# Warm ocean processes and carbon cycling in the Eocene

**Journal:** Philosophical Transactions A  
**Manuscript ID:** RSTA-2013-0099  
**Article Type:** Research  
**Date Submitted by the Author:** 31-Jan-2013  
**Complete List of Authors:** John, Eleanor; Cardiff University, Earth and Ocean Sciences  
Pearson, Paul; Cardiff University, School of Ocean & Earth Sciences  
Coxall, Helen; Stockholm University, Department of Geological Sciences  
Birch, Heather; Cardiff University, School of Ocean & Earth Sciences  
Wade, Bridget; University of Leeds, School of Earth & Environment  
Foster, Gavin; University of Southampton, Ocean & Earth Science  
**Issue Code:** Click here to find the code for your issue: DM1011  
**Subject:** Biogeochemistry < EARTH SCIENCES, Climatology < EARTH SCIENCES, Geochemistry < EARTH SCIENCES, Geology < EARTH SCIENCES, Palaeontology < EARTH SCIENCES  
**Keywords:** Eocene, Planktonic foraminifera, Biological pump, Stable isotopes, Carbon cycling, Temperature
Warm ocean processes and carbon cycling in the Eocene

BY ELEANOR H. JOHN¹*, PAUL N. PEARSON¹, HELEN K. COXALL², HEATHER BIRCH¹, BRIDGET S. WADE³, AND GAVIN L. FOSTER⁴

¹School of Earth & Ocean Sciences, Cardiff University, Cardiff CF10 3AT, UK
²Department of Geological Sciences, Stockholm University, Svante Arrhenius väg 8, SE-106 91 Stockholm, Sweden
³School of Earth & Environment, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK
⁴Ocean & Earth Science, National Oceanography Centre Southampton, University of Southampton, European Way, SO14 3ZH, UK

Abstract

Sea surface and subsurface temperatures over large parts of the ocean during the Eocene epoch (55.5–33.7 Ma) exceeded modern values by several degrees which must have affected a number of oceanic processes. Here we focus on the effect of elevated water column temperatures on the efficiency of the biological pump, particularly in relation to carbon and nutrient cycling. We use stable isotope values from exceptionally well-preserved planktonic foraminiferal calcite from Tanzania and Mexico to reconstruct vertical carbon isotopes gradients in the upper water column, exploiting the fact that individual species lived and calcified at different depths. The oxygen isotope ratios of different species’ tests are used to estimate the temperature of calcification, which we converted to absolute depths using Eocene temperature profiles generated by General Circulation Models. This approach, along with potential pitfalls, is illustrated using data from modern core-top assemblages from the same area. Our results indicate that during the early and middle Eocene, isotope gradients were steeper (and larger) through the upper thermocline than in the modern ocean. This could have been caused by a number of oceanic phenomena but is also consistent with a shallower average depth of organic matter remineralisation. This supports previously proposed hypotheses that invoke high metabolic rates in a warm Eocene ocean, leading to more efficient recycling of organic matter and reduced burial rates of organic carbon.

Index words: Eocene; planktonic foraminifera; biological pump; stable isotopes; carbon cycling temperature.

1. Introduction
There are many concerns about the impact of anthropogenic global warming on the oceans, including changes to thermal structure, circulation patterns, oxygenation and pH (e.g., [1, 2]). The effect of a warmer ocean on the efficiency of the marine biological pump has also been emphasised, due to the fact that respiration rates in remineralising microbes are temperature-dependent (e.g., [3-6]) and may be important for understanding the response of the carbon cycle to current warming trends on short and geological timescales. To predict the effects of warming, these processes can be modelled (e.g., [4]); another approach is to examine them for warm climate states in the past.

During the Eocene epoch (55.5-33.7 Mya), global mean temperatures were undoubtedly higher than today and the poles are thought to have been largely ice-free. Evidence for Eocene warmth in marine and terrestrial realms is diverse and includes records of the distribution of biological taxa (e.g., the presence of cold-blooded animals and frost-intolerant plant species at high latitudes; [7-9]) and analysis of leaf morphology (e.g., [10]). The oxygen stable isotope ratio ($\delta^{18}O$) of deep sea benthic foraminifera [11-14] shows that bottom waters likely exceeded 10-12 °C in the early Eocene, cooling to 5 °C by the end of the epoch (e.g., [13, 14]). This trend was interrupted by intervals of relatively stability or transient warming events, such as at the Middle Eocene Climatic Optimum (MECO; [15, 16]). Sea surface temperatures, reconstructed using the $\delta^{18}O$ values of well-preserved planktonic foraminifera [17] and organic proxies also indicate warmer temperatures than the modern throughout the Eocene, particularly at high latitudes (e.g., [18, 19]). Tropical temperatures remained relatively warm and roughly constant during the Eocene, which suggests that the cooling occurred mainly at high latitudes [17, 18]. Although there is some quantitative disagreement between proxies, the general implication that large areas of the open ocean were warmer than the modern for most of the Eocene is sound, and it is unlikely that global Eocene temperatures have been exceeded since.

Elevated seawater temperatures could have affected the state of the Earth system in many ways, for example causing changes in ocean circulation, evaporation patterns, cloud formation, latent heat transfer to the atmosphere and increased storminess over large areas [20, 21]. Higher ocean temperatures may also have affected the biological pump, that is, the biologically-mediated transport of organic carbon out of the surface ocean to the ocean interior before it is remineralised back to CO$_2$ (e.g. [22]; Fig. 1). Bacterial respiration is one of the main ways that sinking organic matter is decomposed and carbon and nutrients that were fixed near the surface through photosynthesis are recycled at depth. Because the metabolic rates of these remineralising bacteria are temperature-dependent, elevated ocean temperatures may result in more efficient recycling of carbon and nutrients higher in the water column thus affecting the amount of sinking carbon that
reaches the deep sea and sea floor sediments. Because microbial respiration produces CO$_2$ this would also alter the distribution of dissolved inorganic carbon (DIC) in the water column as well as potentially affecting atmospheric CO$_2$. If the oceans were indeed globally warmer during the Eocene, these effects may also have been global and therefore need to be addressed if we are to understand global carbon cycling. This was emphasised by Olivarez Lyle and Lyle [23] who postulated that higher Eocene temperatures and enhanced remineralisation rates were responsible for reduced organic carbon burial rates in the deep sea. Such effects may have been an important feedback on global climate throughout the Phanerozoic [4, 24].

Bacterial remineralisation of organic matter also results in the redistribution of carbon isotopes in the water column: photosynthetic carbon fixation in the photic zone preferentially removes $^{12}\text{C}$ leaving the remaining DIC pool with elevated $\delta^{13}\text{C}_{\text{DIC}}$ values; upon sinking, microbes respire this organic matter and return the isotopically light carbon to the DIC pool. This is reflected in a general decrease in $\delta^{13}\text{C}_{\text{DIC}}$ values with depth in the upper part of the water column (Fig. 1). Potentially, depth stratified planktonic foraminifera can also record this process of organic matter remineralisation as a decrease in the $\delta^{13}\text{C}$ of their test calcite with increased water depth habitat (e.g., [25]). The actual shape of $\delta^{13}\text{C}_{\text{DIC}}$:depth profiles are highly variable worldwide and among the main controls on the shape of the profile are the depth and efficiency of remineralisation processes in the water column.

In this contribution we investigate these effects by using assemblages of exceptionally well-preserved planktonic foraminifera from the Eocene of Tanzania and Mexico to reconstruct the vertical gradient of stable carbon isotope ratios in DIC ($\delta^{13}\text{C}_{\text{DIC}}$) in the water column for various timeslices throughout the epoch. This has not previously been carried out using foraminifera that have not been subject to the micron-scale recrystallization that is common in deep sea carbonates; this is important because such recrystallization can dampen surface-to-deep $\delta^{13}\text{C}_{\text{DIC}}$ offsets. We use these profiles to decipher information about water column processes, including the efficiency of the biological pump during the Eocene in comparison with today.

2. The Metabolic Hypothesis and the $Q_{10}$ relationship

There is a rich literature on the effects of temperature on biological activity. Arrhenius [26] described the exponential increase in inorganic reaction rates with temperature in terms of ‘$Q_{10}$’, the fractional increase in reaction rate for every 10 °C increase in temperature. It has long been known that metabolic rates in ectothermic organisms also follow the $Q_{10}$ pattern and show a very
approximate doubling per 10 °C increase (i.e. \( Q_{10} = \sim 2.0 \)). This includes marine and terrestrial microbial decomposers whose measured \( Q_{10} \) activities lie between \(~ 2 \) and 4 [27-31]. The \( Q_{10} \) pattern can also be used to describe the temperature dependence of metabolic rates in a more diverse range of life forms, from unicellular ectotherms to large endothermic mammals, with other factors such as body size playing important additional roles; these relationships have been expanded to describe entire complex ecosystems in terms of the role that temperature plays in regulating an ecosystem’s 'metabolism' [32-34].

Theory predicts that metabolic rates in all oceanic planktonic communities should be strongly dependent on temperature (e.g., [32-36]). Importantly, while both rates of respiration and rates of photosynthesis should increase with increasing temperature, the effect of temperature is stronger on heterotrophic communities (respirers) than it is on autotrophic communities (photosynthesisers) [36] leading to an increasing dominance of heterotrophic activity in warmer waters. This has been demonstrated in the modern oceans [3, 6, 37]. Based on a large database of 1156 volumetric estimates of oceanic planktonic metabolism and temperature measurements, Regaudie-de-Gioux and Duarte [6] demonstrated strong relationships between both gross primary production and community respiration rates and temperature and found average \( Q_{10} \) values for the whole ocean of 1.56 for gross primary production and 2.52 for community respiration. The rates of increase in metabolism with temperature were comparable in the two hemispheres but different between ocean basins and between seasons, reflecting changes in planktonic community structure. The positive relationship between temperature and the ratio of heterotrophic/autotrophic activity appears to be strong below 20-21 °C [3, 6] with a weaker relationship at higher temperatures due to an overall dominance of heterotrophs [3]. Feedbacks on the global carbon cycle are likely because areas of net heterotrophy represent sources of \( \text{CO}_2 \) to the atmosphere provided there is an allochthonous source of food for the microbes [37].

These relationships also have a bearing on the biological pump as enhanced rates of organic carbon remineralisation could reduce the amount of carbon reaching the deep ocean and the seafloor. Laws et al. [3] used a complex pelagic food web model to investigate controls on modern export production including ecological interactions, controls on the metabolic rates of different organisms and other dynamic processes. They concluded that temperature variations could account for >80 % of the variance in their modelled export production. Several studies have used modelling results to emphasise the affect of temperature-dependent remineralisation on the strength of the organic carbon pump, atmospheric \( \text{CO}_2 \) and nutrient distribution in the ocean, primarily on glacial-interglacial timescales where we have a wealth of data to cross-check with the model. Matsumoto
[4] used results from an intermediate-complexity climate model to account for around a third of the changes in CO$_2$ between Plio-Pleistocene glacials and interglacials by invoking suppressed microbial activity and a stronger organic pump strength during colder glacials. This led to a lower relative export rate of CaCO$_3$ versus C$_{org}$ to the deep seafloor (i.e., a lower ‘rain ratio’). From a comprehensive map of rain ratios and their high resolution regional ocean ecosystem model Matsumoto [4] proposed that today’s rain ratios are controlled at least in part by temperature through both enhanced remineralisation of organic matter and temperature dependence of community composition. Chikamoto et al. [38]’s model simulations include temperature-dependent remineralisation rates and these authors came to similar conclusions about the importance of temperature in controlling export production.

Although some authors have warned that global increases in ocean temperature could result in both increased $p$CO$_2$ levels and decreased rates of burial of organic carbon (e.g. [4]), these ideas have been little discussed in relation to the warm oceans of the Eocene or indeed other warm climates of the past. However, it seems clear that the effects of temperature on the biological pump could have strong implications for our understanding of controls on carbon cycling in ancient greenhouse worlds. Gu et al. [39] proposed that a warmer ocean would increase rates of methanogenesis in seafloor sediments thus providing a source for the isotopically light carbon released during Eocene hyperthermals. However, a warmer ocean would presumably also affect rates of aerobic respiration of sinking organic matter in this context. Olivarez Lyle and Lyle [23] suggested that the discrepancy between percentages of biogenic Ba (an indicator of primary productivity) and organic matter preserved in early Eocene sediments from the equatorial Pacific could be explained through increases in microbial respiration rates in a warmer ocean and a subsequent reduction in the burial rate of organic carbon. They also suggest that increased dissolved inorganic carbon (DIC) concentrations in the water column (caused by enhanced biogenic production of CO$_2$) relative to alkalinity inputs from weathering on land and subsequent shoaling of the carbonate compensation depth (CCD) would lead to reduced inorganic carbon burial. This relatively simple model involving positive feedbacks was suggested as a mechanism for maintaining high $p$CO$_2$ levels in greenhouse worlds and inversely low greenhouse gas concentrations in icehouse worlds ([23], see also [24]).

There are various complications with these ideas. For example, it is difficult to conceive how elevated $p$CO$_2$ levels can be maintained by these processes in light of the tight inorganic feedbacks that mediate atmospheric CO$_2$ change, such as silicate weathering [40]. It has also been suggested that calcium carbonate, the dominant test mineralogy among Eocene plankton, is a more effective ballasting agent than biogenic opal, which dominates planktonic communities today, more rapidly.
transporting organic matter to the seafloor for subsequent burial [41-43] although recent work suggests that the importance of mineral ballasting may have been over-estimated [44]. The effects of enhanced remineralisation on oxygen concentrations should also be carefully considered as oxygen (produced during photosynthesis) is consumed during microbial respiration. The effects on the distribution of oxygen minimum zones (OMZ) in the oceans should also be considered although at present the distribution of OMZs is mainly controlled by large-scale circulation patterns. Despite these considerations, it is clear that there were likely radical differences between the ways in which the marine biological pump operated in the warm Eocene compared with today; this study represents an attempt to detect such differences using the stable isotope record of foraminiferal calcite.

3. The Tanzania foraminifer stable isotope record

Foraminifera are unicellular protists that are abundant in oceanic environments. Some species are benthic; others live as plankton, with habitats distributed through the upper part of the water column (e.g., [45]). Foraminifera secrete ‘tests’ (shells) of calcium carbonate that accumulate on the sea floor after death and can be a major component of pelagic sediments. A suite of geochemical proxies can be extracted from foraminifer tests to provide information about the water in which they calcified; here we focus on a combination of oxygen and carbon isotope ratios.

The oxygen isotope ratio of calcite is dependent in part on the temperature of the water in which it calcified: δ¹⁸O values increase with water depth in accordance with the accompanying decrease in temperature (e.g., [12, 46]). The carbon isotope ratio of calcite depends largely on that of the bicarbonate ion, HCO₃⁻, from which it precipitated [47] which, in turn, reflects air-sea exchange processes in the surface ocean and biological activity. There is a non-linear relationship between δ¹³C_DIC and depth because of the photosynthetic fixation of isotopically light carbon in the surface ocean and its subsequent remineralisation at depth (Fig. 1). However, stable isotope ratios in foraminiferal tests are also affected by other factors, which mean that calcification does not occur in isotopic equilibrium with ambient seawater (see below). Insights into such disequilibrium effects in modern assemblages were made by Birch et al. [48]; Section 4) and their observations are applied in this study.

Here we use stable isotope ratios of planktonic foraminifera from Eocene hemipelagic sediments of Tanzania as published as Supplementary Information to Pearson et al. [17] and in Wade and Pearson [49] and from an Eocene shale of eastern Mexico (the Guayabal Formation), as published in Pearson et al. [50]. The significance of the carbon isotope data has not previously been discussed.
These Tanzanian and Mexican data are particularly valuable as they are derived from exceptionally well-preserved assemblages with no evidence of micron-scale recrystallization ([17, 50]; see also [51]). This is important because such diagenesis can have a large effect on the stable isotope composition of foraminiferal tests, including $\delta^{13}C$ [17, 52], despite claims to the contrary (e.g., [53]). The Tanzanian assemblages represent those typical of open ocean conditions, complete with deep dwelling forms, and were deposited in an upper bathyal environment [54, 55]. The single Mexican dataset also represents a typical open ocean assemblage. The ages of the core samples are determined by foraminiferal and nannofossil biostratigraphy [17, 50]. Recent advances in Eocene biostratigraphy have resulted in significant changes in the ages of several bioevents in the earliest middle Eocene; we have therefore updated the age of each sample in comparison to the previous publications as per Wade et al. [56]. The Tanzanian samples range in age between 54.90–33.75 Ma and the single Mexican sample is dated at 42.05 ± 1.55 Ma. During these times relatively warm conditions prevailed in Tanzania and eastern Mexico with reconstructed sea surface temperatures in the range 30-34.5 °C [17, 49, 50] (compared with 29-30 °C for the modern; [48]).

4. Multi-species and dissolved inorganic carbon in the modern

In this section we describe the approach of reconstructing water column $\delta^{13}C_{\text{DIC}}$ gradients using stable isotope data from foraminiferal assemblages by summarising data from a modern core-top assemblage from offshore Tanzania, as studied by Birch et al. [48]. Although limited to one location, this study is useful in presenting data from a wide range of planktonic foraminifera shell sizes (80-800 µm, taxon dependent) for each species investigated. The results provide new insights into foraminiferal test $\delta^{13}C$ variability that refine our ability to recognise several vital effects, including disequilibrium effects, in geochemical data from fossil assemblages.

Birch et al. [48] measured $\delta^{13}C$ and $\delta^{18}O$ values in 12 species of planktonic foraminifera from a single core-top sample. Using a series of sieves with increasing mesh size, a total of 60 species-specific, size-controlled splits were separated (each consisting of multiple shells) so that the effects of size and species on the isotope ratios could be investigated in detail. Figure 2 shows the $\delta^{13}C$ and $\delta^{18}O$ data from the multispecies size fraction splits plotted against each other. The variability along the $\delta^{18}O$ axis primarily reflects the depth of calcification (with warmer waters, i.e. lower $\delta^{18}O$ values, near the surface) and seasonal variations. Birch et al. first used their $\delta^{18}O$ values to determine temperature using the equation of Erez and Luz [57] and then overlaid this temperature on the measured water column temperature profile to estimate absolute depth of calcification. They used water column $\delta^{13}C_{\text{DIC}}$ measurements from a range of locations near their study site to
determine the approximate values that would result if the foraminifer tests had calcified in approximate isotopic equilibrium with ambient seawater temperature and $\delta^{13}C_{\text{DIC}}$ under conditions of ‘normal’ water column structure. Measurements from a range of settings (~2500 m to >5000 m water depth) within ~800 km of their study site [82] yielded similar shaped profiles and absolute values and a compilation of these values is represented by a grey band in Figure 1 (see [48] for details). The width of the band was also intended to account for seasonal effects. The fact that Birch et al.’s data do not all fall close to this band or any single line in Figure 2 implies that other factors are influencing the $\delta^{13}C$ values. The position of the data with respect to the typical ‘equilibrium line’ helps demonstrate four main types of effect (illustrated in Figure 2):

1) **The metabolic fractionation effect.** Foraminifera that are smaller than the 212 µm sieve size (either adults of relatively small species or the juvenile stages of larger species) tend to have $\delta^{13}C$ values that are more negative than ambient seawater, the offset being greatest for the smallest size fractions [58]. This is thought to be due to the incorporation of a fraction of isotopically light carbon from organic matter that has previously been respired by the foraminifer itself. The fraction of metabolic carbon in the foraminifer test decreases as the foraminifer grows, as the rate of metabolic activity decreases and exchange of carbon with ambient seawater improves [58-63].

2) **The photosynthetic fractionation effect.** Many species of near-surface dwelling planktonic foraminifera have a symbiotic relationship with photosynthesizing algae, mainly dinoflagellates. These algae preferentially remove $^{12}C$ during photosynthesis, leaving the remaining seawater isotopically heavy with respect to ambient DIC; such locally elevated $\delta^{13}C$ values may then be recorded by the foraminifera [25, 64-69]. As foraminifera grow to larger sizes, so the cloud of algae surrounding the foraminifer test increases and the photosynthetic effect is increasingly pronounced in successive size fractions. This becomes particularly marked in the tests of symbiotic species over about 355 µm in diameter [48].

3) **The pH fractionation effect.** A few species are adapted to deep-water habitats close to the oxygen minimum zone where the pH is reduced. Such species may have $\delta^{13}C$ values that show a positive offset from equilibrium values and it has been postulated that this is due to pH-dependent fractionation effects [47, 48, 70].

4) **The seasonal upwelling effect.** Certain species, including *Globigerina bulloides* and the small species *Globigerinita glutinata*, as discussed in the study of Birch et al. [48], together with *Neogloboquadrina dutertrei* [71-73] are indicative of more productive tropical surface conditions linked to seasonal upwelling [72-74]. The $\delta^{13}C$ composition of such species’ tests is therefore more similar to that of deeper-dwelling species because they record the isotopic
chemistry of cool, $^{12}$C-rich, upwelling deep waters. It should be noted however that these species only make up a small proportion of those presented in Figure 1 which otherwise resembles an oligotrophic assemblage [48].

To counteract these effects when reconstructing the water column $\delta^{13}$C$_{DIC}$ gradient, Birch et al. [48] recommend that surface mixed layer $\delta^{13}$C values are best estimated using foraminifera in the middle of their size range, i.e. 212-355 $\mu$m (Fig. 2), and if deep-dwelling species show unexpected scatter in their $\delta^{13}$C values, then ambient $\delta^{13}$C is best estimated using the more negative values. From Figure 2 it can be seen that these relatively simple rules apply reasonably well to the modern data set. Some scatter is always expected due to seasonal and inter-annual variability in water column structure and chemistry at any given site. Another complication is that some species might change their position in the water column during its life cycle; in particular, some surface dwelling symbiotic forms sink in their final life stages to reproduce, forming a crust of gametogenic calcite [64]. The measured stable isotope values in adult size fractions of such species will plot on a mixing line between the two depth habitats (Figs. 2, 3). This effect is not obvious in the modern data of Birch et al. [48] although it may be responsible for some of the differences in $\delta^{18}$O between symbiont-bearing species such as Globigerinoides sacculifer, G. ruber and Orbulina universa. It does, however, seem to be more pronounced in data from certain genera of fossil planktonic foraminifera (see below). Figure 3 is a simple interpretative cartoon modified from Pearson and Wade [75] summarizing these effects and how they can be identified in the fossil data sets used in this study.

5. Eocene reconstructions

We reconstructed water column $\delta^{13}$C$_{DIC}$ profiles for several Eocene timeslices by the following four steps:

1) We plotted the $\delta^{18}$O and $\delta^{13}$C values for each species/size fraction against each other and used the criteria of Birch et al. [48, 76] discussed above to identify those data points that are considered to represent disequilibrium/upwelling effects or that plot along a mixing line between two distinct depth habitats (Fig. 3). We used an optimal growth stage/shell size window of 212-355 $\mu$m.

2) The $\delta^{18}$O values for the chosen species/size fractions were converted into calcification temperatures using the equation of Kim and O’Neil [77]. We used an Eocene ice volume correction of -0.75‰ according to Cramer et al. [78] and we applied a seawater latitude correction of +0.83 [79] assuming a palaeolatitude of 19°S.
3) The depth of calcification for each of these samples was estimated by fitting these $\delta^{18}O$ temperatures to modelled Eocene water column temperature profiles for offshore Tanzania and the south-east Gulf of Mexico [80, 81].

4) We plotted the corresponding $\delta^{13}C$ values against the reconstructed calcification depth for each data point. The resulting Tanzanian $\delta^{13}C_{\text{DIC}}$ depth profiles were compared to the modern profile for offshore Tanzania (a composite of the profiles used in Birch et al. [48], from the World Ocean Database 2009 [82], is shown in Fig. 5 A-Giv).

To carry out step 3), Eocene temperature:depth profiles for offshore Tanzania and the south-east part of the Gulf of Mexico were extracted from published Eocene General Circulation Model reconstructions. In the case of Tanzania these were generated by the NCAR (National Center for Atmospheric Research) model and also the HadCM3 (Hadley Centre Model, version 3) model for comparison. The NCAR model profile [81] was generated for a continental margin adjacent to the east African coast centred around a latitude of ~18.2 °S and for a slope extending from 0 m water depth down to a water depth of 1500 m (Fig. 4). Experiments using different climate forcings of 1120, 2240 and 4480 ppmv atmospheric $pCO_2$ changed the absolute temperatures but not the shape of the temperature:depth profiles. We selected the profile generated by the $pCO_2$ condition that produced sea surface temperatures consistent with those estimated from the mixed layer foraminiferal $\delta^{18}O$ data from our multispecies dataset [17]. For example, the profile generated using 4480 ppmv $pCO_2$ was used for the early Eocene assemblages, and those generated using 2240 ppmv and 1120 ppmv $pCO_2$ were used for the middle Eocene and late Eocene timeslices, respectively. In the different $pCO_2$ scenarios, the temperature gradient between the surface and 1500 m was always 18-20°C and, at all depths, even near the coast and at maximum water depths, most of the temperature gradient is above 600 m; i.e. this reconstruction should be relevant even for the shallower palaeodepth estimates. For the HadCM3 model [80], a forcing of 1680 ppmv $pCO_2$ was applied and the generated profile (Fig. 4) represents that for a grid box centred around 41.25° E and 20° S for a water depth of up to ~4500 m. The shapes of the profiles generated by the two different models are consistent and both show distinct differences compared with the modern profile for offshore Tanzania (from in situ temperature measurements; Fig. 4). Not only are the Eocene temperature:depth profiles offset to warmer temperatures over the entire water column compared with the modern Tanzania profile, the overall surface-to-deep temperature offsets are smaller. The thermocline is also broader in the Eocene profiles with a roughly constant rate of temperature change down to 600 m compared with a modern thermocline that extends down to ~150 m. To determine the absolute depths for our foraminifera sample data, we used a logarithmic regression of the data generated by the NCAR model from the surface to a depth of 600 m (as this was most
consistent with the hemipelagic slope setting and benthic δ¹⁸O temperature estimates). The δ¹⁸O-derived temperatures for each data point (derived in Step 2) were input into the equation generated by this regression to give an absolute water depth. For the single dataset from the Guayabal Formation, Mexico, a temperature:depth profile was also generated using the NCAR model [81] and a climate forcing of 2240 ppmv pCO₂ for an area in the south-east part of the Gulf of Mexico from the coast down to 1500 m water depth (Fig. 4). Modern temperature:depth measurements for this area were obtained from the World Ocean Atlas 2009 database [83]; the curve in Figure 4 represents a composite of 7 profiles between 19.5 and 22.5 N and -95.5 and -96.5 W. Both profiles are also shown in Figure 4. A logarithmic regression of the data generated by the NCAR model from the surface to a depth of ~300 m (consistent with the neritic zone palaeoenvironment of the Guayabal Formation) and absolute water depths determined as for Tanzania. The significance of the model results are discussed in Tindall et al. [80] and Huber et al. [81].

The carbon and oxygen isotope crossplots and the step-by-step reconstruction of the δ¹³C:depth profiles are illustrated in Figure 5. The mixed layer species, that is those with the lowest δ¹⁸O values, in the early and middle Eocene samples are mainly from the muricate genera Acarinina, Morozovella, Morozovelloides and Igorina which are interpreted as having had obligate symbiotic algae [67, 84, 85]. The majority of symbiotic δ¹³C enrichment in these species, which has the effect of exaggerating the surface-to-deep δ¹³C gradient, has been minimised by only using species within the 212-355 µm test size range, as discussed above (Fig. 5Aii-Fii). Other near-surface calcifiers include the apparently non-symbiotic genera Pseudohastigerina, Planoglobanomalina [86] and Chiloguembelina [87]. Other genera present include Dentoglobigerina, Turborotalia, Parasubbotina, Subbotina, Hantkenina and Catapsydrax whose lower δ¹³C and higher δ¹⁸O values indicate calcification at greater depths. Species belonging to the genera Globigerinatheka, Orbulinoides, and Guembelitrioides tend to have isotopic compositions suggestive of mixed layer calcification followed by further gametogenic calcification at greater depth. This is consistent with observations as these genera typically show gametogenic calcite crusts (e.g., [84, 88]; hence these data were not used to generate the δ¹³C:depth profiles (Fig. 5).

The one late Eocene assemblage (Fig. 5G) differs in composition from the others in part due to the large assemblage turnover in planktonic foraminifera in the late middle Eocene that resulted in the extinction of the morozovelloidids and larger acarininids [89]. Constructing a realistic δ¹³C profile for this assemblage is problematic given the limited mixed layer data. We include the plots for completeness but restrict our interpretation to the early and middle Eocene reconstructions pending further investigation of late Eocene assemblages.
There are two common features to the early and middle Eocene profiles:

1) The carbon isotope profile appears to have been much steeper through the upper thermocline than is typical of the oceans in this area and most of the world. The modern $\delta^{13}$C profile for this part of the Indian Ocean [48, 82] shows a fairly constant rate of decrease down to ~1 km, with little change beyond this depth. Conversely, the early and middle Eocene profiles consistently show a sharp decrease in $\delta^{13}$C concentrated between the mixed layer and ~100-150 m depth.

2) The overall surface-to-deep offsets in the early and middle Eocene $\delta^{13}$C profiles are large relative to today, even when the Suess effect is taken into account. In the modern western Indian Ocean at this latitude the total gradient is ~1-1.5 ‰. On a global scale, modern surface-to-deep gradients rarely exceed 2 ‰ [90]. Similar gradients have also characterised at least the last 20 million years [91]. However, the early and middle Eocene profiles show $\delta^{13}$C offsets of 2-4 ‰. Similar values, and overall surface-to-deep gradients (2-3 ‰), have been previously reported for the early and middle Eocene even from recrystallised foraminifera from a variety of latitudes in the Atlantic, Pacific, Indian and Mediterranean basins (e.g., [50, 53, 92]); recrystallisation should dampen surface-to-deep $\delta^{13}$C gradients as measured in foraminifera tests and so many of these datasets may underestimate the offsets. In terms of absolute values, surface values in our dataset are mostly elevated compared with today; deepwater values are comparable.

We consider it unlikely that features 1) and 2) are an artefact of the modelled water column temperature:depth profile. For example, if the modelled profiles had underestimated the temperature gradient in the upper ocean and the profile shape was more similar to the modern, the reconstructed $\delta^{13}$DIC:depth gradients would be even steeper through the upper thermocline as the range of $\delta^{18}$O values (and therefore temperature) measured in the assemblage is small. However, if the models had overestimated the temperature:depth gradient and water column temperatures were actually more vertically homogenous, we could admittedly have generated a $\delta^{13}$DIC:depth gradient that was artificially steep in the upper ocean. Nonetheless, the large range of $\delta^{13}$DIC values measured in the Tanzanian and Mexican foraminifera assemblages suggests that strong vertical mixing was not occurring at those sites.

Another potential source of uncertainty relates to the issue of Eocene water depths and coastal proximity which can be difficult to determine precisely for hemipelagic deposits and may have varied with time. The Kilwa Group of Tanzania comprises several kilometre successions of
relatively monotonous clays and claystones with occasional turbidite interbeds [54, 55]. The palaeoshoreline is estimated to have been generally about 50 km from the site of deposition [93] and palaeodepths have previously been estimated at 300-500 m based on upper bathyal benthic foraminiferal assemblages (e.g., [55]). However, the deeper limit of this estimate is very uncertain, and given the narrow shelf and steep slope that is typical of the East Africa margin, it is quite possible that palaeodepths were considerably greater than this. Both the foraminifera and nannofossil assemblages indicate a fairly constant, open, deep, and relatively oligotrophic environment; there are no restricted assemblages or conspicuous shelf-restricted or eutrophic taxa [51]. Coring of modern hemipelagic sediments offshore Tanzania has revealed that silty clays of similar facies to the Kilwa Group are currently being deposited at depths of 500 m to 1800 m within 50 km of the shoreline [94] hence a more conservative depth estimate for the Eocene sediments would be 300 – 1800 m. For both modern and Eocene environments it is likely that onshore currents brought gyre water onto the continental slope, lending an oceanic rather than coastal character to the water column. Therefore, although we acknowledge that these issues do introduce uncertainty into our approach, we also argue that it is not reasonable to rule out the idea that the Eocene and modern datasets represent similar palaeoenvironments.

In addition, although all Eocene planktonic foraminifera are extinct, we can envisage no plausible vital effect or other fractionation factor that would have affected the surface dwelling forms in a way that could produce such heavy δ¹³C values as seen in Figure 5. Even if we have inadvertently included values affected by symbiotic effects, such effects are only ~1 ‰ or less in the modern and can therefore not explain the differences fully. An obvious question, then, is to ask whether these surface dwellers had more pronounced symbiotic effects than modern forms. It may also be that the isotopic fractionation factor associated with primary production (i.e. that associated with symbionts) was higher before the late Eocene due to effects relating to elevated pCO₂ levels, growth rates and/or volume to surface area ratios in primary producers [95, 96]. However, published relationships between δ¹³C and test size for muricate species (acarininids and morozovellids) from warm Palaeocene/Eocene oceans have similar or indeed shallower gradients to modern planktonic foraminifera with obligate symbionts, such as *Globigerinoides ruber* and *Gs. sacculifer* [67, 76, 97, 98] suggesting that, if anything, the symbiotic effect was less pronounced. Hence the data suggest that vertical carbon cycling operated very differently in the early and middle Eocene than is typical in the modern ocean.

6. Interpretation
The fact that the $\delta^{13}C_{\text{DIC}}$ decreases so sharply through the upper thermocline and to such a degree in the Eocene time slices compared with most modern oceanic environments is notable. One control on the depth of the $\delta^{13}C_{\text{DIC}}$ minimum is oceanic circulation and different oceanic circulation/mixing patterns in the Eocene compared with the modern, for example a shallower mixed layer (perhaps due to reduced wind induced mixing), or enhanced oceanic stratification relating to a warmer climate, could have contributed to the sharper, shallower decrease in $\delta^{13}C_{\text{DIC}}$. Additionally, faster rates of remineralisation of sinking organic matter below the mixed layer could partly explain the shape of the profile. Indeed, the shape of the profiles imply that the majority of remineralisation of sinking organic matter was occurring at a much shallower depth than is typical in the modern. Reconstructed sea surface temperatures offshore Tanzania and the Gulf of Mexico in the Eocene were only about ~2-4 °C greater than today which is not sufficient to affect remineralisation rates greatly, particularly at temperatures so much higher than ~20 °C. However, at a depth of ~150 m, Eocene water temperatures were ~10 °C higher than today (Fig. 4; [80, 81]); this means that if, for example, heterotrophic community respiration had a $Q_{10}$ value of 2 (a conservative estimate, e.g. [6]), respiration rates could quite reasonably have been twice as high at these depths than in the modern. Therefore, any temperature-related increase in microbial metabolic activity rates would have been more pronounced below the mixed layer than at the surface, that is, in the zone of net respiration rather than net photosynthesis. We acknowledge that there are controls on the shape of the vertical $\delta^{13}C_{\text{DIC}}$ profile other than temperature-dependent remineralisation and that to understand how these factors affect how $\delta^{13}C_{\text{DIC}}$ changes with depth requires detailed modelling. However, we propose here that the shape of the $\delta^{13}C_{\text{DIC}}$:depth profile could have resulted, at least in part, from the fact that there was a much greater temperature difference at depths below the mixed layer (Fig. 4) which in turn led to more rapid rates of organic matter remineralisation.

If biogenic remineralisation of organic carbon was more efficient in the Eocene water column due to elevated water temperatures, given that warmer-than-modern water temperatures extended to high latitudes, these findings may have had global significance. As proposed by Olivarez Lyle and Lyle [23], Stanley [24], and other authors focusing on the importance in terms of modern climates (e.g., [3, 4, 6]) this may have affected the transport of organic matter to the deep ocean and may have ultimately reduced rates of organic carbon burial and indeed inorganic burial through an increase in the DIC reservoir a shoaling of the carbonate compensation depth (CCD). This could have pushed $pCO_2$ levels even higher thus supporting a positive feedback mechanism keeping $pCO_2$ levels high during greenhouse periods (when remineralisation rates are high) and low during icehouse conditions (when remineralisation rates are lower). However, the possibility of global effects are probably best investigated using carbon cycle modeling, because, for example, any
consideration of impacts on the global carbon cycle must also take into account organic carbon burial and remineralisation rates in continental shelf environments (e.g., [96, 99, 100]). Rapid subsurface bacterial remineralisation would also have caused a marked upward displacement of the oxygen minimum zone which would have in turn have affected the locus and rate of organic carbon deposition on the continental shelves and margins [24]. Moreover on long timescales (e.g. $10^3$-$10^6$ years) negative feedback mechanisms caused by enhanced silicate weathering could counteract any increases in $pCO_2$ caused by a reduction in deep sea carbon burial (e.g., [99, 101, 102]).

The second observation, that is, the larger surface-to-deep $\delta^{13}C$ gradient, has been reported in several cases and seems to be a common feature of the Eocene ocean [53, 92]. More complete remineralisation of organic matter should in theory produce a greater surface-to-deep offset as more light carbon is being pumped into the ocean interior although this is unlikely to be the sole cause of the elevated gradients; more complete remineralisation should serve to reduce the $\delta^{13}C_{DIC}$ in the deeper ocean rather than elevate surface values. Instead, the surface ocean $\delta^{13}C_{DIC}$ could have been elevated due to higher rates of primary productivity which would have transferred proportionally more $^{12}C$ to organic tissues than occurs today. This would imply higher oceanic nutrient availability, perhaps from enhanced silicate weathering under greenhouse climates (e.g., [99, 100, 102, 103]) or efficient turnover of deep waters [104]. Alternatively, oceanic DIC concentrations could have been generally lower in the Eocene, as indicated by some carbon cycle models (e.g., [100]), which would enhance observed $\delta^{13}C_{DIC}$:depth gradients even without a change in rates of primary productivity in the surface ocean. This remains a possibility although several models suggest broadly unchanged DIC (and alkalinity) over the Cenozoic [105].

In summary, our data from the warm Eocene ocean provide prima facie support for the idea that the remineralisation of sinking organic carbon in the water column was much more efficient than is currently the case. We plan to investigate this possibility further by incorporating metabolic rate effects into carbon cycle models. Models should also be used to take into account other controls on the shape of the $\delta^{13}C_{DIC}$: depth profile, many of which may relate to elevated water temperatures, such as changes in oceanic circulation and enhanced oceanic stratification. This information about warm climates from the past may have important implications for the future: if anthropogenic emissions move the world oceans towards warm Eocene-like conditions, there may be similar profound consequences for water column structure and biological activity, and potentially far-reaching effects on the marine carbon cycle.

Acknowledgements:
We thank M. Huber and J. Tindall for their contribution to the Eocene modelled temperature:depth profiles. This work was supported by a NERC standard grant awarded to GLF and PNP.
References:


16. GA1116.


sedimentology of the Upper Cretaceous to Paleogene Kilwa Group, southern coastal Tanzania.


68. Norris, R. D., 1996. Symbiosis as an evolutionary innovation in the radiation of Paleocene


Figure captions

Fig. 1. Schematic cartoon of the modern biological pump showing production of organic matter, its consumption by higher organisms and the respiration of CO$_2$. The profile on the right shows a $\delta^{13}$C$_{DIC}$ profile from a site offshore modern Tanzania (data taken from site 425 of [90]) to illustrate the typical decrease in $\delta^{13}$C$_{DIC}$ with depth due to preferential fixation of isotopically light carbon in the surface ocean during photosynthesis and the subsequent return of this light carbon as sinking organic matter is respired by microbes.

Fig. 2. Multi-species $\delta^{18}$O and $\delta^{13}$C crossplot for a modern core-top foraminifera assemblage from ~200 km offshore Tanzania (Latitude 8°51.5538’S Longitude 41°26.4102’E) at a water depth of 3006 m [94] Modified from Figure 7 of Birch et al. ([48]; full caption given therein). The site is oligotrophic, as shown by the CTD (conductivity temperature depth probe) data and the assemblage composition, which is dominated by typical oligotrophic species with only a very minor fraction of species that represent seasonal upwelling (e.g., Globigerinita glutinata). Planktonic foraminifera $\delta^{18}$O values were converted to temperature according to the relationship of Erez and Luz [57] and using a modern seawater $\delta^{18}$O$_w$ value of 0.47 ‰. The grey band represents a composite water column $\delta^{13}$C$_{DIC}$ measurements taken from 7 sites within ~ 800 km of their study site (from World Ocean Database) and incorporating a +/- 0.5‰ window to account for seasonal variations. Data points falling outside of this band are thought to represent calcification out of isotopic equilibrium with DIC or by foraminifera that calcified during episodes of seasonal upwelling (i.e., G. bulloides and G. glutinata). For the species with obligate symbionts (*), the largest individuals have $\delta^{13}$C values up to 1.0 ‰ higher than the equilibrium envelope due to photosynthetic activity by symbiotic algae. The smallest individuals of most species have $\delta^{13}$C values that are 0.2-2.0 ‰ lower than the envelope because of size-related metabolic effects. The $\delta^{13}$C measured in mid-sized shells (in the ~212-355 µm size fraction) in fossil assemblages should therefore provide the closest approximation of $\delta^{13}$C$_{DIC}$. Gs. = Globigerinoides, Ga. = Globigerinita, Gt. = Globoturborotalita, O. = Orbulina, Gg. = Globigerina, Gr. = Globorotalia; Ge. = Globigerinella, Gd. =Globorotaloides , T. =Truncorotalia.

Fig. 3. Cartoon showing how data points plotting in different fields of the $\delta^{18}$O and $\delta^{13}$C crossplots can be interpreted after Pearson and Wade [75].

Fig. 4. A. Temperature:depth profiles from modern measurements from offshore Tanzania (CTD data from, 41° 77 E, 10° 65 S, water depth of 2219 m [94]) and those generated by the HadCM3
(dashed) and NCAR (solid) models [80, 81]. Only the NCAR profile produced using a 2240 ppmv
$pCO_2$ climate forcing is illustrated here; the sea surface temperatures in the modelled profile are
consistent with the temperatures derived from middle Eocene mixed layer foraminiferal $\delta^{18}O$
values. The profiles generated by 1120 ppmv (used for the late Eocene timeslice) and 4480 ppmv
(used for the early Eocene timeslices) $pCO_2$ simply shift the profile to higher or lower temperatures.

B. Temperature:depth profile for the modern (a composite of 7 measured depth profiles from the
World Ocean Database 2009 [82] between 19.5 and 22.5 N and -95.5 and -96.5 W) and profile
generated by the NCAR model for the middle Eocene [81].

**Fig. 5.** A-H. Step-by-step reconstruction of $\delta^{13}C$:depth gradients using this data and modelled
temperature:depth profiles. i) Cross plots of $\delta^{13}C$ and $\delta^{18}O$ data from Pearson et al. [50], Pearson et
al. [17] and Wade and Pearson [49] showing names of multiple species of planktonic (and benthic)
foraminifera and the size fraction in which they were analysed (given in $\mu m$), where appropriate.
Note that in Fig. 5H, species names have been updated from the original dataset in Pearson et al.,
[50]. *Ps. pseudowilsoni* in this case was originally named *Paragloborotalia pseudomayeri* in
Pearson et al. [50]. Strictly speaking, *Pa. pseudomayeri* is a synonym of *Turborotalia pomeroli*
[106] but at the time of data collection, the authors [50] actually designated this species name to
what would now be referred to as *Ps. pseudowilsoni*. A. = Acarinina; C = Catapsydrax; Cb =
Cribrohantkenina; Cg = Chiloguembelina; Ga. = Globoturborotalita; Gk. = Globigerinatheka;
Gm. = Guembelitrioides; I. = Igorina; M. = Morozovellain A-C, Morozovelloides in D-F; Pg. =
Planoglobanomalina; Ph. = Pseudohastigerina; Ps. =Parasubbotina; S. = Subbotina; Ta. =
Turborotalita. ii) The same cross plots redrawn to show mixed layer temperature (generated from
the lowest $\delta^{18}O$ value), denoted by a dashed line. Empty squares represent those data points that
were not used to construct the final $\delta^{13}C$ profile following the criteria of Birch et al. (2012). Note
that no data points were eliminated from the Guayabal Formation assemblage (H) because during
the initial data collection, foraminifera were chosen from all size fractions >250 $\mu m$. iii)

Temperature:depth profile showing how the $\delta^{18}O$-generated temperatures were used to generate
absolute depths. iv) $\delta^{13}C$:depth profiles for each sample (black) and the modern profile (green) for
offshore Tanzania (averaged profile from several nearby sites). Note that studies suggest that
surface Indian Ocean $\delta^{13}C_{DIC}$ values have decreased by ~ 0.6 ‰ since 1900 [107] due to the ‘Suess
effect’ i.e. the influence of isotopically light carbon emitted through burning fossil fuels. This has
not been included in the figure but should be noted.
For Review Only

Higher heterotrophs

Zooplankton

Phytoplankton

CO$_2$ CO$_2$

Respiration

Respiration

Respiration

Photosynthesis

Bacteria

Burial

δ$^{13}$C$_{DIC}$

Water depth (m)

Sea surface

High δ$^{13}$C$_{DIC}$ - pref. fixation of light C in organic matter

δ$^{13}$C$_{DIC}$ values decrease as organic matter is respired

http://mc.manuscriptcentral.com/issue-ptrsa
Metabolic depletion <250 μm

Symbiotic enrichment >355μm

Symbiotic species that sink and encrust at depth may have values that plot on a mixing line between surface and deep habitats

δ\text{13}C equilibrium line
**A**

- **i**
  - Triangularis 212-250
  - S. triangular 300-355
  - M. velascoensis 212-355
  - M. velascoensis 212-250
  - M. velascoensis 250-300
  - M. velascoensis 350-355
  - M. subb. 300-355
  - S. triangular 300-355
  - S. triangular 250-300
  - A. coalingensis 250-300

- **ii**
  - All datapoints used in reconstructed δ¹³C:depth profiles

- **iii**
  - Water temperature (°C)

- **iv**
  - δ¹³C DIC

**B**

- **i**
  - A. pseudosubsphaerica 212-250
  - Ps. pseudowilsoni 212-250
  - Ps. pseudowilsoni 212-250
  - S. inoaquispina 212-250
  - S. eocaena 212-250
  - S. roesnaesensis 212-250
  - Mixed benthics 300-425

- **ii**
  - Metabolic depletion?

- **iii**
  - Some gametogenic calcite?

- **iv**
  - δ¹³C DIC

**Notes:**
- δ¹³C
- Water temperature
- Water depth
- Metabolic depletion
- Gametogenic calcite