

Calcification response to climate change in the Pliocene?

C. V. Davis et al.

# Calcification response to climate change in the Pliocene?

C. V. Davis<sup>1,\*</sup>, M. P. S. Badger<sup>1,2</sup>, P. R. Bown<sup>3</sup>, and D. N. Schmidt<sup>1</sup>

<sup>1</sup>School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Rd, Bristol, BS8 1RJ, UK

<sup>2</sup>Organic Geochemistry Unit, The Cabot Institute and Bristol Biogeochemistry Research Centre, School of Chemistry, University of Bristol, Cantock's Close, Bristol, BS8 1TS, UK

<sup>3</sup>Department of Earth Sciences, University College London, London WC1E 6BT, UK

\*now at: Bodega Marine Laboratory, University of California Davis, Bodega Bay, CA 94923 USA

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Correspondence to: M. P. S. Badger (marcus.badger@bristol.ac.uk)

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Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Abstract

As a result of anthropogenic  $p\text{CO}_2$  increases future oceans are growing warmer and lower in pH and oxygen, conditions that are likely to impact planktic communities. Past intervals of elevated and changing  $p\text{CO}_2$  and temperatures can offer a glimpse into the response of marine calcifying plankton to changes in surface oceans under conditions similar to those projected for the future. Here we present new records of planktic foraminiferal and coccolith calcification from Deep Sea Drilling Project Site 607 (mid North Atlantic) and Ocean Drilling Program Site 999 (Caribbean Sea) from the Pliocene, the last time that  $p\text{CO}_2$  was similar to today, and extending through a global cooling event into the Intensification of Northern Hemisphere Glaciation (3.3 to 2.6 million years ago). Test weights of both surface-dwelling foraminifera *Globigerina bulloides* and thermocline-dwelling foraminifera *Globorotalia puncticulata* vary, with a potential link to regional temperature variation in the North Atlantic, whereas in the tropics *Globigerinoides ruber* test weight remains stable. In contrast, reticulofenestrid coccoliths show a narrowing size range and a decline in the largest lith diameters over this interval. Our results suggest no major changes in plankton calcification during the high  $p\text{CO}_2$  Pliocene or during the transition into an icehouse world.

## 1 Introduction

Over the last 250 yr atmospheric  $p\text{CO}_2$  levels have increased from pre-industrial (pre-1750) levels of 280 parts per million (ppm) to 393 ppm in 2012 (Dlugokencky and Tans, 2013). As a consequence, the future ocean is predicted to be warmer, more acidic and oxygen poorer (Solomon et al., 2007). The environmental impacts of anthropogenic atmospheric  $p\text{CO}_2$  and resultant climatic changes are predicted to be widespread across all ecosystems with potential influences on biogeochemical cycles and ecosystem services (Turley et al., 2010). Previous research has largely focused on documenting the response of marine calcifiers to environmental parameters in laboratory culture

BGD

10, 6839–6860, 2013

### Calcification response to climate change in the Pliocene?

C. V. Davis et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Calcification response to climate change in the Pliocene?

C. V. Davis et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

experiments (Spero et al., 1997; Bijma et al., 1999; Riebesell et al., 2000; Langer et al., 2006; Iglesias-Rodriguez et al., 2008). In the natural environment, however, the plasticity within the population, the selection of ecophenotypes and genotypes with different environmental preferences, their migration, adaptation and evolution are possible mechanisms which may act to dampen the effect of ocean acidification on marine organisms and the processes they influence. Laboratory culture experiments therefore incompletely represent whole ecosystem responses to environmental change.

In contrast, marine sediments provide a record of past environmental perturbations in natural environments with their associated complexity, thereby allowing assessment of the potential for marine organisms to migrate, acclimatize and/or adapt to changing environmental conditions. Importantly, the geological record allows upscaling from experiments on single specimens or strains to large scale ecosystem changes and their associated biogeochemical impacts.

Coccolithophores and foraminifers are key groups in the marine ecosystem and carbon cycle, together contributing the majority of pelagic carbonate production (Schiebel, 2002). Surface ocean temperature and pH have been shown to affect the physiology and ecology of both foraminifera (Bé and Tolderlund, 1971; Hemleben et al., 1989; Bijma et al., 1990; Schmidt et al., 2004a) and coccolithophores (Gibbs et al., 2004; Thierstein and Young, 2004; Zondervan, 2007) and their calcification both, in laboratory cultures and field studies (Bijma et al., 1999; Barker and Elderfield, 2002; Langer et al., 2006, 2009; de Moel et al., 2009; Beaufort et al., 2011). The response, however, is strongly strain and species specific (Langer et al., 2006, 2009) and the experiments are often short term with few exceptions (Müller et al., 2010; Lohbeck et al., 2012). In general, high CO<sub>2</sub> results in smaller and less calcified coccoliths and lighter foraminifer tests; however larger cells supported by higher CO<sub>2</sub> lead in a few cases to an overall increase in lith size under high atmospheric pCO<sub>2</sub> conditions (Iglesias-Rodriguez et al., 2008).

Surface ocean carbonate chemistry has remained remarkably constant over the recent evolutionary history of modern plankton (Hönisch et al., 2012) with typical

surface ocean variations between glacial and interglacials of no more than 0.2 pH units (Hönisch and Hemming, 2005; Foster, 2008). We therefore focus on deeper time records to test the effect of warmer, lower pH oceans on calcifying plankton.

The Pliocene is the most recent epoch with atmospheric  $p\text{CO}_2$  levels (around 380–415 ppm) consistently above pre-industrial levels but with continental placement and vegetation similar to modern (Pagani et al., 2010; Seki et al., 2010; Bartoli et al., 2011; Badger et al., 2013). Our study encompasses the end of the Pliocene Warm Period (~3.3 to 3.0 Ma) and the subsequent interval of global cooling culminating at ~2.6 Ma, in the Intensification of Northern Hemisphere Glaciation (INHG) (Ravelo et al., 2004).

We assess potential changes in the abundance and calcification of planktic foraminifers and coccolithophores, zooplankton and phytoplankton respectively, at two sites from the tropics and the mid-latitudes. Changes in atmospheric  $p\text{CO}_2$  should have a synchronous effect across most of the world's surface oceans while temperature changes will be more accentuated in the higher latitudes than in the tropics (Lawrence et al., 2009) thereby allowing us to address the relative importance of these synergistic factors.

## 2 Materials and methods

Sediments were taken from Deep Sea Drilling Project (DSDP) Site 607 in the mid-North Atlantic (41°00' N 32°57' W; 3426 m water depth) and from Ocean Drilling Program (ODP) Site 999 in the Caribbean Sea (12°45' N, 78°44' W; 2828 m water depth; Fig. 1). The age models for both sites were calculated from Lisiecki and Raymo's LR04 benthic foraminifera derived global  $\delta^{18}\text{O}$  stack (Lisiecki and Raymo, 2005) and were used to calculate linear sedimentation rates and mass accumulation rates (MARs).

Calcium carbonate ( $\text{CaCO}_3$ ) MARs, an indication of carbonate production in the surface waters, were calculated from shipboard observations of  $\text{CaCO}_3$  content, density and water content (Shipboard Scientific Party, 1997), while planktic foraminiferal mass accumulation rates (FMAR) were calculated from the bulk MARs and the sand

**BGD**

10, 6839–6860, 2013

### Calcification response to climate change in the Pliocene?

C. V. Davis et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

---

**Calcification  
response to climate  
change in the  
Pliocene?**C. V. Davis et al.

---

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[⏪](#)[⏩](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

fraction of the sediment which consists predominantly of planktic foraminifers, and only a small number (< 1 %) of benthic foraminifers. Changes in the relative contribution of foraminifers to coccolithophores to sediment production were calculated by dividing foraminiferal MAR by carbonate MAR.

5 Sediment samples were washed over a 63  $\mu\text{m}$  sieve and dry sieved at 150  $\mu\text{m}$ . In each sample, at least 150 tests and test fragments (defined as any test with visible damage to at least two chambers or entirely lacking at least one chamber) were counted from the > 150  $\mu\text{m}$  size fraction as a measure of dissolution and an indicator of preservation (Berger, 1968, 1970). Sea surface temperature (SST) data was taken  
10 from Naafs et al. (2010) for Site 607, Groeneveld (2005) and Badger et al. (2013) for Site 999. Additional data from 2.6 to 2.8 Ma were generated following the procedures detailed in Badger et al. (2013).

Relative changes in average foraminiferal test weight can be interpreted as changes in test thickness and the extent of calcification (Barker, 2002; Barker et al., 2003).  
15 Therefore, between 10 and 30 foraminifera of *Globigerina bulloides* and *Globorotalia puncticulata* at Site 607 and *Globigerinoides ruber* at Site 999 were picked from the 300–355  $\mu\text{m}$  size fraction and size normalised following the protocol in Barker (2002). *Gs. ruber* specimens were picked to reflect sensu stricto specimens, excluding kumerform and sensu lato specimens as these are known to have different habitats  
20 (Steinke et al., 2005) and therefore potentially different reactions to environmental drivers. For each sample, foraminifera were weighed on a six-point Sartorius MC5 microbalance to obtain a population average weight. Sixty-three populations of *G. bulloides*, fifty-two of *G. puncticulata* and seventy of *Gs. ruber* were analysed. *G. puncticulata* was largely absent in the North Atlantic prior to 3.23 Ma (Lutz, 2011) and was not  
25 found in significant numbers. Error was estimated by repeat measurements of eight *G. bulloides* populations; three of which were re-picked from the original sample and another five reweighed. The error ranged from 2.58 to 2.32  $\mu\text{g}$ , which is in line with the error of the balance ( $\pm 2 \mu\text{g}$ ).

The average diameter of each specimen in the same orientation was measured from digital images using ImageJ. A sample average test length was calculated to allow size normalisation. Weighed populations of *G. puncticulata* were not size normalized due to the greater uncertainty in estimating volume from external measurements given the high variability of how conical individual tests are (see Barker 2002 for discussion on the morphologically similar species *G. inflata*). For each sample, the size of all flat-lying reticulofenestrid liths was measured on a strew slide using an Hitachi S-3500N Scanning Electron Microscope (SEM). Between 82–178 liths in each sample were imaged and the maximum diameter measured using ImageJ.

### 3 Results

Carbonate MARs are nearly twice as high at Site 607 than at Site 999 (Fig. 2b). There is an orbital variability in the carbonate MARs at Site 607 while, in contrast, at Site 999 the carbonate MAR is more stable, in line with less environmental variability. Test fragmentation does not change significantly at Site 607 with an average value of  $16.3\% \pm 4.8\%$  ( $1\sigma$ ), indicating consistently good preservation, consistent with the Shipboard Report (Fig. 3, Shipboard Scientific Party, 1987). In contrast, at Site 999 fragmentation decreases from 40–60% (at 3.0 Ma) to 20–40% (at 2.6 Ma) potentially caused by bottom water changes related to the final closure of the Central American Seaway (CAS) (Haug et al., 2001).

The foraminiferal contribution to the sediment is small at both sites, with 24 wt% at Site 999 and 8 wt% at Site 607 (Fig. 3g). While foraminiferal MAR are variable ( $0.050$  to  $0.240 \text{ g cm}^{-2} \text{ kyr}^{-1}$  at Site 999,  $0.016$  to  $0.109 \text{ g cm}^{-2} \text{ kyr}^{-1}$  at Site 607), there is no consistent trend over our studied interval. The relative importance of foraminifers to the carbonate production increases from 2.7 Ma onwards at Site 607, while there is no change at Site 999.

Foraminiferal weight ranges from  $13.4$  to  $22.4 \mu\text{g}$  for *G. bulloides*,  $15.7$  to  $21.1 \mu\text{g}$  for *Gs. ruber*, and  $24.8$  to  $40.9 \mu\text{g}$  for *G. puncticulata* (Fig. 3d, e). Unexpectedly, the deep

BGD

10, 6839–6860, 2013

## Calcification response to climate change in the Pliocene?

C. V. Davis et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

dweller *G. puncticulata* shows significantly higher weight variability than the surface dweller. At Site 999 at 2.7 Ma, *Gs. ruber* weight drops which cannot be due to dissolution as preservation is improving. In contrast, at Site 607 there is no overall change in weight throughout the record.

5 Average coccolith size is stable at Site 607, while at Site 999 average lith size increases towards 3 Ma, is high from 2.94 to 2.80 Ma and drops thereafter – the increase between 2.94 and 2.80 Ma being driven by an increase in the number of liths larger than 5  $\mu\text{m}$  (Fig. 3b, c). It is important to note though, that Site 607 records a strong  
10 variability of relative contribution of large liths and a clear loss of those large liths from 2.7 Ma.

## 4 Discussion

Coccolithophores and foraminifera are both thought to respond to changes in atmospheric  $p\text{CO}_2$ . This has raised concerns about the future of the alkalinity pump (Ridgwell and Zeebe, 2005), the export of carbonate from the surface ocean to the deep  
15 sea, and the effect of a change in carbonate ballasting on the efficiency of the biological pump (Klaas and Archer, 2002). Therefore, the prediction would be that the carbonate MAR should be lower in a high  $p\text{CO}_2$  world than today and that it would increase at the time of postulated drop in  $p\text{CO}_2$ .

20 However, despite the environmental change associated with the INHG (Haug and Tiedemann, 1998) we see no clear shift in carbonate MAR. The largest signal in the carbonate MAR is not at the end of the Pliocene warm interval (Pagani et al., 2010; Seki et al., 2010) but across the glacial-interglacial changes most prominent at Site 607 and much larger than at Site 999 (Fig. 2). Overall carbonate MAR is higher at Site 607 compared to Site 999 which is unsurprising given the generally oligotrophic setting  
25 in the Caribbean (Jain and Collins, 2007), and the higher productivity at the higher latitude site (Behrendfeld and Falkowski, 1997).

BGD

10, 6839–6860, 2013

### Calcification response to climate change in the Pliocene?

C. V. Davis et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

## Calcification response to climate change in the Pliocene?

C. V. Davis et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



The contrasting records at these two distant sites suggest that local, rather than global or regional drivers are responsible for the changes in MAR. As the surface ocean at both sites are in equilibrium with the atmosphere today (Takahashi et al., 2002) (and there is no reason to think that this was not the case in the Pliocene) any atmospheric  $p\text{CO}_2$  change should affect both sites in the same way and with the same timing; in contrast, any changes arising from a local environmental affect such as SST (Fig. 4) would be muted in the Caribbean ( $\sim 23\text{--}25^\circ\text{C}$ , Groeneveld, 2005) compared with the North Atlantic ( $\sim 17\text{--}22^\circ\text{C}$ , Naafs et al., 2010), and this is what we in fact see. While it is tempting to compare the differences in  $p\text{CO}_2$  change between glacial and interglacials in the Pliocene to the late Pleistocene ( $\sim 40$  ppm, Badger et al., 2013 vs  $\sim 100$  ppm, Siegenthaler et al., 2005) and the amplitude of changes in carbonate production, too many other factors, such as temperature, stratification and nutrient availability, will be influenced by the same forcing, making a direct comparison difficult. Also, while  $p\text{CO}_2$  and SST are globally tightly coupled, at Site 607 the migration of the North Atlantic Current and the northern extent of the subtropical gyre will likely amplify the response (Naafs et al., 2010).

Foraminifera make up a minor proportion of carbonate production by mass, and the  $\sim 3$  times higher wt% at Site 999 is likely due to the larger species present (Schmidt et al., 2004a, 2006) and their higher overall mass. At Site 999, foraminiferal weights are surprisingly stable and show no significant variation across any environmental changes, including the closure of the CAS. At Site 607, *G. bulloides* weight changes by around a third, associated with glacial-interglacial cycles; similar variability in test weight is seen through the Pleistocene glacial-interglacial cycles at a similar location and related to  $p\text{CO}_2$  forcing (Barker and Elderfield, 2002; Moy et al., 2009). The latter is similar to our site in a dynamic environment in the central subantarctic zone in the proximity to a frontal system (Moy et al., 2009). Absolute test weights and range of test weight in North Atlantic Pliocene and Pleistocene *G. bulloides* are similar despite the higher  $p\text{CO}_2$  during the Pliocene. Interestingly, though the weights found in the

sediment samples in the Moy (2009) study (though not their trap data), are significantly higher than in our data or the Barker and Elderfield (2002) study for the same species.

Given the predicted smaller  $p\text{CO}_2$  variability between Pliocene glacial-interglacial cycles compared to the Pleistocene, we would have expected smaller foraminiferal test weight changes in the Pliocene (half the magnitude observed here), if this was the main or even sole driver. We would also expect to see changes at both sites of similar magnitude if global  $p\text{CO}_2$  were the main driver. As for the carbonate MAR data, the contrasting records at these two sites suggest that regional drivers are responsible for the changes in test weight and not changes in  $p\text{CO}_2$ . The magnitude of temperature change during the Pliocene at Site 607 and Pleistocene at Site NEAP 8K of Barker and Elderfield (2002) was similar, while the temperature in the Caribbean during the Pliocene was very stable. The large glacial-interglacial temperature difference at Site 607 of  $\sim 6^\circ\text{C}$  is the result of the proximity to the North Atlantic Current, as mentioned above. Changes in temperature and frontal dynamics influence the growth of planktic foraminifers, with smaller individuals growing under less optimal conditions due to the environmental variability close to frontal systems (Schmidt et al., 2003). The effect of the frontal system on thermocline structure at Site 607 may also be the cause of the higher test weight variability in the thermocline dwelling *G. punticulata*, which is larger than the surface dweller *G. bulloides*. Changes in thermocline structures have been shown to influence planktic foraminiferal growth, with larger sizes in more stratified waters (Schmidt et al., 2004b).

The overall reaction of coccolithophores to these environmental changes is difficult to predict due to the wide range of responses to multiple forcings, including ocean acidification (Langer et al., 2006; Ridgwell et al., 2009; Beaufort et al., 2011). Additionally, the average reticulofenestrid coccolith size within an assemblage reflects the diversity of species, strains and/or phenotypic variability within populations, all of which may have their own environmental preferences. Coccolith size may therefore reflect a complex interplay of extinction, migration and size changes within the population.

Calcification response to climate change in the Pliocene?

C. V. Davis et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Calcification response to climate change in the Pliocene?

C. V. Davis et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



In general, the Pliocene is an interval of relatively high evolutionary turnover in coccolithophores (Bown, 2005). There are at least four *Discoaster* extinctions (Gradstein et al., 2012) indicating significant changes within the nanoplankton communities, but these do not directly impact our data, which solely represent the dominant taxa, the reticulofenestrads. The different size trends seen at the two sites represent different proportions of species/genotypes/ecophenotypes in the reticulofenestrads populations, but these are relatively subtle shifts, which generally fall below the resolution of traditional taxonomic groupings and hence their relationship to environmental change is uncertain. It is unlikely that these trends reflect dissolution because fragmentation is relatively stable across the record at Site 607 and improves at Site 999 while large liths disappear which are less prone to dissolution (Fig. 2).

The overall trend towards smaller liths through the Pliocene into the Quaternary has been previously documented and linked to species turnover and extinction events (Young, 1990; Gibbs et al., 2005). A decline in the larger reticulofenestrads coccoliths which we find at Site 607 has also been observed in the Atlantic, Pacific, Indian and Arctic oceans (Young, 1990; Sato and Kameo, 1996; Kameo and Takayama, 1999; Kameo and Bralower, 2000; Sato et al., 2002). This trend cannot be driven by the extinction of the largest ( $> 7 \mu\text{m}$ ) reticulofenestrads (*Reticulofenestra pseudoumbilicus*) as this occurred just prior to our study interval, at 3.7 Ma. Other, more subtle but discrete events, such as the disappearance of reticulofenestrads coccoliths  $> 5 \mu\text{m}$  (*Reticulofenestra ampla* of Sato et al., 1991), are seen at Site 607 around  $\sim 2.7$  Ma, and the global nature of this trend suggests that these are widespread evolutionary changes. Evolution, changes in abundance, and extinction of large-sized genera, such as *Calcidiscus*, *Coccolithus*, *Helicosphaera*, and *Reticulofenestra*, and the rise of small-coccolith producing taxa, such as *Emiliana* and *Gephyrocapsa* have been linked to size changes in coccolithophore assemblages (Herrmann et al., 2012). In contrast, the size record at the Caribbean site is dominated by a short-lived increase in larger liths ( $> 5 \mu\text{m}$ ) between 2.8 and 3.0 Ma, and may represent a migration event into the Caribbean. The predicted change in  $p\text{CO}_2$  is clearly not influencing the lith size in reticulofenestrads and the size

differences between the Caribbean (smaller liths) and North Atlantic (larger liths) is presumably reflecting different ecological preferences within the small to medium sized reticulofenestrids.

The brief influx of large specimens in the Caribbean could reflect the complex environmental change in the area during the final stages of the closure of the CAS but again this is not time equivalent with the suggested changes in  $p\text{CO}_2$  and hence not related to  $p\text{CO}_2$ . The final closure of the CAS has been suggested for 2.7 Ma (Bartoli et al., 2005; Schmidt, 2007) which coincides with the first major glaciation of the Pliocene at 2.73 Ma (Lisiecki and Raymo, 2005) and a number of changes in our biotic records. The loss of large reticulofenestrid coccolithophores in the North Atlantic, a relative increase of foraminifera as carbonate producers at the same site, and a minor reduction of foraminiferal weight in the Caribbean all suggest significant changes in the North Atlantic in general. The convergence of the lith records might suggest that the environments at both sites became more similar and may be linked to increase in warm-water transport to the north due to the closure of the shallow-water throughflow (Haug et al., 2001) or to increased vertical stratification in high latitudes (Sigman et al., 2004).

## 5 Conclusions

Sea surface temperature or related environmental parameters, some of which might be linked to the closure of the Central Tropical Seaways, appear to have a larger effect on planktic carbonate producers than  $p\text{CO}_2$  alone during the Pliocene. The drop in  $p\text{CO}_2$  at the end of the Pliocene had no effect on carbonate mass accumulation, reticulofenestrid coccolith size or foraminiferal weight. While these environmental changes may not be forcing critical stress on either plankton group (in terms of evolution or extinction events), these may be causing organisms to adjust their biogeographical distribution to suit environmental tolerances (i.e. Renaud and Schmidt, 2003). Both groups of organisms adapted to the environmental changes during the Pliocene, including the higher

**BGD**

10, 6839–6860, 2013

### Calcification response to climate change in the Pliocene?

C. V. Davis et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

$p\text{CO}_2$  levels that are comparable to those predicted for the next decades, but also the onset of more intense glaciations. The stark contrast of our results compared to those predicted from experiments on both groups suggests that rates of change rather than absolute  $p\text{CO}_2$  values might drive a calcification response in these groups.

5 **Supplementary material related to this article is available online at:**  
**[http://www.biogeosciences-discuss.net/10/6839/2013/  
bgd-10-6839-2013-supplement.pdf](http://www.biogeosciences-discuss.net/10/6839/2013/bgd-10-6839-2013-supplement.pdf)**

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**Calcification  
response to climate  
change in the  
Pliocene?**

C. V. Davis et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Calcification response to climate change in the Pliocene?

C. V. Davis et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)



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C. V. Davis et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)




[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

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## Calcification response to climate change in the Pliocene?

C. V. Davis et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

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C. V. Davis et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

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## Calcification response to climate change in the Pliocene?

C. V. Davis et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)

[⏪](#)

[⏩](#)

[◀](#)

[▶](#)

[Back](#)

[Close](#)

[Full Screen / Esc](#)

[Printer-friendly Version](#)

[Interactive Discussion](#)

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# BGD

10, 6839–6860, 2013

## Calcification response to climate change in the Pliocene?

C. V. Davis et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

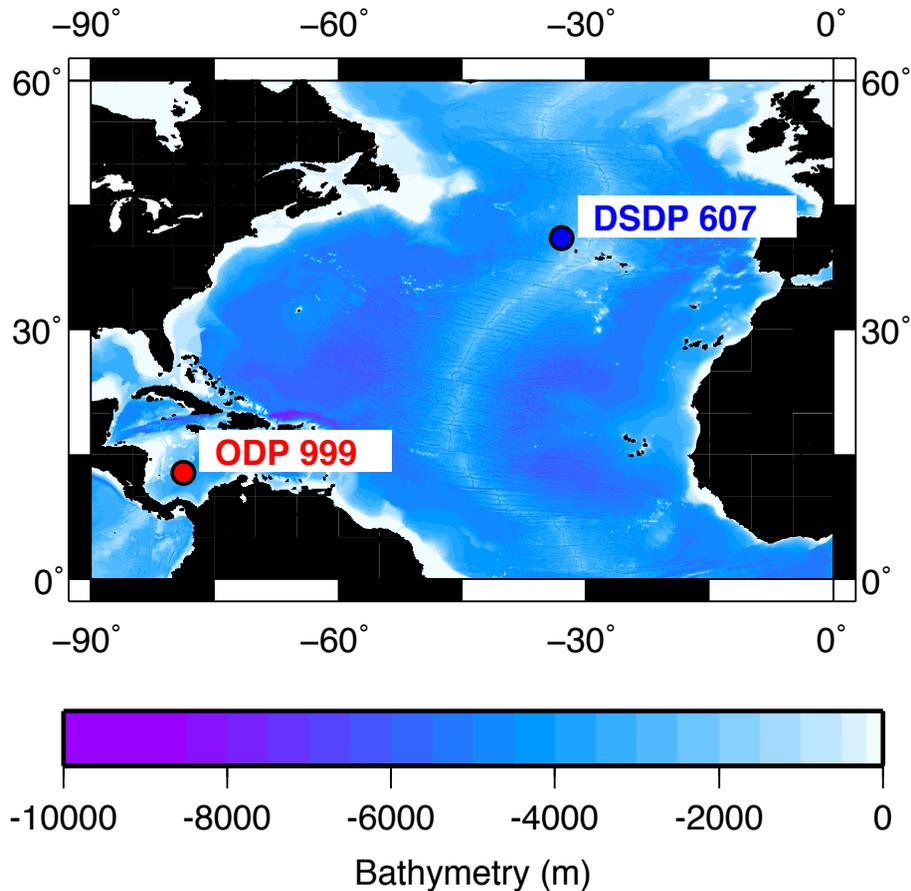
Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



**Fig. 1.** Location map of study sites DSDP Site 607 (blue) and ODP Site 999 (red). Bathymetry from (Amante and Eakins, 2009). Colours coding for both Sites will be used in all the following figures.

## BGD

10, 6839–6860, 2013

### Calcification response to climate change in the Pliocene?

C. V. Davis et al.

[Title Page](#)

[Abstract](#)

[Introduction](#)

[Conclusions](#)

[References](#)

[Tables](#)

[Figures](#)



[Back](#)

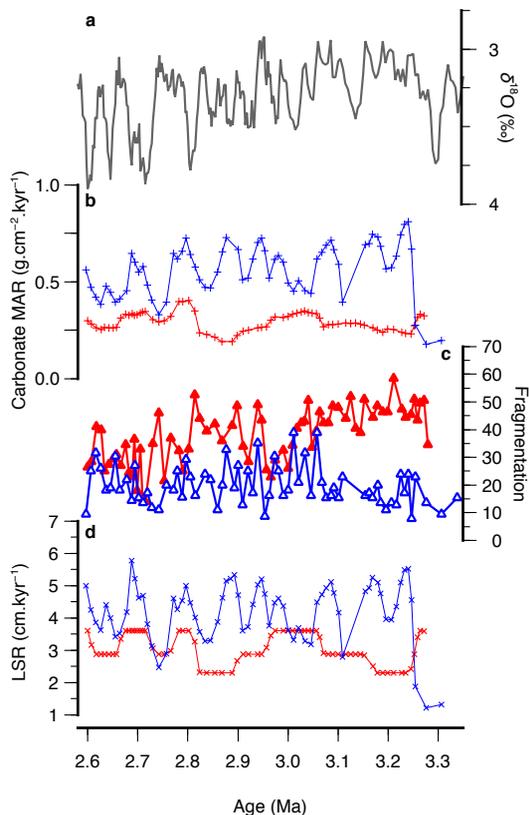
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[Full Screen / Esc](#)

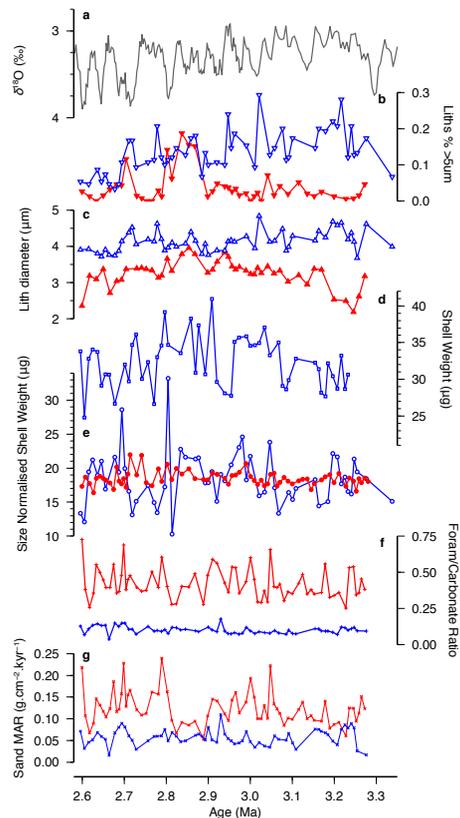
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[Interactive Discussion](#)

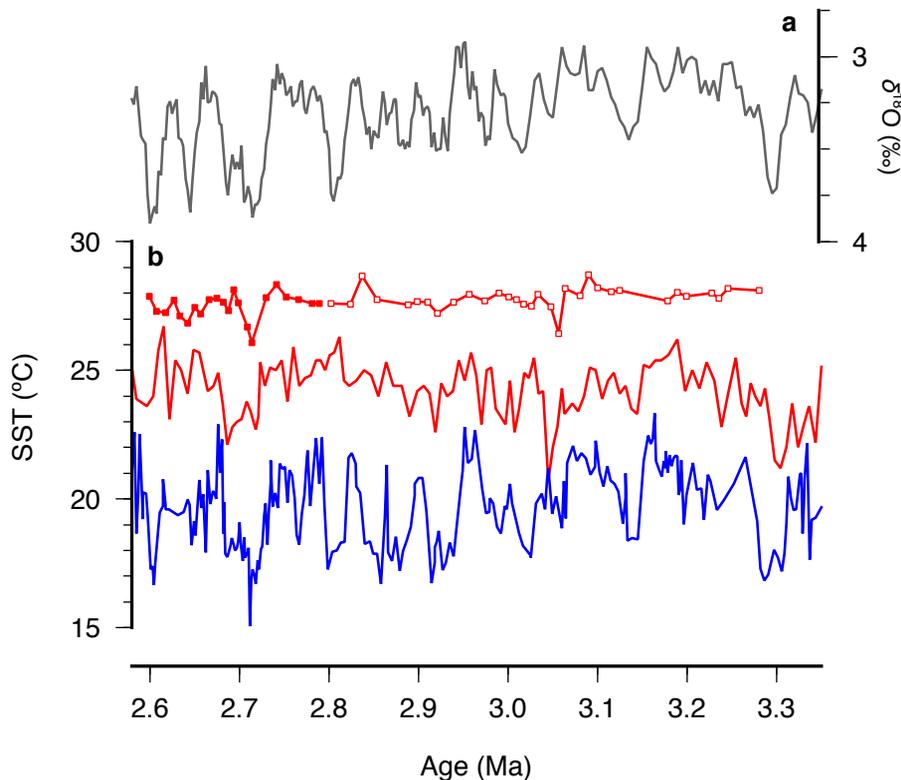




**Fig. 2.** (a) Benthic foraminifera oxygen isotope ( $\delta^{18}\text{O}$  (‰)) stack (LR04; Lisiecki and Raymo, 2005), (b) carbonate mass accumulation rate (MAR,  $\text{g cm}^{-2} \text{kyr}^{-1}$ ), (c) planktic foraminifera fragmentation (whole to fragment index, high values indicating more dissolution) and (d) linear sedimentation rates (LSR,  $\text{cm kyr}^{-1}$ ) calculated from LR04 based age models and shipboard physical properties. For all panels, red represents ODP Site 999 and blue DSDP 607.



**Fig. 3.** (a) Benthic foraminifera oxygen isotope ( $\delta^{18}\text{O}$  (‰)) stack (LR04; Lisiecki and Raymo, 2005), (b) percentage of measured lith with diameter greater than 5  $\mu\text{m}$ , (c) average lith diameter, (d) thermocline dweller *G. puncticulata* mean test weight, (e) size normalised test weight of the surface dwellers *G. bulloides* and *Gs. ruber*, (f) Foraminifera: carbonate ratio and (g) sand mass accumulation rate ( $\text{g cm}^{-2} \text{ kyr}^{-1}$ ). For all panels red represents ODP Site 999 and blue DSDP 607.



**Fig. 4.** (a) Benthic foraminifera oxygen isotope ( $\delta^{18}\text{O}$  (‰)) stack (LR04; Lisiecki and Raymo, 2005) and (b) SST ( $^{\circ}\text{C}$ ) records from alkenone unsaturation index from Naafs et al. (2010) (Site 607; blue line), Badger et al. (2013) (Site 999; red open squares and line), and this study (Site 999; red filled squares and line) and from Mg/Ca ratio of *Globigerinoides sacculifer* (Groeneweld, 2005). For all panels red represents ODP Site 999 and blue DSDP Site 607.