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The role of Antarctic sea ice in the Earth system: Perspectives informed by 130,000 years of sea ice records

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Abstract. Antarctic sea-ice cover reached historically low levels in 2023, consistent with the simulated decrease in sea-ice extent in response to anthropogenic warming. Antarctic sea ice is closely linked to multiple components of the Earth system, thus its demise could precipitate widespread, cascading changes across the cryosphere, atmosphere, and ocean. However, the nature and strength of these interconnections are poorly understood, and they are often inadequately represented in models. In this review paper we use modern observations, models and paleoclimate archives covering the last glacial cycle to gain insights into how reductions in sea ice may affect other components of the Earth system. We review how Antarctic sea ice interacts with ocean and atmosphere circulation, ice sheets and ice shelves, marine productivity, and the carbon cycle over the last glacial cycle, for which we have the most robust sea-ice reconstructions. The review finds strong evidence from theory and models for impacts of Antarctic sea ice on the Earth system. Paleo-proxy reconstructions provide examples where changes in sea ice co-occur with changes in the carbon cycle, marine productivity, and ocean circulation. However, challenges remain in isolating the impact of sea ice in a highly interconnected system.

Short Summary (500 characters)

The impact of recent dramatic declines in Antarctic sea ice on the Earth system are uncertain. We reviewed how sea ice affects ocean circulation, ice sheets, winds, and the carbon cycle by considering theory and modern observations alongside paleo-proxy reconstructions. We found evidence for connections between sea ice and these systems but also conflicting results, which point to missing knowledge. Our work highlights the complex role of sea ice in the Earth system.

1 Introduction

The year 2016 marked the beginning of a low Antarctic sea-ice state after a multi-decadal period of increasing sea-ice extent that peaked in 2014 (Purich and Doddridge, 2023). The emergence of the low sea-ice state, reaching a record low in 2023 for both summer minima and winter maxima (Gilbert and Holmes, 2024), may indicate that a regime shift recently occurred (Hobbs et al., 2024). The recent observed changes are consistent with the

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decline in sea ice that is projected to occur under anthropogenic warming (e.g., Diamond et al., 2024; Eayrs et al., 2021; Fox-Kemper, et al., 2021).

The impacts of the current (Josey et al., 2024) and projected changes in Antarctic sea ice are likely to be widespread and to extend across many parts of the Earth system. This is because sea ice is coupled to the ocean, continental ice, the atmosphere, and the biosphere, (Fig. 1), through large fluxes of heat, salt, and carbon. For example, the magnitude of the freshwater fluxes associated with the annual freeze and melt cycle of Antarctic sea ice is greater than the combined freshwater fluxes associated with precipitation minus evaporation and glacial ice melt in the Southern Ocean (Abernathey et al., 2016).

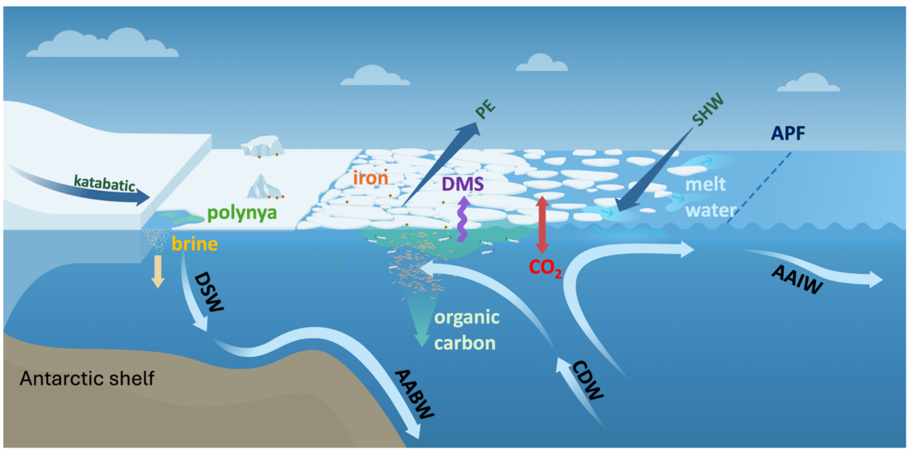

Figure 1: Schematic overview of the role of Antarctic sea ice in the Earth system. Shown are major water masses discussed in the text, including dense shelf water (DSW) which forms Antarctic Bottom Water (AABW), produced through brine rejection during sea-ice production, Circumpolar Deep Water (CDW), upwelling due to surface wind stress, and Antarctic Intermediate Water (AAIW), freshened by sea-ice melt. Biogeochemical processes include ice-associated blooms and carbon export stimulated by continental iron delivered by glacial ice and sea ice, the release of dimethyl sulphide (DMS) and air-sea exchange of carbon dioxide (CO_2). The major Antarctic wind systems, the Katabatic winds, the Polar

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Easterlies (PE) and Southern Hemisphere Westerlies (SHW) are indicated, as well as the oceanic Antarctic Polar Front (APF).

Changes in Antarctic sea ice have been linked with a suite of physical and biogeochemical ocean processes (Fig. 1). Sea-ice presence along the Antarctic coast buttresses ice shelves, stabilising the ice shelf and associated glaciers (Christie et al., 2022). Sea ice also provides a buffer against wave energy, thus limiting physical breakage of ice shelves (Massom et al., 2018; Teder et al., 2022, 2025). Through its impact on ocean circulation, changes in sea-ice formation and brine rejection can impact delivery of heat to ice shelf cavities (e.g., Bintanja et al., 2013; Christie et al., 2022; Lauber et al., 2023; Sun et al., 2023). Changes in sea-ice extent and production rate influence the buoyancy fluxes that are essential in driving changes in the production of dense shelf water (DSW) which forms Antarctic Bottom Water (AABW) south of the Antarctic Polar Front (APF) and Antarctic Intermediate Water (AAIW) north of the APF (Abernathey et al., 2016; Pellichero et al., 2018). Sea-ice extent can also affect atmospheric circulation through its influence on albedo and heat exchange between the ocean and the atmosphere, and thus the position and intensity of westerly winds (e.g., Raphael et al., 2011).

The influence of sea ice extends to the biosphere. Sea-ice extent and seasonal melting influencing the intensity and timing of ice-edge phytoplankton blooms (Giddy et al., 2023), and the cycling of nutrients, both locally (e.g., iron - Lannuzel et al. 2016) and remotely through its influence on intermediate and deep-water circulation (Sarmiento et al., 2004). Sea ice also provides a capping effect, acting as a lid that reduces oceanic outgassing of carbon dioxide (CO_2) (Stephens and Keeling, 2000; Morales-Maqueda, et al., 2003). Through these physical and biogeochemical processes, sea ice has a significant influence on ocean carbon uptake and the global carbon cycle (e.g., Gupta et al., 2020; Kurahashi-Nakamura et al., 2007; Shadwick et al., 2021).

Antarctic sea-ice extent is known to have changed dramatically on glacial-interglacial timescales (Chadwick et al., 2022a; Crosta et al., 2022), and these changes have been implicated as drivers of substantial Earth system changes. Specifically, winter sea-ice cover around Antarctica expanded to approximately twice its current extent during the Last Glacial Maximum (LGM) from 19,000-23,000 years ago (19-23 ka) (Fig. 2; Gersonde et al., 2005; Lhardy et al., 2021). Summertime sea-ice cover likely increased less, leading to enhanced seasonality in areal coverage (Green et al., 2022; Lhardy et al., 2021). In contrast, Antarctic

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sea-ice extent is thought to have been substantially reduced during past warm periods such as the last interglacial (LIG) period (130-116 ka), also known as Marine Isotope Stage 5e (MIS 5e). Note that the Marine Isotope Stage naming system refers to alternating glacial and interglacial periods; cooler periods with larger ice sheets are labelled by even numbers, and warmer periods with smaller ice sheets by odd numbers (Fig. 2b,c). For example, cooler glacial periods of Earth's history such as MIS 2 and 6 were characterized by larger ice sheets, lower sea levels and lower atmospheric CO_2. Warmer interglacial periods such as MIS 1 and 5e had smaller ice sheets, higher sea levels and higher CO_2. Within the colder, glacial periods there is also evidence for rapid millennial scale fluctuations in the ice sheets/sea levels.

Sea salt sodium (ssNa) measurements in ice cores (Fig. 2c; Wolff et al. 2010) suggest there was a substantial reduction in Antarctic sea ice during the peak of the LIG. Simulations suggest a 40-60% reduction in the wintertime sea-ice extent between ~129 and 127 ka, relative to the pre-industrial, is required to explain water isotope measurements from ice cores (Holloway et al., 2016, 2017). Detailed Antarctic sea-ice reconstructions based on marine sediment cores (Chadwick et al., 2020, 2022a, c, 2023) and sea surface temperature compilations (Capron et al., 2017; Chadwick et al., 2022b; Chandler and Langebroek, 2021; Gao et al., 2025; Hoffman et al., 2017) are also consistent with substantial Southern Ocean warming and sea-ice loss during the peak of the LIG. South of 40°S, annual-mean reconstructed sea surface temperatures were 2.2 to 2.7°C warmer than pre-industrial temperatures, while summer sea-surface temperatures ranged from 1.2 to 2.2°C higher than the preindustrial period. Earth System Models show September (winter) sea-ice area was reduced by 40-60% relative to pre-industrial model simulations (Gao et al., 2025; Sime et al., 2025).

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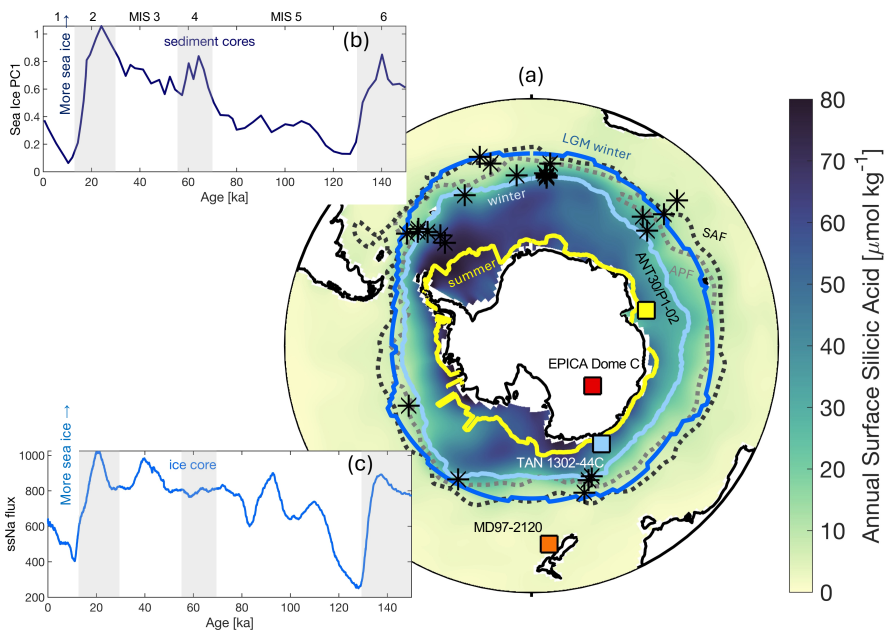

Figure 2: Key Southern Ocean features and proxy records discussed in this paper. a) location map showing in yellow, ANT30/P1-02 (Wu et al., 2018), in orange, MD97-2120 (Pahnke and Zahn, 2005; Ronge et al., 2015) in blue, TAN 1302-44 (Pesjak et al., 2023), in red, EPICA Dome C (Wolff et al., 2010). The cores used in the sea-ice compilation of Chadwick et al. (2022a) are indicated by asterisks. The modern locations of the Subantarctic Front (SAF) and Antarctic Polar Front (APF) (Orsi et al., 1995) are indicated by the dashed dark and light grey lines, respectively. The modern August (winter) and February (summer) sea-ice edges are shown in light blue and yellow, respectively, derived from the biogeochemical Southern Ocean State Estimate as used in Weis et al. (2024). The estimated August sea-ice edge during the LGM, from Paul et al. (2021), is shown in dark blue. The background colour is the annual average surface silicic acid concentration [µmol kg^{-1}] from WOA23 (Reagan et al., 2024), showing how this nutrient is 'trapped' in the Southern Ocean sea ice zone. Insets show b) principal component 1 (PC1) of the sea-ice records from Chadwick et al. (2022a) indicating the dominant temporal trend and c) the ice core sea-ice

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proxy, sea salt sodium (ssNa) flux, in units of μg m^{-2} y^{-1} from EPICA Dome C from Wolff et al. (2010).

The magnitude and timing of sea-ice changes through the last glacial cycle varied by zone and sector of the Southern Ocean. In particular, the pattern of sea-ice advance during glacial stages varied between sectors. As described in Chadwick et al. (2022a), in the Indian and Pacific sectors, sea-ice extent remained low until 80 -70 ka and then gradually increased to a maximum at 25-20 ka during MIS 2. In the East Atlantic sector, sea ice increased rapidly during MIS 4, decreased during MIS 3, and then gradually increased, reaching a maximum during MIS 2. In the Scotia Sea and central Atlantic sectors, sea-ice extent increased earlier in the glacial cycle, around 100 ka, and remained relatively high until deglaciation. The ice core sea ice proxy, nssNa flux, also responded early in the glacial cycle, increasing 4-fold between 130 and 110 ka. While these proxy records provide important constraints on the behaviour of sea ice in the past, it's important to recognise their limits. In particular, very few sea-ice records cover the whole of the last glacial cycle, and none is located south of the current summer sea-ice limit (Chadwick et al., 2022a).

Changes in sea ice over the last glacial cycle are thought to have impacted ocean and atmospheric circulation, ice shelves, marine productivity, nutrient cycling, and the carbon cycle. This paper represents the second of two review papers presented by the Cycles of Sea Ice Dynamics in the Earth system (C-SIDE) PAGES Working Group, examining changes in Antarctic sea ice over the last full glacial-interglacial cycle. The first paper (Crosta et al., 2022) described the marine and ice core proxies used to reconstruct sea-ice changes over the last glacial cycle. The goal of this review is to describe how changes in Antarctic sea-ice are linked to physical and biogeochemical processes in the ocean, atmosphere and cryosphere over the last glacial cycle. We review how sea ice in the Southern Ocean coordinates climate/carbon-cycle feedbacks via direct and indirect impacts on grounded ice, biology, the atmosphere, and the ocean. More specifically, we identify five key aspects of this coordinating role: ocean circulation, ice shelves, winds, marine biological productivity, and the integrated effects of these impacts for marine carbon storage. We present marine sediment and ice core proxy evidence (Fig. 2) to provide examples of how these interactions played out across the last glacial cycle.

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2 Sea ice and ocean circulation

Sea-ice formation and melting exert a substantial influence on water mass formation in the Southern Ocean. The dominant water mass in the Southern Ocean is Circumpolar Deep Water (CDW), which is a mixture of deep waters entering the Southern Ocean from the different ocean basins – including North Atlantic Deep Water (NADW), Indian Deep Water (IDW) and Pacific Deep Water (PDW), which are entrained and mixed in the Antarctic Circumpolar Current (Talley, 2013). Ekman divergence due to the Southern Hemisphere westerlies causes CDW to upwell to the surface where it splits into southern and northern branches (Fig. 3; Pellichero et al., 2018; Rintoul et al., 2001). Both branches are transformed by sea-ice processes into new water masses. The northern branch is transported equatorward and gains buoyancy from surface warming, sea-ice melt, and precipitation, resulting in water masses of intermediate densities that are subducted below the surface waters to the north to form Subantarctic Mode Water (SAMW) and Antarctic Intermediate Water (AAIW) (Abernathey et al., 2016; Orsi et al., 1995; Pellichero et al., 2018; Saenko et al., 2002). SAMW and AAIW are part of the upper cell of the global Meridional Overturning Circulation (MOC) (Marshall and Speer, 2012). The southern branch, in contrast, flows poleward, where it experiences surface buoyancy loss through surface cooling and brine rejection during sea-ice formation, contributing to the formation of dense shelf water that forms AABW (Naveira Garabato et al., 2002; Talley, 2013; Vernet et al., 2019; Whitworth and Nowlin, 1987) which is part of the lower cell of the MOC (Marshall and Speer, 2012). The LGM is a good test bed to understand the relationship between sea ice and the oceanic circulation due to northward expansion of LGM sea-ice cover (Chadwick et al., 2022a; Gersonde et al., 2005; Green et al., 2022) and the extensive proxy and modelling studies of the LGM oceanic circulation.

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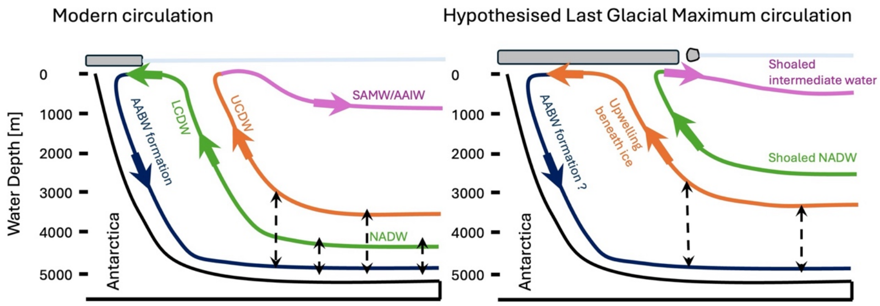

Figure 3: Simplified schematic illustrating the modern Southern Ocean overturning circulation (left) and hypothesised Last Glacial Maximum (LGM) circulation (right). Greater sea-ice cover during the LGM is hypothesised to have produced denser bottom waters through more intense brine rejection. Under present-day conditions there is mixing between the lower branch of the North Atlantic Deep Water (NADW) and the Antarctic Bottom Water (AABW). Under conditions of expanded sea-ice extent NADW shoals and the abyssal cell closes on itself, where CDW upwells mostly under sea-ice and is transformed into AABW with little air–sea gas exchange (Ferrari et al., 2014). Other water masses pictured are Lower and Upper Circumpolar Deep Water (LCDW and UCDW), Indian and Pacific Deep Water (IDW and PDW) and Subantarctic Mode Water (SAMW) and Antarctic Intermediate Water (AAIW). Figure after Talley (2013), Sikes et al., (2017), Shub et al. (2024), Nadeau et al. (2019) and Ronge et al. (2015).

2.1 Sea ice and the upper cell of the global MOC

The upper cell of the MOC forms far from the Antarctic continent but is strongly influenced by sea-ice melt. The water mass transformation analysis of Abernathey et al. (2016) suggests that increased formation and northward transport of sea ice may increase the rate at which CDW is transformed into more buoyant, low-salinity water masses of the upper cell (i.e., AAIW and SAMW). Modelling studies also highlight the importance of wind-driven sea-ice transport and melt to AAIW formation (Saenko and Weaver, 2001), predicting a shoaling of AAIW and a northward shift of the latitude of AAIW subduction during periods of sea-ice expansion (e.g., Fig. 3; Li et al., 2021; Ronge et al., 2015). Interestingly, Li et al (2021) find

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that AAIW also shoals under a global warming scenario, due to the increase in temperature and reduction in density of AAIW, despite a southward shift in the latitude of subduction.

The depth of AAIW in the past can be inferred by using a suite of sediment cores collected across a range of water depths, thus creating a 'paleo CTD cast.' The characteristics of sub-surface water can then be inferred using the $\delta^{13}C$ of DIC reconstructed from benthic foraminifera and the bottom water seawater Nd isotopic composition (εNd) reconstructed using ferro-manganese coatings on foraminifera, fish debris, or bulk sediment. Evidence from $\delta^{13}C$ and εNd suggests that the AAIW was shallower in the southwest Pacific Ocean during glacial periods (Fig. 4c; Hu et al., 2016; Pahnke and Zahn, 2005; Ronge et al., 2015), which is consistent with greater sea-ice melt during austral summer and a reduction in the density of Antarctic surface waters that are subducted to form AAIW (Green et al., 2022). Jones et al. (2022) demonstrated a link between periods of sea-ice expansion and AAIW shoaling in the southwest Pacific Ocean, specifically during the middle (MIS 4) and peak (MIS 2) portions of the last glacial cycle. The response of AAIW in the southeast Pacific Ocean during glacial periods is less clear. Evidence from $\delta^{13}C$ and redox elements implies increased oxygen content and deepening/thickening of the AAIW during the LGM (Martínez-Méndez et al., 2013; Muratli et al., 2010). In contrast, more recent work based on foraminiferal assemblages, $\delta^{13}C$, and $\delta^{18}O$ instead suggests AAIW in the southeast Pacific shoaled and that its subduction region moved northward (Haddam et al., 2020), consistent with the modelled

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pattern due to sea-ice expansion (Li et al., 2021) and the pattern observed in the southwest Pacific Ocean.

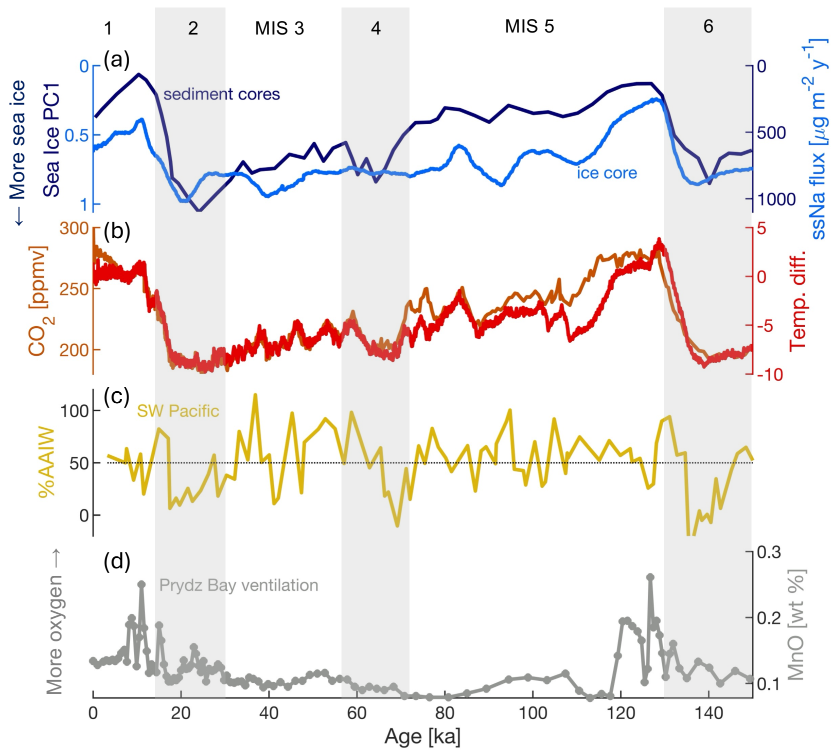

Figure 4: Sea ice and related changes in the Southern Ocean and Antarctica over the past 150 ka. (a) Sea Ice Index as Principal Component 1 of the sea-ice records from Chadwick et al. (2022a) and the ice core sea-ice proxy, ssNa, from EPICA Dome C from Wolff et al. (2010). (b) The Antarctic composite CO_2 (Bereiter et al., 2015) and the Antarctic temperature stack as an anomaly from the pre-industrial reference (Parrenin et al., 2013). Note these records are also shown in Fig. 3 insets in the opposite orientation. (c) The estimated fraction of Antarctic Intermediate Water in the Southwest Pacific at the location of core MD97-2120 (Ronge et al. 2015; Pahnke and Zahn, 2005), and (d), the weight percent of manganese oxide from core ANT30/P1-02 off Prydz Bay (Wu et al. 2019), an indicator of bottom water ventilation and proxy for AABW formation. Locations of records are shown in Fig. 2. Marine Isotope Stage (MIS) numbers, as indicated by the oxygen isotopic records of

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marine carbonates (Lisiecki and Raymo, 2005), are listed along the upper x-axis. Glacial stages are highlighted by grey vertical bars.

2.2 Sea ice and the lower cell

Sea-ice extent also affects the lower cell of the MOC through its impact on surface buoyancy loss around Antarctica. Dense Shelf Water (DSW), which is the precursor to AABW, is formed by brine rejection during sea-ice formation on the Antarctic continental shelf. Changes in sea-ice formation might thus impact DSW formation and therefore AABW.

Porewater chlorinity tells us the Southern Ocean was filled with very salty water during the LGM, consistent with an intensified sea-ice cycle and more brine production (Adkins et al., 2002). With the expansion of ice sheet across the Antarctic continental shelf around much of the continent during the glacials (Bentley et al., 2014), one puzzle is whether this more intense brine rejection was an open ocean process or whether AABW continued to form in small ice sheet free pockets on the shelf as occurs today. Caburlotto et al. (2010) argue, based on sedimentological and microfossil evidence, that dense water continued forming in Adelie Land during the LGM, potentially associated with a smaller and more northward located polynya. Additionally, Smith et al. (2010) interpret the existence of benthic and planktonic foraminiferal deposits in the northwest Weddell Sea as evidence for the continued presence of a polynya during the LGM, and suggest polynyas were widespread around Antarctica during the LGM, including in the Ross Sea, SE Weddell, and Dronning Maud Land. The continued existence of polynyas at the edge of the continental shelf may have also allowed brine production and deep-water formation to occur over the continental slope.

A range of proxy data implies that southern-sourced waters probably filled a larger volume of the Atlantic basin during the LGM. Benthic $\delta^{13}C$, $\delta^{18}O$, Cd/Ca, and radiocarbon records from the Atlantic Ocean suggest a well-ventilated, nutrient-poor water mass in the upper (<2 km), while the lower Atlantic (>2 km) was occupied by ^{13}C-depleted, high Cd, poorly ventilated, nutrient-rich water mass (Curry and Oppo, 2005; Duplessy et al., 1988; Hoffman and Lund, 2012; Lynch-Stieglitz et al., 2007; Marchitto and Broecker, 2006; Oppo et al., 2018; Ullermann et al., 2016). Model-data comparisons and inversion studies suggest the LGM Atlantic water mass geometry was due to shoaling of NADW during the LGM (Fig. 3; Hesse et al., 2011; Menviel et al., 2017; Oppo et al., 2018; Pöppelmeier et al., 2023; Tagliabue et

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al., 2009), and most likely a weakening of NADW as well (Meissner et al., 2003; Menviel et al., 2017; Pöppelmeier et al., 2023).

Mechanistically, Ferrari et al. (2014) proposed that the northward migration of the summer sea-ice edge at the LGM could have contributed to the shoaling of the water mass boundary between NADW and AABW. They suggest this occurred by shifting northward the latitude separating the upper and lower cells of the overturning circulation- that is, the latitude separating the region of buoyancy loss, to the south, and buoyancy gain, to the north. If AABW volume is directly related to this latitude, which corresponds roughly to the summertime Antarctic sea-ice extent, then the volume of AABW should expand during glacial intervals and contract during interglacial intervals, as suggested by the proxy record. In idealised modelling, the observed LGM water mass geometry can be produced by increasing either the extent or the production rate of Antarctic sea ice (Jansen and Nadeau, 2016; Nadeau et al., 2019). However, LGM simulations as part of PMIP3 and PMIP4 show no direct relationship between the summer sea-ice extent, and thus perennial sea-ice cover, and the water mass boundary between NADW and AABW (Green et al., 2022). In addition, model simulations by Hines et al. (2019) suggest the depth of the water mass boundary between NADW and AABW is set by the density of NADW, which is set by the meltwater input in the North Atlantic, rather than by sea-ice extent in the Southern Ocean.

The proxy record also raises questions about the link between sea ice and water mass geometry. First, the sea-ice proxy evidence suggests there was only limited expansion of the summer sea-ice edge during the LGM (Crosta et al., 2022; Gersonde and Zielinski, 2000; Green et al., 2022). The idealised modelling introduced above (Ferrari et al. 2014; Jansen and Nadeau 2016) has generally not considered the seasonal cycle in sea-ice coverage. It is therefore unclear how an enhanced seasonal sea-ice cycle would impact the location of the transition from negative to positive buoyancy forcing given the summer sea-ice edge may not have changed significantly. Furthermore, while ample evidence suggests that the boundary between NADW and AABW deepened during glacial Termination I (i.e., the MIS 2/1 transition) as the summer ice edge retreated, benthic $\delta^{18}O$ results from the South Atlantic Ocean suggest the NADW-AABW boundary *shoaled* during Termination II (i.e., the MIS 6/5e transition) (Shub et al., 2024). If anything, we would expect the boundary to deepen given a more limited sea-ice extent in the Southern Ocean during MIS 5e, particularly in the Atlantic sector (Crosta et al., 2022; Holloway et al., 2017). This unexpected behaviour raises questions about the direct link between sea ice production and extent and AABW volume and suggests the relationship may be more complex.

Regardless of whether it can be attributed to expanded sea ice, the proxy evidence summarised above indicates a greater volume of glacial AABW (sometimes called southern component water), relative to NADW, existed during the LGM. However, this does not necessarily mean AABW was produced at a greater rate. Indeed, a *lower* rate of AABW production during the LGM has been inferred from peaks in the concentration of the redox-sensitive metal Mn in deglacial sediments offshore three major sites of AABW production: north of the Weddell Sea (Jaccard et al., 2016), off Cape Darnley (Wu et al., 2018), and off the Adelie Land margin (Jimenez-Espejo et al., 2020). A low rate of AABW production during the LGM may have decreased oxygen delivery to these sites, with a subsequent increase in AABW production and oxygen delivery preserving a relict sedimentary Mn peak. A decrease in oxygen delivery by AABW is consistent with evidence for widespread deep ocean oxygen depletion throughout the deep Pacific during the LGM (Anderson et al., 2019; Pavia et al., 2021) and global deep ocean (Wang et al., 2024) during the LGM. However, while a lower rate of AABW production is not necessarily incompatible with a larger volume of AABW (De Boer and Hogg, 2014), the inferred changes in deep ocean oxygen, even proximal to Antarctica, cannot be uniquely attributed to decreased AABW production. It may be that greater Antarctic sea-ice cover decreased the preformed oxygen content of AABW by inhibiting air-sea gas exchange during AABW formation, something we explore in more detail in section 6.

3 Interactions between ice sheets, sea ice, and coastal polynyas

A complex suite of interconnected processes influences the relationship between ocean circulation, sea ice, ice shelves, and ice sheets. These complex relationships involve: (1) enhancement of ice shelf stability by the presence of a sea-ice barrier, (2) the role of ice tongues and landfast ice in the formation of coastal polynyas that are sites of active sea-ice formation, and (3) connections among sea ice, land ice, meltwater and surface water salinity.

3.1 Sea ice as a buffer for ice shelves and ice sheets

The presence of a sea-ice buffer protects the adjacent ice shelf from motion generated by waves and ocean swell (Bromirski et al., 2010; Lauber et al., 2023; MacAyeal et al., 2006;

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Robinson and Haskell, 1990; Teder et al., 2022, 2025). In the absence of sea ice, this motion can weaken the ice shelf margin and lead to calving, ice sheet retreat, and ice shelf disintegration. However, not all ice shelves are alike; preconditioning by flooding and hydrofracturing can weaken ice shelves and make them more susceptible to the impact of proximal sea-ice loss (Massom et al., 2018). Deterioration of the sea-ice margin has been shown to decrease ice shelf stability at several Antarctic Peninsula ice shelves, including the Larsen A and B, and the Wilkins Ice Shelf (Massom et al., 2018), while its presence has been observed to facilitate ice shelf growth (Christie et al., 2022). The protective role of a sea-ice barrier is also discussed by Bassis et al. (2021) who proposed that sea ice and/or calved ice debris at the ice front can slow or perhaps even halt the catastrophic collapse of marine ice cliffs, a process that has the potential to cause rapid retreat of grounded ice sheets (DeConto and Pollard, 2016).

3.2 Fast ice, polynyas, ice shelf cavities and bottom water formation

Ice shelf and sea-ice processes are intimately linked with the behaviour of polynyas, which are persistent, open areas with little or thin ice cover in regions where thicker sea ice would otherwise be expected (Barber and Massom, 2007). Most coastal polynyas are "latent heat" polynyas that form when winds blow across the ocean with a surface temperature at the freezing point and push newly formed sea ice downstream, leaving an open water area on the downwind side of obstructions such as landfast sea ice (fast ice) or ice tongues. Fast ice is sea ice that is mechanically fastened to coastal features, and it can be annual or multi-year. Near Antarctica, these coastal polynyas tend to be located on the western side of fast ice (or ice shelves), due to easterly winds (Van Achter et al., 2022). This fast ice plays a critical role in keeping the polynya open and determining the size and sea ice production of Antarctic coastal polynyas (Fraser et al., 2019, 2023). Today, coastal polynyas serve as important sea-ice factories and foci for DSW formation, as salt rejection during sea ice formation results in the sinking of these salty, dense brines which act as the precursor to AABW formation (Nihashi and Ohshima, 2015; Ohshima et al., 2016).

Dense shelf-water formation in coastal polynyas can be diminished where freshwater input from upstream basal melt of ice sheets reducing the salinity of the surface water, a process that also increases the stratification of the water column (Silvano et al., 2016, 2018). Increased stratification is also observed at the Totten Glacier in East Antarctica and in the

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Amundsen Sea, near the Dotson and Getz Ice Shelves (Silvano et al. 2018) where no evidence for production of Dense Shelf Water exists.

The presence of fast ice can also result in the offshore displacement of sea-ice formation, as modelled for the Totten Glacier and the Moscow University Ice Shelf region, along the Sabrina Coast, East Antarctica (Van Achter et al., 2022). The displacement is caused by the cover of fast ice, which impedes active sea-ice formation. The presence of this fast ice at the sea surface results in a more stratified water column proximal to ice shelf cavities, since dense shelf water is not forming and convecting there. In their simulations Van Achter et al., (2022) found this reduced barrier to CDW intrusion can facilitate increased warmer CDW influx. The warm water influx, in turn, is associated with increased basal ice shelf melt, with resulting retreat of the grounded ice sheet.

Solar heating of surface waters in front of ice shelves has been shown to increase basal melting of the shelves (Jacobs et al., 1992; Malyarenko et al., 2019; Stern et al., 2013; Stewart et al., 2019). Although these warm waters are relatively buoyant, downwelling of these warm waters into the sub-ice shelf cavity, which must be driven by forcings external to the ice shelf, is thought to increase basal ice shelf melting, as observed in the Ross Ice Shelf cavity (Malyarenko et al., 2019; Stewart et al., 2019). Decreased sea-ice cover, and associated increase in solar heating, might therefore play a role in future ice shelf stability.

The coastal processes described above characterize the Antarctic continental shelf today. However, during glacial climates when grounded ice expanded across the continental shelves around Antarctica (Bentley et al., 2014), continental margin polynyas like today may not have existed, as discussed in section 2. Under glacial conditions, sea-ice formation and brine rejection forming dense waters may have shifted to an open-ocean mode of deep convection analogous to the Weddell Sea polynya of the mid 1970s (De Lavergne et al., 2014; Gordon, 2014) and 2016-2017 (Zhou et al., 2023). However, there is currently no paleo-evidence to confirm this hypothesized change in the style of AABW formation.

3.3 Ice sheet melt and sea ice

Increased ice sheet melt can contribute to sea-ice expansion. The average extent of Antarctic sea ice is known to have increased during the earliest part of the satellite era between 1979 and 2014 (Parkinson, 2019; Turner et al., 2015). One contributor to this observed increase may have been the surface freshening of the polar ocean in response to freshwater inputs

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from ice sheet retreat, ice shelf runoff, and melting icebergs (Bintanja et al., 2013, 2015; Swart and Fyfe, 2013). Bintanja et al. (2013) described a negative feedback between ice sheet melt and sea ice; as polar warming increases, the influx of cool freshwater to the surface ocean from melting of the ice sheet enhances sea-ice formation during the autumn and winter and may, in turn, counter the initial warming. In fact, some models forced by large freshening of surface waters have shown increased sea-ice extent and surface cooling, primarily due to increased stratification of the upper ocean, decreased convection, and reduced upwelling of warmer waters (Purich et al., 2018).

Other modelling studies link basal melting of ice shelves to changes in ocean dynamics and warming through a series of feedbacks involving sea ice (Fogwill et al., 2015; Kusahara et al., 2023; Naughten et al., 2018; Timmermann and Goeller, 2017; Timmermann and Hellmer, 2013). Naughten et al. (2018) show that warming reduces winter sea-ice formation and the resulting reduction in brine rejection allows for increased stratification. This increased stratification allows a warm bottom layer of CDW or modified CDW to penetrate beneath ice shelves, ultimately leading to increased basal melt. This process might play a role in the Amundsen Sea (Naughten et al., 2018) and the Weddell Sea (Timmermann and Hellmer, 2013). A decline in summer sea-ice cover, on the other hand, exposes a greater fraction of the ocean surface to solar radiation and longwave radiation, leading to warming of surface waters; if these warm waters are subducted beneath ice shelves it also causes basal melting (Naughten et al., 2018; Timmermann and Goeller, 2017). Regions that might be affected by this process include the Filchner, Larsen, and Wilkins Ice Shelves, the eastern half of the eastern Weddell region, the Australian sector of East Antarctica, and the Ross Ice Shelf front (Naughten et al., 2018). This scenario has been further explored through modelling work suggesting that extreme warming events and an associated decrease in coastal sea ice can ultimately lead to ice sheet mass loss, via the intrusion of warm water across the continental shelf, penetrating beneath ice shelves and resulting in their basal melt (Kusahara et al., 2023). While stratification in the ocean can prevent mixing of CDW onto the continental shelf, other factors can also play a role, including offshore upwelling and the strength of the Antarctic Slope Current (Nakayama et al., 2021). A suite of factors must be considered when addressing the complex relationship between sea ice and ice shelves. Given the role ice shelves have been shown to play in the larger Antarctic ice sheet stability (Gudmundsson,

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2013; Scambos et al., 2004), attention to sea-ice processes impacting ice shelf stability is warranted.

3.4 Paleo insights into interactions between land ice and sea ice

While detailed examination of the relationships between sea ice and ice shelves in the paleo record is limited, some studies have addressed the topic. Smith et al. (2019) provide a comprehensive review of the sedimentary signature of a retreating ice sheet/shelf, documenting key sedimentary features that are characteristic of the sub-ice shelf setting. The sequence of glacio-marine sediments (see Smith et al. (2019), Figure 4) can be used to track the change from grounded ice, to floating ice, and finally to an open marine or seasonally sea-ice covered setting. However, determining the relationship between sea ice and ice shelves is complicated by difficulties in distinguishing the presence of ice shelves versus multi-year or perennial sea ice in the paleo-record (Hillenbrand et al., 2009). In both cases, light limitation in the underlying ocean precludes *in situ* primary production, and thus the sediments have a limited to absent biological fingerprint. Studies often use the term "ice canopy" to describe a paleo-setting thought to reflect thick ice cover, without specifying whether that is land ice or sea ice (Lamping et al., 2020; Totten et al., 2015, 2022).

Changes in ice shelves in one region of Antarctica can have an indirect influence on sea ice downstream. Ashley et al. (2021) used diatom assemblages and biomarker data from a high-resolution Holocene sediment core from Wilkes Land margin, East Antarctica, to look at sea ice changes and found an increase in sea ice at ~4.5 ka. They suggested a link between this sea ice expansion and the retreat of the grounding line in the Ross Sea that resulted in the formation of a large sub-ice shelf cavity and a subsequent increase in basal melting and outflow of super cooled Ice Shelf Water. This outflow cooled the downstream waters along the Wilkes Land margin and facilitated the increased production of sea ice. This process may also have occurred westward in Prydz Bay where a similar sea-ice increase was observed (Denis et al., 2010). Importantly, in smaller ice shelf cavities, such as in the Amundsen Sea, the opposite response may occur today. In these locations, melting occurs as a result of incursion of relatively warm CDW, with the influence of inflow of warm deep water far

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outpacing the impact of cool ice sheet meltwater, resulting in a warm sub-ice shelf cavity and reduced proximal sea ice (Jourdain et al., 2017).

An association between ice shelf melt and-sea ice cover during the Holocene is presented by Crosta et al. (2018). Using $\delta^{18}O$ of diatoms as a proxy for ice shelf meltwater in sediment cores from the Antarctic Peninsula (Pike et al., 2013), Adélie Land (Crespin et al., 2014), and Prydz Bay, Crosta et al. (2018) inferred an increase in glacial ice sheet melt and discharge around the Antarctic continental margin from ~ 4 ka onward with a coeval increase in spring sea ice in coastal regions (Crosta et al., 2018). The ice shelf melt is not driven by air temperatures as ice cores show a cooling at this time, and thus, melt must be driven by ocean warming. Proxy records of sub-surface ocean temperatures (Etourneau et al., 2013; Kim et al., 2012; Shevenell et al., 2011) and water column mixing (Denis et al., 2010) are interpreted to reflect greater episodic presence of CDW on the continental shelves, with the warmer CDW driving ice sheet melt which facilitated sea-ice formation, enhanced by decreasing spring insolation. Weber et al. (2014) also modelled the impact of the Antarctic ice discharge event during the Antarctic Cold Reversal of the last deglaciation (14.8 - 14.4 ka) and found it was associated with ocean cooling and an expansion of sea ice due to the increase in freshwater and associated stratification. The melting consequently resulted in a surface ocean cooling and an expansion of sea ice due to the increase in freshwater and associated stratification (Menviel et al., 2010, Golledge et al., 2014, Weber et al., 2014).

While the preceding examples provide evidence of sea ice responding to changes in the ice sheet and ice shelves ice, a record of diatom assemblages and ice-rafted debris from the Adelie Land region of the Wilkes Land margin provides an example of sea ice potentially influencing the ice shelf (Fig. 5; Pesjak et al., 2023). This work shows that during the last deglacial transition, sea-ice cover decreased early in parallel with warming, and was followed by an increase in ice rafted debris. This sequence of events supports the link between sea ice as a buffer for ice shelves and the potential role of decreased sea-ice cover in facilitating basal melt and ice shelf disintegration.

The sensitivity of the Antarctic ice sheet to sea-ice extent (and vice versa) has been examined over longer time scales using model simulations combined with paleoclimate reconstructions from sediment cores recovered from the Antarctic margin (McKay et al., 2016). DeConto et al. (2007) modelled the relationship between the Cenozoic growth of the cryosphere and the development of sea ice surrounding the Antarctic continent. Their work illustrated that

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reductions in atmospheric greenhouse gas concentrations were required to initiate ice sheet growth, and this growth occurred prior to the significant presence of sea-ice cover. Once continental-scale ice sheets were established, sea ice developed, but its seasonal distribution around the Antarctic margin was strongly influenced by the configuration of the Antarctic ice mass, as well as orbital forcing. In contrast, while the expanded sea-ice distribution impacted coastal regions of Antarctica, it had little impact on the ice sheet interior, suggesting the relatively low sensitivity of the Cenozoic Antarctic ice sheet to variability in sea ice.

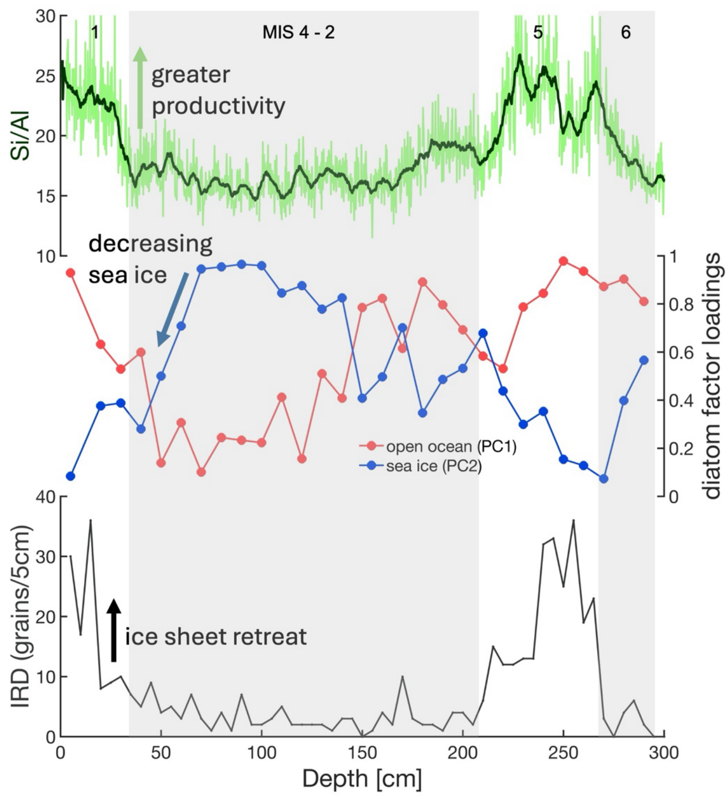

Figure 5: Proxy records of the last glacial cycle (~150 – 0 ka) from core TAN130244 from the Adelie Land margin, East Antarctica (Fig. 2; Pesjak et al. 2023). The Si/Al ratio is an indicator of siliceous productivity, which increases when sea-ice cover decreases. The decrease in sea ice cover at ~50 cm, as indicated by a decline in principal component (PC)

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factor loadings associated with sea-ice diatoms (PC2), precedes ice sheet retreat, as indicated by increased concentration of ice rafted debris (IRD) near 25 cm.

4 Interactions between sea ice and atmospheric circulation

While sea-ice formation, transport, and melt are driven by ocean and atmospheric temperatures, precipitation, and winds, the presence of sea ice also affects the state of the ocean (section 2) and atmosphere (this section). The atmospheric effects are both local, occurring immediately above the ice, and far-field, with impacts occurring from pole to pole (England et al., 2020). Sea ice blocks the exchange of heat and moisture between the ocean and the atmosphere, generally causing the atmosphere directly above sea ice to be cooler and drier than an ice-free ocean (Maykut, 1986). Because the winter sea ice edge sits in the atmospheric polar frontal zone, a region of uplift at the boundary between the polar and the midlatitude (Ferrell) cells, relatively small changes in Antarctic sea-ice extent have the potential to generate large shifts in atmospheric circulation (Raphael et al., 2011).

The recent and projected decline of Antarctic sea-ice cover (Eayrs et al., 2021; Purich and Doddridge, 2023) has stimulated modelling efforts to understand the climate implications of sea-ice loss. Many model-based studies have noted shifts in the position and/or intensity of the southern hemisphere westerly winds (SHW) in response to sea-ice variability, with most finding an equatorward shift and weakening in the SHW when Antarctic sea-ice extent decreases (Ayres et al., 2022; Raphael et al., 2011). This response occurs because the loss of sea ice warms the overlying atmosphere around Antarctica, expanding latitudinally the zone of low pressure associated with the downward limb of the polar cell. This, in turn, tends to push the Farrell cell equatorward, weakening the atmospheric pressure gradient that drives the SHW. Note that the equatorward shift of the SHW linked to sea-ice decline is opposite to the overall model predictions for SHW behaviour under climate warming, which uniformly suggest a poleward shift of the SHW with increasing CO_2 (Goyal et al., 2021; Yin, 2005). The sea-ice effect therefore acts to offset the response of the winds to warming.

The most compelling studies that identify a causal relationship between sea-ice variability and climate use a modelling framework known as “ghost flux” experiments, which adjust heat fluxes and sea-ice albedo to isolate the impact of changes in sea-ice extent (Deser et al., 2015). Applied initially to the Arctic, these ghost flux experiments with Antarctic sea-ice loss show large climate impacts that extend well beyond the sea-ice zone. This impact includes a

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pole-to-pole response: a warming of the Antarctic interior (Ayres et al., 2022), an increase in katabatic winds, cloud cover, and precipitation over coastal Antarctica (Tewari et al., 2023), a decrease in ACC transport, an equatorward shift of the SHW, a warming of the equatorial Pacific SSTs (England et al., 2020), and even a sea-ice loss in the Arctic (Ayres et al., 2022). The impact of sea ice on the SHW, and the far-field climate responses, are driven by ocean-atmosphere coupling (Ayres et al., 2022; England et al., 2020). Coupled ocean-atmosphere climate models are therefore necessary to fully quantify the impact of sea ice on the atmosphere.

Few studies have examined the response of the SHW to greater-than-present Antarctic sea-ice cover. Those that have did not use the ghost flux method. Raphael et al. (2011) studied the atmospheric response to imposed climatological maxima and minima in sea-ice extent and found a relatively symmetric response. The sea-ice minima were associated with an equatorward shift of the SHW and an expansion of the polar cell while the opposite was found when sea-ice maxima were imposed. In contrast, Kidston et al. (2011) found an asymmetric response. While a 7-degree latitudinal decrease in ice extent, in either winter or summer, did nothing to the winds, a 7-degree increase in sea-ice extent, in winter only, caused a poleward shift of the SHW. The latter sea ice scenario is analogous to conditions during the LGM. The impact of sea-ice variability on winds thus appears sensitive to the latitude of the ice edge: when it is far from the polar jet, such as in summer, or under scenarios of decreased ice extent, the jet is minimally impacted by changes in sea-ice cover.

The response to increased sea-ice extent is model-dependent, with an important factor being the interaction between the jet and the ice edge. A CMIP5-PMIP3 model intercomparison study (Sime et al., 2016) found that, among models with an accurate representation of pre-industrial sea-ice extent, those with a greater increase in sea-ice extent during the LGM also had a greater poleward shift of the SHW. However, in models with an inaccurate pre-industrial sea-ice extent, where the ice edge was located far from the jet, changes in sea-ice extent did not impact the position of the jet. Without the effect of sea ice and associated sea-surface cooling near the modern-day jet, models tended to simulate poleward-shifted westerlies in warm climates and equatorward-shifted westerlies in cold climates. However, in these simulations with a less-accurately placed modern-day sea-ice edge, the presence of expanded LGM sea ice reversed the equatorward trend in cooler climates so that the winds in colder, LGM simulations were more likely to have been shifted slightly poleward. Thus,

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accurately reconstructing LGM sea-ice extent is the key to understanding LGM SHW wind changes. This state dependence may explain why there is so much disagreement among models about the sign and magnitude of the deglacial wind shifts, but near uniform agreement among models that the winds will shift poleward in warming climate scenarios. It may be that the offsetting effect of sea ice on winds, acting in opposition to the climate warming signal, operates at different strengths in the various models, resulting in a wide range of predicted wind shifts when simulating the deglacial change. An open question is how important the sea-ice effect on the SHW is in the real climate system. The paleo record may provide clues.

Reliable paleo reconstructions of atmospheric attributes such as winds and precipitation are challenging to produce (Huiskamp and McGregor, 2021; Kohfeld et al., 2013; Shulmeister et al., 2004). However, recent proxy records suggest the sea-ice effect on the SHW is of second order. On glacial-interglacial timescales, Kohfeld et al. (2013) compiled environmental reconstructions in the Southern Hemisphere that could plausibly be affected by a change in the SHW (e.g., moisture, dust, SST). They concluded that making inferences about wind shifts based on paleo-evidence alone is difficult, as the data are consistent with multiple scenarios. Kohfeld et al. (2013) found that a scenario with either stronger winds or an equatorward shift of the SHW during the LGM is consistent with most observations but cautioned that no change, or even a poleward shift, could not be ruled out. More recently, Gray et al. (2023) inferred a poleward shift of the SHW during the last deglaciation from the latitude of SST gradients in the Southern Ocean, which they reconstructed from a compilation of planktonic $\delta^{18}O$ measurements. This reconstruction is consistent with the predicted wind direction response under future warming scenarios, but opposite in sign to the typical model-derived response to a decrease in sea ice described above. These results suggest that the decrease in sea ice during deglaciation (Crosta et al., 2022), which would on its own yield an equatorward shift in SHW, was not enough to offset the poleward tendency due to climate warming. Interestingly, the proxy-reconstructed wind shift is more than 4 degrees of latitude greater than that predicted by any of the CMIP4/3 models investigated (Gray et al., 2023). While there are many possible explanations for this discrepancy, including biases in the observational constraints, one possibility is that the sea-ice effect on

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SHW is too strong in the models, overcompensating for the warming-driven trend that shifts SHW poleward.

Ice core records also suggest sea-ice variability has little impact on winds over millennial time scales. Buizert et al. (2018) studied events during MIS 3, when Antarctic and Greenland climates changed asynchronously (Buizert et al., 2015). Using water isotopes in five Antarctic ice cores, Buizert et al. (2018) infer an equatorward shift of the SHW nearly synchronous with Northern Hemisphere warming events, and, therefore out of synchrony with Antarctic warming. How did Antarctic sea ice change during these millennial events that affected the SHW? While no ocean-based sea-ice records exist that resolve these millennial events, the sea salt sodium (ssNa) ice core proxy provides some insight. Both the European Project for Ice Coring in Antarctica Dronning Maud Land (EDML)(Fischer et al., 2007) and the Talos Dome Ice Core (TALDICE) (Buiron et al., 2012) show abrupt decreases in ssNa, interpreted as a rapid decrease in sea-ice extent, at the start of each Antarctic warming event, followed by a gradual recovery as Antarctica cooled. The ssNa signal in the five cores examined by Buizert et al. (2018) is weak and not observed in all cores. Yet, the sign and timing of the sea-ice signal, and its relationship to the inferred wind changes, do not support a strong link between changes in sea ice and changes in atmospheric circulation over millennial timescales. The sea-ice response tracks Antarctic temperature, with a decrease in extent as Antarctica warmed, while the wind response was closely tied to Northern Hemisphere warming. The abrupt equatorward shift in the winds therefore occurred against a backdrop of increasing Antarctic sea-ice extent and was associated with abrupt Northern Hemisphere warming rather than with any notable shift in Antarctic sea-ice dynamics. Rae et al. (2018) highlight a similar dynamic during millennial variability of the last deglaciation: Antarctic ice core deuterium suggests a northward shift of the SHW coinciding with abrupt Northern Hemisphere warming (Markle et al., 2017) and preceding the Southern Hemisphere cooling and increase in Antarctic sea-ice extent by about 200 years (Buizert et al., 2015). The observed changes in sea ice and SHWs over millennial scales thus suggest that the expected ‘sea-ice’ effect on winds is a second-order process compared to other climate feedbacks associated with warming or cooling.

The available proxy record summarised above suggests sea ice does not play a primary role in driving SHW variability. However, given the limitations of the proxies, the difficulty of discerning leads and lags, particularly in lower resolution marine records, and the diversity of

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model responses to greater than present sea-ice extent, the case is not closed. Given the widespread teleconnections and far-field response to declining sea ice, an avenue for future research is to move beyond the response of the SHW to see if a diagnostic "sea-ice fingerprint" can be found across multiple parts of the climate system associated with past periods of greater or lesser sea-ice extent. Such an approach would require new modelling efforts to isolate the climate signature associated with sea-ice variability in past climate states, both warmer and colder than present, paleo data synthesis of multiple affected proxies (e.g., precipitation, temperature and potentially wind systems), and generation of new proxy records from undersampled regions. Analysis of model output could help identify regions where atmospheric effects are particularly sensitive to Antarctic sea-ice variability.

5 Impact of sea ice on marine biological activity and biogeochemistry

Sea ice plays an important role in regulating productivity and the cycling of climate-active gases in the Southern Ocean. Sea ice also impacts biogeochemical cycles through its influence on the circulation of the Southern Ocean (see section 2), which affects the supply of nutrients to the productive surface ocean via upwelling, the residence time of surface water in contact with the atmosphere and sunlight, and the export of intermediate waters to the global ocean. In this section, we review the role of sea ice in each of these domains, integrating findings from process studies, paleo proxies, and modelling studies.

5.1 Impact on primary production

The dominant role of sea ice in structuring Southern Ocean food webs is reflected in the long-standing use of sea ice, together with oceanographic fronts, to delimit ecological zones (Deppeler and Davidson, 2017; Treguer and Jacques, 1992). According to this classification, the Southern Ocean is comprised of five zones, from farthest to closest to Antarctica (see Fig. 2): 1) the Subantarctic Zone, between the Subtropical Front and the Subantarctic Front (SAF), 2) the Polar Frontal Zone, between the SAF and the Antarctic Polar Front (APF), 3) the Permanently Open Ocean Zone (POOZ), between the APF and the northern limit of winter sea ice, 4) the Seasonal Sea Ice Zone (SSIZ), the region between the winter maximum and summer minimum in sea-ice extent, which includes the highly productive Marginal Ice

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Zone (MIZ) at its northern limit; and 5) the Antarctic Continental Shelf Zone (CZ), a small geographic zone that includes highly productive polynyas.

Within the sea-ice-impacted zones (i.e., poleward of the POOZ), sea ice directly influences primary productivity by modulating solar radiation, providing habitat for some species by acting as a source of phytoplankton to seed the marginal ice zone when the ice melts (Leventer, 1998), and delivering iron at a crucial part of the growth season (Lannuzel et al., 2023). Sea ice itself hosts a diverse microbial community that represents a concentrated food source for zooplankton (Swadling et al., 2023). The autotrophic community is dominated by diatoms, mainly large species, while also containing flagellates (Arrigo, 2014). Rates of annual primary productivity within sea ice are low, representing only about 1% of the rates observed in open ocean Antarctic environments POOZ and SSIZ (Arrigo et al., 1997). However, productivity and biomass in sea ice are highly variable regionally, and vertically within the sea ice column. Biomass within the deepest sea ice layers (often attached to the base of the sea ice) can reach very high levels (Kattner et al., 2004), at times higher than in surrounding waters (McMinn et al., 2010; Van Leeuwe et al., 2018). High chlorophyll concentrations are observed seasonally in the MIZ, associated with the retreating ice edge (Moore and Abbott, 2000; Vernet et al., 2008). However, the annual productivity of these regions is lower than in the POOZ, because of less light at higher latitudes (Moore and Abbott, 2000) and light limitation due to ice cover and snow cover on ice (Roukaerts et al., 2016). In some regions, including the Weddell Sea, greater sea-ice growth and melt are associated with elevated phytoplankton biomass in the following spring/summer, whereas this relationship is absent or reversed in other regions (Giddy et al., 2023). Very high phytoplankton biomass is present in polynyas, averaging twice the concentrations in the open Southern Ocean (Arrigo et al., 2015). Greater sea-ice cover tends to decrease productivity in polynyas while greater sea-ice melt increases productivity (Moreau et al., 2023).

Sea ice plays an important role in the cycling of iron in the Southern Ocean. It provides a link between continental sources of iron – from glaciers, landmasses, and sediments – and the high macro nutrient offshore regions where iron is needed (Lannuzel et al., 2016). Both pack ice and fast ice are enriched in iron by about an order of magnitude above surface Southern Ocean seawater concentrations, with fast ice, formed in closer proximity to iron sources, having higher concentrations than pack ice (Lannuzel et al., 2016). Sea-ice melt in spring results in a large pulse of iron being released to seawater over a short period of time

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(Lannuzel et al., 2008). This springtime iron release coincides with increasing light levels, warming, and a stabilised water column, triggering algal blooms in the seasonal ice zone (Sedwick and DiTullio, 1997).

Across the Southern Ocean as a whole, sea ice appears to play a dominant role in regulating the annual opal flux to the seafloor. Where sea ice is present for at least part of the year, the length of the ice-free season determines the upper limit of opal burial in the underlying sediments (Chase et al., 2015; Ragueneau et al., 2000). Indeed, some of the earliest proxies of sea-ice extent were based on the association between the northern extent of the band of high opal concentration in sediments – the opal belt – and the seasonal ice edge (Burckle and Cirilli, 1987; Cooke and Hays, 1982).

Numerous marine proxy records from south of the APF suggest opal flux in this region was lower during the LGM than today (Amsler et al., 2022; Bareille et al., 1998; Chase et al., 2003; Jaccard et al., 2013; Kohfeld et al., 2005, 2013; Studer et al., 2015; Thöle et al., 2019). In Antarctic proximal records, low productivity during the LGM is associated with increased sea-ice cover (e.g., Fig. 5); productivity records such as Ba/Al are often used as chronological tools given the reliably low productivity during glacial climates (Presti et al., 2011). Given the sensitivity of opal flux to sea-ice season length, lower glacial opal export might be attributed to an expansion of sea ice and a shorter growing season (Ghadi et al., 2020). However, at some sites with lower glacial productivity, located within the POOZ today, sea ice was present only during winter during glacial periods, suggesting sea ice and light limitation are not the primary cause of low productivity (Jaccard et al., 2013). Furthermore, higher nitrogen isotope ratios in glacial sediments from south of the APF suggest more complete consumption of nitrate by the phytoplankton community (Ai et al., 2020; Francois et al., 1997; Robinson et al., 2014; Studer et al., 2015). The combination of more complete nitrate consumption and lower opal flux is not consistent with light limitation, either by sea ice or deeper mixed layers. The proxies have instead been interpreted as a glacial decrease in the vertical supply of nitrate to surface waters, sometimes referred to as near-surface stratification (Francois et al., 1997; Sigman et al., 2020), caused either by a stronger halocline in response to a more intense sea-ice cycle (Shin et al., 2003) and/or less intense or northward

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shifted SHW leading to less upwelling (Galbraith and de Lavergne, 2019; Toggweiler et al., 2006).

Ice core records of biogenic sulphur provide another means of reconstructing marine productivity. Intriguingly, records from both Dome C and Dronning Maud Land, capturing integrated productivity across the Indian and Atlantic sectors, respectively, suggest there was minimal glacial-interglacial change in productivity in either region (Kaufmann et al., 2009), in contrast to the marine sediment evidence from south of the APF summarised above. However, given that marine sediment records north of the APF consistently indicate higher glacial productivity, in response to Fe fertilisation (e.g., Jaccard et al., 2013; Kohfeld et al., 2005), it may be that the ice cores are reflecting an averaging of these opposing signals. There are also questions about how to precisely isolate the biogenic sulphate from other sulphate sources including sea salt, mineral dust and volcanic inputs. A recent study combined sulphate concentration and isotopic data from the EPICA ice core in Dronning Maud Land to better constrain the sources of sulphate to the ice core, concluding that biogenic sulphur dominates the budget and reflects productivity in the SSIZ of the Atlantic sector (Fischer et al., 2025). The authors found a 16% reduction in biogenic sulphur production during the last interglacial (LIG) compared to the penultimate glacial period (MIS 6), which they interpret as a decrease in integrated biological productivity in the region south of ~50ºS in the Atlantic sector. They further note an 'intermittent' and slight decrease in biogenic sulphur production during the LIG around 126 ka, associated with peak warming (Capron et al., 2014; Civel-Mazens et al., 2024; Schneider Mor et al., 2012), a minimum in sea-ice extent (Chadwick et al., 2022c), and evidence for a large reduction in AABW production (Hayes et al. 2014). They argue for a causal chain whereby warmer-than-present temperatures during the early LIG caused a decrease in sea-ice production, which curtailed AABW production and consequently decreased the upwelling of nutrient-rich CDW. A major caveat of these findings is that biogenic sulphur is produced by only a subset of primary producers (see section 5.2), so it may not represent total productivity. The paucity of high-resolution sediment cores in the sea-ice region, challenges with dating opal and siliciclastic dominated sediments, and a lack of understanding of the mechanistic links between sea ice

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and productivity mean many questions remain about how sea ice influenced productivity during past climates.

Even in the POOZ and SAZ, where sea ice is absent, sea ice still impacts productivity indirectly. The nitrogen isotopic composition of nitrate suggests roughly half the nitrate supply to the SAZ is derived from equatorward transport of surface Antarctic waters across the APF (Sigman et al., 1999). Decreased nutrient utilisation in the SSIZ, associated with increased sea-ice duration, should result in a greater supply of nutrients to the SAZ (Matsumoto et al., 2014), all else being equal. Conversely, decreases in sea-ice duration, as predicted with climate change, should result in a reduced supply of nutrients to the SAZ across the APF.

Antarctic sea ice can also affect nutrient supply to the low-latitude oceans. Intermediate waters represent an important pathway transporting nutrients from the Southern Ocean to the tropical thermocline (Sarmiento et al., 2004). To the degree that sea-ice extent and transport are coupled, the impact of sea-ice dynamics on nutrient export from the Southern Ocean may therefore involve complementary physical and biological mechanisms. A decrease in sea-ice extent and meltwater transport would reduce the production of intermediate waters and could also reduce their nutrient content by encouraging greater nutrient drawdown in southern source waters. In contrast to this view, Crosta et al. (2007) argue that during the LGM, the increase in biologically-driven silicic acid leakage from the Southern Ocean was accompanied by a decrease in intermediate water production, such that the biological and physical processes acted in opposition. The extent to which decreasing sea ice in the Southern Ocean could lead to altered nutrient supply to the tropics should be further investigated as it has important consequences for low-latitude biological productivity and carbon cycling under future climates.

5.2 Production of climate-active dimethyl sulphide

Biological processes occurring within sea ice are important to the global sulphur cycle through their impact on the flux of dimethyl sulphide (DMS) to the atmosphere. DMS is a semi-volatile sulphur compound produced in ocean surface waters primarily by the degradation of dimethylsulphoniopropionate (DMSP), a compound produced by algae in response to nutrient, light, thermal, and osmotic stress (Malin and Erst, 1997). The oxidation of DMS produces sulphate aerosols, which act as cloud condensation nuclei and are therefore important in regulating precipitation and albedo (Charlson et al., 1987). Within the Southern

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Ocean, which is the largest natural source of DMS to the atmosphere (Lana et al., 2011), DMSP is produced by phytoplankton in both open ocean and sea-ice environments. Haptophytes such as *Phaeocystis* spp. are considered strong producers of DMSP while diatoms are believed to be weak producers (Kirst et al., 1991). Sea ice can accumulate high levels of DMS, as algal production of DMSP is elevated in sea ice, and high grazing rates convert DMSP to DMS within the sea-ice environment (Kirst et al., 1991). Sea-ice algae may also release DMSP during ice melt, in response to rapidly decreasing salinity (Trevena and Jones, 2006). For these reasons, very large fluxes of DMS to the atmosphere can occur during the spring ice melt (Webb et al., 2019). High concentrations of DMS have also been observed in low salinity lenses associated with stratified conditions in sea-ice leads in the Southern Ocean (Zemmelink et al., 2005), likely associated with similar biogeochemical conditions as found during the spring melt.

Given its climate-active status, and its link to marine productivity, there has been much interest in reconstructing past changes in DMS emissions using ice core records. Indeed, the methanesulphonic acid (MSA) sea-ice proxy (Crosta et al. 2022) is based on the association between MSA and DMS, and between DMS production and sea-ice extent. However, MSA has a preservation bias in ice cores and is not suitable for long-term reconstructions (e.g. Weller et al., 2004). Non-sea salt sulphate ($nssSO_4$) in Antarctic ice cores is also derived primarily from the oxidation of marine biogenic DMS and shows no post-depositional loss, offering a more robust reconstruction of DMS fluxes (Wolff et al., 2010). Remarkably, the flux of $nssSO_4$ in the EPICA Dome C ice core is very constant (within 15%) over the past 800,000 years and shows no glacial-interglacial variability (Wolff et al., 2010). If this minimal variability in $nssSO_4$ is interpreted parsimoniously as indicating a constant production of DMS south of the Antarctic Polar Front across multiple glacial cycles, it suggests that the sulphur cycle was minimally impacted by sea-ice variability and was likely not important in climate feedbacks over this time (Wolff et al., 2006). As discussed above, a more recent and comprehensive study of sulphate sources to Dronning Maud Land, including isotopic information, finds evidence for a slight decrease in biogenic sulphur emissions during the last interglacial compared to the last glacial period (Fisher et al. 2024).

6 Sea ice and glacial-interglacial changes in the carbon cycle

Because of its influence on air-sea gas exchange, stratification, and ocean circulation, Antarctic sea ice can modulate oceanic carbon storage over glacial-interglacial timescales.

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Indeed, it is reasonable to hypothesise that the close correspondence between Antarctic temperature and atmospheric CO_2 during the Pleistocene (EPICA Community Members, 2004; Fig. 4b) is mediated through the influence of Antarctic sea ice, and the multiple mechanisms by which it influences the global carbon cycle. Here, we summarise current thinking on the link between sea ice and atmospheric CO_2 on glacial-interglacial timescales.

The most direct way for sea ice to impact the carbon cycle is by restricting sea-to-air flux of CO_2. Laboratory experiments (Loose and Schlosser, 2011) and the ^{222}Ra inventory method (Rutgers Van Der Loeff et al., 2014) have confirmed that under conditions of near-complete ice cover, gas exchange is reduced by about an order of magnitude compared to open ocean conditions. This 'capping' effect was first proposed by Stephens and Keeling (2000) as a mechanism to explain the low glacial atmospheric CO_2 levels. Using a box model, they showed that a reduction in atmospheric CO_2 of 67 ppm can be achieved if the open ocean area south of the APF is reduced to 10% of its pre-industrial value. Such a large increase in sea-ice extent is unrealistic given diatom proxy data indicate that glacial summer sea-ice extent was comparable to modern day (Benz et al., 2016; Burckle et al., 1982; Gersonde et al., 2005; Lhardy et al., 2021). Additionally, the effectiveness of the blocking mechanism is limited because greater areal coverage of sea ice results in higher surface ocean dissolved inorganic carbon concentrations, which in turn increases the sea-to-air CO_2 gradient and fluxes (Morales Maqueda, 2002). Indeed, subsequent work found that the response of pCO_2 to Antarctic sea ice is much greater in box models than in ocean general circulation models (Archer et al., 2003; Gottschalk et al., 2019).

The lack of knowledge on physical processes of gas exchange in areas of open water adjacent to sea ice adds more uncertainty to the capping hypothesis. Typically, gas exchange under conditions of partial ice cover is estimated by applying a linear dependence of gas exchange on the fraction of open water (Takahashi et al. 2009), based on the assumption that gas exchange in the surrounding open waters proceeds at the same wind-speed dependent rate that it does in the absence of ice. The validity of this assumption is not clear. A study of CO_2 exchange in the Southern Ocean based on the eddy covariance technique (Butterworth and Miller, 2016) found generally good agreement with the linear scaling assumption. However, laboratory experiments suggest gas exchange in open water near sea ice is enhanced 50-70% relative to open waters with no ice present (Loose et al., 2014, 2016), indicating that an assumption of linear dependence on open water area underestimates the true rate of gas

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exchange. In contrast, a study of gas exchange in the Arctic based on ^{222}Ra inventories found the assumption of a linear dependence on open water results in overestimates of the rate of gas exchange (Rutgers Van Der Loeff et al., 2014).

One objection to the capping hypothesis is that decreased productivity and carbon uptake by phytoplankton due to the greater light limitation would counter the reduction in sea to air CO_2 flux due to greater sea-ice cover (Gupta et al., 2020; Kurahashi-Nakamura et al., 2007; Sun and Matsumoto, 2010). Proxy data show decreased carbon export in the Antarctic Zone during the glacial period (e.g., Kohfeld et al., 2005), supporting the suggestion that the gas exchange and light impacts of sea ice may have offset each other. However, as discussed above, the combination of reduced export and increased nutrient utilisation is inconsistent with light limitation and has instead been attributed to a decrease in the supply of nutrients to the surface (Francois et al., 1997; Jaccard et al., 2013; Sigman and Boyle, 2000). A decrease in vertical nutrient supply could enhance ocean carbon sequestration despite lower export production, by limiting the supply of carbon-rich waters to the surface.

A more active sea-ice cycle during the glacial period may have induced surface stratification that decreased nutrient supply and favoured ocean carbon sequestration. An intensified sea-ice cycle may have caused the decrease in surface nutrient supply, by producing a low-salinity lid in regions of net ice melt, leading to increased density stratification of the surface ocean (Francois et al., 1997; Sigman and Boyle, 2000, 2001). Greater surface stratification during summer may have even promoted a short but highly productive growing season, further limiting CO_2 outgassing (Moore et al. 2000). The production and vertical export of highly concentrated brines off the shelf may have also freshened the surface and induced stratification even in regions of net ice production (Bouttes et al., 2010; Sigman et al., 2020). The combination of reduced supply and increased consumption of nutrients, and by extension dissolved inorganic carbon, would act to strongly limit the amount of CO_2 allowed to escape from the Antarctic Zone.

Brine rejection may have also increased ocean carbon storage by increasing deep-ocean stratification and reorganizing deep-ocean circulation (Bouttes et al., 2010; Ferrari et al., 2014; Jansen, 2017; Jansen and Nadeau, 2016), as described section 2. In idealised experiments, either an increase in sea-ice extent or an increase in sea-ice formation rate leads to a reorganisation of the overturning circulation, such that upwelling CDW encounters greater sea-ice cover, providing less opportunity for gas exchange (Ferreira et al., 2018;

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Nadeau et al., 2019). In the model experiments, the simulated increase in idealised water mass age, a tracer that is sensitive to air-sea exchange, was due almost entirely to restricted gas exchange beneath sea ice rather than to slower overturning (Nadeau et al., 2019). This inference based on models is consistent with radiocarbon evidence, which indicates a significant increase in the global mean radiocarbon 'age' of the ocean (Skinner et al., 2017), with a significant contribution from increased surface reservoir ages (i.e. 'preformed radiocarbon ages') (Skinner et al., 2023). The key difference from the initial Stephens and Keeling (2000) proposal is the coupling of sea ice capping with a change in the overturning circulation, which provides a mechanism for restricting the upwelling to occur beneath ice cover, thus strongly limiting the opportunity for CO_2 to escape to the atmosphere.

Marzocchi and Jansen (2019) demonstrated that a 40 ppm reduction in atmospheric CO_2 can be induced in an idealised model forced only with atmospheric cooling. In their model, as in the idealised modelling of Ferreira et al. (2018), the dominant mechanism of glacial CO_2 lowering is the strengthening of the "disequilibrium pump", in other words, the suppression of air-sea gas exchange under expanded sea ice. Importantly, the impact of sea ice on disequilibrium is only apparent when LGM sea ice and circulation act together, such that DIC-rich waters only upwell to the surface mostly beneath sea ice (Marzocchi and Jansen, 2019; Nadeau et al., 2019). A similar premise underlies proposals for a water-mass "volumetric effect" on marine carbon sequestration (Skinner, 2009), which would operate via the maintenance of high "disequilibrium DIC" levels in southern-sourced waters (Eggleston and Galbraith, 2018), in particular via sea-ice effects in a glacial climate state (Galbraith and de Lavergne, 2019). This interaction between sea ice and circulation may explain why the largest decrease in atmospheric CO_2 occurred at the MIS 5-4 boundary, when both sea ice (Chadwick et al., 2022a) and circulation experienced large changes (Kohfeld and Chase 2017). A similar argument would apply to CO_2 rise across the last deglaciation (e.g., Rae et al., 2018).

The glacial inception at the MIS5e to 5d boundary (115 – 125 ka) provides another example of the importance of coupled changes in sea ice and circulation to affect atmospheric CO_2. Ai et al. (2020) noted that during the initiation of the most recent glacial cycle, Antarctic temperature and sea ice (based on the ssNa ice core proxy) began to transition to the glacial state (i.e., decreased temperature and increased sea ice) about 3 ka before CO_2 began to decrease (Fig. 4b). The lag between the expansion of sea ice and the decrease in CO_2

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suggests the direct effect of sea ice in blocking gas exchange is not, on its own, sufficient to decrease atmospheric CO_2 (in particular for moderate changes in sea-ice extent). But it is worth noting that the sediment-core based sea-ice reconstruction diverges from the ice-core based reconstruction during this time period (Fig. 4a), with the sediment-based reconstruction showing a more gradual increase in sea ice that better tracks atmospheric CO_2, suggesting a role for sea ice in the absence of circulation changes. The finding of progressively greater carbon storage in the deep South Atlantic, first during MIS 5d and then during the MIS 5-4 transition (Garity and Lund, 2025), both of which were times of expanding sea ice cover (Fig. 4), is consistent with the sea-ice capping mechanism. More sea-ice reconstructions from the glacial inception are needed to resolve the potential contribution of increasing sea ice in driving the associated CO_2 decline.

A major caveat is that the models that show large sea ice impacts on oceanic overturning circulation and carbon storage are highly idealised. The models either lack a seasonal cycle, or have a seasonal cycle (Ferreira et al., 2018) but with more summer sea ice than indicated by the proxy record (Gersonde et al., 2005), or lack details of inter-basin differences. Results from more complex models show a variable response of CO_2 to sea-ice. A coarse resolution earth system model suggests there is considerable scope for sea ice to limit the release of CO_2 from the upwelling of CDW (Stein et al., 2020). These authors simulated a 10-fold decrease in the timescale for air-sea interaction during peak glacial climate, due both to increased sea-ice coverage blocking gas exchange and due to a reduction in surface water residence time. The sea-ice related carbon sequestration estimated by Stein et al. (2020) agrees well with that estimated by Marzocchi and Jansen (2019) and Ferreira (2018). In contrast, using a more complex model, Khatiwala et al. (2019) conducted a series of experiments to isolate different mechanisms of CO_2 change between glacial and interglacial states. They found that expanded sea ice led to a slight *decrease* in ocean carbon uptake, in response to a dominant effect of reduced biological carbon uptake, as suggested by Sun and Matsumoto (2010). Isolating the effects of sea ice in model experiments can be challenging (Kohfeld and Ridgwell, 2009) and clearly there is model to model variability, even amongst models that appear to be consistent with available (and sufficiently ambiguous) proxy evidence. Future model sensitivity and model-proxy comparisons studies focused on the amount and seasonality of sea ice required

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to initiate changes in the overturning circulation are needed to constrain the impact of sea ice on the carbon cycle.

7 Summary and perspective

This review has highlighted the central role of sea ice in many sectors of the climate system, including the atmosphere, ocean, cryosphere, and biosphere (Table 1). While we focus here on modern studies, as well as paleo-records spanning the last glacial cycle (150 – 0 ka), the processes described are also applicable to more ancient, recent, and future conditions. The paleo data provide a foundation that supports our understanding of the diminishing sea ice we are observing in the Southern Ocean today. What are the implications of decreased sea-ice coverage for ocean and atmosphere circulation, nutrient distributions, and biological productivity, both in the Southern Ocean and in more distal regions of the world's oceans? How will carbon fluxes and carbon storage be impacted? Answers to these questions are complicated because the inter-relationships are complex, and our existing data sets are far from complete and often present ambiguous, under-determined or conflicting interpretations. Paleoclimate data shed light on how these interactions have played out in the past, which furthers our understanding of the processes involved and the interconnections between Antarctic sea ice and other parts of the climate system. We note, however, that climate system changes observed in response to sea-ice decline from a glacial to an interglacial state may not be the same as the response to current and future decreases in sea ice. To increase our knowledge and further improve our understanding, we need paleo-records with higher temporal resolution and better chronologic control in more areas of the Southern Ocean. A focus on millennial-scale warming events and warmer-than-present interglacial periods, is particularly relevant to future projections. As we gain a better understanding of the changes in the Southern Ocean across the whole of the last glacial cycle and across multiple, interconnected components of the Earth system, we build towards a valuable dataset against which to evaluate climate models.

Author contributions

ZC: Conceptualization, Visualization, Writing – original draft, Writing – review & editing; KEK: Conceptualization, Funding acquisition, Project administration, Writing – original draft, Writing – review & editing; AL: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing; DL: Conceptualization, Writing – original draft,

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Writing – review & editing; XC: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing; LM: Conceptualization, Writing – original draft, Writing – review & editing; HCB: Conceptualization, Funding acquisition, Writing – original draft, Writing – review & editing; MC: Conceptualization, Writing – review & editing; SLJ: Conceptualization, Writing – review & editing; JJ: Conceptualization, Writing – review & editing; AM: Conceptualization, Funding acquisition, Writing – review & editing; KJM: Conceptualization, Funding acquisition, Writing – review & editing; ES: Conceptualization; LCS: Conceptualization, Writing – original draft, Writing – review & editing; LS: Conceptualization, Writing – review & editing

Competing interests

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Table 1: Summary of expected impacts of sea ice decline on components of the earth system, the paleo evidence and the associated uncertainties.

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Earth system component	**Expected impact of decreased sea ice**	**Paleo evidence** *Evidence counter to the expectation is presented in italics*	**Uncertainties**
Ocean – upper cell	Shoaling predicted with future warming but deepening with deglacial warming (Li et al. 2021)	Deeper AAIW in SW Pacific Ocean during warm climates (e.g., Ronge et al., 2015) Decreased AAIW presence linked temporally to sea ice contraction (Jones et al. 2022; Fig. 4)	Reconstructing production rates from paleo evidence is difficult In the southeast Pacific, there is disagreement among the proxy evidence.
Ocean – lower cell	Decreased AABW production	Water mass tracers show the boundary between AABW and NADW deepened during Termination I and shoaled during the LGM (e.g., Oppo et al. 2018) *Benthic* δ^{18}O *shows the boundary between AABW and NADW shoaled during Termination II (Shub et al., 2024)* *Deglacial Mn peaks close to Antarctica (e.g., Wu et al. 2019; Jimenez-Espejo et al. 2020) suggest reinvigoration of AABW production with warming*	Reconstructing production rates from paleo evidence is difficult Same response could be driven by density changes in NADW (Hines et al. 2019). PMIP models show no relationship between sea ice extent and NADW/AABW boundary depth (Green et al. 2022) Bottom water oxygen changes can have multiple sources Bottom water formation is not well represented in models

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Ice sheets and ice shelves	Loss of ice shelf buttressing (Massom et al. 2018) Warming of waters that enter ice shelf cavities and accelerate melting (Naughten et al. 2018)	Sea ice decline precedes ice sheet decline during last termination (Fig 5 Pesjak et al. 2023) *In some cases, sea ice appears to respond to glacial ice melt, in some cases increasing with increased input of glacial meltwater (e.g., Crosta et al. 2018)*	Limited paleo evidence proximal to Antarctica Hard to distinguishing glacial ice from perennial sea ice
Atmosphere	Weakened and northward-shifted SHW	*SHW shifted south with deglacial warming (Gray et al. 2023), opposite to sea ice effect. Do CMIP models underestimate the deglacial SHW shift due to the sea ice retreat?* *SHW shifted north during millennial-scale Antarctic cooling, more closely linked to NH warming (Buizert et al. 2018).*	Difficult to isolate the effect of sea ice as it is opposite the warming effect Paleo-reconstruction of wind is challenging
Biological productivity	Increased light could increase biological productivity while reduced iron or reduced upwelling of macro-nutrients could hinder biological productivity	Close to Antarctica and poleward of the APF marine sediment records generally show higher productivity during interglacial periods (Kohfeld et al. 2005) Ice core biogenic sulphur record suggests lower productivity in the Atlantic seasonal sea ice zone during last interglacial period, compared to the preceding glacial (Fisher et al. 2024)	Relatively few well-dated marine records far south of the APF Biogenic sulphate does not represent all primary producers

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DMS	Less DMS production	Biogenic sulphate production decreased by 16% during the last interglacial period compared to the preceding glacial (Fisher et al. 2024)	Atlantic sector only
Carbon cycle	Less ocean storage of carbon especially if coupled to circulation changes (Marzocchi and Jansen 2019)	Largest glacial drop in CO_2 occurs at MIS5-4 boundary, when sea ice and circulation change together (Kohfeld and Chase 2015) *At glacial inception, sea ice increases before CO_2 drops (Ai et al. 2020)*	Difficult to isolate and quantify multiple countervailing effects of sea ice (gas-exchange versus biological productivity) in models, but most studies suggest a limited direct impact of sea-ice changes on atmospheric CO_2 (e.g., Gottschalk et al., 2019, Choudhury et al., 2022). Difference between sediment and ice core reconstructions of sea ice (see Fig. 4). New sediment-based reconstruction of sea-ice tracks CO_2 better.

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