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RESEARCH ARTICLE

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Planktic Foraminiferal Resilience to Environmental Change Associated With the PETM

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Key Points:

- No substantial change in planktic foraminiferal carbonate production (size-normalized weight, test size, or abundance) during the Palaeocene-Eocene Thermal Maximum
- Sea surface warming and the resulting migration of taxa increased carbonate production in the Southern Ocean
- Pelagic carbonate composition changes due to differing impacts on foraminifers and coccolithophores which we link to nutrient availability

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Carbonate-forming organisms play an integral role in the marine inorganic carbon cycle, yet the links between carbonate production and the environment are insufficiently understood. Carbonate production is driven by the abundance of calcifiers and the amount of calcite produced by each individual (their size and weight). Here we investigate how foraminiferal carbonate production changes in the Atlantic, Pacific and Southern Ocean in response to a 4–5°C warming and a 0.3 surface ocean pH reduction during the Palaeocene-Eocene Thermal Maximum (PETM). To put these local data into a global context, we apply a trait-based plankton model (ForamEcoGENIE) to the geologic record for the first time. Our data illustrates negligible change in the assemblage test size and abundance of foraminifers. ForamEcoGENIE resolves small reductions in size and biomass, but these are short-lived. The response of foraminifers shows spatial variability linked to a warming-induced poleward migration and suggested differences in nutrient availability between open-ocean and shelf locations. Despite low calcite saturation at high latitudes, we reconstruct stable foraminiferal size-normalized weight. Based on these findings, we postulate that sea surface warming had a greater impact on foraminiferal carbonate production during the PETM than ocean acidification. Changes in the composition of bulk carbonate suggest a higher sensitivity of coccolithophores to environmental change during the PETM than foraminifers.

1. Introduction

Calcifying organisms are key in regulating the marine carbon cycle via the production and subsequent burial of their calcium carbonate exoskeleton (CaCO₃; Ridgwell & Zeebe, 2005). In the modern ocean, planktic foraminifers contribute 23%–56% of pelagic carbonate production and 32%–80% of total CaCO₃ flux to the sea floor (Buitenhuis et al., 2013; Schiebel, 2002), alongside coccolithophores and pteropods. This marine carbon sink is considered vulnerable to environmental change through sensitivity to warming and changes in carbonate chemistry (Cooley et al., 2022), but the links are insufficiently understood. Carbonate production is driven by the abundance of calcifiers and the amount of calcite produced by each individual (their size and weight; see Text S3 in Supporting Information S1). Warming influences organisms directly via physiological processes (e.g., metabolism) and indirectly via physical oceanographic changes (e.g., sea surface stratification increasing oligotrophy). However, what drives an individual's carbonate production is heavily debated (Beer et al., 2010; Davis et al., 2013; de Moel et al., 2009; de Nooijer et al., 2009; Henehan et al., 2017; Weinkauf et al., 2013, 2016).

The amount of calcite produced by each individual is often reconstructed as size-normalized weight (SNW), which has been postulated to be lower in response to ocean acidification as calcification is more energy intensive in seawater with a lower pH (Beer et al., 2010; de Nooijer et al., 2009; Henehan et al., 2017). However, several studies found no evidence for dependency on the carbonate system in specific taxa and regions. Instead, they emphasize the importance of temperature and productivity in modulating calcification (de Moel et al., 2009; Weinkauf et al., 2013, 2016), as well as species-specific responses to the carbonate system (Beer et al., 2010; Foster et al., 2013; Henehan et al., 2017).

Foraminiferal abundance, biogeography and test size are a function of sea surface temperature (SST) and food availability. Abundance is greatest in high productivity settings (Bé & Tolderlund, 1971). Biogeography shows a strong temperature sensitivity, with species already shifting poleward in response to anthropogenic warming (Beaugrand et al., 2013; Field et al., 2006; Jonkers et al., 2019; Pörtner et al., 2014). Additionally,

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food and light availability modulate the composition of foraminiferal assemblages. Oligotrophic, open-ocean gyres are dominated by spinose species. In upwelling zones these are replaced by non-spinose asymbiotic taxa (Anderson et al., 1979; Schiebel & Hemleben, 2017). While for many species size is largest at their optimal conditions (Schmidt, Renaud, et al., 2004; Schmidt, Thierstein, & Bollmann, 2004; Schmidt et al., 2006), some taxa have shown no relationship with food, temperature, or abundance (Rillo et al., 2020). Irrespective, it is agreed that low-latitude and symbiont bearing species are generally larger today than those without symbionts (Schmidt, Renaud, et al., 2004; Schmidt, Thierstein, & Bollmann, 2004; Schmidt et al., 2006). Such differences between taxa appear to persist through time as during the Palaeogene, *Morozovella* and *Acarinina* are larger than their asymbiotic counterparts, *Subbotina* (Petruzzo, 2007). Additionally, the temperature sensitivity of the symbiont could result in warming-induced bleaching which exacerbates a decrease in individual and assemblage test size as shown in laboratory experiments with symbiont elimination (Bé et al., 1982).

While important insights have been gained from experiments which assess the impacts of acidification and warming on this important pelagic calcifier (Henehan et al., 2017; Russell et al., 2004), these experiments do not assess the potential for acclimation and species replacement to fulfill the function of foraminifera in the inorganic carbon cycle. To address this gap, we reconstruct the planktic foraminiferal record during a geological period of warming, acidification, and changes in productivity. The Palaeocene-Eocene Thermal Maximum (PETM) is characterized by a massive release of isotopically light carbon around 56 Ma ago (Dunkley Jones et al., 2013). This led to a sea surface pH decline of ~0.3 pH (Babila et al., 2018; Gutjahr et al., 2017; Penman et al., 2014) and sea surface warming of 4–5°C (Dunkley Jones et al., 2013; Gutjahr et al., 2017; Inglis et al., 2020; Zachos et al., 2003) over ≤5 Kyr (Haynes & Hönisch, 2020; Kirtland Turner, 2018; Kirtland Turner et al., 2017). Increased stratification due to warming resulted in widespread open-ocean oligotrophy (Bralower, 2002; Kelly et al., 1998; Petruzzo, 2007). Intensified weathering increased nutrient runoff in coastal regions, thereby enhancing local productivity (Bains et al., 2000; Gibbs et al., 2006; Stoll & Bains, 2003; Thomas & Shackleton, 1996). Physiological impacts such as bleaching in foraminifers (Shaw et al., 2021) and a reduction in calcification for coccolithophores (O’Dea et al., 2014) have been described. However, most previous analyses of the ecological response of foraminifers to the PETM focused on presence-absence changes which describe turnover and local diversity modifications as species moved poleward and “excursion” taxa emerged (Kelly et al., 1996; Speijer et al., 2012). Research considering the wider implications of a reorganization of the planktic ecosystem in response to the PETM is limited.

Here we investigate how the PETM environment impacted foraminiferal carbonate production by reconstructing their abundance, individual size, and weight (see Text S3 in Supporting Information S1 for a detailed explanation of how we conceptualize carbonate production). We generate foraminiferal data from tropical, mid latitude, and polar ocean sites. To put these local data into a global context, we apply an ecosystem model for asymbiotic planktic foraminifers—ForamEcoGenIE—to the geologic record for the first time. The model provides an independent but complementary prediction of the foraminiferal response to warming and can disentangle the impact of warming on oceanography (nutrient distribution) from the direct impact on plankton physiology (growth and grazing rate).

Based on the literature described above we hypothesise that: (a) warming induced a poleward migration of larger taxa, thus increasing size at high latitudes; (b) warming decreased assemblage test size at low latitudes due to symbiont bleaching reducing the size of individuals and/or increasing the relative abundance of smaller, symbiont-barren species; and (c) ocean acidification decreased SNW. Furthermore, our approach allows us to not only look at foraminiferal carbonate production but also separate whether foraminifers responded to the warming impact on nutrients or physiology. We also assess the differing vulnerabilities of the main carbonate producers.

2. Materials and Methods

2.1. Materials

To investigate spatial and temporal trends in the planktic foraminiferal response across the PETM, we analyzed samples from three ocean sites (Figure 1): the tropical Pacific Ocean Drilling Program (ODP) Site 1209; Southern Ocean ODP Site 1135; and North Atlantic Integrated Ocean Drilling Program (IODP) Site U1409. Overall,

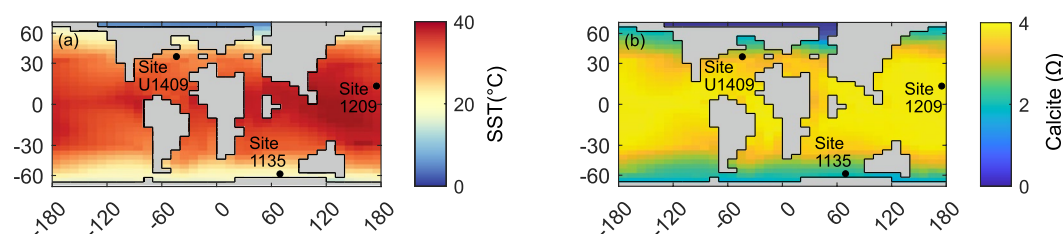


Figure 1. Site locations superimposed on modeled sea surface temperature and calcite saturation state for the peak-PETM (see Figure S7 in Supporting Information S1) as resolved by ForamEcoGENIE.

modeled calcite saturation is very high with the lowest values at the high latitudes (Figure 1b). The age model for Site 1209 follows Westerhold et al. (2018), for Site 1135 Jiang and Wise (2009), and for Site U1409 Penman et al. (2016). Samples were chosen relative to the Carbon Isotope Excursion (CIE) and represent Pre-CIE, CIE, CIE recovery and Post-CIE. At Site 1135 a 4 m core gap precludes the CIE (Figure S6 in Supporting Information S1), resulting in limited pre-CIE samples. Average sedimentation rate is 0.41 cm/kyr at Site 1209, 0.40 cm/kyr at Site 1135, and 0.62 cm/kyr at U1409; this results in an average sampling resolution of 21, 13, and 10 kyr per sample, respectively.

2.2. Methods

2.2.1. Foraminiferal Ecology: Abundance and Accumulation

31 samples from Site 1209, 93 samples from Site U1409, and 75 samples from Site 1135 were washed over a 63 μm sieve to separate the coarse (foraminiferal) fraction from the fine (nanofossil) fraction. Although sieving at this size fraction may reduce the abundance of smaller taxa such as *Globanomalina*, *Chiloguembelina*, *Igorina*, these are rare (Petruzzo, 2007) compared to *Morozovella*, *Acarinina*, and *Subbotina* which dominate PETM assemblages.

Bulk accumulation ($\text{g}/\text{cm}^2/\text{kyr}$) is derived from the linear sedimentation rate (cm/kyr) and dry bulk density (g/cm^3). Carbonate accumulation ($\text{g}/\text{cm}^2/\text{kyr}$; Equation 1) is the product of bulk accumulation ($\text{g}/\text{cm}^2/\text{kyr}$) and % carbonate (% CaCO_3 ; Bralower et al., 2002; Coffin et al., 2000; Norris et al., 2014).

$$\text{Carbonate Accumulation} = \text{Bulk accumulation} \times \text{wt\% CaCO}_3 \quad (1)$$

Foraminiferal accumulation rate (FMAR; $\text{g}/\text{cm}^2/\text{kyr}$; Equation 2) is a function of their carbonate production (individual test size, individual weight, and collective abundance) minus dissolution related loss.

$$\text{Foram Mass Accumulation Rate (FMAR)} = \frac{\text{Carbonate accumulation} \times \text{Coarse Fraction \%}}{100} \quad (2)$$

FMAR is calculated from the coarse fraction contribution to bulk carbonate accumulation and assesses whether changes in foraminiferal relative contribution are driven by changes in foraminifers or a change in dilution by nanofossils (primarily coccolithophores). The relative abundance of foraminifers to coccolithophores was calculated as the coarse fraction to fine fraction ratio of bulk carbonate. Analysis of smear slides at 1000X magnification with oil immersion confirmed that the fine fraction ($<63 \mu\text{m}$) was primarily composed of coccolithophores (Figure S15 in Supporting Information S1), and not broken fragments of foraminifers or authentic calcite; therefore we use the fine fraction accumulation as a proxy for coccolithophore carbonate production. Published data (Bralower et al., 2002; Norris et al., 2014) and manual checks of the images used to generate foraminiferal size data confirmed the rarity of benthic foraminifers at Site 1209, U1409 and 1135, thereby negating any impact on size or bulk weight. Therefore, FMAR represents planktic foraminiferal accumulation.

For subsequent analyses, coarse fraction samples were dry sieved at 150 μm . Fragmentation was assessed by determining the ratio of broken versus whole foraminiferal specimens of 200 specimens in an aliquot of the population, following the method of Le and Shackleton (1992). Foraminifers at Site U1409 are strongly dissolved

during the CIE (Figure 2b). As dissolution post-deposition can artificially alter size trends, the corresponding data for the CIE at U1409 is omitted from analysis. At Site 1209 and 1135, test dissolution is minimal as indicated by fragmentation consistently remaining below 20% (Figure 2b). Minimal fragmentation at Site 1209 during the CIE contrasts published data (Zachos et al., 2003) which records up to 60% fragmentation. Our samples were recounted and fragmentation remained below 20%. Differences between our data and the published (Zachos et al., 2003) could be due to differences in fragmentation susceptibility of samples that are >125 μm and >150 μm.

2.2.2. Foraminiferal Carbonate Production: Assemblage Test Size and Size-Normalized Weight (SNW)

Planktic foraminiferal assemblage test size was determined using automated microscopy following Bollmann et al. (2004). The >150 μm samples were split to aliquots of 1,000–3,000 specimens, imaged at 160X magnification and the morphological parameters of each specimen were extracted in Olympus Stream Motion. To remove foraminiferal and lithic fragments from analyses, parameters were set to exclude particles with a maximum diameter smaller than 150 μm, sphericity lower than 0.5 and mean gray value below 80. We acknowledge that this sphericity parameter removed *Chiloguembelina* from assemblage size counts. However, these contribute little to the total assemblage (e.g., <4% abundance at any given time at Site 1209; Petrizzo, 2007). The rare benthic foraminifers were removed via manual assessment of all images. The 95th percentile of the maximum diameter was calculated for the remaining material (Schmidt et al., 2004a, 2004b), of which the average repeat measurement error is ~3 μm (Schmidt et al., 2003; Todd et al., 2020).

To explore the impact of changes in the carbonate system on calcification, the size-normalized weight (SNW) of *Morozovella subbotinae* and *Subbotina patagonica* was calculated (Equation 3) following the approach established by Barker and Elderfield (2002). These species were selected due to their wide distribution, abundance, and different ecologies. *M. subbotinae* is a symbiont bearing surface dweller, while *S. patagonica* is a thermocline dwelling asymbiotic taxa (Pearson et al., 2006). To assess for post depositional in-fills or dissolution that may compromise weight measurements, selected specimens were broken and observed under the HITACHI S-3500N scanning electron microscope (SEM) at the University of Bristol. Samples were analyzed at a working distance (WD: distance between the sample surface and lower end of electron carrier pole) range of 15.1–15.6 mm at 25 kV. We excluded Site U1409 from this analysis due to the severe dissolution as shown by high fragmentation (Figure 2b). The SEM result indicated post-diagenetic infilling for most of the specimens at Site 1209 (see Text S1 in Supporting Information S1; Figures S1a–S1f in Supporting Information S1). These SNW data are compromised and are not discussed any further. Although there are differences in preservation and the test walls are recrystallized, the foraminifers Site 1135 are cleaner (Figure S1g–S1k in Supporting Information S1). As such, we carried out SNW analysis here.

For Site 1135, 10 specimens of each species were picked from the 250–300 μm size fraction and weighed using a Mettler Toledo balance (sieve-based weight; SBW). These 10 specimens were oriented along their maximum length and their diameter was measured using Olympus Stream Motion. The average weight of specimens in a sample was calculated and size-normalized (Equation 3).

$$\text{SNW}_{\text{diameter}} = \frac{\text{Mean SBW}_{\text{sample}} \times \text{Mean diameter}_{\text{size fraction}}}{\text{Mean diameter}_{\text{sample}}} \quad (3)$$

2.3. ForamEcoGenIE

2.3.1. Model Structure

ForamEcoGenIE is an extension of the size-structured, trait-based, 3-D plankton ecosystem model, “EcoGenIE” (Ward et al., 2018; Wilson et al., 2018), which is embedded in the carbon-centric Earth system model of intermediate complexity, “cGENIE” (Ridgwell et al., 2007). cGENIE is implemented on a 36 × 36 horizontal grid and a 16 vertical layer ocean with non-uniform depth spacing. ForamEcoGenIE can model the large-scale properties of ocean circulation, resolving nutrient distribution and plankton biogeography (see Text S2 and S4 in Supporting Information S1; Figures S4 and S5 in Supporting Information S1).

In EcoGENIE, plankton are defined as either phytoplankton or zooplankton of different cell sizes. Cell size determines key traits such as growth and grazing rates via allometric scaling (Ward et al., 2012). Phytoplankton are limited by light and phosphorus, while zooplankton growth is a function of prey density and size. ForamEcoGENIE builds on the EcoGENIE food web and resolves asymbiotic planktic foraminifera (hereafter, foraminifers) based on the parameterization by Grigoratou et al. (2019; see Text S2 in Supporting Information S1). Further to the published model of Grigoratou et al. (2019), we resolved two additional size classes of foraminifera. These represent the juvenile (19 μm) and neanic (60 μm) specimens, alongside the previously resolved adult (190 μm) specimens (Table S1 in Supporting Information S1).

Only symbiont-barren foraminifers are resolved due to the difficulty in parameterizing symbiosis (Grigoratou et al., 2019; Grigoratou, Monteiro, Ridgwell, et al., 2021). Considering that Paleogene species lacked “true spines” in the modern sense (i.e., protrusions from the test during the Paleogene were much shorter than spines in modern species), we did not aim to represent spines by implementing a change in surface area to volume ratio as in Grigoratou, Monteiro, Ridgwell, et al. (2021). Consequently, we do not delineate between spinose and non-spinose taxa here.

Furthermore, we do not explicitly represent the calcification process and how it interacts with ocean acidification due to the limited understanding of its traits and trade-offs. Instead, foraminifera are based on the same parameterization as zooplankton but with additional costs and benefits associated with the test. For example, calcification is represented by a reduced growth rate due to the energetic cost (10%–50%) of producing a test. Benefits include reduced mortality due to protection from predation and infection (Grigoratou et al., 2019). By representing calcification through cost-benefit rather than explicitly modeling it, this reduces uncertainty associated with the complex and not well understood environmental factors affecting the process. As we do not explicitly model foraminiferal calcification and its link to the environment, we do not represent or assess interactions of pelagic carbonate production with deep-sea input or the input of weathering products. However, we do qualitatively compare the change in calcite saturation state modeled by cGENIE and its inbuilt carbon cycle to changes in foraminiferal carbonate production that we reconstructed from the fossil record (e.g., SNW).

To test ForamEcoGENIE with the novel size structure, model performance in the modern ocean was assessed against foraminiferal abundance data from plankton tows (Bé & Tolderlund, 1971; see Text S4; Figure S4 in Supporting Information S1). ForamEcoGENIE successfully reproduces the biomass and size distribution of modern asymbiotic non-spinose foraminifera (Figure S4 and S5 in Supporting Information S1). The biomass distribution resulting from the novel size structure is comparable to that published for one size class (Grigoratou, Monteiro, Wilson, et al., 2021). More information on the ForamEcoGENIE structure is provided in Supporting Information S1. Although we test ForamEcoGENIE performance in the modern, the model is applicable to past climates as the plankton parameterization is trait-based and therefore does not rely on prescribed characteristics as other models do. The non-foraminiferal part of the model, EcoGENIE, has successfully been applied to the Warm Early Eocene Climate (Wilson et al., 2018), providing support for its power in reconstructing past ecosystems.

It is important to note that the current version of ForamEcoGENIE exclusively models asymbiotic taxa, and thus does not assess the important trait of symbiosis of the Palaeogene taxa *Morozovella* and *Acarinina*. It considers many of the characteristics of Paleogene foraminifera though, including the cost and benefits of their test formation, as well as competition within the plankton ecosystem. Despite this limitation, ForamEcoGENIE allows us to measure global changes in biomass and size of asymbiotic planktic foraminifera and disentangle the impact of warming on oceanography (nutrients) from the direct impact on plankton physiology (growth and grazing rate).

2.3.2. Model Experiments

ForamEcoGENIE was spun-up to steady-state from initial conditions for 10,000 years using the boundary conditions for a late Palaeocene early Eocene climate (Ridgwell & Schmidt, 2010) and ecosystem parameters from Ward et al. (2018) and Grigoratou et al. (2019). As in Wilson et al. (2018), the ecosystem model does not include an iron cycle (see Text S4 and Figure S3 in Supporting Information S1) or sediments (i.e., no land-sea weathering interaction). This spin-up formed the starting point for the transient PETM experiment. A time-varying trajectory of atmospheric CO_2 was prescribed as per Gutjahr et al. (2017) who simulated the trajectory by

assimilating sea surface pH and carbon isotope records to constrain carbon sinks and sources across the PETM using cGENIE.

Model outputs are presented for the “peak PETM” (maximum $p\text{CO}_2$ and SST, minimum pH and surface ocean $\delta^{13}\text{C}$) and after the PETM (200 Kyr after the initial perturbation; hereafter “post PETM”; Figure S7 in Supporting Information S1). We infer changes in foraminiferal carbonate production in response to warming by analyzing changes in asymbiotic foraminiferal size (biomass-weighted geometric mean foraminiferal cell size; μm) and biomass (mmol C m^{-3} ; see Text S3 in Supporting Information S1); the latter being indicative of abundance and biogeography. These changes are presented relative to the first time slice of the PETM (time = 0 kyr; hereafter “pre-CIE”).

To investigate what drives asymbiotic foraminiferal biomass and size, we separate the impact of warming on ocean circulation (i.e., nutrient distribution) from the direct impact of warming on foraminifers (i.e., on their physiology; growth and grazing rate). To do this we run an additional experiment where the plankton ecosystem is separately forced with cooler “pre CIE” SSTs whilst the BIOGEM module continues to be forced with the CO_2 trajectory from Gutjahr et al. (2017) which observes the warmer PETM temperatures.

3. Results

3.1. Stability of Foraminiferal Carbonate Production During the PETM

Across our sites and through time, foraminiferal carbonate production remained more stable than anticipated for the PETM. We explored the drivers of foraminiferal carbonate production by examining changes in foraminiferal abundance (CF % and FMAR), assemblage test size and size-normalized weight (SNW). We omitted the CIE at Site U1409 from analysis due to post-depositional dissolution of foraminifers (79% fragmentation during the CIE; Figure 2b). At Site 1209 and 1135, test fragmentation consistently remained below 20% (Figure 2b).

Across the entire PETM record, assemblage test size followed the expected latitudinal trend, with average test size increasing from the poles (320.89 μm) to the tropics (408.32 μm ; Table S3 in Supporting Information S1). Size was significantly smaller at the high latitude Site 1135 than at the low and mid latitude sites ($p < 0.001$), but similar between Sites 1209 and U1409 ($p > 0.05$; Figure 2c, Table S3 in Supporting Information S1).

Against expectation, size changed minimally during the CIE (Figure 2c). Although size at Site 1209 increased at this time, this change is within the range of pre PETM variability. In contrast, at Site 1135 we observed a small increase in size of 16.93 μm relative to pre CIE (Table S4 in Supporting Information S1). However, it is important to note that pre CIE data for Site 1135 is predominantly 1000 Kyr before the onset due to a 4 m core gap.

A decrease in SNW was expected during the PETM in response to ocean acidification. At Site 1135 the SNW of *M. subbotinae* ranges from 11.91 to 15.54 μg and for *S. patagonica* from 10.49 to 16.04 μg (Figure 2d). Although some infilling by calcareous nanofossils may artificially increase SNW at Site 1135, this impact would be minimal (see Text S1 in Supporting Information S1). Irrespective, despite widespread ocean acidification in the surface ocean, calcification continued at Site 1135 and SNW exhibits little variability during the PETM (Figure 2d).

3.2. Stability in the Foraminiferal Contribution to Bulk Carbonate

Across the length of the record and across different sites, foraminifers consistently contributed less to pelagic carbonate (1%–21%) than nanofossils (Figure 2e). At Site 1135 the foraminiferal contribution to bulk carbonate remained stable through time—as indicated by negligible change in foraminiferal percent (CF%) and FMAR during the CIE ($14.80\% \pm 1.78$; $0.08 \text{ g/cm}^2/\text{kyr} \pm 0.01$) compared to before the CIE ($13.00\% \pm 3.22$; $0.09 \text{ g/cm}^2/\text{kyr} \pm 0.02$; Figures 2e and 2f; Table S4 in Supporting Information S1). Both stable CF% and FMAR suggest that the coccolithophore contribution did not change strongly at Site 1135.

In contrast, at Site 1209 the relative contribution of foraminifers to bulk carbonate is higher during the CIE ($12.51\% \pm 2.23$) than before ($3.87\% \pm 1.95$; $p < 0.01$; Figure 2e; Table S4 in Supporting Information S1). This relative change is driven by a decrease in the nanofossil contribution to bulk carbonate during the CIE, as

indicated by an increase in CF% yet a stable FMAR (Figures 2e and 2f). During the CIE recovery at Site U1409, FMAR more than doubles relative to Pre-CIE accumulation (Pre-CIE: $0.05 \text{ g/cm}^2/\text{kyr} \pm 0.03$; CIE Recovery: $0.15 \text{ g/cm}^2/\text{kyr} \pm 0.03$; Table S4 in Supporting Information S1; $p < 0.05$; Figure 2f), whilst the relative foraminiferal contribution to total sediment (CF%), remains more stable (Figure 2e). This decoupling implies that both foraminifers and nannofossils at Site U1409 increased their abundance and/or weight during the CIE recovery.

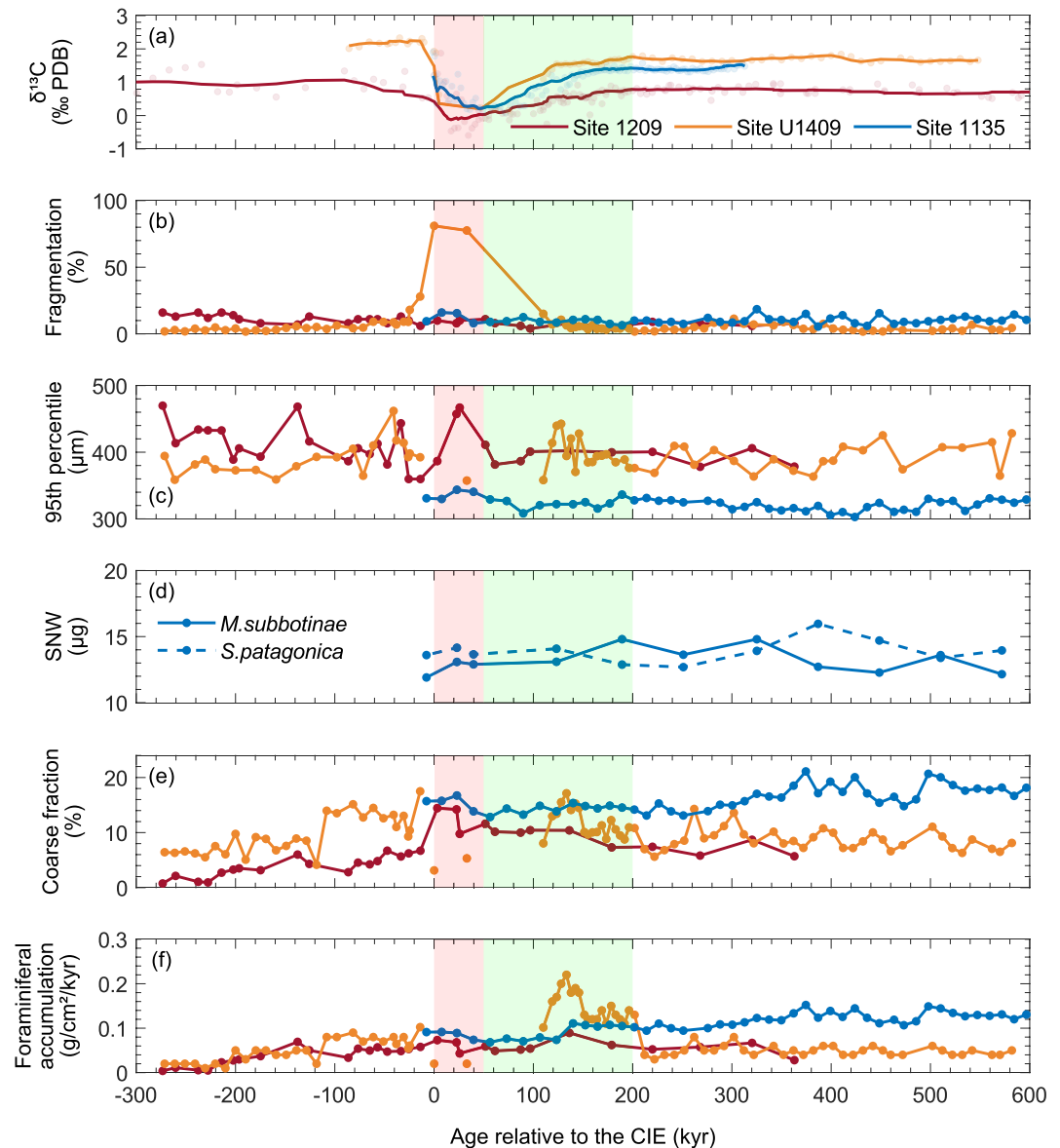


Figure 2. The planktic foraminiferal record at Sites 1209, U1409 and 1135 across the PETM CIE (red highlight) and CIE recovery (green highlight). (a) Carbon isotope ($\delta^{13}\text{C}$ [‰]) records for Site 1135, 1209 and U1409 from Jiang and Wise (2007), Westerhold et al. (2018), and Penman et al. (2016) respectively; negative values indicate the carbon isotope excursion (CIE) (b) Planktic foraminiferal fragmentation (%); higher values indicate greater dissolution post deposition. (c) 95th percentile of the maximum diameter (μm); measuring foraminiferal assemblage size (d) The size-normalized weight (SNW; μg) of *M. subbotinae* and *S. patagonica*. (e) Coarse Fraction (%); relative contribution of foraminifers to bulk carbonate; (f) Foraminiferal accumulation rate ($\text{g/cm}^2/\text{kyr}$); higher accumulation indicates an increased flux of foraminiferal carbonate to the sea floor. *N.B.* Discrete datapoints for Site U1409 correspond to periods of high fragmentation, therefore these data were omitted from analysis. For Site 1135 there is a 4-m core recovery gap precluding the PETM; for extended pre-CIE Site 1135 data see Figure S6 in Supporting Information S1.

3.3. Scaling Up to Global Impacts: Modeled Response of Foraminiferal Carbonate Production and the Wider Planktic Ecosystem to PETM Environmental Change

ForamEcoGENIE provides an independent method to predict the global-scale response of asymbiotic foraminifera to environmental and ecological change during the PETM. Foraminiferal size (Figure 3a) and biomass (Figure 3b) covary with changes in overturning stream function (ocean circulation strength; Figure 3d) and POC flux (nutrient availability; Figure 3e). An initial weakening of ocean circulation strength is mirrored by a reduction in nutrient flux from the surface ocean (Figures 3d and 3e). At the same time, average global foraminiferal size and biomass decline below pre-CIE values (Figures 3a and 3b, Table 1). After this initial perturbation, average global planktic foraminiferal size is larger than before the CIE. This is driven by the

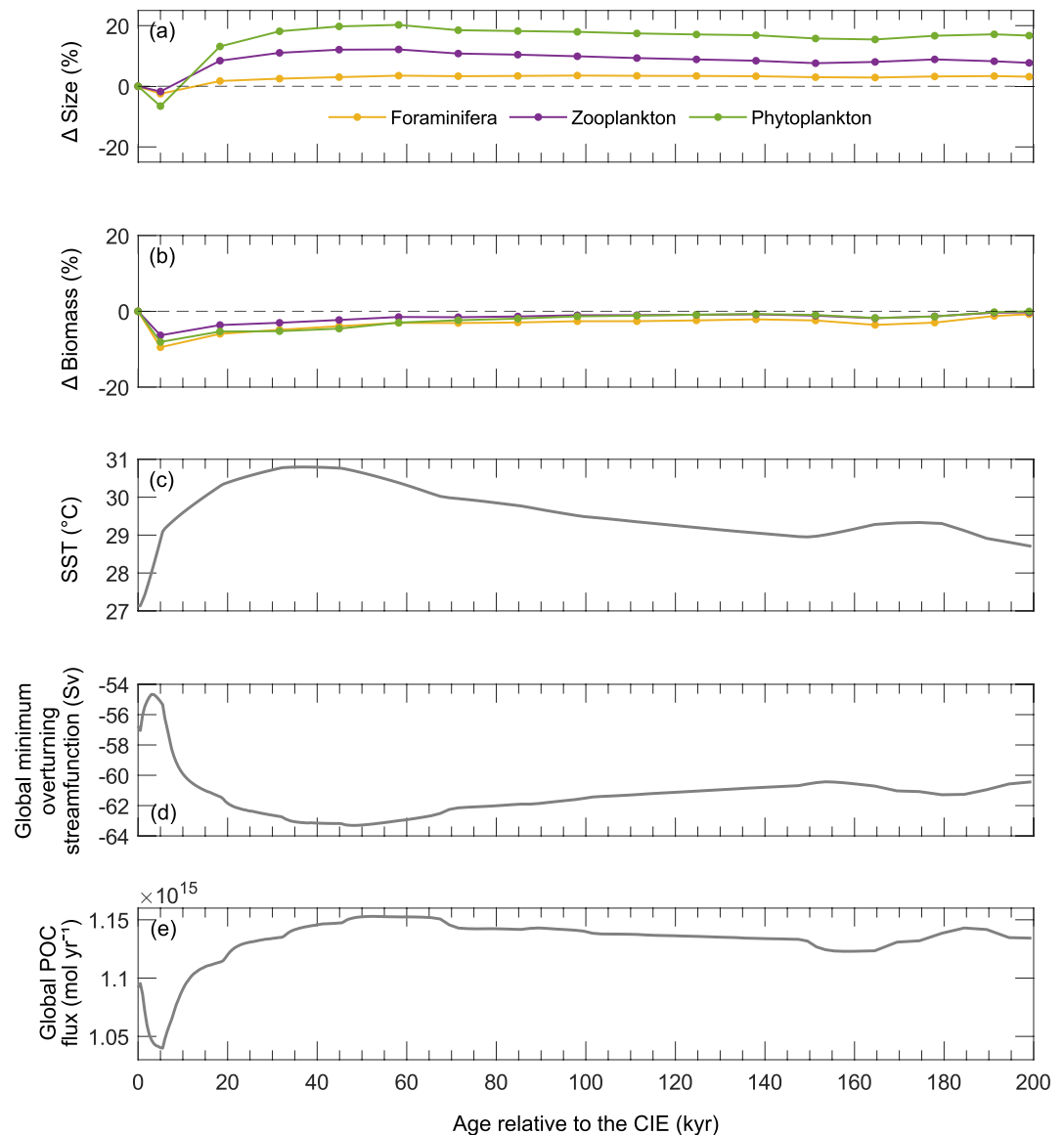


Figure 3. Timeseries showing the percent change ($\Delta\%$) in average global (a) size and (b) biomass of asymbiotic foraminifers, zooplankton and phytoplankton from the CIE onset to post-PETM as resolved by ForamEcoGENIE. Percentage change is relative to the first timeslice of the PETM experiment (“Pre-CIE”; dashed line). *N.B.* “Zooplankton” does not include planktic foraminifers. Model timeseries for (c) sea surface temperature ($^{\circ}\text{C}$) (d) Global minimum overturning streamfunction (Sv) and (e) Global particulate organic carbon flux (mol yr^{-1}).

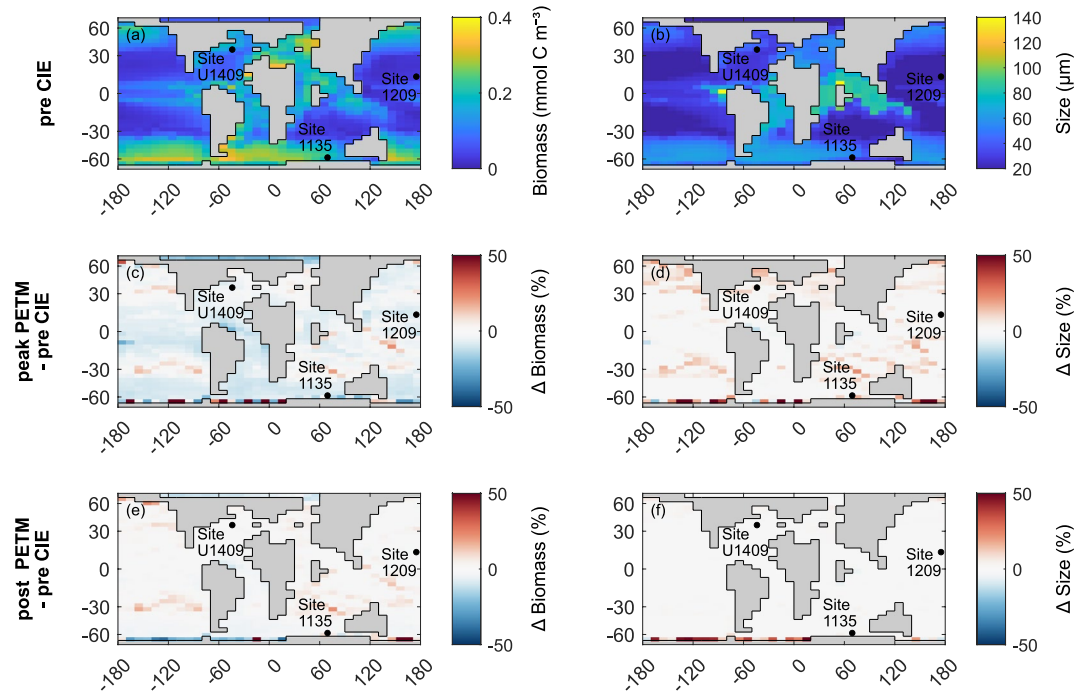


Figure 4. Top panels show absolute values for asymbiotic foraminiferal biomass (a) and size (b) during the pre CIE. Relative anomaly (Δ) in foraminiferal biomass (c, e) and size (d, f) during the peak PETM (middle panels) and 200 kyr after the initial perturbation “post-PETM” (bottom panels), relative to the “pre CIE”.

size increase south of 60° and at the edge of frontal zones relative to pre-CIE (Figures 4d and 4f). Although foraminiferal biomass does not fully recover to pre-CIE stocks, average global losses are less than 5% 30kyrs into the PETM (Figure 3b). Though much of the world observes minor decreases in foraminiferal biomass during the peak PETM, these are largely offset by a strong biomass increase south of 60° and at the edge of frontal zones (Figure 4c, Figures S11 and S12 in Supporting Information S1). Phytoplankton and zooplankton follow the same trend as foraminiferal size, but the magnitude of change is greater (especially for phytoplankton; Figure 3a; Table S5 in Supporting Information S1). Global biomass of the three plankton functional types near track each other (Figure 3b).

3.4. Disentangling the Impact of Warming on Ocean Circulation From Foraminiferal Physiology

We separate the impact of warming on ocean circulation (i.e., nutrient distribution) from the impact of warming directly on asymbiotic foraminifera (i.e., on their physiology; growth and grazing rate; Figure 5). The small global biomass reduction is predominantly driven by losses associated with the temperature-sensitivity of the ecosystem (Figure 5e). However, this reduction is offset by circulation driving an increase in foraminiferal biomass, particularly at the edge of frontal systems (Figures 5a and 5c). Similarly, at the low latitudes the combined impact of circulation driven size change (Figure 5d) and ecologically driven size change (Figure 5f) result in no net change (Figure 5b). Whereas, the size and biomass increase south of 60° is driven by the ecological response to warming (Figures 5e and 5f).

Table 1

Global Anomaly ($\Delta\%$) of Asymbiotic Foraminiferal Biomass and Size, as Modeled by ForamEcoGenIE

Global anomaly	Peak PETM–Pre CIE	Post PETM–Pre CIE
<i>Asymbiotic planktic foraminifers</i>		
Δ Total Biomass (%)	−4.88	−0.78
Δ Mean Size (%)	+2.51	+3.16

Note. Anomalies calculated for the peak PETM and post PETM are relative to the first time slice of the PETM experiment (“pre CIE”; Figure S7 in Supporting Information S1).

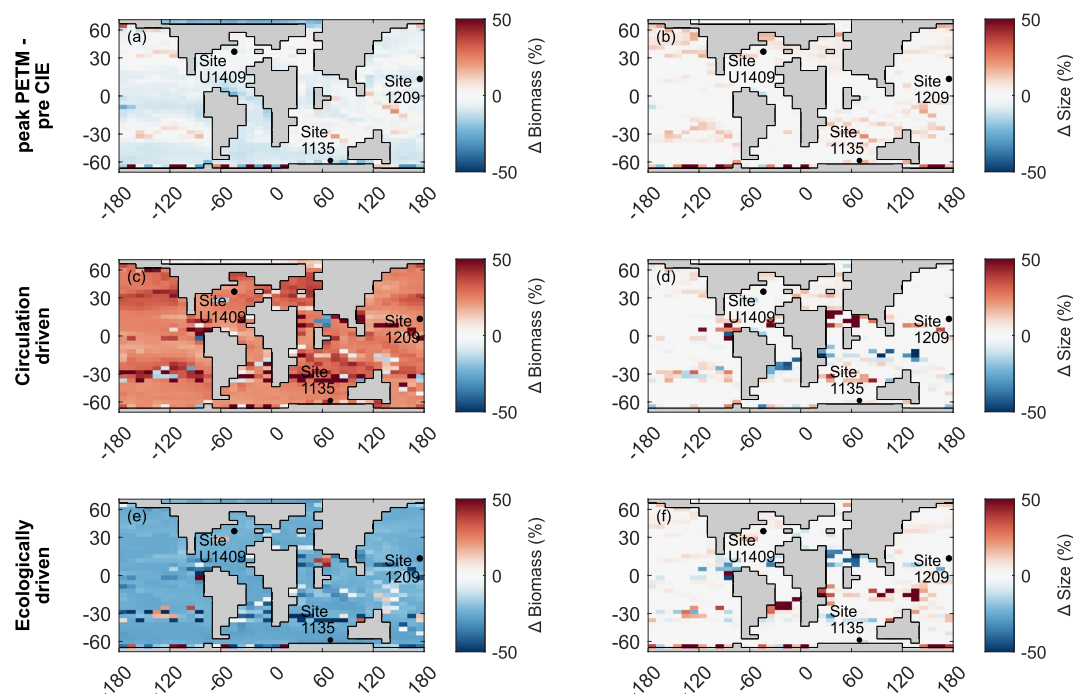


Figure 5. Separating the impact of temperature on ocean circulation (middle panels) and on asymbiotic foraminiferal physiology (bottom panels). Relative anomaly in biomass (left-hand panels) and size (right-hand panels) for the (a–b) full experiment as seen in Figures 4c and 4d (peak PETM–Pre CIE). Middle panels (c–d) correspond to the PETM experiment with the ecosystem separately forced with cooler Pre CIE SSTs minus the Pre CIE output. This shows the temperature impact on ocean circulation. Bottom panels (e–f) correspond to the peak PETM minus PETM experiment with the ecosystem separately forced with cooler Pre CIE SSTs. This shows the direct temperature impact on foraminiferal physiology.

4. Discussion

Planktic foraminifera play a key role in the inorganic carbon cycle (Buitenhuis et al., 2013; Schiebel, 2002) yet it is not well understood how their carbonate production responds to environmental change. Here, we used a combined data-modeling approach to assess the vulnerability of pelagic calcifiers to environmental change and find unexpected resilience of planktic foraminiferal carbonate production in response to the PETM. We define resilience as the ability of a population to resist a disturbance and/or recover from disturbance (Capdevila et al., 2020). Resistance is loss avoidance, which can be achieved via compensation (e.g., migration to avoid heat stress) and recovery is the ability to return to an undisturbed state (Hodgson et al., 2015). Through two independent methodologies we observe resistance and recovery of planktic foraminifera and their biogeochemical function to PETM environmental change. This narrative of resilience corroborates that planktic foraminifera—unlike benthic foraminifera—underwent a rapid turnover rather than extinction during the PETM (Fraass et al., 2015; Kelly et al., 1998).

4.1. Resilience to Environmental Change

Despite the global environmental change associated with the PETM, we demonstrate resistance of planktic foraminifera, with no significant reduction in assemblage test size, weight (for Site 1135), or abundance at this time (Figure 2). The modeled asymbiotic planktic foraminiferal range expansion (Figure 4a) corroborates published data, as larger, warm water taxa became more abundant at the high latitudes (Pardo et al., 1999; Thomas & Shackleton, 1996). Based on the model output we suggest that this shift is due to the ecosystem's physiological response to warming (increased growth and/or grazing rate), rather than changing ocean circulation and increased nutrient availability (Figure 5). These range shifts were temporary, with the re-establishment of tropical foraminiferal diversity following the PETM once environmental conditions returned to baseline (Hupp et al., 2022).

Despite surface ocean acidification (Gutjahr et al., 2017), calcification is not negatively impacted at Site 1135 as shown by stable SNW throughout the PETM. It is interesting to note that the weights at high latitude Site

1135 are comparable to modern values at $\sim 60^\circ\text{N}$ (10–14 μg for *G. bulloides* and 7–10 μg for *N. pachyderma* in the same size class; Barker et al., 2004). This comparability raises interesting questions about the lowest weight a test needs to be to fulfill its function, and the importance of carbonate ion concentration in calcification of foraminifers as the lower carbonate ion concentration associated with the higher Paleogene CO_2 did not result in a lower weight.

Whilst an assemblage test size increase at high latitudes due to migration was expected, a decrease at low latitudes was assumed given evidence of low latitude symbiont bleaching during the CIE (Shaw et al., 2021) and during other Eocene hyperthermals (Edgar et al., 2013; Wade et al., 2008). This assemblage size decrease would have resulted in the larger, symbiont-bearing taxa such as *Morozovella* and *Acarinina* being replaced by the smaller asymbiotic taxa such as *Subbotina* (Petrizzo, 2007), or a size reduction of the bleached individual itself. Our model does not resolve this size change as it does not include symbiosis or the benefit symbiosis might have on calcification. Interestingly, the data does not indicate dwarfing at Site 1209 (Figure 2c). We suggest several reasons for this lack of overall size reduction. First, the assemblage could have a greater heat tolerance than the individuals for whom bleaching was reported. For example, thermally resistant symbionts have been found in modern corals and shallow dwelling benthic foraminifers (Rowan, 2004; Schmidt et al., 2016). Second, newly emerging taxa (Kelly et al., 1998) may have had higher heat tolerance themselves in addition to their symbionts, or third, planktic foraminifers avoided heat stress via depth habitat migration (Barnet et al., 2020). Irrespective, we speculate that the environmental change associated with the PETM occurred at a slow enough rate to facilitate this resilience.

4.2. Drivers of Carbonate Production

Foraminiferal carbonate production is a function of test size, weight and abundance. Unexpectedly, the stable foraminiferal accumulation (Figure 2f) indicates that the replacement species (such as excursion taxa) had little impact on total carbonate production. In contrast, the model predicts an initial global reduction in foraminiferal biomass and size (Figures 3a and 3b)—and by inference carbonate production. This discrepancy could be because the comparatively lower temporal resolution of data misses this short-term modeled decrease. Alternatively, given that excursion taxa *A. sibaiensis* and *M. allisonensis* were symbiotic species, the modeled reduction could reflect the inability of ForaminiferalEcoGENIE to represent an increased abundance of symbiont bearing foraminifers.

Foraminiferal SNWs remained stable at Site 1135 during the CIE (Figure 2d) despite the high latitudes being the least saturated with respect to carbonate (Gibbs et al., 2016; Figure 1b). This unexpected stability could be linked to a relatively low carbon input rate over millennia during the PETM which was not severe or fast enough to reduce calcification (Babila et al., 2018, 2022; Gutjahr et al., 2017; cf. Hupp et al., 2022; Penman et al., 2014). However, our understanding of what drives foraminiferal calcification in the modern ocean is hampered by species-specific and regionally variable interactions between SNW, carbonate chemistry and other drivers (Beer et al., 2010; Davis et al., 2013; de Moel et al., 2009; de Nooijer et al., 2009; Henehan et al., 2017; Weinkauff et al., 2013, 2016). Particularly, it is unclear whether calcification is controlled by the energetic cost associated with lower carbonate saturation state (Ω) and a reduction in CO_3^{2-} (Waldbusser et al., 2016), or whether HCO_3^- or metabolically derived CO_2 are more important controls (Cyronak et al., 2016). Furthermore, adaptive mechanisms could minimize the impacts of ocean acidification. The latter has been observed in corals, which can partially offset ocean acidification impacts by upregulating pH at the site of calcification (Chauvin et al., 2011; McCulloch et al., 2012; Meyer & Riebesell, 2015; Wall et al., 2015). This energy demanding up-regulation is supported by nutrient availability. Hence where food is limited due to warming-induced stratification, the effectiveness of this upregulation could be reduced as seen for example, in bivalves (Melzner et al., 2011). For pelagic organisms, food availability is strongly linked to ocean circulation making nutrients available. Our model results provide evidence for the reduction in ocean circulation strength and nutrient availability being short-lived (Figures 3d and 3e; Kirtland Turner et al., 2017). This may explain why foraminiferal SNW is not negatively impacted as food is not limiting. Our data agrees with findings from coccolithophores (Gibbs et al., 2016) that during the PETM sea surface warming driven relocation, not ocean acidification, drove carbonate production.

During the PETM recovery phase, several sites show an increase in carbonate accumulation, including the North Atlantic Site U1409 (Figure 2f; Penman et al., 2016) and the South Atlantic sites 1262, 1263, and 1266 (Kelly et al., 2010). Based on our data this increase cannot be explained by a size increase at Site U1409. Combining

our findings with Penman et al. (2016) suggest that the increase in FMAR was caused by increasing abundance and/or increased calcification (SNW). Increased calcification could directly result from carbonate overshoot (Kelly et al., 2005, 2010); as in an oversaturated ocean, calcification is enhanced as it is less energy demanding. Increased abundance at this coastal location could be supported by increased nutrient input from intensified continental weathering during the PETM (Pogge von Strandmann et al., 2021). Such a response would not be captured in ForamEcoGEnIE as the model does not resolve the link between carbonate chemistry and calcification, or the intensified land-sea nutrient cycling that is characteristic of the PETM recovery.

We speculate that differences in nutrient regime are also important in modulating the response of the two main fossilized pelagic carbonate producers. An increase in asymbiotic size and biomass at the edge of ocean frontal systems highlights the importance of nutrient availability associated with ocean circulation in driving the foraminiferal response to warming (Figure 5). In the open-ocean, warming-enhanced sea surface stratification and changes in large-scale ocean circulation reduced nutrient availability (Bralower, 2002; Kelly et al., 1998; Lunt et al., 2010; Petrizzo, 2007). At the open-ocean oligotrophic Site 1209, the relative contribution of coccolithophores to carbonate decreased during the CIE—suggesting that foraminifers were more resilient to this nutrient poor environment (Figure 2f). This is unlikely an artefact of preservation as in sea floor sediments foraminifers preferentially dissolve below the lysocline compared to coccolithophores (Subhas et al., 2019). Gibbs et al. (2016) noted a complete disappearance of some coccolithophore groups from low latitudes during the PETM and similarly attributed this to increased oligotrophy. We speculate that foraminifers are better adapted to nutrient poor conditions because of their wider feeding strategy (Grigoratou et al., 2019) which enables foraminifers to occupy a greater range of niches than coccolithophores.

4.3. Resilience in the Wider Planktic Ecosystem

Overall, the pelagic ecosystem was only temporarily perturbed during the PETM, with dinoflagellates, radiolarians and diatoms primarily responding via a short-term poleward migration (Crouch et al., 2001; Hollis, 2006; Sluijs et al., 2006; Speijer et al., 2012). Higher up the food chain evolutionary analyses identifies no major turnover or reduction in open-ocean fish diversity associated with the PETM (Sibert et al., 2018). Although coastal and shallow dwelling tetraodontiform fish underwent extinction, this is likely because they are less able to evade heat by living deeper in the water column (Arcila & Tyler, 2017). Benthic foraminifers experienced a significant PETM extinction, with 30%–50% of species lost (Speijer et al., 2012; Thomas, 2007; Thomas & Shackleton, 1996). This extinction has often been attributed to hypoxic deep-water, a shoaling of the carbonate compensation depth, decreased food availability, or a combination of these (Griffith et al., 2021; Hayek et al., 2019; Stassen et al., 2015; Thomas, 2007; Zhou et al., 2016). However, the response of benthic foraminifers also shows regional modulations which suggest that temperature was not the main driver but that food and saturation impacted benthic foraminiferal growth (Schmidt et al., 2018). Recent modeling advances such as resolving diatom diversity (Tréguer et al., 2017), mixotrophy (Gibbs et al., 2020) and symbiosis (Ying et al., 2023) will allow us to evaluate more components of the pelagic ecosystem and improve our understanding of its response to perturbation.

5. Conclusions

Foraminiferal carbonate production can be conceptualized as an individual's test size, an individual's weight, and their collective abundance. To assess potential vulnerability to environmental change, we generated a record of carbonate production during the PETM. To upscale from individual locations to a global response, we applied a trait-based model for asymbiotic planktic foraminifers to this time period. Together, data and model suggest resilience (i.e., overall stability and/or recovery) of planktic foraminiferal carbonate production to PETM environmental change. We simulate a warming-induced poleward migration and a high latitude size increase. Our data shows no evidence of heat stress (symbiont bleaching) and consequent dwarfing at low latitudes. Despite ocean acidification, calcification continued at high-latitude Site 1135 as shown by a stable size normalized weight. As such, we postulate that sea surface warming had a greater impact on foraminiferal carbonate production during the PETM than ocean acidification. We also use ForamEcoGEnIE to disentangle the impact of warming on oceanography (nutrient distribution) from the direct impact on foraminiferal physiology (growth and grazing rate) and find that the high latitude size and biomass increase is due to the temperature sensitivity of the ecosystem (i.e., physiology). Our data suggest differing vulnerabilities of the carbonate producing plankton, with a greater vulnerability of coccolithophores in the tropics than planktic foraminifers. We suggest that planktic foraminiferal

resilience was facilitated by the relatively slow rate of environmental change during the PETM and therefore do not suggest that impacts would be similarly small in response to more rapid climate change.

Data Availability Statement

The code for the version of the “muffin” release of the cGENIE Earth system model used in this paper is tagged as v0.9.42 (Ridgwell, Reinhard, et al., 2023). Configuration files for the specific experiments presented in the paper can be found in the directory: MS/Barrettetal.2022. Details of the experiments, plus the command line needed to run each one, are given in the readme.txt file in that directory. All other configuration files and boundary conditions are provided as part of the code release. A manual detailing code installation, basic model configuration, tutorials covering various aspects of model configuration and experimental design, and results output and processing is available from Zenodo (Ridgwell, Hülse, et al., 2023). Planktic foraminiferal fossil record data plotted in Figure 2 can be found on Pangaea (Barrett et al., 2023) and the associated unprocessed data (including images for size-normalised weight and assemblage size analysis) can be found on the University of Bristol data repository, data.bris (Barrett & Monsuru, 2023).

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