Surviving rapid climate change in the deep sea during the Paleogene hyperthermals

Laura C. Foster^{a,1}, Daniela N. Schmidt^a, Ellen Thomas^{b,c}, Sandra Arndt^d, and Andy Ridgwell^d

^aDepartment of Earth Sciences, University of Bristol, Bristol BS8 1RJ, United Kingdom; ^bDepartment of Geology and Geophysics, Yale University, New Haven, CT 06520; ^cDepartment of Earth and Environmental Sciences, Wesleyan University, Middletown, CT 06459; and ^dSchool of Geographical Sciences, University of Bristol, Bristol BS8 1SS, United Kingdom

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Predicting the impact of ongoing anthropogenic CO₂ emissions on calcifying marine organisms is complex, owing to the synergy between direct changes (acidification) and indirect changes through climate change (e.g., warming, changes in ocean circulation, and deoxygenation). Laboratory experiments, particularly on longer-lived organisms, tend to be too short to reveal the potential of organisms to acclimatize, adapt, or evolve and usually do not incorporate multiple stressors. We studied two examples of rapid carbon release in the geological record, Eocene Thermal Maximum 2 (~53.2 Ma) and the Paleocene Eocene Thermal Maximum (PETM, ~55.5 Ma), the best analogs over the last 65 Ma for future ocean acidification related to high atmospheric CO₂ levels. We use benthic foraminifers, which suffered severe extinction during the PETM, as a model group. Using synchrotron radiation X-ray tomographic microscopy, we reconstruct the calcification response of survivor species and find, contrary to expectations, that calcification significantly increased during the PETM. In contrast, there was no significant response to the smaller Eocene Thermal Maximum 2, which was associated with a minor change in diversity only. These observations suggest that there is a response threshold for extinction and calcification response, while highlighting the utility of the geological record in helping constrain the sensitivity of biotic response to environmental change.

marine calcifiers | greenhouse gases | ecosystem stress response

Since the industrial revolution, approximately one-third of carbon dioxide (CO₂) released in the atmosphere has been absorbed by the oceans, which has resulted in a lowering of seawater carbonate saturation and a reduction of the average surface pH by 0.1 pH unit, with further reduction by 0.14–0.35 pH units predicted toward the end of the 21st century (1). Such changes in seawater chemistry are predicted to significantly affect marine calcifiers. Culturing experiments, however, have documented a complex range of responses, including dissolution of carbonate shells/skeletons, slower growth, reproductive failure, and reduced activity (1), which makes specific predictions difficult. Evaluating the potential impact of ocean acidification on whole ecosystems is even more complicated, because acidification acts synergistically with other stressors such as global warming and deoxygenation, and competitive advantage/disadvantage is difficult to forecast. In addition, ocean acidification occurs progressively and on a century time scale—much longer than can be replicated in the laboratory. Experiments, particularly on longer-lived organisms, hence tend to be too short to detect the potential for organisms to acclimatize, adapt, or evolve in response to changing environments and cannot predict which traits are most useful. In contrast, the geological record of rapid carbon release may function as an analog for our next century and allows us to examine long-term adaptative strategies of organisms to multiple stressors.

During the hyperthermals of the Paleocene and Eocene (65.5–33.7 Ma), isotopically light carbon was rapidly released into the ocean–atmosphere system, leading to global warming and deep-sea carbonate dissolution (2). The most prominent of these, the Paleocene Eocene Thermal Maximum (PETM, ~55.5 Ma), has

been cited as one of the best analogs for the future (3), although such events are likely to represent only minimum estimates of future biotic and ecosystem changes because the rate of change in surface saturation during the PETM probably was an order of magnitude lower than the present and future rate (4). The release of isotopically light carbon during the PETM resulted in rapid (<10,000 y) global warming with a maximum temperature increase of the surface ocean locally as large as 9–10 °C and of the deep sea 4–5 °C (5–9). The warming led to migration of low-latitude species toward higher latitudes and fast evolutionary turnover (10, 11). The carbon input caused a global negative Carbon Isotope Excursion (CIE) of >2.5‰ (6) and lowered ocean pH and carbonate ion concentration ([CO₃²⁻]), resulting in a rapid shoaling of the Calcite Compensation Depth (CCD) (2). Associated with this global perturbation were a range of biotic changes, most prominently in deep-sea benthic foraminifera, which experienced their only significant global extinction (35–50%) in the last 90 million years (9). Marine calcifying plankton (foraminifera and calcareous nannoplankton), in contrast, did not suffer severe extinction, despite the rapid, in part transient, evolutionary turnover, and carbonate production by nannoplankton may not have been significantly affected (12).

Eocene Thermal Maximum 2 (ETM-2, ~53.2 Ma) occurred about 2 million years after the PETM and provides the opportunity for a comparative study, because it is qualitatively similar to the PETM, with only about half its magnitude (13). Benthic foraminiferal assemblages declined in diversity with postexcursion assemblages similar to the low-diversity post-PETM ones (13–15), but without significant extinction. Carbonate dissolution occurred and the lysocline rose, but the CCD did not shoal to (or beyond) the depth of the sites in the southeast Atlantic where dissolution was complete during the PETM (16). The geological record thus provides an ideal opportunity to assess the sensitivity of marine organisms to contrasting magnitudes of global warming, ocean acidification, and related stressors, thereby assessing potential future thresholds for adaptation and acclimatization.

To examine the response of benthic foraminifera to hyperthermal environmental changes, we selected samples from Ocean Drilling Program (ODP) sites 1262 (27°11.15'S, 1°34'2'E) and 1263 (28°31.98'S, 2°46.77'E) on Walvis Ridge (southeastern Atlantic Ocean), paleodepths 3.5 and 1.5 km, respectively. We combined assemblage analysis with synchrotron radiation X-ray tomographic microscopy (SRXTM) at the Tomographic Microscopy and Coherent Radiology Experiments (TOMCAT) beamline at the Swiss Light source, Paul Scherrer Institute to generate high-resolution (0.37 μm), 3D images of specimens of two deep-sea benthic

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¹To whom correspondence should be addressed. E-mail: l.c.foster@bristol.ac.uk.

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15 keV with UPLAPO 20× objective (numerical aperture 0.7; field view of $0.75 \times 0.75 \mu\text{m}^2$; pixel size $0.37 \times 0.37 \mu\text{m}^2$). A total of 61 specimens were scanned. The exposure time ranged between 300 and 400 ms. Projections were rearranged into corrected sinograms and reconstructed using optimized fast Fourier transform transformations and gridding procedures (37). The final data were exported as TIFF images (8-bit, 2×2 binned). Further processing to produce 3D isosurface and sample thickness was done using Avizo software. Size normalization for the penultimate chamber was done by measuring the maximum width of the foraminifera. For the volume

normalization, the volume of calcite and the overall volume of the foraminifera were calculated.

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