

Response to Reviewer #2

We thank the reviewer for a critical but very constructive review of our manuscript that has forced us to carefully review established concepts within dinocyst paleoecology in the light of the new data presented in our manuscript. As advised by the reviewer, we will include an overview of potential heat-stress evidence during the PETM in our revised manuscript. Below, we provide a point-by-point response to the comments.

This contribution provides detailed new dinoflagellate assemblage data through the PETM from the western tropical Atlantic, supported by additional new bulk sediment chemistry and magnetic susceptibility measurements. Overall it is clearly presented, well written and a solid contribution to the dataset of surface ecosystem responses to the PETM warming event. I do have a couple of concerns and some minor comments that need to be addressed by the authors before publication.

1. One of the key points made within this paper is that, to quote from the abstract: “The combined paleoenvironmental information from Site 959 and a close by shelf site in Nigeria implies the general absence of eukaryotic surface-dwelling microplankton during peak PETM warmth is most likely caused by heat stress.” My concern is that evidence presented from selected sites is framed to make inferences about global responses and environmental drivers: “Site 959 and a close by shelf site in Nigeria: ∴ implies the general absence of ∴”. Within a few words they’ve gone from local and specific (“close by”) to a “general absence”. This is a problem because this group of authors are foremost in the analysis of PETM dinoflagellate (and other) records. The quality of their regular outputs, and regard within the community, gives them a very strong influence on shaping the accepted narrative and interpretation of data. With this in mind, I think they have to be exceptionally careful about the claims that are made and that these fully take into account uncertainty in going from the observed data to interpretation.

Author response:

We thank the reviewer for being critical on this and we fully agree we need to be careful regarding claims. We did not intend to claim that eukaryotes died off in the entire tropical band. ‘General absence’ was not intended to suggest that, but rather to reflect the equatorial eastern Atlantic region, notably the study area covering Site 959 and the Nigerian realm we studied for our 2017 paper. We will specify this in our revised manuscript.

In this case they may well be correct and are presenting a substantive account of the true ecosystem responses, but my concern is that only references that support this “heat stress” and tropical exclusion of eukaryotes are cited – self-citations and Aze et al. (2014) and Yamaguchi & Norris (2015). A stronger case would include a wider overview and consideration of tropical sites where there is less or no evidence for the exclusion of eukaryotes.

Author response:

We agree and will include a section in the revised paper to discuss this issue. We stress that the combined evidence from Site 959 and Nigeria is quite unique because there is independent information on (excessively high) temperature and other environmental parameters from two very different but close by geological settings. Only this allows extracting the SST the dominant forcing factor. For most other sites, this is impossible to accomplish. Indeed, dissolution of carbonates and overall low-organic carbon content of sediments hampers tracking biotic change and how this relates to various environmental factors for the open ocean equatorial and tropical (20 °S – 20 °N) sites (e.g. ODP Site 999, 1001, 1220, 1221, 1258, 1260). The records from Site 865 and 1209 do not show a planktic eukaryote demise, but it should be noted that SST reconstructions from these sites do not show the excessively high temperatures (>35°C) recorded at Site 959, Nigeria or Tanzania and that these SST trends are consistent with model results (Frieling et al., 2017). The southern Tethyan shelf (Egypt) may also be considered shallow enough to avoid carbonate dissolution through CCD rise. However, the PETM in Egypt is marked by black shales devoid of carbonates and yet, as Speijer and Wagner, (2002) note, contain no dinocysts, spores or pollen. These observations could be interpreted as supportive evidence for heat-stress among planktic eukaryotes, albeit less confidently. This will be discussed in the new section.

For example, the Tanzanian section discussed by Aze et al. (2014) also has records of coccolithophore communities and calcareous dinoflagellates throughout the PETM – calcareous dinoflagellates are

actually shown to increase in abundance during the PETM (Bown and Pearson, 2009).

Author response:

This is a nice observation. It should be noted that calcareous dinoflagellates have very different ecologies than organic cyst producing dinoflagellates. Indeed, the calcareous dinocysts increase in relative abundance – but remain present in very low absolute abundance as do coccolithophores. One speculative interpretation of these data would be that also these organisms were outcompeted by the more heat-stress resilient prokaryotes. This will be included in the additional section in the revised paper.

Similar records of persistence of coccolithophore communities and increase in calc. dinos are shown from the tropical Pacific, ODP Site 1209 (Gibbs et al., 2006b). In Site ODP 1209 there is an increase in phytoplankton turnover (Gibbs et al., 2006a), which may be related to heat stress, but there is little evidence for a total exclusion of eukaryotic microplankton from this tropical location.

Author response:

As the reviewer rightfully points out, the abundances of coccolithophores and calcareous dinocysts are unaffected by any heat-stress at IODP Site 1209. However, Site 1209 may not be as hot as Site 959, Nigeria or Tanzania during the PETM. Maximum recorded Mg/Ca SST estimates for Site 1209 are 32-33 °C, equivalent to those in the latest Paleocene in Nigeria (Frieling et al., 2017). Also this evidence will be included in the additional section in the revised paper.

There may be reasons for this increase in calc. dinos. in both the Tanzanian and Pacific tropical sites, and this might support some of this groups' interpretations, but there needs to be some recognition that these other records exist and then an integration of data to form a more solid interpretation of the wider (/global) patterns of change. In this instance, is there a case for any ecological exclusion of dinoflagellates be limited to the (eastern) equatorial Atlantic? I don't think there is strong evidence (yet) to extrapolate from these two relatively close sites (Nigeria and ODP 959) to a global response in the tropical oceans. Any associated sea surface temperature records from these locations might also just represent localized effects that aren't replicated in either the tropical Pacific or Indian Oceans.

Author response:

We agree and did not intend to suggest otherwise. We will make sure to adapt the text accordingly to argue that only the hottest parts of the ocean may have been affected. As indicated in Frieling et al. (2017), the studied region was likely one of those based on the climate model simulations.

2. The use and referencing of a submitted manuscript "Frieling et al. submitted" is frustrating. This was not provided to reviewers. Although I don't think the conclusions of this manuscript rely on what may be contained within this other submission, one feels that we're being asked to review this paper with 20% of the interpretation (and data?) hidden from view. Ideally, I would rather this manuscript was not published until either the "submitted" manuscript was published or made available for reviewers and editors of this submission. For example, key interpretation of the CIE, its onset and the temperature data are all likely contained in this other submission. I would recommend that the editor at least be able to see this other submitted manuscript in confidence prior to any final publication of this paper, so that they can judge the degree of overlap.

Author response:

Reviewer #1 also raised this comment. The companion paper ("Frieling et al., submitted") was submitted early 2017 and we did not anticipate a delay of this magnitude. We would be more than happy to share the submitted paper with the editor and reviewers or publication of the current manuscript may be halted until publication of the first submitted manuscript. We will await editorial advice on this issue. In addition, we will replicate the needed information in this manuscript, with proper citation.

3. Related to the development of a narrative for PETM dinoflagellate records presented by this group over a number of years, I'm intrigued by the interpretation presented of changes in abundance of key indicator species that previously have been used to infer sea level change through the PETM in shelf sites (page 8).

"From 804.4 mbsf, we find an increase in abundance of dinocysts belonging to, or closely related to the genus Areoligera (Areoligera complex sensu Sluijs and Brinkhuis, 2009). A relative abundance

increase of this genus was previously interpreted to reflect sea level rise at several shelf and slope sites during the PETM (Sluijs et al., 2008). However, Site 959 is located in an open ocean setting, which means water depth and shore proximity proportionally do not change as much as may be expected from sites on the continental shelf, especially if estimates of the amplitude of sea level rise across the onset of the PETM (5-20m, e.g., (Speijer and Morsi, 2002; Sluijs et al., 2008) are considered. The increase in *Areoligera* is further associated with a decrease in *Spiniferites*, consistent with other PETM records (e.g., Sluijs et al., 2008), including a recently published record from Nigeria (Frieling et al., 2017). Since we cannot distinguish between transported and local signals, we may either record a signal that is transported off the shelf, or a local signal that is similar to, but not related to sea level.”

I find this a little odd. If the dinoflagellate records are so subject to transport across shelf to the slope and deep ocean, what use are they in reconstructing relative position, from the marginal to oceanic? Which I thought was a substantial component of dinoflagellate paleoenvironmental interpretations? The other option presented is that this assemblage change is: “similar to, but not related to sea level.” This seems more likely than pervasive long distance transport. But if there is an alternate environmental cause of this assemblage change in the open ocean sites, then doesn't this also somewhat question whether the interpretation - of the same assemblage changes through the PETM from shelf-records - as being caused by sea-level is open to some reinterpretation? Could there rather be a broader dinoflagellate assemblage change (increase in *Areoligera*) that is rather related to the wider environmental changes in the tropical / sub-tropical Atlantic and less controlled by sea level? If there are such major PETM environmental changes in the tropics / sub-tropics, such as the heat stress the authors propose plus potential changes in stratification and nutrient supply, wouldn't these be more likely the drivers of dinoflagellate assemblage changes than a relatively modest change in sea level? If so, then this seems like an appropriate place to put the previous interpretations into this new context for the non-expert reader. Again, I'd emphasize, that when this group of authors dominate the generation of PETM dinoflagellate records and the interpretation of them, it's also their responsibility to the external readership to directly address such questions as new data and interpretations arise.

Author response:

We thank the reviewer for being critical about this section, it incompletely described previous work and therefore did not make full sense. We therefore include a more substantial discussion on this matter in our revised manuscript, based on the following arguments.

The main challenge here is that the Site 959 record is the first PETM organic-walled dinocyst record from the open ocean. Generally, organic cyst-forming dinoflagellates are bound to the continental margin because upon production dinoflagellate cysts sink to the ocean floor, where it spends a benthic stage of the life cycle (Fensome et al., 1996). After excystment, the dinoflagellate swims up to the sea surface but in open ocean settings, this is impossible. Therefore, only a few species are capable of sustaining in the open ocean (Zonneveld et al., 2013). What we omitted in the paper is to describe how the dinocyst assemblages do reflect this offshore setting, notably with the very high abundances of *Spiniferites*, which is a genus that is relatively more abundant with increasing distance to coastlines in the Paleogene and the modern (e.g., (Brinkhuis, 1994; Pross and Brinkhuis, 2005; Zonneveld et al., 2013). In such a setting, we would not necessarily expect common to abundant *Areoligera*, because on the shelf, *Areoligera* has been proven to be related to relatively near-shore, high-energy conditions based on independent information on sea level, grain size and relative contributions of terrestrial organic sedimentary components (e.g., Sluijs et al., 2006, 2008a, 2008b; Sluijs and Brinkhuis, 2009). In our view, therefore, the interpretations regarding the effect of sea level on the relative abundance of *Areoligera* during the PETM are solid.

It should be noted, however, that the PETM is associated with a drop in *Areoligera* abundance and a concomitant rise in *Spiniferites* in the relatively offshore locations in New Jersey, such as Bass River (Sluijs & Brinkhuis, 2009), and the Tawanui slope section in New Zealand (Crouch and Brinkhuis, 2005). In the pro-delta settings of Site 1172 on the East Tasman Plateau (Sluijs et al., 2011), the ACEX core in the Arctic Ocean (Sluijs et al., 2008a) and Spitsbergen (Harding et al., 2011), the PETM sees an influx of *Areoligera* into Paleocene freshwater dominated dinocyst assemblages, evidencing a more marine setting. In the nearby shelf site in Nigeria, *Areoligera* is a common constituent of the assemblage only directly before the PETM (Frieling et al., 2017), perhaps recording both the eustatic rise at the PETM and a latest Paleocene regression (Speijer and Morsi, 2002). With this overview, we lay out there is no global increase in *Areoligera*, but rather that the signal depends on the location of the site on the shelf, relative to the coastline and river outflows and the distal end of the margin.

This does leave the question open how to explain *Areoligera* abundances at Site 959 and this is not an

easy one given the limited available information from open ocean sites. We concur with the reviewer that long distance offshore transport is unlikely, particularly because we do not find accompanying abundances of terrestrial organic components (branched GDGTs, pollen and spores). We however note that there is a concomitant increase in the relative abundance of Goniodomids, which are typically associated with warm (seasonally) stratified waters in the Paleogene (e.g. Sluijs et al., 2011, 2014) and modern ocean (Zonneveld et al., 2013). It is inferred from both model results and carbonate proxy data there is a strong but shallow permanent thermocline (and this likely also pertains to the pycnocline) in this region (Frieling et al., 2017), which could act as a substitute seafloor to cyst-forming dinoflagellates, similar to recorded during phases of strong stratification in the Arabian Sea during the last glacial cycle (Reichart et al., 2004). We therefore speculate that the higher percentages of *Areoligera* here may be facilitated by strong(er) stratification in the latest Paleocene, rather than to sea level change. The waters of above the thermocline may emulate the high-energy environment *Areoligera* prefers.

Other comments:

1. Given that Thomas Westerhold is a co-author, I'm surprised that there is no mention, use or citation of the latest age model assessment for the PETM: Westerhold et al. 2017. Clim. Past Discuss. <https://doi.org/10.5194/cp-2017-74>. And specifically the durations provided for the PETM in this paper appear to be at odds with Westerhold et al. 2017.

Author response:

The revised text is made consistent with all available literature, including this paper that is still in review.

2. Use of capitalization for informal sub-epochs / sub-series: e.g. Page 2, line 3: “during the Late Paleocene and Early Eocene: :?”. See Pearson et al. 2017. Episodes, <http://dx.doi.org/10.18814/epiugs/2017/v40i1/017002>

Author response:

Fixed.

Bown, P., and Pearson, P., 2009, Calcareous plankton evolution and the Paleocene/Eocene thermal maximum event: New evidence from Tanzania: Marine Micropaleontology, v. 71, no. 1-2, p. 60-70.

Gibbs, S., Bown, P., Sessa, J., Bralower, T., and Wilson, P., 2006a, Nannoplankton extinction and origination across the Paleocene-Eocene Thermal Maximum: Science, v. 314, no. 5806, p. 1770.

Gibbs, S., Bralower, T., Bown, P., Zachos, J., and Bybell, L., 2006b, Shelf and openocean calcareous phytoplankton assemblages across the Paleocene-Eocene Thermal Maximum: Implications for global productivity gradients: Geology, v. 34, no. 4, p. 233-236.

References used in author response

Brinkhuis, H.: Late Eocene to Early Oligocene dinoflagellate cysts from the Priabonian type-area (northeast Italy): Biostratigraphy and paleoenvironmental interpretation, Palaeogeogr. Palaeoclimatol. Palaeoecol., 107(1-2), 121-163 1994.

Crouch, E. M. and Brinkhuis, H.: Environmental change across the Paleocene-Eocene transition from eastern New Zealand: a marine palynological approach, Mar. Micropaleontol., 56(3), 138-160, 2005.

Fensome, R. A., Riding, J. B. and Taylor, F. J. R.: Dinoflagellates, in Palynology: principles and applications. , edited by J. Jansonius and D. C. McGregor, pp. 107-169, American Association of Stratigraphic Palynologists Foundation., 1996.

Frieling, J., Gebhardt, H., Huber, M., Adekeye, O. A., Akande, S. O., Reichart, G.-J., Middelburg, J. J., Schouten, S. and Sluijs, A.: Extreme warmth and heat-stressed plankton in the tropics during the Paleocene-Eocene Thermal Maximum, Sci. Adv., 3(3), e1600891, doi:10.1126/sciadv.1600891, 2017.

Harding, I. C., Charles, A. J., Marshall, J. E. A., Pälike, H., Roberts, A. P., Wilson, P. A., Jarvis, E., Thorne, R., Morris, E., Moremon, R., Pearce, R. B. and Akbari, S.: Sea-level and salinity fluctuations during the Paleocene–Eocene thermal maximum in Arctic Spitsbergen, *Earth Planet. Sci. Lett.*, 303(1–2), 97–107, doi:<http://dx.doi.org/10.1016/j.epsl.2010.12.043>, 2011.

Pross, J. and Brinkhuis, H.: Organic-walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene ; a synopsis of concepts, *Paläontologische Zeitschrift*, 79(1), 53–59, 2005.

Reichart, G.-J., Brinkhuis, H., Huiskamp, F. and Zachariasse, W. J.: Hyperstratification following glacial overturning events in the northern Arabian Sea, *Paleoceanography*, 19(2), doi:[10.1029/2003PA000900](https://doi.org/10.1029/2003PA000900), 2004.

Sluijs, A. and Brinkhuis, H.: A dynamic climate and ecosystem state during the Paleocene-Eocene Thermal Maximum – inferences from dinoflagellate cyst assemblages at the New Jersey Shelf, *Biogeosciences*, 6(8), 1755–1781, doi:[10.5194/bg-6-1755-2009](https://doi.org/10.5194/bg-6-1755-2009), 2009.

Sluijs, A., Pross, J. and Brinkhuis, H.: From greenhouse to icehouse; organic-walled dinoflagellate cysts as paleoenvironmental indicators in the Paleogene, *Earth-Science Rev.*, 68(3–4), 281–315, doi:<http://dx.doi.org/10.1016/j.earscirev.2004.06.001>, 2005.

Sluijs, A., Schouten, S., Pagani, M., Woltering, M., Brinkhuis, H., Sinninghe Damsté, J. S., Dickens, G. R., Huber, M., Reichart, G.-J., Stein, R., Matthiessen, J., Lourens, L. J., Pedentchouk, N., Backman, J., Moran, K. and the Expedition, S.: Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum, *Nature*, 441(7093), 610–613, doi:[10.1038/nature04668](https://doi.org/10.1038/nature04668), 2006.

Sluijs, A., Röhl, U., Schouten, S., Brumsack, H. J., Sangiorgi, F., Sinninghe Damsté, J. S. and Brinkhuis, H.: Article late Paleocene - Early Eocene paleoenvironments with special emphasis on the Paleocene-Eocene thermal maximum (Lomonosov Ridge, Integrated Ocean Drilling Program Expedition 302), *Paleoceanography*, 23(1), doi:[10.1029/2007PA001495](https://doi.org/10.1029/2007PA001495), 2008a.

Sluijs, A., Brinkhuis, H., Crouch, E. M., John, C. M., Handley, L., Munsterman, D., Bohaty, S. M., Zachos, J. C., Reichart, G. J., Schouten, S., Pancost, R. D., Damsté, J. S. S., Welters, N. L. D., Lotter, A. F. and Dickens, G. R.: Eustatic variations during the Paleocene-Eocene greenhouse world, *Paleoceanography*, 23(4), 1–18, doi:[10.1029/2008PA001615](https://doi.org/10.1029/2008PA001615), 2008b.

Sluijs, A., Bijl, P. K., Schouten, S., Röhl, U., Reichart, G.-J. and Brinkhuis, H.: Southern ocean warming, sea level and hydrological change during the Paleocene-Eocene thermal maximum, *Clim. Past*, 7(1), 47–61, doi:[10.5194/cp-7-47-2011](https://doi.org/10.5194/cp-7-47-2011), 2011.

Sluijs, A., Van Roij, L., Harrington, G. J., Schouten, S., Sessa, J. A., Levay, L. J., Reichart, G.-J. and Slomp, C. P.: Warming, euxinia and sea level rise during the paleocene-eocene thermal maximum on the gulf coastal plain: Implications for ocean oxygenation and nutrient cycling, *Clim. Past*, 10(4), 1421–1439, doi:[10.5194/cp-10-1421-2014](https://doi.org/10.5194/cp-10-1421-2014), 2014.

Speijer, R. P. and Morsi, A.-M. M.: Ostracode turnover and sea-level changes associated with the Paleocene-Eocene thermal maximum, *Geology*, 30(1), 23–26, 2002.

Speijer, R. P. and Wagner, T.: Sea-level changes and black shales associated with the late Paleocene thermal maximum; organic-geochemical and micropaleontologic evidence from the southern Tethyan margin (Egypt-Israel); Catastrophic events and mass extinctions; impacts and beyond, *Spec. Pap. - Geol. Soc. Am.*, 356, 533–549, doi:[10.1130/0-8137-2356-6.533](https://doi.org/10.1130/0-8137-2356-6.533), 2002.

Zonneveld, K. A. F., Marret, F., Versteegh, G. J. M., Bogus, K., Bonnet, S., Bouimetarhan, I., Crouch, E., de Vernal, A., Elshanawany, R., Edwards, L., Esper, O., Forke, S., Grøsfjeld, K., Henry, M., Holzwarth, U., Kieft, J.-F., Kim, S.-Y., Ladouceur, S., Ledu, D., Chen, L., Limoges, A., Londeix, L., Lu, S.-H., Mahmoud, M. S., Marino, G., Matsouka, K., Matthiessen, J., Mildenhall, D. C., Mudie, P., Neil, H. L., Pospelova, V., Qi, Y., Radi, T., Richerol, T., Rochon, A., Sangiorgi, F., Solignac, S., Turon, J.-L., Verleye, T., Wang, Y., Wang, Z. and Young, M.: Atlas of modern dinoflagellate cyst distribution based on 2405 data points, *Rev. Palaeobot. Palynol.*, 191, 1–197, doi:[10.1016/j.revpalbo.2012.08.003](https://doi.org/10.1016/j.revpalbo.2012.08.003), 2013.