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REVIEWS

The polar ocean and glacial cycles in atmospheric CO_2 concentration

Daniel M. Sigman[1], Mathis P. Hain[1,2] & Gerald H. Haug[2,3]

Global climate and the atmospheric partial pressure of carbon dioxide ($p_{\mathrm{CO}_2}^{\mathrm{atm}}$) are correlated over recent glacial cycles, with lower $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ during ice ages, but the causes of the $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ changes are unknown. The modern Southern Ocean releases deeply sequestered CO_2 to the atmosphere. Growing evidence suggests that the Southern Ocean CO_2 'leak' was stemmed during ice ages, increasing ocean CO_2 storage. Such a change would also have made the global ocean more alkaline, driving additional ocean CO_2 uptake. This explanation for lower ice-age $p_{\mathrm{CO}_2}^{\mathrm{atm}}$, if correct, has much to teach us about the controls on current ocean processes.

The oscillation over the last 2.5 million years between ice ages (cold periods with large Northern Hemisphere ice sheets) and interglacials (warmer periods like today with much less northern ice) are probably triggered by orbital changes. However, the observed amplitude and timing of these climate cycles still awaits a full explanation. The observed variation in the atmospheric partial pressure (that is, concentration) of CO_2 (ref. 1 and Fig. 1) may cause a substantial fraction of ice-age cooling, and its climate forcing is distributed globally, which may help to explain why ice ages are global, not simply regional, phenomena. In addition, $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ changes early in the sequence of glacial cycle events[2], and it may trigger subsequent feedbacks. However, the cause of the $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ variation must be resolved if we are to understand its place in the causal succession that produces glacial cycles.

The ocean is the largest reservoir of CO_2 that equilibrates with the atmosphere on the thousand-year timescale of glacial/interglacial changes in $p_{\mathrm{CO}_2}^{\mathrm{atm}}$, so the ocean must drive these changes[3]. CO_2 was more soluble in the colder ice-age ocean, which should have lowered $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ by ~30 p.p.m., but much of this appears to have been countered by other ocean changes (in salinity and volume) and a contraction in the terrestrial biosphere[4]. The most promising explanations for the bulk of the $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ decrease involve ocean biogeochemistry and its interaction with the ocean's physical circulation[4]. Biological productivity in the ocean lowers $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ through the 'biological pump'—the sinking of biologically produced organic matter out of surface waters and into the voluminous ~4-km-thick ocean interior before decomposition ('regeneration') of that organic matter back to CO_2. By transferring organic carbon out of the ~100-m-thick surface layer of the ocean, the biological pump lowers the partial pressure of CO_2 in surface waters, which draws CO_2 out of the atmosphere. Moreover, the storage of regenerated CO_2 in the deep sea focuses acidity there. This reduces the burial of calcium carbonate in seafloor sediments and thus makes the global ocean more alkaline, which increases the solubility of CO_2 in sea water, further lowering $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ (Box 1).

Early in the quest to explain the reduction in $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ during ice ages, geochemists identified the potential importance of the high-latitude surface ocean, especially the Southern Ocean, through its effect on the global efficiency of the biological pump[5–7]. In the Southern Ocean, the nutrient-rich and CO_2-charged waters of the deep ocean ascend into the surface layer and are returned to the subsurface before the available pools of the two universally required 'major' nutrients, nitrogen and phosphorus, are fully used by phytoplankton (floating algae) for carbon fixation (because of their parallel cycling, we do not distinguish between nitrogen and phosphorus below, referring to them together simply as "nutrient"[8]). This incomplete use of nutrient allows for the escape of deeply sequestered

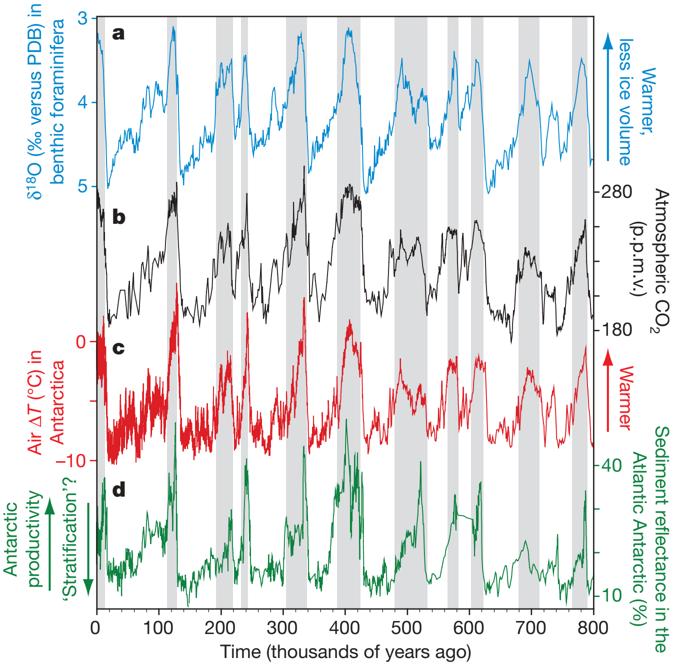

Figure 1 | Records of changing climate, atmospheric CO_2, and Southern Ocean conditions over the last 800 thousand years. a, A compilation of benthic foraminiferal $\delta^{18}O$ records[92] that reflect changes in continental glaciation and deep ocean temperature. **b,** $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ as reconstructed from Antarctic ice cores[93]. **c,** Antarctic air temperature as reconstructed from the deuterium content of an Antarctic ice core[94]. **d,** The sediment reflectance of an Antarctic deep sea sediment record from Ocean Drilling Program (ODP) site 1094 (ref. 95), which varies with the concentration of biogenic opal produced by phytoplankton in the surface ocean, providing a measure of the export of biogenic material (including organic carbon) out of the surface ocean (see text). Grey bars indicate warm intervals ('interglacials').

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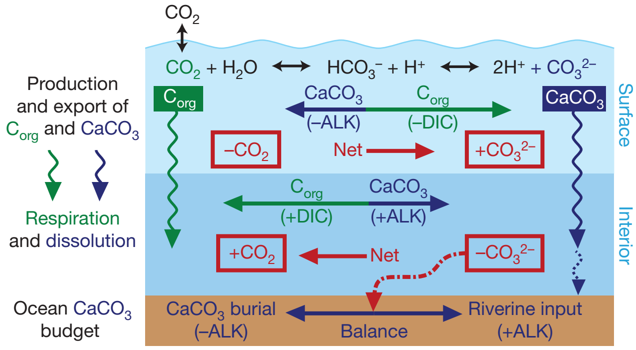
[1]Department of Geosciences, Guyot Hall, Princeton University, Princeton, New Jersey 08544, USA. [2]DFG Leibniz Center for Earth Surface Process and Climate Studies, Institute for Geosciences, Potsdam University, Potsdam D-14476, Germany. [3]Geological Institute, Department of Earth Sciences, ETH Zürich, Zürich 8092, Switzerland.

Box 1 | The ocean's inorganic carbon chemistry

For a given temperature, the CO_2 concentration that the ocean works to impose on the atmosphere is determined by the dissolved CO_2 concentration in surface water, which in turn depends on two chemical properties: (1) the concentration of dissolved inorganic carbon (DIC), which includes dissolved CO_2, bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}); and (2) alkalinity (ALK), which is roughly sea water's acid-buffering capacity, the excess base in sea water that causes dissolved CO_2 to be deprotonated to HCO_3^- and CO_3^{2-}. If all else is considered constant, higher alkalinity causes more of the DIC to be CO_3^{2-} and less of it to be dissolved CO_2; thus, an increase in mean ocean alkalinity lowers $p_{\mathrm{CO_2}}^{\mathrm{atm}}$. In the opposite sense, increasing DIC while holding alkalinity constant raises the concentration of dissolved CO_2 and, less intuitively, lowers the concentration of CO_3^{2-} by making the water more acidic.

The biological pump lowers $p_{\mathrm{CO_2}}^{\mathrm{atm}}$ by decreasing the concentration of DIC in surface waters—its most direct effect—but also by increasing whole-ocean alkalinity. Consider the thought experiment of turning on or strengthening the biological pump (also known as the 'soft tissue' pump, referring specifically to the sinking of non-mineral organic matter, C_{org} in Box 1 figure). The biological pump removes DIC from the surface as C_{org} and transfers it by sinking and subsequent decomposition into the deep ocean, where the regenerated DIC lowers the deep CO_3^{2-}. This decrease in the CO_3^{2-} of deep water affects its saturation state with respect to the biogenic calcium carbonate ($CaCO_3$) that is produced mostly in low-latitude surface waters and sinks to the deep sea floor. Specifically, the decrease in deep CO_3^{2-} shoals the 'calcite saturation horizon', the ocean depth below which sea water is undersaturated with respect to the $CaCO_3$ mineral calcite (the solubility of calcite is pressure-dependent and thus increases with depth). This, in turn, shoals the 'lysocline', the depth transition from shallower sea floor where calcite is preserved and buried to the deeper sea floor where it is dissolved back into the ocean. The net result is a decrease in the global ocean's burial rate of $CaCO_3$. Because $CaCO_3$ burial is the main mechanism by which the ocean loses alkalinity, a decrease in $CaCO_3$ burial causes an excess in the input of alkalinity to the ocean from rivers. Steady state is restored when rising whole-ocean alkalinity increases the deep ocean CO_3^{2-} and $CaCO_3$ burial rate back to their original levels. By that time, the increase in whole-ocean alkalinity has lowered $p_{\mathrm{CO_2}}^{\mathrm{atm}}$.



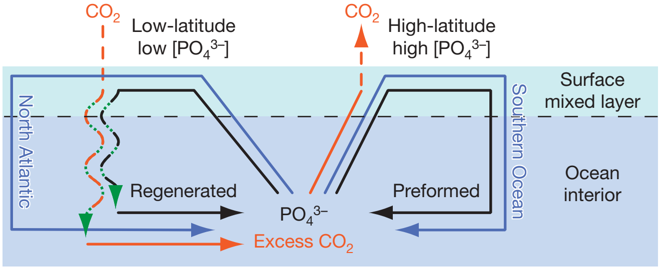


Figure 2 | Symbolic diagram of the ocean's biological pump. The blue, black and orange lines show the transport of water, major nutrient (represented by phosphate, PO_4^{3-}), and CO_2, respectively. The solid, wavy and dashed lines indicate transport by water flow, sinking organic matter, and air–sea exchange, respectively. The loop on the left shows the high efficiency imparted to the pump by the low-latitude, low-nutrient surface regions. Nutrient-bearing subsurface water is converted into nutrient-depleted sunlit surface water. This is coupled with the complete biological assimilation of the major nutrients nitrate and phosphate in the production of particulate organic matter, which then sinks into the ocean interior, where it is decomposed to 'regenerated' nutrient and excess CO_2 (CO_2 added by regeneration of organic matter), sequestering CO_2 away from the atmosphere and in the deep ocean. The nutrient-poor surface waters do not return immediately into the interior but must rather become cold and thus dense; this occurs in the high-latitude North Atlantic. The loop on the right shows the low efficiency imparted by the high-latitude, high-nutrient surface regions, currently dominated by the Southern Ocean, especially its Antarctic Zone near the Antarctic margin. There, nutrient-rich and excess CO_2-rich water comes into the surface and descends again with most of its dissolved nutrient remaining (now referred to as 'preformed'). In so doing, this loop releases to the atmosphere CO_2 that had been sequestered by the regenerated nutrient loop. Among many simplifications, this diagram omits $CaCO_3$ production and dissolution.

CO_2 back to the atmosphere, raising $p_{\mathrm{CO_2}}^{\mathrm{atm}}$. Three basic mechanisms have been recognized by which this Southern Ocean leak in the biological pump may have been reduced during ice ages: (1) a decrease in the exchange of Southern Ocean surface waters with the ocean interior[9,10], (2) an increase in the degree to which Southern Ocean surface nutrient is consumed by phytoplankton[9,11], and (3) an increase in sea-ice coverage, causing a decrease in the ability of CO_2 to escape from supersaturated Southern Ocean surface waters[12].

Rather than reviewing all aspects of glacial/interglacial $p_{\mathrm{CO_2}}^{\mathrm{atm}}$ change[4,13], we focus here on the hypothesis that the Southern Ocean is its primary driver. This hypothesis, though still speculative, has gained support from the shortcomings of low-latitude alternatives[4,14–16] and from recent data on the sequence of events at the end of the last ice age[17–22]. We focus here not on the current status of the palaeoclimate data but rather on how the hypothesis itself relates to our broader understanding of the ocean, including its carbon and nutrient chemistry, physical circulation, and biological fertility. A central outcome of this review is that ongoing debates about the Southern Ocean in the past correspond directly to longstanding questions about the modern polar ocean.

The biological pump and ocean alkalinity

The efficiency of the biological pump is usefully framed in terms of the proportion of "preformed" versus "regenerated" nutrient in the ocean interior[8,23,24] (Fig. 2). Regenerated nutrient derives from organic matter that was produced in the surface ocean by the photosynthesis of phytoplankton, sank into the ocean interior, and was there regenerated to the inorganic forms of carbon and nutrient (wavy downward arrows on the left in Fig. 2). Thus, the presence of regenerated nutrient in the ocean interior is linked to, and records, biological sequestration of CO_2 there. Preformed nutrient originates as nutrient dissolved in the ocean surface that is left unused by phytoplankton and is carried into the interior by ocean circulation (straight downward arrows on the right in Fig. 2). Preformed nutrient represents a missed opportunity for the ocean to sequester CO_2, such that the production of new deep water with high preformed nutrient effectively releases ocean-stored excess CO_2 to the atmosphere (CO_2 escaping on the right in Fig. 2). The ratio of regenerated to preformed nutrient is thus a measure of the efficiency of the biological pump, with a completely efficient pump if the nutrient in the ocean interior is entirely regenerated.

In the vast low-latitude ocean, nutrient upwelled or mixed into the surface waters is nearly completely consumed and returned to the ocean interior as sinking organic matter. Therefore, the low latitudes impose a low preformed nutrient concentration on the ocean interior (Fig. 2, left side). However, the warm and buoyant surface waters of the low latitudes cannot directly re-enter the cold and dense deep ocean. Rather, low-latitude surface water is a major ingredient of North Atlantic Deep Water (NADW), giving NADW a low preformed nutrient content (Fig. 2). Thus, NADW formation is a primary agent by which the low-latitude surface ocean affects the global biological pump, driving it towards high efficiency and thus lowering $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ (refs 24, 25). Unintuitively, much of the NADW-associated storage of regenerated nutrient and respired CO_2 is in the Indo-Pacific, at the end of NADW's path (Fig. 3a, dark blue region in the Pacific).

In contrast, the Southern Ocean is the region that imposes the highest preformed nutrient concentration on the interior and is thus responsible for most of the inefficiency in the global biological pump. First, within the core of the Southern Ocean, associated with the Antarctic Circumpolar Current (ACC), the westerly winds upwell nutrient-rich and CO_2-charged deep water into the surface and blow it equatorward (Fig. 3a). This nutrient-bearing water is then subducted into the mid-depth ocean, as Antarctic Intermediate Water (AAIW) near the Antarctic Polar Front or as Subantarctic Mode Water (SAMW) within the Subantarctic Zone (SAZ in Fig. 3a). Second, denser and deeper water forms in the polar Antarctic Zone

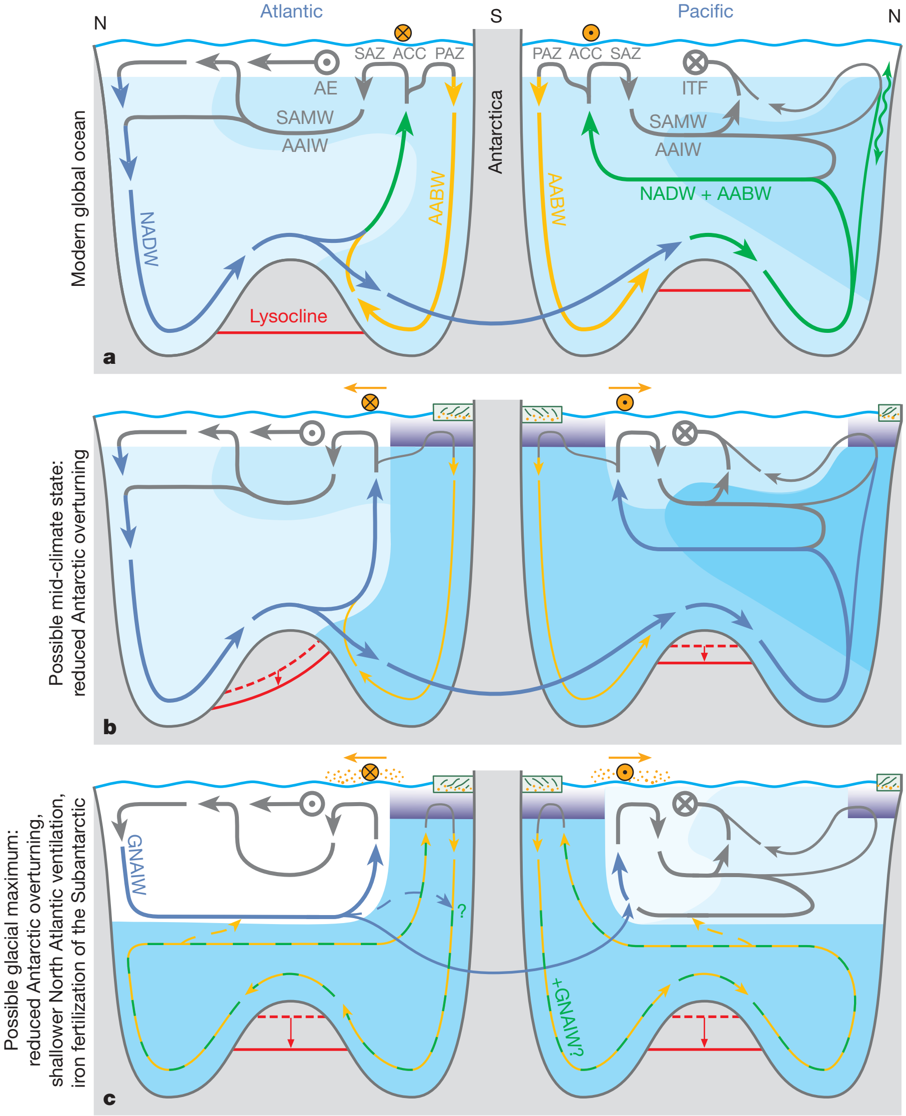


Figure 3 | Summary cartoon of the global ocean today and in two possible ice-age states. a, The global ocean today; **c**, a possible glacial maximum; **b**, a hypothetical intermediate climate state. NADW, North Atlantic Deep Water; GNAIW, Glacial North Atlantic Intermediate Water; AABW, Antarctic Bottom Water (simplistically taken here to represent all Antarctic-formed deep water[27]); AAIW, Antarctic Intermediate Water; SAMW, Subantarctic Mode Water; ITF, Indonesian Through-Flow; AE, Agulhas Eddies (ITF and AE return surface water from the Pacific to the Atlantic, with circled points showing transport out of the page and crosses showing transport into the page); SAZ, Subantarctic Zone; ACC, Antarctic Circumpolar Current; PAZ, Polar Antarctic Zone. Line colours of interior flows indicate their ventilation source region: blue, NADW or GNAIW; yellow, AABW; green, mixed NADW and AABW. Line thickness changes among panels denote changes in flow rate. The steady-state lysocline depth is indicated as a solid red line, with the dashed red line indicating a transient shoaling going into that stage, causing a transient decrease in seafloor CaCO_3 burial that increases ocean alkalinity. Deeper blue shading in the interior indicates a higher concentration of regenerated nutrient and thus regenerated (that is, excess) CO_2. In **b** and **c**, PAZ ventilation of the deep ocean is decreased relative to **a** (see the much thinner yellow flow lines in **b** and **c**). This may be the result of an equatorward shift in the westerly winds (orange symbols above the sea surface) that reduces northward transport of surface waters (slight thinning of this and downstream flow lines) and thus allows the freshwater cap in the PAZ to strengthen (purple shading in the Antarctic and also the North Pacific); in the text, other possible mechanisms for reduced PAZ overturning are also considered. Increased sea ice in the glacial Antarctic may have reduced CO_2 evasion during the winter and/or encouraged algal nutrient consumption in the summer by shoaling the mixed layer and releasing a winter's worth of aeolian iron deposition. In **c**, the ice-age dust increase (orange stipples) enhances nutrient extraction in the Southern Ocean surface, especially in the SAZ; the dust increase is shown only over the SAZ although it occurred globally. Finally, in **c**, GNAIW has replaced NADW, further slowing the ventilation rate of the abyss. This NADW-to-GNAIW switch should have focused the accumulation of dissolved inorganic carbon in the abyss and thus magnified the Southern-Ocean-driven deep sea CaCO_3 dissolution event that raised the pH of the ocean and thus further lowered $p_{\mathrm{CO}_2}^{\mathrm{atm}}$. Speculatively, **b** may represent a mid-glacial state (see text and Fig. 4).

(PAZ) to the south of the ACC. With regard to the Southern Ocean 'leak' in the biological pump, the PAZ is probably the most critical region: it has the highest unused nutrient content, and it partially ventilates (fills with atmosphere-equilibrated surface water) the voluminous abyssal ocean[26]. In the PAZ, Antarctic Bottom Water (AABW in Fig. 3a) forms along the Antarctic continental margin, isolated to some degree from 'open' (off-shore) surface waters. However, other new ocean interior waters form that more directly reflect open PAZ conditions[27].

The Southern Ocean leak in the biological pump can be stemmed by (1) reducing the preformed nutrient content of the region's input of new water into the ocean interior, (2) reducing the volume of the interior that it ventilates, or both. Focusing for the moment on the PAZ, if productivity increases so as to decrease the region's surface nutrient concentration, then $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ decreases owing to a decrease in the preformed nutrient content of PAZ-formed deep water (process (1) above). If PAZ overturning and productivity decrease in step, so as to maintain a constant surface nutrient concentration, then $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ decreases solely owing to a decrease in the volumetric importance of PAZ-formed deep water (process (2) above). If PAZ overturning decreases while productivity increases or does not decrease as much as does the nutrient supply from below, then $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ decreases as a result of both processes (1) and (2). In contrast, sea-ice-driven gas-exchange reduction lowers $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ by partially decoupling CO_2 fluxes from the preformed nutrient metric: it prevents CO_2 release out of high-nutrient, CO_2-supersaturated surface waters, resulting in new deep water with high preformed nutrient but also high excess CO_2.

Some palaeoceanographic data support a reduction in the Southern Ocean CO_2 leak through a combination of processes (1) and (2) above. Most productivity indicators[18,28] (but not all[29]) suggest that the 'export' of sinking organic carbon out of the Antarctic surface was reduced during ice ages (Fig. 1d), while some other types of data are interpreted to indicate that surface nutrient was more completely consumed[9,30]. For export to have been lower while nutrient consumption was higher, the supply of nutrient (and thus water) to the Antarctic surface from the deep ocean below must have been reduced during ice ages[9]. In return, the Southern Ocean as a whole should have reduced its formation of new subsurface water (Fig. 3b), and what did form may have had less preformed nutrient.

The reduction in Southern Ocean subsurface water formation may have been limited to AAIW and SAMW. However, an arguably expected physical consequence of reduced import of water from below is that PAZ-sourced deep water formation should also have decreased (Fig. 3b; see next section). Such a decrease in the PAZ deep water formation rate is supported by evidence of proportionally less atmospherically derived radiocarbon in Southern-Ocean-sourced deep water[31–33] and of less efficient transfer of radiocarbon from atmosphere to ocean during the last ice age than today[34], although these findings could also result from sea-ice limitation of gas exchange[35]. Below, depending on the context, the term Antarctic "stratification"[9] refers to these coupled inferences about Antarctic ice-age conditions (Fig. 3b and c): that is, the reduced input of subsurface water and nutrient into its surface layer, and the reduced ventilation of the deep ocean by the PAZ.

Because the regeneration of organic matter consumes oxygen (O_2), any biological pump mechanism for lowering ice-age $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ decreases the dissolved O_2 content of the ocean interior[3]. The ice-age deep Pacific apparently had less O_2 (ref. 36), implying more regenerated (less preformed) nutrient and thus more storage of respired CO_2, as expected if the Antarctic formed less deep water and/or formed deep water with less preformed nutrient. An early concern with the biological pump mechanisms was that the ice-age data do not indicate the widespread depletion of O_2 (suboxia) in the ocean interior, which box models predicted[5–7]. However, Southern Ocean mechanisms for lowering ice-age $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ focus their increased O_2 consumption in the ocean's deeper waters (Fig. 3b and c), where regenerated CO_2 storage can increase greatly without reaching suboxia[37,38].

Such an increase in deep ocean excess CO_2 also activates a powerful feedback involving ocean 'alkalinity' that amplifies the total CO_2 drawdown (Box 1). Reduced CO_2 release from the Antarctic, regardless of mechanism, would increase the concentration of dissolved inorganic carbon and thus lower the concentration of carbonate ion (CO_3^{2-}) in the deep ocean. This reduces the burial rate of calcium carbonate (Box 1; transient shoaling of the 'lysocline' in Fig. 3b), forcing an increase in whole-ocean alkalinity, which draws additional CO_2 into the ocean. Including this effect, box model results suggest that shutting down PAZ deep water formation or completely covering the PAZ with ice, separate from any change in the more equatorward Southern Ocean, would lower $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ by ~40 p.p.m., although this value depends on uncertain aspects of the models[8,10,12,25,39]. In the likely case that neither Antarctic overturning nor CO_2 gas exchange were completely shut off, more complete nutrient consumption in the Antarctic would have complemented these mechanisms, lowering $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ by this amount or more.

Whereas the sinking flux of organic matter out of the Antarctic surface was apparently reduced during the last ice age, it was greater than today in the Subantarctic Zone[40,41], with some evidence for more complete nutrient consumption[42]. More complete nutrient consumption at the Subantarctic surface reduces the preformed nutrient transported into the mid-depth ocean (100–1,500 m, the light-blue upper ocean interior in Fig. 3c). The increase in the efficiency of the global biological pump due to this change would have been modest because of the modest volume of the ocean interior volume ventilated by SAMW and AAIW (Fig. 3a). However, Subantarctic nutrient drawdown would also have shifted regenerated CO_2 downward from mid-depths to the abyssal ocean where the lysocline is found[38]. This then activates the alkalinity feedback that further lowers $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ (Box 1). Moreover, the decrease in the nutrient content of mid-depths (and/or a proposed increase in the ratio of silicate to nitrate and phosphate[43]) may have affected low-latitude phytoplankton productivity, decreasing the production and rain of CaCO_3 to the seafloor[44,45]. If so, the ocean would gain alkalinity so as to rebalance CaCO_3 burial with the river input of dissolved CaCO_3, further lowering $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ in the process[37,45]. Including these effects on ocean alkalinity, a $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ decrease of 40 p.p.m. is possible for Subantarctic nutrient drawdown[42,45,46]. Combined with the proposed polar Antarctic changes, the $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ decrease observed during peak ice ages is within reach.

We noted above that NADW formation is central to the highly efficient low-latitude biological pump, introducing low preformed nutrient water into the ocean interior (Fig. 2). During the Last Glacial Maximum, when $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ was lowest, North Atlantic ventilation apparently formed Glacial North Atlantic Intermediate Water (GNAIW) rather than the NADW observed today, leaving the abyssal ocean depths (>2.0–2.5 km) less directly ventilated by the North Atlantic[47] (Fig. 3c). The water that filled the deeper Atlantic apparently derived from the Southern Ocean, as AABW does today but over a much greater depth and volume. If the Antarctic was the primary ventilator of this abyssal Atlantic water, the NADW-to-GNAIW switch would have caused the voluminous deep ocean to drift back towards the Antarctic high-preformed nutrient endmember, causing the ocean to release CO_2 back to the atmosphere (Fig. 2). This would seem to represent an impediment for the polar-ocean-based explanations for lower ice-age $p_{\mathrm{CO}_2}^{\mathrm{atm}}$.

However, in the context of the proposed Southern Ocean conditions, other aspects of the NADW-to-GNAIW transition affect $p_{\mathrm{CO}_2}^{\mathrm{atm}}$ in the opposite sense. First, GNAIW appears to have been lower in preformed nutrient than modern NADW[47], partially offsetting its smaller volume. Second, an ice-age increase in nutrient consumption in Southern Ocean surface waters[9,30,42] would have reduced the cost in preformed nutrient of shifting from North Atlantic to Southern Ocean ventilation. Third, the shoaling from NADW to GNAIW would have worked to shift the ocean's burden of excess

CO_2 from the mid-depth ocean into the abyss, increasing whole-ocean alkalinity much as the proposed Southern Ocean changes do[38]. Fourth, a geochemical synergy develops: the Southern Ocean changes concentrate excess CO_2 in the abyss, while the lack of direct ventilation from the North Atlantic allows this excess CO_2 to accumulate there (Fig. 3c). This maximizes the deep-sea $CaCO_3$ dissolution event and the resulting whole-ocean alkalinity increase and $p_{CO_2}{}^{atm}$ decrease[10,37,38]. Thus, the NADW-to-GNAIW transition in combination with the proposed Southern Ocean changes may cause a net decline in $p_{CO_2}{}^{atm}$ greater than that caused by Southern Ocean changes alone.

Polar ventilation of the deep ocean

If ocean geochemistry offers up Southern Ocean change as a mechanism for reaching ice-age $p_{CO_2}{}^{atm}$, numerical models of ocean physics threaten to strip it away. These models tend to predict more—not less—Antarctic overturning in ice-age simulations[48] and instead predict increased Antarctic stratification and reduced deep water formation under anthropogenic global warming[49]. The model behaviour can be rationalized in terms of relatively simple dynamics. For example, global warming tends to strengthen the poleward transport of water vapour through the atmosphere, which should work to stratify the polar ocean under warmer climates[49]. In contrast, the postulated tendency for Antarctic overturning to decrease as global temperatures fall is harder to explain, and it has never been adequately simulated.

Some proposed physical mechanisms for slower Antarctic ventilation of the deep ocean during cold climates have focused on the low salinity of its surface water, which derives from net evaporation at low latitudes and net precipitation at high latitudes. One such proposal involves the Southern Hemisphere westerly winds. Upon cooling, the westerly winds may move equatorward and perhaps weaken, both of which would reduce the northward export of Antarctic surface waters and the resulting upwelling of relatively salty deep water[50] (Fig. 3b). The low-salinity, low-density lid that characterizes the modern Antarctic surface would strengthen because the net freshwater input to the Antarctic would no longer be so strongly dissipated by the upwelling of deep water[51]. The increased Antarctic density stratification would, in turn, discourage Antarctic deep water formation. A second proposal involves the lower sensitivity of sea water density to temperature at low temperatures, referred to here as the equation-of-state (EOS) mechanism[52–54]. In polar regions such as the Antarctic, wintertime temperatures are lowest at the surface, encouraging vertical mixing and, in the extreme cases, deep water formation; however, the low salinity of the Antarctic surface works against temperature's drive for overturning. In the EOS mechanism, global ocean cooling reduces the effect of temperature on polar ocean density structure. This makes the low salinity of Antarctic surface waters the dominant factor, thus strengthening the density stratification and discouraging Antarctic deep water formation. Valid criticisms exist for both hypotheses. The winds may not have changed as required; even if they did, their effect on Antarctic upwelling may have been buffered by eddies[55]. The EOS mechanism is implicit in the physics of ocean models, yet it has only occasionally arisen as an important factor.

Another proposal focuses on the rate of dense water removal from the deep ocean[56]. During ice ages, the Antarctic may have formed much denser deep water than today[57], which may have led to stronger density gradients in the ocean interior. Because the energy required for mixing two waters increases with the waters' density difference, extremely dense ice-age Antarctic-sourced abyssal water may have mixed with overlying waters much more slowly than does modern Antarctic-sourced deep water[56,58]. With less mixing-driven loss of dense Antarctic-sourced deep water from the ocean interior, the demand for this water would have decreased. Moreover, the resulting reduction in Antarctic overturning may have allowed fresh water to accumulate at the Antarctic surface, explaining the stronger upper water column stratification inferred for the ice-age Antarctic. While plausible, this hypothesis is unintuitive, as it posits that the formation of denser Antarctic deep water would cause less of it to form, and numerical ocean models do not as yet support it.

An additional hurdle for the Antarctic stratification hypothesis arises from the observed shoaling of North-Atlantic-formed deep water during the last ice age. If ocean models accomplish this shoaling, they do so by increasing the formation rate and density of Antarctic overturning[48]. That is, for Antarctic-sourced deep water to fill a greater volume of the ocean interior during the last ice age, the models must form more of it. The main recognized cause for this behaviour is a global requirement for continuous dense deep water production[59,60], driven by the loss of the ocean's densest deep waters to wind-driven upwelling south of the Drake Passage[61] and the downward mixing of buoyant water in the low latitudes[62]. If the formation rate of dense deep water decreases in the North Atlantic, there is greater demand for deep water formation in the Southern Ocean.

In defence of the stratification hypothesis, the models' calculation of mixing between different density waters in the ocean interior is highly suspect[60], and yet this mixing is central to the models' tendency for inverse behaviour between North Atlantic and Antarctic overturning[51]. The models can have too much deep mixing, and they generally do not take into account the fact that more energy is required to mix across a greater density difference[60,63]. Deep mixing may be the Achilles' heel of the models that has prevented them from capturing a climate change that greatly decreases the global demand for new deep water and thus allows reduced deep water formation in both the North Atlantic and the Antarctic.

At the same time, a complete hypothesis for reduced Antarctic overturning must match the observation that the deep Atlantic was dominated by a water mass that penetrated northwards from the deep Southern Ocean[47]. In the case of uniquely dense Antarctic-formed bottom water during ice ages[57], the proposed reduction in its mixing with overlying North-Atlantic-sourced mid-depth water[56] may have allowed Southern-Ocean-sourced water to accumulate in the abyss[64], even if it was forming slowly. Similarly, the proposed ice-age westerly wind shift, by decreasing both upwelling[51] and deep mixing[56] in the Southern Ocean, might have preserved Southern-Ocean-sourced dense deep water and allowed its volume to expand.

Alternatively, two different processes may be at work, one that decreases Antarctic overturning (Fig. 3b) and a second that shoals the contact between North-Atlantic-sourced and Southern-Ocean-sourced deep water in the ice-age Atlantic (Fig. 3c). Indeed, some data suggest a temporal decoupling of these processes, both on the million-year timescale[65] and within individual ice ages[66].

Yet another view of the disconnect between the Antarctic stratification hypothesis and ocean model behaviour is that it argues instead for sea-ice-driven reduction in $p_{CO_2}{}^{atm}$. If in fact ice-age deep ocean ventilation was dominated by a rapidly overturning polar Antarctic Zone and if PAZ productivity was not higher than today, then extensive sea-ice cover slowing gas exchange emerges as the only mechanism that could prevent increased CO_2 evasion from the PAZ during ice ages[12]. Indeed, in the modern PAZ, sea-ice cover appears to impede wintertime CO_2 escape[67]. In this scenario, the ice-age evidence for Antarctic stratification[9], rather than applying to the entire Antarctic, might be explained by the melting of sea ice that had been transported northward from as-yet-unstudied sites nearer the Antarctic continent where intense ice formation and dense water production occurred[8]. However, a major reduction in CO_2 degassing requires ice coverage to be nearly complete in the regions of deep water formation[12], the physical plausibility of which has been questioned[68]. Moreover, deep water formation may gravitate to open water, where the heat flux out of the ocean is much greater.

Algal nutrient consumption in the Southern Ocean

More complete consumption of nutrient in the ice-age Southern Ocean was introduced above as both a sign of other ocean changes (for example, Antarctic stratification) and a potentially important

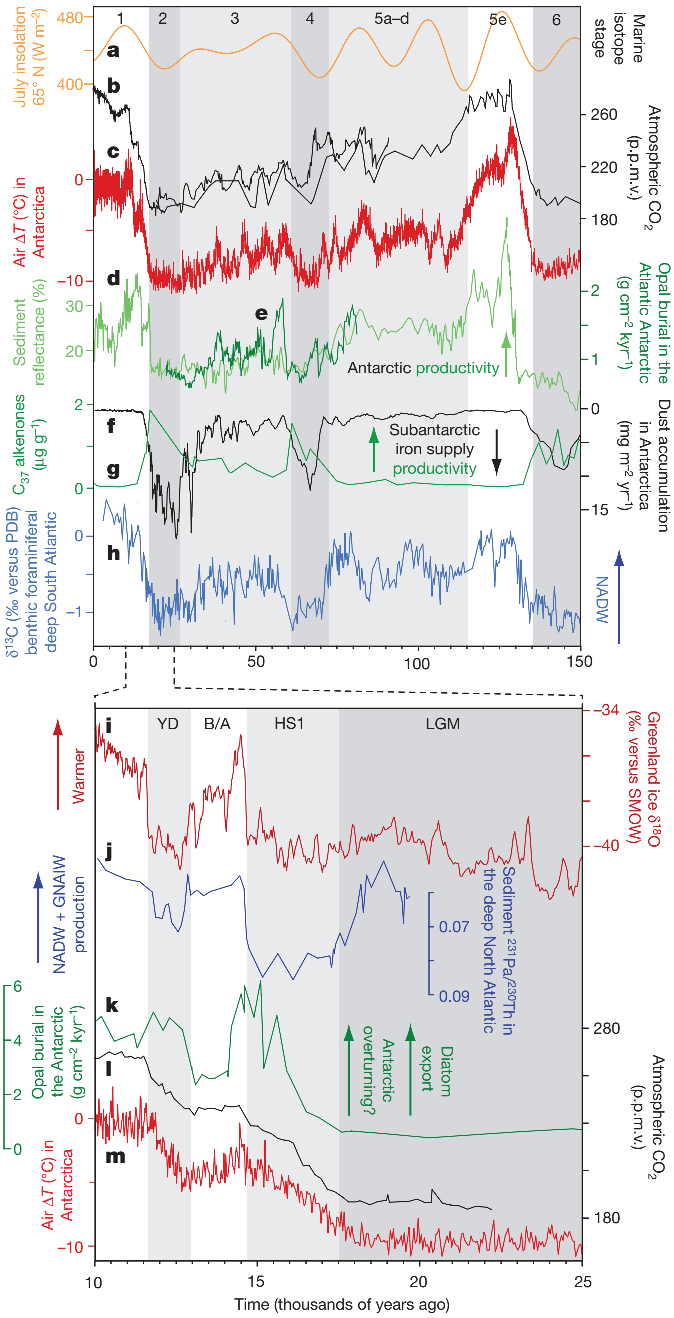


Figure 4 | Palaeoclimate records over the most recent full glacial cycle and the last deglaciation, suggesting the roles of the Southern Ocean and North Atlantic in glacial/interglacial atmospheric CO_2 change. The top panel (**a**–**h**) shows the most recent full glacial cycle, and the bottom panel (**i**–**m**) shows the last deglaciation. **a**, Summer insolation at 65° N, Milanković and Köppen's hypothesized driver of ice growth (low insolation) and decay (high isolation)[96]. **b**, **l**, Atmospheric CO_2 concentration as reconstructed from Antarctic ice cores[19,78,97]. **c**, **m**, Antarctic temperature reconstructed from the deuterium content of an Antarctic ice core[94]. **d**, The Antarctic sediment reflectance record[95] also shown in Fig. 1 (left axis), which varies with the concentration of biogenic opal, and more direct reconstructions of Antarctic biogenic opal flux[18] (right axis of **e**, and **k**). **f**, Dust accumulation in an Antarctic ice core[98], a rough measure of dust flux changes over the Southern Ocean. **g**, Concentration of alkenones in a Subantarctic sediment record[41], suggesting higher Subantarctic productivity when dust-borne iron supply was higher. **h**, $\delta^{13}C$ in benthic foraminifera from a sediment core from a depth of 4,600 m in the South Atlantic[66], suggesting that the first major switch away from NADW formation (and to GNAIW) occurred near the boundary of the marine isotope stages (MIS) 4 and 5. **i**, The GISP2 (Greenland) record of ice $\delta^{18}O$, a measure of local air temperature[99], when compared with the Antarctic reconstruction of temperature[19], shows that the Antarctic led deglacial warming, with a hiatus in Antarctic warming during Greenland's Bølling–Allerød (B/A) warm period and a resumption of Antarctic warming during Greenland's Younger Dryas (YD) cold period. **j**, The $^{231}Pa/^{230}Th$ activity ratio of a North Atlantic sediment core[20] suggests a sharp reduction in North Atlantic export of subsurface water beginning 17.5 thousand years ago and coinciding with the Heinrich Event 1 ice rafting event. The Heinrich 1 stadial (HS1), the ensuing circum-North Atlantic cold interval, is labelled, as is the Last Glacial Maximum (LGM). North Atlantic subsurface water formation apparently resumed in the Bølling–Allerød warm period, followed by another reduction at the onset of the Younger Dryas cold period. During both HS1 and the Younger Dryas, Antarctica warmed (**m**), Antarctic biogenic opal production increased (**k**), and atmospheric $p_{CO_2^{atm}}$ rose (**l**), suggestive of increased Antarctic overturning and CO_2 release. SMOW and PDB refer to Standard Mean Ocean Water and Pee Dee Belemnite, both isotopic reference materials.

contributor in its own right to ice-age $p_{CO_2^{atm}}$ reduction. But why might such a nutrient change have occurred?

In the Antarctic, both light[69] and the trace nutrient iron[70] are thought to control the productivity of phytoplankton and the export of their organic matter. If iron is the central limiter of annual Antarctic productivity, then the degree of consumption of the major nutrients (nitrate and phosphate) should depend on the supply ratio of iron relative to the major nutrients. If iron supply to the Antarctic surface is always dominantly from underlying deep water and the deep iron concentration does not change with time, then the iron-to-nutrient supply ratio would be constant even while the nutrient supply declined with ice-age stratification, and surface nutrient concentration would not change[71]. However, if surface iron inputs were significant during ice ages (from dust, melting ice, or shallow bathymetric features) and/or if deep iron concentration were elevated by such inputs, then ice-age stratification would have increased the iron-to-nutrient supply ratio—the supply of iron would have decreased less than would the supply of major nutrients—and the degree of surface nutrient consumption should have increased, leaving less major nutrient in the surface.

If light is the dominant limiter of Antarctic productivity, the scenario of perennial stratification as well as the prevalence of productivity-conducive sea-ice edge conditions during ice ages should have encouraged algal growth during the summer and led to more complete consumption of surface nutrient[29]. Summertime sea-ice cover would have sharply reduced light and thus decreased nutrient consumption, but year-round ice cover is not supported for most of the ice-age Antarctic[72].

In short, most views of polar phytoplankton limitation lead to the expectation that Antarctic stratification would have resulted in similar or more complete consumption of the surface nutrient pool, with environments closer to atmospheric iron sources and/or melting sea ice more likely to show the greatest increase in nutrient consumption. This is broadly consistent with ice-age Antarctic nitrogen isotope data suggesting that consumption was most complete in the more polar Antarctic, near the summer sea-ice front[30].

The evidence from the ice-age Subantarctic for increased productivity and nutrient drawdown is perhaps also to be expected, because it is one of the best candidate regions for natural iron fertilization[46]. It falls in the same latitude band and wind path as the major Southern Hemisphere dust sources, which intensified during ice ages[73] (Fig. 3). Moreover, for its iron supply, it depends more on dust than does the Antarctic, which receives much of its iron from upwelled deep water[71]. Even if light were the limiting factor in the Subantarctic, increased ice-derived fresh water from the Antarctic may have stabilized its surface waters and thus spurred phytoplankton growth.

Perhaps the most difficult observation to explain from the ice-age Subantarctic is the dramatic increase in biogenic opal production in its Atlantic sector[40]. If nutrient supply into the Antarctic were reduced during ice ages and most nutrient was consumed in that region, then the nutrient supply from the Antarctic surface to the Subantarctic should have dropped, which would have limited the productivity increase that more complete nutrient consumption can explain. An answer might be found in the proposed northward shift in wind-driven upwelling (Fig. 3)[30]. Alternatively, 'leakage' of silicate from the Antarctic to the Subantarctic may have increased during ice ages[43], fuelling the production of high-opal biogenic matter in the ice-age Subantarctic[45].

Evidence from the timing of changes

To this point, we have focused on the concepts—geochemical, physical and biological—linking the polar oceans to $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ change. Yet these concepts were explored largely because of strong indications from palaeoclimate measurements, such as the timing of $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ change at the end of the last ice age.

At the end of the last ice age, the most rapid Antarctic warming began about 18 thousand years ago (Fig. 4c, m). The rises in $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ (Fig. 4l) and in Antarctic opal flux[18] (Fig. 4k), which is a measure of the export of biogenic material out of the surface ocean, had very similar timing. This argues for a central role for Antarctic surface/deep water exchange in glacial/interglacial $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ change[19]. Moreover, the first major deglacial increases in both Antarctic temperature and $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ also seem to coincide with the Heinrich Event 1 (H1) in the North Atlantic[17,74] (Fig. 4i, j). This event is characterized by debris-bearing icebergs, freshening of polar North Atlantic surface waters, an abrupt decrease in North Atlantic subsurface water formation, and circum-North-Atlantic cooling[20,75]. Although some orbitally driven Antarctic warming may have predated Heinrich Event 1[76,77], the event has arisen as the probable trigger of the abrupt Antarctic changes that led to the first major pulse of deglacial $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ rise[17]. Moreover, a similar sequence of events appears to initiate the $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ rise during the Younger Dryas interval (YD in Fig. 4), the Heinrich-associated cold intervals within the last ice age[78,79], and at previous deglaciations[80,81]. Increasing Northern Hemisphere summer insolation may trigger the North Atlantic events that appear to initiate major deglaciations (Fig. 4a), which would explain in part the apparent orbital pacing of deglaciations[74].

The deglacial sequence currently has multiple plausible explanations, which draw on the concepts discussed above. As a first option, the freshwater-driven shutdown in ocean ventilation by the North Atlantic, which removed a source of dense water to the ocean interior, may have resulted in a "density vacuum"[59] in the deep ocean, precipitating an increase in Antarctic deep water formation to fill that vacuum[74,79]. The associated Antarctic overturning released biologically sequestered CO_2 into the atmosphere and melted highly reflective Antarctic sea ice, causing regional and global warming. An alternative follows from the wind-shift hypothesis for reduced ice-age Antarctic overturning[50]. The reduced upper-ocean and atmospheric transport of heat from South to North due to the Heinrich Event 1 shutdown of North Atlantic overturning warmed the Southern Hemisphere[22,82], which may have shifted the Southern Hemisphere westerly wind belt southward[83]. This may then have driven increased Antarctic upwelling[17,18,84], which would have eroded the Antarctic salinity-driven stratification and thus encouraged the Antarctic to form deep water[50,51]. A third alternative is in the vein of the sea-ice gas-exchange hypothesis[12]: the Southern Hemisphere warming reduced Antarctic sea-ice cover that had previously prevented the release of CO_2 from supersaturated Antarctic surface waters. Antarctic ice core evidence of decreasing dust flux before Heinrich Event 1[85] suggests that iron fertilization should not have prevented CO_2 release associated with these circulation or sea-ice changes. Distinguishing among these and other deglacial scenarios may help to identify the ice-age conditions that sequestered CO_2 in the first place.

The larger-scale structure of the $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ record may also provide insight. Over at least the last 400 thousand years, the declines in $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ to their minima during peak ice ages tend to occur over tens of thousands of years and/or in steps (Fig. 1). This temporal behaviour is roughly intermediate between the Antarctic ice core temperature reconstructions, which indicate fast cooling into ice ages, and the more gradual glacial increase in ocean calcite $\delta^{18}O$ (Fig. 1). The slow and/or multi-stepped decline in $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ may result in part from the progressive activation of distinct $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$-reducing processes[39].

How might a Southern Ocean control on $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ explain this temporal structure? Focusing on the last glacial cycle, the Antarctic cooling early in the last ice age, 115 thousand years ago (Fig. 4c), suggests reduced Antarctic overturning or increased sea-ice suppression of gas exchange as driving part of the ~40 p.p.m. of $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ decline at that time (Fig. 4b)[39]. This change may also mark the largest single step in cooling of the ocean interior[86], with its attendant oceanic uptake of CO_2. In contrast, the second major decline in $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ 70 thousand years ago, which coincides with a major dust flux increase to Antarctic ice cores (Fig. 4f) and Subantarctic sediment cores[41], has been attributed by some to iron fertilization of the Southern Ocean, the Subantarctic in particular[42,46,87] (Fig. 4g). This may also have been the time of sharpest transition from NADW to GNAIW[66] (Fig. 4h), which may have increased the ability of the Southern Ocean changes to lower $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ (Fig. 3c). Of course, attribution of the individual components of $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ change is only a first step towards a coherent theory for glacial $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ cycles, which must explain the timing of the drivers themselves.

Synthesis and implications

The Southern Ocean is strongly implicated as an important driver of glacial/interglacial $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ changes. One possible control valve is the circulation-driven release of deeply sequestered CO_2 through the Antarctic surface: reduced water exchange between the Antarctic surface and the underlying deep ocean may have closed this valve during the last ice age. However, other possible drivers or contributors to $p_{\mathrm{CO}_2}{}^{\mathrm{atm}}$ change have been identified. First, enhanced ice coverage in the Antarctic may have provided an alternative or complementary barrier to CO_2 release from the Antarctic, especially in extreme polar regions where wintertime overturning persisted. Second, despite lower productivity, Antarctic phytoplankton may have more completely consumed a reduced nutrient supply to the Antarctic surface, further increasing CO_2 storage in the deep ocean. Third, phytoplankton productivity was apparently higher in the Subantarctic Zone, perhaps owing to natural iron fertilization, and may have more efficiently stripped out nutrient before it escaped into the low-latitude upper ocean, adding to the abyssal accumulation of excess CO_2. Fourth, increased storage of CO_2 in the deep sea should have driven a $CaCO_3$ dissolution event on the sea floor, making the global ocean more alkaline and thus increasing its capacity to store CO_2. Fifth, the shoaling of North-Atlantic-sourced deep water during ice ages may have assisted the above mechanisms by isolating the deep ocean as a slowly ventilated reservoir in which the Southern-Ocean-driven CO_2 storage was focused, maximizing the $CaCO_3$ dissolution caused by the deeply sequestered CO_2 and thus enhancing the ocean's shift to more alkaline conditions. One view of these mechanisms as a whole is of the effective segregation of the ocean during the last ice age into (1) a slowly ventilated, CO_2-rich deep ocean most directly under the control of a stratified and/or ice-covered Antarctic and (2) a nutrient-poor and CO_2-poor upper ocean ventilated by the North Atlantic and the more equatorward regions of the Southern Ocean (Fig. 3c).

Despite the relative complexity of our narrative, the robust coupling of $p_{\mathrm{CO_2}}^{\mathrm{atm}}$ to climate over glacial cycles calls for a simple explanation. Thus, amid ongoing efforts in palaeo-environmental reconstruction, we must also search for new paths to more general insights. As one example, a mechanistic understanding of the ice-age Antarctic may arise, counter-intuitively, from the high-latitude North Pacific[88]. This region appears to have undergone glacial/interglacial changes similar to those reconstructed for the Antarctic[89–91] (Fig. 3b). If so, ice-age Antarctic conditions must not have been controlled by regional specifics (for example, the bathymetry of the Antarctic continental shelf or modest shifts in the summertime sea-ice front) but rather must have involved a more fundamental climate response of the polar ocean[52].

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