among zooplankton and fish communities, decreased for bacteria, protists, epibenthos and seabirds, and did not vary significantly for macrobenthos, relative to a colder year (Mueter et al., 2021a).

The documented changes in Arctic biodiversity bring about functional reconfigurations with implications for ecosystem function and vulnerability (Ingvaldsen et al., 2021). Many boreal species differ from Arctic ones in terms of functional characteristics, as exemplified by fish and copepods (e.g., Aune et al., 2018). Boreal fish species are often large, and predatory, with a generalist diet, whereas Arctic fish are rather small benthivores like sculpins (Frainer et al., 2017; Emblemsvåg et al., 2022a; Emblemsvåg et al., 2022b). In East Greenland, the incoming boreal functional traits do not compensate for the loss of Arctic traits, which leads to a decrease in functional diversity across depths (Emblemsvåg et al., 2022a). In contrast, in the Barents Sea, functional diversity increases with the northward shift of functionally-rich boreal communities (Frainer et al., 2021), but this situation might be transitory as predation and competition between newly co-occurring boreal and Arctic species might lead to the decline of Arctic species (Pecuchet et al., 2020). The alteration in functional diversity is correlated with a change in dominance of different life history strategies, including an expansion of so-called "periodic" species, which have a greater adaptive capacity owing to higher reproductive output, broader diet, and migratory behaviour (Bernardo et al., 2024). Higher functional diversity is thought to increase adaptive capacity and affect ecosystem stability and resilience to perturbations. However, these studies have so far been limited to fish communities, and a pan-Arctic overview is lacking.

3.4.2 Impacts on apex predators

Changes in environmental conditions in the Arctic also affect seabirds and marine mammals, which are often emblematic and/or Red-listed and are thus also an important component of biodiversity, despite low species richness compared to smaller groups. For example, seabirds colonies are experiencing changes in densities and species composition around the Svalbard Archipelago (Descamps and Strøm, 2021), and in the northern Bering Sea and eastern Chukchi Sea (Kuletz et al., 2020). Similarly, changes in marine mammals are observed with changes in habitat conditions: killer whales are increasingly observed in the Chukchi Sea and elsewhere as sea-ice retreats (Ferguson et al., 2010; Stafford, 2019), in East Greenland an increase in the abundance of several boreal cetaceans (humpback, fin, killer, and pilot whales and dolphins) has been seen as summer sea ice has disappeared and water temperatures have increased (Heide-Jørgensen et al., 2023), while narwhals seem to distribute preferentially where temperatures are colder, and might abandon their warmer habitats of Mideast and Southeast Greenland (Chambault et al., 2020; Heide-Jørgensen et al., 2023). Sea surface temperatures are also linked to seasonal displacements of bowhead whales in Baffin Bay (Chambault et al., 2018). With sea ice decline, polar bears are pushed to more frequent long-distance swimming (Pilfold et al., 2017). Gray whales, associated with warmer waters, occur more frequently in the Chukchi Sea to feed on abundant prey when ice conditions allow. However, recent warm events have been associated with unusual mortality events in gray whales (Stewart et al., 2023), suggesting that increased availability of prey in newly ice-free areas was insufficient to compensate for decreasing prey availability in more southern feeding areas. Concomitant displacements have been observed for Arctic ice-associated species, with poorer body condition and population status (Kovacs et al., 2011; Laidre et al., 2015). Environmental changes and prey behaviour are also altering migration patterns and timing of marine mammal species (Kuletz et al., 2024).

Changes in distribution of lower trophic level communities affect the diet of many apex predators, modifying trophic interactions and food webs (de la Vega et al., 2021). Spatial or compositional shifts in epibenthic invertebrate communities in the Bering and Chukchi Sea could affect prey species of benthivorous marine mammals like Pacific walrus and bearded seals, which are important subsistence resources for Alaska Native communities (Richman and Lovvorn, 2003; Logerwell et al., 2022), as well as benthivorous seabirds like the endangered Steller's eiders (Richman and Lovvorn, 2003). However, current latitudinal and regional variability in ringed seals and beluga diets would suggest that those species could adapt to changes in prey (Yurkowski et al., 2016a). For polar bears, some individuals are more opportunistic than others, and those that specialise on seals are most sensitive to climate change impacts (Thiemann et al., 2008). Apart from changes in diet and habitat loss, Arctic top predators will likely face an increasing number of anthropogenic pressures, such as increased noise and pollution from shipping, plastic pollution, increasing disease and parasite occurrence, (Kovacs and Lydersen, 2008; Merkel et al., 2021). Top predators have been shown to sometimes adapt to the change in diet (e.g., Yurkowski et al., 2016b; Vihtakari et al., 2018; Sauser et al., 2023), although not always successfully, as changes in prey quality, notably fat content, would affect species fitness (e.g., Descamps et al., 2022; Anderson et al., 2023; Sauser et al., 2023). The decline of iconic marine mammals in the Arctic is a major conservation concern, with implications for biodiversity and cultural ecosystem services in the Arctic.

3.4.3 Food-web impacts

Apex- and mesopredator incoming boreal species establish new feeding links in Arctic marine ecosystems, thereby reorganising food-webs, leading to increased food-web connectance and decreased modularity, which is associated with low resilience (Kortsch et al., 2015; Blanchet et al., 2019; Pecuchet et al., 2020; Jordán et al., 2024). A core function of Arctic food webs that is affected by borealization is the sympagic-pelagic-benthic carbon coupling through the sinking of ice-algae when ice melts. This function is particularly important for benthic biomass and biodiversity (Boetius et al., 2013; Kędra et al., 2015; Hansen et al., 2020). Indeed, several studies have shown the strong reliance of megabenthic communities to this coupling in the Barents Sea, northeast Greenland shelf (Cautain et al., 2022; Cautain et al., 2024), on Siberian shelves (Schmid et al., 2006; Lalande et al., 2009), in the Northern Bering Sea and Chukchi Sea (Koch et al., 2020), in Baffin Bay (Yunda-Guarin et al., 2020) and in the Canadian high-Arctic (Yurkowski et al., 2020). The anticipated - though poorly documented (see Zhulay et al., 2023 for the Chukchi Borderland) - decline in benthic-pelagic coupling has important implications for ecosystem functioning (Niemi et al., 2024). Food web and ecosystem models can explore the consequences of declining sea ice and new trophic interactions in an integrative approach. In the Beaufort Sea, the shelf and slope ecosystem with strong riverine influence and changes in salinity has likely driven lower diversity and changes in biomass, consumption and trophic levels of marine mammals and fish, including Arctic key species (Sora et al., 2024). In the Barents Sea, multiple pressures have caused changes in the food-web over time, but an ecosystem model suggests that increased productivity fuelled the food web through bottom-up effects after the 1990's (Pedersen et al., 2021). In Baffin Bay, an ecosystem model revealed that polar cod is a key component of the food-web structures (Pedro et al., 2023). An exploration of past dynamics could reveal the impacts of changes in the polar cod stock on the ecosystem.

4 Discussion

4.1 Spatial extent of borealization: the "spillover" effect

Local changes in environmental conditions, driven by alterations in large scale circulation patterns and fluid (water, air) masses properties, are reported across the pan-Arctic. The strongest impacts seem to affect the inflow shelves, where high connectivity to very different systems result in a high interannual variability and sensitivity to external forcings. Borealization has thus progressed more rapidly on these shelves, affecting all trophic levels (Csapó et al., 2021). Ecosystems inflow shelves are currently transitioning towards a more boreal functioning but retain some Arctic characteristics. The potential degree of borealization in the future is discussed below. A new emerging signal, as revealed by many recent studies reviewed here, is that interior and outflow shelves are also experiencing borealization through climate-induced modifications of local environmental conditions (sea-ice cover, river runoff, temperature) that render habitat suitable for species that are transported or actively relocate there (Figure 6).

However, the extent of this "spillover" effect of borealization across space, time and functional groups is uncertain, due to several knowledge and data gaps. Indeed, a recent biodiversity assessment for the whole Arctic domain has highlighted the lack of data for the Siberian seas (Kara, Laptev, East Siberian seas) and the Canadian Arctic (Canadian Arctic Archipelago, Beaufort Sea, Hudson and Baffin Bay, Alfaro-Lucas et al., 2023). In addition, for all shelves and for the Arctic basins, data are largely restricted to the summer and autumn seasons, with recent but limited knowledge on winter and polar night processes (Berge et al., 2015; Berge et al., 2020; Gerland et al., 2019), and transition periods between ice-free and ice-covered seasons (Shogren et al., 2020). More seasonal and spatial coverage, including land-sea connectivity at more extensive spatial scales than currently conducted, are important for understanding physical processes such as sea ice loss, water freshening, nutrient and carbon cycles (Brown et al., 2020; Shogren et al., 2020; Timmermans and Marshall, 2020), as well as biological processes (Berge et al., 2015; Geoffroy and Priou, 2020). Deployment of dedicated autonomous technologies are often suggested to fill this data gap. In addition, approaches such as participatory modelling tools have a strong potential to fill the knowledge gaps around e.g., winter processes, using local ecological knowledge (Pedro et al., 2023). A more comprehensive overview and monitoring of Arctic ecosystem borealization would also necessitate the allocation of research resources to characterise and better understand processes of relatively understudied compartments such as microbial communities, epibenthos and infauna (CAFF, 2017).

4.2 Through the spyglass: a boreal Arctic in the future?

Predicting the extent to which Arctic borealization will continue in the future across ecosystem compartments is a priority that has received much attention from the scientific community. Climatic scenarios from the coupled model intercomparison project (CMIP) suggest various trajectories for future Arctic climatic and

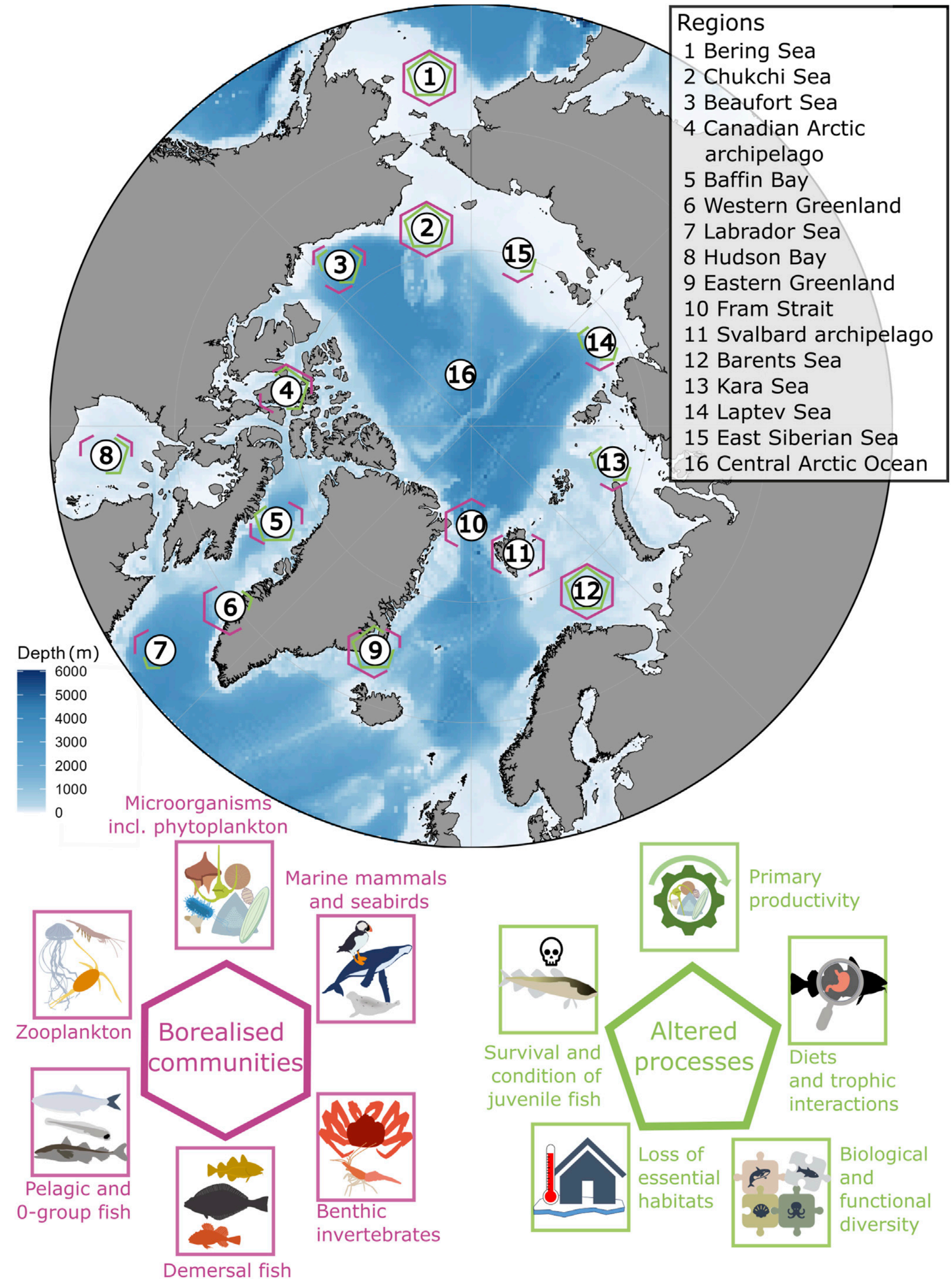

FIGURE 6
Map of evidence of borealization of communities and ecosystem processes across regions. Regions that are indicated are based on the naming used in the literature cited in the main text.

oceanographic conditions, but all scenarios display similar trajectories until the 2040s. The Artic will likely continue to warm at a faster rate than mid-latitude systems. Arctic amplification could continue under a low emission scenario, where ice albedo feedback would maintain the phenomenon, but it would be less prominent in a high-emission scenario (Ono et al., 2022). The increase in heat transport from the Atlantic and the Pacific will likely continue and progress poleward through the Bering Strait and the Barents Sea (Drinkwater et al., 2021; Dörr et al., 2024). All shelves will become ice free in the summer, irrespective of the climatic scenario, and the Barents Sea could become ice free in winter by the end of the century (Årthun et al., 2021). Expanding open water areas and increasing precipitation will contribute to large and rapid changes in hydrological cycles (McCrystall et al., 2021). Increased river runoffs should increase stratification and subsurface warming in the central Arctic Ocean (Nummelin et al., 2016).

It is challenging to assess the degree of borealization of biogeochemical processes and microbial communities at pan-Arctic scales. Primary production is arguably the microbial process that has received most attention in the literature, and numerous studies suggest an evolution towards a more boreal functioning in the future (Ardyna and Arrigo, 2020; Noh et al., 2024). The Pacific and Atlantic inflow shelves will likely experience the strongest increase in primary productivity, although this is more uncertain for the western Barents Sea, where oceanographic models project variable directions and magnitudes of change depending on how stratification processes are represented (Mueter et al., 2021b; Mousing et al., 2023). However, increasing cloud cover (Bélanger et al., 2013) and strong seasonality in light conditions at higher latitudes are likely to limit the transition towards a completely boreal phenology, and primary production should retain some characteristics of an Arctic system, which would lead to arctic-boreal hybrid functioning. Yool et al. (2015) projected that, by 2,100, despite an increase in productivity driven by the loss of sea ice, the Arctic will not be more productive than the Atlantic, with both systems entering a low nutrient regime. In contrast, the Pacific, richer in nutrients, might experience a longer rise in productivity (Yool et al., 2015). However, the trajectory of nutrient limitation remains a significant knowledge gap, leaving predictions of Arctic productivity in the future uncertain (Slagstad et al., 2015; Mueter et al., 2021b; Mousing et al., 2023). While observational data on other microbial processes across the pan-Arctic remain limited, experimental studies offer valuable insights into potential shifts in crucial microbial functions. For example, temperature variations might influence bacterial metabolic rates, phytoplankton community structure and chlorophyll a concentrations and, consequently, carbon cycling (Kritzberg et al., 2010).

The climate driven environmental changes will continue to trigger distributional shifts and changes in biodiversity across functional groups and Arctic regions. These shifts are quantitatively explored based on species distribution models fitted to species' current thermal preferences. Ensemble modelling predicts an increase in phytoplankton species richness all over the globe under the highest warming scenario, by the end of the century, except in the Arctic, where no trend is expected (Benedetti et al., 2021). Other projections with similar time horizons suggest that poleward shifts in zooplankton distribution could continue at a pace of 8.7 km/decade, accompanied by a change in seasonal occurrence peak up to 13 days earlier, a high species turnover, and a northward shift of many boreal gelatinous zooplankton, sometimes only into sub-polar regions (Villarino et al., 2015; Benedetti et al., 2021; Pantiukhin et al., 2023; Pantiukhin et al., 2024; Cheung et al., 2015) also predicted a northward range expansion for Pacific pelagic fish species of 30.1 ± 2.34 (S.E.) km decade^{-1}. However, regional predictions for Canadian waters predict a decline in biomass in both the Pacific and Atlantic sides (Bryndum-Buchholz et al., 2020). In contrast, projections under a high emission scenario reveal an increase in total forage fish biomass in Hudson Bay, but with decreasing fish size and a shift from lipid rich polar cod to smaller boreal fish (Florko et al., 2021). Overall, responses to climate change are likely region-specific, as well as species specific and are thus challenging to predict (Mueter and Litzow, 2008; Alabia et al., 2018; Husson et al., 2020; Calvet et al., 2024). The impact of climate change on benthic habitats may depend on the spatial scale of the projection. In the Bering and Chukchi seas, the habitat of many assemblages of epibenthic invertebrates is predicted to be reduced by 50% by 2050 and almost 100% by 2,100, with the exception of eurythermal species such as the basket star *Gorgonocephalus cf. arcticus* (Logerwell et al., 2022). At the pan-Arctic scale, however, habitat change for benthic species might be limited in the future (Renaud et al., 2019). Habitat loss should mainly affect currently cold and aragonite-oversaturated areas such as northern Barents Sea and east Greenland Sea (Renaud et al., 2019), and cold-stenothermal species such as gastropods and bivalve mussels *Musculus* spp. in the Bering and Chukchi Sea, leading to large losses of biodiversity locally (Logerwell et al., 2022). At the ecosystem-level, long-term projections using species distribution ensemble models suggest an increase in species richness and functional redundancy poleward with an increase in predatory taxa that will threaten Arctic species and decrease the modularity of Arctic food webs in the Bering and Chukchi seas (Alabia et al., 2020). It is predicted that the co-occurrence of boreal and arctic fish species in borealized regions will vary from 1 year to the other, with more Arctic species in cold years and more boreal species in warm years (Geoffroy et al., 2023), as seen in the Labrador and Bering seas (Marsh and Mueter, 2020).

The poleward progression of communities could lead to many changes in seascapes, with shifts in essential habitat localisation and altered connectivity, leading to declining stocks and a potential increase in population mixing and hybridization by the end of the century. Habitat forming species such as macroalgae are likely to continue their colonisation of coastal Arctic regions, with more of the Canada, Greenland and Svalbard coasts becoming suitable habitats due to less ice cover for three important macroalgae species by 2,100 (Jueterbock et al., 2013). In contrast, in the soft-sediment dominated Beaufort Sea, kelp production has been shown to be limited by wind speed that resuspends river and coastal sediments and limits light penetration to the seabed (Bonsell and Dunton, 2018). This is likely to affect nursery and feeding habitats, although their variations are only partially understood and might be affected by multiple factors. Along the Norwegian coast, Northeast Arctic cod spawning locations have been fluctuating with a northward trend, seemingly under the effect of population demography, while the effect of climatic factors is uncertain (Höffle et al., 2014; Opdal and Jørgensen, 2015). Similarly, spawning locations of Northeast Arctic haddock (*Melanogrammus aeglefinus*) are likely driven by density dependence, rather than temperature (Langangen et al., 2018). Finally, predation by boreal species has been shown to influence capelin's spawning area (Olsen et al., 2024). It is thus challenging to model future locations of spawning sites. Nevertheless, modelling studies based on thermal preferences and bottlenecks of species early life stages can give a first estimate. Capelin is anticipated to shift spawning north-eastward in the Barents Sea (Huse and Ellingsen, 2008). For Northeast Arctic cod, further northward shifts in spawning sites could affect juveniles' survival and increase their sensitivity to spawning timing (Endo et al., 2024).

Population mixing will likely increase and would probably occur via the Northeast and Northwest Passages (Vermeij and Roopnarine, 2008; Kelly et al., 2010; Wisz et al., 2015). This has likely already started, as suggested by the first observations of interoceanic dispersals (e.g., a Pacific diatom in the Atlantic waters, Reid et al., 2007). The Greenland halibut Pacific and Atlantic populations, with so far limited genetic mixing (Orlova et al., 2019), are now increasingly interacting along the Eurasian Arctic, suggesting that a potential reunification of those populations is possible in the future (Orlov and Volvenko, 2024).

To summarize, all climatic scenarios point to a profound transformation of the Arctic oceanic functioning. Under those conditions, many species will shift, but not all, and not all the way into the Arctic Basin, where conditions will remain harsh. Ecosystems' primary productivity, biodiversity, functioning and food webs will be altered. All this suggests that Arctic marine ecosystems might not entirely transform into a boreal functioning, but rather stabilize in a hybrid state between Arctic and boreal ecosystem at a latitudinal limit north of the current one, with transient borealization during warmer periods.

4.3 Into the fog: uncertainties and key questions

Large uncertainties and bias surround projected trajectories for the Arctic and sub-Arctic ecosystems. Arctic Ocean circulation is complex, with numerous feedback and potentially tipping processes among and between the cryosphere, hydrosphere and atmosphere, and several possible future evolutions depending on climate change intensity (Lannuzel et al., 2020; Timmermans and Marshall, 2020). The most recent version of the Coupled Model Intercomparison Project (CMIP6) has persistent bias on Arctic water masses representations, inherited from the previous version, which necessitate major improvements, notably by using higher model resolutions (Khosravi et al., 2022). For example, other studies showed that heat transport from lower latitudes might be underestimated by model with too coarse spatial resolution (Xu et al., 2024).

Projections of community shifts in the future are also associated with considerable uncertainties, although hard to estimate and thus rarely mentioned in the studies. The potential for further borealization of the ecosystem depends on species habitat preferences, the location and connectivity of their essential habitats (spawning, nursery, feeding grounds), and their capacity to acclimatise and then adapt to new abiotic and biotic conditions. Projecting species future habitats using species distribution models is a first approach to anticipating species movement. However, those models are often based on strong assumptions, such as environmental niche stability, and are built around limited number of environmental covariables, ignoring the impact of population dynamics and interspecific interactions on species distributions. Among environmental variables, factors that do not vary over time are not always included. Indeed, while temperature, salinity or oxygen, which will be affected by future climate change, can be used as time-varying predictors of most fish species' suitable habitats, poleward displacement might be limited by non-dynamic factors such as depth, light regimes, or seabed type. Considering a species' traits and life cycle can help estimate the likelihood of that species to shift northward. Using this approach, it is assumed that cod and haddock have reached their northern limit at the shelf break of the Barents Sea and minke whale or harp seals will likely follow the ice edge, while other species, such as capelin, redfish or snow crab will likely be able to expand further into the Arctic (Hollowed et al., 2013b; Hollowed et al., 2013a; Haug et al., 2017; Mullowney et al., 2023).

When conditions in the Arctic are limiting, species that will not be able to shift their distribution will have to acclimate, then adapt, or die (Hoffmann and Parsons, 1990), and this will impact the pace and extent of borealization across regions and functional groups. Adaptation to environmental stress manifests itself mainly via two mechanisms: the species plasticity (capacity of a genotype to express different phenotypes under varying environmental stress), and the selection, on evolutionary scales, of certain phenotypes. Species phenotypic plasticity includes, among others, behavioural flexibility and physiological tolerance, both of which are challenging to observe in natural environments (Beever et al., 2017) and manifest differently across a species' range (Donelson et al., 2019). Plasticity can be a way to cope temporarily with environmental stress, but can also hinder adaptation in some cases (Fox et al., 2019). It is thus important to assess species adaptive capacity to understand species responses to climate change and support conservation and management efforts (Hoffmann and Sgrò, 2011). This can be done by considering the species fundamental adaptive capacity, characterised via its functional traits such as longevity, mobility, and dispersal capacity (Beever et al., 2016). Such approaches, along with experiments on species thermal adaptivity, are often suggested as potential improvements to species distribution models (Drost et al., 2014; Drost et al., 2016; Logerwell et al., 2022). Evolutionary models could integrate that information and incorporate interspecific interactions to further explore possible trajectories of co-evolution for Arctic marine systems.

Finally, lasting borealization, emerging from species completing their life cycle, implies that environmental conditions are suitable for all life stages (Wassmann et al., 2015), of which early life stages and spawning adults are often the bottlenecks (Dahlke et al., 2020). Several species have been suggested to be able to complete their life cycle in areas where it was previously not observed, for example, the boreal capelin in Hudson Bay (Gaston and Elliott, 2014), the copepod *C. finmarchicus* and the Atlantic hyperiid amphipod *Themisto compressa* at the Fram Strait, with the latter two species much poorer in lipid than their Arctic counterparts (Kraft et al., 2013; Tarling et al., 2022). Connectivity between the habitats and along dispersal routes is thus a key consideration when projecting population shifts and species range shifts. Knowledge on thermal preferences of early life stages enabled modellers to estimate changes in spawning sites for cod and polar cod under various gas emission scenarios (Dahlke et al., 2020; Sanders et al., 2022). Results of these studies all suggest a deterioration of the current spawning sites for both species under high emission scenarios, and more limited impacts for low emission scenarios. In addition, some local conditions such as depth may act as barriers to dispersal of fish species across the pan-Arctic (Bouchard et al., 2018).

4.4 Risks and vulnerability of borealized socio-ecological systems

Despite some uncertainties and knowledge gaps, there is a clear consensus on the ongoing borealization of Arctic ecosystems, and its likely continuation in the future. Arctic endemic communities and ecosystems are most at risk, if they are unable to adapt to the multiple environmental stressors or to compete with new incoming species (Kędra et al., 2015). Sympagic species or species with a strong link to the ice, through their diet or life cycle, are particularly at risk (Kohlbach et al., 2016), while some may survive in the pelagic zone (Kunisch et al., 2020). The ice association is well documented for example, for polar cod. In the Chukchi Sea, its body condition appears to be lower during warm years, suggesting that the region is warming beyond the species' thermal limits (Copeman et al., 2022). With sea ice loss, polar cod will lose its spawning habitat (Huserbråten et al., 2019), and new incoming species could outcompete it (Mueter et al., 2016). However, some studies suggest that competition for food might be limited at least for early life stages, through niche partitioning (Falardeau et al., 2014; Bouchard et al., 2022). Moreover, in the Canadian Arctic Archipelago and Central Arctic Ocean, the relaxation of the most extreme conditions with climate change could benefit polar cod, at least in the short term (Bouchard et al., 2017; Steiner et al., 2019; Geoffroy et al., 2023). There, larval survival of polar cod increases in years with earlier ice-breakup and warmer sea surface temperatures (Bouchard et al., 2017).

With sea-ice loss and increased open water area, carbon sinking and ocean acidification are likely to increase (Lannuzel et al., 2020; Terhaar et al., 2020; Qi et al., 2022), adding to the effect of warming to affect species habitats and distributions. The extent of the impacts of ocean acidification on marine populations is still not well understood. Experimental studies show that acidification affect coastal phytoplankton species growth, colony length and chain length, although the effect vary across species (Thoisen et al., 2015). In addition, increased acidification could lower phytoplankton growth rates and amplify the decrease in primary production with warming (Coello-Camba et al., 2014), and alter microbial community composition (Brussaard et al., 2013; Sugie et al., 2020). Finally, acidification can lead to the dissolution of Arctic benthic invertebrate shells (Comeau et al., 2009; Niemi et al., 2021) and, in combination with warming temperatures, increased consumption by Arctic brittle stars (Wood et al., 2011). However, some Arctic bivalves are more resilient to decreasing pH (Goethel et al., 2017).

In addition to those climate-driven pressures, Arctic ecosystems will experience increasing pressures from many other anthropogenic sources. Microplastic contamination is already affecting benthic organisms in the Chukchi Sea and other areas of the Arctic through local sources and transport (Fang et al., 2018; Bergmann et al., 2022). New ice-free conditions along the shelves and seasonally in the Central Arctic Ocean would allow Arctic shipping year-round starting in the 2070s (Min et al., 2022), leading to increased concentrations in pollutants (Svavarsson et al., 2021). This increase in shipping would also be prompted by industrial opportunities newly accessible in a future seasonally ice-free Arctic, such as mineral, oil and gas extraction, of fishing. Indeed, large global models project a high potential for Blue Economy in the Arctic, with potential for new fisheries, owing to increased local productivity and incoming new stocks (Cheung et al., 2015). However, the latest FAO report stresses the high risk associated with potential fishing in the Arctic due to very high uncertainties around the future biomass projections associated with the two main Earth system models used to force the simulations (Tittensor et al., 2021; Blanchard and Novaglio, 2024). In addition, climate is not the only factor affecting Arctic fisheries, and complex cross-scale, cross-domain (ecology, society, economy) processes can greatly affect the future of pan-Arctic fisheries (Niiranen et al., 2018). The potential growth of biomass of commercial stocks thus call for new management approaches (Christiansen et al., 2014; McBride et al., 2014) and careful consideration of potential new fishing opportunities. For example, a study investigating the potential for a fishery on walleye pollock that are expanding into the western Chukchi Sea highlight strong uncertainties around the amount of biomass entering the region, the state of the stock, and the possibility of harvesting considering the harsh local fishing conditions (Maznikova et al., 2023). Such complex systems are challenging to apprehend, and models are often a key tool to anticipate future changes. To date, few models explore regional ecosystem response to potential effects of climate change scenarios on ecosystem services and human wellbeing, with or without considering other human pressures such as fisheries. The few projections that have been completed anticipate a decrease in fish biomass or high uncertainties in biomass trajectories, thus challenging the hypothesis of a future Blue Growth in the Arctic (Bryndum-Buchholz et al., 2020; Whitehouse et al., 2021).

In the meantime, some traditional local fisheries are threatened by ecosystem changes. For example, the winter ice fishery on Greenland Halibut (*Reinhardtius hippoglossoides*) is now being threatened by the progressive loss of sea ice (Hussey et al., 2017). Fishermen in Greenland are shifting their traditional fishing practices in response to changes in ice cover, and are observing new species (Schiøtt et al., 2022). Local ecological knowledge, including knowledge from Indigenous communities whose livelihoods and cultures are tightly linked to Arctic ecosystems, is increasingly highlighted as a most valuable tool to face future challenges and apply an adaptive strategy to the fast changing Arctic (Riedlinger and Berkes, 2001; Schwoerer et al., 2021). Local fishermen and hunters have detailed knowledge on seasonal and spatial scales that are rarely covered by any scientific survey, and are highly useful to combine with scientific knowledge and data do detect changes in Arctic ecosystems and threats to traditional livelihoods (Chila et al., 2022; Falardeau et al., 2022; Bouchard et al., 2023; Dunmall et al., 2024). Better inclusion of this rich source of information could be done through community-based monitoring and co-construction of scenarios to directly inform management (Nilsson et al., 2021; Falardeau et al., 2022). Indeed, balancing ecosystem and livelihood conservation and the increasing economic interests in the Arctic necessitate consideration of the whole socio-ecological system, but a holistic, interdisciplinary and systematic approach is currently lacking to properly picture the complexity of the Arctic socio-ecological system and the pressures that affect it (Falardeau and Bennett, 2020; Eerkes-Medrano and Huntington, 2021). Identified gaps include for example: the heterogenous knowledge base across the Arctic, limited research on cumulative impacts of climate change with other anthropogenic pressures, a lack of knowledge on some feedbacks between ecosystem services and human well-being, and a lack of projection into the future for human systems (Falardeau and Bennett, 2020). Considering the local and global importance of

Arctic climatic and biological processes, urgent mitigation and adaptive actions are needed (Overland et al., 2019).

Author contributions

BH: Conceptualization, Writing–original draft, Writing–review and editing. BB: Writing–review and editing. FC: Conceptualization, Formal Analysis, Writing–review and editing. SD: Conceptualization, Writing–review and editing. EE: Writing–review and editing. MF: Writing–review and editing. MG: Writing–review and editing. RH: Writing–review and editing. RBI: Conceptualization, Writing–review and editing. LJ: Writing–review and editing. CL: Writing–review and editing. LM: Writing–review and editing. FM: Writing–review and editing. RP: Writing–review and editing. MW: Writing–review and editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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