Transient response of Southern Ocean ecosystems during Heinrich stadials

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Abstract

Antarctic ice core records suggest that atmospheric CO2 increased by 15 to 20 ppm during Heinrich stadials (HS). These periods of abrupt CO2 increase are associated with a significant weakening of the Atlantic meridional overturning circulation (AMOC), and a warming at high southern latitudes. As such, modelling studies have explored the link between changes in AMOC, high southern latitude climate and atmospheric CO2. While proxy records suggest that the aeolian iron input to the Southern Ocean decreased significantly during HS, the potential impact on CO2 of reduced iron input combined with oceanic circulation changes has not been studied in detail. Here, we quantify the respective and combined impacts of reduced iron fertilisation and AMOC weakening on CO2 by performing numerical experiments with an Earth system model under boundary conditions representing 40,000 years before present (ka). Our study indicates that reduced iron input can contribute up to 6 ppm rise in CO2 during an idealized Heinrich stadial. This is caused by a 5% reduction in nutrient utilisation in the Southern Ocean, leading to reduced export production and increased carbon outgassing from the Southern Ocean. An AMOC weakening under 40ka conditions and without changes in surface winds leads to a ~0.5 ppm CO2 increase. The combined impact of AMOC shutdown and weakened iron fertilisation is almost linear, leading to a total CO2 increase of 7 ppm. Therefore, this study highlights the need of including changes in aeolian iron input when studying the processes leading to changes in atmospheric CO2 concentration during HS.

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Key Points: 10

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11	•	Simulated marine ecosystems and CO ₂ respond linearly to the combined impact
12		of freshwater addition and reduced iron flux into the ocean.
13	•	A maximum of 7 ppm increase in CO_2 is simulated due to the AMOC shutdown
14		and weakened iron fertilisation under MIS 3 boundary conditions.
15	•	Reduced aeolian iron flux in the Southern Ocean during Heinrich Stadials can lead
16		up to 6 ppm rise in CO_2 .

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17 Abstract

Antarctic ice core records suggest that atmospheric CO₂ increased by 15 to 20 ppm dur-18 ing Heinrich stadials (HS). These periods of abrupt CO_2 increase are associated with a 19 significant weakening of the Atlantic meridional overturning circulation (AMOC), and 20 a warming at high southern latitudes. As such, modelling studies have explored the link 21 between changes in AMOC, high southern latitude climate and atmospheric CO₂. While 22 proxy records suggest that the aeolian iron input to the Southern Ocean decreased sig-23 nificantly during HS, the potential impact on CO₂ of reduced iron input combined with 24 oceanic circulation changes has not been studied in detail. Here, we quantify the respec-25 tive and combined impacts of reduced iron fertilisation and AMOC weakening on CO_2 26 by performing numerical experiments with an Earth system model under boundary con-27 ditions representing 40,000 years before present (ka). Our study indicates that reduced 28 iron input can contribute up to 6 ppm rise in CO_2 during an idealized Heinrich stadial. 29 This is caused by a 5% reduction in nutrient utilisation in the Southern Ocean, leading 30 to reduced export production and increased carbon outgassing from the Southern Ocean. 31 An AMOC weakening under 40ka conditions and without changes in surface winds leads 32 to a ~ 0.5 ppm CO₂ increase. The combined impact of AMOC shutdown and weakened 33 iron fertilisation is almost linear, leading to a total CO_2 increase of 7 ppm. Therefore, 34 this study highlights the need of including changes in aeolian iron input when studying 35 the processes leading to changes in atmospheric CO_2 concentration during HS. 36

37 1 Introduction

Paleoproxy records from Greenland ice cores have shown the occurrence of abrupt 38 climate variability during the last glacial period (Johnsen et al., 1972; Dansgaard et al., 39 1982; Kindler et al., 2014). Such variability, referred to as Dansgaard-Oeschger (D/O)40 variability, is characterized by an abrupt rise in Greenland air temperatures on decadal 41 timescales (D/O event), followed by a gradual cooling over hundreds or thousands of years 42 to cold (stadial) stages (G. Bond et al., 1993; Dansgaard et al., 1993). About twenty-43 five such climatic oscillations have been recorded in Greenland ice cores (Kindler et al., 44 2014) out of which 14 D/O events occurred during Marine Isotope Stage 3 (MIS 3, 65-45 27 thousand years before present (ka BP hereafter)). D/O stadials are associated with 46 layers of ice rafted debris in North Atlantic marine sediment cores, indicating iceberg dis-47 charges into the ocean from the surrounding ice sheets (Van Kreveld et al., 2000). Some 48 stadials are characterised by especially thick layers of ice rafted debris originating from 49 the Laurentide ice-sheet (Heinrich, 1988; W. Broecker et al., 1992; Elliot et al., 1998; Snoeckx 50 et al., 1999; Grousset et al., 2000), and are referred to as Heinrich Events (HEs). The 51 origin and timing of D/O variability is still debated (W. S. Broecker et al., 1990; W. S. Broecker, 52 1994; G. C. Bond & Lotti, 1995; Hodell et al., 2010; Marcott et al., 2011; Barker et al., 53 2015; Menviel et al., 2020). 54

Paleoproxy records and modelling studies have suggested that Henirich stadials (HS), 55 stadials which contain a HE, were associated with a significant weakening of the AMOC 56 (Menviel et al., 2020). Such an AMOC weakening would lead to a reduction in the north-57 ward heat transport in the Atlantic, therefore causing a significant cooling in the North 58 Atlantic and Greenland region (Ganopolski & Rahmstorf, 2001; Meissner et al., 2002; 59 Huber et al., 2006; Kageyama et al., 2010; Buizert et al., 2014; Kindler et al., 2014; Henry 60 et al., 2016; Menviel et al., 2020). Due to the reduced northward oceanic heat transport 61 in the Atlantic, the AMOC weakening would lead to a warming in the South Atlantic, 62 and at high southern latitudes (Crowley, 1992; Stocker, 1998; Blunier & Brook, 2001; 63 Seidov & Maslin, 2001; Stocker & Johnsen, 2003; Jouzel et al., 2007; Timmermann et 64 al., 2010; Pedro et al., 2018). 65

Antarctic ice core records reveal that there was a rise in atmospheric CO_2 concentration during Heinrich stadials (HS) (Ahn & Brook, 2008, 2014; Parrenin et al., 2013;

Bereiter et al., 2015; T. K. Bauska et al., 2021). Observations also suggest that concur-68 rent to each HS in the North Atlantic during MIS 3, there was an Antarctic warm event 69 (also known as Antarctic Isotope Maxima, AIM) coinciding with the CO₂ increase (Buizert 70 et al., 2015; T. K. Bauska et al., 2021). For example, during Heinrich stadial 4 (H4), which 71 is associated with an intense ice rafted debris deposition in the North Atlantic (Hemming, 72 2004), the temperature in Greenland decreased by $\sim 5^{\circ}$ C (Huber et al., 2006; Kindler et 73 al., 2014), while Antarctic temperatures rose by 2-3°C (Jouzel et al., 2007), and global 74 CO₂ concentration increased by 15 to 20 ppm (Ahn & Brook, 2014; Bereiter et al., 2015; 75 T. Bauska et al., 2018) (Figure 1a-c). 76

A compilation of numerical studies by Gottschalk et al. (2019) suggests that sim-77 ulated atmospheric CO_2 levels can vary between -7 to +14 ppm in response to an AMOC 78 shutdown under interglacial boundary conditions, whereas under glacial boundary con-79 ditions, this range can vary between -5 to +6 ppm. Modelling studies have further sug-80 gested that the rise in CO_2 during HS was caused by a decrease in deep Pacific and South-81 ern Ocean carbon resulting from stronger North Pacific Deep Water (NPDW) formation 82 and enhanced Southern Ocean outgassing (Huiskamp & Meissner, 2012; Menviel et al., 83 2014, 2018). Enhanced Southern Ocean outgassing could result from stronger convec-84 tion or enhanced wind-driven upwelling as also suggested from paleo-proxy ventilation 85 records (Anderson et al., 2009; Skinner et al., 2020). 86

Marine sediment cores from the South Atlantic (Martínez-García et al., 2011) and 87 the South Pacific (Lamy et al., 2014) as well as Antarctic ice cores (Fischer et al., 2010; 88 Lambert et al., 2012) have highlighted millennial-scale fluctuations in the atmospheric 89 dust flux deposition at high southern latitudes that are opposite to changes in atmospheric 90 CO_2 levels (Figure 1d). The associated changes in aeolian iron input to the ocean have 91 been suggested to impact CO₂ concentration by modulating Southern Ocean nutrient 92 utilisation (Martin, 1990; Martínez-García et al., 2014). For aminifera-bound $\delta^{15}N$ (FB-93 δ^{15} N) records (Martínez-García et al., 2014; Studer et al., 2015) suggest that the greater 94 iron supply can stimulate higher nutrient utilisation in the ocean, by liberating the iron 95 limitation effect, and causing higher export production (EP). 96

Many modelling studies have assessed the impact of changes in iron input to the 97 ocean on Southern Ocean EP and atmospheric CO_2 by performing sensitivity experiments 98 under Last Glacial Maximum (Aumont et al., 2003; Bopp et al., 2003; Oka et al., 2011; qq Lambert et al., 2015; Muglia et al., 2017; Khatiwala et al., 2019; Yamamoto et al., 2019; 100 Lambert et al., 2021; Saini et al., 2021) and pre-industrial (PI) (Aumont & Bopp, 2006; 101 Tagliabue et al., 2009, 2014) boundary conditions. However, even though the link be-102 tween aeolian iron input and Southern Ocean EP should also hold for millennial scale 103 climate changes (Anderson et al., 2014), the response of marine ecosystems and ocean 104 biogeochemistry to changes in iron dust flux during millennial-scale events of the last glacial 105 period has not been simulated in detail. So far, only one experiment studied the impact 106 of millennial-scale changes in dust flux on atmospheric CO_2 by forcing the Bern3D model 107 with reconstructed dust deposition from DOME C ice core under PI boundary condi-108 tions (Parekh et al., 2008). They simulated the largest increase in atmospheric CO_2 (+9 109 ppm) during H4 as a response to the lowest reconstructed aeolian dust flux. 110

Alkenone based EP evidence from a marine sediment core east of New Zealand, in-111 dicates higher productivity during HS over the past 70,000 years in this region (Sachs 112 & Anderson, 2005). This is in agreement with the higher amount of opal flux during HS 113 obtained from four cores in the Antarctic zone (south of $\sim 60^{\circ}$ S in the Pacific sector and 114 south of $\sim 50^{\circ}$ S in the Atlantic sector) (Anderson et al., 2009). However, recent stud-115 116 ies (Anderson et al., 2014; Martínez-García et al., 2014) based on alkenone concentrations, opal and organic carbon fluxes measured in sub-Antarctic Atlantic sediment cores 117 (close to $\sim 40^{\circ}$ S), point towards a reduction in biological productivity during HS when 118 the dust supply declined (Lambert et al., 2012). This is also in agreement with the records 119 of higher deep ocean oxygenation during HS in the sub-Antarctic Atlantic (Gottschalk 120



Figure 1. Time series of (a) Greenland air temperature anomalies compared to today (°C) reconstructed from the NGRIP ice core (Kindler et al., 2014); (b) Antarctic deuterium (δ D) concentration (‰) anomaly from today as recorded in EPICA DOME C ice core (Jouzel et al., 2007), representing temperature variability in Antarctica; (c) atmospheric CO₂ concentrations (ppm) from EPICA DOME C ice core (Bereiter et al., 2015); (d) dust flux (mg/m²/yr) from EPICA DOME C ice core (Lambert et al., 2012); Grey shade represents Heinrich stadials during MIS 3 (65-27 ka).

et al., 2016; Jaccard et al., 2016), which is an indicator of less remineralized organic carbon in the deep ocean. However, lower carbon sequestration in the ocean can also be due to increased ventilation as recorded from radiocarbon changes in the deep Southern Ocean during H4 (Gottschalk et al., 2016). Therefore, the Southern Ocean biological efficiency is impacted by more than just iron limitation. As there are only a few cores at sparse locations, it is thus challenging to draw robust conclusions about EP changes in the Southern Ocean during HS.

In addition, while many studies assessed the impact of an AMOC shutdown or an 128 increase in aeolian iron input on the carbon cycle, no modelling study has yet looked into 129 the combined impact of an AMOC shutdown and a decrease in aeolian iron flux on the 130 carbon cycle under appropriate glacial boundary conditions. A study by Jochum et al. 131 (2022) analysed the impact of longer stadials and reduced iron flux on global atmospheric 132 CO_2 concentration. However, they investigated this response with an experiment resem-133 bling LGM climate conditions and iron flux reduced by 50% from PI dust flux. Here, we 134 investigate the response of marine ecosystems and atmospheric CO_2 to the individual 135 and combined impacts of AMOC shutdown and reduced iron flux input in the South-136 ern Ocean under MIS 3 boundary conditions. We focus on the changes in ecosystems and 137 atmosphere-ocean CO_2 exchange in the Southern Ocean as the iron fertilisation effect 138 is crucial in this region (Saini et al., 2023). 139

 $_{140}$ 2 Methods

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2.1 Model

The experiments are performed with the version 2.9 University of Victoria Earth 142 System Climate Model of intermediate complexity (UVic ESCM). It includes the MOM2 143 ocean general circulation model (Pacanowski, 1995) coupled to a sea ice model (Semtner, 144 1976; Hibler, 1979; Hunke & Dukowicz, 1997), a land surface scheme and a dynamic veg-145 etation model (Meissner et al., 2003), a sediment model (Archer & Maier-Reimer, 1994; 146 Meissner et al., 2012) with fixed weathering flux, and a vertically integrated 2-D energy 147 and moisture balance atmospheric model (Fanning & Weaver, 1996). All model compo-148 nents are on a grid with a spatial resolution of 3.6 by 1.8 degrees and there are 19 ver-149 tical depth levels in the ocean. Seasonally varying solar insolation (Berger, 1978) at the 150 top of the atmosphere and seasonal variations in wind stress and wind fields (Kalnay et 151 al., 1996) are used as external forcing to drive the model. An ideal age tracer is added 152 to track water mass age (Koeve et al., 2015). A detailed description of the model struc-153 ture and physics can be obtained from (Weaver et al., 2001; Meissner et al., 2003; Eby 154 et al., 2009; Mengis et al., 2020). 155

The climate model incorporates the recently developed ecosystem model called Kiel Marine Biogeochemistry Model (KMBM), v3 (Kvale et al., 2021; Saini et al., 2021), which represents the ocean carbon cycle. This model includes prognostic equations for diatoms (silicifying plankton) and coccolithophores (calcifying plankton), in addition to general phytoplankton and diazotrophs. It also includes a prognostic iron cycle (Nickelsen et al., 2015) featuring hydrothermal sources (Yao et al., 2019), and fully incorporated silica and CaCO₃ cycles. Full description of the ecosystem model can be found in Kvale et al. (2021).

163 2.2 Experimental design

A control simulation (40ka-control) using constant atmospheric CO₂ levels set at 200 ppm (Bereiter et al., 2015), with orbital forcing (Berger, 1978) and ice sheet topography (obtained from an offline ice sheet simulation (Abe-Ouchi et al., 2013)) corresponding to 40ka BP is integrated for 10,000 years to reach an equilibrium state. We use iron (LGM-fe) and silica (LGM-Si) dust fluxes based on the Last Glacial Maximum (LGM) dust deposition map from Lambert et al. (2012) and a iron/silica to dust percentage map from Zhang et al. (2015), applying a 3% iron solubility factor in the ocean. After 10,000 years of spin up, the model is run with prognostic CO₂ for another 1,000 years (Figure 2, black line).

To simulate an idealized HS, we add a meltwater pulse of 0.05 Sv (equivalent to a 2 m global sea level rise) into the North Atlantic (52°W:5.4°E; 78°N:86°N) for 500 years (FW, Figure 2a, orange line, phase 1). This meltwater causes an AMOC shutdown. The model is run for another 500 years without any meltwater input (phase 2). To simulate an AMOC recovery, a salt flux addition to the North Atlantic is required in the UVic ESM. A negative meltwater input (-0.15 Sv) is thus added in the North Atlantic for 200 years. The model is then run for another 300 years (phase 3).

To understand the impact of reduced iron flux, we run another experiment called 180 FE (Figure 2, red line), during which there is no freshwater forcing, but the global iron 181 flux into the ocean is abruptly decreased by 90% to 2.744 Gmol yr⁻¹ (Figure 2g). This 182 experimental design was chosen based on EPICA DOME C ice core records, where the 183 optical particle counts as well as soluble calcium (Ca^{2+}) and non-sea salt soluble calcium 184 (nssCa²⁺) records indicate a reduction of dust flux by about 84% during H4, between 185 40ka and 38ka (Lambert et al., 2012). We run the model for 1000 years and then switch 186 the iron flux back to the original LGM-fe flux value $(27.44 \text{ Gmol yr}^{-1})$ in phase 3. 187

Finally, in our third experiment, FWFE (Figure 2, green line), we analyse the im-188 pact of the combination of a freshwater discharge into the North Atlantic and a simul-189 taneous reduction in the iron input. Therefore, the iron flux is reduced by 90% and 0.05190 Sv of meltwater is added in the North Atlantic during the first 500 years (phase 1). For 191 the following 500 years, the iron flux stays reduced while no additional meltwater is added 192 in the North Atlantic (phase 2). In phase 3, the salt is applied, the iron flux is changed 193 back to the original value and the model is run for 200 years. After that the model con-194 tinues to run for another 300 years with the same iron flux and no freshwater pertur-195 bation. 196

In each of these simulations, the North Atlantic Deep Water (NADW) transport is calculated as the maximum meridional Atlantic overturning streamfunction at 30°N between 1500 and 3500m depth. Antarctic Bottom Water transport (AABW) is calculated as the minimum meridional global overturning streamfunction at 35°S below 3000m depth. North Pacific Deep Water transport is calculated as the maximum meridional Indo-Pacific overturning streamfunction at 30°N below 700m depth.

In addition, simulated dissolved inorganic carbon (DIC) is decomposed into its three main contributors: respired organic carbon (C_{reg}) , DIC generated by dissolution of calcium carbonate (C_{CaCO_3}) and preformed carbon (C_{pref}) following the methods described below.

2.3 CO₂ decomposition

Changes in sea surface pCO₂, which influence the magnitude and direction of airsea flux exchange, are controlled by changes in sea surface temperature (SST), sea surface salinity (SSS), alkalinity (ALK) and DIC.

The sea surface pCO_2 anomalies can be decomposed into the individual contributions using the equations given below (Sarmiento & Gruber, 2006):

$$\Delta p CO_2 = \Delta p CO_2^{SST} + \Delta p CO_2^{SSS} + \Delta p CO_2^{ALK} + \Delta p CO_2^{DIC}$$
(1)

The SST contribution is derived from:

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$$\Delta p C O_2^{SST} = e^{(\gamma_{SST} \times \Delta SST)} \times p C O_2^{ref} - p C O_2^{ref} \tag{2}$$

where $\gamma_{SST} = 0.0423$ (Sarmiento & Gruber, 2006), and pCO_2^{ref} represents the sea surface pCO_2 value of the 40ka-control simulation.

216 Contributions from DIC, ALK, SSS are derived from:

$$\Delta p C O_2{}^X = \gamma_X \times \Delta X \times p C O_2{}^{ref} / \bar{X} \tag{3}$$

where, X represents DIC, ALK or SSS; \bar{X} is the mean of X during PI; and γ_X is equal to 13, -11 and 1 for DIC, ALK and SSS respectively (Sarmiento & Gruber, 2006; Smith & Marotzke, 2008; Egleston et al., 2010; Jiang et al., 2019).

220 3 Results

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$3.1\ \ {\rm Carbon}\ {\rm cycle}\ {\rm response}\ {\rm to}\ {\rm an}\ {\rm AMOC}\ {\rm shutdown}$

As a response to the freshwater discharge in the North Atlantic in experiment FW 222 (Figure 2a) during phase 1, the NADW transport decreases gradually from a maximum 223 of ~ 8 Sv and shuts off completely after 400 years of meltwater addition (Figure 2c) and 224 until the end of phase 2. NPDW transport strengthens by ~ 3 Sv over 1000 years, while 225 AABW transport weakens initially by ~ 1.5 Sv during phase 1 and then increases slightly 226 during phase 2 (Figure 2d,e). Younger age of water masses at intermediate depths south 227 of 30°S (Figure 2f, 3d-f) indicates enhanced Antarctic Intermediate water (AAIW) trans-228 port in the South Pacific by the end of phase 2. 229

As described elsewhere (Saenko et al., 2004; Okazaki et al., 2010), a weakening in
 NADW transport is accompanied by an enhanced NPDW formation in the North Pa cific and AAIW formation in the Southern Ocean due to an increase in surface salinity
 arising from oceanic and atmospheric teleconnections with the North Atlantic (Figure 3b).

In agreement with earlier studies (Menviel et al., 2020), an inter-hemispheric thermal seesaw pattern, with a 3.3 degrees decrease in North Atlantic (35°W:10°W,47°N:55°N) sea surface temperatures (SSTs) and a 0.4 degrees increase in Southern Ocean SST, is simulated during the AMOC shutdown (Figure 3a). There is no significant change in the Southern Hemisphere annual mean sea ice edge, which is situated at 53°S in the Indian and Atlantic sectors and at 62°S in the Pacific sector (Figure 3a).

The combination of greater ocean stratification (attributable to higher SSTs and SSS), moderate increase in AAIW formation and the reduction in AABW transport lead to less surface nutrient availability during phase 1. Therefore, there is an overall decrease in both diatoms (by 3%) and coccolithophores (by 6%) abundance in the Southern Ocean during phase 1 (Figure 2h,j).

However, during phase 2, a further increase in AAIW formation, combined with 245 a slow recovery of AABW leads to an increase in ventilation and deepening of the mixed 246 layer depth (MLD) in the Southern Ocean (Figure 3c), which causes greater nutrient avail-247 ability particularly in the Pacific sector. The locally increased nutrients are quickly taken 248 up by the diatoms (being prescribed higher growth rates and half saturation constants 249 for nutrients than coccolithophores (Kvale et al., 2021; Saini et al., 2021)), increasing di-250 atom's abundance by $\sim 16\%$ in the Pacific sector of the Southern Ocean, while coccol-251 ithophores decline (Figure 4a,b). This increase in diatoms is responsible for the total South-252 ern Ocean diatom increase (+6.7%) shown in Figure 2h during phase 2. On the contrary, 253 coccolithophores decrease by $\sim 9.6\%$ in the Southern Ocean as they are outcompeted by 254 diatoms (Figure 4b,2j). Overall, EP is 8.6% lower (Figure 2i,4c) and NPP 5% lower in 255 the Southern Ocean (not shown) during the AMOC shutdown. 256



Figure 2. Transient evolution of simulated biological and physical variables. Time series of (a) freshwater flux (Sv) applied to the North Atlantic and (g) global iron flux (Gmol yr⁻¹), used as forcings in experiments (orange) FW, (red) FE, and (green) FWFE. Please note that the green line overlaps the orange line in (a) and the red line overlaps the green line in (g). The black line represents 200 years of 40ka-control experiment with prognostic CO₂. Time series of simulated (b) global atmospheric CO₂ concentration (ppm) anomaly compared to 40ka-control, (c) NADW (Sv), (d) AABW (Sv), and (e) NPDW transport (Sv), (f) Southern Ocean ideal age anomaly averaged over intermediate depths (600-1700m, years) compared to 40ka-control; time series anomalies of simulated (h) Southern Ocean depth integrated diatoms (PgC), (i) Southern Ocean export production at 177.5m depth (PgC), (j) Southern Ocean depth integrated coccolithophores (PgC), (k) global terrestrial carbon (GtC) and (l) global ocean carbon (GtC) compared to 40ka-control. The Southern Ocean (SO in the figure) is defined as the region south of 30°S, and all the biological tracers are integrated over the Southern Ocean.

Table 1. Changes in atmospheric CO_2 , terrestrial and ocean carbon at the end of phase 2 (yr 1000) compared to the 40ka-control simulation.

Experiments	Change in CO ₂ (ppm)	Atmospheric carbon (GtC)	Terrestrial carbon (GtC)	Total Ocean carbon (GtC)	Atlantic, north of 30°S (GtC)	Pacific, north of 30°S (GtC)	Indian, north of 30°S (GtC)	Southern Ocean, south of 30°S (GtC)
FW	$ \begin{array}{c} +0.5 \\ +6 \\ +7 \end{array} $	1	7.5	-8	140	-120	-19	-9
FE		12	23	-35	8	10	-3	-50
FWFE		14	31	-45	145	-110	-21	-59



Figure 3. FW experiment at year 1000 (end of phase 2) minus 40ka-control anomalies of (a) sea surface temperature (°C), (b) sea surface salinity (psu), (c) ventilation depth (m), and zonally averaged ideal age (years) over the (d) Atlantic, (e) the Pacific, and (f) Indian sector; where red in d-f indicates reduction in ventilation. Overlaid contours in (a) represent the 15% annual mean sea-ice concentration in (red) 40ka-control and in (green) FW experiment at the end of phase 2.

In contrast, significantly weaker NADW transport and higher stratification, thus 257 higher residence time, leads to a greater amount of regenerated phosphate (P_{reg}) at in-258 termediate depths in the North Atlantic and in the deep Atlantic ocean (Figure S1). Cor-259 respondingly, DIC, in the form of regenerated carbon (C_{reg}) (Figure S2), accumulates 260 in the Atlantic Ocean. Positive DIC anomalies are simulated below 500m depth in the 261 North Atlantic and below 1500m depth in the South Atlantic (Figure 5a). At the end 262 of phase 2, the Atlantic Ocean carbon reservoir has thus increased by 140 GtC (Table 1). 263 On the contrary, the Pacific Ocean loses 120 GtC, because of increased ventilation as-264 sociated with stronger NPDW and AAIW transports (Figure 2e,f, 3d-f, Table 1). 265

Enhanced intermediate depth ventilation in the Southern Ocean (Figure 2f), and 266 to some extent lower Southern Ocean EP, leads to a decrease in DIC, and particularly 267 in C_{reg} , in the upper 1000m of the Southern Ocean (Figure 5a-c, S2a-c). This anomaly 268 spreads at intermediate depths within AAIW (Figure 5a-c). The positive DIC anoma-269 lies in the deep Pacific and Indian Ocean (Figure 5b,c) are mainly due to increased pre-270 formed carbon (C_{pref}) resulting from the lower nutrient utilisation at high southern lat-271 itudes (Figure S1, S2d-f). In the Indian Ocean, an increase in C_{reg} is also simulated be-272 low 2500m depth (Figure S2c). Overall, DIC decreases by 19 GtC in the Indian Ocean 273 and by 9 GtC in the Southern Ocean (Table 1, Figure 5c). 274

At the surface of the Southern Ocean, between $\sim 47^{\circ}$ S and 60° S, higher DIC con-275 centration due to reduction in EP and higher ventilation, increases the surface ocean par-276 tial pressure of CO_2 (p CO_2 , Figure 6b). Conversely, an increase in surface alkalinity in 277 the Southern Ocean (Figure S3), associated with the decrease in coccolithophore pop-278 ulation (Figure 4b), partly compensates the effect of higher DIC and ventilation on sur-279 face ocean pCO_2 (Figure 6b). In addition, higher SST and SSS lead to a reduction of 280 CO_2 solubility in sea water (Figure 6b). Therefore, higher surface DIC and a weakened 281 solubility pump cause a CO_2 outgassing in the Southern Ocean (red regions south of $30^{\circ}S$ 282



Figure 4. Diatoms, coccolithophores and EP anomalies for experiments (top) FW, (center) FE, and (bottom) FWFE at year 1000 (end of phase 2) compared to the 40ka-control simulation. Anomalies in depth integrated (a,d,g) diatoms (gC m⁻²) and (b,e,h) coccolithophores (gC m⁻²). (c,f,i) Export production anomalies at 177.5m (gC m⁻²yr⁻¹). Paleo-proxy estimated anomalies at 39ka compared to 40ka are added on top of the simulated anomalies for qualitative comparison of model and data: (a, d, g) opal flux (triangles) (Anderson et al., 2009; Thöle et al., 2019; Amsler et al., 2022) and brassicasterol concentration (circle) (Sachs & Anderson, 2005); (c, f,i) alkenone flux (diamonds) (Sachs & Anderson, 2003, 2005) and organic carbon flux (square) (Anderson et al., 2014; Thöle et al., 2019). Dark (light) orange represents significantly (slightly) higher values, while dark (light) blue represents significantly (slightly) lower values.



Figure 5. Zonally averaged DIC anomalies $(mmol m^{-3})$ over (left) the Atlantic, (center) the Pacific, and (right) Indian ocean for experiments (top) FW, (center) FE, and (bottom) FWFE at year 1000 (end of phase 2) compared to the 40ka-control simulation.

²⁸³ in Figure 7b), and particularly in the southeast Pacific between $\sim 47^{\circ}$ S:60°S. In contrast, ²⁸⁴ the increase in surface alkalinity leads to carbon drawdown from the atmosphere into the ²⁸⁵ Southern Ocean (blue regions south of 40°S in Figure 7b). Overall, the Southern Ocean ²⁸⁶ carbon outgassing decreases by $\sim 8\%$. We also see an anomalous outgassing from the north-²⁸⁷ east Atlantic (Figure 7b), which is due to a decrease in surface alkalinity (Figure 6a) in ²⁸⁸ response to the freshwater flux addition in this region.

The changes in carbon exchange with the atmosphere causes the global ocean carbon to decrease by 8 GtC by the end of phase 2 (Table 1, Figure 2l). This is accompanied by a 7.5 GtC increase in terrestrial carbon reservoir (Figure 2k), and about 1 GtC carbon uptake by the atmosphere leading to an insignificant rise in CO₂ (Figure 2b) at the end of phase 2.

²⁹⁴ During the AMOC recovery in phase 3, the NADW transport increases to ~ 14 Sv ²⁹⁵ before equilibrating at 7 Sv once the salt flux is turned off (Figure 2c). NPDW trans-²⁹⁶ port also reduces back to near initial conditions, while AABW transport stabilizes to a ²⁹⁷ slightly higher value, at 11 Sv (Figure 2d,e). The addition of the salt flux causes a ~ 1 ²⁹⁸ ppm rise in CO₂, after which it reduces back to the initial value.

Diatoms increase by 21% compared to phase 2 in the Indian Ocean sector south of the annual sea ice edge, and coccolithophores increase by 6% mostly everywhere north of the annual sea ice edge (Figure S4a,b). This increases the total Southern Ocean EP by 7.6% at the end of phase 3 compared to phase 2 and brings EP back to a similar value as in 40ka-control.

3.2 Carbon cycle response to a reduction in aeolian iron flux.

When the aeolian iron input to the ocean is abruptly reduced (Figure 2g), the CO_2 305 increases by 6 ppm over 1000 years in experiment FE (Figure 2b). There are no changes 306 in ocean circulation in this experiment, and therefore the changes in CO_2 are due to the 307 reduction in the biological pump efficiency and the land carbon changes responding to 308 higher CO_2 and temperatures. Plankton abundances south of ~47°S are reduced due 309 to decreased iron flux in the Southern Ocean (Figure 4d.e). Diatoms decrease by 19% 310 in the Atlantic, 5.7% in the Pacific and $\sim 9.5\%$ in the Indian sector south of $\sim 47^{\circ}$ S, while 311 coccolithophores decrease by 27% south of $\sim 47^{\circ}$ S. This leads to reductions in EP (Fig-312 ure 4f) and NPP south of $\sim 47^{\circ}$ S. 313

Reduced nutrient utilization within the Antarctic zone causes an advection of ex-314 cess nutrients northward (Figure S5), increasing diatoms (by 88% in the Indian region) 315 and coccolithophores (by 23% in total) abundances and thus EP and NPP north of $47^{\circ}S$ 316 in the Southern Ocean (Figure 4d-f). Thereby, EP decreases by 17% south of 47° S and 317 increases by 29% between $47^{\circ}S$ and $30^{\circ}S$ as a response to nutrient reorganization, with 318 an overall 5.5% decrease in diatoms and 1.6% decrease in coccolithophores in the South-319 ern Ocean. The total Southern Ocean EP decreases by 7% at the end of phase 2 (Fig-320 ure 2i) due to a 5% decrease in nutrient utilisation in this sector. 321

The lower EP south of 47°S causes an increase in surface DIC. However, this also leads to reduced DIC, in the form of regenerated DIC (C_{reg}) within AABW (Figure 5df and S6a-c). These negative DIC anomalies are further advected into the deep Atlantic and Indo-Pacific basins (Figure 5d-f). In contrast, greater DIC content is simulated north of 47°S in the upper 2500m depth in all the basins. There is also a small increase in surface alkalinity in the Southern Ocean (Figure S3) due to the overall decrease in Southern Ocean coccolithophores (Figure 2j).

No significant changes in surface alkalinity, SST and SSS are simulated between 329 47° S and 60° S (Figure 6c). In contrast, higher surface DIC leads to $\sim 48\%$ increase in 330 CO_2 outgassing between 47°S and 60°S (Figure 6c and red regions south of 40°S in Fig-331 ure 7c). This leads to a 50 GtC carbon loss from the Southern Ocean in experiment FE 332 (Table 1). In total, while the global ocean loses 35 GtC (Figure 2l), the atmosphere gains 333 12 GtC, while 23 GtC are absorbed by the terrestrial biosphere (Figure 2k). During phase 334 3, CO_2 decreases gradually as the ocean biogeochemistry recovers to the initial condi-335 tions of 40ka-control. 336

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3.3 Carbon cycle response to an AMOC shutdown and iron flux reduction

In this section we analyse the combined effect of an AMOC shutdown due to freshwater input in the North Atlantic (Figure 2a, experiment FWFE), and a reduced global iron flux (Figure 2g, experiment FWFE). A 7 ppm CO₂ increase is simulated in this experiment (1 ppm higher than FE and 6.5 ppm higher than FW).

As can be seen in Figure 2c-f, the changes in ocean circulation in FWFE are similar to those of the FW experiment, with slightly larger anomalies in AABW transport and slightly smaller anomalies in NPDW transport. Figures 2 and 4 clearly show that the diatom, coccolithophore and EP responses in FWFE experiment are a linear combination of the responses simulated in FW and FE.

Diatoms increase south of 47° S in the Pacific sector due to circulation changes as in experiment FW. However, because of the parallel reduction in iron supply (which causes 6% diatom reduction in this sector), the net increase is limited to 9.5% (instead of 16% as simulated in FW) compared to 40ka-control. Similarly, the diatoms decrease south of 47°S in the Atlantic (-16%, +3% from circulation and -19% from the iron effect) and



Figure 6. Time series of sea surface pCO_2 (ppm) anomalies resulting from changes in (blue) ALK, (orange) DIC, (green) SSS, and (red) SST for (a) FW averaged over the North Atlantic, (b) FW averaged over the Southern Ocean (47°S:60°S), (c) FE over the Southern Ocean (47°S:60°S), and (d) FWFE averaged over the Southern Ocean (47°S:60°S), compared to the 40ka-control simulation. The dashed black line represents simulated sea surface pCO_2 (ppm), while the solid black line shows the sum of the ALK, DIC, SSS and SST contributions. Please note the scale differs between the sub-panels.



Figure 7. Surface carbon flux (gC $m^{-2}yr^{-1}$) for (a) 40ka-control; surface carbon flux anomalies for (b) FW, (c) FE, and (d) FWFE experiments at year 1000 (end of phase 2) compared to the 40ka-control simulation. Red indicates ocean outgassing.

Indian sectors (-14%, -3.2%) from circulation and -9.5% from the iron effect) and the in-353 crease north of 47° S in the Indian sector (+63%) is also a net outcome from changes in 354 both circulation and iron supply. Consequently, due to the weak positive anomalies in 355 the Pacific, and the stronger negative anomalies in the Atlantic and Indian sectors, the 356 Southern Ocean diatom abundance is 6% lower compared to FW but 5.8% higher com-357 pared to FE (Figure 2h) at the end of phase 2. Coccolithophores on the other hand de-358 crease by 11.4% over the Southern Ocean (Figure 2j) compared to the 40ka-control (where 359 9.6% decrease is simulated due to the circulation changes as in FW and 1.6% is simu-360 lated due to changes in iron as in FE). With these changes in the plankton population, 361 the total Southern Ocean EP reduces by 14% in FWFE at the end of phase 2 (Figure 4i). 362

The larger simulated decrease in C_{reg} in the FWFE simulation (Figure S7a-c) com-363 pared to that in FW and FE, due to the weaker (-13%) Southern Ocean nutrient util-364 isation (Figure S8), causes a larger decrease in DIC below 200m depth in the Southern 365 Ocean (Figure 5g-i). Simulated air-sea CO_2 fluxes in the FWFE experiment (Figures 6d 366 and 7d) as well as the changes in ocean carbon (Table 1) in the Southern Ocean are a 367 combination of FW and FE carbon changes. Therefore, a total of ~ 45 GtC are lost from 368 the ocean in experiment FWFE (Table 1, Figure 2l). Terrestrial carbon increases by 31 369 GtC (Figure 2k), while atmospheric carbon increases by 14 GtC by the end of phase 2. 370

371 4 Discussion

Our study indicates that to understand the mechanisms behind atmospheric CO₂ increase during HS, an investigation of dust related impacts is crucial in addition to previously explored feedbacks from oceanic circulation changes.

In our idealized experiment simulating a HS under MIS 3 boundary conditions, the 375 simulated SST anomalies in the North Atlantic $(\sim -3^{\circ}C)$ are consistent with the alkenone 376 based SST proxies from the Iberian Margin (Martrat et al., 2007) and the North Atlantic 377 (Cacho et al., 1999). On the contrary, the simulated Southern Ocean SST anomalies $(+0.4^{\circ}C)$ 378 are significantly lower than what is inferred from marine records $(+\sim 2^{\circ}C)$ (Pahnke et 379 al., 2003; Kaiser et al., 2005; Barker et al., 2009; Caniupán et al., 2011) but are still within 380 the range of previously simulated responses to an AMOC shutdown (Kageyama et al., 381 2013; Menviel et al., 2014, 2015). 382

The changes in global circulation (Figure S9), and therefore the changes in South-383 ern Ocean physics, impact marine ecosystems in this region. As pointed out earlier, high 384 resolution paleo evidence of changes in EP during HS are limited. The simulated decrease 385 in coccolithophores and EP at $\sim 45^{\circ}$ S east of the South Island of New Zealand in our FW 386 simulation (Figure 4b,c) is in contradiction with the increase in alkenone (proxy for EP) 387 and C_{37} methyl ketones (a marker for coccolithophores) concentrations recorded in a ma-388 rine sediment core, MD97-2120 (Sachs & Anderson, 2005), at this location near Chatham 389 Rise during H4 (Figure 4c). Our experiment FWFE, which includes the combined im-390 pact from the iron flux reduction (Figure 4e,f) and freshwater forcing (Figure 4b,c), im-391 proves this model data agreement by simulating an increase in coccolithophores and EP 392 at this location (Figure 4h,i). The simulated increase in diatom abundance east of New 393 Zealand, due to deeper MLD in experiments FW and FWFE, is in agreement with bras-394 sicasterol concentrations (a marker for diatoms) (Figure 4a,g) observed in the Chatham 395 rise core (Sachs & Anderson, 2005). Increased diatom abundance south of $\sim 50^{\circ}$ S in the 396 Atlantic in FW and FWFE and a decrease in diatoms between $\sim 50^{\circ}$ S and $\sim 55^{\circ}$ S in the 397 Indian sector in FE and FWFE, are also in agreement with the marine sediment opal 398 flux records from the Southern Ocean (Anderson et al., 2009; Thöle et al., 2019; Am-399 sler et al., 2022). In the sub-Antarctic, simulated diatom changes north of $\sim 50^{\circ}$ S in FW 400 are consistent with the proxy records from Atlantic (Sachs & Anderson, 2003; Ander-401 son et al., 2014) and Indian sectors (Thöle et al., 2019; Amsler et al., 2022), while in the 402

FE and FWFE simulations, the diatom increase is consistent with only one record (Amsler et al., 2022) in the Indian sector.

The simulated EP increase at $\sim 45^{\circ}$ S in simulations FE and FWFE is in contra-405 diction with the reduced alkenone and organic carbon fluxes (Sachs & Anderson, 2003; 406 Anderson et al., 2014) recorded in marine sediment cores in the subantarctic Atlantic. 407 However, the simulated EP decrease south of 40° S in experiment FW is in agreement 408 with these paleo EP records. The simulated increase in EP in the Indian sector is con-409 sistent with the organic carbon flux proxy (Thöle et al., 2019). In experiment FWFE, 410 changes in the simulated diatom abundance and in EP show a $\sim 60\%$ and 40% agreement 411 with the available proxy records, respectively. 412

The simulated EP decrease in FW, along with the simulated decline south of $\sim 47^{\circ}$ S 413 in FE and FWFE experiments, is in agreement with the EP response to an AMOC shut-414 down obtained with another version of the UVic model (Menviel et al., 2014). Based on 415 the above-mentioned proxy evidence and our simulated results, we suggest that an EP 416 decrease due to reduced iron supply during HS could most likely have occurred south 417 of $\sim 45^{\circ}$ S in the Southern Ocean. Clearly, better constraints on changes in EP and plank-418 ton abundances during HS, along with additional proxy records of the last glacial millennial-419 scale climate variability are required. 420

Enhanced AAIW transport and reduction in Southern Ocean EP lead to an increase in intermediate and deep ocean oxygen concentrations south of ~40°S in all of our simulations (Figure S10). This is in agreement with the reconstructed bottom water oxygen concentrations (Gottschalk et al., 2016), and authigenic Uranium based deep oxygenation records (Jaccard et al., 2016) in sub-Antarctic Atlantic marine sediment cores at ~45°S and ~55°S respectively.

A total of $7ppm CO_2$ increase is simulated in experiment FWFE due to the com-427 pounding effects of changes in oceanic circulation and a reduced iron dust flux in the South-428 ern Ocean. Most of this CO_2 increase is due to the reduced iron availability (experiment 429 FE). This is caused by a larger carbon loss (50 GtC compared to 9 GtC) from the South-430 ern Ocean in experiment FE compared to FW. In simulation FW, outgassing in the North 431 Atlantic is compensated by the higher carbon sequestration (140 GtC in FW compared 432 to 8 GtC in FE, Table 1) in the deep North Atlantic Ocean due to the AMOC shutdown, 433 and by the decrease in outgassing in the Southern Ocean. Due to the CO_2 fertilization 434 effect, the CO_2 increase in FWFE simulation enhances terrestrial primary productivity. 435 This leads to a 12 GtC increase in terrestrial vegetation, as well as an increase in litter 436 fall, leading to a 19 GtC increase in soil carbon. The total terrestrial carbon thus increases 437 by ~ 31 GtC. The simulated changes in terrestrial carbon in this study are in contradic-438 tion to previous modelling studies which show a decrease in terrestrial carbon in response 439 to an AMOC shutdown (Scholze et al., 2003; Köhler et al., 2005; Menviel et al., 2008) 440 but are in agreement with freshwater simulations performed with another version of the 441 UVic ESCM (Huiskamp & Meissner, 2012). However, it should be noted that the dis-442 crepancies in these results could be related to having different vegetation models, dif-443 ferent boundary conditions, and different freshwater flux forcings. 444

The 7 ppm rise is significantly lower than the maximum observed CO_2 increase of 445 20 ppm during HS within MIS 3 (Ahn & Brook, 2008; Bereiter et al., 2015; T. K. Bauska 446 et al., 2021). It is also lower than the simulated increase of 9 ppm simulated by Parekh 447 et al. (2008) as a response to reduced dust flux, although using a much simpler biogeo-448 chemical model than our study and under PI conditions. Jochum et al. (2022) simulated 449 an increase of ~ 8 ppm in CO₂ in their experiment with a longer stadial and a reduction 450 in PI iron flux by 50%. The discrepancy between our simulated CO_2 changes and the 451 estimates from proxy records can somewhat be explained by the lack of enhanced ven-452 tilation in the Southern Ocean in our simulations. Previous modelling studies have sug-453 gested that enhanced Southern Ocean ventilation could have contributed to the atmo-454

spheric CO_2 increase (Menviel et al., 2014, 2015) during HS. Some of these changes in 455 Southern Ocean ventilation changes could result from intensified Southern Hemisphere 456 westerlies (Menviel et al., 2018; Huiskamp et al., 2016). In addition, recent studies have 457 also highlighted the role of changes in AAIW in driving atmospheric CO_2 increases (Menviel 458 et al., 2018; Yu et al., 2022). Due to the coarse resolution of the ocean model and lack 459 of a dynamic atmosphere (and thus constant Southern Hemisphere westerlies) in the ex-460 periments presented above, it is possible that changes in Southern Ocean circulation and 461 thus their impact on atmospheric CO_2 are not appropriately captured. 462

463 There is also uncertainty involving the total amount of dissolved iron available for uptake by phytoplankton under different climates. In the experiments presented here, 464 we use 3% iron solubility, which is based on the most plausible estimate of glacial iron 465 solubility (3-5%) (Conway et al., 2015; Shoenfelt et al., 2018; Saini et al., 2023). A higher 466 iron solubility as initial MIS3 conditions would lead to greater CO_2 release when the iron 467 supply is reduced (Saini et al., 2023). We also do not consider the impact of potential 468 changes in ligand concentrations in the ocean which can also impact iron solubility (Parekh 469 et al., 2006, 2008). Additionally, better constraints on the pattern and amount of dust 470 fluxes under different climates are required to constrain the contribution of iron fertil-471 isation during millennial events. 472

473 Open Research Section

The modelling data from all the simulations are temporarily available at https:// datadryad.org/stash/share/sVMbSADOs_UdVAIvhvE_psxF-I_RUts-WOZtPjsOUr4 for the review process. The data will be published on the DRYAD repository through https:// doi.org/10.5061/dryad.k3j9kd5dt, once the manuscript is accepted.

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Transient response of Southern Ocean ecosystems during Heinrich stadials

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Key Points: 10

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11	•	Simulated marine ecosystems and CO ₂ respond linearly to the combined impact
12		of freshwater addition and reduced iron flux into the ocean.
13	•	A maximum of 7 ppm increase in CO_2 is simulated due to the AMOC shutdown
14		and weakened iron fertilisation under MIS 3 boundary conditions.
15	•	Reduced aeolian iron flux in the Southern Ocean during Heinrich Stadials can lead
16		up to 6 ppm rise in CO_2 .

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17 Abstract

Antarctic ice core records suggest that atmospheric CO₂ increased by 15 to 20 ppm dur-18 ing Heinrich stadials (HS). These periods of abrupt CO_2 increase are associated with a 19 significant weakening of the Atlantic meridional overturning circulation (AMOC), and 20 a warming at high southern latitudes. As such, modelling studies have explored the link 21 between changes in AMOC, high southern latitude climate and atmospheric CO₂. While 22 proxy records suggest that the aeolian iron input to the Southern Ocean decreased sig-23 nificantly during HS, the potential impact on CO₂ of reduced iron input combined with 24 oceanic circulation changes has not been studied in detail. Here, we quantify the respec-25 tive and combined impacts of reduced iron fertilisation and AMOC weakening on CO_2 26 by performing numerical experiments with an Earth system model under boundary con-27 ditions representing 40,000 years before present (ka). Our study indicates that reduced 28 iron input can contribute up to 6 ppm rise in CO_2 during an idealized Heinrich stadial. 29 This is caused by a 5% reduction in nutrient utilisation in the Southern Ocean, leading 30 to reduced export production and increased carbon outgassing from the Southern Ocean. 31 An AMOC weakening under 40ka conditions and without changes in surface winds leads 32 to a ~ 0.5 ppm CO₂ increase. The combined impact of AMOC shutdown and weakened 33 iron fertilisation is almost linear, leading to a total CO_2 increase of 7 ppm. Therefore, 34 this study highlights the need of including changes in aeolian iron input when studying 35 the processes leading to changes in atmospheric CO_2 concentration during HS. 36

37 1 Introduction

Paleoproxy records from Greenland ice cores have shown the occurrence of abrupt 38 climate variability during the last glacial period (Johnsen et al., 1972; Dansgaard et al., 39 1982; Kindler et al., 2014). Such variability, referred to as Dansgaard-Oeschger (D/O)40 variability, is characterized by an abrupt rise in Greenland air temperatures on decadal 41 timescales (D/O event), followed by a gradual cooling over hundreds or thousands of years 42 to cold (stadial) stages (G. Bond et al., 1993; Dansgaard et al., 1993). About twenty-43 five such climatic oscillations have been recorded in Greenland ice cores (Kindler et al., 44 2014) out of which 14 D/O events occurred during Marine Isotope Stage 3 (MIS 3, 65-45 27 thousand years before present (ka BP hereafter)). D/O stadials are associated with 46 layers of ice rafted debris in North Atlantic marine sediment cores, indicating iceberg dis-47 charges into the ocean from the surrounding ice sheets (Van Kreveld et al., 2000). Some 48 stadials are characterised by especially thick layers of ice rafted debris originating from 49 the Laurentide ice-sheet (Heinrich, 1988; W. Broecker et al., 1992; Elliot et al., 1998; Snoeckx 50 et al., 1999; Grousset et al., 2000), and are referred to as Heinrich Events (HEs). The 51 origin and timing of D/O variability is still debated (W. S. Broecker et al., 1990; W. S. Broecker, 52 1994; G. C. Bond & Lotti, 1995; Hodell et al., 2010; Marcott et al., 2011; Barker et al., 53 2015; Menviel et al., 2020). 54

Paleoproxy records and modelling studies have suggested that Henirich stadials (HS), 55 stadials which contain a HE, were associated with a significant weakening of the AMOC 56 (Menviel et al., 2020). Such an AMOC weakening would lead to a reduction in the north-57 ward heat transport in the Atlantic, therefore causing a significant cooling in the North 58 Atlantic and Greenland region (Ganopolski & Rahmstorf, 2001; Meissner et al., 2002; 59 Huber et al., 2006; Kageyama et al., 2010; Buizert et al., 2014; Kindler et al., 2014; Henry 60 et al., 2016; Menviel et al., 2020). Due to the reduced northward oceanic heat transport 61 in the Atlantic, the AMOC weakening would lead to a warming in the South Atlantic, 62 and at high southern latitudes (Crowley, 1992; Stocker, 1998; Blunier & Brook, 2001; 63 Seidov & Maslin, 2001; Stocker & Johnsen, 2003; Jouzel et al., 2007; Timmermann et 64 al., 2010; Pedro et al., 2018). 65

Antarctic ice core records reveal that there was a rise in atmospheric CO_2 concentration during Heinrich stadials (HS) (Ahn & Brook, 2008, 2014; Parrenin et al., 2013;

Bereiter et al., 2015; T. K. Bauska et al., 2021). Observations also suggest that concur-68 rent to each HS in the North Atlantic during MIS 3, there was an Antarctic warm event 69 (also known as Antarctic Isotope Maxima, AIM) coinciding with the CO₂ increase (Buizert 70 et al., 2015; T. K. Bauska et al., 2021). For example, during Heinrich stadial 4 (H4), which 71 is associated with an intense ice rafted debris deposition in the North Atlantic (Hemming, 72 2004), the temperature in Greenland decreased by $\sim 5^{\circ}$ C (Huber et al., 2006; Kindler et 73 al., 2014), while Antarctic temperatures rose by 2-3°C (Jouzel et al., 2007), and global 74 CO₂ concentration increased by 15 to 20 ppm (Ahn & Brook, 2014; Bereiter et al., 2015; 75 T. Bauska et al., 2018) (Figure 1a-c). 76

A compilation of numerical studies by Gottschalk et al. (2019) suggests that sim-77 ulated atmospheric CO_2 levels can vary between -7 to +14 ppm in response to an AMOC 78 shutdown under interglacial boundary conditions, whereas under glacial boundary con-79 ditions, this range can vary between -5 to +6 ppm. Modelling studies have further sug-80 gested that the rise in CO_2 during HS was caused by a decrease in deep Pacific and South-81 ern Ocean carbon resulting from stronger North Pacific Deep Water (NPDW) formation 82 and enhanced Southern Ocean outgassing (Huiskamp & Meissner, 2012; Menviel et al., 83 2014, 2018). Enhanced Southern Ocean outgassing could result from stronger convec-84 tion or enhanced wind-driven upwelling as also suggested from paleo-proxy ventilation 85 records (Anderson et al., 2009; Skinner et al., 2020). 86

Marine sediment cores from the South Atlantic (Martínez-García et al., 2011) and 87 the South Pacific (Lamy et al., 2014) as well as Antarctic ice cores (Fischer et al., 2010; 88 Lambert et al., 2012) have highlighted millennial-scale fluctuations in the atmospheric 89 dust flux deposition at high southern latitudes that are opposite to changes in atmospheric 90 CO_2 levels (Figure 1d). The associated changes in aeolian iron input to the ocean have 91 been suggested to impact CO₂ concentration by modulating Southern Ocean nutrient 92 utilisation (Martin, 1990; Martínez-García et al., 2014). For aminifera-bound $\delta^{15}N$ (FB-93 δ^{15} N) records (Martínez-García et al., 2014; Studer et al., 2015) suggest that the greater 94 iron supply can stimulate higher nutrient utilisation in the ocean, by liberating the iron 95 limitation effect, and causing higher export production (EP). 96

Many modelling studies have assessed the impact of changes in iron input to the 97 ocean on Southern Ocean EP and atmospheric CO_2 by performing sensitivity experiments 98 under Last Glacial Maximum (Aumont et al., 2003; Bopp et al., 2003; Oka et al., 2011; qq Lambert et al., 2015; Muglia et al., 2017; Khatiwala et al., 2019; Yamamoto et al., 2019; 100 Lambert et al., 2021; Saini et al., 2021) and pre-industrial (PI) (Aumont & Bopp, 2006; 101 Tagliabue et al., 2009, 2014) boundary conditions. However, even though the link be-102 tween aeolian iron input and Southern Ocean EP should also hold for millennial scale 103 climate changes (Anderson et al., 2014), the response of marine ecosystems and ocean 104 biogeochemistry to changes in iron dust flux during millennial-scale events of the last glacial 105 period has not been simulated in detail. So far, only one experiment studied the impact 106 of millennial-scale changes in dust flux on atmospheric CO_2 by forcing the Bern3D model 107 with reconstructed dust deposition from DOME C ice core under PI boundary condi-108 tions (Parekh et al., 2008). They simulated the largest increase in atmospheric CO_2 (+9 109 ppm) during H4 as a response to the lowest reconstructed aeolian dust flux. 110

Alkenone based EP evidence from a marine sediment core east of New Zealand, in-111 dicates higher productivity during HS over the past 70,000 years in this region (Sachs 112 & Anderson, 2005). This is in agreement with the higher amount of opal flux during HS 113 obtained from four cores in the Antarctic zone (south of $\sim 60^{\circ}$ S in the Pacific sector and 114 south of $\sim 50^{\circ}$ S in the Atlantic sector) (Anderson et al., 2009). However, recent stud-115 116 ies (Anderson et al., 2014; Martínez-García et al., 2014) based on alkenone concentrations, opal and organic carbon fluxes measured in sub-Antarctic Atlantic sediment cores 117 (close to $\sim 40^{\circ}$ S), point towards a reduction in biological productivity during HS when 118 the dust supply declined (Lambert et al., 2012). This is also in agreement with the records 119 of higher deep ocean oxygenation during HS in the sub-Antarctic Atlantic (Gottschalk 120



Figure 1. Time series of (a) Greenland air temperature anomalies compared to today (°C) reconstructed from the NGRIP ice core (Kindler et al., 2014); (b) Antarctic deuterium (δ D) concentration (‰) anomaly from today as recorded in EPICA DOME C ice core (Jouzel et al., 2007), representing temperature variability in Antarctica; (c) atmospheric CO₂ concentrations (ppm) from EPICA DOME C ice core (Bereiter et al., 2015); (d) dust flux (mg/m²/yr) from EPICA DOME C ice core (Lambert et al., 2012); Grey shade represents Heinrich stadials during MIS 3 (65-27 ka).

et al., 2016; Jaccard et al., 2016), which is an indicator of less remineralized organic carbon in the deep ocean. However, lower carbon sequestration in the ocean can also be due to increased ventilation as recorded from radiocarbon changes in the deep Southern Ocean during H4 (Gottschalk et al., 2016). Therefore, the Southern Ocean biological efficiency is impacted by more than just iron limitation. As there are only a few cores at sparse locations, it is thus challenging to draw robust conclusions about EP changes in the Southern Ocean during HS.

In addition, while many studies assessed the impact of an AMOC shutdown or an 128 increase in aeolian iron input on the carbon cycle, no modelling study has yet looked into 129 the combined impact of an AMOC shutdown and a decrease in aeolian iron flux on the 130 carbon cycle under appropriate glacial boundary conditions. A study by Jochum et al. 131 (2022) analysed the impact of longer stadials and reduced iron flux on global atmospheric 132 CO_2 concentration. However, they investigated this response with an experiment resem-133 bling LGM climate conditions and iron flux reduced by 50% from PI dust flux. Here, we 134 investigate the response of marine ecosystems and atmospheric CO_2 to the individual 135 and combined impacts of AMOC shutdown and reduced iron flux input in the South-136 ern Ocean under MIS 3 boundary conditions. We focus on the changes in ecosystems and 137 atmosphere-ocean CO_2 exchange in the Southern Ocean as the iron fertilisation effect 138 is crucial in this region (Saini et al., 2023). 139

 $_{140}$ 2 Methods

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2.1 Model

The experiments are performed with the version 2.9 University of Victoria Earth 142 System Climate Model of intermediate complexity (UVic ESCM). It includes the MOM2 143 ocean general circulation model (Pacanowski, 1995) coupled to a sea ice model (Semtner, 144 1976; Hibler, 1979; Hunke & Dukowicz, 1997), a land surface scheme and a dynamic veg-145 etation model (Meissner et al., 2003), a sediment model (Archer & Maier-Reimer, 1994; 146 Meissner et al., 2012) with fixed weathering flux, and a vertically integrated 2-D energy 147 and moisture balance atmospheric model (Fanning & Weaver, 1996). All model compo-148 nents are on a grid with a spatial resolution of 3.6 by 1.8 degrees and there are 19 ver-149 tical depth levels in the ocean. Seasonally varying solar insolation (Berger, 1978) at the 150 top of the atmosphere and seasonal variations in wind stress and wind fields (Kalnay et 151 al., 1996) are used as external forcing to drive the model. An ideal age tracer is added 152 to track water mass age (Koeve et al., 2015). A detailed description of the model struc-153 ture and physics can be obtained from (Weaver et al., 2001; Meissner et al., 2003; Eby 154 et al., 2009; Mengis et al., 2020). 155

The climate model incorporates the recently developed ecosystem model called Kiel Marine Biogeochemistry Model (KMBM), v3 (Kvale et al., 2021; Saini et al., 2021), which represents the ocean carbon cycle. This model includes prognostic equations for diatoms (silicifying plankton) and coccolithophores (calcifying plankton), in addition to general phytoplankton and diazotrophs. It also includes a prognostic iron cycle (Nickelsen et al., 2015) featuring hydrothermal sources (Yao et al., 2019), and fully incorporated silica and CaCO₃ cycles. Full description of the ecosystem model can be found in Kvale et al. (2021).

163 2.2 Experimental design

A control simulation (40ka-control) using constant atmospheric CO₂ levels set at 200 ppm (Bereiter et al., 2015), with orbital forcing (Berger, 1978) and ice sheet topography (obtained from an offline ice sheet simulation (Abe-Ouchi et al., 2013)) corresponding to 40ka BP is integrated for 10,000 years to reach an equilibrium state. We use iron (LGM-fe) and silica (LGM-Si) dust fluxes based on the Last Glacial Maximum (LGM) dust deposition map from Lambert et al. (2012) and a iron/silica to dust percentage map from Zhang et al. (2015), applying a 3% iron solubility factor in the ocean. After 10,000 years of spin up, the model is run with prognostic CO₂ for another 1,000 years (Figure 2, black line).

To simulate an idealized HS, we add a meltwater pulse of 0.05 Sv (equivalent to a 2 m global sea level rise) into the North Atlantic (52°W:5.4°E; 78°N:86°N) for 500 years (FW, Figure 2a, orange line, phase 1). This meltwater causes an AMOC shutdown. The model is run for another 500 years without any meltwater input (phase 2). To simulate an AMOC recovery, a salt flux addition to the North Atlantic is required in the UVic ESM. A negative meltwater input (-0.15 Sv) is thus added in the North Atlantic for 200 years. The model is then run for another 300 years (phase 3).

To understand the impact of reduced iron flux, we run another experiment called 180 FE (Figure 2, red line), during which there is no freshwater forcing, but the global iron 181 flux into the ocean is abruptly decreased by 90% to 2.744 Gmol yr⁻¹ (Figure 2g). This 182 experimental design was chosen based on EPICA DOME C ice core records, where the 183 optical particle counts as well as soluble calcium (Ca^{2+}) and non-sea salt soluble calcium 184 (nssCa²⁺) records indicate a reduction of dust flux by about 84% during H4, between 185 40ka and 38ka (Lambert et al., 2012). We run the model for 1000 years and then switch 186 the iron flux back to the original LGM-fe flux value $(27.44 \text{ Gmol yr}^{-1})$ in phase 3. 187

Finally, in our third experiment, FWFE (Figure 2, green line), we analyse the im-188 pact of the combination of a freshwater discharge into the North Atlantic and a simul-189 taneous reduction in the iron input. Therefore, the iron flux is reduced by 90% and 0.05190 Sv of meltwater is added in the North Atlantic during the first 500 years (phase 1). For 191 the following 500 years, the iron flux stays reduced while no additional meltwater is added 192 in the North Atlantic (phase 2). In phase 3, the salt is applied, the iron flux is changed 193 back to the original value and the model is run for 200 years. After that the model con-194 tinues to run for another 300 years with the same iron flux and no freshwater pertur-195 bation. 196

In each of these simulations, the North Atlantic Deep Water (NADW) transport is calculated as the maximum meridional Atlantic overturning streamfunction at 30°N between 1500 and 3500m depth. Antarctic Bottom Water transport (AABW) is calculated as the minimum meridional global overturning streamfunction at 35°S below 3000m depth. North Pacific Deep Water transport is calculated as the maximum meridional Indo-Pacific overturning streamfunction at 30°N below 700m depth.

In addition, simulated dissolved inorganic carbon (DIC) is decomposed into its three main contributors: respired organic carbon (C_{reg}) , DIC generated by dissolution of calcium carbonate (C_{CaCO_3}) and preformed carbon (C_{pref}) following the methods described below.

2.3 CO₂ decomposition

Changes in sea surface pCO₂, which influence the magnitude and direction of airsea flux exchange, are controlled by changes in sea surface temperature (SST), sea surface salinity (SSS), alkalinity (ALK) and DIC.

The sea surface pCO_2 anomalies can be decomposed into the individual contributions using the equations given below (Sarmiento & Gruber, 2006):

$$\Delta p CO_2 = \Delta p CO_2^{SST} + \Delta p CO_2^{SSS} + \Delta p CO_2^{ALK} + \Delta p CO_2^{DIC}$$
(1)

The SST contribution is derived from:

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$$\Delta p C O_2^{SST} = e^{(\gamma_{SST} \times \Delta SST)} \times p C O_2^{ref} - p C O_2^{ref} \tag{2}$$

where $\gamma_{SST} = 0.0423$ (Sarmiento & Gruber, 2006), and pCO_2^{ref} represents the sea surface pCO_2 value of the 40ka-control simulation.

216 Contributions from DIC, ALK, SSS are derived from:

$$\Delta p C O_2{}^X = \gamma_X \times \Delta X \times p C O_2{}^{ref} / \bar{X} \tag{3}$$

where, X represents DIC, ALK or SSS; \bar{X} is the mean of X during PI; and γ_X is equal to 13, -11 and 1 for DIC, ALK and SSS respectively (Sarmiento & Gruber, 2006; Smith & Marotzke, 2008; Egleston et al., 2010; Jiang et al., 2019).

220 3 Results

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$3.1\ \ {\rm Carbon}\ {\rm cycle}\ {\rm response}\ {\rm to}\ {\rm an}\ {\rm AMOC}\ {\rm shutdown}$

As a response to the freshwater discharge in the North Atlantic in experiment FW 222 (Figure 2a) during phase 1, the NADW transport decreases gradually from a maximum 223 of ~ 8 Sv and shuts off completely after 400 years of meltwater addition (Figure 2c) and 224 until the end of phase 2. NPDW transport strengthens by ~ 3 Sv over 1000 years, while 225 AABW transport weakens initially by ~ 1.5 Sv during phase 1 and then increases slightly 226 during phase 2 (Figure 2d,e). Younger age of water masses at intermediate depths south 227 of 30°S (Figure 2f, 3d-f) indicates enhanced Antarctic Intermediate water (AAIW) trans-228 port in the South Pacific by the end of phase 2. 229

As described elsewhere (Saenko et al., 2004; Okazaki et al., 2010), a weakening in
 NADW transport is accompanied by an enhanced NPDW formation in the North Pa cific and AAIW formation in the Southern Ocean due to an increase in surface salinity
 arising from oceanic and atmospheric teleconnections with the North Atlantic (Figure 3b).

In agreement with earlier studies (Menviel et al., 2020), an inter-hemispheric thermal seesaw pattern, with a 3.3 degrees decrease in North Atlantic (35°W:10°W,47°N:55°N) sea surface temperatures (SSTs) and a 0.4 degrees increase in Southern Ocean SST, is simulated during the AMOC shutdown (Figure 3a). There is no significant change in the Southern Hemisphere annual mean sea ice edge, which is situated at 53°S in the Indian and Atlantic sectors and at 62°S in the Pacific sector (Figure 3a).

The combination of greater ocean stratification (attributable to higher SSTs and SSS), moderate increase in AAIW formation and the reduction in AABW transport lead to less surface nutrient availability during phase 1. Therefore, there is an overall decrease in both diatoms (by 3%) and coccolithophores (by 6%) abundance in the Southern Ocean during phase 1 (Figure 2h,j).

However, during phase 2, a further increase in AAIW formation, combined with 245 a slow recovery of AABW leads to an increase in ventilation and deepening of the mixed 246 layer depth (MLD) in the Southern Ocean (Figure 3c), which causes greater nutrient avail-247 ability particularly in the Pacific sector. The locally increased nutrients are quickly taken 248 up by the diatoms (being prescribed higher growth rates and half saturation constants 249 for nutrients than coccolithophores (Kvale et al., 2021; Saini et al., 2021)), increasing di-250 atom's abundance by $\sim 16\%$ in the Pacific sector of the Southern Ocean, while coccol-251 ithophores decline (Figure 4a,b). This increase in diatoms is responsible for the total South-252 ern Ocean diatom increase (+6.7%) shown in Figure 2h during phase 2. On the contrary, 253 coccolithophores decrease by $\sim 9.6\%$ in the Southern Ocean as they are outcompeted by 254 diatoms (Figure 4b,2j). Overall, EP is 8.6% lower (Figure 2i,4c) and NPP 5% lower in 255 the Southern Ocean (not shown) during the AMOC shutdown. 256



Figure 2. Transient evolution of simulated biological and physical variables. Time series of (a) freshwater flux (Sv) applied to the North Atlantic and (g) global iron flux (Gmol yr⁻¹), used as forcings in experiments (orange) FW, (red) FE, and (green) FWFE. Please note that the green line overlaps the orange line in (a) and the red line overlaps the green line in (g). The black line represents 200 years of 40ka-control experiment with prognostic CO₂. Time series of simulated (b) global atmospheric CO₂ concentration (ppm) anomaly compared to 40ka-control, (c) NADW (Sv), (d) AABW (Sv), and (e) NPDW transport (Sv), (f) Southern Ocean ideal age anomaly averaged over intermediate depths (600-1700m, years) compared to 40ka-control; time series anomalies of simulated (h) Southern Ocean depth integrated diatoms (PgC), (i) Southern Ocean export production at 177.5m depth (PgC), (j) Southern Ocean depth integrated coccolithophores (PgC), (k) global terrestrial carbon (GtC) and (l) global ocean carbon (GtC) compared to 40ka-control. The Southern Ocean (SO in the figure) is defined as the region south of 30°S, and all the biological tracers are integrated over the Southern Ocean.

Table 1. Changes in atmospheric CO_2 , terrestrial and ocean carbon at the end of phase 2 (yr 1000) compared to the 40ka-control simulation.

Experiments	Change in CO ₂ (ppm)	Atmospheric carbon (GtC)	Terrestrial carbon (GtC)	Total Ocean carbon (GtC)	Atlantic, north of 30°S (GtC)	Pacific, north of 30°S (GtC)	Indian, north of 30°S (GtC)	Southern Ocean, south of 30°S (GtC)
FW	$ \begin{array}{c} +0.5 \\ +6 \\ +7 \end{array} $	1	7.5	-8	140	-120	-19	-9
FE		12	23	-35	8	10	-3	-50
FWFE		14	31	-45	145	-110	-21	-59



Figure 3. FW experiment at year 1000 (end of phase 2) minus 40ka-control anomalies of (a) sea surface temperature (°C), (b) sea surface salinity (psu), (c) ventilation depth (m), and zonally averaged ideal age (years) over the (d) Atlantic, (e) the Pacific, and (f) Indian sector; where red in d-f indicates reduction in ventilation. Overlaid contours in (a) represent the 15% annual mean sea-ice concentration in (red) 40ka-control and in (green) FW experiment at the end of phase 2.

In contrast, significantly weaker NADW transport and higher stratification, thus 257 higher residence time, leads to a greater amount of regenerated phosphate (P_{reg}) at in-258 termediate depths in the North Atlantic and in the deep Atlantic ocean (Figure S1). Cor-259 respondingly, DIC, in the form of regenerated carbon (C_{reg}) (Figure S2), accumulates 260 in the Atlantic Ocean. Positive DIC anomalies are simulated below 500m depth in the 261 North Atlantic and below 1500m depth in the South Atlantic (Figure 5a). At the end 262 of phase 2, the Atlantic Ocean carbon reservoir has thus increased by 140 GtC (Table 1). 263 On the contrary, the Pacific Ocean loses 120 GtC, because of increased ventilation as-264 sociated with stronger NPDW and AAIW transports (Figure 2e,f, 3d-f, Table 1). 265

Enhanced intermediate depth ventilation in the Southern Ocean (Figure 2f), and 266 to some extent lower Southern Ocean EP, leads to a decrease in DIC, and particularly 267 in C_{reg} , in the upper 1000m of the Southern Ocean (Figure 5a-c, S2a-c). This anomaly 268 spreads at intermediate depths within AAIW (Figure 5a-c). The positive DIC anoma-269 lies in the deep Pacific and Indian Ocean (Figure 5b,c) are mainly due to increased pre-270 formed carbon (C_{pref}) resulting from the lower nutrient utilisation at high southern lat-271 itudes (Figure S1, S2d-f). In the Indian Ocean, an increase in C_{reg} is also simulated be-272 low 2500m depth (Figure S2c). Overall, DIC decreases by 19 GtC in the Indian Ocean 273 and by 9 GtC in the Southern Ocean (Table 1, Figure 5c). 274

At the surface of the Southern Ocean, between $\sim 47^{\circ}$ S and 60° S, higher DIC con-275 centration due to reduction in EP and higher ventilation, increases the surface ocean par-276 tial pressure of CO_2 (p CO_2 , Figure 6b). Conversely, an increase in surface alkalinity in 277 the Southern Ocean (Figure S3), associated with the decrease in coccolithophore pop-278 ulation (Figure 4b), partly compensates the effect of higher DIC and ventilation on sur-279 face ocean pCO_2 (Figure 6b). In addition, higher SST and SSS lead to a reduction of 280 CO_2 solubility in sea water (Figure 6b). Therefore, higher surface DIC and a weakened 281 solubility pump cause a CO_2 outgassing in the Southern Ocean (red regions south of $30^{\circ}S$ 282



Figure 4. Diatoms, coccolithophores and EP anomalies for experiments (top) FW, (center) FE, and (bottom) FWFE at year 1000 (end of phase 2) compared to the 40ka-control simulation. Anomalies in depth integrated (a,d,g) diatoms (gC m⁻²) and (b,e,h) coccolithophores (gC m⁻²). (c,f,i) Export production anomalies at 177.5m (gC m⁻²yr⁻¹). Paleo-proxy estimated anomalies at 39ka compared to 40ka are added on top of the simulated anomalies for qualitative comparison of model and data: (a, d, g) opal flux (triangles) (Anderson et al., 2009; Thöle et al., 2019; Amsler et al., 2022) and brassicasterol concentration (circle) (Sachs & Anderson, 2005); (c, f,i) alkenone flux (diamonds) (Sachs & Anderson, 2003, 2005) and organic carbon flux (square) (Anderson et al., 2014; Thöle et al., 2019). Dark (light) orange represents significantly (slightly) higher values, while dark (light) blue represents significantly (slightly) lower values.



Figure 5. Zonally averaged DIC anomalies $(mmol m^{-3})$ over (left) the Atlantic, (center) the Pacific, and (right) Indian ocean for experiments (top) FW, (center) FE, and (bottom) FWFE at year 1000 (end of phase 2) compared to the 40ka-control simulation.

²⁸³ in Figure 7b), and particularly in the southeast Pacific between $\sim 47^{\circ}$ S:60°S. In contrast, ²⁸⁴ the increase in surface alkalinity leads to carbon drawdown from the atmosphere into the ²⁸⁵ Southern Ocean (blue regions south of 40°S in Figure 7b). Overall, the Southern Ocean ²⁸⁶ carbon outgassing decreases by $\sim 8\%$. We also see an anomalous outgassing from the north-²⁸⁷ east Atlantic (Figure 7b), which is due to a decrease in surface alkalinity (Figure 6a) in ²⁸⁸ response to the freshwater flux addition in this region.

The changes in carbon exchange with the atmosphere causes the global ocean carbon to decrease by 8 GtC by the end of phase 2 (Table 1, Figure 2l). This is accompanied by a 7.5 GtC increase in terrestrial carbon reservoir (Figure 2k), and about 1 GtC carbon uptake by the atmosphere leading to an insignificant rise in CO₂ (Figure 2b) at the end of phase 2.

²⁹⁴ During the AMOC recovery in phase 3, the NADW transport increases to ~ 14 Sv ²⁹⁵ before equilibrating at 7 Sv once the salt flux is turned off (Figure 2c). NPDW trans-²⁹⁶ port also reduces back to near initial conditions, while AABW transport stabilizes to a ²⁹⁷ slightly higher value, at 11 Sv (Figure 2d,e). The addition of the salt flux causes a ~ 1 ²⁹⁸ ppm rise in CO₂, after which it reduces back to the initial value.

Diatoms increase by 21% compared to phase 2 in the Indian Ocean sector south of the annual sea ice edge, and coccolithophores increase by 6% mostly everywhere north of the annual sea ice edge (Figure S4a,b). This increases the total Southern Ocean EP by 7.6% at the end of phase 3 compared to phase 2 and brings EP back to a similar value as in 40ka-control.

3.2 Carbon cycle response to a reduction in aeolian iron flux.

When the aeolian iron input to the ocean is abruptly reduced (Figure 2g), the CO_2 305 increases by 6 ppm over 1000 years in experiment FE (Figure 2b). There are no changes 306 in ocean circulation in this experiment, and therefore the changes in CO_2 are due to the 307 reduction in the biological pump efficiency and the land carbon changes responding to 308 higher CO_2 and temperatures. Plankton abundances south of ~47°S are reduced due 309 to decreased iron flux in the Southern Ocean (Figure 4d.e). Diatoms decrease by 19% 310 in the Atlantic, 5.7% in the Pacific and $\sim 9.5\%$ in the Indian sector south of $\sim 47^{\circ}$ S, while 311 coccolithophores decrease by 27% south of $\sim 47^{\circ}$ S. This leads to reductions in EP (Fig-312 ure 4f) and NPP south of $\sim 47^{\circ}$ S. 313

Reduced nutrient utilization within the Antarctic zone causes an advection of ex-314 cess nutrients northward (Figure S5), increasing diatoms (by 88% in the Indian region) 315 and coccolithophores (by 23% in total) abundances and thus EP and NPP north of $47^{\circ}S$ 316 in the Southern Ocean (Figure 4d-f). Thereby, EP decreases by 17% south of 47° S and 317 increases by 29% between 47° S and 30° S as a response to nutrient reorganization, with 318 an overall 5.5% decrease in diatoms and 1.6% decrease in coccolithophores in the South-319 ern Ocean. The total Southern Ocean EP decreases by 7% at the end of phase 2 (Fig-320 ure 2i) due to a 5% decrease in nutrient utilisation in this sector. 321

The lower EP south of 47°S causes an increase in surface DIC. However, this also leads to reduced DIC, in the form of regenerated DIC (C_{reg}) within AABW (Figure 5df and S6a-c). These negative DIC anomalies are further advected into the deep Atlantic and Indo-Pacific basins (Figure 5d-f). In contrast, greater DIC content is simulated north of 47°S in the upper 2500m depth in all the basins. There is also a small increase in surface alkalinity in the Southern Ocean (Figure S3) due to the overall decrease in Southern Ocean coccolithophores (Figure 2j).

No significant changes in surface alkalinity, SST and SSS are simulated between 329 47° S and 60° S (Figure 6c). In contrast, higher surface DIC leads to $\sim 48\%$ increase in 330 CO_2 outgassing between 47°S and 60°S (Figure 6c and red regions south of 40°S in Fig-331 ure 7c). This leads to a 50 GtC carbon loss from the Southern Ocean in experiment FE 332 (Table 1). In total, while the global ocean loses 35 GtC (Figure 2l), the atmosphere gains 333 12 GtC, while 23 GtC are absorbed by the terrestrial biosphere (Figure 2k). During phase 334 3, CO_2 decreases gradually as the ocean biogeochemistry recovers to the initial condi-335 tions of 40ka-control. 336

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3.3 Carbon cycle response to an AMOC shutdown and iron flux reduction

In this section we analyse the combined effect of an AMOC shutdown due to freshwater input in the North Atlantic (Figure 2a, experiment FWFE), and a reduced global iron flux (Figure 2g, experiment FWFE). A 7 ppm CO₂ increase is simulated in this experiment (1 ppm higher than FE and 6.5 ppm higher than FW).

As can be seen in Figure 2c-f, the changes in ocean circulation in FWFE are similar to those of the FW experiment, with slightly larger anomalies in AABW transport and slightly smaller anomalies in NPDW transport. Figures 2 and 4 clearly show that the diatom, coccolithophore and EP responses in FWFE experiment are a linear combination of the responses simulated in FW and FE.

Diatoms increase south of 47° S in the Pacific sector due to circulation changes as in experiment FW. However, because of the parallel reduction in iron supply (which causes 6% diatom reduction in this sector), the net increase is limited to 9.5% (instead of 16% as simulated in FW) compared to 40ka-control. Similarly, the diatoms decrease south of 47°S in the Atlantic (-16%, +3% from circulation and -19% from the iron effect) and



Figure 6. Time series of sea surface pCO_2 (ppm) anomalies resulting from changes in (blue) ALK, (orange) DIC, (green) SSS, and (red) SST for (a) FW averaged over the North Atlantic, (b) FW averaged over the Southern Ocean (47°S:60°S), (c) FE over the Southern Ocean (47°S:60°S), and (d) FWFE averaged over the Southern Ocean (47°S:60°S), compared to the 40ka-control simulation. The dashed black line represents simulated sea surface pCO_2 (ppm), while the solid black line shows the sum of the ALK, DIC, SSS and SST contributions. Please note the scale differs between the sub-panels.



Figure 7. Surface carbon flux (gC $m^{-2}yr^{-1}$) for (a) 40ka-control; surface carbon flux anomalies for (b) FW, (c) FE, and (d) FWFE experiments at year 1000 (end of phase 2) compared to the 40ka-control simulation. Red indicates ocean outgassing.

Indian sectors (-14%, -3.2%) from circulation and -9.5% from the iron effect) and the in-353 crease north of 47° S in the Indian sector (+63%) is also a net outcome from changes in 354 both circulation and iron supply. Consequently, due to the weak positive anomalies in 355 the Pacific, and the stronger negative anomalies in the Atlantic and Indian sectors, the 356 Southern Ocean diatom abundance is 6% lower compared to FW but 5.8% higher com-357 pared to FE (Figure 2h) at the end of phase 2. Coccolithophores on the other hand de-358 crease by 11.4% over the Southern Ocean (Figure 2j) compared to the 40ka-control (where 359 9.6% decrease is simulated due to the circulation changes as in FW and 1.6% is simu-360 lated due to changes in iron as in FE). With these changes in the plankton population, 361 the total Southern Ocean EP reduces by 14% in FWFE at the end of phase 2 (Figure 4i). 362

The larger simulated decrease in C_{reg} in the FWFE simulation (Figure S7a-c) com-363 pared to that in FW and FE, due to the weaker (-13%) Southern Ocean nutrient util-364 isation (Figure S8), causes a larger decrease in DIC below 200m depth in the Southern 365 Ocean (Figure 5g-i). Simulated air-sea CO_2 fluxes in the FWFE experiment (Figures 6d 366 and 7d) as well as the changes in ocean carbon (Table 1) in the Southern Ocean are a 367 combination of FW and FE carbon changes. Therefore, a total of ~ 45 GtC are lost from 368 the ocean in experiment FWFE (Table 1, Figure 2l). Terrestrial carbon increases by 31 369 GtC (Figure 2k), while atmospheric carbon increases by 14 GtC by the end of phase 2. 370

371 4 Discussion

Our study indicates that to understand the mechanisms behind atmospheric CO₂ increase during HS, an investigation of dust related impacts is crucial in addition to previously explored feedbacks from oceanic circulation changes.

In our idealized experiment simulating a HS under MIS 3 boundary conditions, the 375 simulated SST anomalies in the North Atlantic $(\sim -3^{\circ}C)$ are consistent with the alkenone 376 based SST proxies from the Iberian Margin (Martrat et al., 2007) and the North Atlantic 377 (Cacho et al., 1999). On the contrary, the simulated Southern Ocean SST anomalies $(+0.4^{\circ}C)$ 378 are significantly lower than what is inferred from marine records $(+\sim 2^{\circ}C)$ (Pahnke et 379 al., 2003; Kaiser et al., 2005; Barker et al., 2009; Caniupán et al., 2011) but are still within 380 the range of previously simulated responses to an AMOC shutdown (Kageyama et al., 381 2013; Menviel et al., 2014, 2015). 382

The changes in global circulation (Figure S9), and therefore the changes in South-383 ern Ocean physics, impact marine ecosystems in this region. As pointed out earlier, high 384 resolution paleo evidence of changes in EP during HS are limited. The simulated decrease 385 in coccolithophores and EP at $\sim 45^{\circ}$ S east of the South Island of New Zealand in our FW 386 simulation (Figure 4b,c) is in contradiction with the increase in alkenone (proxy for EP) 387 and C_{37} methyl ketones (a marker for coccolithophores) concentrations recorded in a ma-388 rine sediment core, MD97-2120 (Sachs & Anderson, 2005), at this location near Chatham 389 Rise during H4 (Figure 4c). Our experiment FWFE, which includes the combined im-390 pact from the iron flux reduction (Figure 4e,f) and freshwater forcing (Figure 4b,c), im-391 proves this model data agreement by simulating an increase in coccolithophores and EP 392 at this location (Figure 4h,i). The simulated increase in diatom abundance east of New 393 Zealand, due to deeper MLD in experiments FW and FWFE, is in agreement with bras-394 sicasterol concentrations (a marker for diatoms) (Figure 4a,g) observed in the Chatham 395 rise core (Sachs & Anderson, 2005). Increased diatom abundance south of $\sim 50^{\circ}$ S in the 396 Atlantic in FW and FWFE and a decrease in diatoms between $\sim 50^{\circ}$ S and $\sim 55^{\circ}$ S in the 397 Indian sector in FE and FWFE, are also in agreement with the marine sediment opal 398 flux records from the Southern Ocean (Anderson et al., 2009; Thöle et al., 2019; Am-399 sler et al., 2022). In the sub-Antarctic, simulated diatom changes north of $\sim 50^{\circ}$ S in FW 400 are consistent with the proxy records from Atlantic (Sachs & Anderson, 2003; Ander-401 son et al., 2014) and Indian sectors (Thöle et al., 2019; Amsler et al., 2022), while in the 402

FE and FWFE simulations, the diatom increase is consistent with only one record (Amsler et al., 2022) in the Indian sector.

The simulated EP increase at $\sim 45^{\circ}$ S in simulations FE and FWFE is in contra-405 diction with the reduced alkenone and organic carbon fluxes (Sachs & Anderson, 2003; 406 Anderson et al., 2014) recorded in marine sediment cores in the subantarctic Atlantic. 407 However, the simulated EP decrease south of 40° S in experiment FW is in agreement 408 with these paleo EP records. The simulated increase in EP in the Indian sector is con-409 sistent with the organic carbon flux proxy (Thöle et al., 2019). In experiment FWFE, 410 changes in the simulated diatom abundance and in EP show a $\sim 60\%$ and 40% agreement 411 with the available proxy records, respectively. 412

The simulated EP decrease in FW, along with the simulated decline south of $\sim 47^{\circ}$ S 413 in FE and FWFE experiments, is in agreement with the EP response to an AMOC shut-414 down obtained with another version of the UVic model (Menviel et al., 2014). Based on 415 the above-mentioned proxy evidence and our simulated results, we suggest that an EP 416 decrease due to reduced iron supply during HS could most likely have occurred south 417 of $\sim 45^{\circ}$ S in the Southern Ocean. Clearly, better constraints on changes in EP and plank-418 ton abundances during HS, along with additional proxy records of the last glacial millennial-419 scale climate variability are required. 420

Enhanced AAIW transport and reduction in Southern Ocean EP lead to an increase in intermediate and deep ocean oxygen concentrations south of ~40°S in all of our simulations (Figure S10). This is in agreement with the reconstructed bottom water oxygen concentrations (Gottschalk et al., 2016), and authigenic Uranium based deep oxygenation records (Jaccard et al., 2016) in sub-Antarctic Atlantic marine sediment cores at ~45°S and ~55°S respectively.

A total of $7ppm CO_2$ increase is simulated in experiment FWFE due to the com-427 pounding effects of changes in oceanic circulation and a reduced iron dust flux in the South-428 ern Ocean. Most of this CO_2 increase is due to the reduced iron availability (experiment 429 FE). This is caused by a larger carbon loss (50 GtC compared to 9 GtC) from the South-430 ern Ocean in experiment FE compared to FW. In simulation FW, outgassing in the North 431 Atlantic is compensated by the higher carbon sequestration (140 GtC in FW compared 432 to 8 GtC in FE, Table 1) in the deep North Atlantic Ocean due to the AMOC shutdown, 433 and by the decrease in outgassing in the Southern Ocean. Due to the CO_2 fertilization 434 effect, the CO_2 increase in FWFE simulation enhances terrestrial primary productivity. 435 This leads to a 12 GtC increase in terrestrial vegetation, as well as an increase in litter 436 fall, leading to a 19 GtC increase in soil carbon. The total terrestrial carbon thus increases 437 by ~ 31 GtC. The simulated changes in terrestrial carbon in this study are in contradic-438 tion to previous modelling studies which show a decrease in terrestrial carbon in response 439 to an AMOC shutdown (Scholze et al., 2003; Köhler et al., 2005; Menviel et al., 2008) 440 but are in agreement with freshwater simulations performed with another version of the 441 UVic ESCM (Huiskamp & Meissner, 2012). However, it should be noted that the dis-442 crepancies in these results could be related to having different vegetation models, dif-443 ferent boundary conditions, and different freshwater flux forcings. 444

The 7 ppm rise is significantly lower than the maximum observed CO_2 increase of 445 20 ppm during HS within MIS 3 (Ahn & Brook, 2008; Bereiter et al., 2015; T. K. Bauska 446 et al., 2021). It is also lower than the simulated increase of 9 ppm simulated by Parekh 447 et al. (2008) as a response to reduced dust flux, although using a much simpler biogeo-448 chemical model than our study and under PI conditions. Jochum et al. (2022) simulated 449 an increase of ~ 8 ppm in CO₂ in their experiment with a longer stadial and a reduction 450 in PI iron flux by 50%. The discrepancy between our simulated CO_2 changes and the 451 estimates from proxy records can somewhat be explained by the lack of enhanced ven-452 tilation in the Southern Ocean in our simulations. Previous modelling studies have sug-453 gested that enhanced Southern Ocean ventilation could have contributed to the atmo-454

spheric CO_2 increase (Menviel et al., 2014, 2015) during HS. Some of these changes in 455 Southern Ocean ventilation changes could result from intensified Southern Hemisphere 456 westerlies (Menviel et al., 2018; Huiskamp et al., 2016). In addition, recent studies have 457 also highlighted the role of changes in AAIW in driving atmospheric CO_2 increases (Menviel 458 et al., 2018; Yu et al., 2022). Due to the coarse resolution of the ocean model and lack 459 of a dynamic atmosphere (and thus constant Southern Hemisphere westerlies) in the ex-460 periments presented above, it is possible that changes in Southern Ocean circulation and 461 thus their impact on atmospheric CO_2 are not appropriately captured. 462

463 There is also uncertainty involving the total amount of dissolved iron available for uptake by phytoplankton under different climates. In the experiments presented here, 464 we use 3% iron solubility, which is based on the most plausible estimate of glacial iron 465 solubility (3-5%) (Conway et al., 2015; Shoenfelt et al., 2018; Saini et al., 2023). A higher 466 iron solubility as initial MIS3 conditions would lead to greater CO_2 release when the iron 467 supply is reduced (Saini et al., 2023). We also do not consider the impact of potential 468 changes in ligand concentrations in the ocean which can also impact iron solubility (Parekh 469 et al., 2006, 2008). Additionally, better constraints on the pattern and amount of dust 470 fluxes under different climates are required to constrain the contribution of iron fertil-471 isation during millennial events. 472

473 Open Research Section

The modelling data from all the simulations are temporarily available at https:// datadryad.org/stash/share/sVMbSADOs_UdVAIvhvE_psxF-I_RUts-WOZtPjsOUr4 for the review process. The data will be published on the DRYAD repository through https:// doi.org/10.5061/dryad.k3j9kd5dt, once the manuscript is accepted.

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Supporting Information for "Transient response of Southern Ocean ecosystems during Heinrich stadials"

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1. Figures S1 to S10

Introduction

The supplementary figures from S1 to S10 complements the respective detailed description provided in the main article.



Figure S1. Zonally averaged (top) P_{reg} anomalies (μ mol m⁻³) over (left) the Atlantic, (center) the Pacific, and (right) Indian ocean for FW experiment at year 1000 (end of phase 2) compared to the 40ka-control simulation. Bottom: Same as top for total phosphate (P_{total} , μ mol m⁻³) anomalies.





Figure S2. Zonally averaged (top) C_{reg} anomalies (mmol m⁻³) over (left) the Atlantic, (center) the Pacific, and (right) Indian ocean for FW experiment at year 1000 (end of phase 2) compared to the 40ka-control simulation. Bottom: Same as top for C_{pref} (mmol m⁻³) anomalies.



Figure S3. Surface alkalinity anomalies (mmol m^{-3}) for experiment (left) FW, (centre) FE, and (right) FWFE at year 1000 (end of phase 2) compared to the 40ka-control simulation.



Figure S4. Depth integrated (left) diatom and (right) coccolithophore anomalies (gC m⁻²) for FW experiment at year 1500 (end of phase 3) compared to FW at year 1000 (end of phase 2).



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Figure S5. Zonally averaged (top) P_{reg} anomalies (μ mol m⁻³) over (left) the Atlantic, (center) the Pacific, and (right) Indian ocean for FE experiment at year 1000 (end of phase 2) compared to the 40ka-control simulation. Bottom: Same as top for total phosphate (P_{total} , μ mol m⁻³) anomalies.



Figure S6. Zonally averaged (top) C_{reg} (mmol m⁻³) anomalies over (left) the Atlantic, (center) the Pacific, and (right) Indian ocean for FE experiment at year 1000 (end of phase 2) compared to the 40ka-control simulation. Bottom: Same as top for C_{pref} (mmol m⁻³) anomalies.





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Figure S7. Zonally averaged (top) C_{reg} (mmol m⁻³) anomalies over (left) the Atlantic, (center) the Pacific, and (right) Indian ocean for FWFE experiment at year 1000 (end of phase 2) compared to the 40ka-control simulation. Bottom: Same as top for C_{pref} (mmol m⁻³) anomalies.



Figure S8. Zonally averaged (top) P_{reg} anomalies (μ mol m⁻³) over (left) the Atlantic, (center) the Pacific, and (right) Indian ocean for FWFE experiment at year 1000 (end of phase 2) compared to the 40ka-control simulation. Bottom: Same as top for total phosphate (P_{total} , μ mol m⁻³) anomalies.



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Figure S9. Global overturning streamfunctions (Sv) in experiment (left) 40ka-control and in experiment (right) FW at year 1000 (end of phase 2).





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Figure S10. Zonally averaged oxygen anomalies (mmol m⁻³) over (left) the Atlantic, (center) the Pacific, and (right) Indian ocean for experiments (top) FW, (center) FE, and (bottom) FWFE at year 1000 (end of phase 2) compared to the 40ka-control simulation.