

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

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**Abstract:** The global ocean’s oxygen (O<sub>2</sub>) 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 65 average temperature rose by at least 5 °C (17), while atmospheric  $\text{CO}_2$  is believed to have more 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 70 oxygenation. However, the response of the ODZs during this episode of abrupt warming remains 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 ( $\text{NO}_3^-$ ) reduction in the water column, causing residual nitrate to be enriched in  $^{15}\text{N}$  (25). Circulation as well as assimilation, sinking, and regeneration propagate the  $^{15}\text{N}$ -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.  
90 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).  
95 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,  
100 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  
105 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  
110 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  
115 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  
120 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).

125 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  $\text{O}_2$  supply  
140 and demand (34). A rise in temperature increases metabolic  $\text{O}_2$  demand relative to organismal  $\text{O}_2$   
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  $\text{O}_2$  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  $\text{O}_2$  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  $\text{O}_2$  requires a decline in respiratory  $\text{O}_2$   
consumption at depth relative to the rate of circulation-driven  $\text{O}_2$  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  $\text{O}_2$  changes we observe. Changes in  $\text{O}_2$  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  $\text{O}_2$  and its mixing into the thermocline therefore was not the cause of the PETM  
increase in  $\text{O}_2$  in the tropical shallow subsurface. Warming without a change in the respiratory  $\text{O}_2$   
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  $\text{O}_2$ , 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).

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**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 TEX<sub>86</sub>-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 °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.

Conceptualization: SM, CD, DMS, AMG

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

Supervision: DMS, AMG

Writing – original draft: SM, DMS, AMG

Writing – review & editing: all authors

**Competing interests:** Authors declare that they have no competing interests.

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)

