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Ocean warming, not acidification, controlled coccolithophore response during past greenhouse climate change

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ABSTRACT

Current carbon dioxide emissions are an assumed threat to oceanic calcifying plankton (coccolithophores) not just due to rising sea-surface temperatures, but also because of ocean acidification (OA). This assessment is based on single species culture experiments that are now revealing complex, synergistic, and adaptive responses to such environmental change. Despite this complexity, there is still a widespread perception that coccolithophore calcification will be inhibited by OA. These plankton have an excellent fossil record, and so we can test for the impact of OA during geological carbon cycle events, providing the added advantages of exploring entire communities across real-world major climate perturbation and recovery. Here we target fossil coccolithophore groups (holococcoliths and braarudosphaerids) expected to exhibit greatest sensitivity to acidification because of their reliance on extracellular calcification. Across the Paleocene-Eocene Thermal Maximum (56 Ma) rapid warming event, the biogeography and abundance of these extracellular calcifiers shifted dramatically, disappearing entirely from low latitudes to become limited to cooler, lower saturation-state areas. By comparing these range shift data with the environmental parameters from an Earth system model, we show that the principal control on these range retractions was temperature, with survival maintained in high-latitude refugia, despite more adverse ocean chemistry conditions. Deleterious effects of OA were only evidenced when twinned with elevated temperatures.

INTRODUCTION

Increasing atmospheric CO₂ is currently driving a decrease in surface ocean pH and carbonate saturation, a phenomena termed ocean acidification (OA; Royal Society, 2005). Continuing OA is expected to induce a range of adverse impacts on ocean ecosystem function, biodiversity, and marine biogeochemical cycles (Aze et al., 2014), with organisms that form shells from calcium carbonate (CaCO₃) considered particularly at risk. The most widespread pelagic calcifiers are calcareous nannoplankton, predominantly coccolithophorid algae, with our current understanding of their response to OA predominantly based on observations of reduced calcification in short-term culture experiments (days to a year) (e.g., Riebesell et al., 2000). The interpretation of experimental results, however, is not straightforward, and they reveal a complex range of responses, including both higher and lower rates of calcification with acidification (Meyer and Riebesell, 2015), and synergistic effects with environmental parameters, such as temperature, modulating the acidification influence (Sett et al., 2014). More recent and sophisticated experiments have also shown that coccolithophore species may have the ability to adapt and evolve to OA over relatively short time scales (100 to thousands of generations) (Lohbeck et al., 2012). Because calcareous plankton have remarkably com-

plete fossil records, we can now supplement experimental data by studying past climate change events that encompassed environmental changes relevant to the future, affording the opportunity to assess responses and complex net outcomes across entire calcareous nannoplankton populations.

The Paleocene-Eocene Thermal Maximum (PETM, 56 Ma) was a transient carbon-release event characterized by 4–5 °C of surface ocean warming (Dunkley Jones et al., 2013) and an ~0.3 pH unit decrease (Penman et al., 2014), making it our closest geological analogue to modern fossil fuel burning (Hönisch et al., 2012). There is currently little substantive support for significant OA effects on calcifying plankton during this event, with some evidence of coccolith thinning (O’Dea et al., 2014) and putative skeletal malformation (Raffi and De Bernardi, 2008), but plentiful evidence for temperature- and nutrient availability-controlled migration and population composition changes (Bralower, 2002; Gibbs et al., 2006b). There is thus a need to identify diagnostic indicators that are sufficiently sensitive and selective to OA. Here we attempt to distinguish OA response by assessing a novel indicator of biomineralization function in coccolithophores, specifically the distribution of the extracellular calcifying holococcoliths (Figs. 1A–1C) and braarudosphaerids (Fig. 1D) across the PETM.

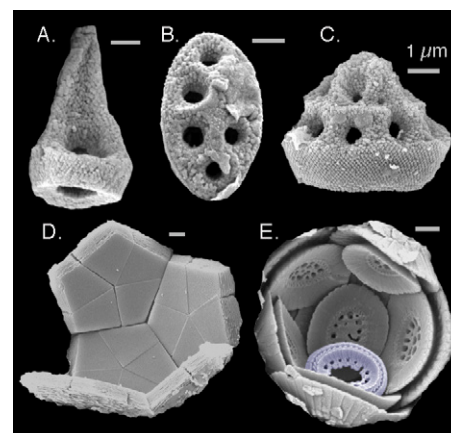


Figure 1. Examples of extracellular and intracellular calcifying calcareous nannoplankton, all imaged by scanning electron microscopy (SEM). A: Holococcolith *Zygrhablithus bijugatus* from Lodo Gulch (central California, USA), sample LO-03–29. B: Holococcolith *Holodiscolithus solidus* from Lodo Gulch, sample LO29. C: Holococcolith *Semihololithus biskayae* from Tanzania, sample TDP14/9–1. D: *Braarudosphaera bigelowii* (SEM) from Tanzania, sample TDP14/9–1. E: *Toweius pertusus* coccosphere (SEM), which includes an intracellularly forming protococcolith (highlighted in purple), from Bass River (New Jersey, USA) sample BR27.

Holococcoliths and heterococcoliths are the exoskeletal calcite plates of coccolithophores, produced during different life-cycle phases and generated by different biomineralization modes. Heterococcoliths form in the diploid life-cycle phase and comprise radial arrays of interlocking crystals with complex shapes (Fig. 1E), produced within the cytoplasm in a coccolith vesicle (Young and Henriksen, 2003). Their calcite is chemically distinct from abiotic calcite (Cros et al., 2013), implying a strong physiological control on the intracellular calcification processes (Mackinder et al., 2011), including a degree of buffering to external pH (Taylor et al., 2011). In contrast, holococcoliths form in the haploid life-cycle phase and comprise numerous minute crystallites (~0.1 μm; Figs. 1A–1C) produced within a membrane-bound space but outside the cell wall (Rowson et al., 1986). We therefore call these taxa extracellular coccolithophore calcifiers (ECCs). We also include in this ECC

group the braarudosphaerids (Fig. 1D), which are distinctive coccolithophores with pentagonal liths that also appear to be produced extracellularly (Bown et al., 2014). The external location of this biomineralization and its trace element chemistry (Cros et al., 2013) strongly imply that extracellular calcification may be more sensitive to changes in seawater chemistry than intracellular calcification. Therefore, by assessing the relative prevalence of ECCs across the PETM and comparing this with environmental changes predicted by an Earth system model, we provide a unique test for whether OA may pose a threat to coccolithophores in the near future.

METHODS

Holococcolith and Braarudosphaerid Meta-Analysis

Our meta-analysis of published and unpublished ECC occurrences comes from a global array of more than 20 sites that provide stratigraphic range data for individual or grouped holococcolith species and braarudosphaerids (Fig. 2; Figs. DR1 and DR2 in the GSA Data Repository¹; the site list is provided in the caption of Fig. DR1). We grouped these data as delicate holococcoliths, *Zygrhablithus bijugatus* (a large holococcolith with high preservation potential), and braarudosphaerids (Fig. DR2). Data were binned into six stratigraphic intervals distinguished using carbon isotope records (Fig. DR2): (1) pre-PETM, (2) onset (the rapid shift to lower carbon isotope values), (3) peak (minimum $\delta^{13}\text{C}$ values), (4) plateau (stable carbon isotope values), (5) recovery (values increase), and (6) post-PETM (return to near pre-event levels). Coarser resolution bins were used for comparing distribution data and modeled environmental parameters (Figs. 2 and 3): pre-PETM–background (0 yr, metadata from intervals 1, 5, and 6), characterized by the widespread occurrences of ECCs in the background normal conditions; carbon isotope excursion (CIE) onset (+6000 yr, metadata from interval 2), where there is the most dramatic range contraction of the ECCs; and plateau (+40,000 yr, including metadata from intervals 3 and 4), where environmental conditions are still perturbed but there is some degree of recovery of ECC distribution.

Earth System Modeling

We employed the cGENIE Earth system model (Ridgwell and Schmidt, 2010; Kirtland Turner and Ridgwell, 2013) to generate sea-surface environmental parameters across the PETM (see the Data Repository). The model

¹GSA Data Repository item 2016014, supplementary methods, figures and tables, is available online at www.geosociety.org/pubs/ft2016.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

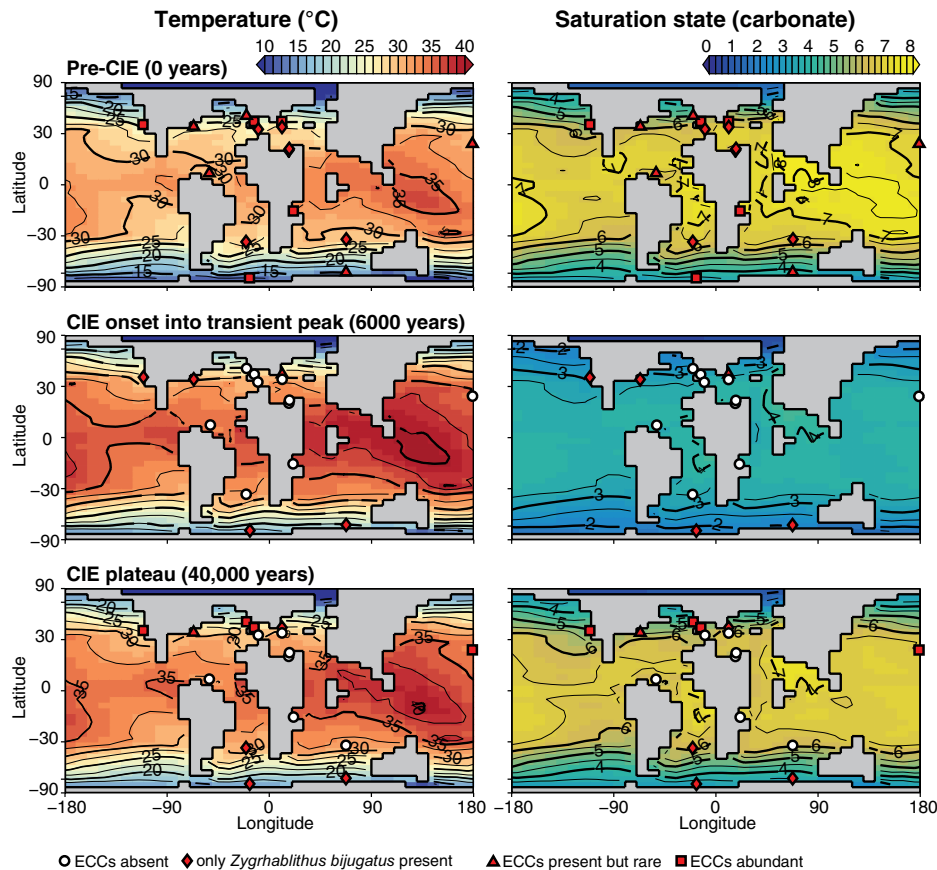


Figure 2. Extracellular coccolithophore calcifier (ECC) occurrence and cGENIE (Grid Enabled Integrated Earth systems; <http://www3.imperial.ac.uk/lesc/projects/archived/gridenabledintegrated>) model sea-surface temperature and carbonate saturation state output for Paleocene-Eocene Thermal Maximum (PETM) time slices. ECC occurrence (red symbols) and absence (open circles) for pre/post, onset to peak, and plateau PETM time slices (Fig. DR2; see footnote 1) for each site is superimposed upon mean annual model outputs for pre-CIE (carbon isotope excursion, 0 yr), CIE onset into transient peak (6000 yr) and CIE plateau (40,000 yr).

was configured following the seasonally forced early Eocene configuration of Kirtland Turner and Ridgwell (2013). To generate a scenario for PETM warming and recovery that could be related to specific carbon isotopic features (e.g., pre-CIE, onset, and plateau of Fig. DR2), we used the time history of carbon release devised by Zeebe et al. (2009), comprising an initial pulse of highly isotopically depleted carbon followed by an extended and slower rate leak of less isotopically depleted carbon. However, in order to generate sufficient surface warming in the model, consistent with data-based assessments (Dunkley Jones et al., 2013), we doubled the emissions rates specified by Zeebe et al. (2009) and halved the isotopic value, giving an isotopic excursion of -4.5‰ and mean ocean warming of 4.2 °C . This scenario was run for 200 k.y.; the first 60 k.y. time histories of key atmospheric and ocean surface properties are shown in Figure DR4. In Figure 3 and Figure DR5, we used mean modeled environmental parameters, and in Figure DR6 we plotted the seasonal ranges of carbonate saturation state and sea-surface temperature.

RESULTS AND DISCUSSION

Holococcolith Gap

At the PETM onset-peak, we find that ECCs show striking relative abundance and biogeographic shifts, declining across their range and disappearing entirely from low latitude sites (Fig. 2). For most of the species analyzed, these changes represent temporary stratigraphic gaps (the holococcolith gap; Fig. DR2), and similar global distributions were reestablished during the PETM recovery interval. However, for several holococcolith species the disappearance was a true extinction (e.g., *Semihololithus biskayae*; Bown and Pearson, 2009). Braarudosphaerids also temporarily disappear, or become very sporadic, at the event onset, and the most abundant holococcolith, *Z. bijugatus*, exhibits a dramatic range contraction, withdrawing from the low and middle latitudes, with rare occurrences restricted to the higher latitudes.

Multiple environmental and ecological factors influence the abundance and distribution of coccolithophore taxa, making it difficult to definitively identify the causes of perturbations

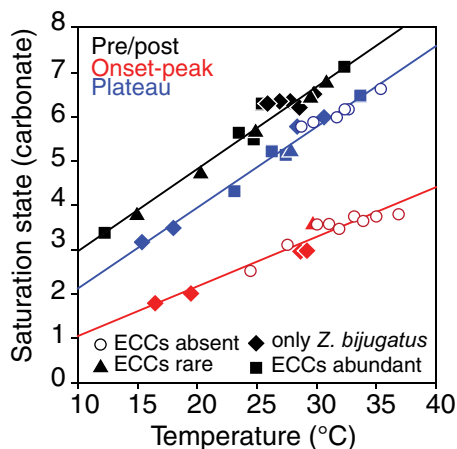


Figure 3. Model outputs for carbonate saturation state against sea-surface temperature, with extracellular coccolithophore calcifier (ECC) occurrence, at Paleocene-Eocene Thermal Maximum (PETM) time slices. ECC occurrence is shown for each site, with records compiled for pre/post, onset to peak, and plateau time slices, which correspond to the 0 yr, 6000 yr, and 40,000 yr time slices used for model outputs (as in Fig. 2), respectively (Fig. DR2 [see footnote 1]). The linear regression between modeled parameters at each time slice is shown. *Z.—Zygrhablithus*.

in the fossil record. The holococcolith gap is unusual, however, because it affects only a subset of the coccolithophore population, linked by a significant common factor, i.e., biomineralization mode. In contrast to the exclusions seen in the ECCs, the remaining majority of the nanoplankton community was less affected by the PETM onset, with changes typified by increasing abundances of low-latitude, warm-water-favoring taxa and expansion of their ranges into the higher latitudes (e.g., Bralower, 2002).

By comparing the model-generated environmental parameters (salinity, phosphate, temperature, pH, and calcite saturation state) across the PETM with the ECC distribution patterns, the factors that best explain the holococcolith gap are temperature and calcite saturation state (and/or pH), the parameters that have a clear latitudinal pattern (Figs. 2 and 3; for other parameters, see Figs. DR5 and DR6). Despite the limitation and noise within this simple meta-analysis, and the incidence of several outlier occurrences, we can clearly identify a region of parameter space that broadly coincides with the decline and absence of ECCs, which is characterized primarily by high temperatures (Fig. 3). Against expectation, these data do not indicate a simple biomineralization vulnerability because the ECC refugia occur at high latitudes, coincident with some of the lowest saturation states in the surface ocean at that time (Figs. 2 and 3). This inference is independent of the modeled rate of PETM onset, which occurs over 6 k.y. in our assumed emissions scenario (Zeebe et al., 2009). This

is because the mismatch between the observed spatial patterns of exclusion and modeled saturation state is key, the general trend being declining surface ocean saturation away from the equator and toward the poles. Similarly, this also rules out a major role for preservation, which is a particular concern at the PETM where increased dissolution is typically observed at and just below the event onset. Preservation bias at the PETM should result in fragile holococcoliths being least likely to be preserved at the high latitudes and at deeper sites, where carbonate saturation is lowest; however, our data show that this is not the case. Furthermore, the holococcolith gap occurs in shallower, low-latitude sites where excellent preservation is maintained even across the event onset (e.g., Tanzania and Bass River; Figs. DR2 and DR3). Although we cannot entirely discount the effects of preservation, the overall global pattern of ECC disappearance cannot be explained simply by variations in preservation.

ECC Exclusion Scenarios

To interpret the ECC exclusion, we found it helpful to consider a suite of plausible exclusion regimes (Fig. 4). We have already ruled out a dominant OA control (Fig. 4A), and while temperature clearly plays an important role, a simple temperature threshold does not adequately explain the presence-absence distribution (Fig. 4B). This may be explained by a trade-off relationship (Fig. 4C), the impacts of OA being partly offset by more favorable kinetics at higher temperatures, as seen in corals (McCulloch et al., 2012; Chauvin et al., 2011). However, the observed region of ECC exclusion is different from that predicted by this

trade-off, perhaps due to the reduced nutrients associated with temperature-driven stratification in the pelagic habitat. So, while higher temperatures would favor faster metabolic processes and could enable greater regulation of chemistry at the site of calcification, lower nutrient availability would inhibit growth.

The low-latitude exclusion of ECCs is best explained by a conceptual model where tropical sea-surface temperatures exceed some threshold above which there is a decreased tolerance to a second environmental parameter, in this case calcite saturation (Fig. 4D). The exclusion boundary would be crossed at a higher saturation state when temperatures were higher (Fig. 4D). It is therefore not the absolute value of this second parameter that is important per se, but rather the relative change in value, as suggested by the absence of ECCs even where saturation states were as high as 6.5. In this case, when close to the temperature threshold, a relatively small saturation decrease excludes ECCs, but at cooler temperatures a larger saturation change can be accommodated. While ocean chemistry is playing a role, it is not the primarily negative role that many studies of modern and fossil coccolithophores have presumed; i.e., the paradigm that reduced saturation state leads to reduced calcification.

ECC Life-Cycle Sensitivity

Why were ECCs in particular so strongly affected at the PETM? Although current understanding of modern coccolithophores life cycles is limited, there is evidence that different life-cycle phases exploit distinct ecological niches, the holococcolith-bearing phases inhabiting oligotrophic, high-light surface waters and hetero-

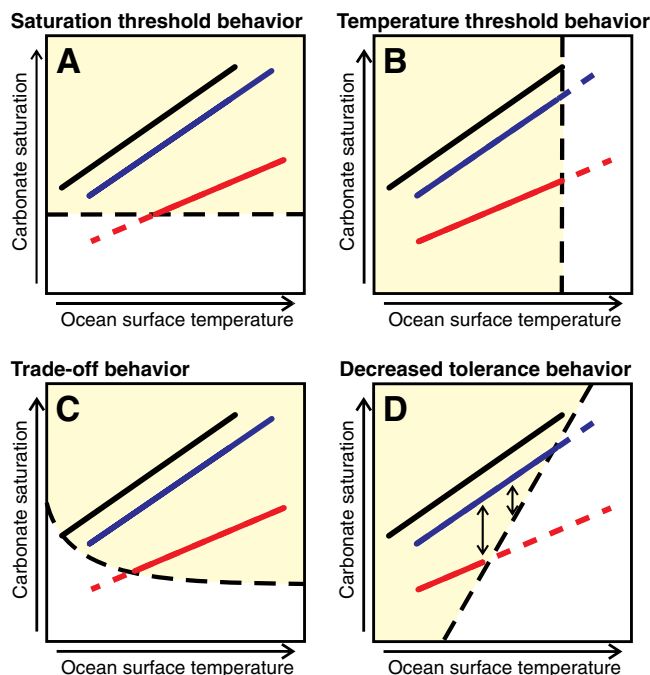


Figure 4. Theoretical extracellular coccolithophore calcifier (ECC) behaviors within modeled sea-surface temperature-carbonate saturation state space. Colors correspond to Paleocene-Eocene Thermal Maximum time slices (see Fig. 3). Solid lines show ECC presence, dashed lines show reduced ECC abundance or absence. Thin dashed black lines illustrate a theoretical threshold beyond which ECCs are largely present (shaded yellow) and absent (unshaded). A: Due to saturation state. B: Due to temperature. C: Due to trade-off. D: Due to decreased tolerance behaviors. The arrows in D highlight decreasing tolerance to saturation state with increasing temperature.

coccolith-bearing phases favoring deeper waters where nutrients are plentiful but light is limiting (Cros and Estrada, 2013). This ability to exist and flourish in two different life-cycle stages is virtually unique to coccolithophores and almost certainly confers advantage through expansion of habitable niche space and diversification of survival strategies (Cros and Estrada, 2013). However, in the case of these PETM ECCs, it appears that resilience to climate change may actually have been impaired by vulnerability in one of their life-cycle phases. Without very low saturation states, it is difficult to envisage direct biomineralization inhibition being responsible for their exclusion, although there may be a physiological vulnerability associated with the cost of maintaining external biomineralization in suboptimal growth conditions.

Although the shift in ECC distribution was dramatic, few extinctions actually occurred at the PETM and overall there is substantive geological evidence for resilience in coccolithophores to future OA. In particular, the vast majority of nanoplankton were left unscathed by the PETM, with only mildly elevated turnover rates (Gibbs et al., 2006a) indicating remarkable resilience because of, or in spite of, their life-cycling strategy. However, it is the rate of carbon emissions that is crucial to determining the magnitude of decline in surface-water carbonate saturation state (Hönisch et al., 2012). While the OA impacts on calcifying plankton at the PETM appear minimal, we must consider that today's carbon emission rates are significantly higher than at the PETM (Hönisch et al., 2012) and that any OA impact across this event has to be considered conservative compared to any that may be predicted for our modern climate scenario.

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