Invited review

The Southern Ocean during the ice ages: A review of the Antarctic surface isolation hypothesis, with comparison to the North Pacific

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ABSTRACT

The Southern Ocean is widely recognized as a potential cause of the lower atmospheric concentration of CO_2 during ice ages, but the mechanism is debated. Focusing on the Southern Ocean surface, we review biogeochemical paleoproxy data and carbon cycle concepts that together favor the view that both the Antarctic and Subantarctic Zones (AZ and SAZ) of the Southern Ocean played roles in lowering ice age CO_2 levels. In the SAZ, the data indicate dust-driven iron fertilization of phytoplankton growth during peak ice age conditions. In the ice age AZ, the area-normalized exchange of water between the surface and subsurface appears to have been reduced, a state that we summarize as "isolation" of the AZ surface. Under most scenarios, this change would have stemmed the leak of biologically stored CO_2 that occurs in the AZ today. SAZ iron fertilization during the last ice age fits with our understanding of ocean processes as gleaned from modern field studies and experiments; indeed, this hypothesis was proposed prior to evidentiary support. In contrast, AZ surface isolation is neither intuitive nor spontaneously generated in climate model simulations of the last ice age.

In a more prospective component of this review, the suggested causes for AZ surface isolation are considered in light of the subarctic North Pacific (SNP), where the paleoproxies of productivity and nutrient consumption indicate similar upper ocean biogeochemical changes over glacial cycles, although with different timings at deglaciation. Among the proposed initiators of glacial AZ surface isolation, a single mechanism is sought that can explain the changes in both the AZ and the SNP. The analysis favors a weakening and/or equatorward shift in the upwelling associated with the westerly winds, occurring in both hemispheres. This view is controversial, especially for the SNP, where there is evidence of enhanced upper water column ventilation during the last ice age. We offer an interpretation that may explain key aspects of the AZ and SNP observations. In both regions, with a weakening in westerly wind-driven upwelling, nutrients may have been "mined out" of the upper water column, possibly accompanied by a poleward "slumping" of isopycnals. In the AZ, this would have encouraged declines in both the nutrient content and the formation rate of new deep water, each of which would have contributed to the lowering of atmospheric CO_2. Through several effects, the reduction in AZ upwelling may have invigorated the upwelling of deep water into the low latitude pycnocline, roughly maintaining the pycnocline's supply of water and nutrients so as to (1) support the high productivity of the glacial SAZ and (2) balance the removal of water from the pycnocline by the formation of Glacial North Atlantic Intermediate Water. The

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proposed return route from the deep ocean to the surface resembles that of Broecker's (1991) "global ocean conveyor," but applying to the ice age as opposed to the modern ocean.

1. Introduction

The causes of glacial/interglacial CO_2 change are critical to the feedbacks underlying ice age climate cycles. Because of its strong control on atmospheric CO_2 on thousand-year time scales, the ocean has long been recognized as central to glacial/interglacial CO_2 change (Broecker, 1982a,b). In the 1980s, the Southern Ocean was identified as a major leak of biologically stored CO_2 from ocean to atmosphere, suggesting the closure of this leak as a mechanism for lowering atmospheric CO_2 during ice ages (Sarmiento and Toggweiler, 1984; Siegenthaler and Wenk, 1984; Knox and McElroy, 1984). In the early 1990s, the focus pivoted to the role of the low latitudes in the calcium carbonate ($CaCO_3$) budget of the ocean (Archer and Maier-Reimer, 1994). However, in the late 1990s, arguments against these low latitude mechanisms were recognized (Sigman et al., 1998; Tyrrell et al., 1999). Accordingly, the search for the drivers of CO_2 change refocused on the Southern Ocean, which continues to dominate thinking on the topic (reviewed by Sigman and Boyle, 2000; Fischer et al., 2010; Sigman et al., 2010; and Hain et al., 2014a).

Here, we review previous model and measurement results and seek new perspective on the role of the Southern Ocean in glacial/interglacial CO_2 change. We first describe the current role of the Southern Ocean in the global overturning circulation and ventilation of the ocean interior (section 2). We then describe the geochemical potential of Southern Ocean changes to lower atmospheric CO_2 to ice age levels (section 3). We then review the evidence for a strengthening of the ocean's biological pump during the ice ages (section 4). In doing so, we summarize coupled reconstructions of export production and surface nitrate concentrations in the Southern Ocean to argue that its two major zones, the Antarctic Zone (AZ) to the South and the Subantarctic Zone (SAZ) to the North, played distinct and complementary roles in the drawdown of CO_2 during ice ages.

Our attention then focuses on the highly divergent hypotheses for the physical cause of the AZ changes (section 5). The glacial AZ condition was first described as "stratification" (François et al., 1997). However, this term implied stronger density stratification as the ultimate physical cause, which is possible but unproven, thus our choice of the less specific term of surface "isolation." As a prospective aspect of this analysis, we draw on evidence from the subarctic North Pacific (SNP) in an effort to distinguish among hypothesized causes for ice age AZ surface isolation, leading us to favor changes in the westerly wind-driven upwelling as instrumental (section 6). Our proposal for the ice age ocean is presented in light of this conclusion (sections 7 and 8). It is then applied to address two important questions. These relate to the two "cells" of circulation passing through the Southern Ocean surface, specifically, their respective roles in (1) ventilating the deep ocean and (2) feeding the upper limb of global meridional overturning circulation that produces North Atlantic Deep Water (section 9).

## 2. Architecture of Southern Ocean overturning

The overturning circulation of the Southern Ocean and its connections to the global ocean have been usefully separated into "upper" and "lower" cells (Fig. 1 a; Toggweiler et al., 2006; Lumpkin and Speer, 2007). In the upper cell, the southern hemisphere westerly winds drive upwelling in the AZ and northward wind-driven transport toward the Polar Frontal Zone (PFZ) and SAZ. There, water is subducted near the Antarctic Polar Front to form Antarctic Intermediate Water (AAIW) or near the Subantarctic Front to form Subantarctic Mode Water (SAMW). These waters flow northward in the shallow subsurface (~200−1100 m) to the lower latitude ocean, where they may return to the surface. In the Southern Ocean, this cell is understood to be the "residual" of the Ekman (wind-driven) transport and the largely opposing response of eddies to the sea level height (and thus pressure and density) gradients that result from it (Marshall and Speer, 2012). The wind-driven transport tends to tilt the isopycnals, causing them to outcrop in the polar region; the eddies, responding to the resulting northward increase in sea level height and pycnocline thickness, work to flatten the isopycnals. The balance between these counteracting processes yields the observed pycnocline tilt (Fig. 1 a, lower contact of the light gray region).

The surface exposure of the lower cell is entirely within the Antarctic Zone (Fig. 1 a): waters brought from the deep Southern Ocean interior to the AZ surface are returned to the deep Southern Ocean. In the "polar" AZ (PAZ; poleward of the Southern Antarctic Circumpolar Front), formation of Antarctic Bottom Water (AABW) near the coast of Antarctica is an established mechanism for this return flow (Orsi et al., 1999, 2002; Fukachami et al., 2010). Other mechanisms may exist that more directly involve the non-coastal AZ, such as open ocean deep convection associated with transient open ocean polynyas (Broecker et al., 1999; Campbell et al., 2019) and perennial, widespread open ocean mixing at the base of the AZ winter mixed layer that links to isopycnal exchange in the interior (Abernathey and Ferreira, 2015). The relationship between the two cells within the Southern Ocean will arise as a central question in section 9.

On the global scale, the upper and lower cells are connected elsewhere in the ocean, actually representing one complex cell (Fig. 1 a; Talley, 2013). Upper cell water from the Southern Ocean flows northward and into the mid-depth to shallow ocean, eventually contributing to the formation of North Atlantic Deep Water (NADW, Toggweiler and Samuels, 1995). NADW, largely through mixing with deep water in the Southern Ocean, gives rise to Lower Circumpolar Deep Water (LCDW). The exposure of NADW and LCDW in the AZ surface feeds AABW formation; according to Talley (2013), Upper Circumpolar Deep Water (UCDW) is also a significant feedwater for AABW. Without reaching the AZ surface, LCDW can also be entrained into newly formed AABW. AABW (with some proportion of entrained LCDW) then flows through the deep Indo-Pacific, where it accumulates regenerated nutrients, carbon, and alkalinity from sinking material. This water upwells as it gains buoyancy from mixing with overlying waters, becoming Pacific Deep Water (PDW) and then UCDW as it flows back to the Southern Ocean. As UCDW, this water upwells largely as part of the Southern Ocean's upper cell, closing the global circulation.

It is useful to distinguish between the upper and lower cells in terms of the ocean interior volumes that they occupy and the surface regions that are responsible for the ventilation of these respective volumes (Toggweiler et al., 2006). The upper cell occupies the shallower interior (including the global ocean's
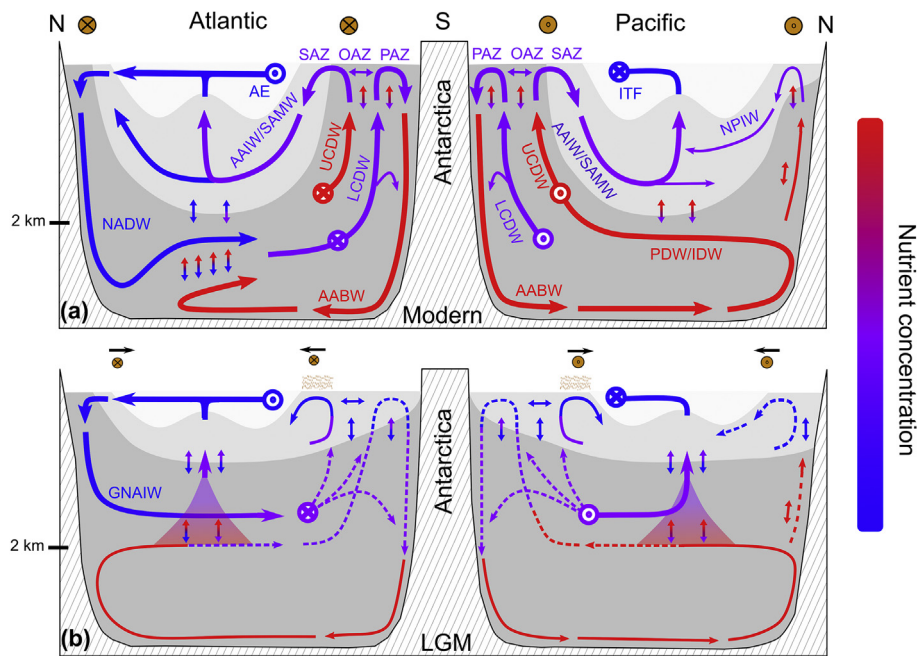
Fig. 1. Schematic of the global ocean's interior circulation today (a) and a proposal for the Last Glacial Maximum (b, LGM). Abbreviations are as follows: PAZ, Polar Antarctic Zone; OAZ, Open Antarctic Zone; SAZ, Subantarctic Zone; NADW, North Atlantic Deep Water; GNAIW, Glacial North Atlantic Intermediate Water; PDW, Pacific Deep Water; IDW, Indian Deep Water; UCDW, Upper Circumpolar Deep Water; LCDW, Lower Circumpolar Deep Water; AABW, Antarctic Bottom Water; AAIW, Antarctic Intermediate Water; SAMW, Subantarctic Mode Water; ITF, Indonesian Throughflow; AE, Agulhas Eddies (ITF and AE return surface water from the Pacific to the Atlantic). Circled points and crosses show water and westerly wind transports out of and into the page, respectively (with the winds as orange circles). Line thickness changes among panels largely denote changes in flow rate, with thin dashed lines representing the greatest declines from modern; in the modern, the thinner flow lines in the SNP denote weaker wind-driven upwelling than in the AZ. Double-direction arrows indicate lateral mixing between surface PAZ and OAZ in the Southern Ocean, vertical mixing across the base of the mixed layer in the AZ and SNP, and vertical (i.e., diapycnal) mixing in the ocean interior. Line colors indicate nutrient (nitrate phosphate) concentration according to the color scale (red highest and blue lowest). All panels show the global ocean's upper and lower overturning cells (i.e., those beginning in the SAZ and PAZ, respectively); the depiction follows Toggweiler et al. (2006) but shows the interconnection of the cells described by Talley (2013) and highlighted by Ferrari et al. (2014). The gray scale indicates relative water densities, with light gray shading indicating the global pycnocline, the proposed poleward "slumping" of which is shown in (b) for the LGM and is explained in the text. For explanation of (a), see section 2. Additional phenomena in (b) include an equatorward shift and weakening in the westerly winds (black horizontal arrows and wind symbol size reduction) and increased dust-borne iron supply to the SAZ (brown stipples). For further explanation of (b), see sections 6, 7, and 9.

pycnocline, down to roughly 1.2 km depth) and a portion of the deeper ocean. The AZ and SAZ ventilate its shallower limb, as AAIW and SAMW, while the North Atlantic ventilates its deeper limb as NADW. The lower cell, which is believed to be mainly ventilated from the AZ, occupies abyssal levels and the portion of the deep ocean not ventilated from the North Atlantic. With this distinction, one can imagine a competition between the AZ and the North Atlantic to ventilate the ocean interior (specifically, the abyssal and deep waters), and many model studies of ice age CO_2 drawdown can be understood in terms of this competition (Toggweiler, 1999; Sigman et al., 1999; Archer et al., 2003; Toggweiler et al., 2003; Sigman and Haug, 2003; Köhler et al., 2005; Marinov et al., 2008; Hain et al., 2010; Kwon et al., 2012; Menviel et al., 2018), as described below.

However, important connections have been recognized between the two cells in the modern ocean (Talley, 2013). For example, the AABW formed as part of the lower cell evolves by diffusion into PDW and in turn into UCDW, the wind-driven upwelling of which feeds the upper cell in the modern ocean (Fig. 1 a). These connections between the two cells in the Southern Ocean surface imply that any change in the proportion of the global deep ocean sourced from the AZ *vs.* the North Atlantic also has implications for the routing of waters through the Southern Ocean surface. Ferrari et al. (2014) argue that a more complete decoupling of the circulation into two cells (as in Fig. 1 b) was a fundamental climate-related event of the ice ages that allowed for the drawdown of atmospheric CO_2. Thompson et al. (2019) propose that variations in the coupling between the two cells contribute to the anti-

correlated millennial-scale climate changes in the northern and southern hemispheres during the ice ages.

The modern global ocean circulation schematic in Fig. 1 a neglects an important contributor to the overturning circulation. In the ocean interior, small-scale turbulent mixing between waters of different densities transports heat downward from the surface and thus increases the buoyancy of deep water. The buoyancy increase in the existing deep water allows new dense water from high latitude ventilation regions to flow into the ocean basins below it, which in turn causes the diffuse upwelling of deep water in the ocean interior (Munk, 1966). The upwelling has the potential to import deep water directly into the pycnocline (Talley, 2013). In section 9.4, we suggest that this upwelling into the pycnocline was more important during the ice ages when the Southern Ocean upper cell was sluggish (colored cones and upward arrows in the Fig. 1 b). To emphasize the possibility of its ice age acceleration, we include the process in Fig. 1 b but exclude it in Fig. 1 a.

3. Geochemistry of Southern Ocean mechanisms for lowering atmospheric CO_2

3.1. Southern Ocean-focused processes

Changes at the Southern Ocean surface can lower atmospheric CO_2 by several categories of geochemical mechanism (Figs. 2 and 3; the discussion below follows Hain et al., 2010). The most central to this review is an increase in the efficiency of the global ocean's "biological pump" (or, more specifically, its "soft-tissue pump").

Here, the biological pump refers to the sequestration of CO_2 in ocean waters below the surface wind-mixed layer, through the production, export, and subsurface remineralization of photosynthetic organic matter. The maximal amount of carbon sequestered in the ocean interior by the biological pump is roughly set by the phosphate concentration of the ocean. We can also frame this in terms of nitrate so long as (1) the nitrogen-to-phosphorus (N/P) ratio of organic matter is relatively well conserved over time and (2) feedbacks keep nitrate in a relatively constant ratio to phosphate in the ocean. These two assumptions are defensible (e.g., Deutsch et al., 2007; Marconi et al., 2017; Ren et al., 2017) and help to simplify the current discussion. The efficiency of the biological pump refers to the degree to which the ocean's "major nutrient" (phosphate or nitrate) reservoir is involved in the process of carbon storage. This is usefully tracked with the unused ("preformed") nutrient concentration with which the ocean interior is ventilated (Ito and Follows, 2005). A lower preformed nutrient concentration for the global ocean interior indicates more complete usage of the nutrient reservoir in carbon storage (corresponding to more "regenerated" nutrients in the ocean interior) and thus a more efficient biological pump. Today, only about half of the ocean's nutrient inventory is associated with biologically sequestered carbon, while the other half (the preformed half) was not used for export production when it was last at the surface (Hain et al., 2010). The vast majority of preformed nutrients originate from the Southern Ocean surface (Fig. 3 a; Toggweiler et al., 2003).

A decline in mean ocean preformed nutrient concentration could be accomplished by (1) a decrease in the unused nutrient concentration of the Southern Ocean surface waters that ventilate the ocean interior (Sigman and Boyle, 2000; Marinov et al., 2006) or (2) a reduction in Southern Ocean ventilation of the interior relative to some other ventilating source with a lower preformed nutrient concentration (in particular, the North Atlantic) (Fig. 3 a) (Toggweiler et al., 2003; Marinov et al., 2008; Kwon et al., 2012). Either of these changes or a combination of them would increase the deep ocean storage of regenerated CO_2 and thereby lower atmospheric CO_2. Importantly, these Southern Ocean "ventilation reduction" and "nutrient drawdown" mechanisms do not have additive effects on atmospheric CO_2 (Fig. 2). For example, if Southern Ocean ventilation of the interior ceased while other ocean ventilation processes continued, Southern Ocean surface nutrient status would no longer modulate the efficiency of the global biological pump. Conversely, with more complete consumption of nutrients in the Southern Ocean surface, the region's tendency to leak regenerated CO_2 from the deep ocean to the atmosphere would be lower, such that reduction in Southern Ocean ventilation of the interior would have a weaker CO_2 impact.

Atmospheric CO_2 is lowered "directly" by increased sequestration of regenerated CO_2 in the ocean interior (the soft-tissue pump, *sensu stricto*) and "indirectly" by the transient $CaCO_3$ dissolution event in the deep ocean that it causes, which raises whole ocean alkalinity (Broecker and Peng, 1987). The proportional strength of the whole alkalinity effect can vary according to the mechanism involved (Sigman et al., 1998), but it most often augments the CO_2 drawdown by roughly a third of the drawdown due to deep ocean CO_2 sequestration alone (Hain et al., 2010).

At the same time that a reduction in Southern Ocean overturning strengthens the soft-tissue pump and thus tends to decrease atmospheric CO_2, this effect is partially countered by a strengthening of the "carbonate pump" (Fig. 3 b). In the carbonate pump, the rain of $CaCO_3$ in fossiliferous material (coccoliths or foraminifera tests) out of the surface ocean extracts alkalinity from surface waters and sequesters it in the deep ocean (as "regenerated alkalinity"), with consequences for surface carbonate chemistry, atmospheric CO_2 and whole ocean alkalinity that are analogous to,
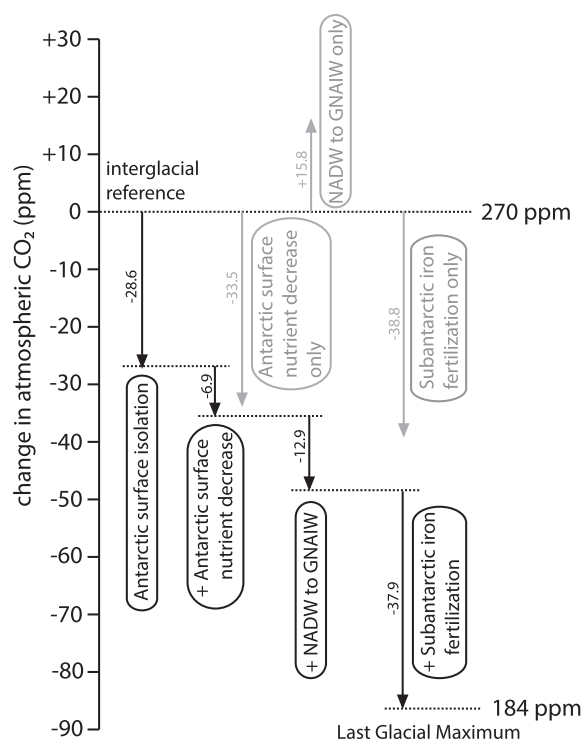
Fig. 2. Simulated changes in the concentration of atmospheric CO_2 (in parts per million by volume, ppm) due to proposed ice age changes in the Southern Ocean as well as in the character of North Atlantic-formed deep water (from Hain et al., 2010). NADW and GNAIW refer to North Atlantic Deep Water and Glacial North Atlantic Intermediate Water. The interglacial reference case of the model has an atmospheric CO_2 concentration of 270 ppm. The gray arrows indicate the CO_2 change caused by a given forcing if active by itself, whereas the black arrows indicate successive addition of forcings from left to right. First, AZ surface isolation, removing essentially all deep ventilation from the AZ surface, causes a CO_2 decline of 29 ppm. In these experiments, the only water exchanges that are reduced are those related to ventilation of the "lower cell" of Southern Ocean overturning (i.e., AZ-formed deep water); this strategy was taken to distinguish the CO_2 effect of AZ surface isolation from that of reducing the nutrient supply to SAZ surface waters. Second, AZ surface nutrient concentration is lowered to ~50% of its interglacial value. If conducted alone, without AZ surface isolation, the nutrient drawdown causes a 33 ppm decline; however, without a circulation change, a nutrient drawdown would require an increase in export production, counter to ice age observations (e.g., Jaccard et al., 2013). In contrast to its effect when applied alone, when nutrient drawdown is applied in concert with AZ surface isolation, it only contributes an additional 7 ppm decline beyond the 29 ppm from AZ surface isolation. Again, in these experiments, this is implemented in a way that SAZ surface nutrients are not affected. Third, a shift from the formation of NADW to GNAIW, when conducted in the context of the first two changes, contributes an additional 13 ppm decline. In contrast, when the change to GNAIW is conducted alone, without the Southern Ocean changes, it raises atmospheric CO_2 by 16 ppm because it gives over more of the ocean interior to ventilation by the high-nutrient AZ. SAZ iron fertilization (implemented as an export production increase that causes a ~43% decline in SAZ surface nutrient concentration) lowers atmospheric CO_2 by 38 ppm, whether it is conducted alone or in combination with any of the other changes. The AZ surface is an important source of nutrients to the SAZ. If, in the model, AZ nutrient drawdown is allowed to cause nutrient decline in the SAZ as well, then the AZ changes lower CO_2 more than indicated here, while the SAZ iron fertilization lowers CO_2 correspondingly less, resulting in no change in the net CO_2 decline from the combined forcings. A CO_2 decline of 86 ppm occurs from simultaneous implementation of all four changes, producing an atmospheric CO_2 concentration of 184 ppm, which is similar to observations for the LGM. LGM conditions for the temperature, salinity, and volume of the ocean are not implemented here and in combination may have reduced ice age CO_2 by an additional ~30 ppm (Kohfeld and Ridgwell, 2009); the simulations described here were for an isothermal ocean, such that imposed circulation changes did not alter the average ocean temperature. There is also no implementation of an ice age decline in the terrestrial biosphere and soil carbon inventories, which may have raised atmospheric CO_2 by ~15 ppm (Sigman and Boyle, 2000).
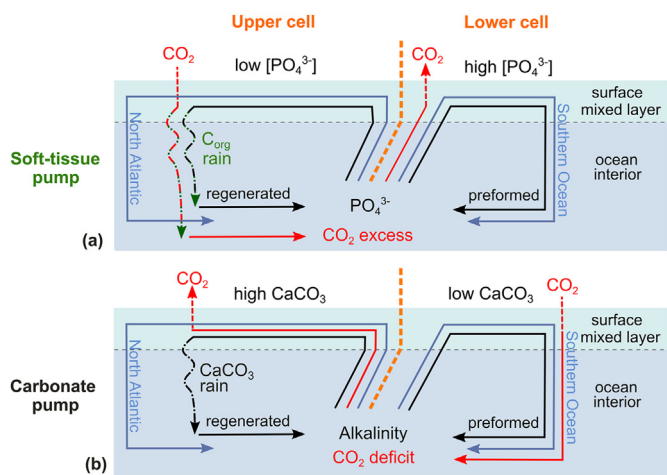
Fig. 3. Schematic view of the roles of the two Southern Ocean overturning cells in the soft-tissue pump (a) and the carbonate pump (b). In both panels, the blue and red lines show the transport of water and CO_2, respectively. In (a), the black lines show the transport of major nutrients (represented by phosphate); in (b), the black lines show the transport of alkalinity. The solid, wavy and dashed arrows indicate transport by water flow, sinking organic matter, and air−sea exchange, respectively. The deep ocean interior is filled with cold, dense waters originating from polar ocean regions, either the northern North Atlantic (left side) or the Southern Ocean (right side). In (a), the upper cell of Southern Ocean overturning, after upwelling in the AZ, flows through the low-latitude, low-nutrient surface regions, where the growth of phytoplankton completely extracts its dissolved nutrients. The particulate organic matter from this growth sinks into the ocean interior, where it is decomposed to "regenerated" nutrient and excess CO_2 (CO_2 added by regeneration of organic carbon), sequestering CO_2 away from the atmosphere and in the deep ocean. The nutrient-poor low latitude surface waters cannot return immediately into the interior but must first become dense by cooling; today, this occurs dominantly in the high-latitude North Atlantic, included on the left side of the diagram. The lower cell of Southern Ocean overturning imports deep water into the Polar Antarctic Zone near the margin of Antarctica. Because of vigorous vertical circulation, rapid nutrient supply, and poor light and iron conditions in the AZ, 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"). Soft-tissue organic matter consists of assimilated carbon and nutrients, such that preformed nutrients in the ocean interior record a "missed opportunity" for deep ocean carbon sequestration by the soft-tissue pump. Put another way, the lower cell releases to the atmosphere CO_2 that had been sequestered by the upper cell. There is a similar effect of the two regions of ventilation on the carbonate pump (b), but this translates to an opposing effect on atmospheric CO_2 (see red arrows). Biogenic $CaCO_3$ rain is important in the low-latitude ocean. Therefore, when nutrient-bearing water is cycled through the upper cell of ocean overturning, the rain of $CaCO_3$ sequesters alkalinity in the deep ocean (as "regenerated alkalinity"), which raises the concentration of CO_2 in surface waters and pushes CO_2 into the atmosphere. In contrast, the Southern Ocean is dominated by biogenic opal, such that the lower cell brings regenerated alkalinity to the surface, allows it to take up CO_2, and then sends it back into the interior as "preformed alkalinity." As a result, if more of the ocean is ventilated by the North Atlantic, the carbonate pump is also made more efficient, which cancels part of the CO_2 decline driven by the increased efficiency of the soft-tissue pump. The figure is adapted from Hain et al. (2014a).

but the opposite of, the sequestration of regenerated carbon via the soft-tissue pump (Hain et al., 2010). With overturning in the Southern Ocean, the regenerated alkalinity from deep ocean dissolution is allowed to return to surface waters where it can take up CO_2 from the atmosphere before the water is circulated back into the ocean interior (i.e., as "preformed" alkalinity). Slowing this overturning causes a rise in regenerated relative to preformed alkalinity in the ocean interior, which indicates less ocean CO_2 sequestration. This is a significant limitation on the ability of a slowing of Southern Ocean overturning to lower atmospheric CO_2, with two related consequences. First, it encourages consideration of glacial scenarios of more complete surface nutrient consumption in the AZ. In the diatom-dominated AZ, the sinking biogenic material includes little $CaCO_3$, so this change would strengthen the soft-

tissue pump without also strengthening the carbonate pump, maximizing the CO_2 reduction. Second, given the data pointing to a glacial reduction in AZ export production (section 4.2), SAZ changes are also required to lower atmospheric CO_2 to observed glacial levels (Fig. 2).

An additional consideration regarding a slowing of the lower cell of Southern Ocean overturning is that its geochemical components of CO_2 change are affected by whether it occurs in the context of modern-like North Atlantic Deep Water formation or of North Atlantic ventilation to a shallower level, such as the formation of Glacial North Atlantic Intermediate Water (GNAIW; Boyle, 1988). The switch from NADW to GNAIW formation tends to raise atmospheric CO_2 by ~15 ppm, due to the resulting increased role of the high-preformed nutrient AZ surface in ventilating the deep ocean (Hain et al., 2010). However, slowing of the Southern Ocean's lower cell and/or a decline in its preformed nutrient concentration then become somewhat more efficient in lowering CO_2 from that level. This is firstly because the transition from NADW to GNAIW increases the role of the AZ in deep ocean ventilation. Secondly, any AZ-driven change in CO_2 storage is focused in the abyssal layer of the ocean near the calcite lysocline, such that its tendency to increase ocean alkalinity is maximized (Boyle, 1988; Toggweiler, 1999). These CO_2 effects of a NADW-to-GNAIW shift are important in multiple contexts (Sigman et al., 2010), two of which are mentioned here. First, the NADW-to-GNAIW shift appears to occur mid-way through development of the last ice age (at ~70 ka; Piotrowski et al., 2005), thus potentially affecting the relationship between Southern Ocean changes and atmospheric CO_2 at that time. Second, the shoaling of NADW to GNAIW is central to a set of prominent hypotheses for lower cell change over glacial cycles (e.g., Ferrari et al., 2014, sections 5.1.3 and 5.1.4).

To this point, enhanced CO_2 storage due to Southern Ocean change has been described as a consequence of the CO_2 fluxes across the interface between the surface mixed layer and the underlying deep ocean. However, reducing the evasion of CO_2 from surface mixed layer to the atmosphere represents an important alternative. Stephens and Keeling (2000) proposed that increased sea ice cover in the AZ would have had this effect. With respect to the lower cell of Southern Ocean overturning, a strong limitation on gas exchange during the ice ages, with or without ice, would have reduced AZ CO_2 release, similar to the AZ circulation and biogeochemical mechanisms for CO_2 sequestration (Archer et al., 2003; Khatiwala et al., 2019). As with the competition between the nutrient drawdown and ventilation reduction mechanisms described above, the gas exchange-limitation mechanism for reducing atmospheric CO_2 is not strictly additive with other mechanisms: if one of three mechanisms completely stemmed the leak of CO_2 out of the AZ surface, then the others would have no further effect (Hain et al., 2010). One caveat to this is with respect to the upper cell. Preventing ocean CO_2 release by gas exchange limitation does not apply to the upper cell, as excess CO_2 kept in AZ surface water would be able to escape from this surface water as it flows northward out of the region of dense sea ice cover.

3.2. Effects involving the lower latitude ocean

The Southern Ocean as a whole supplies nutrients to the lower latitude ocean, through equatorward transport into the SAZ and subduction of nutrient-rich water to intermediate depths, which includes the formation of both AAIW and SAMW (Fig. 1 a). Here, the distinct roles of the AZ and SAZ deserve our attention. The AZ (and more specifically, the Open Antarctic Zone, OAZ, equatorward of the Southern Antarctic Circumpolar Front) is upstream of the SAZ in the Southern Ocean's "upper" overturning cell, with water and nutrients upwelled in the AZ flowing northward into the SAZ surface.

This AZ nutrient supply fuels the production and export of both organic carbon and $CaCO_3$ in the SAZ. The SAZ, in turn, passes its unused nutrients to the lower latitudes mostly through the SAMW formation (Sarmiento et al., 2004). If nutrient consumption becomes more complete in either the AZ or the SAZ, and/or if the upper cell weakens, then there should be a downstream decrease in nutrient supply to the low latitude thermocline and thus the low latitude surface, reducing the low latitude production of organic matter and possibly also of $CaCO_3$.

In the case of increased nutrient consumption in the Southern Ocean, a CO_2 decrease in addition to that associated with the Southern Ocean alone is expected because of the decreased nutrient transport from the Southern Ocean to the lower latitudes (Keir, 1988). First, the change reduces the load of preformed nutrient in the mid-depth ocean by converting it into regenerated nutrient in the deep ocean, modestly enhancing long term CO_2 storage in the deep ocean and increasing the transient $CaCO_3$ dissolution event that is induced by this CO_2 storage. Second, reduced nutrient supply to the lower latitudes may reduce the $CaCO_3$ rain by restricting the $CaCO_3$-rich export production of the low latitudes. This would reduce the strength of the global carbonate pump and also decrease the rain of $CaCO_3$ to the seabed. Both of these $CaCO_3$-related changes would reduce atmospheric CO_2, the latter by causing a rise in global ocean alkalinity so as to deepen the steady-state lysocline (Sigman et al., 1998; Hain et al., 2010). The nutrient supply change could be caused by either the AZ or the SAZ. However, the SAZ is the final gateway to the vast low latitude ocean and thus has more direct control on low latitude effects.

4. Biogeochemical proxy evidence

4.1. Global and deep ocean evidence

Broecker (1982a,b) first proposed a stronger ocean biological pump as the cause of the lowering of atmospheric CO_2 during the last ice age. He considered three possible tests for this proposal. The first derives from the low $^{13}C/^{12}C$ ratio of the organic carbon that is produced by photosynthesis in the surface ocean and respired back to CO_2 in the deep ocean. During the ice age in comparison to today, the increased storage of respired CO_2 in the ocean interior should have resulted in a stronger carbon isotopic gradient between surface waters and the ocean interior. Second, due to the greater accumulated respiration required to generate that respired CO_2, the average oxygen (O_2) concentration of the ocean interior should have been lower. Third, with the deglacial transition to the Holocene, the escape of CO_2 from the ocean interior to the atmosphere should have caused a rise in the pH and thus the carbonate ion concentration of deep water. This should have resulted in a transient peak in deep sea $CaCO_3$ preservation and burial, which compensated for (i.e., reversed) the rise in deep ocean carbonate ion concentration. This transient $CaCO_3$ burial event, while serving as a useful indicator, would also have lowered ocean alkalinity from elevated glacial levels, thereby contributing to deglacial CO_2 rise (Broecker and Peng, 1987).

While each of these phenomena warrants its own discussion, a fair summary is that the biological pump hypothesis is supported by the data on each, although with caveats that call for further work (Shackleton, 1983; Yu et al., 2010; Jaccard and Galbraith, 2012). For the stable carbon isotopes, uncertainties include the potential for variation in the $^{13}C/^{12}C$ ratio of the organic carbon produced in surface waters and for air/sea disequilibrium in regions of deep water formation (Lynch-Stieglitz et al., 1995; Hofmann et al., 1999; Schmitt et al., 2012; Broecker and McGee, 2013; Schmittner et al., 2013; Khatiwala et al., 2019). The lower O_2 of the glacial ocean

interior is more conclusive evidence for ice age strengthening of the biological pump (François et al., 1997; Jaccard et al., 2009; Galbraith and Jaccard, 2015; Hoogakker et al., 2018; Anderson et al., 2019). The stronger nature of this constraint arises in large part from the fact that air/sea equilibration is faster for O_2 than for the carbon isotopes, which reduces the potential for changes in the "preformed" (initial) O_2 concentration of deep water (Stephens and Keeling, 2000). For deep ocean carbonate ion, a deglacial peak can be caused by a variety of processes that work to release CO_2 from the ocean interior upon deglaciation, so its interpretation in terms of biological pump change is non-unique (Broecker and Peng, 1987; Sigman et al., 1998).

It is important to note that these deep ocean signals do not inherently distinguish among mechanisms for strengthening the biological pump, for example, low latitude *versus* high latitude mechanisms. However, certain temporal and spatial features in the deep ocean during the last ice age point strongly to the Southern Ocean as the driver of the changes in the biological pump. The first finding in this regard was the very low $^{13}C/^{12}C$ of glacial-age Southern Ocean-sourced abyssal water (Curry and Oppo et al., 2005). More recent work has observed that, on a millennial time scale, deep ocean O_2 declined specifically when glacial Southern Ocean surface conditions changed in a way expected to lower atmospheric CO_2 (Jaccard et al., 2016). Moreover, deglacial changes in pH and carbonate ion concentration have been observed to vary among the different Southern Ocean-ventilated water masses in a way that is consistent with Southern Ocean-driven storage of CO_2 in the deep ocean during the Last Glacial Maximum (LGM) (Rae et al., 2018; Allen et al., 2020). Additional support has been found in deep ocean radiocarbon data for the LGM and subsequent deglaciation: it appears that the radiocarbon content of the deep ocean, relative to that of the atmosphere, was lower during the LGM and rose during the deglaciation with a timing consistent with Southern Ocean CO_2 release (e.g., Sikes et al., 2000; Marchitto et al., 2007; Rose et al., 2010; Skinner et al., 2010; Burke and Robinson, 2012; Zhao et al., 2018). However, there are major uncertainties in the significance of the radiocarbon data. Perhaps most importantly, the radiocarbon content of the modern Southern Ocean surface is not at equilibrium with the overlying atmosphere, such that a lower radiocarbon content in the deep ocean relative to the atmosphere during the LGM may have reflected either a reduction in surface-deep exchange or a reduction in the degree of equilibration at the sea surface (Hughen et al., 1998; Campin et al., 1999; Stephens and Keeling, 2000; Schmittner et al., 2003; Hain et al., 2011, 2014b; Galbraith and de Lavergne, 2019).

4.2. Southern Ocean surface nitrate and export production during the ice ages

Our focus going forward is on proxies of biogeochemical conditions in the Southern Ocean surface (Fig. 4). The $^{15}N/^{14}N$ ratio (hereafter, $\delta^{15}N$) of organic matter bound in the fossils of diatoms, planktonic foraminifera, and deep sea corals suggests more complete nitrate consumption (i.e., higher biological pump efficiency) in Southern Ocean surface waters during the ice ages and thus supports a key role for the Southern Ocean in ice age reductions in atmospheric CO_2 (Fig. 4 d, e, i, j; Martínez-García et al., 2014; Studer et al., 2015; Wang et al., 2017). For the AZ, this is qualitatively consistent with previous measurements of the $\delta^{15}N$ of bulk sediment, but it overturns the previous conclusion for the SAZ (François et al., 1997). The discrepant results for the SAZ are explicable in terms of changing diagenetic overprint on the bulk organic matter in the sediment that does not apply to the fossil-protected N (Martínez-García et al., 2014), and diagenesis may also have played a role in the bulk sedimentary $\delta^{15}N$ changes observed in the AZ
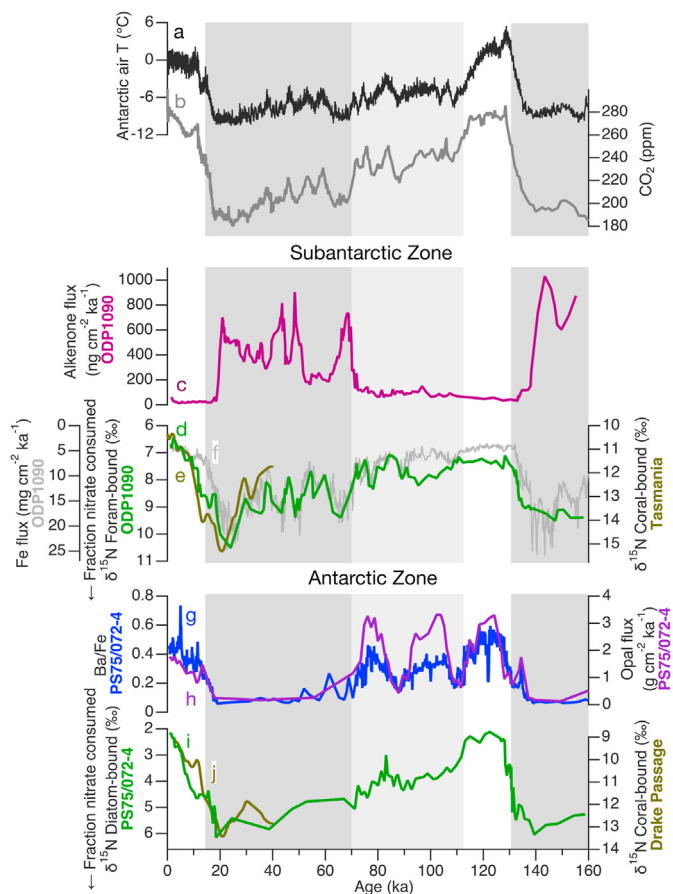
Fig. 4. Reconstructions of biogenic flux and fossil-bound nitrogen isotopic composition from the SAZ and AZ over the last full glacial cycle. The Antarctic air temperature reconstruction from EPICA Dome C ice deuterium is shown in black (a; Jouzel et al., 2007), and the atmospheric CO_2 reconstruction compiled from Antarctic ice cores is shown in gray (b; Lüthi et al., 2008). The dark gray background indicates the main glacial intervals MIS 6 and 2−4, the white indicates the full interglacial intervals (MIS 5e and 1), and the light gray indicates a period early in the development of the last ice age (MIS 5a-d). In the SAZ, ^{230}Th-normalized fluxes of alkenones (c, purple) and iron (f, light gray) and foraminifera-bound δ^{15}N (d, dark green) are from the Atlantic sector core ODP Site 1090 (Martínez-García et al., 2014). Plotted with the ODP Site 1090 foram-bound δ^{15}N is a compilation of deep sea coral-bound δ^{15}N from the SAZ south of Tasmania (e, olive; Wang et al., 2017). In the AZ, sediment barium-to-iron ratio (g, blue), ^{230}Th-normalized opal flux (h, purple), and pennate diatom-bound δ^{15}N (i, green) are from the Pacific sector core PS75/072-4 (Studer et al., 2015). Coral-bound δ^{15}N is also shown from the AZ in the Drake Passage (j, olive; Wang et al., 2017). Throughout, δ^{15}N is in permil, referenced to air N_2. In the SAZ, both biogenic flux and δ^{15}N are higher in glacial stages, suggesting higher export production and more complete nitrate consumption in response to higher dust-borne iron fluxes to the SAZ, supporting the iron fertilization hypothesis first proposed by John Martin. In the AZ, biogenic flux is lower in the glacial stages than interglacial stages, suggesting lower export production, while δ^{15}N is higher in glacial stages, suggesting a higher degree of nitrate consumption. The combined changes in these two parameters indicate a reduction in gross nitrate supply to the surface mixed layer during glacial stages.

(Studer, 2013). Regardless, the combined fossil-bound organic matter δ^{15}N changes from the AZ and SAZ provide a compelling picture of Southern Ocean-wide nitrate drawdown during the ice ages (Wang et al., 2017, and references therein). An important caveat is that there are as yet no data from near the Antarctic continent, where AABW forms.

In the AZ, the rise in the completeness of nitrate consumption coincides with proxy evidence for a lower rate of export production (the production and subsequent sinking of organic matter out of the surface ocean; Fig. 4 g, h; Mortlock et al., 1991; Kumar et al.,

1993; François et al., 1997; Jaccard et al., 2013). These two changes together point to lower gross nitrate supply to the surface and thus an apparent ice age reduction in the exchange of water between the surface and the underlying ocean (here termed AZ "surface isolation") (François et al., 1997). Because AZ surface isolation would have reduced the supplies of both nitrate and iron to this iron-limited environment, productivity should have declined, as observed (Lefèvre and Watson, 1999; Studer et al., 2015). However, it is expected that productivity would have declined less than the nitrate supply, due to other routes of iron supply to the AZ surface (Boyd et al., 2012) and the potential for intensive iron recycling (Rafter et al., 2017). If so, the degree of nitrate consumption should have risen, as the data indicate (Studer et al., 2015). Recent support for AZ surface isolation comes from evidence for a strong surface-to-deep water δ^{18}O gradient in the AZ during the glacial maxima of the late Pleistocene (Hasenfratz et al., 2019).

In the SAZ, north of the AZ, more complete nitrate consumption coincided with higher export production as well as increased dust flux to the ocean (Fig. 4 c, d, e, f; Martínez-García et al., 2014, and references therein). These data argue for dust-borne iron fertilization of the SAZ, enhancing export production and thus leading to more complete nitrate consumption in this zone as well. With this combination of AZ and SAZ physical and biological changes (Jaccard et al., 2013), if supported by ocean cooling and not undercut by an unexpectedly large terrestrial biosphere reduction, the full (~90 ppm) ice age CO_2 decline is achievable (Fig. 2; Hain et al., 2010).

4.3. Timing of changes: Antarctic Zone vs. Subantarctic Zone

Evidence points to AZ changes as important in initiating the decline in atmospheric CO_2 going into ice ages (Jaccard et al., 2013; Studer et al., 2015), such as the 30−40 ppm CO_2 decline at ~110 ka early in the last glacial cycle (Fig. 4 b, i). In contrast, SAZ iron fertilization became an important player only during the latter part of the last ice age (Kohfeld et al., 2005; Martínez-García et al., 2014; Kohfeld and Chase, 2017), potentially explaining the 30−40 ppm CO_2 decline at 60−70 ka (Fig. 4 b, c, d, e, f). The SAZ represents the "final stop" of Southern Ocean surface waters before they are subducted into the shallow arm of the upper cell. Thus, for AZ and SAZ mechanisms for lowering atmospheric CO_2 to be fully complementary, the AZ mechanism must involve the lower cell, which the SAZ does not directly affect. Following the logic above (section 3.1), there are two options for the ice age AZ to contribute uniquely to lower atmospheric CO_2: (i) the AZ-sourced lower cell must have ventilated less of the interior (i.e., AZ ventilation of the deep ocean slowed, surrendering this process to the North Atlantic; e.g., Kwon et al., 2012), and/or (2) the preformed nutrient concentration in the lower cell waters must have declined (i.e., the burden of unused nutrients in the AZ surface must have declined). As summarized above, there is evidence for distinct timings of AZ and SAZ biogeochemical changes during the ice ages (Kohfeld et al., 2005; Jaccard et al., 2013; Martínez-García et al., 2014; Studer et al., 2015). However, given that the SAZ is downstream of the AZ in the circulation of the upper cell, it has been puzzling that AZ changes during the last ice age had no clear effect on the productivity or nutrient status of the SAZ (Martínez-García et al., 2014). We will revisit this point in section 9.2.

5. Physical and biological mechanisms for Southern Ocean-driven reduction in atmospheric CO_2

Why would the Southern Ocean have undergone these changes?

While the evidence for iron fertilization in the ice age SAZ is remarkable, it fits with our understanding of ocean processes as gleaned from modern field studies and experiments (Boyd et al., 2010). Indeed, John Martin originally proposed it based on modern ocean and culture studies, given the evidence from Antarctic ice cores for increased atmospheric dust loads during the ice ages (Martin, 1990). In contrast, a reduction in AZ subsurface/surface exchange (i.e. the reconstructed AZ "surface isolation") is unexpected at a mechanistic level, and it is not broadly accepted across oceanography and climate science.

Skepticism within the paleoceanographic community derives in part from the decades-long effort to map changes in the water mass structure of the ocean interior. One of the central paleoceanographic interpretations of data from the ice age Atlantic is that southern hemisphere-sourced water was more volumetrically dominant, occupying the depths below 2.5 km in most of the basin (Rutberg et al., 2000; Lynch-Stieglitz et al., 2007). For decades, this was almost universally accepted as corresponding to more vigorous deep water formation in the AZ, and much of the community still holds this view. Subsequently, it was found that this abyssal volume (and abyssal water in other basins) was very slowly ventilated with respect to atmospheric radiocarbon (Sikes et al., 2000; Keigwin, 2004), consistent with slow formation of deep waters that nevertheless were adequately dense to occupy most the deep Atlantic. Very slow ventilation in the AZ may mean that the last true ventilation of the reconstructed southern-sourced abyssal volume occurred in the North Atlantic (Hain et al., 2010). In this scenario, North Atlantic-ventilated water was transported at intermediate depths into the Southern Ocean. Rather than being vigorously ventilated there, it entrained only a small volume of very slowly forming Antarctic Bottom Water, with the resulting mixture being adequately dense to sink deeper in the water column and spread throughout the global abyssal ocean (Kwon et al., 2012). This view appears to be consistent with Neodymium isotope data, which suggest that North Atlantic-sourced water was a significant contributor to the filling of the abyssal Atlantic (Howe et al., 2016). Benthic foraminiferal carbon isotope data have been interpreted to argue against such a situation (e.g., Sikes et al., 2017); however, the carbon isotopes may be influenced by remineralization and air/sea gas exchange. Nevertheless, given the evidence for a large, coherent, mostly southern-sourced abyssal volume during the last ice age (Lynch-Stieglitz et al., 2007), it is fair to be skeptical of the proposal of slower AZ ventilation of the interior. Moreover, modern AZ surface waters are radiocarbon-poor due to the slow rate of air/sea gas exchange, so the low radiocarbon content of the glacial abyssal ocean, by itself, does not require slower overturning through the AZ surface (Campin et al., 1999; Schmittner et al., 2003; Galbraith and de Lavergne, 2019).

Another important cause for skepticism of ice age AZ surface isolation is a lack of support from climate models and other numerical models of ocean circulation. In models run to steady state under LGM background conditions as part of the Paleoclimate Modelling Intercomparison Project, the response among at least a subset of the models is for AZ overturning to be enhanced (Otto-Bleisner et al., 2007; Wainer et al., 2012). This appears to be largely a consequence of enhanced sea ice formation, which densifies AZ surface waters due to brine rejection. Similar behavior has also been observed in other model simulations with the sole background change of lower atmospheric CO_2 concentration (Stouffer and Manabe, 2003) or with a broader range of prescribed changes (Jansen, 2017; Galbraith and de Lavergne, 2019). This has been interpreted as consistent with model simulations of ongoing global warming; in these simulation, polar ocean overturning tends to decline (Sarmiento et al., 1998), due in part to a rise in the precipitation excess relative to evaporation at high latitudes.

Numerical model simulations have been used to explore the hypothesis of AZ surface isolation during the ice ages (Toggweiler et al., 2006; Tschumi et al., 2008; Menviel et al., 2018); however, these studies rely on purposefully imposed changes in the winds or in freshwater discharge from the Antarctic continent. To our knowledge, AZ surface isolation has never occurred spontaneously in a climate model under ice age boundary conditions.

If physical models do not produce AZ surface isolation, the question arises: What mechanism do models offer to explain the lower CO_2 of ice ages? Reduced sea-to-air CO_2 release due to sea ice cover occurs in at least some model simulations (Ferreira et al., 2018; Marzocchi et al., 2019). Nevertheless, the plausibility of this explanation remains unclear (Kurahashi-Nakamura et al., 2007; Sun and Matsumoto, 2010). Among other factors, it depends on the sensitivity of gas exchange rate to sea ice cover (e.g., Loose and Schlosser, 2011). With regard to paleoceanographic observations, one issue with the hypothesis of sea ice-driven gas exchange limitation is that wintertime sea ice formation and associated deep mixing would increase gross nitrate supply to the surface, whereas the nitrogen isotope and export production proxy data suggest a reduction in gross nitrate supply. There are two possible solutions to this apparent discrepancy. First, the AZ summer mixed layer may have been much shallower during ice ages, perhaps due to summertime sea ice melt, allowing a higher degree of nitrate consumption to coincide with a reduction in area-normalized export production (Keeling and Visbeck, 2001). Simulation of such mixed layer shoaling suggests that it alone cannot quantitatively explain the paleoproxy data (Kemeny et al., 2018), but it cannot be precluded. Second, the AZ core sites studied so far may have "missed" the regions that hosted intense sea ice formation and deep ocean ventilation during the ice ages. Instead, the upper water columns of studied sites may have been stabilized by receiving sea ice and associated fresh water from the regions of sea ice formation and overturning (see Sigman and Haug, 2003, their Figure 9). However, there is a lack of evidence for these alternatives. Accordingly, we seek a plausible ocean circulation (as opposed to gas exchange) mechanism by which the AZ surface waters reduced their leakage of CO_2 to the atmosphere during the ice ages.

5.1. Hypotheses for Antarctic Zone "surface isolation"

A number of proposals exist for the cause of AZ surface isolation during ice ages. One category involves the conditions of the Southern Ocean upper water column (sections 5.1.1., 5.1.2, and 5.1.3), while another category involves the deep ocean (sections 5.1.4 and 5.1.5).

5.1.1. Decreased wind-driven upwelling

Perhaps the best-known hypothesis is that a northward shift and/or weakening of the Southern hemisphere westerly winds during ice ages reduced Ekman upwelling in the AZ and that this in turn led to decreased ventilation of the deep Southern Ocean (Toggweiler et al., 1999, 2006; Sigman and Boyle, 2000). This change would have slowed the nitrate supply to the AZ surface, consistent with the paleobiogeochemical evidence.

In the modern ocean, AZ upwelling and the associated Southern Ocean upper cell is linked in the global circulation to NADW formation (Fig. 1 a) (Toggweiler and Samuels, 1995; Marshall and Speer, 2012). NADW formation transfers into the ocean interior water that has been stripped of nutrients as it passed through low latitudes, with these nutrients being returned to the ocean in the low latitudes as sinking organic matter, storing respired CO_2 in the ocean interior (Fig. 3a). Thus, if weaker Ekman upwelling in the AZ during ice ages also weakened NADW formation, this would work to reduce the efficiency of the global ocean's biological pump. This

change would tend to raise − not lower − atmospheric CO_2. Thus, in order to substantially lower atmospheric CO_2, the weakening of the upper cell must also lead to the weakening of the lower cell, which is today responsible for much of the inefficiency in the global ocean's biological pump (section 3.1). Mechanisms by which weaker wind-driven upwelling (a weakening of the upper cell) may have reduced either the preformed nutrient content in the lower cell or the degree of ventilation of the ocean interior by the lower cell are discussed in section 8 to 9. Here, we should specifically note the mechanism that arose in Toggweiler et al. (2006): with a longer residence time for AZ surface waters, a stronger halocline developed, impeding deep water formation (see also De Boer et al., 2008).

5.1.2. Sea ice effects

Both models and data suggest that the polar ocean experienced more extensive sea ice during the ice ages, especially with regard to wintertime coverage (Gersonde et al., 2005; Otto-Bleisner et al., 2007). These findings of more extensive sea ice and a more active sea ice cycle have led to hypotheses for the cause of glacial/interglacial CO_2 change (e.g., the gas exchange limitation hypothesis of Stephens and Keeling, 2000, section 3.1).

A hypothesis more related to the evidence for AZ surface isolation was put forward by Bouttes et al. (2010), referred to here as the "brine export" hypothesis. The growth of the Antarctic ice sheet and the lowering of sea level would likely have reduced the areas of the Antarctic continental shelves. This has been proposed to shift the intense sea ice formation from shallow shelves today to deep waters during the ice ages (Paillard and Parrenin, 2004). Bouttes et al. (2010) proposed that, during the ice ages, this caused the efficient export of a more pure (undiluted) brine into the deep ocean. If so, this would have freshened the AZ even in the regions of net sea ice formation, enhancing the salinity-driven density stratification, and thus slowing the ventilation of the deep ocean by the AZ.

The brine export hypothesis is challenged by the lack of a modern analogue. The brines generated from sea ice today are observed to entrain mixed layer water, such that modern sea ice formation can export salt to the deep ocean only if the bulk surface mixed layer water of a given region becomes adequately dense to sink, leading to ventilation of the ocean interior (Grimm et al., 2016; Ohshima et al., 2013; Shcherbina et al., 2003). Nevertheless, the hypothesis warrants inclusion in our list of proposed mechanisms.

5.1.3. Effects of a more expansive Antarctic Zone

Ferrari et al. (2014) and Watson et al. (2015) developed scenarios for the glacial ocean that focus on the areal extent of the region of buoyancy loss in the glacial AZ (essentially the PAZ). Ferrari et al. (2014) propose that the northward expansion of Antarctic sea ice caused or heralded a similar expansion in the AZ region of buoyancy loss. For a given overturning rate for the Southern Ocean's lower cell, this would have increased the residence time of water in the AZ surface between ascending from depth and sinking back into the interior (Ferrari et al., 2014; Watson et al., 2015). With this longer residence time of water at the surface, similar or even reduced biological productivity could have led to more complete nitrate consumption. Moreover, it would imply a slower removal of buoyancy of the AZ surface and thus slower deep water formation near the Antarctic margin (Watson et al., 2015). Moreover, we note here that a longer residence time of surface waters in the AZ may have allowed the AZ halocline to strengthen, further slowing deep water formation. This effect on the halocline was introduced above as a potential consequence of a decline in wind-driven upwelling (section 5.1.1).

A complementary mechanism focused on the Southern Ocean's

upper cell is that the westerly winds and Southern Ocean fronts shifted equatorward during the ice ages, increasing the area of the entire AZ, not solely the region of buoyancy loss (e.g., Lawrence et al., 2013). If such a change occurred, the upwelling would have become more remote from the PAZ, also increasing the residence time of PAZ surface waters. Once again, this would have slowed the per-area nutrient supply and may have allowed the PAZ halocline to strengthen, reducing the tendency for deep ventilation by the region.

5.1.4. Reduced abyssal mixing

Another hypothesis is of a glacial decline in abyssal mixing due to the shoaling of the upper branch of the lower cell away from bathymetric features, which in effect reduces the demand for new deep water to form in the AZ (Watson and Naveira Garabato, 2006; Lund et al., 2011; Ferrari et al., 2014; De Boer and Hogg, 2014). Deep ocean mixing decreases the density of deep waters and thus encourages new deep water formation. Studies of this mixing suggest that it is particularly intense over rough seafloor topography (Wunsch and Ferrari, 2004). The contact between NADW and AABW in the modern ocean is adequately deep for mixing over the Atlantic seafloor to efficiently mix the two water masses. One of the most well-known findings from the ice age ocean is that there was a ~1 km shoaling of the contact zone between North Atlantic sourced deep water (above) and southern sourced deep water (below) (Lynch-Stieglitz et al., 2007). Shoaling this contact during ice ages may have allowed the seafloor-induced mixing to occur entirely within southern sourced abyssal water (i.e., AABW), dramatically slowing the rate of buoyancy gain in this water. Accordingly, the draw for new AABW would have been reduced.

Atmospheric CO_2 declined roughly halfway to LGM levels early in the progression of the last ice age, at 110-115 ka, and it was approximately at this time that Antarctic air temperature fell and that AZ diatom-bound $\delta^{15}N$ shows a clear rise (Fig. 4 a, b, i). All of these observations suggest that AZ surface isolation and the associated reduction in deep ocean ventilation began at ~115 ka. In contrast, the shoaling of the NADW/AABW contact apparently did not become a persistent glacial feature until ~70 ka, at the marine isotope stage (MIS) 5/4 boundary (Piotrowski et al., 2005). Thus, there are some signs of a temporal mismatch between the predictions of the hypothesis and observations. However, not all versions of this hypothesis focus on the NADW/AABW contact as the critical parameter in affecting deep mixing (Watson and Garabato, 2006).

5.1.5. Effect of homogenous cooling on the ocean's density structure

In the AZ, wintertime temperatures are lowest at the surface, encouraging vertical mixing and, in the extreme cases, deep water formation. However, the halocline works against temperature's drive for overturning.

A proposal for AZ surface isolation during ice ages involves the lower sensitivity of density to temperature at low temperatures, referred to here as the "equation of state" (or "EOS") mechanism (Sigman et al., 2004; DeBoer et al., 2007). In the EOS mechanism, global ocean cooling reduces the effect of temperature on polar ocean density structure, effectively increasing the leverage of the low salinity of the AZ upper ocean to strengthen density stratification. In the case of a homogenously colder water column, the decrease in temperature from deep water into the polar ocean surface causes a weaker density increase from deep to surface. In contrast, the shift toward a colder water column does not cause a significant change in the effect of surface water freshness to lower its density relative to deep waters. In net, under homogenous cooling, the surface waters become less dense relative to deep waters. This discourages wintertime vertical mixing and deep

water formation. Once this decline in surface/deep exchange has been initiated, the longer residence time of surface waters may allow the halocline to strengthen, further strengthening the density stratification.

6. The subarctic North Pacific as a point of comparison

The modern SNP has significant similarities with the AZ. Within their upper water columns, the depth profiles of temperature, salinity, density, and nutrients, as well as their seasonality, are remarkably similar, especially when comparing the AZ to the western SNP and Bering Sea (Talley et al., 2011). Both regions host Ekman-(i.e., westerly wind driven-)upwelling of nutrient-rich subsurface waters, which leads to nutrient-richness at the surface (Gargett, 1991). In both regions, iron limitation prevents complete consumption of the major nutrient supply to the surface mixed layer (de Baar et al., 2005).

At the same time, the two regions do have important differences. The SNP lacks the deep circumpolar channel that characterizes the Southern Ocean and that allows the Ekman upwelling to draw large quantities of deep, dense, nutrient-rich water to the surface. Rather, the nutrient richness of the SNP upper water column appears to depend partly on diffusion-driven upwelling at the base of the pycnocline, which is enhanced by turbulence near steep bathymetric features (Fig. 1 a) (Nishioka et al., 2020). Ekman upwelling then conveys the nutrient-rich intermediate water to the surface. Perhaps the most fundamental distinction is that the SNP currently does not ventilate the deep ocean at significant rates (Warren et al., 1983). In this regard, the SNP possesses an analogue to the Southern Ocean's "upper cell" but lacks a clear analogue to the Southern Ocean's "lower cell."

As described below, the AZ and SNP also have notable similarities in their paleobiogeochemical records of glacial/interglacial cycles. In the context of the search for a mechanism for AZ surface isolation, we consider here the possibility that a single mechanism explains the observations from both regions. This would provide a possible basis, albeit a tentative one, for favoring one mechanism over others.

6.1. Glacial/interglacial changes

During the late Pleistocene ice ages, as with the AZ, the SNP was characterized by reduced export production as indicated by low burial fluxes of biogenic components (e.g., Jaccard et al., 2005) and by a high degree of surface nitrate consumption as indicated by nitrogen isotopic data (Brunelle et al., 2007, 2010; Galbraith et al., 2008; Ren et al., 2015; Worne et al., 2019) (Fig. 5). Looking further back in time, the onset of major ice age cycles ~2.7 million years ago coincided with a sharp drop in export production in both the SNP and the AZ (Haug et al., 1999; Sigman et al., 2004), and SNP nitrogen isotope studies have found that this was also accompanied by an increase in surface nitrate consumption (Studer et al., 2012). As for the AZ, these coupled changes have been interpreted to reflect a reduced supply of nitrate into the sunlit surface layer of the SNP under cold conditions. This may have been due to a reduction in surface/subsurface exchange (Jaccard et al., 2005; Brunelle et al., 2007, 2010; Galbraith et al., 2008; Ren et al., 2015) and/or a decline in subsurface nutrient concentration (Gray et al., 2018). Given the evidence for the similarity of glacial/interglacial change in the AZ and SNP, in our view, the default starting hypothesis should be of the same basic mechanism of change in the two regions (Haug and Sigman, 2009).
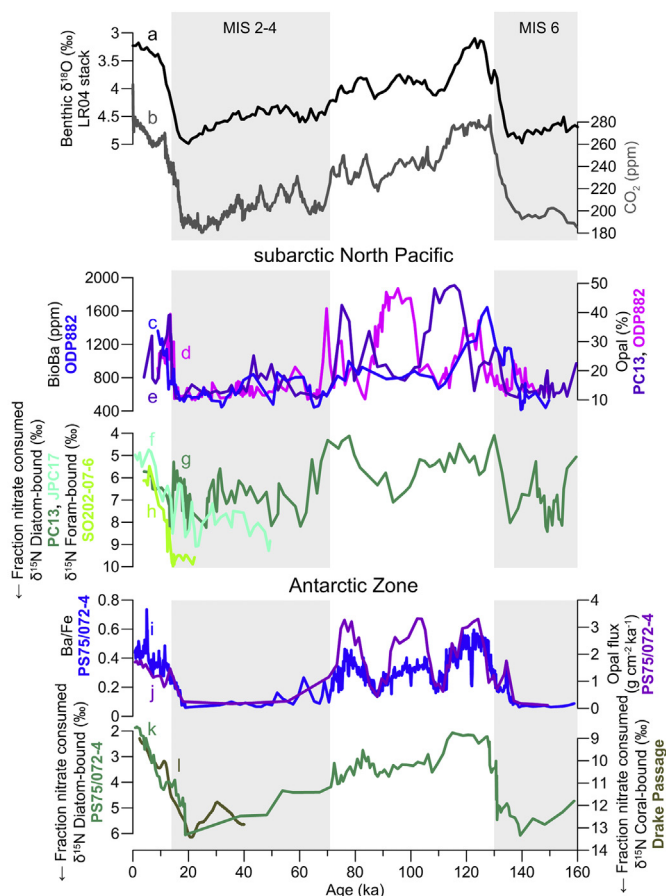
Fig. 5. Comparison of reconstructions of biogenic flux and fossil-bound nitrogen isotopic composition from the AZ and western SNP, which argue for reduced nitrate supply in both regions during ice ages. The benthic foraminifera $\delta^{18}O$ stack of Lisiecki and Raymo (2005) is shown in black, and the atmospheric CO_2 reconstruction compiled from Antarctic ice cores is shown in gray (Lüthi et al., 2008). The gray background indicates the main glacial intervals MIS 6 and 2−4, and the white indicates the predominantly interglacial intervals MIS 5 and 1. In the AZ, ^{230}Th-normalized opal accumulation and barium-to-iron ratio (purple and blue) and pennate diatom-bound $\delta^{15}N$ (dark green) are from Pacific sector core PS75/072-4 (Studer et al., 2015). Plotted with the diatom-bound $\delta^{15}N$ is a compilation of deep sea coral-bound $\delta^{15}N$ from the AZ in the Drake Passage (olive; Wang et al., 2017). In the western SNP, biogenic barium concentration (blue) is from ODP Site 882, biogenic opal concentration records are from ODP Site 882 and Roundabout PC13 (pink and purple), diatom-bound $\delta^{15}N$ (dark green) is from PC13, and foraminifera-bound $\delta^{15}N$ (grass green) is from INOPEX core SO202-07-6 (Jaccard et al., 2005; Brunelle et al., 2010; Ren et al., 2015). Diatom-bound $\delta^{15}N$ is also shown from *Healy*-0202 JPC17 in the central Bering Sea back to 50 ka (aqua) (Brunelle et al., 2007). In both regions, biogenic fluxes are lower in glacial stages than interglacial stages, while $\delta^{15}N$ is higher in glacial stages, the former suggesting lower export production and the latter suggesting a higher degree of nitrate consumption. Following the arguments of François et al. (1997), the combined changes in these two parameters require a reduction in gross nitrate supply to the surface mixed layer during glacial stages. Both SNP diatom-bound $\delta^{15}N$ records show a local minimum during Heinrich Stadial 1 (HS1) at the end of MIS 2; this minimum does not occur in foraminifera-bound $\delta^{15}N$ (Ren et al., 2015; see Fig. 6) and appears to be an artifact deriving from sponge spicules due to the very low abundance of diatom opal in this depth interval of the western SNP sediment cores (Studer et al., 2013).

6.2. Deglacial changes

In contrast to the similarity of the glacial/interglacial changes in the AZ and SNP, the two regions have an important distinction in the timing of changes at the last deglaciation (Fig. 6). At the end of the last ice age, the most rapid Antarctic warming began at ~18 ka, and atmospheric CO_2 began to rise at approximately the same time. The first rise in AZ opal flux and decline in diatom-bound $\delta^{15}N$ had
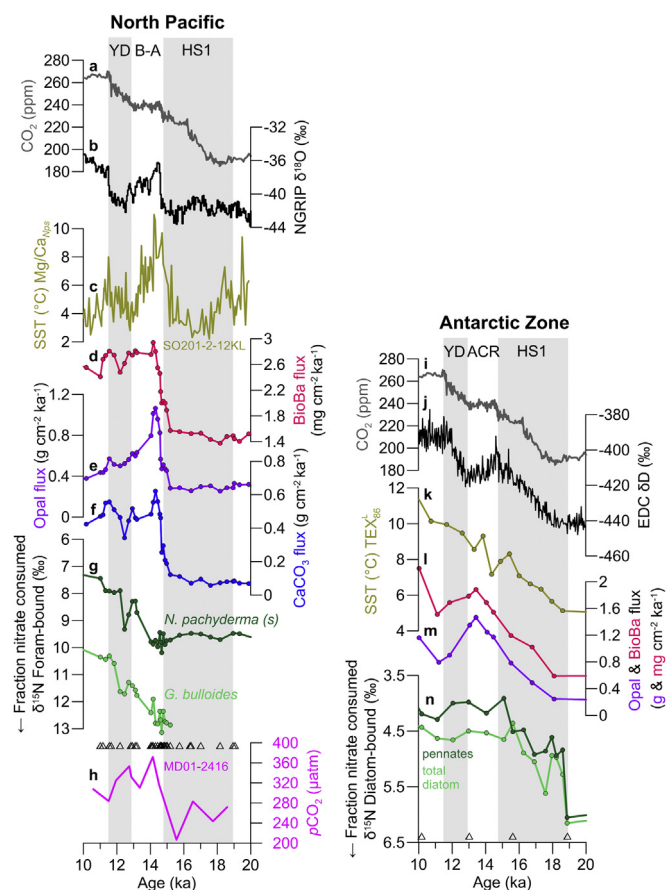
Fig. 6. Comparison of reconstructions of biogenic flux and diatom- or foraminifera-bound nitrogen isotopic composition from the AZ and western SNP across the last glacial termination (i.e., the last deglaciation). In the AZ (right), ^{230}Th-normalized opal and biogenic barium accumulation (purple and pink), pennate and total diatom-bound δ^{15}N (dark and light green), and TEX$_{86}^L$-based sea surface temperature (bronze) are from the same Pacific sector core (PS75/072-4) as shown in Figs. 4 and 5. In the western SNP (left), ^{230}Th-normalized fluxes of biogenic barium (pink), biogenic opal (purple), and CaCO$_3$ (blue) and the δ^{15}N of foraminifera-bound N (*N. pachyderma* (s) in dark green, *G. bulloides* in light green) are from core SO202-07-6 (Ren et al., 2015); Mg/Ca-based sea surface temperature (bronze) is from core SO-201-2-12KL (Riethdorf et al., 2013); and boron isotope-based surface water pCO$_2$ (pink) is from core MD01-2416 (Gray et al., 2018). The ice δ^{18}O record from Greenland ice core NGRIP and the ice δD record from Antarctic ice core EPICA Dome C are shown in black on the left and right, reflecting northern and southern hemisphere high latitude air temperature (NGRIP Community Members, 2004; Jouzel et al., 2007). The gray background indicates northern hemisphere cold phases first identified in the circum-North Atlantic (Heinrich Stadial 1 (HS1) and the Younger Dryas (YD)), and the white indicates warmer northern hemisphere intervals (the Bolling-Allerod (B–A), also indicated as the Antarctic Cold Reversal (ACR), and the post-Younger Dryas). Triangles indicate age control points for SO202-07-6 (left) and PS75/072-4 (right) (Studer et al., 2015; Ren et al., 2015). The SO202-07-6 age model is well-resolved (Serno et al., 2015; Ren et al., 2015) and clearly indicates that the deglacial increase in surface/subsurface exchange in the SNP does not occur until the B-A. The SNP δ^{15}N decline may have been delayed by subsurface nitrate δ^{15}N changes during the B-A (Ren et al., 2015), such that SNP nitrate consumption may have fallen earlier in the B-A than is suggested by the timing of the δ^{15}N decline. While the age model at AZ core PS75/072-4 derives largely from planktonic δ^{18}O (Studer et al., 2015) and is less certain, the first rise in TEX$_{86}$L-based sea surface temperature in the core, when aligned with the warming reflected in Antarctic ice core δD, indicates that the AZ biogeochemical changes began during HS1 and not during the B-A, and this is consistent with other studies (Anderson et al., 2009; Jaccard et al., 2013).

similar timing (Fig. 6) (Anderson et al., 2009; Studer et al., 2015). These data point to an increase in the supply rate of nitrate to AZ surface waters that began at a similar time as the rises in atmospheric CO$_2$ and Antarctic air temperature. This suggests a role for AZ surface/deep water exchange in the deglacial CO$_2$ rise.

These first deglacial Antarctic changes approximately coincide with the Heinrich Stadial 1 (HS1) in the North Atlantic (Anderson et al., 2009). This event is characterized by circum-North-Atlantic cooling, debris-bearing icebergs, freshening of polar North Atlantic surface waters, and a dramatic reduction in North Atlantic subsurface water formation (Hemming, 2004; McManus et al., 2004). The possible mechanistic connections between the North Atlantic and Antarctic through this deglacial sequence have received much consideration, with proposals for both atmospheric and deep ocean pathways by which the North Atlantic changes could drive an increase in AZ overturning (Crowley, 1992; Broecker, 1998; Lamy et al., 2007; Marchitto et al., 2007; Schmittner et al., 2007; Sigman et al., 2007; Schmittner and Galbraith, 2008; Toggweiler, 2009; Anderson et al., 2009; Barker et al., 2009; Denton et al., 2010; Meckler et al., 2013).

With regard to these millennial time scale deglacial changes, the SNP alternated with the AZ. The first major Antarctic warming occurs at HS1, when the SNP remains cold. The SNP undergoes its first major warming coincident with the Bolling-Allerod (B-A) warm interval of the circum-North Atlantic (Praetorius and Mix, 2014), when warming pauses or reverses in Antarctica. Similarly, while the AZ shifts toward Holocene biogeochemical conditions at HS1, in the SNP, opal flux declines weakly from already very low LGM levels into HS1, and foraminifera-bound δ^{15}N shows no sign of a change from glacial values (Ren et al., 2015). The SNP undergoes its first major surface biogeochemical change at the B-A (Galbraith et al., 2007), when the combined biogenic flux and foraminifera-bound δ^{15}N data indicate an increase in nitrate supply to the SNP surface (Fig. 6 d, e, f, g). Apparently coincident with this, surface pCO$_2$ rises, consistent with more rapid supply of regenerated nutrients and carbon from the ocean interior (Fig. 6 h; Gray et al., 2018). In summary, in the AZ and SNP, nitrate supply to the surface appears to rise upon warming in that region and/or its hemisphere.

Taking these deglacial observations together with those for the larger scale glacial/interglacial changes in both regions, a simple coupling is suggested between regional climate and nitrate supply from below, with reduced circulation-driven nitrate supply under a climate that is colder on a regional basis. That is, the control on nitrate supply in the AZ and SNP appears to be *regional* – not global – climate. One caveat to this interpretation is that deglacial enhancement of AZ overturning might not have been a response to its own regional climate; hypotheses exist for a trigger from declining North Atlantic overturning through the ocean interior (Broecker, 1998; Schmittner et al., 2007; Sigman et al., 2007; Schmittner and Galbraith, 2008; Meckler et al., 2013). However, the SNP experienced enhanced nitrate supply at the same times that NADW formation strengthened (McManus et al., 2004), such that compensatory behavior in the North Atlantic and SNP does not help to explain the deglacial timing of SNP changes. To explain the SNP changes, it appears that one must look to the SNP region.

6.3. Comparison of the Antarctic Zone mechanisms with subarctic North Pacific changes

Based on the discussion above, hypothesized explanations for the reconstructed changes in subsurface-to-surface nutrient supply in the AZ and SNP can be evaluated on their potential to explain two observations (Table 1). The first is the similarity of glacial/interglacial changes in the AZ and SNP; specifically, subsurface-to-surface nutrient supply in both regions appears to decline strongly during the ice ages. The second is the millennial-scale evidence for distinct timings of deglacial change in the two regions. This evidence from the last deglaciation suggests that the rate of subsurface-to-surface nutrient supply increased when

Table 1
Agreement of proposed "surface isolation" mechanisms with two observations.

mechanism	Glacial "surface isolation" in both AZ and SNP[f]	Millenial synchroneity of deglacial end to "surface isolation"
westerly winds[a]	**Yes**	**No**
abyssal mixing[b]	No	Yes
equation of state[c]	Yes?[g]	No[h]
brine export[d]	Yes?	Yes
expanded region of buoyancy loss[e]	No	No
Observations	**Yes**	**No**

[a] Toggweiler et al. (2006); Toggweiler (2009).
[b] Watson and Naveira Garabato (2006); Lund et al. (2011); Ferrari et al. (2014); De Boer and Hogg (2014).
[c] Sigman et al. (2004); De Boer et al. (2007, 2008).
[d] Bouttes et al. (2010).
[e] Ferrari et al. (2014); Watson et al. (2015).
[f] AZ, Antarctic Zone; SNP, western subarctic North Pacific.
[g] ? indicates points of greatest uncertainty (see text).
[h] EOS mechanism would strengthen surface isolation during a deglacial warming, opposite to observations.

deglacial warming began in each region's respective hemisphere. We now revisit the proposed mechanisms for ice age AZ isolation discussed above (section 5.1), assessing their consistency with these two observations.

6.3.1. Glacial/interglacial changes

Given the lack of deep water formation in the modern SNP, the similarity of the glacial/interglacial paleoproxy changes between the AZ and SNP (Fig. 5) cannot reflect an ice age reduction in deep ocean ventilation by each region. This argues against mechanisms that are driven from the deep ocean or strictly involve deep water formation. The hypothesis of reduced abyssal mixing falls into this category.

On an annual basis, density-driven wintertime deep mixing is critical for importing nutrients to the mixed layer. However, without upwelling to restore the nutrient content of the upper water column with nutrients (ultimately from deep water), summertime nutrient consumption and wintertime mixing would eventually deplete the upper water column of its nutrients. Conversely, a reduction in wintertime mixing depth alone might not greatly reduce the annual nutrient supply, as the upwelling would raise high-nutrient deep water to the base of the euphotic zone. This argument suggests that the observed ice age reduction in nutrient supply to the AZ and SNP is better explained by a reduction in upwelling than by a reduction in upper ocean vertical mixing. However, nutrient supply is a physically complex process, and so, for the time-being, we allow that either change could be consistent with the data (Table 1). For example, the "brine export" and EOS hypotheses, if they acted in the SNP, would have reduced vertical mixing in the upper water column, which may have slowed the nutrient supply to the surface.

The proposal of an expansion of the area of buoyancy loss in the PAZ is focused on the flow associated with the Southern Ocean's lower cell (Ferrari et al., 2014; Watson et al., 2015), which has no analogue in the SNP (Table 1). However, an expansion of the AZ and SNP as a whole, for example, as a result of equatorward migration of the westerlies (e.g., Lawrence et al., 2013), would have slowed the per-area nutrient supply associated with the wind-driven upwelling in both regions. Thus, a scenario of zone expansion may have contributed to the observed changes in both the AZ and SNP over glacial cycles. Parenthetically, models and data appear consistent with an expansion of the SNP under glacial conditions. Climate models consistently predict an equatorward shift in the westerly winds in the North Pacific (Wang et al., 2018), and planktonic foraminifera oxygen isotope data are consistent with an equatorward expansion of the North Pacific subpolar gyre (Gray et al., 2020).

6.3.2. Deglacial changes

The timing of deglacial biogeochemical change in the AZ and SNP provides a complementary criterion for evaluating the underlying physical mechanism of AZ surface isolation during the ice ages. Specifically, the distinct timings of the deglacial increase in gross nutrient supply in the AZ and the SNP argue against any driver that would have the same timing in the two hemispheres.

The "brine export" hypothesis is based on ice age sea level lowering, which shifts sea ice formation off the Antarctic shelf (Bouttes et al., 2010). Given the largely global nature of deglacial sea level rise, the distinct timings of AZ and SNP deglacial changes (Fig. 6) appear inconsistent with this mechanism operating on the margins of both the AZ and the SNP and driving the observed paleobiogeochemical changes (Table 1).

The asynchrony of the AZ and SNP deglacial changes also argue against mechanisms operating through the ocean interior. Thus, a glacial reduction in abyssal mixing and the effect of deep ocean cooling on the temperature sensitivity of seawater density (the EOS hypothesis) are not supported as the triggers of the deglacial loss of AZ isolation (Table 1). One caveat is that it may take substantial time for a signal to propagate through the ocean interior. However, the ~3 kyr difference between AZ and SNP changes (Fig. 6) appears too great to be explained by a circulation-associated delay in the SNP. Finally, the EOS mechanism would also be influenced by region-specific surface water temperature changes. However, deglacial surface warming would have increased surface isolation in a given region, the opposite of the observations (Table 1).

Mechanisms driven by the atmosphere will, for the most part, tend to be consistent with the observational test of deglacial timing, with their greatest deglacial change occurring upon warming in their region or hemisphere (Table 1). From the perspective of this test, changes in westerly wind-driven upwelling (Toggweiler et al., 2006) and/or in the areal extents of the AZ and SNP (Lawrence et al., 2013; Ferrari et al., 2014; Watson et al., 2015) are both plausible.

6.3.3. Summary of the Antarctic Zone/subarctic North Pacific comparison

To the degree that AZ and SNP changes in reconstructed gross nutrient supply share a driving mechanism, comparison of the AZ and SNP offers constraints on the origins of the "surface isolation" of the ice age AZ (Table 1). The AZ surface isolation mechanism that fares best when held up against the comparison of data from the AZ and the SNP is the westerly wind-driven upwelling mechanism of Toggweiler et al. (2006) (Fig. 1 b), so long as this mechanism also applies to the northern hemisphere westerly winds (Table 1). The other mechanisms fail in at least one of two respects. Some fail to explain the observation that an ice age reduction in subsurface-to-surface nitrate supply occurs in both the AZ and the SNP (left

column in Table 1). Some are inconsistent with the evidence from the last deglaciation that the changes in nitrate supply in each region respond to regional/hemispheric atmospheric temperature, not global atmospheric or deep sea temperature (right column in Table 1).

These conclusions have several qualifications that should be raised here. First, while the AZ/SNP comparison argues against a deep ocean trigger for the AZ and SNP changes, abyssal mixing appears to have been reduced at some point during the ice ages, at which point it may have contributed to AZ surface isolation. This is discussed below (section 9.1.2). Second, the same driver need not have applied to all changes in both the AZ and the SNP. For example, the reconstructed deglacial increase in AZ surface/subsurface exchange at HS1 appears to be a response to declining North Atlantic overturning, through a westerly wind change, as a response to changes in the ocean interior, or both (Sigman et al., 2007; Schmittner and Galbraith, 2008; Anderson et al., 2009; Denton et al., 2010; Meckler et al., 2013). In addition, teleconnections between the North Atlantic and the SNP have been observed in models (Mikolajewicz et al., 1997; Saenko et al., 2004; Schmittner, 2005; Okumura et al., 2009). However, these connections would have enhanced nitrate supply to the SNP surface during HS1, not the B-A. So our timing-based argument in favor of a glacial reduction in wind-driven upwelling remains valid.

6.4. Upper water column changes in the glacial subarctic North Pacific and Antarctic Zone

Here, we note a substantial body of data that has led to an interpretation of the glacial SNP that is different from our interpretation of SNP surface isolation. Previous studies find evidence for reduced nutrients and better ventilation of the upper water column (down to ~1.5 km) of the SNP from the ice age through the early deglaciation (Keigwin, 1998; Okazaki et al., 2010; Max et al., 2014; Gray et al., 2018). Based on foraminiferal stable carbon isotope, radiocarbon, and micropaleontological data, these studies argue that the LGM and/or HS1 were periods of enhanced intermediate water formation in the SNP. These interpretations are supported by the finding in some models that a shutdown in North Atlantic overturning encourages ventilation of the mid-depths in the SNP (Okazaki et al., 2010; Gong et al., 2019). Enhanced intermediate water formation would appear to be at odds with the SNP surface isolation during the glacials for which we have argued above. In this interpretation, the nutrient impoverishment of the glacial SNP surface is due not to a decline in the nutrient supply from below but rather to increased input of low-nutrient subtropical water flowing into the SNP to feed intermediate water formation (Gray et al., 2018).

We propose a related but distinct explanation for these observations from the SNP. In this explanation, the reduction in nutrients and the lower radiocarbon ages of the mid-depths during the LGM and HS1 were, at least in part, due to the reduction in westerly wind-driven upwelling in the SNP for which we have argued above (Fig. 1 b). Slower upwelling would have yielded a lower rate of upward advection of nutrient-rich and ^{14}C-depleted interior water toward the surface. Without this upward advection but with continued vertical mixing (e.g., deep winter mixing), the sinking flux of biogenic material would have "mined out" the nutrients from the upper water column of the glacial SNP (Fig. 1 b, blue color of the mixing arrows in the SNP) while raising the ^{14}C content of the upper water column.

The formation of North Pacific Intermediate Water (NPIW) could have played a similar role. If, during the LGM and HS1, surface waters were lower in nutrient concentration, then NPIW formation could have transmitted this nutrient reduction to the SNP

subsurface at the depths that it ventilates today (the upper ~1 km). Without the counteracting effect of the upward advection of nutrients from wind-driven upwelling, NPIW formation need not have been faster to achieve this effect. Thus, whereas there have been interpretations of an increase in NPIW formation and vertical mixing during the LGM and HS1 (Okazaki et al., 2010; Max et al., 2014; Gray et al., 2018), we call solely for the persistence of these processes, possibly even at rates lower than modern, but uncountered by westerly wind-driven upwelling. Reciprocally, so long as enhanced NPIW formation during the LGM and HS1 did not significantly increase the nitrate supply to the SNP surface, then our reconstruction of reduced nitrate supply does not argue against it.

In addition, the reduction in westerly wind-driven upwelling would have contributed to mid-depth nutrient depletion in both the SNP and the AZ during the ice ages through its effect on pycnocline structure. The pycnocline tilt away from the polar regions is driven by Ekman upwelling and partially counteracted ("compensated") by eddies (Marshall and Speer, 2012; Gent, 2016). During the ice ages, without strong Ekman upwelling in the SNP and AZ, the compensation by the poleward eddy-induced advection would have been more complete, allowing for the pycnocline to "slump" poleward while thinning at lower latitudes (Fig. 1, change in light gray regions between panels a and b).

A change in nutrient gradients would largely parallel the slumping of the pycnocline, reducing the nitrate concentration of the shallow subsurface in the SNP and AZ (Fig. 1 b, change from purple to blue lines in the SNP and AZ). With this change, each year's upwelling and vertical mixing would supply less nitrate to the surface mixed layer of the SNP and AZ. Thus, glacial reductions in both (1) the rate of subsurface water supply to the surface and (2) the nitrate concentration of that subsurface water would have contributed to the decline in nitrate supply to the SNP and AZ surface. This can explain why the nitrate supply rate to the AZ surface mixed layer is calculated to be so low during ice ages (Kemeny et al., 2018). Thus, this interpretation fits with our goal of explaining the similar biogeochemical changes in the AZ and SNP during the ice ages, rather than proposing distinct, region-specific explanations. At the same time, the proposed poleward slumping of isopycnals is, in some regards, similar to the proposal by Gray et al. (2018) of a northward incursion of subtropical surface waters into the SNP as part of a mid-depth overturning cell.

7. Proposal: Bihemispheric changes in westerly wind-driven upwelling since the last ice age

In summary, we propose that, during the last ice age, an equatorward shift and weakening of the westerly winds reduced upwelling in the AZ and SNP (Fig. 1 b). This reduced biological export production but increased the degree of nitrate consumption (Fig. 1 b; change in line color from purple to blue in the AZ and SNP surface).

Another consequence of the weakening of the westerlies concerns the shape of the pycnocline and its depth. The wind-driven Ekman transport in the AZ acts to steepen isopycnals while the largely opposing response of eddies to the tilted isopyncnals (i.e., eddy advection) works to slump isopycnals back to horizontal (Marshall and Speer, 2012). Accordingly, the weakening of the westerlies may have caused a poleward slumping of the global pycnocline (the light gray region in Fig. 1). Moreover, the weakening in the Southern Ocean's upper cell and the poleward slumping of the pycnocline may have contributed to a shoaling of the low latitude pycnocline (thinning of the light gray region in the low latitudes in Fig. 1 b) (Gnanadesikan, 1999).

As pursued in section 9, the proposed changes in the AZ upper water column may have slowed deep ocean ventilation by the AZ

(indicated by the thinner and dashed flow lines in Fig. 1 b). Both more complete nutrient consumption and reduced deep ocean ventilation in the AZ would have reduced the leakage of biologically sequestered CO_2 to the atmosphere. In contrast, the lack of significant ventilation of the ocean interior by the SNP today argues that this region's changes only marginally contributed to the lowering of ice age CO_2 levels.

8. Models and data regarding ice age wind-driven upwelling

Since a wind-driven decrease in the upper cell of Southern Ocean during ice ages was first proposed, it has been explored and debated vigorously (Sigman and Boyle, 2000; Keeling and Visbeck, 2001; Sigman and Boyle, 2001; Toggweiler et al., 2006; Volker and Kohler, 2013). Northward migration of the winds is mechanistically intuitive and seems to have some empirical support (Lamy et al., 2004, 2007; Bard and Rickaby, 2009; Ljung et al., 2015). However, both paleoclimate data (Shulmeister et al., 2004; Kohfeld et al., 2013) and models (Menviel et al., 2008; Rojas et al., 2009; Chavaillaz et al., 2013; Rojas, 2013; Sime et al., 2013; Timmermann et al., 2013) have so far proven ambiguous as to their support for/refutation of a net weakening of the winds in the latitude range of the modern-day AZ.

With regard to the North Pacific, in PMIP simulations of the LGM, models tend to shift the winds equatorward, weakening the westerlies over the western SNP and Bering Sea. However, the polar easterlies also tend to move into the region. Gray et al. (2018, 2020) find that these simulations lead to higher Ekman divergence over the SNP as a whole. In the models, this is driven by strong Ekman divergence along the eastern margin of the Gulf of Alaska. However, in the modern SNP, the isopycnals are deeper in the Gulf of Alaska than in the western SNP and Bering Sea (Olsen et al., 2019). As a result, the western SNP and Bering Sea, not the Gulf of Alaska, are the regions with the strongest combination of upwelling and deep mixing, the densest wintertime surface waters, and thus the highest nitrate supply rates and surface nitrate concentrations (Gargett, 1991; Ohno et al., 2009; Nakanowatari et al., 2017; Nishioka et al., 2020). Accordingly, upwelling along eastern margin of the Gulf of Alaska during the ice ages (Gray et al., 2018) may have drawn subsurface water from the lower density upper water column, effectively recycling waters through upper several hundred meters and homogenizing their characteristics. We thus believe it possible that an equatorward shift of winds would have reduced the upwelling-driven supply of deep nutrients to the SNP as a whole. Nevertheless, there is currently a notable lack of climate model support for the wind-driven upwelling explanation for both AZ and SNP surface isolation during the ice ages (Sime et al., 2013; Gray et al., 2020), and this is a major concern.

In terms of the ocean's response, the upper cell of the Southern Ocean is the residual circulation resulting from the superposition of the Ekman upwelling and eddy advection, with the latter largely opposing the former at the surface (Marshall and Speer, 2012). Even with a decline in northward Ekman transport, it has been argued that a parallel decline in the compensating transport by eddies will result in little change in the net upwelling and northward transport (Keeling and Visbeck, 2001; Böning et al., 2008; Fischer et al., 2010). However, model studies indicate that eddies only partially compensate for changes in westerly wind stress, reducing the change in the net northward surface transport in the AZ but not preventing it (Hallberg and Gnanadesikan, 2006; Abernathey et al., 2011; Morrison and Hogg, 2012; Munday et al., 2013). In support of this view, benthic foraminifera carbon isotope data point to accelerated AAIW formation coincident with southern hemisphere warming upon deglaciations (Bostock et al., 2004; Pahnke and

Zahn, 2005; Jung et al., 2009), suggesting that the upper cell does change in strength. Thus, we do not see this "eddy compensation" as a process that will prevent an ice age reduction in Ekman transport from resulting in a reduction in net AZ upwelling. Rather, as described in section 7, we propose that the continued (albeit weakened) poleward eddy advection played an important role in depleting nutrients from the glacial AZ upper water column.

Toggweiler et al. (2006) emphasized the northward migration of the southern hemisphere westerly winds out of the deep channel around Antarctica (bounded to the North by South America and the other continents) as being important to achieving a reduction in AZ overturning that no longer imported deep water to the surface. Yet a glacial/interglacial mechanism relying on a deep channel cannot apply to the SNP. Steep bathymetric features in the SNP have been argued to enhance vertical mixing and diffusion-driven upwelling in the deep SNP (Sarmiento et al., 2004), and this may allow Ekman upwelling in the western SNP to bring deep water and nutrients to the surface (Nishioka et al., 2020). With mechanisms for linking Ekman upwelling to deep nutrient reservoirs in both the AZ and the SNP, a similar wind-driven mechanism can explain glacial/interglacial changes in nutrient supply in the two regions.

9. A glacial reduction in the upper cell of the Southern Ocean: arising questions

Above, we argue for an ice age decline in westerly wind-driven Southern Ocean overturning and a parallel change in the SNP. However, this proposal raises three critical questions, each of which relates to the fact that westerly wind-driven transport of AZ surface waters is northward and into mid-depths, not southward and into the voluminous deep ocean. That is, westerly wind-driven upwelling is directly tied to the upper cell, whereas its connections to the lower cell are unclear (Fig. 1 a).

9.1. Capacity to reduce ice age CO_2

The first question regarding the inference of a weakened Southern Ocean upper cell involves its potential to lower atmospheric CO_2. The CO_2 impacts of the upper cell overturning are strongly influenced by nutrient conditions in the SAZ. As described above, dust-borne iron fertilization appears to modulate SAZ nutrient consumption over glacial/interglacial cycles (Kumar et al., 1995; Martínez-García et al., 2009, 2011, 2014). Thus, the greatest independent leverage that the AZ has on atmospheric CO_2 is through the deep ocean (Fig. 1). Put another way, if the changes in the AZ did not involve the region's ventilation of the deep ocean, then their CO_2 effects would have been limited, consistent with some numerical model experiments of Southern Ocean wind changes (Menviel et al., 2008; Gottschalk et al., 2020).

As described in section 3.1, there are two related geochemical mechanisms for increasing the efficiency of the global ocean's biological pump: "nutrient drawdown" and "ventilation reduction." In "nutrient drawdown", the supply of nutrients and excess CO_2 is more completely consumed in the AZ region(s) that ventilate the ocean interior. In "ventilation reduction," the AZ becomes less important in ventilating the ocean interior relative to regions such as the North Atlantic. Current theory does not directly couple westerly wind-driven Southern Ocean overturning (i.e., the upper cell) to AZ ventilation of the deep ocean (i.e., the lower cell) (Fig. 1 a). Thus, we seek mechanisms for how a reduction in the Southern Ocean's upper cell could either (1) increase the degree of nutrient consumption in the AZ surface waters that then reenter the deep ocean, or (2) inhibit ventilation of the deep ocean by AZ surface waters. Below, we offer proposals for both scenarios (Fig. 7).
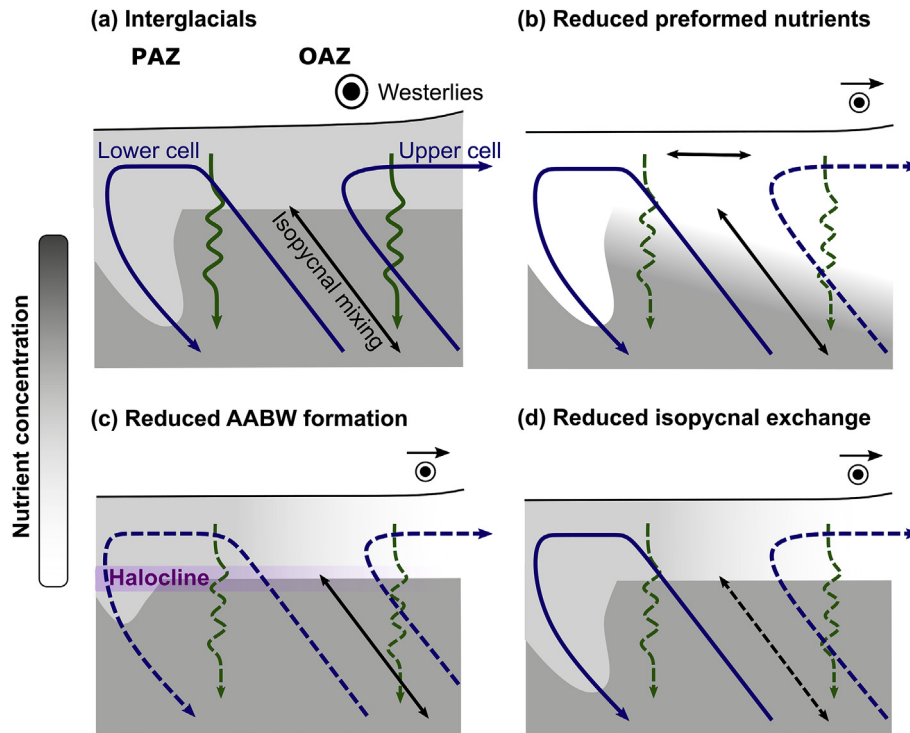
Fig. 7. Mechanisms through which a weakening in the upper cell of Southern Ocean circulation could lead to the storage of more CO_2 in the deep ocean during ice ages. Southward is to the left in each panel. Gray shading qualitatively indicates the nutrient (nitrate or phosphate) concentration, and dotted arrows indicate a reduction in magnitude relative to the interglacial condition. (a) The modern condition of strong upper and lower cells and incomplete surface nutrient consumption. (b, c, d) Reduced upper cell strength (dotted lines) relative to the interglacial case, leading to three separable but non-exclusive mechanisms for increased deep CO_2 storage. (b) Lower surface nutrient concentration across the entire AZ, including the PAZ, the region mostly directly ventilating the lower cell, leading to a reduction in the preformed nutrient content of the deep ocean. In the OAZ, nutrients are proposed to have been lowered not only at the surface but also in the shallow subsurface; this is proposed to be the result of "nutrient mining" and/or pycnocline slumping (see text). Export production was apparently reduced throughout the glacial AZ – both the OAZ and the PAZ (thinning and dashing of the wavy green arrows). Thus, for surface nutrients to be low in the glacial PAZ without a decline in overturning in the region, lower-nutrient water must have been mixed in from the OAZ (horizontal bidirectional arrow). Note that the deep ocean maintains high nutrient concentrations, with the preformed nutrient concentration decline matched by a rise in regenerated nutrients (and thus more CO_2 storage). (c) The increase in the residence time of AZ surface waters may lead to a strengthening of the halocline, which causes a reduction of deep ocean ventilation by the lower cell (Toggweiler et al., 2006; De Boer et al., 2008). In this case, the PAZ may also have experienced a decline in surface nutrient concentration due to its own changes in overturning (i.e., the reduction in nutrient supply from the lower cell). CO_2 leakage from the region would have decreased without a decline in PAZ surface nutrient concentration, but the CO_2 decrease would have been greater with a surface nutrient decline. In (c), the upper and lower cells are shown shifted northward, as this shift may also have helped the PAZ halocline to strengthen (Lawrence et al., 2013). (d) Decreased isopycnal exchange. Decreased Ekman transport should have caused a weakening in eddy mixing along interior isopycnals that would have reduced deep ocean ventilation (Abernathey and Ferreira, 2015). Not shown here but shown in Fig. 1 b due to its global scale, an equatorward migration of the westerlies may also have slowed the lower cell by shoaling the deep ocean contact zone between the lower limb of the upper cell and the upper limb of the lower cell, so as to be further above the mixing-inducing features of the seafloor (Watson and Naveira Garabato, 2006; Lund et al., 2011; Ferrari et al., 2014; De Boer and Hogg, 2014). However, our comparison of the AZ with the SNP (Figs. 5 and 6; Table 1) argues that such a deep ocean change did not initiate the ice age surface isolation of the AZ.

9.1.1. Reduced preformed nutrients in Antarctic Zone-formed deep water

In two regards, reduction of surface nutrient concentrations in the PAZ is currently the most palatable option for stemming the PAZ leak in the biological pump, being preferable to the slowing of the Southern Ocean's lower cell (section 9.1.2). First, while reducing the circulation of the lower cell would strengthen the soft-tissue pump (lowering atmospheric CO_2), it would also strengthen the carbonate pump (raising atmospheric CO_2) (Fig. 3 b; section 3.1). In contrast, reducing the surface nutrient concentration of the PAZ would strengthen the soft-tissue pump without affecting the carbonate pump, making it a more efficient mechanism for lowering atmospheric CO_2 (Fig. 2). Second, the proposal of a reduced lower cell circulation contradicts most climate model simulations of cold climates, in which extensive sea ice formation leads to the formation of salinity-densified deep water in the PAZ (Otto-Bleisner et al., 2007; Wainer et al., 2012; Jansen, 2017; Galbraith and de Lavergne, 2019). While this contradiction may be the fault of the models, many researchers would probably judge this to be unlikely.

A dramatic reduction in nutrient supply is required to drive the reconstructed decline in surface nitrate concentration without violating the reconstructions of lower AZ export production during the ice ages (Kohfeld et al., 2005; Kemeny et al., 2018). We propose that this is achieved by marshalling three coupled mechanisms for reducing the nutrient supply (Fig. 7 b). The first is the reduction in the overturning rate of the upper cell. Second, we propose that this slowing of the upper cell allowed the nutrients from the AZ upper water column to be "mined out." More specifically, without strong net upwelling, years of nitrate consumption in the summertime surface followed by vertical mixing in the winters (and year-round below the winter mixed layer) would eventually extract nutrients from the upper water column. This could well have reduced nutrient concentrations of the upper water column across the AZ, including in the regions of deep water formation. Third, poleward slumping of the pycnocline (Fig. 1 b and 7 b; see section 6) would have lowered the density and nutrient concentration of the upper water column (including the shallow subsurface) in these regions. The decline in nutrient concentration would have encouraged a decline in the preformed nutrient concentration of AZ-formed deep water (Fig. 7 b), which would, in turn, have increased the efficiency of the global ocean's biological pump, contributing to the ice age decline in atmospheric CO_2.

A decline in the Southern Ocean's upper cell is most likely to lower the nutrient concentration of the more northern portion of the Antarctic Zone, here referred to as the Open Antarctic Zone (OAZ, Fig. 7 b). However, the surface waters of the Polar Antarctic Zone (PAZ) are more directly involved in ventilating the abyssal ocean (Sloyan and Rintoul, 2001; Lumpkin and Speer, 2007), such that a decrease in PAZ nutrients would most directly drive a decline in the preformed nutrient of the Southern Ocean's lower cell, which in turn sets a large part of the AZ influence on the efficiency of the global ocean's biological pump. Thus, a central question for future work is whether the decline in nutrient concentration reconstructed for the surface waters of the OAZ surface waters also applied to the PAZ. Even if the decline in nutrient supply was focused in the OAZ, north-south exchange by surface waters may have been adequate to drive a decline in surface nutrients in the PAZ as well (Fig. 7 b, two-way horizontal arrow in the AZ surface). In addition, as discussed below, a forced reduction in surface/subsurface exchange in the OAZ, by a change in winds or some other factor, may have strengthened the halocline across the AZ. Such halocline strengthening would have reduced the nutrient supply to the AZ, contributing to the tendency for more complete nutrient consumption in both the OAZ and the PAZ.

Finally, as described below, there is a suggestion from numerical model simulations that the OAZ itself plays a role in ventilating the deep ocean (Abernathey and Ferreira, 2015). If so, the surface nutrient concentration decline in the OAZ could itself have lowered the preformed nutrient concentration of the ocean interior and thus strengthened the biological pump. However, the effect would be stronger if the surface AZ nutrient decline extended into the PAZ.

9.1.2. Slowing deep ventilation

A weakening of the upper cell of Southern Ocean overturning might also decrease the overturning rate of the "lower cell," that is, the rate of ventilation by the AZ of the underlying abyssal and deep ocean (Fig. 7 c and d). We know of four possible mechanisms for this.

First, weakening of the Ekman upwelling in the AZ may have allowed the isopycnals to slump poleward (Fig. 1 b). This change, considered alone, would have tended to reduce the density of surface waters across the AZ. As a result, the regions suitable for deep water formation in the AZ may have contracted, reducing AZ-wide ventilation of the deep ocean.

Second, the AZ halocline may have intensified. The strong northward wind-driven overturning that characterizes the modern Southern Ocean leads to a relatively short residence time for water in the AZ surface. This limits the strength of the halocline that can develop in response to net precipitation in the region. With this limit on halocline strength, modern buoyancy forcing at the Antarctic margin, such as wintertime cooling and sea ice formation, are sufficient to densify the surface ocean and drive vigorous deep water formation in some regions of the AZ. In contrast, reduced wind-driven overturning could allow the halocline to strengthen, reducing the ability of buoyancy fluxes at the Antarctic margin to form deep water (Fig. 7 c) (Toggweiler et al., 2006; De Boer et al., 2008; Hasenfratz et al., 2019). Even if the winds moved equatorward more dramatically than they weakened, the decline in upwelling in the region that is the modern AZ, as well as the expansion of its area, would allow for strengthening of the halocline in the more polar latitudes of the AZ (Lawrence et al., 2013).

Third, deep ocean ventilation may be directly connected to the upper cell. Using an eddy-resolving, zonal channel model of the Southern Ocean, Abernathey et al. (2011) find that the lower overturning cell will either remain stable or strengthen under the proposed ice age condition of weakened westerly winds. This is counter to the sense of change that would allow circulation in the

PAZ to enhance CO_2 sequestration in the deep ocean during ice ages. However, Abernathey and Ferreira (2015) observe in the same model that weaker westerly winds lead to reduced eddy mixing and thus lower effective diffusivity along isopycnals in the interior. Taking into account changes in both the advective circulation and the isopycnal diffusivity, the net effect of a westerly wind stress decline is a reduction in the ventilation of the deep ocean and the mid-depth range of upwelling CDW (Abernathey and Ferreira, 2015). The role of isopycnal diffusivity in ventilating UCDW is particularly intriguing because UCDW interacts with the surface in the OAZ. This implies that, beyond its effects on the PAZ, the modern OAZ is playing a role in ventilating the deep ocean and that this role may have been reduced during the ice ages (Fig. 7 d).

Fourth, an equatorward shift in the position of southern hemisphere westerly winds may have activated the abyssal mixing decline that has been proposed previously (section 5.1.4). We have argued above that reduction in abyssal mixing was not the initiator of the AZ and SNP paleobiogeochemical changes. However, it remains possible that such a change contributed to reducing the rate of AZ deep water formation during the glacials, and it is thus included in Fig. 1 b. It is believed that, under peak ice age conditions, GNAIW replaced NADW (Lynch-Stieglitz et al., 2007), a change that Ferrari et al. (2014) interpret as a shoaling of the interface between the upper and lower ocean overturning cells and an associated decoupling of the two cells. Ferrari et al. look to an equatorward shift in the summer sea ice edge (which they take to mark the latitude at which the air-sea heat flux switches sign) as the driver, whereas Jansen (2017) suggests a more general climatic mechanism. The proposed equatorward shift in the winds may also have contributed to an equatorward shift in the surface boundary between the upper and lower cells and thus a shoaling of their deep ocean interface between the upper and lower cells, allowing the lower cell to expand (Fig. 1 b). Shoaling of the boundary between the two cells may have reduced the bathymetry-enhanced mixing between them (Lund et al., 2011; two vertical arrows in Fig. 1 b as opposed to four in Fig. 1 a). This would have, in turn, reduced the demand for newly formed deep water from the AZ (Watson and Naveira Garabato, 2006; Lund et al., 2011; Ferrari et al., 2014; De Boer and Hogg, 2014). Although new abyssal water continued to be sourced from the AZ, the slowness of ventilation from the AZ surface may have made the North Atlantic an important ventilator of this water (Fig. 1 b, purple dashed lines connecting the upper and lower overturning cells in the Southern Ocean) (Hain et al., 2010; Kwon et al., 2012).

9.2. Nutrient supply from the Antarctic Zone to the Subantarctic Zone

The second unanswered question regarding a weakened Southern Ocean upper cell and lower AZ surface nutrients involves the nutrient supply to the SAZ. Today, probably more than half of the nutrients supplied to the SAZ derive from AZ upwelling (Sarmiento et al., 2004; Palter et al., 2010). An ice age reduction in the volume and nutrient concentration of AZ surface waters sent northward would have reduced nutrient supply to the SAZ.

Above, we pointed to reconstructions of enhanced export production and more complete nutrient consumption in the ice age SAZ, coincident with higher dust fluxes to the SAZ, as evidence of iron fertilization that contributed to the ice age atmospheric CO_2 reduction (Fig. 4; Kumar et al., 1995; Martínez-García et al., 2009; 2014). However, at the initiation of the last ice age at ~110 ka, both export production and nutrient consumption proxies in the SAZ show only weak changes, while the same proxies point to a significant decline in nitrate supply to the AZ (Fig. 4; Kohfeld et al., 2005; Jaccard et al., 2013; Martínez-García et al., 2014; Studer

et al., 2015). Given the modern importance of the AZ nitrate supply to the SAZ, two related questions arise. First, why is there no evidence for a major decline in nitrate supply to the SAZ at 110 ka? Second, how was nitrate supply maintained at adequate levels to support the rise in export production during the high dust supply events in the peak ice age intervals?

The weakening in wind-driven upwelling in the AZ may have been partly compensated by increased upwelling to the North, in the modern SAZ. Such a change would most simply be explained by the northward shift in the southern hemisphere westerly winds that Toggweiler et al. (2006) propose. In this way, local upwelling into the modern region of the SAZ may partly compensate for the reduced supply of surface nitrate from the AZ. However, we do not believe that this is the sole mechanism of compensation. Observationally, the glacial rise in biogenic fluxes to the North of the AZ was not of similar magnitude to the decline in biogenic fluxes within the modern AZ (e.g., Chase et al., 2003). Conceptually, a northward shift in the upwelling may have caused the upwelling to be less effective at drawing water from great depth, such that nutrients would have been lost from the upper ocean without some additional mechanism of nutrient resupply from the deep ocean.

9.3. Southern Ocean upper cell: North Atlantic water balance

The third question regarding the inference of a weakened Southern Ocean upper cell during the ice ages involves the water budget for the low latitude upper ocean and North Atlantic sinking. NADW forms from surface, thermocline, and intermediate-depth (~1100 m) waters flowing northward into the region (Talley, 2013); presumably, GNAIW did as well. The Southern Ocean's upper cell supplies most of this water (Toggweiler and Samuels, 1995; Marshall and Speer, 2012). Thus, feedbacks are implied to maintain a rough balance between the formation of AAIW and SAMW in the Southern Ocean and NADW formation in the North Atlantic (Toggweiler and Samuels, 1995). However, North Atlantic sinking was at a minimum during HS1 (McManus et al., 2004), during which AZ subsurface-to-surface nutrient supply accelerated, as apparently did AAIW formation (Pahnke and Zahn, 2005; Pahnke et al., 2008). Moreover, the diatom-bound $\delta^{15}N$ data suggest that AZ subsurface-to-surface nutrient supply decreased significantly after the penultimate interglacial (at ~110 ka), whereas the largest glacial reduction in North Atlantic sinking occurred at the MIS 5/4 transition (at ~70 ka) (Piotrowski et al., 2005). How could the apparent changes in the Southern Ocean's upper cell have been so disconnected from those in North Atlantic sinking?

9.4. Did diffuse upwelling from the deep ocean increase during the last ice age?

Here, we provide a possible answer for the questions raised in sections 9.2 and 9.3. Specifically, we propose that, during the ice ages, an increase in the diffuse upwelling of deep water in the ocean interior compensated for the reduction in the supply of water and nutrients to the upper ocean due to the ice age weakening of the Southern Ocean's upper cell.

In its first conception, the upward flow in the global overturning circulation was thought to be driven by the addition and extraction of buoyancy at the ocean surface and vertical mixing in the ocean interior, allowing a diffuse upwelling of deep water into the low latitude pycnocline (Stommel, 1961; Munk, 1966). However, wind-driven upwelling in the Southern Ocean was eventually identified as the dominant process (Gill and Bryan, 1971; Toggweiler and Samuels, 1995, 1998). We propose here that the ice ages diverged from the modern overturning geometry (Fig. 1 a) toward one more similar to the original conception of upwelling from the deep ocean

into the pycnocline (Fig. 1 b, the upward diffuse cone and arrow at low latitudes). The mechanisms for this are two-fold.

The diffuse upwelling of deep water described by Stommel (1961) and Munk (1966) is driven by diapycnal mixing in the ocean interior, which transports buoyancy from the low latitude surface downward into the deep ocean, causing the deep water to upwell and be replaced by newly formed deep water. The wind-driven upwelling in the Southern Ocean draws water from ~2 km depth in the low latitudes, for example, Pacific Deep Water that becomes UCDW as it is drawn into the AZ. Thus, the Southern Ocean upwelling removes buoyancy that has been mixed down into the deep ocean. With a reduction in the Southern Ocean upwelling, therefore, the downward transport of buoyancy across the low latitude pycnocline would have been more fully compensated by diffuse upwelling across the pycnocline, much as envisioned by Stommel and Munk for the modern ocean. This buoyancy-driven interior upwelling may have been further enhanced by the loss of continental shelves during the ice ages, which may have increased diapycnal diffusion in the ocean interior (Munk and Wunsch, 1998; Wilmes and Green, 2014; Schmittner et al., 2015).

Moreover, the weakening in the Southern Ocean's upper cell may have led to a shoaling in the low latitude pycnocline, complementing the poleward slumping of isopycnals in response to reduced westerly wind-driven equatorward transport of surface waters (Fig. 1 b). In the North Atlantic, such ice age shoaling and steepening of the pycnocline has been observed, although the feature was explained as the result of North Atlantic hydrographic changes (Slowey and Curry, 1992). Typical scaling of the advective/diffusive balance calls for an inverse relationship between pycnocline thickness and upwelling rate (Gnanadesikan, 1999; Palter, 2010). Thus, a thinner glacial pycnocline may have encouraged a greater upwelling rate of deep sub-pycnocline water. Whether this occurred would have depended on how vertical mixing across the pycnocline changed in response to its thickness, a topic that is too complex and uncertain to treat appropriately here.

An increase in deep upwelling can explain the two needs identified above: (1) the source of nutrients to the ice age SAZ surface, and (2) the source of low latitude pycnocline and surface water for Glacial North Atlantic Intermediate Water formation (Fig. 1 b, the red-to-purple shading of the diffuse upwelling cone indicates upward nutrient supply). With regard to (1), the deep nutrients would have entered the global pycnocline, and isopycnal mixing and the deep component of the subtropical gyres would then have transported the nutrients to the shallow subsurface of the SAZ, with wintertime mixing and the northward-shifted wind-driven upwelling then importing the nutrients to the SAZ surface. With regard to (2), the glacial circulation would have resembled the global ocean "conveyor" circulation envisioned by Broecker (1991) for the modern ocean.

10. Conclusions

The available evidence points to the Southern Ocean as playing a central role in the lower atmospheric CO_2 concentrations of the ice ages. Two distinct mechanisms appear to be involved: (1) reduced subsurface/surface exchange in the Antarctic Zone (AZ), affecting CO_2 storage associated with both the lower and upper "cells" of Southern Ocean circulation and (2) iron fertilization in the Subantarctic Zone (SAZ), largely affecting CO_2 storage associated with the upper cell as well as the vertical partitioning of nutrients and CO_2 in the ocean. Both of these mechanisms have important interactions with the ocean's calcium carbonate budget, which further affects atmospheric CO_2. Carbon cycle model calculations suggest that changes in both lower and upper cell are required to approach the full amplitude of observed ice age CO_2 drawdown.

If the paleoceanographic observations have been interpreted correctly, the central question is: Why, from a physical and biological perspective, did the Southern Ocean undergo these changes? The ice age reduction in AZ subsurface/surface exchange (i.e., glacial surface "isolation") is particularly mysterious, as underscored by the common result in climate model simulations that AZ overturning increases under ice age boundary conditions and decreases under global warming. Here, we have used the subarctic North Pacific (SNP) as an analogue to distinguish among existing hypotheses for reduced subsurface/surface exchange in the AZ during ice ages. We find that a weakening of wind-driven upwelling associated with an equatorward shift of the westerly winds upon cooling fares best in its ability to explain changes in both the AZ and the SNP. This change would have reduced the transport of nutrient-bearing subsurface water into the surface layers of these regions. Moreover, we suggest that it would have allowed surface productivity and winter mixing to "mine out" the nutrients and excess CO_2 from the upper water columns of the AZ and SNP, and it may also have permitted the currently strongly tilted isopycnal surfaces of these regions to "slump" poleward, strengthening the vertical density gradient in these regions. We have outlined the requirements for a reduction in the Southern Ocean's upper cell to intensify CO_2 storage in the deep ocean. We also considered how the nutrient supply to the SAZ and the water supply for North Atlantic-sourced deep (or intermediate) water could have been maintained during ice ages, as observations require. For this, we propose that an enhancement of upwelling into the low latitude pycnocline compensated for the reduction in AZ upwelling.

Author statement

Declaration of competing interest

Acknowledgments

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