Polar biocenosis cumulative response to environmental stressors reveals who benefits from marine ice loss

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Abstract

Marine ice is retreating in many sectors of Earth's polar and subpolar regions. The rates are unprecedented, generating great concern in both scientific and public communities. Despite the expected serious implications, we lack a comprehensive understanding of how ice loss and related processes control marine biota and interactions at different spatiotemporal scales under multiple environmental stressors and drivers of change. We systematically review existing knowledge on how the losses of ice shelves, sea ice, and glaciers affect polar marine biocenosis. We include in situ, remote sensing, and modelling studies on sea ice biota, phyto- and zooplankton, fish, seabirds, phyto- and zoobenthos and marine mammals, covering a time span of three decades (1991-2022). We apply a qualitative ecosystem-based risk assessment to assess the individual and cumulative response of ecosystem components and related ecosystem services. The most threats and opportunities are expected to manifest in the shallow coastal zones. They include loss of ice habitat, water column darkening due to sediment input with meltwater, increased sedimentation rates, and mechanical damage due to ice scouring, but also gain of marine habitat, lightening of the water column and nutrient input with meltwater. The cumulative score of all the stressors shows that marine ice loss will lead to autotroph-dominated polar marine systems with detrimental effects on secondary producers, i.e. zooplankton and zoobenthos, and sea ice-obligate species. Although similar stressors are recognised for polar and subpolar regions, some processes may differ in magnitude. This overview aims to provide summarised knowledge to inform science-based solutions for conservation and climate mitigation actions.

Abstract

Marine ice is retreating in many sectors of Earth's polar and subpolar regions. The rates are unprecedented, generating great concern in both scientific and public communities. Despite the expected serious implications, we lack a comprehensive understanding of how ice loss and related processes control marine biota and interactions at different spatiotemporal scales under multiple environmental stressors and drivers of change. We systematically review existing knowledge on how the losses of ice shelves, sea ice, and glaciers affect polar marine biocenosis. We include in situ, remote sensing, and modelling studies on sea ice biota, phyto- and zooplankton, fish, seabirds, phyto- and zoobenthos and marine mammals, covering a time span of three decades (1991-2022). We apply a qualitative ecosystem-based risk assessment to assess the individual and cumulative response of ecosystem components and related ecosystem services. The most threats and opportunities are expected to manifest in the shallow coastal zones. They include loss of ice habitat, water column darkening due to sediment input with meltwater, increased sedimentation rates, and mechanical damage due to ice scouring, but also gain of marine habitat, lightening of the water column and nutrient input with meltwater. The cumulative score of all the stressors shows that marine ice loss will lead to autotroph-dominated polar marine systems with detrimental effects on secondary producers, i.e. zooplankton and zoobenthos, and sea ice-obligate species. Although similar stressors are recognised for polar and subpolar regions, some processes may differ in magnitude. This overview aims to provide summarised knowledge to inform science-based solutions for conservation and climate mitigation actions.

Keywords: cryosphere retreat, ecosystem change, polar biocenosis, Arctic and Southern Ocean

Introduction

Polar regions are experiencing some of the most extreme climate change impacts that have already resulted in serious transformations. In particular, polar marine ecosystems are strongly influenced by the rapidly-changing extent, duration, and seasonality of the cryosphere (Fig.1). Loss of marine ice, i.e. ice shelves, glaciers, and sea ice, is an undeniable indicator of ongoing climatic changes on Earth (Cavalieri and Parkinson 2012, Parkinson and Cavalieri 2012, Pfeffer et al. 2014). The estimates derived from satellite observations and numerical models show that Earth has lost 28 x 1012 t of ice between 1994 and 2017, including Arctic sea ice (7.6 x 1012 t), Antarctic ice shelves (6.5 x 1012 t), the Greenland ice sheet (3.8 x1012 t), the Antarctic ice sheet (2.5 x 1012t), and Southern Ocean sea ice (0.9 x1012t) (Slater et al. 2021). Despite the legally-binding Agreement to constrain warming to 1.5°C above pre-industrial levels (UNFCCC 2015), the cryosphere will continue to lose mass this century (Pattyn et al. 2018) and post-breakup recovery of confined ice shelves is unlikely (kesson et al. 2022).

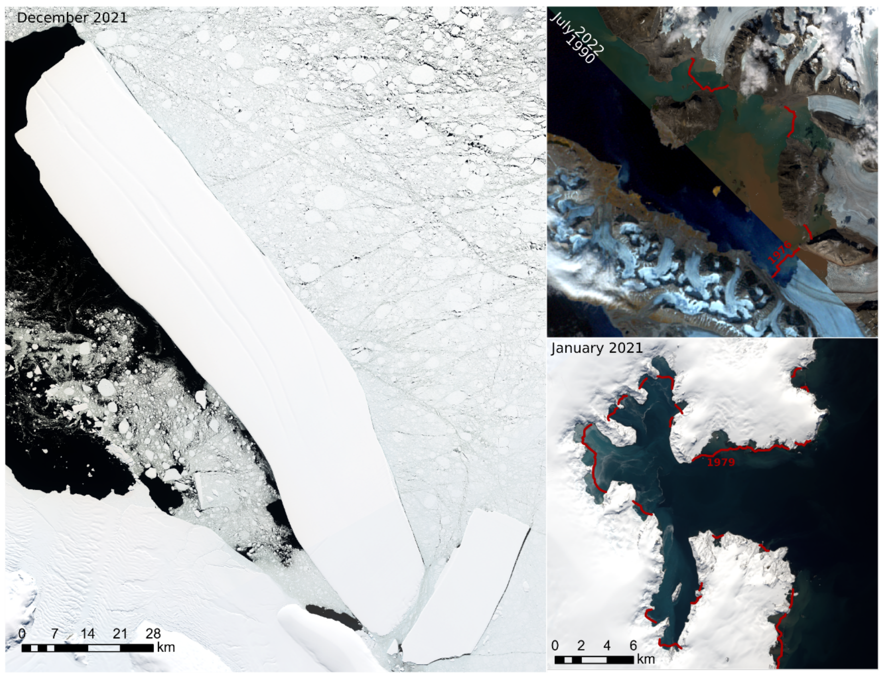

Figure 1. Cryosphere retreat. A) Ice shelf collapse; giant iceberg A-76 calved from the Filchner–Ronne Ice Shelf in May 2021 (74°S Weddell Sea, Antarctica). B) Glacier retreat; the extent of newly ice-free areas and glacial meltwater plumes in Kongsfjorden (top; 79°N Svalbard archipelago) and Admiralty Bay (bottom; 62°S South Shetland islands). Landsat 8 satellite images were obtained from https://www.usgs.gov/ and natural colour composites were generated in ArcGIS Pro 2.8.0.

Impacts of cryosphere retreat in the surrounding marine environment vary in magnitude and scale. They include, but are not restricted to, both habitat loss and expansion, increased stratification of the water column (de Andrés et al. 2020), changes in underwater light regime, general circulation, transport of sediment and nutrients (Sundfjord et al. 2017, Skogseth et al. 2020) and increased ice-scouring (Gutt 2001, Barnes and Souster 2011a). All these are sources of ecological disturbance to the pelagic and benthic biocenosis associated with glacial and periglacial environments. The accumulation of stressors can further increase the vulnerability of polar marine food webs and ecosystem services such as commercial fisheries and climate regulation (Arrigo et al. 2020).

Rapid climate-forced environmental changes of polar marine ecosystems offer ideal scenarios to get further insights into ecological concepts such as equilibrium, resilience, and tipping points (Sahade et al. 2015, Dayton et al. 2019, Gutt et al. 2021). Many ecological elements of polar regions are approaching a level of potentially irreversible regime shifts, particularly in the Arctic and West Antarctic Peninsula, due to the magnitude and consistency of marine ice loss. While ecosystem response to environmental stress tends to be gradual, broad evidence suggests that shifts in community structure are more prone to threshold dynamics, and their tipping points occur at differing critical values of environmental pressure (Hillebrand et al. 2020). Thus, understanding the extent to which marine ice loss affects ecosystem components might help to predict future composition of the polar seas.

Biogeographical patterns of polar marine biocenosis are seldom investigated across various spatiotemporal scales and integrated into ecological studies. However, this integration gives complementary information to assess trends and drivers of ecosystem state, and helps to prioritise conservation efforts (Kennicutt et al. 2015). Elucidating threshold levels of pressure, above which ecosystem response magnitudes and their variances increase disproportionately, creates context for accelerating changes in the polar marine ecosystem and ecosystem-based management. Developing a risk assessment framework has been recently identified as an urgent transition in orientating whole-of-systems dynamics toward robust approaches for managing risks and uncertainties in polar marine ecosystems (Ottersen et al. 2022). To move forward, ecosystem-based management requires assessing the states of ecosystem components, their past and future dynamics, and response to cumulative environmental and anthropogenic pressures.

A decent amount of reviews and meta-analyses exist on the effect of climate-driven disturbances on different polar marine functional groups (Griffiths et al. 2017, Figuerola et al. 2021), while only few of them focus on wider ecosystem components (Morley et al. 2019, Gutt et al. 2021). Here, we review existing knowledge on how the loss of marine ice affects sympagic biota, phyto- and zooplankton, fish, seabirds, phyto- and zoobenthos, and marine mammals in the Arctic and Southern Ocean following the PRISMA EcoEvo extension (O'Dea et al. 2021) (Supplementary Materials). We identified the environmental stressors from marine ice loss and scored them based on a decision tree (modified from (Altman et al. 2011), Fig. S1) to qualitatively assess their potential net effect on ecosystem components (level 1, class 3 ecosystem-based risk assessment, (Holsman et al. 2017)) based on the most recent projections of the cryosphere by the end of this century (2100: reference year of the Representative Concentration Pathways RCP projections, AR6-IPCC, 2022).

Trends of marine ice dynamics

Warming and wetting have persisted as key climatic drivers in polar regions which will very likely continue through this century (Fox-Kemper et al. 2021), particularly in the areas of Atlantic and Pacific water inflow and West Antarctica (Fig. 2). Since 1979, the Arctic has warmed nearly four times faster than the global average (Rantanen et al. 2022), and summer sea surface temperature (SST) has increased about 0.5°C per decade (1982–2017) (Meredith et al. 2019) While the southernmost regions of the Southern Ocean have cooled down, the Antarctic Peninsula is considered an area of recent rapid regional (RRR) warming (Vaughan et al. 2003) where SST has already increased >1°C since the second half of the 20th century (Meredith and King 2005).

Box 1. Definition of key terms related to cryosphere, polar biocenosis, ecosystem services and other processes
1. Cryosphere Marine ice-related definitions were taken from WMO Sea Ice Nomenclature (2014). WMO classifies ice into t

In the Arctic, the loss of sea ice, particularly of multi-year ice (MYI), has accelerated since 2001 and even low emissions scenarios show ice-free summers by 2050. In contrast, sea ice around Antarctica has been comparatively stable over the past several decades of satellite observations, growing in some regions and decreasing in others. However, after record-high sea ice concentration in 2014, an unexpected and precipitous reduction has started that was equivalent to 30 years of sea ice loss in the Arctic (Eayrs et al. 2021). Regional changes during the recent decline were almost opposite to the long-term trend (Rackow et al. 2022) Thus, current climate model simulations are uncertain about sea-ice future in the Southern Ocean.

In both polar regions, glaciers and ice sheets have lost mass especially since 2000 (even in parts of the more stable East Antarctica), and further loss is predicted under all emissions scenarios. In the coastal Arctic and Antarctic Peninsula regions, many marine-terminating glaciers have retreated, and some of them became land-based in the last decades producing newly ice-free areas (Błaszczyk et al. 2013, Jerosch et al. 2018). In the Southern Ocean, over 30,000 km^2 have been exposed since the second half of the last century, particularly in the Antarctic Peninsula region, due to the collapse of several ice shelves (Cook and Vaughan 2010). The East Antarctic Ice Sheet could also retreat substantially if temperatures rise +1.8°C compared to pre-industrial levels (currently at +1.1°C). In contrast to sea ice dynamics, once ice sheet melt accelerates due to higher temperatures, it cannot be stopped or reversed for many thousands of years, even once temperatures stabilise. Importantly, sea-ice loss increases both ice shelves and glaciers activity, and disturbance by drifting icebergs (Smale and Barnes 2008, Barnes and Souster 2011b).

As the polar regions warm, glacial meltwater plumes and riverine input will carry increased sediment and nutrient loads (Syvitski 2002), in particular across all coastal Arctic and the Antarctic Peninsula. Increased run-off from glaciers and ice shelves is also freshening the surface waters of the polar seas (Nummelin et al. 2015). This colder, fresher water prevents nutrients from deeper and saltier waters from reaching the surface, thus increasing stratification.

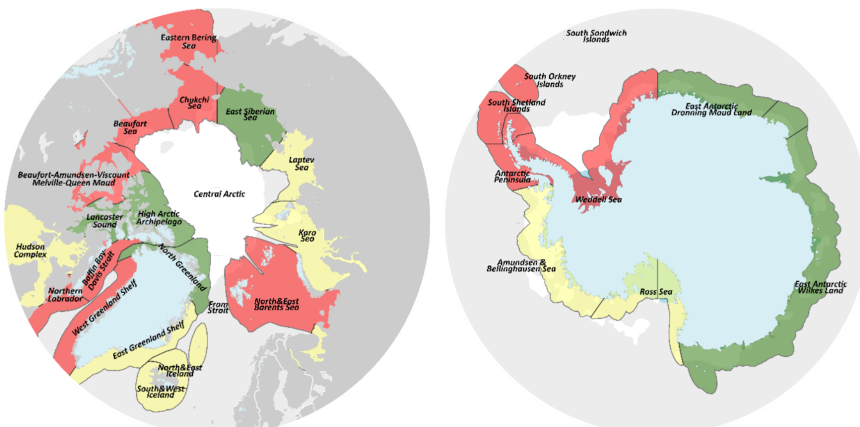

Figure 2. Anticipated level of marine ice loss and related stressors in polar marine ecoregions by the end of this century (high-red, medium-yellow, low-green). Layers source: United States National Ice Center, Esri Data and Maps, National Snow and Ice Data Center, GLIMS Randolph Glacier Inventory, Natural Earth, Maps.com.

Environmental stressors from marine ice loss

Marine habitat expansion due to glaciers and ice shelves retreat

In the Arctic and Southern Ocean, all ecosystem components and services are expected to benefit from marine habitat expansion after ice shelf and glacier loss, with the former exposing much more area (Fig. 3). Planktic organisms can respond rapidly due to short lifespan, high growth rate, and less restricted lateral exchange in the pelagic system (Clarke et al. 2007, Bertolin and Schloss 2009, Cape et al. 2014). Fast colonisation by benthic diatoms, macroalgae and pioneer zoobenthic species has also been observed in the newly formed ice-free areas, while fish were rare (Quartino et al. 2013, Ahn et al. 2016, Campana et al. 2018, Braeckman et al. 2019). Massive blooming of benthic diatoms can either inhibit further colonisation by macroalgal and zoobenthic species or precondition the substratum for the establishment of pseudoperennial and annual macroalgae (Fricke et al. 2008). Benthic grazers play a key role in controlling their abundance during successional processes and reduce the competition for space (Campana et al. 2018). The dietary flexibility of benthic species is a potential ecological driver and central to its success in the colonisation of newly ice-free coastal habitats (Seefeldt et al. 2017). Glacier retreat was also shown to enlarge the foraging grounds for planktivorous seabirds and littoral habitats accessible to benthophages (Stempniewicz et al. 2017). Similarly, ice shelf and glacier retreat enables the formation of sea ice in the newly formed glacial bays, increasing the surface area available for sympagic algae and ice-obligate species. Although rapid shifts towards local primary production have been reported due to ice shelf collapse (Ingels et al. 2018), little is known about how this may affect benthic sub-ice shelf life that has recently been discovered (Griffiths et al. 2021, Owsianowski and Richter 2021). On the one hand, the emergence of highly productive coastal zones can lead to more efficient sinks of anthropogenic carbon and nutrient cycling as well as support higher biodiversity and benefit fish stocks. On the other hand, the environmental conditions of the least-disturbed habitat on the planet, the sub-ice shelf habitats, risk extinction as Earth's ice imbalance continues.

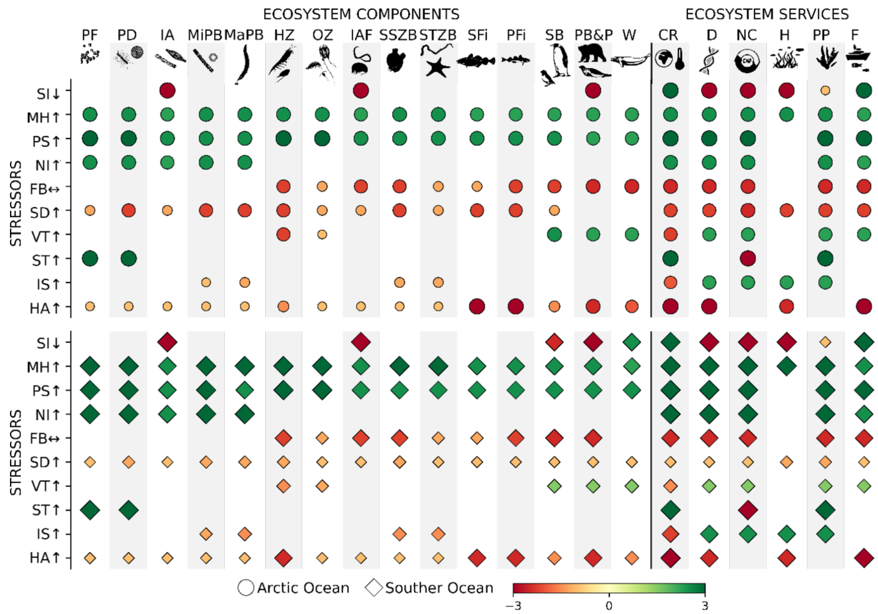

Figure 3. Risk assessment (RA) for ecosystem components (left) and services (right) in response to stressors related to marine ice loss in the Arctic (top, circles) and Southern Ocean (bottom, diamonds). Ecosystem components; planktic flagellates (PF), planktic diatoms (PD), ice algae (IA), microphytobenthos (MiPB), macrophytobenthos (MaPB), primarily herbivorous zooplankton (HZ), omnivorous zooplankton (OZ), ice-associated fauna (IAF), sediment sensitive macrozoobenthos (SSZB), sediment tolerant macrozoobenthos (STZB), subpolar (SFi) and polar fish (PFi), seabirds (SB), polar bears and pinnipeds (PB&P), baleen whales (W). Ecosystem services (excluding cultural); regulating: carbon storage and climate regulation (CR); supporting: genetic and biological diversity (D), nutrient cycling (NC), habitat (H), primary production (PP); provisioning: fisheries (F). Stressors and their expected direction shown in arrows: sea-ice habitat (SI), marine habitat (MH), productive season (PS), nutrient input with meltwater (MI), food base composition change/mismatch (FB), sediment discharge (SD), vertical transport by buoyant plume (VT), stratification (ST), IS (ice scouring), human activity (HA). See more detailed information on Table S2.

Loss of sea ice habitat

An ongoing change from a MYI to less stable FYI, particularly in the Arctic Ocean, is unfavourable for the sympagic community (see Box 1). The highly variable under-ice topography of MYI allows enough light penetration for ice algae (Lange et al. 2017), enables richer biodiversity and species abundances compared to FYI (Melnikov et al. 2002), and offers an attractive feeding ground and refuge for ice-associated species year-round (Gradinger 2001) Furthermore, MYI can act as long-term storage for carbon and other elements, given internal biomass layers and has a potential for seeding spring bottom-ice algal communities in the following year, compared to FYI that undergoes a complete annual cycle of growth and melt. It leads to release of ice fauna and their low abundance and biomass (Ehrlich et al. 2020).

The sea-ice boundary will shift dramatically in both polar regions with further sea ice decline. Loss of FYI in the Arctic and Antarctica will lead to more open water within the ice pack and to lower primary production by ice algae (Lange et al. 2017). In the Arctic, sea ice retreat has led to an expansion of boreal fish and marginalisation of typical Arctic fish species (Aune et al. 2018). At the current state, it is increasing species richness and evenness, and the functional diversity of the fish assemblage. Even though higher diversity is often interpreted as being positive for ecosystem health, the observed trend may be temporal as subpolar species threaten Arctic species via predation and competition and ultimate loss of Arctic species will result in a reduction in functional diversity (Frainer et al. 2021). In the case of marine mammals and seabirds, sea-ice decline results in loss of shelter from inclement weather, open-water predators, but also represents loss of foraging habitats, platforms for birthing, nursing, resting and moulting (Lydersen et al. 2014). However, recent observations suggest that they are increasingly using land habitats in some parts of their range, where they have minimal access to their preferred prey, which has the potential to increase nutritional stress and interactions with humans (Rode et al. 2018). Despite some signs of adaptation, it is generally agreed that the ice-obligate species cannot survive absent sea ice. The abrupt loss of sea ice is creating a dichotomy between ice-dependent mammals and seabirds that are losing habitat (Iverson et al. 2014, Trathan et al. 2020), and some cetaceans that appear to be thriving during periods of rapid sea ice loss with extended open-water seasons enabling the establishment of macrozooplankton and fish populations (Moore et al. 2022).

Longer productive season and food base composition change/mismatch

Sea-ice thinning, reduction of the snow cover, earlier melt and later freeze-up of seasonal sea ice will increase the amount of sunlight reaching the marine ecosystem (Alou-Font et al. 2013, Aumack et al. 2014) and likely drive ecological tipping points in which primary producers flourish and outcompete dark-adapted species (Kortsch et al. 2012). In the areas where sea ice still persists, a longer productive season is predicted to benefit the ice-algae, phytoplankton and phytobenthos in both polar regions (Goldsmit et al. 2021). Higher competition will likely lead to widespread shifts from invertebrate- to algal-dominated states on coastal polar seabeds, reducing biodiversity and altering ecosystem functioning. Future extension of the productive season might drive some endemic shallow invertebrate communities into small refugia where sea-ice duration is maintained, impeding genetic connectivity. In many non-coastal areas, increased light will only allow phytoplankton blooms (Montes-Hugo et al. 2009). Thus, some invertebrate species may persist at depths where the light is too low for benthic algae irrespective of sea-ice.

Changes in sea-ice duration and timing of major bloom events are expected to negatively affect food base composition, particularly for secondary producers. Primarily herbivorous zooplankton which transfer energy-rich lipid compounds and essential fatty acids to higher trophic levels, strongly depend on the sea-ice algae blooms (Ershova et al. 2021). During spring, ice algal-derived carbon is essential for the maturation and reproduction of pelagic grazers before phytoplankton is available for their offspring (Leu et al. 2011). An earlier onset of the ice-associated and pelagic blooms is likely to create a mismatch in carbon source availability and grazer occurrence (Ji et al. 2013). Krill and *Calanus* copepods are a keystone species and a primary food resource for many fish, seabirds, and marine mammals (Cavan et al. 2019, Will et al. 2020). As many species are highly dependent on them, declines in abundance could have cascading effects throughout the food web. Large increases in gelatinous zooplankton biomass could imply an energetic turning point and trophodynamic restructuring.

In regions still covered by seasonal sea ice, more and fresher organic material is exported to the deep sea by the fast-settling ice-associated diatoms and surface-born microbial clades in comparison to slow-settling Phaeocystis aggregates in the ice-free regions (Savidge et al. 1995, Reigstad et al. 2008, Lalande et al. 2019, Fadeev et al. 2021). Weakening of the pelagic-benthic coupling through the decrease in vertical export efficiency and amount of sinking labile organic matter will have repercussions on arctic deep-sea ecosystems. Indeed, benthic biomass and diversity were found to be higher in the seasonally ice-covered areas (Pecuchet et al. 2022) with a shorter but with higher modularity food web. Modelling results indicate that climate-related changes in phytodetrital inputs can lead to important shifts in benthic biomass, community structure, and functional diversity, with loss of various common taxa (Lovvorn et al. 2016). Further warming and reduction in sea-ice coverage will most likely also continue to negatively affect arctic fish species whose food availability largely depends on the coupling between sea-ice cover and the benthic production (e.g. demersal). Most deposit-feeders (and, in turn, their consumers), however, rather depend on the total amount of settling microalgae, and not so much the timing.

Freshwater, nutrient, and sediment inputs. Stratification and vertical transport by buoyant plume

Sea ice and glacier ice melt release large volumes of freshwater. It can have stimulating effects on primary production early in the season by nutrient input and meltwater-induced stratification, which provides favourable conditions for phytoplankton growth and development (Detoni et al. 2015), but prevents the vertical export to the bottom, especially of small cells. Icebergs also leave a trail of trace nutrient enrichment as they gradually melt, enhancing phytoplankton blooms in their path. This phytoplankton bloom fertilisation increase bloom intensity, and increase the potential blue carbon capture, but whether this increases any storage or sequestration by benthic organisms depends on where and when this occurs (Death et al. 2014, Wadham et al. 2019). However, as outlet glaciers continue to retreat, many will lose their connection to the ocean. This decoupling of glaciers (and their meltwater) from the ocean will have important consequences for the timing and spatial distribution of nutrient delivery and the carbon cycle (Meire et al. 2015, Hopwood et al. 2018). Glaciers' retreat on land will also affect seabirds as currently, submarine glacial plumes stun zooplankton by cold and osmotic shock and raise them up to the surface, thus making available to seabirds, in particular to surface-feeders over benthic-feeders and pelagic pursuit-divers.

Meltwater discharge also transports dissolved and particulate matter from land, leading to increased light attenuation and coastal waters darkening/shading. The total primary production may drop drastically due to intensive glacial melt (Hoffmann et al. 2019). Also, low light availability by glacier melt inputs with high turbidity restricts large phytoplankton productivity (diatoms). Whereas marine particulate organic matter provides rich food to higher trophic consumers, terrestrial POM is a low-quality food resource for marine organisms. Therefore, if glaciers continue to melt because of climate change, an impoverishment of the nutritional value of POM may be predictable impacting the food webs of polar coastal regions. Many zoobenthic species were also found to be sensitive to high sedimentation rates. Thus, if the increasing intensity of glacial processes will continue in the upcoming years, the diversity of the encrusting fauna, ascidians in the shallow sublittoral could dramatically decrease (Krzeminska and Kuklinski 2018).

Ice scouring

Iceberg scouring affects around 30% of world's coastline and leads to significant mechanical disturbances (Conlan et al. 1998, Barnes and Souster 2011a) that skews population structure of benthic communities (Smale and Barnes 2008), contributes to the sediment resuspension and increment of inorganic particulate matter on the water column (Moon et al. 2015), and limits the potential immobilisation and, ultimately, sequestration of benthic blue carbon (Barnes et al. 2018). The probability of scouring effect is intertwined with sea ice dynamics, since coastal fast-ice losses and low coverage of seasonal sea ice can facilitate the movement of icebergs, thus producing high-frequency ice scour disturbance events (Zwerschke et al. 2022). After the space clearance, mobile and pioneer benthic organisms (via larval recruitment) are the first to recolonise the scour marks and their surroundings. Slow recolonisation and recovery post-disturbance which follows highly complex successional pathways (approximately 10 to 250 years), is a general tendency for polar benthic ecosystems due to slow growth and life cycles (Gutt and Starmans 2001, Zwerschke et al. 2022). The magnitude of iceberg-driven disturbance varies within and, most contrastingly, between polar regions and the peak effect is asynchronous. Abundance, disturbance area, and maximum age of ice scours are comparatively lower in the Arctic (Gutt et al. 1996). Icebergs drifting in the northern hemisphere are significantly smaller than those in the southern, and since the contributory glaciers and ice shelves have retreated more severely in the Arctic, massive disturbances from mega-icebergs should only be expected in the vicinity of the main ice shelves/glaciers in the Canadian high Arctic and Greenland. On the other hand, almost 90% of glacier fronts have retreated along the western Antarctic Peninsula since the early 1950's (Cook et al. 2005). On ecological time scales, benthos will be increasingly affected in such areas, while ice scour disturbance will drastically drop in Antarctic shallows in the centuries to come; this asynchronous ice disturbance history in polar regions indicate that the Arctic may anticipate future Antarctic.

Human activity

The opening of polar seaways is facilitating opportunities among all types of vessels in areas that were previously covered by MYI, supporting the strong increasing statistical correlations observed between sea ice change and shipping trends in both polar regions (Constable et al. 2022). This will have an impact on ice-associated species by ice breakup, underwater noise, increase the risks of lethal and sublethal collisions of marine megafauna, and risks of invasive species. Loss of marine ice is also related to increasing human activity of other forms, e.g. fisheries and the use of other marine resources. Although the largest more sustainable fisheries are in polar waters, more periodical reassessment of the stocks will be needed particularly considering the imbalance that can be triggered by further changes of the sea ice, and the increase of demand of highly nutritious protein (Constable et al. 2022). Bottom trawling in polar shelves also makes the stored carbon therein more prone to be released back into the carbon cycle, thus blocking the long-term storage (Bax et al. 2021). However, an overarching management framework to protect benthic communities from bottom fisheries in high polar seas is the identification and designation of VMEs (Ashford et al. 2019). Oil, gas, and deep-sea mining exploration and exploitation in Arctic seas is dissonant with the Paris Agreement, and unlike Southern Ocean's governance of The Antarctic Treaty System (ATS) through the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), the northern polar region is more vulnerable to direct human interference.

Cumulative response to environmental stressors

Our ecosystem based risk assessment suggests that future marine ice loss is likely to pave the way for autotroph-dominated polar ecosystems with higher productivity and carbon-capture. The cumulative score of all the stressors shows that marine ice loss will be detrimental to secondary producers, i.e. zooplankton and zoobenthos, and particularly for primarily herbivorous copepods and krill. It is mostly driven by changes in the food base composition and timing after sea ice loss as well as sediment discharge with glacial meltwater that will also affect carbon storage and sequestration as well as regional biodiversity. These effects will likely suppress the effect of colonisation of pioneer species and biodiversity shifts in the newly open coastal zones becoming exposed in the near future. In the long term, there will be regions where ice-algal production will decline with the disappearance of the ice all together leading to new pelagic conditions, while in other areas sea ice will expand over previously ice-shelf covered waters. Such nonlinear responses complicate the prediction of future polar ecosystem dynamics. There is no doubt, however, that the consequences of the large abiotic changes in the polar regions are expected to be severe for ice-obligate species such as polar bears, pinnipeds and seabirds. Currently, they often find refuge at the front of marine terminating glaciers and on ice shelves, or slowly adapt to land habitats. Moreover, climate change-related biodiversity redistribution and range extensions open up new and large-scale opportunities for the recruitment of non-native, invasive species and human activity that have the potential to affect ecosystem functioning and ecosystem services.

The patterns of species loss or change in biomass will likely differ substantially in Arctic and Antarctic regions due to habitat differences related to the nature of the ice-cover, which is floating in the Arctic and land-associated in the Antarctic. Our analysis suggests that the nature of the changes that will occur with marine ice loss in polar regions may differ somewhat in magnitude, with the Arctic having lower cumulative scores and thus being more prone to species loss by the end of this century. Arguably, for all of the environmental stressors assessed here, the Arctic seems to be close to the tipping point of marine ice loss related shifts. In many environmental aspects and to a certain degree, the ongoing changes in the Arctic could be used to foresee possible ecosystem phenologies in Antarctic seas.

The current review shows that there is a great value in a synergistic approach held in compliance with recent state-of-the art assessment and predictions of the environmental stressors. Future reviews and meta-analyses would be facilitated if source studies focussing in species also provide some sort of functional classification of their study subjects that can be used as input for building score matrices or clustering type of responses based (pressure-response).

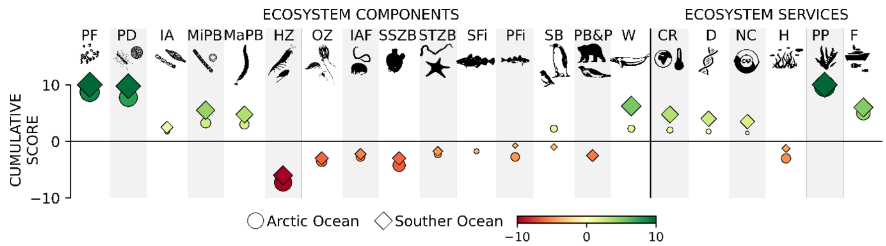

Fig. 5 Cumulative scores of risk assessment (RA) for ecosystem components (left) and services (right) in response to stressors related to marine ice loss in the Arctic (circles) and Southern Ocean (diamonds). Ecosystem components; planktic flagellates (PF), planktic diatoms (PD), ice algae (IA), microphytobenthos (MiPB), macrophytobenthos (MaPB), primarily herbivorous zooplankton (HZ), omnivorous zooplankton (OZ), ice-associated fauna (IAF), sediment sensitive macrozoobenthos (SSZB), sediment tolerant macrozoobenthos (STZB), subpolar (SFi) and polar fish (PFi), seabirds (SB), polar bears and pinnipeds (PB&P), baleen whales (W). Ecosystem services (excluding cultural); regulating: carbon storage and climate regulation (CR); supporting: genetic and biological diversity (D), nutrient cycling (NC), habitat (H), primary production (PP); provisioning: fisheries (F). See more detailed information on Table S2.

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