

## Some don't like it hot

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The oceans are experiencing vast environmental changes that are predicted to accelerate in the future (Stocker et al., 2013). Warming, acidification, deoxygenation, and increased stratification act on a global scale, whereas other factors such as eutrophication, the effect of changes in run-off on the carbonate system, and pollution act more locally to regionally. It is very hard to predict whether these drivers will act synergistically, antagonistically, or additively on marine organisms (Pörtner et al., 2014). Individual drivers can be tested in laboratory experiments (see Pörtner et al. [2014] for a recent assessment), but most of these experiments are too short, with little acclimation or possibility of adaptation. Species interact (Munday et al., 2009; Sanford et al., 2014) and evolve (Collins and Bell, 2004; Lohbeck et al., 2012), which is proving to be highly challenging to test in laboratory settings and mesocosms.

The geological record provides an archive of the integrated, long-term effects of climate change and ocean acidification, as well as other factors, on marine ecosystems (Hönisch et al., 2012). The Paleocene–Eocene Thermal Maximum (PETM), ca. 56 Ma, is a key interval for such comparisons because the effects of the climate perturbation can be found all over the globe and in all ecosystems (see McInerney and Wing [2011] and Sluijs et al. [2007] for reviews). A substantial negative carbon isotope excursion suggests the addition of between 2000–6000 Gt of isotopically light carbon to the atmosphere (Cui et al., 2011; Dickens, 2003). The global surface ocean warmed on average by 4–5 °C, and the subsurface ocean by 5–6 °C (Dunkley Jones et al., 2013). The observation of global shoaling of the carbonate compensation depth (Zachos et al., 2005), combined with recent modeling (Ridgwell and Schmidt, 2010) and boron isotope analysis (Penman et al., 2014) support that ocean acidification occurred in both the surface and the deep ocean. Ecosystem changes have been widely documented (Foster et al., 2013; Gibbs et al., 2006; Scheibner et al., 2005; Kelly et al., 1996; Thomas, 2007; Webb et al., 2009) showing, amongst others, migration toward higher latitudes, changes in ecosystem composition, extinction amongst deep sea species, and calcification responses.

The usefulness of the geological record in improving our understanding of the impacts of future climate change and ocean acidification, though, depends on accurate regional climate reconstructions, which allow a differentiated assessment of the impact on marine biota. Papers in this issue of *Geology*, by Aze et al. (2014, p. 739) and Frieling et al. (2014, p. 767), increase our knowledge in two critical areas: the tropical western Indian Ocean (19°S) and the subpolar West Siberian Seaway (~55°N), with the first PETM temperature reconstructions for these regions. Aze et al.'s novel tropical peak PETM values range from 32 °C to 43 °C, with a warming of 3 °C above background, depending on calibration and whether average or maximum values are considered. Similarly, warming is documented by Frieling et al. to have been ~7 °C, so that temperatures of 27 °C were reached in the West Siberian Seaway, combined with seasonal anoxia.

Both papers contain provocative novel ideas. For example, a complete lack of temperature difference between the Arctic and the West Siberian Seaway provides new targets for climate models. These papers also point to the challenges of working in comparatively shallower-water, near-coastal sections. Sediments at shallow-water sites are often subjected to reworking and unconformities, both of which make identifying base-lines of pre-event climate variability, and hence the relative amplitude of the warming, very difficult.

More importantly, though, both records point at our limitations to calculate absolute temperatures for deep-time records. Using oxygen isotopes (as in Aze et al.) meets the limits of our knowledge because seawater  $\delta^{18}\text{O}$  is not well constrained, resulting in a several-degree uncertainty in temperature reconstructions (Tindall et al., 2010), as large as the climate signal in the event. This is especially true in settings with strong evaporation near the coast, and likely a high variability in the carbonate system, by analogy to modern shelf seas (Artioli et al., 2014). Additional effects such as unknown calibration equations for extinct species and the effect of the surface-water acidification on isotope incorporation just add to the problem (Spero et al., 1997). Given the very recent quantification of the surface-water pH values prior to the PETM and the change within (Penman et al., 2014), the most likely average sea-surface temperature for the PETM in Tanzania was between 33.9 °C and 35.9 °C, which agrees well with temperature ranges in model simulations (Huber and Caballero, 2011; Tindall et al., 2010) for pre-PETM background values, combined with the 3 °C warming found by Aze et al.

So if we take these data at face value, what are the consequences for biology, and what does this tell us about the future? These papers highlight the migration of phytoplankton to follow their niche, and suggest that the extreme warmth led to an absence of calcifiers in tropical waters. Intriguingly, though, this abiotic zone appears several tens of thousands of years after the onset of the extreme temperatures and the acidification, is associated with changes in lithology, and follows a gap in the record. This potentially slow response contradicts everything we know about ecosystem response to decadal temperature variability; for example, the North Atlantic Oscillation (Beaugrand et al., 2009; Beaugrand et al., 2002) or the California upwelling system (Chavez et al., 2003; Chavez et al., 1999). Aze et al. explain the abiotic zone by comparing it to the temperature adaptation of modern foraminifers. One would expect, though, that Paleogene foraminifers which evolved in an ~15 °C warmer environment than today (Huber and Caballero, 2011) were generally adapted to these warmer temperatures. As so often, new papers ask more questions than they answer, such as: why are these abiotic zones not found at other open ocean sites nearer the equator? If the high-end temperatures are reasonable estimates, these might point to physiological limits at which enzymes start denaturalizing. Given the high metabolic rates in response to these high temperatures, the size of the supply of food needed to sustain the organisms is a pressing question and might have played a role in a regional exclusion. More work is needed, though, to move from assessments of past climates to predictive models for policy makers of the impact of future climate change on marine ecosystems, such as the cascading effects of these potential abiotic zones on food webs.

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