

1 **Glacial Southern Ocean expansion recorded in foraminifera-bound nitrogen
2 isotopes from the Agulhas Plateau during the Mid-Pleistocene Transition**

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12 **Plain Language Summary:**

13 The Mid-Pleistocene Transition is a unique period of time, during which the natural rhythm of
14 Earth's climate shifted, the pace of glacial and interglacial cycles changed from 40,000 years to
15 100,000 years as ice sheets expanded, carbon accumulated in the deep ocean, and the planet
16 cooled. The exact cause of these changes is unclear, but internal system feedbacks were likely at
17 play. As climate changes today and the oceans increasingly take up carbon, the Mid-Pleistocene
18 Transition provides a unique case study to investigate Earth's natural climate system and
19 important carbon cycle feedbacks. In this paper we use the nitrogen isotopic composition of
20 plankton shells and other biogeochemical records to show that leading up to the Mid-Pleistocene
21 Transition the Southern Ocean underwent major physical changes and expanded as 100,000 year
22 glacial cycles emerged. Our data indicates that the expansion of the Southern Ocean delivered
23 cold, nutrient rich waters northward where they could mix with warm, salty Indian and Atlantic
24 Ocean waters as hypothesized by other studies.

25 **Key Points:**

- 26• Foraminifera-bound nitrogen isotope values from the Agulhas Plateau record latitudinal
27 migrations of the Subtropical Front.
- 28• Elevated foraminifera-bound nitrogen isotope values after 900 ka are consistent with Southern
29 sourced nitrate.
- 30• Southern Ocean contraction during a “super interglacial” brings more subtropical nitrate to the
31 Agulhas Plateau.

33 **Abstract**

34 The emergence of 100-kyr glacial cycles (The Mid-Pleistocene Transition, MPT) is attributed in
 35 part to slower global overturning circulation and iron stimulation of biological carbon drawdown
 36 in the Southern Ocean. We present foraminifera-bound nitrogen isotope values and polar
 37 planktic foraminifera abundances from the Agulhas Plateau that show that increases in biogenic
 38 sediment accumulation coincide with northward migrations of the Subtropical Frontal Zone
 39 (STFZ) and elevated foraminifera-bound nitrogen isotope values during MPT glacial episodes.
 40 The nitrogen isotope values of two planktic foraminifera species, *Globigerina bulloides* and
 41 *Globorotalia inflata* show remarkable coherence amongst the sea surface temperature gradient
 42 between the STFZ and SAZ, and polar foraminifera abundances, indicating a strong relationship
 43 between nitrogen isotope dynamics above the Agulhas Plateau and migrations of the STFZ.
 44 Northward migration of the STFZ may have been essential to prolonging glacial intervals by
 45 increasing deep ocean carbon storage via a northward shift of the South Westerly Winds (SWW)
 46 and a reduction in upwelling, delivery of fresher surface waters into the upper limb of global
 47 overturning circulation, or inhibiting heat and salt delivery to the Atlantic as Agulhas Leakage.

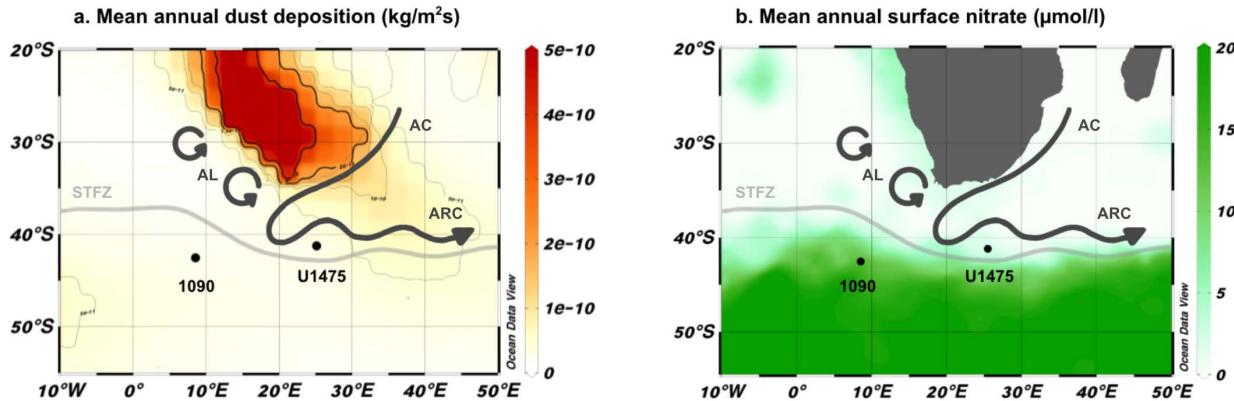
48 **1 Introduction**

49 Around 1 million years ago (Ma), Antarctica and the Southern Ocean witnessed expansion of
 50 polar ice sheets and Southern Ocean sea ice (Starr et al., 2021) and increases in iron delivery and
 51 biological productivity in the Subantarctic Zone (SAZ) (Martínez-García et al., 2009; Kemp et
 52 al., 2010). Alongside evidence for increased deep ocean carbon storage (Farmer et al., 2019),
 53 these surface changes implicate a Southern Ocean driver in the extension and amplification of
 54 glacial-interglacial cycles from 40 kyr to ~100 kyr pacing during the MPT (1,200 - 600 ka)
 55 (Chalk et al., 2017; Hönisch et al., 2009; Pena & Goldstein, 2014; Lear et al., 2016; Hoogakker
 56 et al., 2006; Hasenfratz et al., 2019). Several hypotheses exist to explain the mechanisms
 57 responsible for the MPT. Enhanced biological pump efficiency, increasing carbon export from
 58 the surface (and atmosphere) to the deep ocean, as well as slower ocean circulation, reducing
 59 CO₂ outgassing and extending the residence time of carbon in the deep ocean, have been
 60 proposed. However, without evidence demonstrating an increase in Southern Ocean nutrient
 61 consumption, the relative importance of each process in reducing glacial atmospheric CO₂ across
 62 the MPT remains ambiguous (Martínez-García et al., 2009; Diekmann & Kuhn, 2002; Kemp et
 63 al., 2010; Jaccard et al., 2013; Crundwell et al., 2008). Observed increases in biogenic sediment
 64 accumulation in the glacial Southern Ocean SAZ across the MPT could result from iron
 65 fertilization or Southern Ocean expansion in response to cooling and Antarctic ice sheet growth
 66 (Martínez-García et al., 2009; Diekmann & Kuhn, 2002).

67 The evidence for the northward expansion of the Southern Ocean during the MPT comes from
 68 the Atlantic Sector of the Southern Ocean (Kemp et al., 2010; Diekmann & Kuhn, 2002) and
 69 more recently the Indian-Atlantic Ocean Gateway, south of Africa (Starr et al., 2021; Cartagena-
 70 Sierra et al., 2021; Tangunan et al., 2021). Expansion of the Southern Ocean via northward
 71 migrations of the STFZ and SWW slows global overturning circulation and increases deep ocean
 72 carbon storage (Russell et al., 2006; Toggweiler et al., 2006; Marshall & Speer, 2012; Ferrari et
 73 al., 2014; Sigman et al., 2021). The Indian-Atlantic Ocean Gateway is globally significant due to
 74 the eddies of salty Indian Ocean surface waters that are shed into the Atlantic Ocean as Agulhas

75 Leakage (AL). AL contributes excess salt to the surface return flow of the Atlantic Meridional
76 Overturning Circulation (AMOC) that is needed for deep convection and North Atlantic Deep
77 Water (NADW) formation (Pena & Goldstein, 2014; Caley et al., 2012; Beal et al., 2011).
78 Northward migrations of the STFZ have been proposed to cut off or limit AL on millennial and
79 glacial interglacial timescales as well as during the MPT. Evidence for significantly reduced AL
80 during intervals when the Antarctic Polar Front is thought to have moved at least 7 degrees
81 northward comes from the South Atlantic (Bard and Rickaby, 2009; Kemp et al., 2010; Caley et
82 al., 2012). Recent evidence for increased ice-rafted debris accumulation beneath the STFZ during
83 the early stages of glacial periods across the MPT suggests an expansion of cool, fresh SAZ
84 waters into the subtropics (Starr et al., 2021). This ‘southern escape’ of fresh water potentially
85 increased the buoyancy of the surface return flow of the AMOC, reducing NADW formation,
86 and slowing overturning (Starr et al., 2021; Pena & Goldstein, 2014). Whether by reducing salty
87 AL or adding fresh water via the southern escape, these changes provide a physical means of
88 carbon sequestration during the MPT (Starr et al., 2021; Simon et al., 2013). In this region, such
89 dramatic northward migrations of the Southern Ocean fronts would also deliver excess
90 macronutrients towards the subtropics, closer to South African and South American aeolian dust
91 sources (Martin, 1990; Martínez-García et al., 2011; Martínez-García et al., 2014) (Figure 1).
92 Given sufficient iron supply to Site U1475, the increase in nutrients would fuel local productivity
93 further enhancing glacial carbon drawdown (Martin, 1990; Martínez-García et al., 2011;
94 Martínez-García et al., 2014; Anderson et al., 2014). Indeed, northward STFZ migrations during
95 glacial periods of the past 1.4 million years are met with increased productivity at Site U1475
96 with the most significant northward frontal migrations yielding the greatest increases in biogenic
97 sediment deposition (Tangunan et al., 2021; Cartagena-Sierra et al., 2021).
98

99 While the MPT is widely regarded as an interval of global cooling, significant Southern
100 Hemisphere warming occurs during the MPT “super interglacial”, MIS 31, ~1,100 ka. Prior to
101 the emergence of 100 kyr glacial-interglacial cyclicity, Southern Hemisphere insolation reaches a
102 5 Myr high, collapsing the East Antarctic Ice Sheet and delivering subtropical fauna well into the
103 modern day Subantarctic Zone (Beltran et al., 2020; McKay et al., 2012; Maiorano et al., 2009).
104 It is interesting that this destabilization of Antarctic ice sheets under relatively low atmospheric
105 CO₂ concentrations occurs immediately prior to the re-equilibration of the global climate system
106 with cooler and longer glacial intervals during the MPT. The role MIS 31 plays in the MPT
107 remains ambiguous, highlighting the need for a greater understanding of how Southern Ocean
108 processes influence and are influenced by global climate.



109
110 Figure 1: Map of Site U1475 and Site 1090, in the Indian-Atlantic Ocean gateway, with respect to modern a. mean
111 annual dust deposition ($\text{kg}/\text{m}^2\text{s}$) (Li et al., 2008) and b. mean annual surface nitrate ($\mu\text{mol/l}$) (World Ocean Atlas,
112 2013). STFZ = Subtropical Frontal Zone; AL = Agulhas Leakage; AC = Agulhas Current; ARC = Agulhas Return
113 Current. STFZ position from Orsi et al., (1995).

114
115 Here, we focus on the importance of frontal migrations as recorded in the nitrogen isotope values
116 of foraminifera, in the Indian-Atlantic Ocean Gateway region across the MPT. Nitrogen isotopes
117 provide us with a tool for documenting nutrient consumption within regions of the ocean where
118 surface nitrate is not completely consumed and/or nutrient sources where nitrate is depleted. In
119 the modern Southern Ocean, the nitrogen isotopic composition of nitrate, $\delta^{15}\text{N}_{\text{NO}_3}$, where $\delta^{15}\text{N} =$
120 $[(^{15}\text{N}/^{14}\text{N})_{\text{sample}}/(^{15}\text{N}/^{14}\text{N})_{\text{air}}] - 1$, increases with nutrient drawdown as surface waters are advected
121 north, yielding maximum values at the northern edge of the Southern Ocean generally, and
122 within in the STFZ south of Africa, specifically (Figure 2a; Smart et al., 2020; Ren et al., 2009;
123 Sigman et al., 1999). In the oligotrophic subtropical Indian Ocean, near surface $\delta^{15}\text{N}_{\text{NO}_3}$ -values
124 tend to be lower than in the Southern Ocean surface, due in part to the addition of newly fixed
125 nitrogen with a $\delta^{15}\text{N}$ of $\sim 0\text{‰}$ (Harms et al., 2019). The result is meridional increase in $\delta^{15}\text{N}_{\text{NO}_3}$
126 values across the Southern Ocean that peaks around $42\text{--}43^\circ\text{S}$, reflecting the progressive increase
127 in nutrient consumption, and then a decrease beyond 42°S that reflects mixing of Southern Ocean
128 sourced nitrate with subtropically sourced nitrate in the deep mixed layer of the STFZ (Figure
129 2a). This trend in the $\delta^{15}\text{N}_{\text{NO}_3}$ is reflected in the $\delta^{15}\text{N}$ of particulate organic nitrogen produced by
130 phytoplankton using this nitrate pool and in turn, the particulate nitrogen is consumed by
131 planktonic foraminifera and is the source of their $\delta^{15}\text{N}$ signal (Smart et al., 2020; Ren et al.,
132 2009). We use the $\delta^{15}\text{N}$ values of organic matter within planktonic foraminifera shells ($\delta^{15}\text{N}_{\text{FB}}$) to
133 study the surface nutrient dynamics in this mixing region, where the source of nitrate is the
134 primary control on the $\delta^{15}\text{N}$ value of organic matter, yet the source $\delta^{15}\text{N}$ values are subject to
135 change.

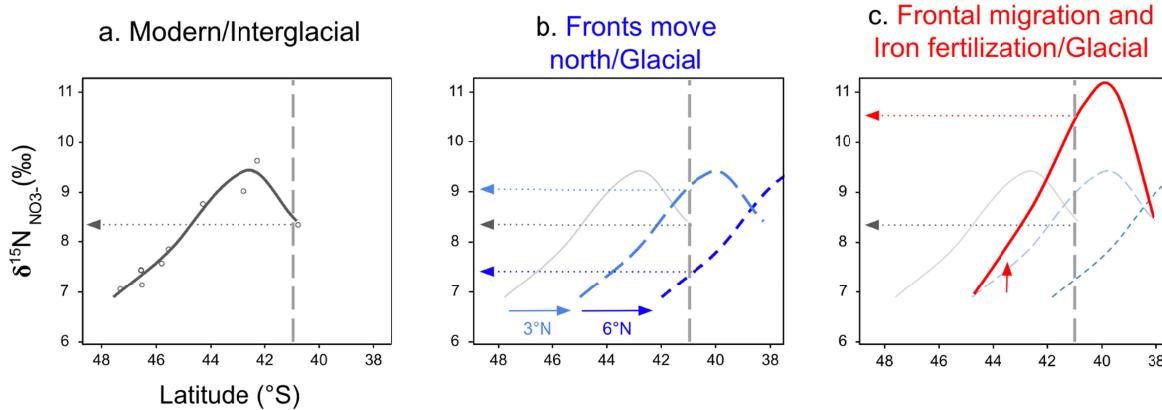
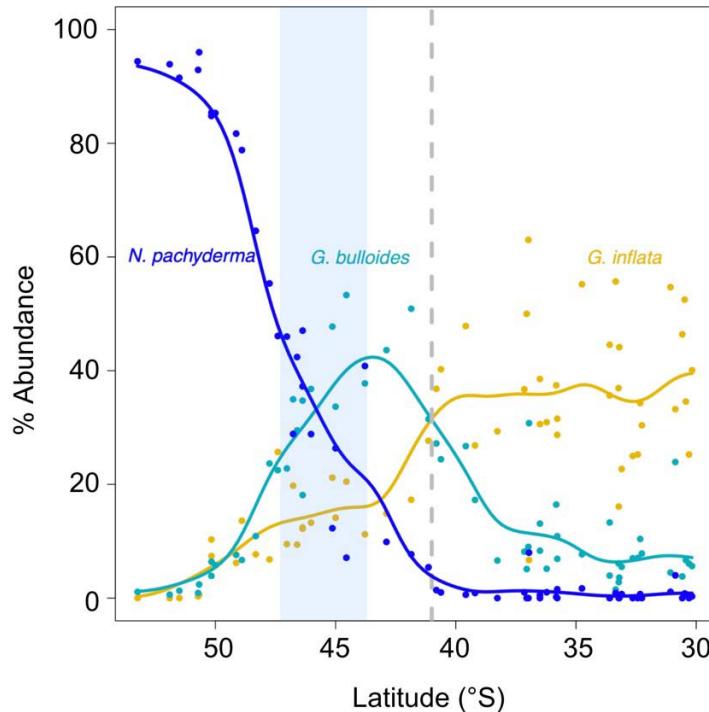


Figure 2: Schematic illustrating the $\delta^{15}\text{N}_{\text{NO}_3}$ latitudinal gradient in the modern ocean and estimated changes resulting from frontal migrations and/or iron fertilization. a. Modern $\delta^{15}\text{N}_{\text{NO}_3}$ latitudinal gradient within the Southern Ocean mixed layer (Smart et al., 2020); b. under hypothesized MPT scenarios of northward frontal migrations; c. and iron fertilization. Vertical dashed line approximates the location of Site U1475, within the present-day STFZ. Dotted arrows indicate expected $\delta^{15}\text{N}_{\text{NO}_3}$ at Site U1475 under each scenario.

To do so, we pair $\delta^{15}\text{N}_{\text{FB}}$ values with polar planktonic foraminifera species abundance, and sea surface temperatures (SST) from International Ocean Discovery Program Site U1475 ($41^{\circ}25'\text{S}$, $25^{\circ}15'\text{E}$; water depth 2669 m) to provide constraints on the relative importance of physical (ocean circulation) and biological (export productivity) processes across the MPT. Site U1475 underlies the Subtropical Frontal Zone (STFZ) where warm, nutrient-poor subtropical waters meet cool, nutrient-rich polar waters at the northern edge of the Southern Ocean SAZ (Figure 1) thus it is sensitive to physical and biogeochemical changes associated with latitudinal migrations of the STFZ. We consider these additional physical water mass proxies in light of complimentary proxy records from ODP Site 1090 ($42^{\circ}54'\text{S}$, $8^{\circ}54'\text{E}$; water depth 3702 m) which serves as an SAZ endmember.

We present records of $\delta^{15}\text{N}_{\text{FB}}$ from *Globigerina bulloides* ($\delta^{15}\text{N}_{\text{FB}} G. \text{bull}$) and *Globorotalia inflata* ($\delta^{15}\text{N}_{\text{FB}} G. \text{inf}$). *G. bulloides* is a cosmopolitan, opportunistic species inhabiting nutrient-rich environments, with maximum abundances south of the STFZ (Figure 3; Bé & Hutson, 1977; Haddam et al., 2016). *G. inflata* is dominant within the thermocline of transitional environments, between subtropical and polar water masses, with greatest abundance in the Indian Ocean north of Site U1475 (Figure 3; Bé & Hutson, 1977; Haddam et al., 2016). Previous studies measured $\delta^{15}\text{N}_{\text{FB}} G. \text{bull}$ to examine SAZ nutrient consumption at ODP 1090, located well within the SAZ. At U1475, within the STFZ, the $\delta^{15}\text{N}_{\text{FB}} G. \text{bull}$ may be biased toward a Southern Ocean signal and subject to potential influence from variations in SAZ nutrient demand related to Fe fertilization but also to the incursion of low latitude source nitrate into the mixing zone. $\delta^{15}\text{N}_{\text{FB}} G. \text{inf}$ values on the other hand, are more likely biased toward the Subtropical, or northern, component of the STFZ mixture. Comparison of the two records may relate to the relative position of the STFZ with respect to the core site.



167
 168 Figure 3: Modern core-top abundance of *N. pachyderma* sinistral (blue), *G. bulloides* (teal), and *G. inflata* (yellow)
 169 versus latitude in the region surrounding Site U1475, between 0 - 50 °E (Haddam et al., 2016). Blue shading
 170 encompasses latitudes in the modern ocean with abundances of *N. pachyderma* similar to observed glacial
 171 abundances during the MPT. Site U1475 denoted with grey dashed vertical line.

172 Our data demonstrate the northward migration of Southern Ocean fronts during MPT glacials.
 173 We show that the establishment of 100 kyr glacials is preceded by dramatic contraction of the
 174 Southern Ocean during the “super interglacial” Marine Isotope Stage 31, ~1,100 ka, and
 175 subsequent expansion of the Southern Ocean in the Indian-Atlantic Ocean Gateway. Expansion
 176 of the Southern Ocean appears to have occurred with an increase in biological carbon
 177 sequestration as due to enhanced biological pump efficiency in the Southern Ocean, while also
 178 altering global ocean circulation through mixing with Agulhas Leakage. Dilution of Agulhas
 179 Leakage by Southern Ocean waters may further heighten deep ocean carbon storage, increasing
 180 the residence time of surface waters and slowing overturning circulation (Starr et al., 2021).

181 **2 Materials and Methods**

182 **2.1 Foraminifera-bound N isotopes**

183 Individual species were identified and ~550 individuals per species were picked from the >250
 184 µm fraction under dissecting microscope for each sample. Approximately 7 mg of picked and
 185 identified foraminifera shells were crushed between glass microscope slides and rinsed with
 186 MilliQ water. Samples were cleaned prior to $\delta^{15}\text{N}_{\text{FB}}$ measurement as follows: crushed tests were
 187 sonicated in 1.5 mL of 2% sodium hexametaphosphate, rinsed 5 times with MilliQ water and
 188 then chemically oxidized with 2 mL of an alkaline persulfate reagent (50 mL of MilliQ water,
 189 3.25 g NaOH, 3.0 g $\text{K}_2\text{S}_2\text{O}_8$) in a pressure cooker for 60 minutes (~100 min with warm up and
 190 cool down) on a slow vent setting, followed by three MilliQ rinses, to remove external N

191 contamination (Smart et al., 2020; Ren et al., 2009). Once samples were clean, organic nitrogen
192 was released into solution by acid dissolution of the foraminiferal calcite with 75 μ L of 6N
193 hydrochloric acid and converted to nitrate by the addition of 3 mL of an alkaline persulfate
194 reagent (100 mL MilliQ water, 1.6 g NaOH, 1.0 g $K_2S_2O_8$; Knapp et al., 2005; Nydahl, 1978).
195 Samples were acidified to a pH between 2-4, using \sim 100 μ L 6N hydrochloric acid, prior to
196 measurement. Nitrate concentrations were measured by chemiluminescence on a Teledyne
197 Instruments (Model 200E) chemiluminescence NO/NO_x analyzer (Braman & Hendrix, 1989).
198 $\delta^{15}N_{FB}$ samples, 10 nmol in size, were measured by bacterial conversion of nitrate to nitrous
199 oxide (Sigman et al., 2001), with measurement of the $\delta^{15}N$ of the nitrous oxide by automated
200 extraction and gas chromatography-isotope ratio mass spectrometry (Casciotti et al., 2002) on a
201 Thermo Delta V Plus IRMS. The potassium nitrate reference materials IAEA-N3 and USGS 34
202 (+4.7‰ and 1.8‰, respectively) were used to standardize results (Gonfiantini et al., 1995).
203 Note, testing of subset of 6 samples, each with full procedural triplicates, for a total of 18
204 samples, showed negligible differences in nitrogen content and $\delta^{15}N_{FB}$ values with and without a
205 reductive cleaning step, and so it was omitted here to avoid unnecessary loss of sample material.

206 Sample replicates and triplicates were analyzed when possible. Full procedural replicates were
207 analyzed for 134 sample splits, representing 66 unique samples, when enough foraminifera were
208 available for duplicate or triplicate analysis. The average standard deviation of procedural
209 replicates is 0.4‰. Full operational blanks and amino acid standards (USGS 65 glycine) were
210 measured in each batch. The average standard deviation of glycine standards measured in
211 triplicate is 0.3‰. We estimated the $\delta^{15}N$ value of the persulfate blank using a dilution series (5,
212 7.5, 10, and 20 μ M of the glycine standard and the fraction of the blank in standards. We applied
213 a blank correction to each sample based on the calculated mean $\delta^{15}N$ value of all of the persulfate
214 blanks for the dataset and the fraction of the blank in the N content of each sample (see SI
215 equation S1). Data were subset to exclude N content outliers (>2 s.d. from mean and where the
216 blank was greater than 20% of the sample N content, with significantly different $\delta^{15}N$ values
217 from other replicates). The exclusion of this data does not alter statistical analyses or the findings
218 of the paper but does improve error.

219 Full propagated analytical error associated with measurement and blank correction, following
220 Higgins et al., (2009), was on average 0.6‰ (Full description in SI equation S2). Propagating the
221 errors, including not only the procedural replicates and their variance, but the relative size of the
222 blanks, the mean of the calculated blank $\delta^{15}N$ values (5 ± 10 ‰). All error bars are propagated
223 errors for each individual sample where calculated and the mean value, 0.6‰, is used where
224 procedural replicates were limited by sample availability. To verify accuracy, we measured the
225 Holocene mean $\delta^{15}N_{FB}$ *G. bull* value at MD02-2588, a co-located CASQ core, of 8.7 ± 0.7 ‰; for
226 comparison, $\delta^{15}N_{FB}$ *G. bull* value of the mudline sample collected at U1476 was measured to be
227 9.2‰ for *G. bulloides* size class 250-400 μ m and 8.4‰ *bulloides* size class >400 μ m (A.
228 Foreman, personal communication, 2023. The age model is based on the benthic oxygen isotope
229 stratigraphy presented by Starr et al. (2021). This age model for Site U1475 was generated with
230 12 radiocarbon dates and 33 benthic oxygen isotope tie points which were graphically aligned
231 with a probabilistic stack of 180 globally distributed benthic oxygen isotope records (Starr et al.,
232 2021).

233 2.2 Biogenic Silica

234 Approximately 200 mg of sediment was analyzed for each sample. Cleaning, chemical treatment,
 235 and measurement followed protocols outlined in (Mortlock & Froelich, 1989). Samples were
 236 measured with a UV Vis spectrophotometer at 812 nm wavelength. Full procedural replicates
 237 were performed on 163 of the 435 samples yielding an average standard deviation of 0.2%.
 238 Samples were referenced to RICCA VerSpec SiO_3^{2-} in 1% NaOH for intercomparison. Opal
 239 mass accumulation rates were calculated by multiplying the fraction of opal by dry bulk density
 240 and sedimentation rates from Starr et al. (2021).

241 2.3 Planktic foraminifera *Neogloboquadrina pachyderma* (sin) counts

242 Bulk planktonic foraminifera are obtained by washing $\sim 10 \text{ cm}^3$ of sediment through a $150 \mu\text{m}$
 243 sieve and drying at $\sim 50^\circ\text{C}$ for 24 h. This dried fraction is split until a total of 300-400
 244 individuals remained. From this amount, we identify the relative abundance of
 245 *Neogloboquadrina pachyderma* tests according to Kennett and Srinivasan (1983) and Loeblich
 246 and Tappan (1988).

247 2.4 Changepoint mean analysis

248 Changepoint mean analysis was executed in R, using ‘cpt.mean()’ function within package
 249 ‘changepoint’ (RStudio Team, 2020) Data are averaged between replicates for each species and
 250 fit to a 6 kyr evenly spaced time series using nearest neighbor interpolation, R package ‘pracma’,
 251 function ‘interp1().’ Changepoint mean analysis was conducted using the following parameters:
 252 test statistic = Normal; method = PELT; penalty = BIC. We consider the 0.6‰ standard
 253 deviation in our interpretations, discussing short term changes greater than 1‰ and identifying
 254 long term changes in the mean. Welch 2-sample t tests on all samples and replicates analyzed in
 255 each section identified in the changepoint mean analysis show that each of the groups are
 256 significantly different ($p < 0.05$) from each other.

257 **3 Data**258 3.1 *Neogloboquadrina pachyderma* (sin) abundance

259 Relative abundance of *N. pachyderma* (sin) varies between glacial and interglacial intervals with
 260 greater abundances consistently observed in glacials. Prior to 936 ka, *N. pachyderma* (sin)
 261 generally increases from 0 – 10 % in interglacials to 20 – 30 % in glacials (Figure 4). From 936 –
 262 917 ka, *N. pachyderma* (sin) dominates the assemblage, reaching 60 % abundance and remains
 263 above 20% throughout MIS 23 (917 – 900 ka, Figure 4). After 900 ka, *N. pachyderma* varies
 264 between 45% and 0% in glacial and interglacial intervals, respectively (Figure 4).

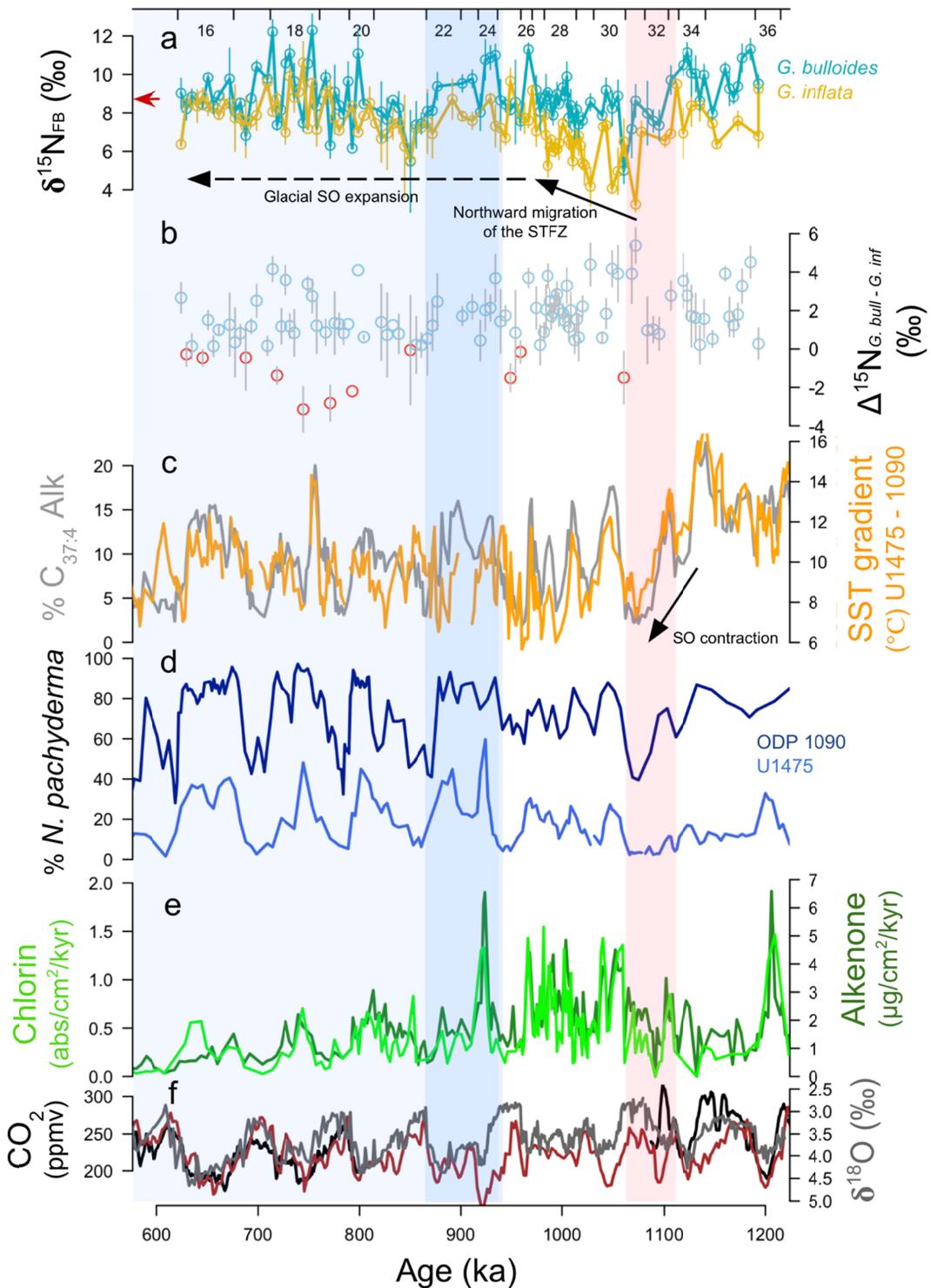
265 3.2 Opal mass accumulation

266 Opal concentrations were overall very low, with an average value of 1.6%, at U1475. As a result,
 267 opal mass accumulation rates are generally low ($< 0.05 \text{ mg/cm}^2/\text{kyr}$), reaching maximum values
 268 ($> 0.1 \text{ mg/cm}^2/\text{kyr}$) early in the MPT, $\sim 1,100$ ka (Figure 5). After this initial peak, opal mass
 269 accumulation declines slightly, remaining near $\sim 0.06 \text{ mg/cm}^2/\text{kyr}$ until ~ 800 ka, after which
 270 opal accumulation remains largely below $0.05 \text{ mg/cm}^2/\text{kyr}$ (Figure 5).

271 3.3 Foraminifera-bound N isotopes

272 Across the MPT, $\delta^{15}\text{N}_{\text{FB } G. \text{ bull}}$ values are generally higher than $\delta^{15}\text{N}_{\text{FB } G. \text{ inf}}$ values (Figure 4).
273 While $\delta^{15}\text{N}_{\text{FB } G. \text{ bull}}$ values are less variable and tend to be highest in the early MPT, prior to 1,100
274 ka, $\delta^{15}\text{N}_{\text{FB } G. \text{ inf}}$ values are less variable and tend to be highest during the mid-late MPT, after ~790
275 ka. Both species exhibit minimum $\delta^{15}\text{N}_{\text{FB}}$ values during the “super interglacial” Marine Isotope
276 Stage (MIS) 31, ~1,070 ka.

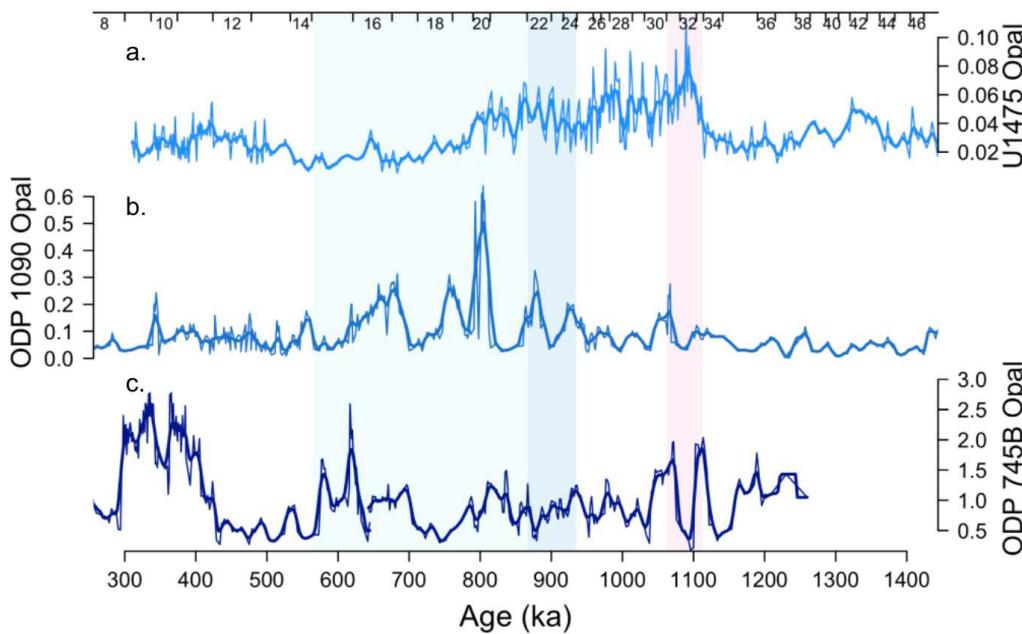
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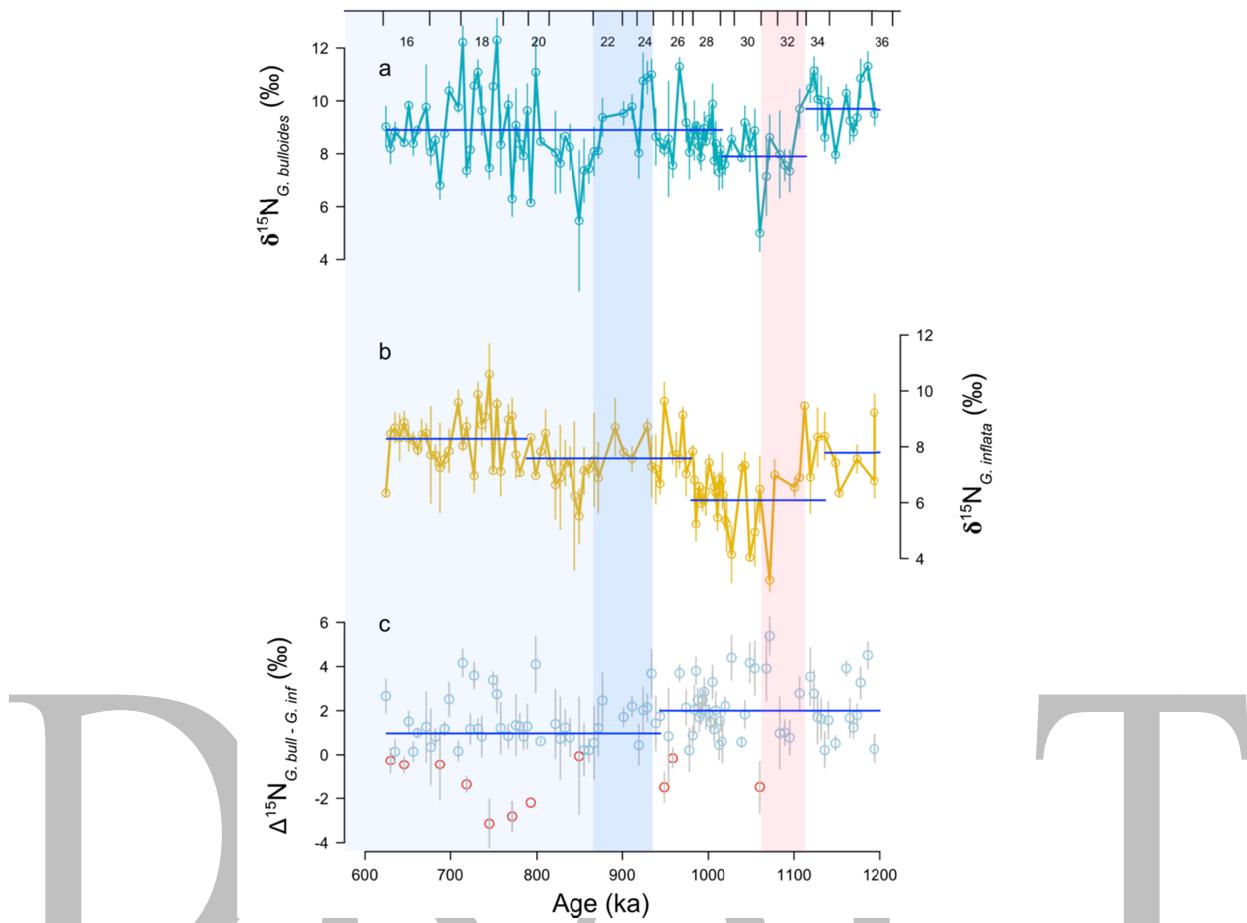
278 Figure 4: Biogeochemical records measured from Sites U1475 and ODP 1090. a. $\delta^{15}\text{N}_{\text{FB}}$ of *G. bulloides* and *G.*
 279 *Inflata*, vertical lines indicate propagated error for each sample. The average Holocene *G. bulloides* value from a co-
 280 located core (MD0202588) are indicated by the red arrow on the y axis; b. $\Delta\delta^{15}\text{N}_{\text{FB}}$, *G. bulloides* – *G. inflata*, where
 281 blue circles indicate positive and red indicate negative values, gray bars span vertical lines span ± 1 standard
 282 deviation; c. U^{37}SST gradient between Site U1475 (Cartagena-Sierra et al., 2021) and ODP 1090 (Martínez-García
 283 et al., 2010) and percent $\text{C}_{37:4}$ alkenones at ODP 1090 (grey, Martínez-García et al., 2010); d. Percent abundance of

284 polar species *N. pachyderma* at Site U1475 and Site 1090 (Becquey & Gersonde, 2002); e. Alkenone and chlorin
 285 mass accumulation rates (Cartagena-Sierra et al., 2021) ($\mu\text{g}/\text{cm}^2/\text{kyr}$ and $\text{abs}/\text{cm}^2/\text{kyr}$; dark and light green
 286 respectively). U1475 age model from Starr et al. (2021); f. Atmospheric CO_2 from EPICA Dome C (black, Bereiter
 287 et al., 2015), $\delta^{11}\text{B}$ -based reconstruction (black, Hönisch et al., 2009), and $\delta^{13}\text{C}_b$ models (red, Lisiecki, 2010); Site
 288 U1475 benthic $\delta^{18}\text{O}$ *Cibicidoides wuellerstorfi* (gray, Starr et al., 2021). Marine Isotope Stages are noted along the
 289 top axis. Light blue shading indicates 100 kyr world, dark blue shading indicates “900 kyr” event, red shading
 290 indicates “super interglacial”.



291

292 Figure 5: Opal mass accumulation rates ($\text{mg}/\text{cm}^2/\text{kyr}$) from the a. Subtropical frontal zone, IODP Site U1475; b.
 293 Subantarctic Zone, ODP Site 1090 (Diekmann & Kuhn, 2002); c. Antarctic Zone, ODP Site 745B (Kaiser et al.,
 294 2021; Billups et al., 2018) showing a southward shift in the relative, site specific, magnitude of biogenic opal
 295 deposition within the Southern Ocean around the MPT. Bold lines show a 10 kyr kernel smoothing. Marine Isotope
 296 Stages are noted along the top axis and red/blue shading corresponds to shading in Figure 4.



297

298 Figure 6: Results from changepoint mean analysis of a. $\delta^{15}\text{N}_{\text{FB}}$ *G. bulloides*; b. $\delta^{15}\text{N}_{\text{FB}}$ *G. inflata*; and c. $\Delta\delta^{15}\text{N}_{\text{FB}}$, *G. bulloides* – 299 *G. inflata*, where blue circles indicate positive and red indicate negative values. Blue lines indicate mean $\delta^{15}\text{N}_{\text{FB}}$ of 300 a statistically similar interval, with significant changes in the mean marked by a change in the y position, or mean 301 $\delta^{15}\text{N}_{\text{FB}}$ value, of the line. Vertical bars span ± 1 standard deviation. Marine Isotope Stages are noted along the top 302 axis and red/blue shading corresponds to shading in Figure 4.

303 4 Discussion

304 4.1 Long timescale changes in $\delta^{15}\text{N}$ above the Agulhas Plateau

305 The long timescale variation in $\delta^{15}\text{N}$, with lower $\delta^{15}\text{N}_{\text{FB}}$ *G. bull* and $\delta^{15}\text{N}_{\text{FB}}$ *G. inf* values around 306 1,100 ka, with a minimum during MIS 31-33, followed by a return to a more elevated mean 307 values by 900 ka, is mirrored in the SST gradient, $\text{Uk}'_{37:4}$, and *N. pachyderma* abundance records 308 suggesting a strong link between surface ocean nutrient dynamics and the climate driven position 309 of the Subtropical Front. Changepoint mean analysis reveals two significant timepoints in each 310 species' $\delta^{15}\text{N}_{\text{FB}}$ record (Figure 6) that highlight the long term trends. From 1,200 – 1,114 ka the 311 $\delta^{15}\text{N}_{\text{FB}}$ *G. bull* values vary around a mean of 9.7‰, a significant changepoint occurs at 1,114 ka 312 when mean $\delta^{15}\text{N}_{\text{FB}}$ *G. bull* is reduced to 7.9‰ until 1,016 ka (Figure 6). After 1,016 ka $\delta^{15}\text{N}_{\text{FB}}$ *G. bull* 313 values vary around a mean of ~ 8.9‰ (Figure 6). In contrast, $\delta^{15}\text{N}_{\text{FB}}$ *G. inf* values vary around a 314 mean of 7.8‰ prior to 1,136 ka, from 1,136 – 980 ka mean $\delta^{15}\text{N}_{\text{FB}}$ *G. inf* is 6.1‰, from 980 – 788 315 ka mean $\delta^{15}\text{N}_{\text{FB}}$ *G. inf* is 7.6‰ and after 788 ka mean $\delta^{15}\text{N}_{\text{FB}}$ *G. inf* rises to 8.3‰ (Figure 6). The 316 potential controls on the $\delta^{15}\text{N}$ records are: 1) variations in the relative contribution from 317

318 Subtropical versus Subpolar water masses, 2) variation in the relative contributions from locally
319 grown versus advected foraminifera, 3) variations in the $\delta^{15}\text{N}$ values of the Subtropical source
320 water, 4) variations in the $\delta^{15}\text{N}$ value of the Subpolar source, and 5) local variations in the
321 relative utilization of nitrate. To some degree, all of these factors are likely to contribute to this
322 record.

323 Subtropical and Subpolar waters converge in the STFZ and their relative contributions likely
324 vary over time with climate. The early MPT, prior to \sim 1,140 ka, is marked by ice sheet
325 expansion, cool SST's, and elevated *N. pachyderma* (sin) abundance at Site 1090 (McKay et al.,
326 2012; Martínez-García et al., 2010; Beltran et al., 2020) (Figure 4; Figure S2). Yet, warm SST's
327 and low *N. pachyderma* (sin) abundance at Site U1475 prior to 1,140 ka indicates the STFZ was
328 located south of Site U1475. Records of Agulhas Leakage indicate transfer of water from the
329 Indian into the Atlantic Ocean, consistent with this inference (Caley et al., 2012). The early MPT
330 interval of ice-sheet expansion is terminated by the "super interglacial" of MIS 31 (\sim 1,070 ka,
331 McKay et al., 2012; Beltran et al., 2020) and a dramatic southward shift of the STFZ.

332
333 Southern Hemisphere insolation reaches a 5 Myr high during MIS 31, \sim 1,070 ka, resulting in
334 dramatic Antarctic ice loss and Southern Hemisphere warming (Beltran et al., 2020; McKay et
335 al., 2012; Maiorano et al., 2009) (Figure S2). Southward displacement of the STFZ is evidenced
336 by reduced presence of polar species *N. pachyderma* (sin) at Site 1090, a sharp reduction in the
337 SST gradient between Sites U1475 and 1090, reduced % C_{37.4} at Site 1090 (Figure 4), and by
338 increased presence of Subtropical Convergence/Agulhas Current nannofossil assemblages at Site
339 1090 from MIS 33-31 (1,114 – 1,062 ka, Maiorano et al., 2009). The reduced SST gradient is
340 largely driven by warming at Site 1090 (Figure S2). This marks a sustained reduction in the SST
341 gradient relative to values observed prior to MIS 33, \sim 1,110 ka (Figure 4). Interestingly, biogenic
342 opal deposition at Site U1475 is highest during the "super interglacial", despite evidence for
343 significant contraction of the Southern Ocean (Figure 5). The STFZ is associated with a
344 deepening of the mixed layer depth and may indicate localized enhanced nutrient supply and
345 consequent production related to this deep mixing (Monterey & Levitus, 1997).

346
347 The extreme southward shift in the STFZ is contemporaneous with significant reductions in the
348 $\delta^{15}\text{N}_{\text{FB}}$ values. This interval is highlighted as a significant changepoint between MIS 33 – 31
349 (Figure 6). Low $\delta^{15}\text{N}_{\text{FB}}$ values are consistent with a greater contribution of nitrogen from the
350 Subtropics, either through the advection of Subtropically sourced nitrate with low $\delta^{15}\text{N}$ values to
351 the core site, resulting in low $\delta^{15}\text{N}$ PON production and consumption by local foraminifera, or
352 the advection of more foraminifera from the Subtropics to the core site. Model results reveal the
353 Agulhas Current is capable of carrying plankton nearly 1,000 km over a typical 30 day lifespan
354 (van Sebille et al., 2015) and so at least some contribution from advected foraminifera is likely.
355 While both potential contributions of nitrogen point to a more important Subtropical source
356 during MIS 31 – 33, the need to make a distinction comes into play if one wants to assign an
357 endmember $\delta^{15}\text{N}$ value to the Subtropical nitrogen or use the relative proportion of Subpolar
358 versus subtropical planktic foraminiferal abundances to weight these endmember values. The
359 possibility of locally grown versus imported foraminifera muddies these ideas further.

360 The need to understand the endmember $\delta^{15}\text{N}$ values is highlighted by the fact that the $\delta^{15}\text{N}_{\text{FB}}$
 361 values observed during MIS 31-33 are exceptionally low relative to the rest of the record, and
 362 also relative to expectations based on to modern southern Indian Ocean values (Harms et al.,
 363 2016; Marshall et al., 2023). These low $\delta^{15}\text{N}_{\text{FB}}$ values require not only an increase in
 364 contributions of Subtropical nitrogen but also a decrease in the $\delta^{15}\text{N}$ of the nitrogen sourced to
 365 the STFZ. A decrease in the $\delta^{15}\text{N}$ of the Subtropically sourced nitrogen can be explained by
 366 increases in nitrogen fixation derived nitrogen in the Agulhas Current region. Today N fixation,
 367 which brings in N with a $\delta^{15}\text{N}$ value of $\sim 1\text{\textperthousand}$, occurs in the source regions to and along the
 368 flowpath of the Agulhas Current (Dupuy et al., 2016; Kolasinski et al., 2012; Marshall et al.,
 369 2023). In addition, throughout interglacial periods of the last 800 kyr, increased denitrification
 370 has been documented in the Arabian Sea (Kim et al., 2018) thus it is probable that during this
 371 “super interglacial” we may see an exceptional response in N fixation to balance N losses from
 372 denitrification. Our data pose an interesting question as to whether a significant change in the
 373 magnitude of Indian Ocean denitrification and N fixation occurs at this time. N isotope data from
 374 upstream locations would be useful in confirming these changes.

375 At the same time that Subpolar nitrate likely became less important at U1475, the $\delta^{15}\text{N}$ of the
 376 Subpolar sourced nitrogen, either as nitrate or in advected Subpolar foraminifera, may also have
 377 decreased. Prior to the super-interglacial warming, we observe high $\delta^{15}\text{N}_{\text{FB}}$ values particularly in
 378 *G. bulloides* coincident with the SST gradient and Site 1090 %C_{37.4} maxima and Southern
 379 Hemisphere insolation minimum (Figure 4, Figure S2). Part of the elevation in $\delta^{15}\text{N}$ values may
 380 be due to the northward shifted Southern Ocean fronts, documented by the Site 1090 *N.*
 381 *pachyderma* (sin) and SST gradient data, and the associated relative contribution of Subpolar
 382 nitrogen at U1475. Yet, the observed $\delta^{15}\text{N}_{\text{FB}}$ *G. bull* values ($11\text{\textperthousand}$) exceed the modern latitudinal
 383 $\delta^{15}\text{N}_{\text{NO}_3}$ maxima expected near the STFZ ($9.5\text{\textperthousand}$) and are $\sim 3\text{\textperthousand}$ greater than the expected $\delta^{15}\text{N}_{\text{FB}}$
 384 *G. bull* (Figure S1). This implies an increase in the $\delta^{15}\text{N}$ value of the source nitrogen. We infer that
 385 relative nutrient consumption was elevating the $\delta^{15}\text{N}$ value of nitrate (Figure 1, Figure 4). This
 386 could be due to a local increase in nutrient consumption or a regional increase and the advection
 387 of this signal northwards from the SAZ. Without an increase in productivity at Sites 1090 or
 388 U1475, enhanced nutrient consumption requires an overall reduction in nutrient supply prior to
 389 1,110 ka. Indeed, ice sheet expansion may have contributed to weaker overturning within the
 390 Southern Ocean that limited nutrient supply and increased relative nitrate consumption
 391 regionally (Starr et al., 2021; Ferrari et al., 2014). After 1,110 ka, Southern Ocean warming
 392 during “super interglacial” MIS 31 coincides with a significant reduction in $\delta^{15}\text{N}_{\text{FB}}$ values and a
 393 decrease in the $\delta^{15}\text{N}$ of nitrogen from both the Subtropical and Subpolar sources is likely.

394 4.3 Transitional expansion of the glacial Southern Ocean prior to the 100 kyr glacial periods

395 The Southern Ocean experienced significant geographic expansion during glacial stages
 396 following 900 ka. *N. pachyderma* (sin) abundances indicate that the glacial expansions began
 397 gradually after MIS 31, ($\sim 1,060$ ka), increasing in each glacial period until MIS 24 (~ 930 ka)
 398 when the STFZ achieved its northernmost position. At ~ 930 ka, *N. pachyderma* (sin)
 399 abundances exceeded 60% at Site U1475, which, based on *N. pachyderma* (sin) surface sediment
 400 distributions suggest an 8 degree northward migration in the average latitude of STFZ (Figures 3
 401 & 4). Higher abundances of *N. pachyderma* (sin) in 100 kyr glacials, after ~ 920 ka, indicates
 402 increased influence of polar waters near Site U1475. The northward shift in polar waters is

403 supported by the relative proportion of the cold, %C_{37.4} alkenones at the nearby SAZ ODP Site
 404 1090 (Martínez-García et al., 2010) (Figure 4) and abundance of ice-rafted debris (IRD) at Site
 405 U1475 (Figure S2, Starr et al., 2021). This northward migration of the STFZ would deliver
 406 nitrate rich waters further north, fueling the enhanced export productivity recorded by chlorin
 407 and alkenone accumulation from ~1,010 – 920 ka (Figure 4). The relatively high $\delta^{15}\text{N}$ of this
 408 southern sourced nitrate is evident in the progressive increase in $\delta^{15}\text{N}_{\text{FB}}$ values (Figure 6).

409 4.4 An expanded glacial Southern Ocean amplifies Fe fertilization in the 100 kyr world

410 The $\delta^{15}\text{N}_{\text{FB}}$ values at Site U1475 after 900 ka likely reflect the increased or dominant presence of
 411 the Southern Ocean waters that, because they are nutrient bearing, also record the nutrient
 412 consumption signal attributable to enhanced iron delivery (Martinez-Garcia et al., 2011). The
 413 STFZ maintains a northward position, as evidenced by *N. pachyderma* (sin) abundance and IRD
 414 deposition, from ~930 – 860 ka and, based on the relatively high $\delta^{15}\text{N}_{\text{FB}}$ values, an extended
 415 period of enhanced nutrient drawdown (Figure 4, Figure S2). Similar to the interval prior to the
 416 super-interglacial, expansion of the Southern Ocean alone cannot fully explain the glacial $\delta^{15}\text{N}_{\text{FB}}$
 417 values recorded at Site U1475. A slowdown in overturning circulation is recorded by the
 418 accumulation of resired organic carbon in the deep ocean (Farmer et al., 2017; Lear et al.,
 419 2016). Expanded Southern Ocean sea ice and enhanced stratification at ~900 ka would have
 420 limited the supply of nutrients and carbon to the surface contributing to the elevated $\delta^{15}\text{N}_{\text{FB}}$
 421 values observed across this interval (Hasenfratz et al., 2019). This interplay between biological
 422 drawdown and physical trapping of carbon occurs across the “900 ka event”, prior to the
 423 establishment of 100 kyr cyclicity in deep ocean biogeochemical records (Ford & Chalk; 2020;
 424 Starr et al., 2021; Farmer et al., 2019; Pena & Goldstein, 2014).

425 In glacial intervals following 900 ka, the supply of southern sourced nutrients to Site U1475
 426 supported modest increases in biological productivity that are reflected in slightly elevated
 427 biogenic sediment accumulation rates while elevated glacial $\delta^{15}\text{N}_{\text{FB}}$ values suggest continued
 428 greater demand for nutrients and reduced Subtropical nitrogen contributions (Figure S3). The
 429 expectation for a slight northward shift in the fronts without any change in the degree of nutrient
 430 consumption regionally is an increase in the $\delta^{15}\text{N}_{\text{NO}_3^-}$ value (due to reduced contribution of low
 431 $\delta^{15}\text{N}$ subtropical NO_3^-). While a larger northward shift in the latitude of the STFZ, as predicted in
 432 MPT glacials by *N. pachyderma* (sin) abundances (Figure 2b), would result in lower $\delta^{15}\text{N}_{\text{NO}_3^-}$,
 433 unless a significant increase in nutrient demand relative to availability accompanies these frontal
 434 migrations. Glacial *N. pachyderma* (sin) abundances indicate a 3 - 6 degree northward migration
 435 of the STFZ, again suggesting that the $\delta^{15}\text{N}_{\text{FB}}$ enrichments, on average 3‰ between average
 436 interglacial minima and glacial maxima cannot be explained without enhanced nutrient
 437 consumption (Figure 2 & 4) (Haddam et al., 2016). We use $\delta^{15}\text{N}_{\text{FB}} G. bull$ values to estimate a
 438 change in Southern Ocean nutrient consumption on glacial-interglacial timescales during the
 439 MPT, assuming the $\delta^{15}\text{N}_{\text{FB}} G. bull$ signal after MIS 31 dominantly reflects changes in relative
 440 consumption. We use measurements from *G. bulloides* to more easily relate to estimates from
 441 Site 1090 spanning the last glacial period.

442 Assuming no net change in supplied nitrate concentration or isotopic composition at 41°S, we
 443 apply a Rayleigh model to estimate changes in the degree of summer nitrate consumption
 444 associated with a 3‰ increase in $\delta^{15}\text{N}_{\text{FB}} G. bull$ (Altabet & Francois, 1994; Fripiat et al., 2019)

445 (Figure S1b). We calculate the integrated phytoplankton biomass N assimilated during summer
 446 nitrate drawdown using the “integrated product” equation, where $\delta^{15}\text{N}_{\text{integ.prod.}} = \delta^{15}\text{N}_{\text{initial}} + e *$
 447 $([\text{NO}_3^-]/([\text{NO}_3^-]_{\text{initial}} - [\text{NO}_3^-])) * \ln([\text{NO}_3^-]/[\text{NO}_3^-]_{\text{initial}})$ and $[\text{NO}_3^-]_{\text{initial}}$ and $\delta^{15}\text{N}_{\text{initial}}$ are the nitrate
 448 concentration and $\delta^{15}\text{N}_{\text{NO}_3^-}$ in the water supplied to the summertime surface mixed layer prior to
 449 nutrient drawdown, $[\text{NO}_3^-]$ is the nitrate concentration after the nutrient drawdown period, and e is the isotope
 450 effect of nitrate assimilation. Here we assume an isotope effect of 6.5‰, consistent
 451 with estimates for SAZ surface layer nitrate drawdown (DiFiore et al., 2010) (Figure S1).
 452 $\delta^{15}\text{N}_{\text{initial}}$ and $[\text{NO}_3^-]_{\text{initial}}$ are taken from water column measurements beneath the mixed layer at
 453 41°S, 10.1‰ and 8.4 µM (Smart et al., 2020). Using these parameters, the $\delta^{15}\text{N}$ of the
 454 photosynthetic biomass produced is estimated to be 4.4‰, and $\delta^{15}\text{N}_{\text{FB } G. \text{ bull}}$ is expected to be
 455 7.5‰, based on a 3.1‰ trophic offset (Smart et al., 2020) (Figure S1b). These estimates are
 456 slightly lower than average interglacial data (8.7‰) and Holocene data (8.7‰) from Site U1475.
 457 Assuming similar conditions to modern, we use the integrated product estimation to link changes
 458 in $\delta^{15}\text{N}_{\text{FB}}$ values to nitrate consumption. Under these conditions, mean glacial maxima $\delta^{15}\text{N}_{\text{FB}}$
 459 values of 10.2‰ and MIS 24 values of 10‰ are consistent with surface ocean nitrate
 460 concentrations below 2.2 µM (Figure S1b). Surface ocean nitrate concentrations indicate near
 461 complete nutrient consumption in glacial intervals with potentially >70% of surface ocean
 462 nutrients at Site U1475 drawn down. Between peak interglacial and glacial conditions, we
 463 estimate that relative nutrient consumption increased from 16% up to 70%, consistent with
 464 nutrient drawdown exceeding the increase in nutrient supply (Figure 4; Figure S1b). This
 465 estimate does not reflect the real nuances discussed above associated with the potential variations
 466 in the source $\delta^{15}\text{N}$ values or relative contributions of advected versus locally grown foraminifera.

467 If glacial mixing of SAZ and subtropical water remains similar amongst glacial periods
 468 following 900 ka, as the consistent glacial abundances of *N. pachyderma* (sin) imply,
 469 maintaining similar mean $\delta^{15}\text{N}_{\text{FB}}$ values with smaller magnitude increases in biogenic sediment
 470 accumulation requires that nutrient supply decreased. This can be explained by a wholesale
 471 slowdown in nutrient supply or a shift in the locus of nutrient consumption and the advection of
 472 the nitrogen isotopic signature of enhanced consumption northwards. Intermittent increases in
 473 biogenic opal accumulation occur in the SAZ after 900 ka and after 400 ka in the AZ perhaps
 474 suggesting a progressive southward shift in productivity (Figure 5) (Diekmann & Kuhn, 2002;
 475 Billups et al., 2018; Kaiser et al., 2021). Our observation supports a more polar Southern Ocean
 476 driver, whether biological or physical, of carbon sequestration during late MPT glacials.

477 Species specific differences in $\delta^{15}\text{N}_{\text{FB}}$

478 In addition to the large scale shifts in the mean $\delta^{15}\text{N}_{\text{FB}}$ seen in both the *G. bulloides* and *G.*
 479 *inflata* datasets, differences between the two records and the differences between species also
 480 vary with the inferred latitudinal migrations of the STFZ (Figure 6). A significant changepoint
 481 occurs in the record of the $\delta^{15}\text{N}_{\text{FB}}$ difference between the species ($\Delta\delta^{15}\text{N}_{\text{FB}} = \delta^{15}\text{N}_{\text{FB } G. \text{ bull}} -$
 482 $\delta^{15}\text{N}_{\text{FB } G. \text{ inf}}$), with decrease in the $\Delta\delta^{15}\text{N}_{\text{FB}}$ across the MPT with a >1 ‰ reduction in the mean
 483 after 933 ka reducing $\Delta\delta^{15}\text{N}_{\text{FB}}$ value from ~ 2.5 ‰ to 1.1 ‰ (Figure 6). The consistent offset
 484 between $\delta^{15}\text{N}_{\text{FB } G. \text{ bull}}$ and $\delta^{15}\text{N}_{\text{FB } G. \text{ inf}}$ values, in which $\delta^{15}\text{N}_{\text{FB } G. \text{ bull}}$ values are higher, is counter to
 485 modern observations collected from net tows and sediment traps in Indian-Atlantic Ocean
 486 Gateway (Smart et al., 2020) (Figures 4 & 6). In the modern ocean, *G. inflata* records a higher

487 $\delta^{15}\text{N}_{\text{FB}}$ value than *G. bulloides* captured in the same net tow. This is attributable to its preference
 488 for a deeper habitat, possibly related to the consumption of a more degraded PON pool for
 489 nutrition (Smart et al., 2020). If depth was the primary control on differences between $\delta^{15}\text{N}_{\text{FB}}$ *G.*
 490 *bull* and $\delta^{15}\text{N}_{\text{FB}}$ *G. inf* values in the Site U1475 record we would expect to see consistently higher
 491 $\delta^{15}\text{N}_{\text{FB}}$ *G. inf* values. Since we do not, we explore the possibility that the differences relate to
 492 seasonal export events and/or foraminiferal habitat preferences and advection.

493 Within the Southern Ocean, *G. bulloides* exhibits two export episodes to the sediments each year,
 494 once in spring and again in fall (Kretschmer et al., 2018; King & Howard, 2005; Jonkers &
 495 Kučera, 2015). In contrast, *G. inflata* export flux peaks once, in spring (Jonkers & Kučera, 2015;
 496 Bé & Hutson, 1977). Thus, seasonal biases may yield higher $\delta^{15}\text{N}_{\text{FB}}$ values in *G. bulloides* if
 497 nutrients are more depleted in fall than in spring. This is not entirely consistent with modern
 498 observations from this region where late summer $\delta^{15}\text{N}_{\text{NO}_3}$ values are reduced by mixing with low
 499 $\delta^{15}\text{N}_{\text{NO}_3}$ subtropical waters indicating that seasonality does not provide a robust explanation
 500 (Smart et al., 2020). Further, as climate cools *G. bulloides* is expected to bias its export towards
 501 warmer seasons while *G. inflata* would be less affected; this could further reduce the $\delta^{15}\text{N}_{\text{FB}}$ *G. bull*
 502 relative to $\delta^{15}\text{N}_{\text{FB}}$ *G. inf* (Jonkers & Kučera, 2015).

503 However, planktic foraminifera are also subject to advection into this mixing zone. North of Site
 504 U1475, *G. inflata* is present in greater abundance than *G. bulloides*, but to the south *G. bulloides*
 505 abundance exceeds *G. inflata* (Figure 2). If we view the STFZ as a convergence zone of
 506 subtropical and subpolar planktic foraminifera, we can explain the observed $\delta^{15}\text{N}_{\text{FB}}$ values of *G.*
 507 *bulloides* and *G. inflata* more easily. On average, the *G. inflata* measured at Site U1475 are
 508 biased towards recording the subtropical signature of the Agulhas Current, where at least some
 509 fraction of the *G. inflata* in the sediment must have integrated the low $\delta^{15}\text{N}$ PON signal into their
 510 shell in the Subtropics to be ultimately deposited along the STFZ. Similarly, Ekman transport of
 511 Southern Ocean surface water would deliver *G. bulloides* grown in the SAZ to Site U1475. Some
 512 contribution of advected *G. bulloides* from the south and *G. inflata* from the north best explains
 513 the higher $\delta^{15}\text{N}$ values of *G. bulloides* compared to *G. inflata*. The difference between $\delta^{15}\text{N}_{\text{FB}}$
 514 values of *G. bulloides* and *G. inflata* is smallest during “super interglacial” MIS 31 and after 933
 515 ka, with the most similar values occurring when *N. pachyderma* (sin) abundances indicate
 516 considerable latitudinal migrations of the STFZ leading to greater similarity in $\delta^{15}\text{N}$ values of the
 517 sources to both species (Figure 4). To put it another way, when the front is furthest from U1475,
 518 either to the north or south, foraminifera $\delta^{15}\text{N}$ values reflect a shared local Subantarctic or
 519 Subtropical food source, whereas when the mixing zone is close to overhead, foraminifera are
 520 advected from different regions.

521 Both species exhibit significant changes in their mean $\delta^{15}\text{N}_{\text{FB}}$ values associated with these
 522 significant frontal migrations, however, *G. inflata*’s changes lag relative to *G. bulloides*,
 523 suggesting that $\delta^{15}\text{N}_{\text{FB}}$ *G. bull* is a sensitive and early indicator of southward migrations of the
 524 STFZ, with reductions in $\delta^{15}\text{N}_{\text{FB}}$ *G. bull* occurring as early as MIS 33 (Figure 6). After MIS 31, the
 525 $\delta^{15}\text{N}_{\text{FB}}$ values of both species significantly increase (Figure 6). The earlier increase in mean
 526 values of *G. bulloides* is consistent with a northward migration of the STFZ and expansion of the
 527 southern sourced $\delta^{15}\text{N}$ signal (Figure 6).

528

529 **5 Conclusions**

530 Across the MPT, $\delta^{15}\text{N}_{\text{FB}}$ records from Site U1475 change in tandem with STFZ migrations. The
 531 largest change in $\delta^{15}\text{N}_{\text{FB}}$ values results from Southern Ocean contraction and dominance of a low
 532 $\delta^{15}\text{N}$ subtropical nutrient signal during the “super interglacial” MIS 31, ~1080 ka. Glacial
 533 intervals prior to MIS 31 were cold in the Subantarctic but still relatively warm in the STFZ with
 534 the front located firmly south of the Agulhas Plateau. Glacials following MIS 31 are
 535 characterized by northward migrations of the STFZ in the Indian-Atlantic Ocean Gateway with
 536 potential for >6 degree northward migration of the STFZ during MIS 24, 936 – 917 ka and
 537 glacials after 900 ka are characterized by greater abundance of polar foraminifera and a reduced
 538 SST gradient between Sites U1475 and 1090, consistent with a more northern STFZ. More
 539 similar $\delta^{15}\text{N}_{\text{FB}}$ values between *G. bulloides* and *G. inflata* after MIS 24 also support a northern
 540 expansion of Southern Ocean nitrate and reduced influence of low $\delta^{15}\text{N}$ subtropical nitrate at Site
 541 U1475 after 900 ka. These data suggest that not only cooling of the Southern Ocean but also its
 542 expansion is necessary to expand the length of ice ages across the MPT.

543 The increases in $\delta^{15}\text{N}_{\text{FB}}$ associated with northward migrations of the front are likely amplified by
 544 changes in nutrient consumption. Despite higher supply of nitrate and reduced subtropical water
 545 contribution in MPT glacials, it seems that nutrient consumption increased, likely related to iron
 546 fertilization. Glacial expansion of the Southern Ocean has the potential to enlarge the total
 547 nutrient replete area and it also may facilitate iron fertilization by bringing these nutrient rich
 548 waters closer to Southern Hemisphere iron sources which would otherwise be unavailable. In this
 549 region, a >6 degree northward migration of the STFZ would deliver nitrate bearing surface waters
 550 into latitudes receiving twice as much annual dust deposition, linking physical and biological
 551 carbon feedbacks (Figure 1; Jaccard et al., 2016). A complimentary iron accumulation record
 552 from Site U1475 would allow us to determine whether northward expansion of the STFZ, and
 553 associated proximity to South African iron sources, could stimulate additional nutrient
 554 drawdown. A $\delta^{15}\text{N}_{\text{FB}}$ record from a site north of Site U1475 would allow us to account for any
 555 reduction of the $\delta^{15}\text{N}_{\text{FB}}$ values at Site U1475 due to mixing with subtropical water or changes in
 556 the proportion of fixation derived N.

557 A northward shift in the position of the STFZ in this region would alter physical ocean
 558 circulation, increasing the residence time of this carbon in the deep ocean. We hope that future
 559 work to generate nutrient consumption and Fe records will clarify the extent to which Fe
 560 fertilization further enhances C sequestration. This interplay between physical and biological
 561 feedbacks in the Indian-Atlantic Ocean Gateway may play a critical role in increasing deep
 562 ocean carbon storage and lengthening glacial cycles during the MPT.

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572 **Open Research:**

573 All new data presented in this paper are archived at Pangaea (Marcks et al., 2022a), (Marcks et
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