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Title: Oxygen rise in the tropical upper ocean during the Paleocene-Eocene Thermal Maximum

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Abstract: The global ocean’s oxygen (O₂) inventory is declining in response to global warming, but the future of the low-oxygen tropics is uncertain. We report new evidence for tropical oxygenation during the Paleocene-Eocene Thermal Maximum (PETM), a warming event that serves as a geologic analogue to anthropogenic warming. Foraminifera-bound nitrogen isotopes indicate that the tropical North Pacific oxygen-deficient zone contracted during the PETM. A concomitant increase in foraminifera size implies that oxygen availability rose in the shallow subsurface throughout the tropical North Pacific. These changes are consistent with ocean model simulations of warming, in which a decline in biological productivity allows tropical subsurface oxygen to rise even as global ocean oxygen declines. The tropical oxygen increase may have helped avoid a mass extinction during the PETM.

One-Sentence Summary: During a geological analogue to anthropogenic warming, the N isotopes and size of microfossils reveal an increase in the oxygenation of the low latitude ocean.

Main Text: Oxygen is fundamental to life, and its distribution in the ocean constrains the habitats of marine biota, from microbes to macrofauna. Historical observations demonstrate a strong correlation between the rise in ocean heat content and declining oxygen inventory over the past 40 five decades (1, 2), with substantial impacts on coastal ecosystems (3, 4). While these global trends are likely to persist into the future (5), their regional manifestations are poorly understood, particularly in the tropical ocean, which contain some of the greatest biodiversity, most productive ecosystems, and highest rates of low oxygen metabolism in the world ocean (6–8). Nitrogen 45 isotope measurements in sedimentary archives from the vicinity of the oxygen-deficient zones (ODZs) provide a window into ODZ response to climate change. Reconstructions from the past century suggest that the ODZ in the eastern tropical North Pacific, the largest ODZ of the global ocean, shrinks when trade winds weaken, a trend anticipated from climate warming (6). Contraction of the North Pacific ODZ has also been inferred during peak warmth in the Eocene 50 and Miocene epochs (9, 10). However, the prominence of centennial variability in signals from the recent past (6), and the potential importance of geological processes in records spanning millions of years (11) leaves doubt about the relevance of these changes for the ODZ under anthropogenic warming. Moreover, the colder climate of the Last Glacial Maximum (LGM) ~20,000 thousand 55 years ago may have also had a smaller ODZ (12), the opposite sensitivity of ODZs to climate implied by the Eocene and Miocene data, although this result has recently been questioned (13). Thus, the fate of ODZs in warming climates and their connection to the broader oxygen conditions of the tropical ocean remain uncertain.

The Paleocene-Eocene Thermal Maximum (PETM) was the largest and fastest known pre- 60 anthropogenic global warming event in the Cenozoic (14). It occurred around 56 million years ago in response to a rapid (< 5000 year) (15) injection of carbon (C) into the ocean-atmosphere system. This caused a decline in the $\delta^{13}\text{C}$ of preserved materials in both marine and terrestrial sedimentary archives, known as the C isotope excursion (CIE), close to the onset of the PETM (16). Global average temperature rose by at least 5 °C (17), while atmospheric CO_2 is believed to have more 65 than doubled (18). The PETM was associated with widespread ocean acidification (19), large faunal turnover on land (16), and the largest extinction of marine benthic organisms of the Cenozoic (20). While the C emission was ~10 times slower than present (21), the amplitude of the reconstructed relative temperature increase resembles future climate projections under scenarios of high greenhouse gas emissions (17). Thus, the PETM may foreshadow the future state of ocean oxygenation. However, the response of the ODZs during this episode of abrupt warming remains 70 highly uncertain (22, 23). Here, we reconstruct changes in the ODZs and surrounding shallow subsurface waters of the tropical ocean during the PETM using foraminifera-bound nitrogen isotopes and microfossil body size.

The stable isotopes of nitrogen (N) have been used to study past changes in the ODZs (12, 24). Denitrification occurring in the ODZs of the ocean water column expresses a large isotopic 75 discrimination, due to incomplete nitrate (NO_3^-) reduction in the water column, causing residual nitrate to be enriched in ^{15}N (25). Circulation as well as assimilation, sinking, and regeneration propagate the ^{15}N -enriched nitrate signal of the ODZs well beyond their spatial extent (26), ultimately elevating nitrate $\delta^{15}\text{N}$ throughout the Pacific and the global ocean. In contrast, sedimentary denitrification consumes N with only weak isotopic discrimination, due to nearly 80 complete nitrate consumption in sediment porewaters (27). Accordingly, mean ocean pycnocline nitrate $\delta^{15}\text{N}$ is largely controlled by the global ratio of water column (WCD) to sedimentary denitrification (SD) (28). Planktic foraminifera provide a window into past seawater nitrate $\delta^{15}\text{N}$. In oligotrophic regions where surface nutrients are fully consumed, the $\delta^{15}\text{N}$ of foraminifera-bound organic matter (FB- $\delta^{15}\text{N}$) reflects the $\delta^{15}\text{N}$ of the pycnocline nitrate (29). Foraminifera-bound

85 organic matter is well protected from alteration by the biomineral matrix (30) and has been used to reconstruct changes in the N cycle over the Cenozoic, the past 65 Myr (9–11).

We report measurements of FB- $\delta^{15}\text{N}$ from 5 well-studied PETM sections (Fig. 1; Table S1). We present measurements of the three dominant planktic foraminifera genera of the PETM, *Subbotina*, *Acaranina* and *Morozovella*, measured in parallel whenever their abundances allowed. We report FB- $\delta^{15}\text{N}$ data from subtropical Atlantic Ocean Drilling Program (ODP) Site 1263 and Southern Ocean ODP Site 690, tropical North Pacific ODP Sites 1209/1210, equatorial Site 865, and Indian Ocean DSDP Site 213 (Fig. 1). At the paleo-locations of Sites 213, 1209/1210, and 1263, nutrient consumption in the surface waters is expected to have been complete, such that these FB- $\delta^{15}\text{N}$ data should record changes in the $\delta^{15}\text{N}$ of the nitrate in the shallow subsurface (29). The Pacific hosts most of the ocean's water column denitrification along its eastern tropical margin (31), and Sites 1209/1210 were paleo-located at the margin of the eastern tropical North Pacific ODZ (Fig. 1), to which the westward transport of the denitrification N isotopic signal is well documented (26). This makes Sites 1209/1210 particularly sensitive to denitrification in the North Pacific ODZ. In contrast, there is no water column denitrification in the modern South Atlantic, the region of Site 1263, and Indian Site 213 is remote from the Arabian Sea ODZ and its denitrification signal.

Oxygen deficient zones during the PETM

At the onset of the PETM, FB- $\delta^{15}\text{N}$ decline at the subtropical sites in the North Pacific (1209/1210), South Atlantic (1263) and Indian Ocean (213) as well as at Site 690 in the Southern Ocean (Fig. 2A, B; Site 865 will be discussed below). The largest decline in FB- $\delta^{15}\text{N}$ is observed in the North Pacific Sites 1209/1210, which show an extreme FB- $\delta^{15}\text{N}$ drop from 16 ‰ to 4 ‰ (Fig. 2A, Fig. S3, S4, S5). This results in a collapse in the reconstructed FB- $\delta^{15}\text{N}$ difference between the Pacific and the Atlantic and Indian basins (Fig. S6), before gradually recovering to pre-PETM values in parallel with foraminiferal carbonate $\delta^{13}\text{C}$ (Fig. 2D). Our FB- $\delta^{15}\text{N}$ data for the pre- and post-PETM interval are consistent with background Paleocene FB- $\delta^{15}\text{N}$ values (9). Importantly, at Sites 1209/1210, FB- $\delta^{15}\text{N}$ declines to near its lowest value without a transition through intermediate values, and this occurs within 3 cm of sediment thickness (Fig. S3), pointing to a geologically instantaneous environmental change.

The observation of a FB- $\delta^{15}\text{N}$ decline at multiple sites from the different ocean basins implies a decrease in mean ocean pycnocline nitrate $\delta^{15}\text{N}$. As the mean ocean pycnocline nitrate $\delta^{15}\text{N}$ is driven by the relative proportions of WCD and SD (28), our results could, in principle, be explained by either a decline in water column denitrification and/or an increase in sedimentary denitrification. However, a global increase in sedimentary denitrification is expected to have the same isotopic impact across basins (28). In contrast, there is a much greater FB- $\delta^{15}\text{N}$ decline in the Pacific, as reflected in the collapse of the Pacific to Atlantic/Indian ocean FB- $\delta^{15}\text{N}$ gradient (Fig. 2A; Fig. S6). This points to a marked decline in North Pacific water column denitrification. Other possible changes, such as in sedimentary denitrification and/or N fixation, may have occurred, but they cannot themselves explain the observed FB- $\delta^{15}\text{N}$ changes (See Supplementary Materials).

Among all our sites, South Atlantic Sites 1263 and 213 combined likely provide the best measure of the PETM decline in mean ocean pycnocline nitrate $\delta^{15}\text{N}$ (32), suggesting that it was $\sim 5\text{‰}$ (Fig. 2A). A simple mass balance of the ocean N budget suggests that this corresponds to a 13–21% decline in the proportion of denitrification occurring in the water column (Fig. 3B, Table S2). Today, North Pacific WCD accounts for $\sim 8\%$ of the total denitrification (31). Thus, the

130 apparent whole pycnocline nitrate $\delta^{15}\text{N}$ decline of $\sim 5\text{‰}$ may require that WCD also decreased in
the ocean's other ODZs.

Foraminifera size and ocean oxygen

To evaluate whether the decline in WCD implied by FB- $\delta^{15}\text{N}$ measurements reflects changes
specific to the ODZs or broader changes in low latitude oxygenation, we estimated changes in
135 seawater $p\text{O}_2$ (partial pressure of diatomic oxygen) using foraminifera shell size (FS- $p\text{O}_2$). Marine
ectotherm species in warm waters grow to smaller body sizes when temperatures rise, a
relationship that is observed experimentally and in natural environments (33). The magnitude of
this “temperature size effect” (TSE) and its patterns of variability across species and a wide range
of temperature and body sizes can be predicted from a mechanistic model of organism O_2 supply
140 and demand (34). A rise in temperature increases metabolic O_2 demand relative to organismal O_2
supply; balance can be restored by a reduction in body size. Changes in ambient $p\text{O}_2$ induce an
analogous “oxygen size effect” (OSE) that is also observed in aquatic species (35, 36) and that
may exacerbate or ameliorate the TSE. The combined impact on body size (B) of changes in
temperature (T) and oxygen pressure can be described as $\Delta B/B \cdot 1/\Delta T = \text{TSE} + \text{OSE}$, where both
145 the TSE and OSE can be related to species traits governing the thermal and geometric dependence
of O_2 supply and demand (see Supplementary Materials). The body size of fossil organisms can
be used as a recorder of past changes in ocean $p\text{O}_2$, provided that seawater temperature and
physiological parameters linking body size to seawater $p\text{O}_2$ and temperature are known. Changes
in T and B are measurable from the fossil record, while the allometric and thermal sensitivities of
150 O_2 supply/demand have been obtained from comparative experimental respirometry on a large
number of living organisms (34) (Fig. S1, S2; Table S3).

We use the model to estimate seawater $p\text{O}_2$ from published planktic and benthic foraminifera
size data and the available SST estimates for the PETM from Pacific Sites 1209/1210 (37, 38).
Since global temperature rose by about $5\text{ }^\circ\text{C}$ at the onset of the PETM (Fig. 3D, Fig. S8) (17), the
155 expected response of foraminifera body size is to decrease according to the TSE. However, in
Pacific Sites 1209/1210, planktic foraminifera belonging to genus *Morozovella*, which represents
the dominant taxon of the PETM foraminifera assemblage in these sites (38), collectively show a
rise in body size at the onset of the PETM (Fig. 2C). Other taxa in the planktic foraminifera
assemblage show a much more muted increase in size (Fig. S7), but none of the planktic species
160 shows dwarfing (38). Our metabolic model indicates that the observed planktic foraminifera size
changes (including the lack of dwarfing) in all dominant taxa correspond to an increase of
subsurface FS- $p\text{O}_2$ in the subtropics during the PETM (Fig. 3C and Fig. S7). These results support
a broader scale rise in tropical shallow subsurface oxygen availability as the driver of the ODZ
contraction indicated by our FB- $\delta^{15}\text{N}$ data. Benthic foraminifera from the same sites show the
165 opposite trend (Fig. 2D), implying that a reduction in $p\text{O}_2$ accompanied warming of the deep ocean
(Fig. 3C).

Mechanisms of upper ocean oxygenation in a warming climate

In the context of a warming ocean, a rise in subsurface O_2 requires a decline in respiratory O_2
consumption at depth relative to the rate of circulation-driven O_2 gross supply. A reduction in
170 respiration during the PETM would require a decrease in export production, driven by reduced
nutrient supply to the equatorial and eastern tropical Pacific surface waters (6, 39). A decline in
nutrient supply may be linked to a reduction either in tropical upwelling (6) or in the nutrient
concentration of the upwelled waters. The former is controlled mainly by tropical trade winds,
while the latter is controlled by the degree of nutrient consumption in the mid-latitude surface

175 regions that ventilate the tropical thermocline (8, 40). Such changes could have occurred even on
a decadal-centennial time scale (41), consistent with the abruptness of the FB- $\delta^{15}\text{N}$ decline and
FS- $p\text{O}_2$ rise, with a near-lack of intermediate values (Fig. 1A). Both of these mechanisms could
contribute to the O_2 changes we observe. Changes in O_2 supply (“ventilation”) by upper ocean
180 circulation cannot be ruled out. However, rapid warming intervals are typically associated with
reduced rates of ventilation (42), which would tend to work against the observed PETM
oxygenation, exacerbating the need for lower tropical productivity. With regard to nutrient
concentration, there have been suggestions of a global increase in nutrient reservoir during the
PETM (43); this alone would increase nutrient supply to tropical surface waters, the opposite of
what is needed to explain the Site 865 data and the ODZ contraction.

185 The FB- $\delta^{15}\text{N}$ data from East Pacific Site 865 reported here support a decline in upwelling-
fueled phytoplankton productivity as the most likely cause of ODZ contraction during the PETM.
In contrast to all other records across the PETM, Site 865 shows a 2‰ rise in FB- $\delta^{15}\text{N}$ for both
symbiont-bearing and -barren foraminifera (Fig. 2A, B). The difference from nearby Site 1210 is
stark: Prior to the PETM, Site 865 shows FB- $\delta^{15}\text{N}$ values 6‰ lower than Site 1210, whereas at the
190 CIE onset, Site 865 FB- $\delta^{15}\text{N}$ is 6‰ higher than at Site 1209/1210 (Fig. 2A, B, Fig S6). During the
PETM, Site 865 was located within 6° of latitude from the equator (Fig. 1, Table S1). In the modern
ocean, the equatorial Pacific hosts high rates of primary production associated with intense
equatorial upwelling, with a large “nutrient tongue” in these surface waters, where the isotopic
discrimination associated with partial nitrate assimilation leads to a low FB- $\delta^{15}\text{N}$ (44). Similar
195 conditions during the Paleogene are supported by both geological evidence of high equatorial
sedimentation rates (45) and the low FB- $\delta^{15}\text{N}$ of Site 865 relative to Site 1210 at that time (Fig.
2A). The net rise in FB- $\delta^{15}\text{N}$ at Site 865 (Fig. 3A) and the reversal of the FB- $\delta^{15}\text{N}$ difference
between Sites 865 and 1210 at the CIE onset (Fig. S6) are best explained by an increase in nutrient
consumption in the equatorial upwelling zone and a contraction of the nutrient tongue during the
200 PETM. Studies of nannofossil assemblages at Site 865 have been interpreted to reflect a shift from
eutrophic toward oligotrophic conditions at the onset of the CIE (Fig. 3A) (46), supporting this
interpretation of the Site 865 FB- $\delta^{15}\text{N}$ record. A decrease in either the tropical upwelling rate or
the nutrient concentration of the upwelling waters could have caused the contraction in the
equatorial Pacific nutrient tongue and the decline in tropical productivity.

205 The foraminifera body size changes into the PETM observed at Sites 1209/1210 also support
an upper ocean mechanism for the oxygenation of the tropical Pacific thermocline. While the body
size of planktic foraminifera did not decline, contrary from expectations from the TSE, that of
benthic foraminifera decreased by ~20%/C, far more than can be attributed to temperature alone.
This implies that the $p\text{O}_2$ of waters at ~2000m decreased while temperatures rose (Fig. 4A). A rise
210 in deep Pacific O_2 and its mixing into the thermocline therefore was not the cause of the PETM
increase in O_2 in the tropical shallow subsurface. Warming without a change in the respiratory O_2
consumption will cause a reduction in $p\text{O}_2$ due to the non-linear thermal solubility of gasses, but
this effect is small. Thus, the apparent decline in abyssal $p\text{O}_2$ implies a reduction of surface
nutrients in the polar or subpolar ocean (47). This may have contributed to the loss of productivity
215 in the tropics and the resulting rise of tropical shallow subsurface O_2 , a mechanism previously seen
in models of past and future global warming (8, 48).

Comparison of reconstructed oxygen changes to numerical simulations

220 We evaluated the magnitude and pattern of pO_2 changes inferred from foraminifera body size
to numerical experiments conducted with an ocean general circulation model (Fig. 4; see
Supplementary Materials). The model is forced with sea surface temperature from proxy
reconstructions across the PETM (17), and circulation changes are imposed from a coupled climate
225 model (42). The model reproduces deep ocean temperatures in the pre- and peak-PETM (Fig. S9),
for which it also simulates the equilibrium distributions of O_2 and nutrients. Across a range of
simulations that vary the magnitude of circulation change and the depletion of surface nutrients
(Fig. S10), the pO_2 rises in the low latitude thermocline while declining in the high latitudes and
the deep ocean (Fig. 4A). These changes are consistent in magnitude and pattern with the pO_2
reconstructed from both planktic and benthic foraminifera body size (Fig. 3C).

230 The observed oxygenation of the subtropical thermocline and the ODZ contraction during the
PETM may be relevant for the coming decades and centuries. This suggestion is supported by the
strong agreement in the rate of subtropical pO_2 change per degree of warming of our
reconstructions with PETM model simulations (Fig. 4A), and with future climate projections for
235 2300 under a high greenhouse gas emissions scenario (Fig. 4B; 48). The inferred contraction of
the equatorial nutrient tongue during the PETM is likewise consistent with Earth System Model
simulations of future global warming, which suggest a decrease in primary production and nutrient
concentrations by the end of the current century (50). Thus, our PETM results support the
expectation that the ODZs of the ocean will likely contract in response to global warming as a
consequence of a reduction in productivity-driven oxygen demand in the surface subtropical
240 Pacific.

Implications for marine biodiversity

Our results have implications for marine life under abrupt climate warming. In the modern
climate, the general increase in biodiversity from the poles toward the equator exhibits a reversal
in the tropics (51) where the prevailing combination of high temperature and low O_2 is inhabitable
245 for a smaller number of species (52). A warming climate pushes ocean temperatures beyond the
metabolic limits of a greater number of species, further accentuating the tropical dip in species
richness, a feature that arose after the LGM (53). Unlike with the deglacial warmings of the
Pleistocene, the rise in tropical O_2 reconstructed for the PETM would have maintained aerobic
habitat that would otherwise have been lost due to thermal acceleration of animal metabolism. This
250 compensation may help to explain the relatively moderate level of pelagic extinction in the fossil
record of the PETM (54, 55). In contrast, increased tropical subsurface O_2 change was not adequate
to ward off massive losses of tropical biodiversity at the end-Permian (48), nor is it predicted to
be in future projections of human-driven global warming (52).

255 References and Notes

1. S. Schmidtko, L. Stramma, M. Visbeck, Decline in global oceanic oxygen content during the past five
decades. *Nature* **542**, 335–339 (2017).
2. T. Ito, S. Minobe, M. C. Long, C. Deutsch, Upper ocean O_2 trends: 1958–2015. *Geophysical Research Letters*
260 **44**, 4214–4223 (2017).
3. L. Stramma, G. C. Johnson, J. Sprintall, V. Mohrholz, Expanding Oxygen-Minimum Zones in the Tropical
Oceans. *Science* **320**, 655–658 (2008).

- 265 4. D. Breitburg, L. A. Levin, A. Oschlies, M. Grégoire, F. P. Chavez, D. J. Conley, V. Garçon, D. Gilbert, D. Gutiérrez, K. Isensee, G. S. Jacinto, K. E. Limburg, I. Montes, S. W. A. Naqvi, G. C. Pitcher, N. N. Rabalais, M. R. Roman, K. A. Rose, B. A. Seibel, M. Telszewski, M. Yasuhara, J. Zhang, Declining oxygen in the global ocean and coastal waters. *Science* **359**, eaam7240 (2018).
- 270 5. H.-O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, B. Rama (eds.), *IPCC, 2022: Climate Change 2022: Impacts, Adaptation and Vulnerability: Working Group II Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge University Press, UK and New York, NY, USA, 2023).
6. C. Deutsch, W. Berelson, R. Thunell, T. Weber, C. Tems, J. McManus, J. Crusius, T. Ito, T. Baumgartner, V. Ferreira, J. Mey, A. van Geen, Centennial changes in North Pacific anoxia linked to tropical trade winds. *Science* **345**, 665–668 (2014).
- 275 7. A. Yamamoto, A. Abe-Ouchi, M. Shigemitsu, A. Oka, K. Takahashi, R. Ohgaito, Y. Yamanaka, Global deep ocean oxygenation by enhanced ventilation in the Southern Ocean under long-term global warming. *Global Biogeochemical Cycles* **29**, 1801–1815 (2015).
8. W. Fu, F. Primeau, J. K. Moore, K. Lindsay, J. T. Randerson, Reversal of Increasing Tropical Ocean Hypoxia Trends With Sustained Climate Warming. *Global Biogeochemical Cycles* **32**, 551–564 (2018).
- 280 9. E. R. Kast, D. A. Stolper, A. Auderset, J. A. Higgins, H. Ren, X. T. Wang, A. Martínez-García, G. H. Haug, D. M. Sigman, Nitrogen isotope evidence for expanded ocean suboxia in the early Cenozoic. *Science* **364**, 386–389 (2019).
- 285 10. A. Auderset, S. Moretti, B. Taphorn, P.-R. Ebner, E. Kast, X. T. Wang, R. Schiebel, D. M. Sigman, G. H. Haug, A. Martínez-García, Enhanced ocean oxygenation during Cenozoic warm periods. *Nature* **609**, 77–82 (2022).
11. X. T. Wang, Y. Wang, A. Auderset, D. M. Sigman, H. Ren, A. Martínez-García, G. H. Haug, Z. Su, Y. G. Zhang, B. Rasmussen, A. L. Sessions, W. W. Fischer, Oceanic nutrient rise and the late Miocene inception of Pacific oxygen-deficient zones. *Proceedings of the National Academy of Sciences* **119**, e2204986119 (2022).
- 290 12. R. S. Ganeshram, T. F. Pedersen, S. E. Calvert, J. W. Murray, Large changes in oceanic nutrient inventories from glacial to interglacial periods. *Nature* **376**, 755–758 (1995).
13. A. S. Studer, F. Mekik, H. Ren, M. P. Hain, S. Oleynik, A. Martínez-García, G. H. Haug, D. M. Sigman, Ice Age-Holocene Similarity of Foraminifera-Bound Nitrogen Isotope Ratios in the Eastern Equatorial Pacific. *Paleoceanography and Paleoclimatology* **36**, e2020PA004063 (2021).
- 295 14. J. Zachos, M. Pagani, L. Sloan, E. Thomas, K. Billups, Trends, Rhythms, and Aberrations in Global Climate 65 Ma to Present. *Science* **292**, 686–693 (2001).
15. S. Kirtland Turner, P. M. Hull, L. R. Kump, A. Ridgwell, A probabilistic assessment of the rapidity of PETM onset. *Nature Communications* **8**, 353 (2017).
- 300 16. F. A. McInerney, S. L. Wing, The Paleocene-Eocene Thermal Maximum: A Perturbation of Carbon Cycle, Climate, and Biosphere with Implications for the Future. *Annual Review of Earth and Planetary Sciences* **39**, 489–516 (2011).
17. J. E. Tierney, J. Zhu, M. Li, A. Ridgwell, G. J. Hakim, C. J. Poulsen, R. D. M. Whiteford, J. W. B. Rae, L. R. Kump, Spatial patterns of climate change across the Paleocene–Eocene Thermal Maximum. *Proceedings of the National Academy of Sciences* **119**, e2205326119 (2022).

- 305 18. R. E. Zeebe, J. C. Zachos, G. R. Dickens, Carbon dioxide forcing alone insufficient to explain Palaeocene–Eocene Thermal Maximum warming. *Nature Geoscience* **2**, 576–580 (2009).
19. D. E. Penman, B. Hönisch, R. E. Zeebe, E. Thomas, J. C. Zachos, Rapid and sustained surface ocean acidification during the Paleocene-Eocene Thermal Maximum. *Paleoceanography* **29**, 357–369 (2014).
20. E. Thomas, N. J. Shackleton, The Paleocene-Eocene benthic foraminiferal extinction and stable isotope anomalies. *Geological Society, London, Special Publications* **101**, 401–441 (1996).
- 310 21. R. E. Zeebe, A. Ridgwell, J. C. Zachos, Anthropogenic carbon release rate unprecedented during the past 66 million years. *Nature Geoscience* **9**, 325–329 (2016).
22. W. Yao, A. Paytan, U. G. Wortmann, Large-scale ocean deoxygenation during the Paleocene-Eocene Thermal Maximum. *Science* **361**, 804–806 (2018).
- 315 23. X. Zhou, E. Thomas, R. E. M. Rickaby, A. M. E. Winguth, Z. Lu, I/Ca evidence for upper ocean deoxygenation during the PETM. *Paleoceanography* **29**, 964–975 (2014).
24. M. A. Altabet, R. Francois, D. W. Murray, W. L. Prell, Climate-related variations in denitrification in the Arabian Sea from sediment $^{15}\text{N}/^{14}\text{N}$ ratios. *Nature* **373**, 506–509 (1995).
25. J. D. Cline, I. R. Kaplan, Isotopic fractionation of dissolved nitrate during denitrification in the eastern tropical north pacific ocean. *Marine Chemistry* **3**, 271–299 (1975).
- 320 26. D. M. Sigman, P. J. DiFiore, M. P. Hain, C. Deutsch, D. M. Karl, Sinking organic matter spreads the nitrogen isotope signal of pelagic denitrification in the North Pacific. *Geophysical Research Letters* **36** (2009).
27. J. A. Brandes, A. H. Devol, Isotopic fractionation of oxygen and nitrogen in coastal marine sediments. *Geochimica et Cosmochimica Acta* **61**, 1793–1801 (1997).
- 325 28. J. A. Brandes, A. H. Devol, A global marine-fixed nitrogen isotopic budget: Implications for Holocene nitrogen cycling. *Global Biogeochemical Cycles* **16**, 67-1-67–14 (2002).
29. H. Ren, D. M. Sigman, R. C. Thunell, M. G. Prokopenko, Nitrogen isotopic composition of planktonic foraminifera from the modern ocean and recent sediments. *Limnol. Oceanogr.* **57**, 1011–1024 (2012).
30. A. Martínez-García, J. Jung, X. E. Ai, D. M. Sigman, A. Auderset, N. N. Duprey, A. Foreman, F. Fripiat, J. Lechliter, T. Lüdecke, S. Moretti, T. Wald, Laboratory Assessment of the Impact of Chemical Oxidation, Mineral Dissolution, and Heating on the Nitrogen Isotopic Composition of Fossil-Bound Organic Matter. *Geochemistry, Geophysics, Geosystems* **23**, e2022GC010396 (2022).
- 330 31. D. Bianchi, J. P. Dunne, J. L. Sarmiento, E. D. Galbraith, Data-based estimates of suboxia, denitrification, and N_2O production in the ocean and their sensitivities to dissolved O_2 . *Global Biogeochemical Cycles* **26** (2012).
- 335 32. F. Fripiat, A. Martínez-García, D. Marconi, S. E. Fawcett, S. H. Kopf, V. H. Luu, P. A. Rafter, R. Zhang, D. M. Sigman, G. H. Haug, Nitrogen isotopic constraints on nutrient transport to the upper ocean. *Nat. Geosci.* **14**, 855–861 (2021).
33. D. Atkinson, Temperature and organism size—a biological law for ectotherms? *Advances in Ecological Research* **25**, 1–58 (1994).
- 340 34. C. Deutsch, J. L. Penn, W. C. E. P. Verberk, K. Inomura, M.-G. Endress, J. L. Payne, Impact of warming on aquatic body sizes explained by metabolic scaling from microbes to macrofauna. *Proceedings of the National Academy of Sciences* **119**, e2201345119 (2022).

35. M. Czarnoleski, J. Ejsmont-Karabin, M. J. Angilletta Jr, J. Kozłowski, Colder rotifers grow larger but only in oxygenated waters. *Ecosphere* **6**, art164 (2015).
- 345 36. A. Kuroyanagi, R. E. da Rocha, J. Bijma, H. J. Spero, A. D. Russell, S. M. Eggins, H. Kawahata, Effect of dissolved oxygen concentration on planktonic foraminifera through laboratory culture experiments and implications for oceanic anoxic events. *Marine Micropaleontology* **101**, 28–32 (2013).
37. K. Kaiho, K. Takeda, M. R. Petrizzo, J. C. Zachos, Anomalous shifts in tropical Pacific planktonic and benthic foraminiferal test size during the Paleocene–Eocene thermal maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* **237**, 456–464 (2006).
- 350 38. M. R. Petrizzo, The onset of the Paleocene–Eocene Thermal Maximum (PETM) at Sites 1209 and 1210 (Shatsky Rise, Pacific Ocean) as recorded by planktonic foraminifera. *Marine Micropaleontology* **63**, 187–200 (2007).
39. J. J. M. Busecke, L. Resplandy, S. J. Ditkovsky, J. G. John, Diverging Fates of the Pacific Ocean Oxygen Minimum Zone and Its Core in a Warming World. *AGU Advances* **3**, e2021AV000470 (2022).
- 355 40. D. P. Keller, I. Kriest, W. Koeve, A. Oschlies, Southern Ocean biological impacts on global ocean oxygen. *Geophysical Research Letters* **43**, 6469–6477 (2016).
41. S. Yang, N. Gruber, M. C. Long, M. Vogt, ENSO-Driven Variability of Denitrification and Suboxia in the Eastern Tropical Pacific Ocean. *Global Biogeochemical Cycles* **31**, 1470–1487 (2017).
- 360 42. T. Ilyina, M. Heinze, Carbonate Dissolution Enhanced by Ocean Stagnation and Respiration at the Onset of the Paleocene-Eocene Thermal Maximum. *Geophysical Research Letters* **46**, 842–852 (2019).
43. N. M. Papadomanolaki, W. K. Lenstra, M. Wolthers, C. P. Slomp, Enhanced phosphorus recycling during past oceanic anoxia amplified by low rates of apatite authigenesis. *Science Advances* **8**, eabn2370 (2022).
44. P. A. Rafter, D. M. Sigman, K. R. M. Mackey, Recycled iron fuels new production in the eastern equatorial Pacific Ocean. *Nature Communications* **8**, 1100 (2017).
- 365 45. T. C. Moore Jr., J. Backman, I. Raffi, C. Nigrini, A. Sanfilippo, H. Pälike, M. Lyle, Paleogene tropical Pacific: Clues to circulation, productivity, and plate motion. *Paleoceanography* **19** (2004).
46. D. Clay Kelly, T. J. Bralower, J. C. Zachos, I. P. Silva, E. Thomas, Rapid diversification of planktonic foraminifera in the tropical Pacific (ODP Site 865) during the late Paleocene thermal maximum. *Geology* **24**, 423 (1996).
- 370 47. J. L. Sarmiento, J. R. Toggweiler, A new model for the role of the oceans in determining atmospheric PCO₂. *Nature* **308**, 621–624 (1984).
48. J. L. Penn, C. Deutsch, J. L. Payne, E. A. Sperling, Temperature-dependent hypoxia explains biogeography and severity of end-Permian marine mass extinction. *Science* **362**, eaat1327 (2018).
- 375 49. Y. Takano, T. Ito, C. Deutsch, Projected Centennial Oxygen Trends and Their Attribution to Distinct Ocean Climate Forcings. *Global Biogeochemical Cycles* **32**, 1329–1349 (2018).
- 380 50. L. Kwiatkowski, O. Torres, L. Bopp, O. Aumont, M. Chamberlain, J. R. Christian, J. P. Dunne, M. Gehlen, T. Ilyina, J. G. John, A. Lenton, H. Li, N. S. Lovenduski, J. C. Orr, J. Palmieri, Y. Santana-Falcón, J. Schwinger, R. Séférian, C. A. Stock, A. Tagliabue, Y. Takano, J. Tjiputra, K. Toyama, H. Tsujino, M. Watanabe, A. Yamamoto, A. Yool, T. Ziehn, Twenty-first century ocean warming, acidification, deoxygenation, and upper-ocean nutrient and primary production decline from CMIP6 model projections. *Biogeosciences* **17**, 3439–3470 (2020).

51. C. Chaudhary, H. Saeedi, M. J. Costello, Bimodality of Latitudinal Gradients in Marine Species Richness. *Trends in Ecology & Evolution* **31**, 670–676 (2016).
52. J. L. Penn, C. Deutsch, Avoiding ocean mass extinction from climate warming. *Science* **376**, 524–526 (2022).
- 385 53. M. Yasuhara, C.-L. Wei, M. Kucera, M. J. Costello, D. P. Tittensor, W. Kiessling, T. C. Bonebrake, C. R. Tabor, R. Feng, A. Baselga, K. Kretschmer, B. Kusumoto, Y. Kubota, Past and future decline of tropical pelagic biodiversity. *Proceedings of the National Academy of Sciences* **117**, 12891–12896 (2020).
54. R. D. Norris, S. K. Turner, P. M. Hull, A. Ridgwell, Marine Ecosystem Responses to Cenozoic Global Change. *Science* **341**, 492–498 (2013).
- 390 55. J. Frieling, H. Gebhardt, M. Huber, O. A. Adekeye, S. O. Akande, G.-J. Reichart, J. J. Middelburg, S. Schouten, A. Sluijs, Extreme warmth and heat-stressed plankton in the tropics during the Paleocene-Eocene Thermal Maximum. *Science Advances* **3**, e1600891 (2017).
56. S. Moretti, Oxygen rise in the tropical upper ocean during the Paleocene-Eocene Thermal Maximum [Dataset], Dryad (2023); <https://doi.org/doi:10.5061/dryad.br15dvdr>.
- 395 57. R. D. Müller, M. Seton, S. Zahirovic, S. E. Williams, K. J. Matthews, N. M. Wright, G. E. Shephard, K. T. Maloney, N. Barnett-Moore, M. Hosseinpour, D. J. Bower, J. Cannon, Ocean Basin Evolution and Global-Scale Plate Reorganization Events Since Pangea Breakup. *Annual Review of Earth and Planetary Sciences* **44**, 107–138 (2016).
- 400 58. F. Nunes, R. D. Norris, Abrupt reversal in ocean overturning during the Palaeocene/Eocene warm period. *Nature* **439**, 60–63 (2006).
59. D. C. Kelly, J. C. Zachos, T. J. Bralower, S. A. Schellenberg, Enhanced terrestrial weathering/runoff and surface ocean carbonate production during the recovery stages of the Paleocene-Eocene thermal maximum. *Paleoceanography* **20** (2005).
- 405 60. T. Westerhold, U. Röhl, R. H. Wilkens, P. D. Gingerich, W. C. Clyde, S. L. Wing, G. J. Bowen, M. J. Kraus, Synchronizing early Eocene deep-sea and continental records – cyclostratigraphic age models for the Bighorn Basin Coring Project drill cores. *Climate of the Past* **14**, 303–319 (2018).
61. C. Pälike, M. L. Delaney, J. C. Zachos, Deep-sea redox across the Paleocene-Eocene thermal maximum. *Geochemistry, Geophysics, Geosystems* **15**, 1038–1053 (2014).
- 410 62. D. Paillard, L. Labeyrie, P. Yiou, Macintosh Program performs time-series analysis. *EOS Transactions* **77**, 379–379 (1996).
63. K. Takeda, K. Kaiho, Faunal turnovers in central Pacific benthic foraminifera during the Paleocene–Eocene thermal maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* **251**, 175–197 (2007).
64. S. Bains, R. M. Corfield, R. D. Norris, Mechanisms of Climate Warming at the End of the Paleocene. *Science* **285**, 724–727 (1999).
- 415 65. B. N. Hupp, D. C. Kelly, J. C. Zachos, T. J. Bralower, Effects of size-dependent sediment mixing on deep-sea records of the Paleocene-Eocene Thermal Maximum. *Geology* **47**, 749–752 (2019).
66. T. J. Bralower, J. C. Zachos, E. Thomas, M. Parrow, C. K. Paull, D. C. Kelly, I. P. Silva, W. V. Sliter, K. C. Lohmann, Late Paleocene to Eocene paleoceanography of the equatorial Pacific Ocean: Stable isotopes recorded at Ocean Drilling Program Site 865, Allison Guyot. *Paleoceanography* **10**, 841–865 (1995).
- 420 67. H. Ren, D. M. Sigman, A. N. Meckler, B. Plessen, R. S. Robinson, Y. Rosenthal, G. H. Haug, Foraminiferal Isotope Evidence of Reduced Nitrogen Fixation in the Ice Age Atlantic Ocean. *Science* **323**, 244–248 (2009).

68. Mehra, O. P., Jackson, M. L., “Iron oxide removal from soils and clays by a dithionite–citrate system buffered with sodium bicarbonate” in *Clays and Clay Minerals*, E. Ingerson, Ed. (Pergamon, 1960), pp. 317–327.
- 425 69. F. Nydahl, On the peroxodisulphate oxidation of total nitrogen in waters to nitrate. *Water Research* **12**, 1123–1130 (1978).
70. R. S. Braman, S. A. Hendrix, Nanogram nitrite and nitrate determination in environmental and biological materials by vanadium(III) reduction with chemiluminescence detection. *Anal. Chem.* **61**, 2715–2718 (1989).
- 430 71. J. N. Leichliter, T. Lüdecke, A. D. Foreman, N. N. Duprey, D. E. Winkler, E. R. Kast, H. Vonhof, D. M. Sigman, G. H. Haug, M. Clauss, T. Tütken, A. Martínez-García, Nitrogen isotopes in tooth enamel record diet and trophic level enrichment: Results from a controlled feeding experiment. *Chemical Geology* **563**, 120047 (2021).
72. D. M. Sigman, K. L. Casciotti, M. Andreani, C. Barford, M. Galanter, J. K. Böhlke, A Bacterial Method for the Nitrogen Isotopic Analysis of Nitrate in Seawater and Freshwater. *Anal. Chem.* **73**, 4145–4153 (2001).
- 435 73. M. A. Weigand, J. Foriel, B. Barnett, S. Oleynik, D. M. Sigman, Updates to instrumentation and protocols for isotopic analysis of nitrate by the denitrifier method. *Rapid Communications in Mass Spectrometry* **30**, 1365–1383 (2016).
74. D. M. Sigman, F. Fripiat, “Nitrogen Isotopes in the Ocean” in *Encyclopedia of Ocean Sciences (Third Edition)*, J. K. Cochran, H. J. Bokuniewicz, P. L. Yager, Eds. (Academic Press, Oxford, 2019), pp. 263–278.
- 440 75. S. Seitzinger, J. A. Harrison, J. K. Böhlke, A. F. Bouwman, R. Lowrance, B. Peterson, C. Tobias, G. V. Drecht, Denitrification Across Landscapes and Waterscapes: A Synthesis. *Ecological Applications* **16**, 2064–2090 (2006).
76. C. Deutsch, A. Ferrel, B. Seibel, H.-O. Pörtner, R. B. Huey, Climate change tightens a metabolic constraint on marine habitats. *Science* **348**, 1132–1135 (2015).
- 445 77. C. Deutsch, J. L. Penn, B. Seibel, Metabolic trait diversity shapes marine biogeography. *Nature* **585**, 557–562 (2020).
78. J. S. Bradshaw, Laboratory experiments on the ecology of foraminifera. *Cushman Found Foram. Res., Contr.* **12**, 87–106 (1961).
- 450 79. J. P. DeLong, J. G. Okie, M. E. Moses, R. M. Sibly, J. H. Brown, Shifts in metabolic scaling, production, and efficiency across major evolutionary transitions of life. *Proceedings of the National Academy of Sciences* **107**, 12941–12945 (2010).
80. J. C. Zachos, M. W. Wara, S. Bohaty, M. L. Delaney, M. R. Petrizzo, A. Brill, T. J. Bralower, I. Premoli-Silva, A Transient Rise in Tropical Sea Surface Temperature During the Paleocene-Eocene Thermal Maximum. *Science* **302**, 1551–1554 (2003).
- 455 81. A. Tripathi, H. Elderfield, Deep-Sea Temperature and Circulation Changes at the Paleocene-Eocene Thermal Maximum. *Science* **308**, 1894–1898 (2005).
82. R. Schiebel, C. Hemleben, *Planktic Foraminifers in the Modern Ocean* (Springer-Verlag, Berlin Heidelberg, ed. 2, 2017; <https://www.springer.com/gp/book/9783662502952>).
- 460 83. C. V. Davis, J. O. Shaw, S. D’haenens, E. Thomas, P. M. Hull, Photosymbiont associations persisted in planktic foraminifera during early Eocene hyperthermals at Shatsky Rise (Pacific Ocean). *PLOS ONE* **17**, e0267636 (2022).

84. T. DeVries, C. Deutsch, P. A. Rafter, F. Primeau, Marine denitrification rates determined from a global 3-D inverse model. *Biogeosciences* **10**, 2481–2496 (2013).
85. T. Dunkley Jones, D. J. Lunt, D. N. Schmidt, A. Ridgwell, A. Sluijs, P. J. Valdes, M. Maslin, Climate model and proxy data constraints on ocean warming across the Paleocene–Eocene Thermal Maximum. *Earth-Science Reviews* **125**, 123–145 (2013).
86. A. Bornemann, R. D. Norris, J. A. Lyman, S. D’haenens, J. Groeneveld, U. Röhl, K. A. Farley, R. P. Speijer, Persistent environmental change after the Paleocene–Eocene Thermal Maximum in the eastern North Atlantic. *Earth and Planetary Science Letters* **394**, 70–81 (2014).
87. J. Frieling, F. Peterse, D. J. Lunt, S. M. Bohaty, J. S. S. Damsté, G.-J. Reichert, A. Sluijs, Widespread Warming Before and Elevated Barium Burial During the Paleocene-Eocene Thermal Maximum: Evidence for Methane Hydrate Release? *Paleoceanography and Paleoclimatology* **34**, 546–566 (2019).
88. J. E. Tierney, M. P. Tingley, A Bayesian, spatially-varying calibration model for the TEX86 proxy. *Geochimica et Cosmochimica Acta* **127**, 83–106 (2014).
89. J. C. Zachos, Rapid Acidification of the Ocean During the Paleocene-Eocene Thermal Maximum. *Science* **308**, 1611–1615 (2005).
90. R. Kozdon, D. C. Kelly, K. Kitajima, A. Strickland, J. H. Fournelle, J. W. Valley, In situ $\delta^{18}\text{O}$ and Mg/Ca analyses of diagenetic and planktic foraminiferal calcite preserved in a deep-sea record of the Paleocene-Eocene thermal maximum. *Paleoceanography* **28**, 517–528 (2013).
91. C. Deutsch, D. M. Sigman, R. C. Thunell, A. N. Meckler, G. H. Haug, Isotopic constraints on glacial/interglacial changes in the oceanic nitrogen budget. *Global Biogeochemical Cycles* **18** (2004).
92. P. Stassen, E. Thomas, R. P. Speijer, Paleocene–Eocene Thermal Maximum environmental change in the New Jersey Coastal Plain: benthic foraminiferal biotic events. *Marine Micropaleontology* **115**, 1–23 (2015).
93. R. Kozdon, D. C. Kelly, J. W. Valley, Diagenetic Attenuation of Carbon Isotope Excursion Recorded by Planktic Foraminifers During the Paleocene-Eocene Thermal Maximum. *Paleoceanography and Paleoclimatology* **33**, 367–380 (2018).
94. B. N. Hupp, D. C. Kelly, J. W. Williams, Isotopic filtering reveals high sensitivity of planktic calcifiers to Paleocene–Eocene thermal maximum warming and acidification. *Proceedings of the National Academy of Sciences* **119**, e2115561119 (2022).
95. G. J. Arreguín-Rodríguez, E. Thomas, S. D’haenens, R. P. Speijer, L. Alegret, Early Eocene deep-sea benthic foraminiferal faunas: Recovery from the Paleocene Eocene Thermal Maximum extinction in a greenhouse world. *PLOS ONE* **13**, e0193167 (2018).
96. J. J. Lee, W. A. Muller, Trophic Dynamics and Niches of Salt Marsh Foraminifera. *American Zoologist* **13**, 215–223 (1973).
97. F. Lombard, J. Erez, E. Michel, L. Labeyrie, Temperature effect on respiration and photosynthesis of the symbiont-bearing planktonic foraminifera *Globigerinoides ruber*, *Orbulina universa*, and *Globigerinella siphonifera*. *Limnology and Oceanography* **54**, 210–218 (2009).
98. G. J. Arreguín-Rodríguez, L. Alegret, E. Thomas, Late Paleocene-middle Eocene benthic foraminifera on a Pacific seamount (Allison Guyot, ODP Site 865): Greenhouse climate and superimposed hyperthermal events. *Paleoceanography* **31**, 346–364 (2016).

- 500 99. D. J. Thomas, J. C. Zachos, T. J. Bralower, E. Thomas, S. Bohaty, Warming the fuel for the fire: Evidence for the thermal dissociation of methane hydrate during the Paleocene-Eocene thermal maximum. *Geology* **30**, 1067 (2002).
100. A. B. Colosimo, T. Bralower, J. C. Zachos, Evidence for lysocline shoaling at the Paleocene/Eocene Thermal Maximum on Shatsky Rise, northwest Pacific. *Proceedings of the Ocean Drilling Program: Scientific Results* **198** (2005).
- 505 101. C. C. von der Borch, J. G. Sclater, et al. (U.S. Government Printing Office, 1974)vol. 22 of *Initial Reports of the Deep Sea Drilling Project*.
102. T. Westerhold, U. Röhl, B. Donner, J. C. Zachos, Global Extent of Early Eocene Hyperthermal Events: A New Pacific Benthic Foraminiferal Isotope Record From Shatsky Rise (ODP Site 1209). *Paleoceanography and Paleoclimatology* **33**, 626–642 (2018).
- 510 103. G. Ravizza, R. N. Norris, J. Blusztajn, M.-P. Aubry, An osmium isotope excursion associated with the Late Paleocene thermal maximum: Evidence of intensified chemical weathering. *Paleoceanography* **16**, 155–163 (2001).
104. H. McCarren, E. Thomas, T. Hasegawa, U. Röhl, J. C. Zachos, Depth dependency of the Paleocene-Eocene carbon isotope excursion: Paired benthic and terrestrial biomarker records (Ocean Drilling Program Leg 208, Walvis Ridge). *Geochemistry, Geophysics, Geosystems* **9** (2008).
- 515 105. A. Sluijs, S. Schouten, M. Pagani, M. Woltering, H. Brinkhuis, J. S. S. Damsté, G. R. Dickens, M. Huber, G.-J. Reichart, R. Stein, J. Matthiessen, L. J. Lourens, N. Pedentchouk, J. Backman, K. Moran, Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. *Nature* **441**, 610–613 (2006).
- 520 106. A. Sluijs, H. Brinkhuis, S. Schouten, S. M. Bohaty, C. M. John, J. C. Zachos, G.-J. Reichart, J. S. S. Damsté, E. M. Crouch, G. R. Dickens, Environmental precursors to rapid light carbon injection at the Palaeocene/Eocene boundary. *Nature* **450**, 1218–1221 (2007).
107. A. K. Tripathi, H. Elderfield, Abrupt hydrographic changes in the equatorial Pacific and subtropical Atlantic from foraminiferal Mg/Ca indicate greenhouse origin for the thermal maximum at the Paleocene-Eocene Boundary. *Geochemistry, Geophysics, Geosystems* **5** (2004).
- 525 108. A. Sluijs, P. K. Bijl, S. Schouten, U. Röhl, G.-J. Reichart, H. Brinkhuis, Southern ocean warming, sea level and hydrological change during the Paleocene-Eocene thermal maximum. *Clim. Past* **7**, 47–61 (2011).

Fig. 1 Locations of sites through the PETM investigated in this study. All numbers refer to the DSDP or ODP Site identifier. Map showing a reconstructed paleogeography according to a plate rotation model (see Supplementary Materials) at 55.8 Ma (PETM). Site locations are moved consistently with the same plate model. Circles and Squares are site locations for FB- $\delta^{15}\text{N}$ measurement and FS- $p\text{O}_2$ reconstruction, respectively.

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Fig. 2. FB- $\delta^{15}\text{N}$ and foraminifera shell size changes during the PETM. (A) FB- $\delta^{15}\text{N}$ of symbiont-bearing foraminifera *Acarinina* (diamonds) and *Morozovella* (circles). In all panels but D, color reflects the relevant DSDP/ODP site (legend). (B) FB- $\delta^{15}\text{N}$ of symbiont-barren foraminifera (*Subbotina*). FB- $\delta^{15}\text{N}$ measurement precision is $\sim 0.2\text{‰}$ (1 S.D.). (C) Shell size of planktic foraminifera of *Morozovella* species for Sites 1209 and 1210, using data from (38). Red line is a 3 point interspecies moving average for both sites and shading represents 1 S.D. confidence envelope. The dataset used for this figure and additional data from other planktic foraminifera in these sites is discussed in the Supplementary Materials. (D) Size of trochospiral benthic foraminifera for Sites 1209 and 1210, using data from (37). Brown line is a 3 point moving average for both sites and shading represents 1 S.D. confidence envelope. (E) Carbonate $\delta^{13}\text{C}$ records from benthic foraminifera *Nuttallides truempyi* or *Cibicidoides* sp. $\delta^{13}\text{C}$, indicating the CIE, a common marker of the PETM (See Supplementary Materials for source data).

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Fig. 3. Comparison of near-equatorial FB- $\delta^{15}\text{N}$ data with reconstructions of low latitude stratification, global ocean denitrification change, and shallow and deep oxygen change.

(A) FB- $\delta^{15}\text{N}$ change in near-equatorial Pacific Site 865 in 3 different taxa *Morozovella* (circles),
555 *Acarinina* (diamonds) and *Subbotina* (squares). Relative abundance of eutrophic conditions
dwelling coccolithophore *Toweius sp.* from (46), suggesting a decline in nutrient supply at the
PETM. (B) Estimated changes in ratio of water column denitrification (WCD) to total
denitrification, based on an isotope budget constructed from Site 1263 FB- $\delta^{15}\text{N}$ data. (C)
560 Timeseries of estimated changes in subsurface (red) and deep ocean (brown) FS- $p\text{O}_2$ relative to
pre-PETM using the metabolic model applied to foraminifera size in subtropical Pacific Sites 1209
and 1210. Red and brown lines are 3 point moving averages, and shading represents 1 S.D.
confidence envelope. (D) Compilation of Mg/Ca- and TEX₈₆-based upper ocean temperature
changes, plotted relative to pre-PETM average values. Black line is a 9 point moving average. Red
565 line represents the upper ocean temperature reconstruction used for shallow subsurface $p\text{O}_2$
estimation in Sites 1209/1210 (See Supplementary Materials for source data).

Fig. 4. Change in ocean pO_2 from past and future climate warming (A) Vertical profile of percentage pO_2 change per degree $^{\circ}C$ of warming, estimated from the metabolic model applied to body size and temperature proxy records from foraminifera in the subtropical Pacific. Shaded curve is the range of low latitude Pacific pO_2 change from an ocean GCM, simulating the rapid warming at the PETM for a range of scenarios for the biological carbon pump efficiency (see Supplementary Materials). (B) Meridional depth section of zonally averaged pO_2 change (atm) from Earth System model projections of future warming in 2300 A.D. for SSP5-8.5 scenario (Supplementary Materials), which yield a similar vertical structure to models of the PETM.

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585 **Author contributions:** S.M. and A.M.-G. designed the study. S.M. measured foraminifera bound nitrogen isotopes in the lab of A.M.-G. C.D. developed the metabolic pO_2 model. S.M., A.M.-G and D.M.S. wrote the first draft of the manuscript. R.S. and L.G. contributed to sample preparation under the supervision of R.S.. E.T. provided sample material for Site 1263, 690. A.T. provided material for Site 685. M.R.P. provided material for Site 1210.

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590 Methodology: SM, CD, RS, LG, DMS, AMG

Investigation: SM, CD

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Resources: ET, RN, AT, PS, VL, MP, GHH, AMG

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595 Project administration: AMG

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600 **Data and materials availability:** Datasets are available in Data tables S1 and S2 at DRYAD (56).

Supplementary Materials

Materials and Methods

605 Supplementary Text

Figs. S1 to S10

Tables S1 to S5

Captions for Data S1 to S2

References (55–106)

