

# **Deglacial upwelling, productivity and CO<sub>2</sub> outgassing in the North Pacific Ocean**

William R Gray<sup>1,2</sup>, James W B Rae<sup>2</sup>, Robert C J Wills<sup>3</sup>, Amelia E Shevenell<sup>4,5</sup>, Ben Taylor<sup>2</sup>, Andrea Burke<sup>2</sup>, Gavin L Foster<sup>6</sup>, Caroline H Lear<sup>7</sup>

<sup>1</sup>Department of Geography, University College London, UK

<sup>2</sup>School of Earth and Environmental Sciences, University of St Andrews, UK

<sup>3</sup>Department of Atmospheric Sciences, University of Washington, Seattle, WA, USA

<sup>4</sup>Department of Earth Sciences, University College London, UK

<sup>5</sup>College of Marine Science, University of South Florida, Tampa, FL, USA

<sup>6</sup>Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, UK

<sup>7</sup>School of Earth and Ocean Sciences, Cardiff University, UK

**The interplay between ocean circulation and biological productivity affects atmospheric CO<sub>2</sub> levels and marine oxygen concentrations. During the warming of the last deglaciation, the North Pacific experienced a peak in productivity and widespread hypoxia, with changes in circulation, iron supply, and light limitation all proposed as potential drivers. Here we use the boron-isotope composition of planktic foraminifera from a sediment core in the western North Pacific to reconstruct pH and dissolved CO<sub>2</sub> concentrations from 24,000 to 8,000 years ago. We find that the productivity peak during the Bølling-Allerød warm interval, 14,700 to 12,900 years ago, was associated with a**

27 **decrease in near-surface pH and an increase in  $p\text{CO}_2$ , and must**  
28 **therefore have been driven by increased supply of nutrient and  $\text{CO}_2$ -rich**  
29 **waters. In a climate model ensemble (PMIP3), the presence of large ice**  
30 **sheets over North America results in high rates of wind-driven upwelling**  
31 **within the subpolar North Pacific. We suggest that this process,**  
32 **combined with collapse of North Pacific Intermediate Water formation at**  
33 **the onset of the Bølling-Allerød, led to high rates of upwelling of water**  
34 **rich in nutrients and  $\text{CO}_2$ , and supported the peak in productivity. The**  
35 **respiration of this organic matter, along with poor ventilation, likely**  
36 **caused the regional hypoxia. We suggest that  $\text{CO}_2$  outgassing from the**  
37 **North Pacific helped to maintain high atmospheric  $\text{CO}_2$  concentrations**  
38 **during the Bølling-Allerød and contributed to the deglacial  $\text{CO}_2$  rise.**

39  
40 The balance between the supply of nutrients and carbon to surface waters via  
41 ocean circulation and their removal via biological productivity is a first order  
42 control on atmospheric  $\text{CO}_2$ . This is particularly important at high latitudes<sup>1,2</sup>,  
43 where Ekman suction, driven by cyclonic wind stress, and winter mixing  
44 supply  $\text{CO}_2$  from the deep ocean to the surface. Depending on the availability  
45 of light and micronutrients, such as iron, this  $\text{CO}_2$  may be captured by  
46 photosynthesis and returned to the deep ocean (the “biological pump”), or  
47 may escape to the atmosphere. The balance between circulation and  
48 biological productivity is also crucial for determining the ocean’s dissolved  
49 oxygen content. Ventilation of the ocean at high latitudes mixes oxygen-rich  
50 waters from the surface into the ocean’s interior, where oxygen is consumed

51 by the respiration of sinking organic matter, coupling the biogeochemical  
52 cycles of oxygen and carbon.

53

54 Dramatic changes in these biogeochemical balances are thought to occur  
55 during Pleistocene deglaciations, with reorganisations of circulation and  
56 productivity at high latitudes leading to changes in oceanic oxygen content  
57 and rapid atmospheric CO<sub>2</sub> rise<sup>1-4</sup>. However, the degree to which these  
58 changes in CO<sub>2</sub> and oxygen are driven by circulation versus biological  
59 productivity remains unknown, limiting our understanding of the mechanisms  
60 driving glacial-interglacial variations in CO<sub>2</sub> and climate. Particularly enigmatic  
61 are the dramatic peaks in productivity observed throughout the North Pacific  
62 Ocean during every deglaciation of at least the last ~1 Ma<sup>5-8</sup>. During the  
63 Bølling-Allerød interval (14.7-12.9 ka) of the last deglaciation (the only  
64 deglaciation for which we currently have records of intermediate-ocean redox)  
65 the productivity maximum is associated with widespread intermediate-ocean  
66 hypoxia in the North Pacific<sup>3,9-11</sup>. Since the discovery of these events more  
67 than 25 years ago<sup>5,10</sup> multiple explanations have been put forward, yet there is  
68 no consensus on the cause of either the productivity or the hypoxia; indeed  
69 the degree to which the productivity and hypoxia are linked, and even the  
70 direction of causation, are still contested. Some studies have proposed the  
71 productivity maximum was caused by an increase in the supply of nutrient and  
72 carbon rich waters<sup>7,12</sup>, while others have suggested alleviation of iron<sup>11,13</sup>  
73 and/or light limitation as the main driver<sup>14</sup>. Early work debated the dominance  
74 of reduced ventilation versus increased productivity as the primary cause of  
75 the hypoxia<sup>9,10</sup>, while more recently it has been proposed that hypoxia was

initially induced by subsurface warming, and that iron release from hypoxic sediments drove the increase in productivity<sup>11</sup>.

Given the large reservoir of dissolved inorganic carbon (DIC) in the North Pacific interior<sup>15</sup> (Figure 1), a change in its supply and removal to and from the surface could have significant impact on the global carbon cycle, and play a role in glacial termination. Understanding the nature of these events is also important as they have been suggested to provide insights in to future changes in hypoxia and productivity in a rapidly warming climate<sup>3,11</sup>.

#### **Boron isotopes and CO<sub>2</sub> supply**

To determine the cause of the Bølling-Allerød productivity maximum, we measured the boron isotope composition ( $\delta^{11}\text{B}$ ) of the planktic foraminifera *N. pachyderma* from deglacial sediments in core MD01-2416 (51.27°N, 167.73°E, 2317 m water depth) (Methods). The core site is located close to the center of the high nutrient and CO<sub>2</sub> pool in the modern subpolar North Pacific (Figure 1), making it ideally suited to track changes in the biogeochemistry of the region.  $\delta^{11}\text{B}$  is a proxy for seawater pH, which tracks seawater CO<sub>2</sub> chemistry, and with an estimate of one other parameter of the carbonate system (here alkalinity), allows the quantification of the CO<sub>2</sub> concentration of past seawater<sup>16</sup> (Methods).

Our results show a general decrease in near-surface pH over deglaciation, with a glacial high of  $8.31 \pm 0.04$  ( $1\sigma$ ) falling to a value of  $8.14 \pm 0.04$  in the early

Holocene, identical to pre-industrial pH at 50m water depth<sup>15</sup> (Figure 2). Punctuating the general decline in pH is a pronounced pH minimum of  $8.07 \pm 0.05$  in the early Bølling-Allerød, coeval with the maximum in productivity. At this time,  $p\text{CO}_2$  in the near surface ocean reached a maximum of  $373 \pm 46 \text{ } \mu\text{atm}$  ( $1\sigma$ ) (Figure 3). The decrease in pH and increase in  $\text{CO}_2$  demonstrates that the supply of carbon and nutrients to the surface ocean was greater than their removal by export production (Supplementary Figure 1). As export production during the Bølling-Allerød was higher than today<sup>6,19</sup>, it follows that the supply of carbon and macronutrients must also have been higher.

### **PMIP3 model ensemble and paleo-circulation tracers**

To investigate the physical mechanisms underlying the increase in nutrient and  $\text{CO}_2$  supply, we looked for large-scale changes in the PMIP3 model ensemble<sup>31</sup> under glacial boundary conditions, alongside paleo-tracers of ocean circulation. Although formation of North Pacific Intermediate Water (NPIW) is extremely limited today<sup>32</sup>, overturning circulation within the basin was significantly enhanced during the last glacial maximum (LGM): benthic foraminiferal  $\delta^{13}\text{C}$  records indicate glacial expansion of NPIW to depths of  $>1500 \text{ m}$ <sup>29,33,34</sup> (Supplementary Figure 2), flushing nutrients and carbon from intermediate waters and deepening the interior ocean nutrient/carbon reservoir. North Pacific ventilation may have been even deeper and more vigorous during early deglaciation<sup>28,30,35</sup>, with possible localised deepwater formation during Heinrich Stadial 1<sup>30,35,36</sup> (HS1) potentially driving the early-

126 deglacial decrease in pH observed in our record (Methods). However, at the  
127 onset of the Bølling-Allerød a rapid decrease in benthic  $\delta^{13}\text{C}$  and increase in  
128 benthic radiocarbon ages indicate a collapse in NPIW formation<sup>28,30</sup>, and a  
129 circulation more similar to the modern<sup>36</sup> (Figure 3 and Supplementary Figure  
130 3).

131  
132 If the Bølling-Allerød was characterised by similar overturning circulation to  
133 today, why was the supply of nutrients and carbon to the surface ocean so  
134 much higher? All eight models in the PMIP3 ensemble show substantial  
135 increase in wind stress curl within the subpolar gyre under glacial boundary  
136 conditions, with an ensemble mean increase of ~60% relative to pre-industrial  
137 (Figure 4). This is driven by the presence of an ice sheet over North America,  
138 which causes a strengthening of the westerlies and a southward shift in the  
139 polar easterlies, substantially increasing meridional wind shear and  
140 associated upwelling by Ekman suction within the subpolar gyre.

141  
142 At the onset of the Bølling-Allerød large ice sheets remained over North  
143 America, with the Laurentide Ice Sheet having lost only ~15% of its mass<sup>37</sup>.  
144 Ekman suction within the subpolar gyre would therefore have been  
145 significantly higher than modern. During the LGM, nutrient flushing by  
146 enhanced NPIW formation would have prevented the increase in Ekman  
147 suction from increasing the nutrient/carbon supply. However, following the  
148 collapse in NPIW at the onset of the Bølling-Allerød, the interior ocean  
149 nutrient/carbon reservoir would have shoaled, becoming accessible to the  
150 surface ocean (Supplementary Figure 3). This combination of nutrient- and

carbon- rich subsurface waters and enhanced Ekman suction led to a substantial increase in nutrient and carbon supply to the surface.

## **Nutrient utilisation and hypoxia**

Higher iron availability from atmospheric dust flux and the alleviation of light-limitation in warm seasonally-stratified waters would have also helped Bølling-Allerød productivity to exceed present-day levels<sup>14,27</sup> (Methods). However, our pH and CO<sub>2</sub> record demonstrates that carbon and nutrient supply overwhelmed iron and light availability, leaving a significantly higher proportion of the upwelled macronutrients and carbon unutilised, and reducing the net efficiency of the biological pump at this location. In contrast to  $\delta^{11}\text{B}$ , foraminiferal  $\delta^{15}\text{N}$  shows little change at the onset of the Bølling-Allerød productivity maximum<sup>19,22,25</sup> (Figure 2). While no change in  $\delta^{15}\text{N}$  during an increase in productivity is consistent with an increase in nutrient supply<sup>19</sup>, previous interpretations have suggested increased nutrient supply was balanced by higher export production, such that there was no net change in the efficiency of the biological pump<sup>19</sup>. However,  $\delta^{15}\text{N}$  is also influenced by the isotopic composition of source water nitrate, which is thought to have increased at the Bølling-Allerød due to enhanced denitrification associated with regional hypoxia<sup>22,25,26,38</sup> (Figure 2). Signals of reduced nutrient utilisation at the Bølling-Allerød are thus likely to be somewhat masked or delayed in  $\delta^{15}\text{N}$  records (Methods).

The increase in export production during the Bølling-Allerød would have increased organic matter respiration, consuming oxygen in the ocean's interior. The supply of oxygen to intermediate waters would also have been reduced, due to the collapse in NPIW formation. Both processes thus contributed to the regional hypoxia observed at this time. The initiation of hypoxia may have acted as a positive feedback on productivity by increasing iron concentrations within upwelling waters<sup>11</sup>, but it was not the primary cause of the increase in productivity.

### **Deglacial CO<sub>2</sub> rise**

The increase in  $p\text{CO}_2$  within the near-surface ocean at the onset of the Bølling-Allerød would have resulted in significant outgassing of CO<sub>2</sub>, with our reconstructed ocean-atmosphere  $p\text{CO}_2$  difference being ~130  $\mu\text{atm}$ . Although *N. pachyderma* calcifies at around ~50 m water depth (Methods) the average annual  $p\text{CO}_2$  difference between 50m depth and the surface ocean is only ~10  $\mu\text{atm}$  at the core site today, thus the surface ocean would have also experienced elevated levels of CO<sub>2</sub> (Methods). A significant release of CO<sub>2</sub> is also supported by the warm temperatures recorded by the Mg/Ca of *N. pachyderma* during this time (Figure 3), which, as well as indicating a relatively near-surface habitat, would also have helped drive CO<sub>2</sub> outgassing from the ocean to atmosphere (Methods). Release of CO<sub>2</sub> from the subpolar Pacific at the onset of the Bølling-Allerød may have contributed to the rapid ~10  $\mu\text{atm}$  increase in atmospheric CO<sub>2</sub> observed at this time<sup>4,12</sup> (Figure 3; Methods). Furthermore, continued CO<sub>2</sub> outgassing from the North Pacific



would have maintained the high levels of atmospheric  $p\text{CO}_2$  observed throughout the Bølling-Allerød, countering the return to more stratified conditions in the Southern Ocean<sup>4,16,39,40</sup> and the ventilation of the Atlantic with low-preformed nutrient NADW<sup>41</sup>, both of which should drive down atmospheric  $p\text{CO}_2$ . The upwelling of  $\text{CO}_2$ -rich waters in the North Pacific may thus allow atmospheric  $p\text{CO}_2$  to stay high – rather than falling – during the Bølling-Allerød, and help drive continued deglaciation.

Results from ocean drilling in the Bering Sea indicate an expansion of NPIW during every glacial period of the last 1.2 million years<sup>42</sup>. All that is required for the model proposed here to explain the regular deglacial North Pacific productivity peaks is that the switch from the enhanced glacial mode of NPIW formation to the reduced interglacial mode precedes the loss of the Laurentide Ice Sheet and its associated enhanced Ekman suction. Brine rejection within the Bering Sea has been suggested as an important process by which NPIW formation was enhanced during glacial periods<sup>42</sup>. Over the last deglaciation there was an almost total loss of sea ice within the Bering Sea following the Northern Hemisphere warming at the Bølling-Allerød<sup>43</sup>, however the Laurentide Ice Sheet did not ablate completely until ~7000 years later<sup>37</sup>. If the expansion of NPIW during glacial periods is driven by enhanced brine rejection, then the loss of sea ice prior to ice sheets during deglacial warming would dictate that increased upwelling of carbon and nutrient rich waters – and associated  $\text{CO}_2$  release – would regularly occur during glacial terminations.

## References

1. Toggweiler, J. R. Variation of Atmospheric CO<sub>2</sub> by Ventilation of the Ocean's Deepest Water. *Paleoceanography* **14**, 571–588 (1999).
2. Sigman, D. M., Hain, M. P. & Haug, G. H. The polar ocean and glacial cycles in atmospheric CO<sub>2</sub> concentration. *Nature* **466**, 47–55 (2010).
3. Jaccard, S. L. & Galbraith, E. D. Large climate-driven changes of oceanic oxygen concentrations during the last deglaciation. *Nature Geoscience* **5**, 151–156 (2011).
4. Marcott, S. A. *et al.* Centennial-scale changes in the global carbon cycle during the last deglaciation. *Nature* **514**, 616–619 (2014).
5. Keigwin, L., Jones, G. A. & Froelich, P. N. A 15,000 year paleoenvironmental record from Meiji Seamount, far northwestern Pacific. *Earth and Planetary Science Letters* **111**, 425–440 (1992).
6. Kohfeld, K. E. & Chase, Z. Controls on deglacial changes in biogenic fluxes in the North Pacific Ocean. *Quaternary Science Reviews* **30**, 3350–3363 (2011).
7. Jaccard, S. L. *et al.* Glacial/interglacial changes in subarctic North Pacific stratification. *Science* **308**, 1003–1006 (2005).
8. Jaccard, S. L., Galbraith, E. D., Sigman, D. M. & Haug, G. H. A pervasive link between Antarctic ice core and subarctic Pacific sediment records over the past 800kyrs. *Quaternary Science Reviews* **29**, 206–212 (2010).
9. Crusius, J., Pedersen, T. F., Kienast, S., Keigwin, L. & Labeyrie, L. Influence of northwest Pacific productivity on North Pacific Intermediate Water oxygen concentrations during the Bølling-Ållerød interval (14.7–

- 250 12.9 ka). *Geol* **32**, 633–636 (2004).
- 251 10. Behl, R. J. & Kennett, J. P. Brief interstadial events in the Santa  
252 Barbara basin, NE Pacific, during the past 60 kyr. *Nature* **379**, 243–245  
253 (1996).
- 254 11. Praetorius, S. K. *et al.* North Pacific deglacial hypoxic events linked to  
255 abrupt ocean warming. *Nature* **527**, 362–366 (2015).
- 256 12. Galbraith, E. D. *et al.* Carbon dioxide release from the North Pacific  
257 abyss during the last deglaciation. *Nature* **449**, 890–893 (2007).
- 258 13. Mix, A. C. *et al.* in *Mechanisms of Global Climate Change at Millennial*  
259 *Time Scales* (eds. Clark, P. U., Webb, R. S. & Keigwin, L.) (American  
260 Geophysical Union, 1999). doi:10.1029/GM112p0127
- 261 14. Lam, P. J. *et al.* Transient stratification as the cause of the North Pacific  
262 productivity spike during deglaciation. *Nature Geoscience* **6**, 622–626  
263 (2013).
- 264 15. Key, R. M., Olsen, A., van Heuven, S. & Lauvset, S. K. Global Ocean  
265 Data Analysis Project, Version 2 (GLODAPv2). *ORNL/CDIAC-162*  
266 (2015). doi:10.3334/CDIAC/OTG
- 267 16. Martínez-Botí, M. A. *et al.* Boron isotope evidence for oceanic carbon  
268 dioxide leakage during the last deglaciation. *Nature* **518**, 219–222  
269 (2015).
- 270 17. Takahashi, T. *et al.* Climatological mean and decadal change in surface  
271 ocean  $p\text{CO}_2$ , and net sea–air  $\text{CO}_2$  flux over the global oceans. *Deep*  
272 *Sea Research Part II: Topical Studies in Oceanography* **56**, 554–577  
273 (2009).
- 274 18. Boyer, T. P. *et al.* *World Ocean Database 2013*. NOAA Atlas NESDIS

- 275           **72**, 209 (2013).
- 276   19.   Ren, H. *et al.* Glacial-to-interglacial changes in nitrate supply and  
277           consumption in the subarctic North Pacific from microfossil-bound N  
278           isotopes at two trophic levels. *Paleoceanography* **30**, 1217–1232  
279           (2015).
- 280   20.   Key, R. M. *et al.* A global ocean carbon climatology: Results from  
281           Global Data Analysis Project (GLODAP). *Global Biogeochem. Cycles*  
282           **18**, GB4031 (2004).
- 283   21.   Gebhardt, H. *et al.* Paleonutrient and productivity records from the  
284           subarctic North Pacific for Pleistocene glacial terminations I to V.  
285           *Paleoceanography* **23**, PA4212 (2008).
- 286   22.   Brunelle, B. G. *et al.* Glacial/interglacial changes in nutrient supply and  
287           stratification in the western subarctic North Pacific since the penultimate  
288           glacial maximum. *Quaternary Science Reviews* **29**, 2579–2590 (2010).
- 289   23.   Jaccard, S. L. *et al.* Subarctic Pacific evidence for a glacial deepening  
290           of the oceanic respired carbon pool. *Earth and Planetary Science*  
291           *Letters* **277**, 156–165 (2009).
- 292   24.   Barron, J. A., Bukry, D., Dean, W. E., Addison, J. A. & Finney, B.  
293           Paleoceanography of the Gulf of Alaska during the past 15,000 years:  
294           Results from diatoms, silicoflagellates, and geochemistry. *Marine*  
295           *Micropaleontology* **72**, 176–195 (2009).
- 296   25.   Galbraith, E. D. *et al.* Consistent relationship between global climate  
297           and surface nitrate utilization in the western subarctic Pacific throughout  
298           the last 500 ka. *Paleoceanography* **23**, PA2212 (2008).

- 299 26. Hendy, I. L., Pedersen, T. F., Kennett, J. P. & Tada, R. Intermittent  
300 existence of a southern Californian upwelling cell during submillennial  
301 climate change of the last 60 kyr. *Paleoceanography* **19**, PA3007  
302 (2004).
- 303 27. Serno, S. *et al.* Comparing dust flux records from the Subarctic North  
304 Pacific and Greenland: Implications for atmospheric transport to  
305 Greenland and for the application of dust as a chronostraphic tool.  
306 *Paleoceanography* **30**, 583–600 (2015).
- 307 28. Max, L. *et al.* Pulses of enhanced North Pacific Intermediate Water  
308 ventilation from the Okhotsk Sea and Bering Sea during the last  
309 deglaciation. *Clim. Past* **10**, 591–605 (2014).
- 310 29. Keigwin, L. Glacial Age Hydrography of the Far Northwest Pacific  
311 Ocean. *Paleoceanography* **13**, 323–339 (1998).
- 312 30. Okazaki, Y. *et al.* Deepwater Formation in the North Pacific During the  
313 Last Glacial Termination. *Science* **329**, 200–204 (2010).
- 314 31. Braconnot, P. *et al.* Evaluation of climate models using palaeoclimatic  
315 data. *Nature Clim. Change* **2**, 417–424 (2012).
- 316 32. Talley, L. D. Distribution and formation of North Pacific intermediate  
317 water. *J. Phys. Oceanogr.* **23**, 517–537 (1993).
- 318 33. Max, L. *et al.* Evidence for enhanced convection of North Pacific  
319 Intermediate Water to the low-latitude Pacific under glacial conditions.  
320 *Paleoceanography* **32**, 41–55 (2017).
- 321 34. Matsumoto, K., Oba, T. & Lynch-Stieglitz, J. Interior hydrography and  
322 circulation of the glacial Pacific Ocean. *Quaternary Science Reviews*  
323 **21**, 1693–1704 (2002).

- 324 35. Rae, J. W. B. *et al.* Deep water formation in the North Pacific and  
325 deglacial CO<sub>2</sub> rise. *Paleoceanography* **29**, 645–667 (2014).
- 326 36. Cook, M. S. & Keigwin, L. Radiocarbon profiles of the NW Pacific from  
327 the LGM and deglaciation: Evaluating ventilation metrics and the effect  
328 of uncertain surface reservoir ages. *Paleoceanography* **30**, 174–195  
329 (2015).
- 330 37. Ullman, D. J., Carlson, A. E., Anslow, F. S., LeGrande, A. N. & Licciardi,  
331 J. M. Laurentide ice-sheet instability during the last deglaciation. *Nature*  
332 *Geoscience* **8**, 534–537 (2015).
- 333 38. Deutsch, C., Sigman, D. M., Thunell, R. C., Meckler, A. N. & Haug, G.  
334 H. Isotopic constraints on glacial/interglacial changes in the oceanic  
335 nitrogen budget. *Global Biogeochem. Cycles* **18**, GB4012 (2004).
- 336 39. Anderson, R. F. *et al.* Wind-Driven Upwelling in the Southern Ocean  
337 and the Deglacial Rise in Atmospheric CO<sub>2</sub>. *Science* **323**, 1443–1448  
338 (2009).
- 339 40. Burke, A. & Robinson, L. F. The Southern Ocean's Role in Carbon  
340 Exchange During the Last Deglaciation. *Science* **335**, 557–561 (2012).
- 341 41. McManus, J. F., Francois, R., Gherardi, J. M. & Keigwin, L. Collapse  
342 and rapid resumption of Atlantic meridional circulation linked to  
343 deglacial climate changes. *Nature* **428**, 834–837 (2004).
- 344 42. Knudson, K. P. & Ravelo, A. C. North Pacific Intermediate Water  
345 circulation enhanced by the closure of the Bering Strait.  
346 *Paleoceanography* **30**, PA002840 (2015).
- 347 43. Méheust, M., Stein, R., Fahl, K., Max, L. & Riethdorf, J.-R. High-  
348 resolution IP25-based reconstruction of sea-ice variability in the western

North Pacific and Bering Sea during the past 18,000 years. *Geo-Mar  
Lett* **36**, 101–111 (2015).

Corresponding Author: WRG; wrg4@st-andrews.ac.uk

## **Acknowledgments**

We thank Michael Sarnthein for providing core material and stimulating discussions, the 'B-team' for their accommodation in the National Oceanography Centre Southampton's laboratories, Anabel Mortes Rodenas for assistance with ICP-MS analysis at Cardiff University, and Jonathan Holmes for support throughout the project. We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling for the coordination of CMIP and thank the climate modeling groups for producing and making available their model output (<https://esgf-node.llnl.gov/search/cmip5/>). We thank three anonymous reviewers for their thoughtful comments and detailed suggestions that substantially improved this paper. This work was funded by NERC studentship NE/I528185/1 awarded to W.R.G., NERC studentship NE/1492942/1 to B.T., NERC grant NE/N011716/1 awarded to J.W.B.R and A.B., and NERC grant NE/I013377/1 awarded to A.E.S.

## **Author contributions**

W.R.G. and J.W.B.R. designed the study and wrote the manuscript; W.R.G., J.W.B.R, G.L.F., C.H.L., and A.E.S. were involved in the generation of the trace element and  $\delta^{11}\text{B}$  data; R.C.W. analysed climate model output; all

authors contributed to the interpretation and preparation of the final manuscript.

#### **Financial competing interests**

The authors declare no competing financial interests.

#### *Figure captions*

**Figure 1. CO<sub>2</sub> and nutrients in the modern subpolar North Pacific** (a) annual surface ocean-atmosphere CO<sub>2</sub> flux<sup>17</sup>, with contours of surface ocean phosphate (PO<sub>4</sub>) in  $\mu\text{mol/kg}$ <sup>18</sup>. The location of core MD01-2416 (51.27°N, 167.73°E, 2317 m water depth) is indicated by a star (b) upper water column profiles of dissolved inorganic carbon (DIC) and phosphate in the western subpolar North Pacific<sup>15</sup>.

**Figure 2. Deglacial changes in the biogeochemistry of the subpolar North Pacific** (a)  $\delta^{11}\text{B}$  of *N. pachyderma* from MD01-2416 (b) pH with LOESS smooth and 1 $\sigma$  and 2 $\sigma$  error envelope (Methods). The star shows pre-industrial pH at this site<sup>20</sup> (50m water depth) and blue lines show equilibrium pH (Methods) (c) Opal MAR from MD01-2416<sup>21</sup> (filled circles, inset-axis), RAMA-PC-44<sup>9</sup> (triangles), PC13<sup>22</sup> (squares), ODP882<sup>23</sup> (open circles) and SO202-07-6<sup>19</sup> (inverse triangles) (d) Excess U (dark pink) and Mo (light pink) from EW0408-85JC<sup>11,24</sup> (e)  $\delta^{15}\text{N}$  of *N. pachyderma* from SO202-07-6<sup>19</sup> (diamonds), diatoms from PC13<sup>22</sup> (squares), and bulk sediments from MD01-2416<sup>25</sup> (dashed line), ODP887<sup>25</sup> (solid line) and ODP1017<sup>26</sup> (dotted line) (f)



<sup>4</sup>He flux from SO202-7-6<sup>27</sup>. YD, B/A and HS1 are the Younger Dryas, Bølling Allerød, and Heinrich Stadial 1. See supplement for core locations.

**Figure 3. Deglacial temperature,  $p\text{CO}_2$  and NPIW formation** (a) *N. pachyderma* Mg/Ca-temperature with LOESS smooth and  $1\sigma$  and  $2\sigma$  error envelope. The star shows modern mean annual temperature at the site<sup>18</sup> (50m water depth) (b)  $p\text{CO}_2$  in the atmosphere<sup>4</sup> and near-surface subpolar North Pacific with LOESS smooth and  $1\sigma$  and  $2\sigma$  error envelope (Methods). The star shows pre-industrial  $p\text{CO}_2$  at the site<sup>20</sup> (50m water depth) (c)  $\delta^{13}\text{C}$  of *Cibicidoides* spp. from the intermediate Bering Sea (SO201-2-85KL) and Okhotsk Sea (SO178-13-6)<sup>28</sup> (Methods). The triangle shows the LGM value for the intermediate-depth (~1000 m) Okhotsk Sea<sup>29</sup> (d) Benthic-planktic  $^{14}\text{C}$  age difference in the intermediate depth (<1500 m) northwest Pacific<sup>30</sup> with  $1\sigma$  error bars and LOESS smooth; CH84-14 (circles), GH02-1030 (triangles), and MR01K03-PC4/PC5 (diamonds). The star shows pre-bomb benthic-planktic  $^{14}\text{C}$  age<sup>20</sup>.

**Figure 4. Wind stress curl in the glacial North Pacific.** (a) PMIP3 ensemble mean difference in wind stress curl in the North Pacific in LGM relative to the pre-industrial (PI) control (positive means greater wind stress curl in LGM), with changes in vector windstress indicated by the arrows (see grey arrow in top left corner for scale) (b) PI and LGM windstress curl between 40°N and 60°N (shown by the black box in a, corresponding to the position of the subpolar gyre under PI conditions) in each of the models. The ensemble means for the PI and LGM are shown by the stars.

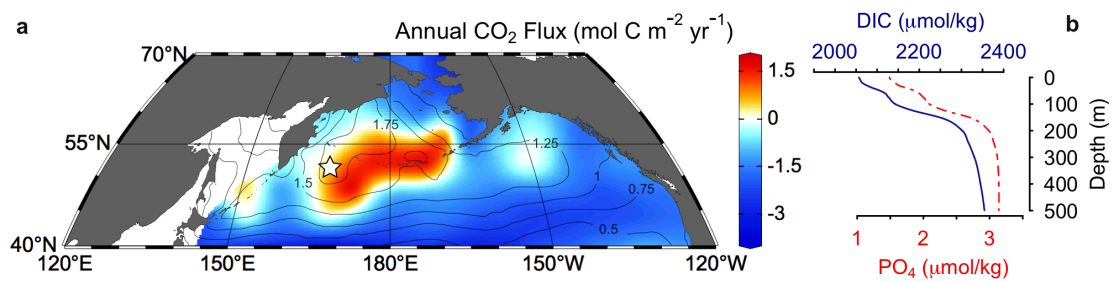


Figure 1

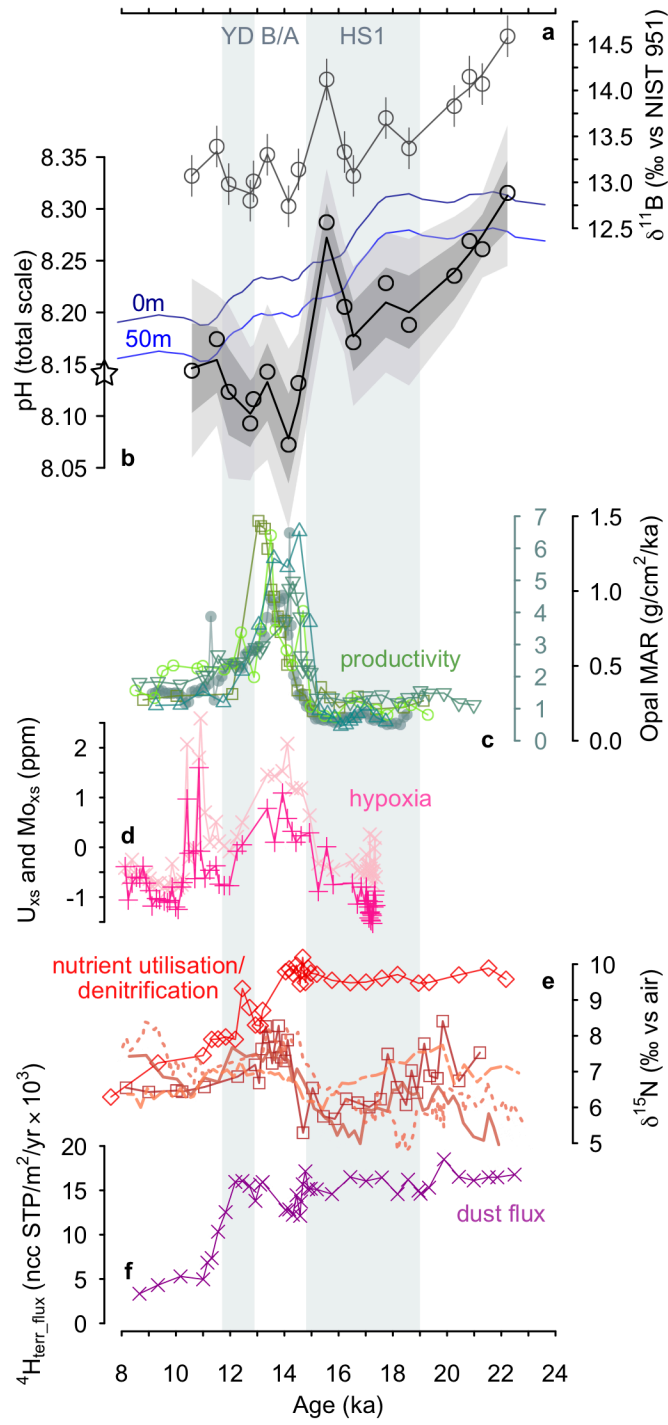


Figure 2

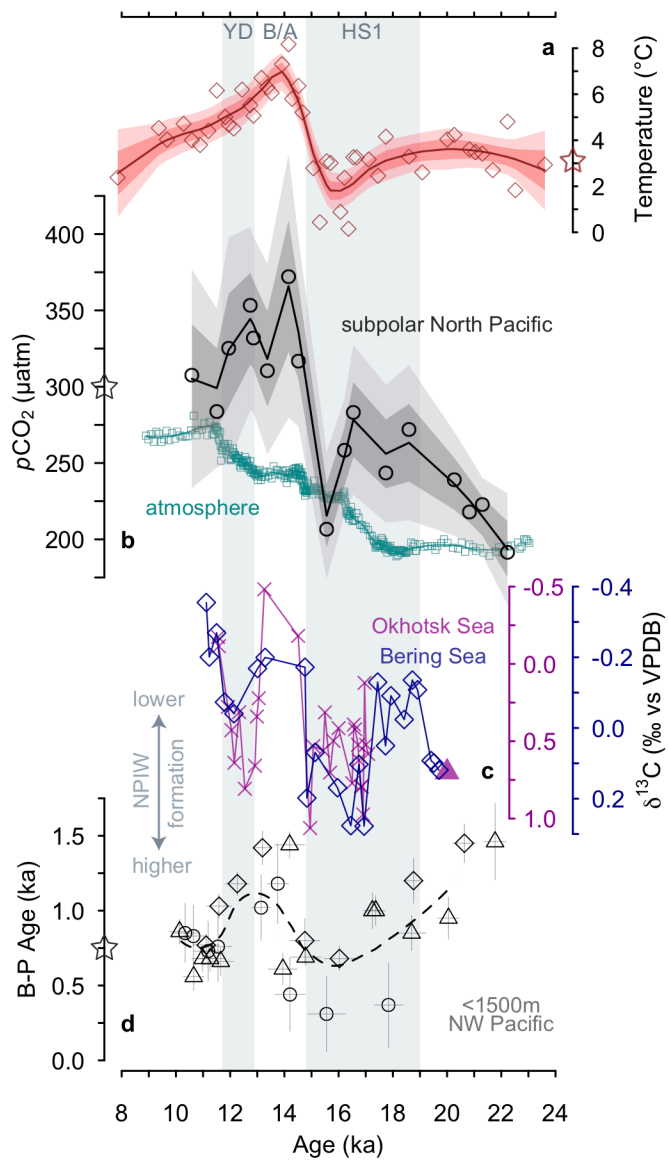


Figure 3

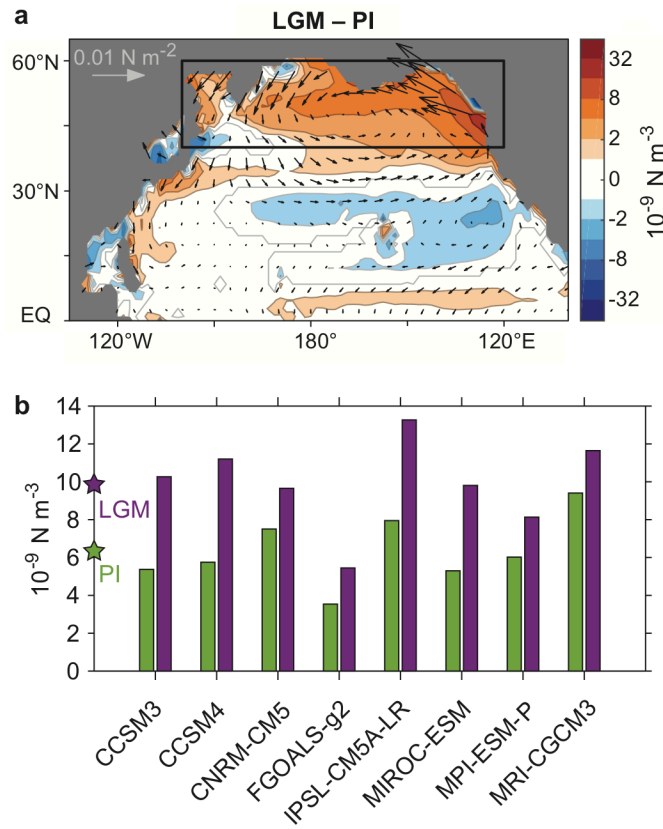


Figure 4

## Methods

### *Data availability*

The authors declare that data supporting the findings of this study are available within the article and its supplementary information files. Data are also available on *Pangaea* (doi.pangaea.de/10.1594/PANGAEA.887381).

### *Habitat depth and seasonality of *N. pachyderma* in the western North Pacific*

Sediment trap data in the modern NW Pacific display two seasonal *N. pachyderma* abundance peaks during the spring and autumn, roughly corresponding to the time of most, and least, stratification respectively. As these fluxes are more or less equal, the geochemical signature of *N. pachyderma* should represent mean annual oceanographic conditions at a water depth of ~50 m<sup>44</sup>, provided that the growing season of *N. pachyderma* did not change substantially in the past.

### *Core materials*

Core MD01-2416 was raised from 51.27°N, 167.73°E, 2317 m water depth on the Detroit Seamount. This site is situated within the subpolar North Pacific High Nutrient Low Chlorophyll zone, making it well suited to track past changes in CO<sub>2</sub> outgassing in this region (Figure 1). %Opal data from the core (Figure 2) were previously published (refs<sup>21,45</sup>), and were converted into mass accumulation rate (MAR) using the age model described below. Foraminifera are well-preserved throughout the deglaciation in this core, likely due to its high sedimentation rate and the relatively muted changes in carbonate ion since the LGM in the deep Pacific<sup>46</sup>.

502

503 *Age model for MD01-2416*

504 We generated a new age model for the core by recalibrating 36 *N.*  
505 *pachyderma*  $^{14}\text{C}$  dates from ref<sup>47</sup>, excluding 6  $^{14}\text{C}$  dates previously  
506 demonstrated to show evidence of reworking<sup>47</sup>. The  $^{14}\text{C}$  dates were calibrated  
507 with INTCAL13<sup>48</sup>. There are likely to be considerable changes in deglacial  
508 reservoir age which are difficult to constrain; we apply a constant reservoir  
509 age of  $950 \pm 450$  yrs, which encompasses the modern seasonal variability  
510 within the region, as well as paleo-reconstructions and model estimates for  
511 the LGM, deglaciation, and the Holocene<sup>20,49-52</sup>. The age model was  
512 constructed using the BACON<sup>53</sup> Bayesian age modelling package in R.  
513 Uncertainty in calibrated age is typically  $\pm 800$  years at the 95% confidence  
514 interval, increasing to greater than  $\pm 1000$  years before  $\sim 21\text{ka}$ . Using the  $^{14}\text{C}$   
515 plateau tuned chronology of ref<sup>47</sup> makes no difference to any of the  
516 conclusions drawn (Supplementary Figure 4).

517

518  *$\delta^{11}\text{B}$  and trace element analysis*

519 Well-preserved *N. pachyderma* were picked from the 150-250  $\mu\text{m}$  size fraction  
520 at a 3-15 cm resolution.  $\sim 400$  individuals were used per  $\delta^{11}\text{B}$  analysis.  
521 Samples were cleaned in a class 100 clean lab at the National Oceanography  
522 Centre Southampton (NOCS) according to the 'Mg' method of ref<sup>54</sup> as detailed  
523 in ref<sup>55</sup>. A  $\sim 5\%$  split of the cleaned foraminiferal samples was analysed after  
524 acidification for a suite of trace elements at NOCS using an Element II HR-  
525 ICP-MS against matrix matched standards.  $\delta^{11}\text{B}$  was analysed at NOCS on a  
526 Neptune MC-ICP-MS following the method of ref<sup>55,56</sup>, which involves removing

the sample matrix prior to analysis using anionic exchange resin, and sample-standard bracketing to correct for instrument induced mass fractionation. Long term reproducibility of this approach is  $\pm 0.23\%$  at the 95% confidence interval<sup>57</sup>.

To increase the resolution of the Mg/Ca record, 26 additional samples were analysed for trace elements only. Between 20-50 individual *N. pachyderma* were cleaned following the oxidative/reductive protocol of ref<sup>58</sup>. The samples were analysed at Cardiff University using an Element II HR-ICP-MS against matrix-matched standards. The same standards were used at both Cardiff University and NOCS to ensure consistency.

Average Al/Ca values are  $\sim 50$   $\mu\text{mol/mol}$ . Six samples have Al/Ca between 100-150  $\mu\text{mol/mol}$ , however these samples do not display elevated Mg/Ca or B/Ca indicating no influence of clay contamination. Average Mn/Ca for samples cleaned using the 'Mg' method is 80  $\mu\text{mol/mol}$ , whereas average Mn/Ca for reductively cleaned samples is  $<10$   $\mu\text{mol/mol}$ . Despite the higher Mn/Ca values of the 'Mg' cleaned samples, both datasets display very similar Mg/Ca (after correction for preferential dissolution of high-Mg calcite during reductive cleaning<sup>54</sup>) and B/Ca values downcore, indicating no influence of Mn-Fe oxyhydroxide coatings. Previously published Mg/Ca data from MD01-2416<sup>21,45</sup> show elevated values compared to the data cleaned by both the 'Mg' method and the reductive method in this study, indicating a possible influence of contamination, so are not used in our temperature reconstruction. Including these data makes no difference to any of the conclusions drawn.



### *Temperature record*

The Mg/Ca values were converted to temperature using the species specific calibration of ref<sup>59</sup> (recalculated by ref<sup>60</sup>). Samples that had been reductively cleaned were adjusted upward by 12.5% to account for preferential dissolution of high-Mg calcite during reductive cleaning<sup>54</sup>. The data were fitted with a non-parametric regression (LOESS) in R. The smoothing parameter ( $\alpha$ ) was optimised using generalised cross validation (GCV). A Monte Carlo approach was used to determine the most likely fit to the data, with the LOESS smooth fitted to ten thousand realisations of the temperature data with an uncertainty of  $\pm 2.3$  °C ( $2\sigma$ ), accounting for the 1.2 °C ( $2\sigma$ ) calibration error<sup>59</sup>, and incorporating terms for uncertainty in salinity ( $\pm 2$  PSU [ $2\sigma$ ] with a sensitivity of 3%/PSU<sup>61,62</sup>), and pH ( $\pm 0.2$  pH units [ $2\sigma$ ] with a sensitivity of -7%/0.1 pH units<sup>62,63</sup>).

pH is known to affect planktic foraminiferal Mg/Ca with a sensitivity of  $\sim$ -7%/0.1 pH units<sup>62,63</sup>. While the pH minimum during the Bølling-Allerød may be influencing the apparent Mg/Ca temperatures, this influence is likely to be minimal. Firstly, as the absolute value of pH during the Bølling-Allerød interval is broadly equivalent to pre-industrial (it is a large anomaly from equilibrium due to lower atmospheric CO<sub>2</sub> concentrations during the Bølling-Allerød) the effect of pH on absolute temperature will be negligible. Secondly, the  $\Delta$ pH at the onset of the Bølling-Allerød is  $\sim 0.15$  units, so given a Mg/Ca sensitivity of -7%/0.1 pH units, this could only account for a 10% increase in Mg/Ca, or  $\sim 1$ -1.5 °C, considerably smaller than the  $\sim 5$  °C warming indicated

by the Mg/Ca record at the onset of the Bølling-Allerød. The effect of higher pH during the LGM means our Mg/Ca temperature record is likely to be underestimating LGM temperature by ~1-1.5 °C. Dissolution can also effect foraminiferal Mg/Ca, though this influence is relatively minor in lower-Mg planktic foraminifera such as *N. pachyderma*<sup>64</sup>. LGM-Holocene changes in bottom water carbonate ion concentration are also relatively minor within the Pacific (~10 µmol/kg)<sup>46</sup>, and our Mg/Ca data show no correlation with %CaCO<sub>3</sub> in this core, so dissolution is unlikely to have a significant influence on our record. Our temperature record shows good agreement with the assemblage derived temperature record of ref<sup>21,45</sup> from the same core. Recent research found that the *G. ruber* Mg/Ca-temperature sensitivity is lower than the widely applied 9%/°C temperature sensitivity<sup>62</sup>; if future calibration work also demonstrates similar results for *N. pachyderma*, our Mg/Ca-temperature record may need minor revision.

### *Carbonate system calculations*

To calculate pH the  $\delta^{11}\text{B}$  of *N. pachyderma* was converted to seawater  $\delta^{11}\text{B}_{\text{borate}}$  using the calibration of ref<sup>65</sup>, where  $\delta^{11}\text{B}_{\text{borate}} = \delta^{11}\text{B}_{\text{Npachyderma}} + 3.38 \pm 0.71\text{‰}$  ( $2\sigma$ ). To fully explore the uncertainty associated with the calibration, we recalibrated the dataset of ref<sup>65</sup>, varying the slope between 0.6 and 1.4 (which incorporates the range previously observed in all other species of planktic foraminifera, refs<sup>16,66,67</sup>) with a flat probability distribution, allowing the intercept to vary (see sensitivity test below). pH was calculated from  $\delta^{11}\text{B}_{\text{borate}}$  using a seawater  $\delta^{11}\text{B}$  value of 39.61‰<sup>68</sup> and the experimentally-determined fractionation factor of 1.0272<sup>69</sup> following ref<sup>70</sup>. The boric acid

dissociation constant ( $K_B$ ) was calculated with the Mg/Ca temperature, and an estimate of salinity generated by taking the salinity at the site today (33.0 PSU), and accounting for the whole ocean change in salinity over deglaciation by scaling the 1.15 PSU glacial salinity increase of ref<sup>71</sup> to the sea level curve of ref<sup>72</sup>. To fully propagate uncertainty in reconstructed pH a Monte-Carlo approach was taken, with ten thousand realisations of the data accounting for the uncertainties in the measurement of  $\delta^{11}\text{B}_{\text{Npachyderma}}$ , the conversion of the  $\delta^{11}\text{B}_{\text{Npachyderma}}$  to  $\delta^{11}\text{B}_{\text{borate}}$ , and of the uncertainty in the temperature and salinity reconstructions on  $K_B$  using the confidence interval of the LOESS temperature smooth and a salinity uncertainty of  $\pm 2$  units ( $2\sigma$ ). Typical uncertainty on the pH reconstruction following this approach is  $\pm 0.084$  ( $2\sigma$ ), which is chiefly due to the uncertainty in the offset between the  $\delta^{11}\text{B}$  of *N. pachyderma* and seawater  $\delta^{11}\text{B}_{\text{borate}}$  ( $\pm 0.078$   $2\sigma$ ). Using a constant value of  $K_B$  (i.e. constant temperature and salinity) has no major influence on reconstructed pH values (see sensitivity test). Preservation has not been shown to influence planktic  $\delta^{11}\text{B}$ <sup>73</sup>.

An additional parameter of the carbonate system is required to calculate  $p\text{CO}_2$  from pH, and total alkalinity is widely used<sup>16,56,65</sup>. Although modeling studies can provide estimates of the change in alkalinity during the LGM<sup>1,74</sup>, there are few data-based constraints on its secular evolution over deglaciation. Here we follow the approach of ref<sup>16</sup>, taking a range in alkalinity between modern day alkalinity at the site ( $2235 \mu\text{mol/kg}$ )<sup>20</sup> plus an estimate of the glacial alkalinity increase based on the modeling results of refs<sup>1,74</sup> ( $+125 \mu\text{mol/kg}$ ), and modern day alkalinity at the site minus  $25 \mu\text{mol/kg}$ , with a 'flat' probability

distribution between these values. With this approach there is an equal probability of total alkalinity being at any value between 2210 and 2360  $\mu\text{mol/kg}$  at any point in the record, fully exploring the likely range in alkalinity without giving weight to any particular value. Note, this range in alkalinity is cautious, being broadly equivalent to the range observed across the surface of the entire open Pacific Ocean today<sup>20</sup>. The  $p\text{CO}_2$  of seawater was calculated using the *seacarb* package in R<sup>75</sup>, using the constants of refs<sup>76-78</sup>. To fully propagate the uncertainty associated with each parameter ten thousand realisations of pH, total alkalinity, temperature and salinity were input, using the uncertainty on each parameter described above. Following this approach, the total uncertainty associated with our  $p\text{CO}_2$  estimates is typically  $\pm 64 \mu\text{atm}$  ( $2\sigma$ ), which again is chiefly due to the uncertainty in the offset between  $\delta^{11}\text{B}_{\text{Npachyderma}}$  and  $\delta^{11}\text{B}_{\text{borate}}$  ( $\pm 55 \mu\text{atm}$ ).  $p\text{CO}_2$  estimates are almost entirely driven by the pH estimates (Supplementary Figure 5). Typical  $p\text{CO}_2$  uncertainty associated with the temperature uncertainty is  $\pm 2 \mu\text{atm}$  ( $2\sigma$ ), and the uncertainty associated with the salinity uncertainty is  $\pm 10 \mu\text{atm}$  ( $2\sigma$ ). Using either a constant ‘modern minus 25  $\mu\text{mol/kg}$ ’ or ‘modern plus 125  $\mu\text{mol/kg}$ ’ total alkalinity changes the  $p\text{CO}_2$  values by only  $\pm 20 \mu\text{atm}$ .

Surface ocean pH at equilibrium with the atmosphere was calculated using alkalinity calculated in the manner described above, and the atmospheric  $\text{CO}_2$  record of ref<sup>4</sup>. Salinity (estimated in the manner described above) and Mg/Ca temperature were used to constrain changes in dissociation constants. Equilibrium pH at 50m is calculated by applying the modern surface-50m pH gradient ( $-0.035$  units); deviations from equilibrium pH therefore represent

changes in the carbonate system beyond those expected from changing atmospheric CO<sub>2</sub>.

Both the pH and  $p\text{CO}_2$  records were fitted with a LOESS smooth in R, with the smoothing parameter ( $\alpha$ ) determined by GCV. To determine the most likely fit to the data a LOESS smooth fitted to ten thousand realisations of the data, accounting for the uncertainties in the pH and  $p\text{CO}_2$  estimates in the manner described above; this approach allows us to identify significant trends within the data and reduce uncertainty in our estimates.

#### *Carbonate system sensitivity tests*

As the current  $\delta^{11}\text{B}_{\text{calcite}}\text{-}\delta^{11}\text{B}_{\text{borate}}$  calibration for *N. pachyderma* comes from a limited range in pH<sup>65</sup>, application of this calibration to the NW Pacific requires extrapolation beyond the calibrated range. We tested the sensitivity of our results to the assumed slope of calibration, building on the test outlined in ref<sup>79</sup>. We re-calibrated the coretop data of ref<sup>65</sup>, forcing the slope within the range previously observed in all other species of planktic foraminifera (refs<sup>16,66,67</sup>), while allowing the intercept to vary (Supplementary Figure 6). This exercise demonstrates that within the range previously observed in all other species of planktic foraminifera, the assumed slope of the  $\delta^{11}\text{B}_{\text{calcite}}\text{-}\delta^{11}\text{B}_{\text{borate}}$  calibration makes no difference to any of the conclusions drawn in this study.

To provide a further constraint on the relationship between  $\delta^{11}\text{B}_{\text{Npachyderma}}$  and  $\delta^{11}\text{B}_{\text{borate}}$ , we measured the  $\delta^{11}\text{B}$  of *N. pachyderma* (following the method

described above) from Holocene sediments in core MD02-2489 (54.39°N, 148.92°E, 3640 m water depth), located in the eastern subpolar Pacific, where modern pH values are significantly higher than in the western subpolar Pacific. Comparing this data along with the Holocene  $\delta^{11}\text{B}_{\text{Npachyderma}}$  data from site MD01-2416 to pre-industrial  $\delta^{11}\text{B}_{\text{borate}}$  (calculated from ref<sup>20</sup>) shows excellent agreement with the *N. pachyderma*  $\delta^{11}\text{B}_{\text{calcite}} - \delta^{11}\text{B}_{\text{borate}}$  calibration proposed by ref<sup>65</sup> over a range of  $\delta^{11}\text{B}$  ~equivalent to our down-core reconstruction (Supplementary Figure 6).

To test the sensitivity of our pH and  $p\text{CO}_2$  reconstructions to temperature, we calculated pH and  $p\text{CO}_2$  assuming constant temperatures of 2 °C, 5 °C and 8 °C (broadly the deglacial range suggested by the Mg/Ca). Supplementary Figure 7 demonstrates that using a constant temperature in our carbonate system calculations would not have any effect on the main findings of this study. Compiling all available proxy temperature data in the western subpolar North Pacific demonstrates that using the reconstructed temperatures suggested by all available proxies (Mg/Ca,  $\text{U}^{\text{k}'}_{37}$ ,  $\text{TEX}_{86}$ , foraminiferal assemblage transfer function; refs<sup>21,80-82</sup>) in our carbonate system calculations results in a substantial outgassing of  $\text{CO}_2$  from the subpolar North Pacific during the Bølling-Allerød.

#### *Overtuning and $\text{CO}_2$ in early deglaciation*

In addition to the large decrease in pH at the onset of the Bølling-Allerød, our record demonstrates a decrease in pH during early deglaciation, reaching a minimum in HS1. Benthic foraminiferal  $\delta^{13}\text{C}$  and radiocarbon records show an

increase in overturning circulation during early deglaciation relative to the LGM<sup>28,30</sup>, with possible local deepwater formation during HS1<sup>30,35</sup> (Supplementary Figure 8). The deepening of the overturning circulation during early-deglaciation would have allowed deeply sequestered nutrients and CO<sub>2</sub> to mix more vigorously through the water column<sup>35</sup>, resulting in the observed decrease in pH and increase in CO<sub>2</sub> in the near-surface ocean, and outgassing of CO<sub>2</sub> to the atmosphere. The increase in overturning would have resulted in a deepening of the mixed layer, such that light may have become limiting to primary production<sup>14</sup>. A return to a shallower overturning circulation (similar to the LGM) during late-HS1 would have lessened the upward mixing of deep carbon, increasing pH. Note, removing the high-pH data point at ~15.5 ka makes no difference to any of the conclusions drawn in this study; even without this high-pH data point there is a ~0.1 pH unit decrease from the mean HS1 value going into the B/A, indicating a substantial increase in nutrient- and CO<sub>2</sub>- supply.

#### *Nutrient utilisation/denitrification controls on $\delta^{15}N$*

Nitrogen isotope records may be influenced by both the degree of nitrate utilisation and the isotopic composition of nitrate in the source water<sup>22,25,38,83,84</sup>. The widespread hypoxia accompanying the Bølling-Allerød productivity maximum is thought to have significantly increased denitrification within the oxygen minimum zones of the northeast Pacific<sup>22,26,83,84</sup>, driving up the  $\delta^{15}N$  of seawater nitrate. This is reflected by the large increase in bulk sediment  $\delta^{15}N$  in cores from the Mexican<sup>83</sup> and Californian<sup>26</sup> continental margins to the Alaskan gyre<sup>25</sup> (Figure 2). This signal is spread throughout the

subsurface North Pacific<sup>25</sup>, influencing the  $\delta^{15}\text{N}$  of nitrate upwelled in the northwest Pacific. Records of  $\delta^{15}\text{N}$  from the northwest Pacific (including bulk-sediment, diatom-bound, and foram-bound  $\delta^{15}\text{N}$ ) show relatively muted changes at the onset of the Bølling-Allerød<sup>19,22,25</sup>. This likely reflects the opposing influences of a decrease in nutrient utilisation, due to higher nutrient supply in this key upwelling region, and the increase in  $\delta^{15}\text{N}$  of source water nitrate due to hypoxia-driven denitrification.

#### *Constraints on CO<sub>2</sub> uptake within the mixed layer*

CO<sub>2</sub> concentrations in the mixed layer are likely to be lower than at the ~50m depth habitat of *N. pachyderma*. However, the mean annual difference between 50 m and surface ocean at this core site today is only ~10  $\mu\text{atm}$ . During the summer months this difference is 21.9  $\mu\text{atm}$ <sup>20</sup>, due export production from the mixed layer, and during winter is close to zero due to mixing of the upper water column. While it is possible this difference was higher in the past, the Mg/Ca of the *N. pachyderma* indicates temperatures of 5-7 °C during the interval of low pH/high CO<sub>2</sub> suggesting that either (a) the *N. pachyderma* are recording a signal close to the surface at this time, (b) the mixed layer was deeper and thus thermal stratification weak, or (c) the *N. pachyderma* are recording a summer signal at this time, which would make the CO<sub>2</sub> concentrations a minimum estimate. All of these scenarios would result in a significant flux of CO<sub>2</sub> to the atmosphere.

#### *CO<sub>2</sub> outgassing and atmospheric CO<sub>2</sub> change*



Net changes in atmospheric CO<sub>2</sub> on millennial timescales are strongly influenced by the inventory of preformed versus remineralised nutrients in the ocean's interior<sup>74,85</sup>. Constraining preformed nutrient inventory is challenging using paleo-proxies. However, given the increased nutrient consumption<sup>19</sup> and high pH/low CO<sub>2</sub> of the near-surface North Pacific during the LGM (Figures 1 and 2), Glacial NPIW would likely have had lower preformed nutrient content than the water in the upper 1500m of the North Pacific today<sup>86</sup>. Overall this would make the biological pump more efficient at the LGM, driving down atmospheric CO<sub>2</sub>. At the onset of the Bølling-Allerød, our data suggest a net weakening in the strength of the North Pacific biological pump and substantial outgassing of CO<sub>2</sub> from near surface waters. The collapse in NPIW formation at this time would also have removed this source of relatively low-preformed nutrient water from the ocean's interior, and thus would also act to increase atmospheric CO<sub>2</sub>.

#### *Benthic $\delta^{13}\text{C}$ records*

The benthic  $\delta^{13}\text{C}$  records (*Cibicidoides* spp.) were corrected for the whole ocean change in  $\delta^{13}\text{C}$  relating to changes in the terrestrial biosphere by scaling the value of ref<sup>87</sup> to global sea level<sup>72</sup>. This only affects the long-term trend, and makes no difference to millennial scale events within the records.

#### *PMIP3 model output*

We analyse the difference in North Pacific wind-stress curl between LGM and Preindustrial (PI) conditions as represented by 8 coupled climate models (listed in Figure 4b). All models but CCSM3 are part of the Coupled Model

Intercomparison Project phase 5 (CMIP5). Orbital parameters, atmospheric greenhouse gas concentrations, coastlines, and ice topography for the LGM simulations are standardized as part of the Paleoclimate Model Intercomparison Project phase 3 (PMIP3) and represent best estimates of the climate state at the LGM, 21 ka before present<sup>10</sup>. We include data from comparable LGM and PI simulations<sup>88,89</sup> using an older model, CCSM3, used extensively in paleoclimate studies. We compute the wind stress curl climatology based on the atmospheric output of each model. The computed wind stress curl is linearly interpolated onto a common grid to compute the ensemble mean (Figure 4a). Individual model results are shown on Supplementary Figure 9.

## References only in Methods

44. Kuroyanagi, A., Kawahata, H. & Nishi, H. Seasonal variation in the oxygen isotopic composition of different-sized planktonic foraminifer *Neogloboquadrina pachyderma* (sinistral) in the northwestern North Pacific and implications for reconstruction of the paleoenvironment. *Paleoceanography* **26**, PA4215 (2011).
45. Sarinthein, M. *et al.* Mid Holocene origin of the sea-surface salinity low in the subarctic North Pacific. *Quaternary Science Reviews* **23**, 2089–2099 (2004).
46. Yu, J. *et al.* Responses of the deep ocean carbonate system to carbon reorganization during the Last Glacial-interglacial cycle. *Quaternary Science Reviews* **76**, 39–52 (2013).

- 801 47. Sarnthein, M., Schneider, B. & Grootes, P. M. Peak glacial  $^{14}\text{C}$   
802 ventilation ages suggest major draw-down of carbon into the abyssal  
803 ocean. *Clim. Past* **9**, 2595–2614 (2013).
- 804 48. Reimer, P. J. *et al.* IntCal13 and Marine13 radiocarbon age calibration  
805 curves 0-50,000 years cal BP. *Radiocarbon* **55**, 1869–1887 (2013).
- 806 49. Takahashi, T., Olafsson, J., Goddard, J. G., Chipman, D. W. &  
807 Sutherland, S. C. Seasonal variation of  $\text{CO}_2$  and nutrients in the high-  
808 latitude surface oceans: A comparative study. *Global Biogeochem.*  
809 *Cycles* **7**, 843–878 (1993).
- 810 50. Butzin, M., Prange, M. & Lohmann, G. Readjustment of glacial  
811 radiocarbon chronologies by self-consistent three-dimensional ocean  
812 circulation modeling. *Earth and Planetary Science Letters* **317-318**,  
813 177–184 (2012).
- 814 51. Kovanen, D. J. & Easterbrook, D. J. Paleodeviations of radiocarbon  
815 marine reservoir values for the northeast Pacific. *Geol* **30**, 243–246  
816 (2002).
- 817 52. Southon, J. R., Nelson, D. E. & Vogel, J. S. A record of past ocean-  
818 Atmosphere radiocarbon differences from the northeast Pacific.  
819 *Paleoceanography* **5**, 197–206 (1990).
- 820 53. Blaauw, M. & Christen, J. A. Flexible paleoclimate age-depth models  
821 using an autoregressive gamma process. *Bayesian Analysis* (2011).  
822 doi:10.1214/11-BA618
- 823 54. Barker, S., Greaves, M. & Elderfield, H. A study of cleaning procedures  
824 used for foraminiferal Mg/Ca paleothermometry. *Geochem. Geophys.*

- 825        *Geosyst.* **4**, 8407 (2003).
- 826    55.    Rae, J. W. B., Foster, G. L., Schmidt, D. N. & Elliott, T. Boron isotopes  
827        and B/Ca in benthic foraminifera: Proxies for the deep ocean carbonate  
828        system. *Earth and Planetary Science Letters* **302**, 403–413 (2011).
- 829    56.    Foster, G. L. Seawater pH,  $p\text{CO}_2$  and  $[\text{CO}_3^{2-}]$  variations in the  
830        Caribbean Sea over the last 130 kyr: A boron isotope and B/Ca study of  
831        planktic foraminifera. *Earth and Planetary Science Letters* **271**, 254–266  
832        (2008).
- 833    57.    Foster, G. L. *et al.* Interlaboratory comparison of boron isotope analyses  
834        of boric acid, seawater and marine  $\text{CaCO}_3$  by MC-ICPMS and NTIMS.  
835        *Chemical Geology* **358**, 1–14 (2013).
- 836    58.    Boyle, E. A. & Keigwin, L. Comparison of Atlantic and Pacific  
837        paleochemical records for the last 215,000 years: Changes in deep  
838        ocean circulation and chemical inventories. *Earth and Planetary  
839        Science Letters* **76**, 135–150 (1985).
- 840    59.    Elderfield, H. & Ganssen, G. Past temperature and  $\delta^{18}\text{O}$  of surface  
841        ocean waters inferred from foraminiferal Mg/Ca ratios. *Nature* **405**, 442–  
842        445 (2000).
- 843    60.    Jonkers, L., Jiménez-Amat, P., Mortyn, P. G. & Brummer, G.-J. A.  
844        Seasonal Mg/Ca variability of *N. pachyderma* (s) and *G. bulloides*:  
845        Implications for seawater temperature reconstruction. *Earth and  
846        Planetary Science Letters* **376**, 137–144 (2013).
- 847    61.    Hönisch, B. *et al.* The influence of salinity on Mg/Ca in planktic  
848        foraminifers – Evidence from cultures, core-top sediments and  
849        complementary  $\delta^{18}\text{O}$ . *Geochimica et Cosmochimica Acta* **121**, 196–213

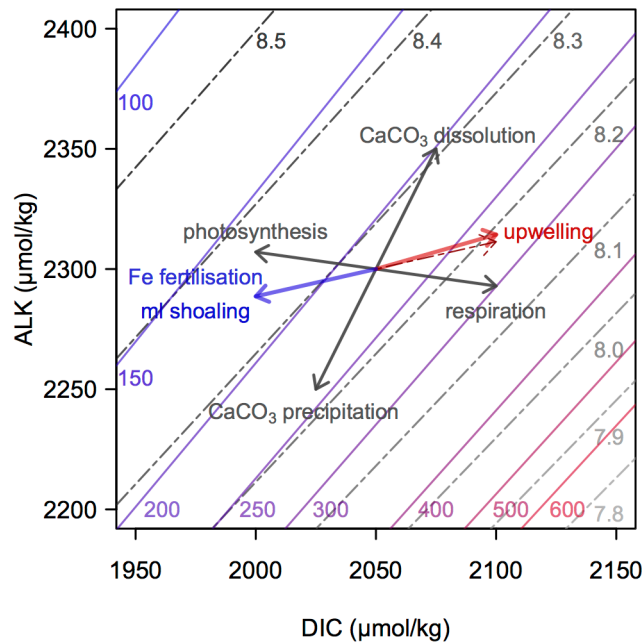
- 850 (2013).
- 851 62. Gray, W. R. *et al.* The effects of temperature, salinity, and the carbonate  
852 system on Mg/Ca in *Globigerinoides ruber* (white): A global sediment  
853 trap calibration. *Earth and Planetary Science Letters* **482**, 607–620  
854 (2018).
- 855 63. Evans, D., Wade, B. S., Hennehan, M. J., Erez, J. & Müller, W. Revisiting  
856 carbonate chemistry controls on planktic foraminifera Mg/Ca:  
857 implications for sea surface temperature and hydrology shifts over the  
858 Paleocene–Eocene Thermal Maximum and Eocene–Oligocene  
859 transition. *Clim. Past* **12**, 819–835 (2016).
- 860 64. Regenberg, M., Regenberg, A., Garbe-Schönberg, D. & Lea, D. W.  
861 Global dissolution effects on planktonic foraminiferal Mg/Ca ratios  
862 controlled by the calcite-saturation state of bottom waters.  
863 *Paleoceanography* **29**, 127–142 (2014).
- 864 65. Yu, J., Thornalley, D. J. R., Rae, J. W. B. & McCave, N. I. Calibration  
865 and application of B/Ca, Cd/Ca, and  $\delta^{11}\text{B}$  in *Neogloboquadrina*  
866 *pachyderma* (sinistral) to constrain CO<sub>2</sub> uptake in the subpolar North  
867 Atlantic during the last deglaciation. *Paleoceanography* **28**, 237–252  
868 (2013).
- 869 66. Hennehan, M. J. *et al.* A new boron isotope-pH calibration for *Orbulina*  
870 *universa*, with implications for understanding and accounting for ‘vital  
871 effects’. *Earth and Planetary Science Letters* **454**, 282–292 (2016).
- 872 67. Hennehan, M. J. *et al.* Calibration of the boron isotope proxy in the  
873 planktonic foraminifera *Globigerinoides ruber* for use in palaeo-CO<sub>2</sub>  
874 reconstruction. *Earth and Planetary Science Letters* **364**, 111–122

- 875 (2013).
- 876 68. Foster, G. L., Pogge von Strandmann, P. A. E. & Rae, J. W. B. Boron  
877 and magnesium isotopic composition of seawater. *Geochem. Geophys.*  
878 *Geosyst.* **11**, Q08015 (2010).
- 879 69. Klochko, K., Kaufman, A. J., Yao, W., Byrne, R. H. & Tossell, J. A.  
880 Experimental measurement of boron isotope fractionation in seawater.  
881 *Earth and Planetary Science Letters* **248**, 276–285 (2006).
- 882 70. Zeebe, R. E. & Wolf-Gladrow, D. A. *CO<sub>2</sub> in Seawater: Equilibrium,*  
883 *Kinetics, Isotopes.* (Elsevier Oceanography Series, 2001).
- 884 71. Adkins, J. F., McIntyre, K. & Schrag, D. P. The salinity, temperature,  
885 and  $\delta^{18}\text{O}$  of the glacial deep ocean. *Science* **289**, 1769–1773 (2002).
- 886 72. Lambeck, K., Rouby, H., Purcell, A., Sun, Y. & Sambridge, M. Sea level  
887 and global ice volumes from the Last Glacial Maximum to the Holocene.  
888 *Proceedings of the National Academy of Sciences* **111**, 15296–15303  
889 (2014).
- 890 73. Edgar, K. M., Anagnostou, E., Pearson, P. N. & Foster, G. L. Assessing  
891 the impact of diagenesis on  $\delta^{11}\text{B}$ ,  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ , Sr/Ca and B/Ca values in  
892 fossil planktic foraminiferal calcite. *Geochimica et Cosmochimica Acta*  
893 **166**, 189–209 (2015).
- 894 74. Hain, M. P., Sigman, D. M. & Haug, G. H. Carbon dioxide effects of  
895 Antarctic stratification, North Atlantic Intermediate Water formation, and  
896 subantarctic nutrient drawdown during the last ice age: Diagnosis and  
897 synthesis in a geochemical box model. *Global Biogeochem. Cycles* **24**,  
898 GB4023 (2010).
- 899 75. Gattuso, J. P. *et al.* *Seacarb: seawater carbonate chemistry with R.* (R

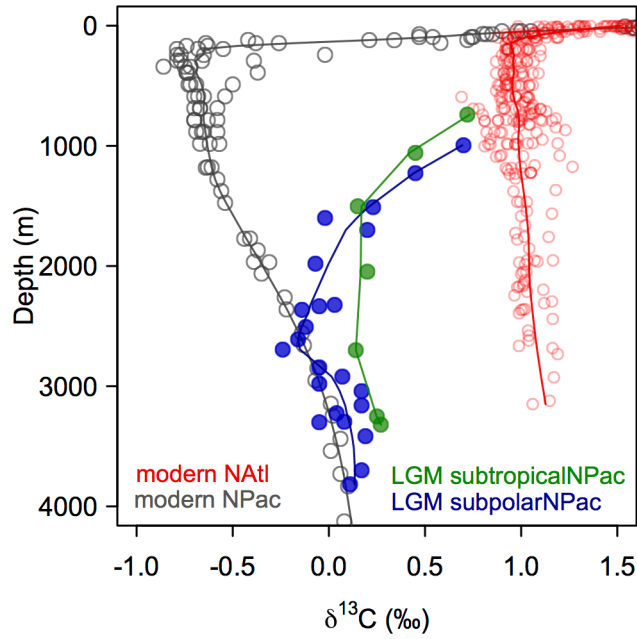
- 900 Package version 3.1.2, 2017).
- 901 76. Millero, F. J., Graham, T. B., Huang, F., Bustos-Serrano, H. & Pierrot,  
902 D. Dissociation constants of carbonic acid in seawater as a function of  
903 salinity and temperature. *Marine Chemistry* **100**, 80–94 (2006).
- 904 77. Dickson, A. G. Standard potential of the reaction:  $\text{AgCl(s)} + 1/2\text{H}_2\text{(g)} =$   
905  $\text{Ag(s)} + \text{HCl(aq)}$ , and the standard acidity constant of the ion  $\text{HSO}_4^-$   
906 in synthetic sea water from 273.15 to 318.15 K. *The Journal of*  
907 *Chemical Thermodynamics* **22**, 113–127 (1990).
- 908 78. Dickson, A. G. & Riley, J. P. The estimation of acid dissociation  
909 constants in seawater media from potentiometric titrations with strong  
910 base. I. The ionic product of water -  $K_w$ . *Marine Chemistry* **7**, 89–99  
911 (1979).
- 912 79. Ezat, M. M., Rasmussen, T. L., Honisch, B., Groeneveld, J. &  
913 deMenocal, P. Episodic release of  $\text{CO}_2$  from the high-latitude North  
914 Atlantic Ocean during the last 135kyr. *Nature Communications* **8**, 1–10  
915 (2017).
- 916 80. Riethdorf, J.-R., Max, L., Nürnberg, D., Lembke-Jene, L. & Tiedemann,  
917 R. Deglacial development of (sub) sea surface temperature and salinity  
918 in the subarctic northwest Pacific: Implications for upper-ocean  
919 stratification. *Paleoceanography* **28**, 91–104 (2013).
- 920 81. Seki, O. *et al.* Reconstruction of paleoproductivity in the Sea of Okhotsk  
921 over the last 30 kyr. *Paleoceanography* **19**, PA1016 (2004).
- 922 82. Seki, O. *et al.* Large changes in seasonal sea ice distribution and  
923 productivity in the Sea of Okhotsk during the deglaciations. *Geochem.*  
924 *Geophys. Geosyst.* **10**, Q10007 (2009).

- 925 83. Ganeshram, R. S., Pedersen, T. F., Calvert, S. E., McNeill, G. W. & R,  
926 F. M. Glacial-interglacial variability in denitrification in the world's  
927 oceans: Causes and consequences. *Paleoceanography* **15**, 361–376  
928 (2000).
- 929 84. Brunelle, B. G. *et al.* Evidence from diatom-bound nitrogen isotopes for  
930 subarctic Pacific stratification during the last ice age and a link to North  
931 Pacific denitrification changes. *Paleoceanography* **22**, PA1215 (2007).
- 932 85. Ito, T. & Follows, M. J. Preformed phosphate, soft tissue pump and  
933 atmospheric CO<sub>2</sub>. *Journal of Marine Research* **63**, 813–839 (2005).
- 934 86. Talley, L. D. Closure of the global overturning circulation through the  
935 Indian, Pacific, and Southern Oceans: Schematics and transports.  
936 *oceanog* **86**, 80–97 (2013).
- 937 87. Peterson, C. D., Lisiecki, L. E. & Stern, J. V. Deglacial whole-ocean  
938  $\delta^{13}\text{C}$  change estimated from 480 benthic foraminiferal records.  
939 *Paleoceanography* **29**, 549–563 (2014).
- 940 88. Otto-Bliesner, B. L. *et al.* Climate sensitivity of moderate-and low-  
941 resolution versions of CCSM3 to preindustrial forcings. *J. Climate* **19**,  
942 2567–2583 (2006).
- 943 89. Otto-Bliesner, B. L. *et al.* Last Glacial Maximum and Holocene Climate  
944 in CCSM3. *J. Climate* **19**, 2526–2544 (2006).

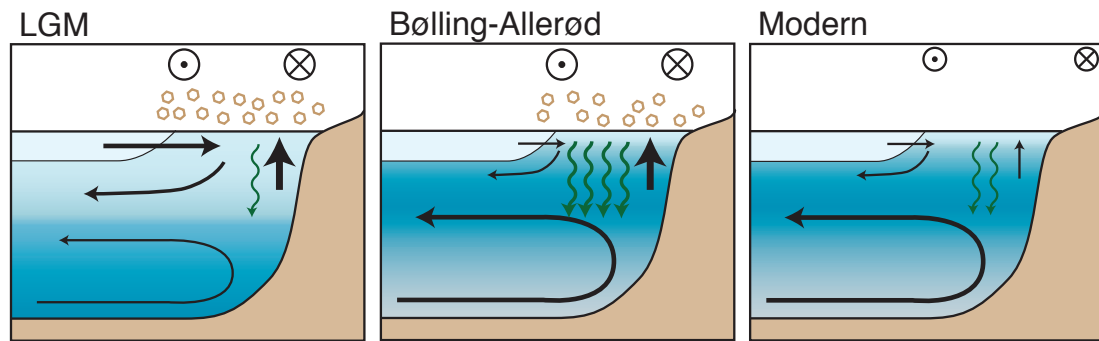




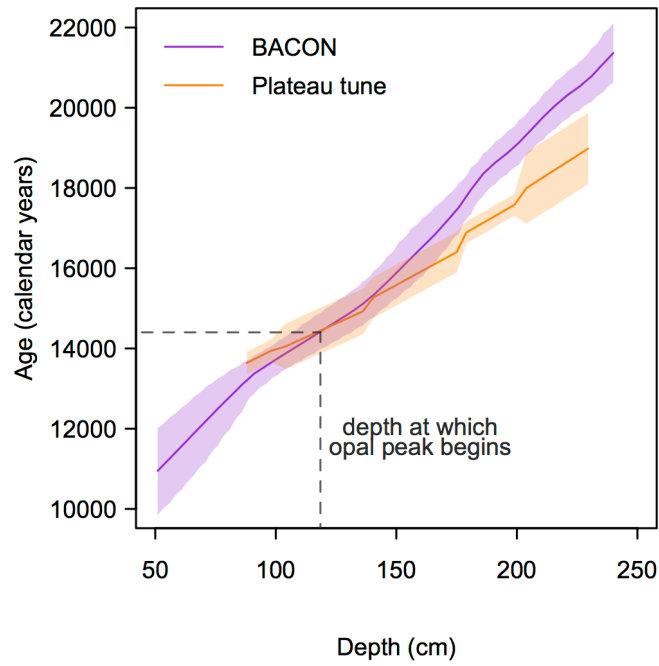
**Supplementary Figure 1** Dissolved Inorganic Carbon (DIC) versus Alkalinity (ALK) with contours of pH on the total scale (grey dashed lines) and  $p\text{CO}_2$  (coloured solid lines) at 5°C, 35 PSU and 0m water depth. The effects of photosynthesis and respiration, as well as the precipitation and dissolution of  $\text{CaCO}_3$  are indicated by the grey arrows. Formation of organic matter by photosynthesis removes DIC and adds ALK in a ratio of ~7:1. Respiration of organic matter adds DIC and removes ALK in the same ratio. Precipitation of  $\text{CaCO}_3$  removes both DIC and ALK with a ratio of 1:2 and dissolution of  $\text{CaCO}_3$  adds DIC and ALK in the same ratio. The effects of an increase in export production from iron fertilisation and mixed layer shoaling are indicated by the blue arrow (assuming a  $\text{C}_{\text{org}}:\text{CaCO}_3$  rain ratio of 4:1). The effect of an increase in upwelling of subsurface waters containing the respired/dissolved products exported from a surface ocean with a  $\text{C}_{\text{org}}:\text{CaCO}_3$  rain ratio of 4:1 is shown by the solid red arrow; the effect of upwelling waters from 250m depth into the surface of the modern western subpolar North Pacific using the values from ref<sup>15</sup> is shown by the dashed red arrow. The upwelling of waters from the ocean's interior brings with it the respired products of photosynthesis, increasing the ratio of DIC to alkalinity (ALK), lowering pH and increasing  $\text{CO}_2$  (red arrow). Increasing export production through the alleviation of iron or light limitation decreases the ratio of DIC/ALK, increasing pH and decreasing  $\text{CO}_2$  (blue arrow).



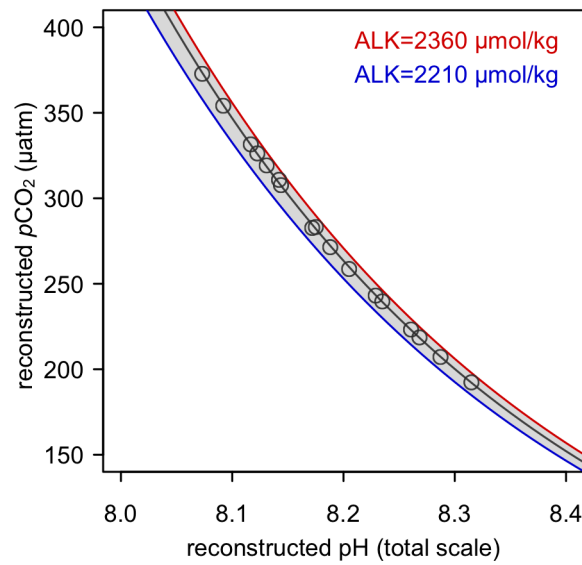
**Supplementary Figure 2**  $\delta^{13}\text{C}$  profiles of the modern (grey) and LGM (blue and green) NW Pacific, and modern North Atlantic (red). Modern values are DIC measurements from ref<sup>15</sup>. LGM values are *Cibicidoides* spp. from refs<sup>29,34</sup>. LGM values have been corrected for the whole ocean change in  $\delta^{13}\text{C}$  using ref<sup>87</sup>.



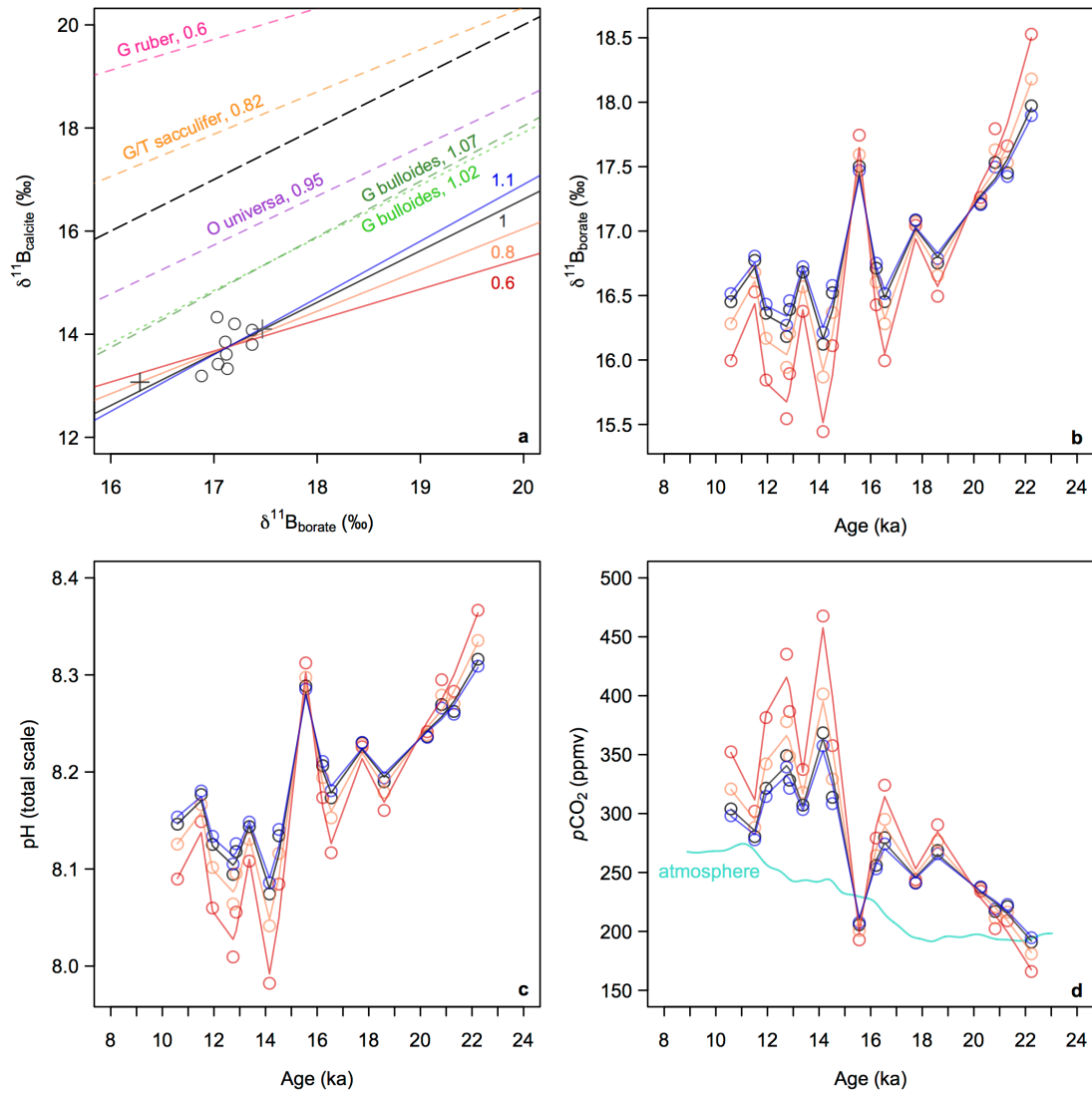
**Supplementary Figure 3** Schematic of circulation and upwelling (black arrows), productivity (green arrows) and atmospheric iron supply (brown symbols) during the LGM, Bølling-Allerød, and in the modern North Pacific. At the LGM, ice sheets on North America shift the easterlies south and strengthen the westerlies, driving increased Ekman suction. However, the upwelled waters have relatively low nutrient contents, due to enhanced ventilation of the upper water column by NPIW, analogous to a shallower version of the modern North Atlantic. During the Bølling-Allerød warming NPIW collapses, increasing the nutrient content of subsurface waters. The continued presence of ice on North America maintains high Ekman upwelling, driving a high flux of nutrients and CO<sub>2</sub> into the surface. Relatively high iron availability from dust, along with reduced light limitation due to seasonal stratification, also contribute to high export productivity, but are not its primary cause. The linked combination of reduced ventilation and high productivity drives hypoxia at intermediate depths.



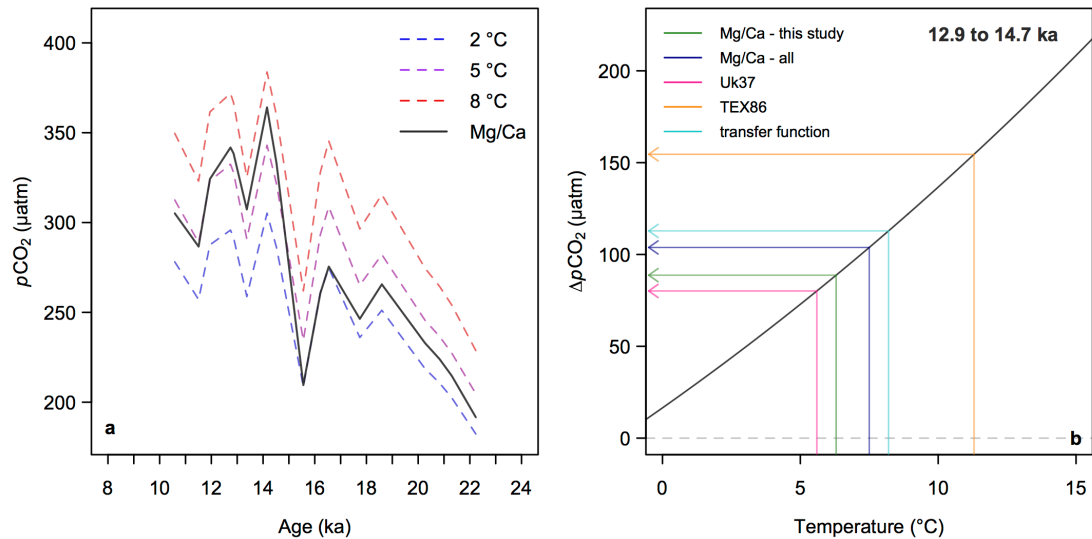
**Supplementary Figure 4** New age model used in this study (purple), and previously published plateau-tuned age model of ref<sup>47</sup>.



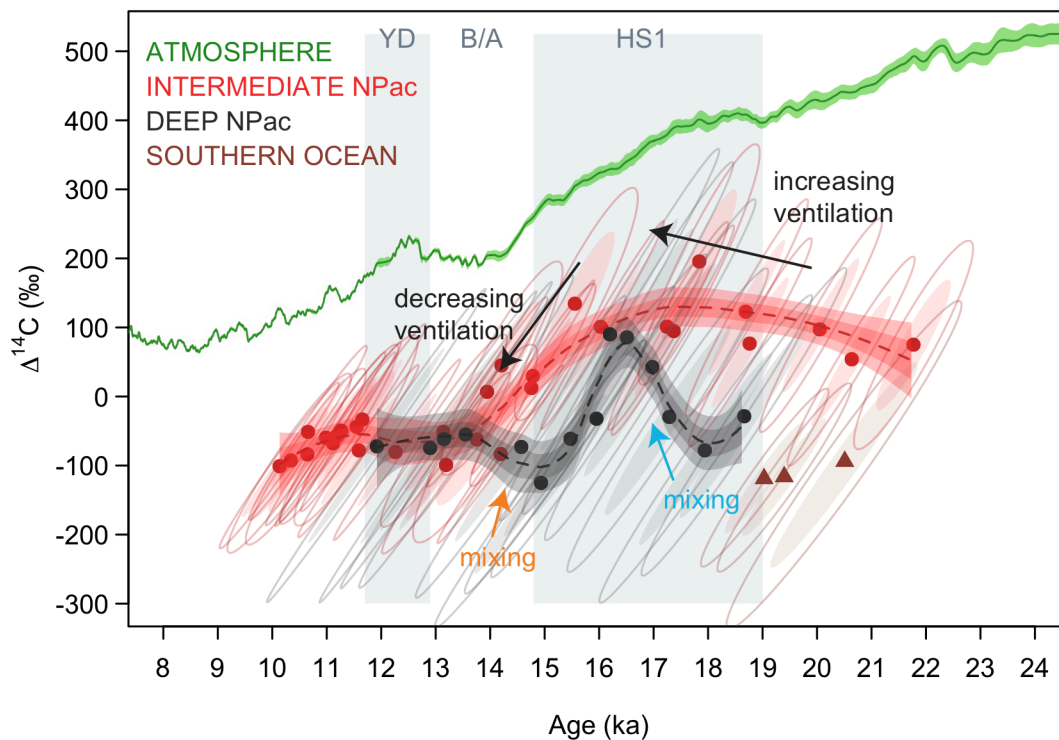
**Supplementary Figure 5** Reconstructed  $p\text{CO}_2$  as a function of reconstructed pH with varying alkalinity. The range in alkalinity represented by the shaded area is equivalent to the range in alkalinity found within the surface of the open Pacific Ocean today<sup>15</sup>.



**Supplementary Figure 6**  $\delta^{11}\text{B}_{\text{calcite}}\text{-}\delta^{11}\text{B}_{\text{borate}}$  calibration sensitivity test (a) the dashed lines show all previously published planktic foraminiferal relationships between  $\delta^{11}\text{B}_{\text{borate}}$  and  $\delta^{11}\text{B}_{\text{calcite}}$  (refs<sup>18,65,66</sup>) with the slope of the relationship indicated. The 1:1 line is shown by the dashed black line. *N. pachyderma* coretop data of ref<sup>65</sup> are shown by the open circles. To test the sensitivity of our results to the assumed slope of the calibration line we re-calibrated the coretop data of ref<sup>65</sup>, forcing the slope of the line within the range previously observed in all other species of planktic foraminifera (0.6 to 1.1, solid lines), and allowing the intercept to vary. Newly generated Holocene  $\delta^{11}\text{B}_{\text{Npachyderma}}$  from MD01-2416 (dark-grey cross) and MD02-2489 (light-grey cross; 54.39°N, 148.92°E, 3640 m water depth) plotted against pre-industrial  $\delta^{11}\text{B}_{\text{borate}}$ , show very good agreement with the calibration proposed by ref<sup>65</sup> used in this study (b) down core  $\delta^{11}\text{B}_{\text{borate}}$  (c) pH and (d)  $\text{pCO}_2$  versus age (with LOESS smooth), assuming different slopes in relationship between  $\delta^{11}\text{B}_{\text{calcite}}$  and  $\delta^{11}\text{B}_{\text{borate}}$  (see panel a). This exercise demonstrates that within the range in slope previously observed in all other species of planktic foraminifera, the assumed slope of the  $\delta^{11}\text{B}_{\text{calcite}}\text{-}\delta^{11}\text{B}_{\text{borate}}$  calibration makes no difference to any of the conclusions drawn in this study.



**Supplementary Figure 7** Temperature-carbonate system sensitivity tests **(a)** reconstructed  $p\text{CO}_2$  versus age at different temperatures (calculated at a constant salinity [33.9] and pressure [5 bar]). The coloured lines are calculated assuming a constant temperature of 2 °C, 5 °C and 8 °C, and the black line shows pH calculated using the Mg/Ca temperatures **(b)** average reconstructed ocean-atmosphere  $p\text{CO}_2$  difference ( $\Delta p\text{CO}_2$ ) during the Bølling-Allerød (12.9 to 14.7 ka) as a function of temperature (using a salinity of 33.9 and pressure of 5 bar). Coloured lines show reconstructed temperature within the western subpolar North Pacific during this interval from all available proxy data (refs<sup>21,80-82</sup>). The temperatures suggested by all proxies suggest a substantial outgassing of  $\text{CO}_2$  to the atmosphere during the Bølling-Allerød.



1131

1132

1133

1134

1135

1136

1137

1138

1139

1140

1141

1142

1143

1144

1145

1146

1147

1148

1149

1150

1151

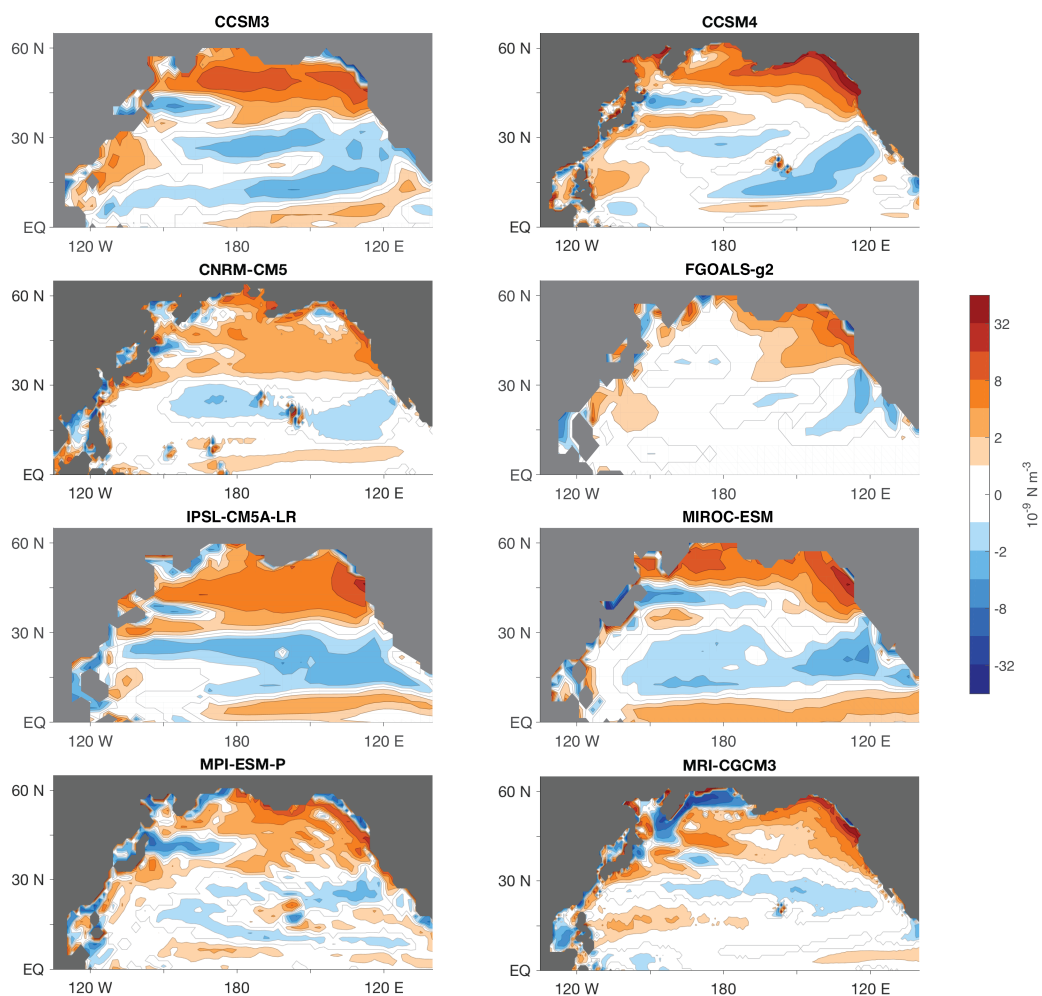
1152

1153

**Supplementary Figure 8** Benthic  $\Delta^{14}\text{C}$  records from the intermediate (<1500m) western North Pacific<sup>30</sup> (red circles, see caption of Figure 3 for core details) and deep North Pacific<sup>35,47</sup> (black circles), with the atmospheric record of ref<sup>48</sup> (green), and the LGM Southern Ocean data of ref<sup>51</sup> (brown triangles). Confidence intervals are 95% (open circles) and 67% (filled circles). LOESS smooth shown by the dashed line with 67% and 95% confidence intervals. An increase in North Pacific overturning circulation is suggested during early deglaciation by increasing  $\Delta^{14}\text{C}$ , with deepwater formation in HS1 resulting in mixing throughout the water column to ~3600m (blue arrow). A reduction in intermediate water formation during the Bølling-Allerød results in old, radiocarbon depleted, deepwaters mixing throughout the water column, and low  $\Delta^{14}\text{C}$  values at intermediate depths (orange arrow). The Southern Ocean record of ref<sup>51</sup> is thought to represent southern sourced deepwater, which flows into the deep Pacific today, and likely during the LGM.



1154



1155

1156

**Supplementary Figure 9** Difference in wind stress curl within the North Pacific under glacial boundary conditions relative to pre-industrial control in PMIP3 climate model ensemble<sup>31</sup>.

1157

1158

1159

1160

1161

1162

1163

1164

1165

1166

1167

1168

1169

1170

1171

1172

1173

**Supplementary Table 1**

The location of cores in the North Pacific from which proxy data are discussed in the manuscript

<b>Core</b>	<b>Lat (°N)</b>	<b>Lon (°E)</b>	<b>Water depth (m)</b>
RAMA-PC-44	53.00	164.65	2980
PC13	49.72	168.31	2393
ODP882	50.37	167.60	3244
SO202-07-6	51.30	167.70	2345
EW0408-85JC	59.55	-144.15	682
ODP887	54.62	-148.75	3647
ODP1017	34.53	-121.10	955
SO201-2-85KL	57.51	170.70	968
SO178-13-6	52.73	144.71	713
CH84-14	41.73	142.55	978
GH02-1030	42.23	144.21	1212
MR01K03-PC4/PC5	41.12	142.40	1366

1174

1175

1176 *Supplementary References*

- 1177 S1. Skinner, L., Fallon, S., Waelbroeck, C., Michel, E. & Barker, S. Ventilation of the Deep  
 1178 Southern Ocean and Deglacial CO<sub>2</sub> Rise. *Science* **328**, 1147–1151 (2010).

1179

1180