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The response of calcifying plankton to climate change in the Pliocene

C. V. Davis1,*, M. P. S. Badger1,2, P. R. Bown3, and D. N. Schmidt1

1Organic Geochemistry Unit, Bristol Biogeochemistry Centre and The Cabot Institute, School of Chemistry, University of Bristol, Cantock’s Close, Bristol, BS8 1TS, UK
2Organic Geochemistry Unit, Cabot Institute and Bristol Biogeochemistry Research Centre, School of Chemistry, University of Bristol, Cantock’s Close, Bristol, BS8 1TS, UK
3Department of Earth Sciences, University College London, London WC1E 6BT, UK
* now at: Bodega Marine Laboratory, University of California Davis, Bodega Bay, CA 94923, USA

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

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Abstract. As a result of anthropogenic pCO2 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 pCO2 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 (weight and size) 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 pCO2 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 punc tculata 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 calcite production during the high pCO2 Pliocene or during the transition into an icehouse world.

1 Introduction

Over the last 250 yr atmospheric pCO2 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 pCO2 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 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). In coccoliths, the response, however, is strongly strain- and species-specific (Langer et al., 2006, 2009, 2011; Ridgewell et al., 2009), and the experiments are often short term with few exceptions (Lohbeck et al., 2012). These multi-generation experiments demonstrate the potential for selection of genotypes with differing environmental tolerances, and adaptation and evolution on relatively short timescales (500 generations). It has been argued that high CO$_2$ in the future will result in smaller and less calcified coccoliths and lighter foraminifer tests; however, larger cells supported by higher CO$_2$ levels (around 380–415 ppm) consistently above pre-industrial levels (around 380–415 ppm) 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. Furthermore, the latitudinal gradient between the sites allows the comparison of species with different biogeographic adaptation.

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 δ$^{18}$O stack (Lisiecki and Raymo, 2005) and were used to calculate linear sedimentation rates and mass accumulation rates (MARs).

Calcium carbonate (CaCO$_3$) MARs, an indication of carbonate production in the surface waters, were calculated from shipboard observations of CaCO$_3$ content, density and water content (Shipboard Scientific Party, 1997), while planktic foraminiferal mass accumulation rates (FMARs) were calculated from the bulk MARs and the sand fraction which share little in common in terms of their hydrology and nutrient regimes that could potentially overprint a synchronous pCO$_2$ signal. Changes in atmospheric pCO$_2$ 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. Furthermore, the latitudinal gradient between the sites allows the comparison of species with different biogeographic adaptation.
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 FMARs by carbonate MAR.

Sediment samples were washed over a 63 µm sieve and dry-sieved at 150 µm. 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 µm size fraction as a measure of dissolution and an indicator of preservation (Berger, 1968, 1970). Sea surface temperature (SST) data were taken from Naafs et al. (2010) for Site 607, Groeneveld (2005) and Badger et al. (2013) for Site 999. Additional SST 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). 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 µm size fraction and size-normalized following the protocol in Barker (2002). Gs. ruber specimens were picked to reflect sensu stricto specimens, excluding kummerform and sensu lato specimens as these are known to have different habitats (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. A total of 63 populations of G. bulloides, 52 of G. puncalcata and 70 of Gs. ruber were analysed. G. puncalcata was largely absent in the North Atlantic prior to 3.23 Ma (Lutz, 2011) and was not 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 µg, which is in line with the error of the balance (±2 µg).

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 normalization. Weighed populations of G. puncalcata 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 reticulofenestriliths from the < 63 µm fraction, made up almost exclusively of coccoliths, was measured on a strew slide using a Hitachi S-3500N scanning electron microscope (SEM). Between 82 and 178 liths in each sample were imaged and the maximum diameter measured using ImageJ.

Fig. 2. (a) Benthic Foraminifera oxygen isotope ($\delta^{18}$O (%)) stack (LR04; Lisiecki and Raymo, 2005), (b) carbonate mass accumulation rate (MAR, g cm$^{-2}$ kyr$^{-1}$), (c) planktic Foraminifera fragmentation (whole to fragment index, high values indicating more dissolution) and (d) linear sediment rates (LSRs, 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.

3 Results

Carbonate MARs are nearly twice as high at Site 607 compared to 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% ± 4.8% (1σ), 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). At neither site did fragmentation couple with the foraminiferal/coccolithophores ratio, which we therefore deem to be influenced by differing abundances of these two calcifiers and not by preferential dissolution of foraminifers.

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 FMARs are variable (0.050 to 0.240 g cm$^{-2}$ kyr$^{-1}$ at Site 999, 0.016 to 0.109 g cm$^{-2}$ 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 µg for *G. bulloides*, 15.7 to 21.1 µg for *Gs. ruber*, and 24.8 to 40.9 µg for *G. punctulata* (Fig. 3d, e). Unexpectedly, the deep dweller *G. punctulata* 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.

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 µm (Fig. 3b, c). It is important to note though that Site 607 records a strong variability of relative contribution of large liths and a clear loss of those large liths from 2.7 Ma.

### Discussion

Coccolithophores and Foraminifera are both thought to respond to changes in atmospheric $p$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 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 $p$CO$_2$ world than today and that it would increase at the time of postulated drop in $p$CO$_2$.

However, despite the environmental change associated with the intensification of Northern Hemisphere glaciation (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 in the Caribbean (Jain and Collins, 2007), and the higher productivity at the higher latitude site (Behrendfeld and Falkowski, 1997).

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 is near equilibrium with the atmosphere today (Takahashi et al., 2002, 2009; and there is no reason to think that this was not the case in the Pliocene), any atmospheric $p$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 effect such as SST (Fig. 4) would be muted.
in the Caribbean (∼23–25 °C, Groeneveld, 2005) compared with the North Atlantic (∼17–22 °C, Naafs et al., 2010), and this is what we in fact see. While it is tempting to compare the differences in $pCO_2$ change between glacial and interglacials in the Pliocene and the late Pleistocene (∼40 ppm, Badger et al., 2013 vs. ∼100 ppm, Siegenthaler et al., 2005), and the amplitude of changes in carbonate production, there are many other factors, such as temperature, stratification and nutrient availability, that will be influenced by the same forcing, making a direct comparison difficult. Also, while $pCO_2$ 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).

We cannot rule out an influence of either bottom water saturation state or pore water saturation state on foraminiferal test weight, the former of which has been shown to have a significant impact in past studies (Lohman et al., 1995). Fragmentation of foraminifer tests suggests a consistent state of preservation for carbonate sediments at Site 607 but an improvement of preservation around ∼2.8 Ma at Site 999. At Site 607, given that there is no indication of changes in the degree of dissolution through our study interval, samples in this core are likely not impacted by changing dissolution. However, it is possible that the observed preservation changes at Site 999 may have an effect on the record. If such an influence were taken into account, this would make shell weight even lighter after ∼2.8 Ma, not heavier as would be expected if foraminiferal weight were following $pCO_2$. Thus, the impacts of changes in pore water and/or bottom water saturation state on test weight do not influence our interpretation of the weight records at Sites 607 and 999.

Foraminifera make up a minor proportion of carbonate production by mass, and the ∼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 one-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 $pCO_2$ forcing (Barker and Elderfield, 2002; 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 $pCO_2$ during the Pliocene. Interestingly though, the weights found in the sediment samples in the Moy et al. (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 $pCO_2$ 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 were the main or even sole driver. We would also expect to see changes at both sites of similar magnitude if global $pCO_2$ 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 $pCO_2$. The magnitudes of temperature change during the Pliocene at Site 607 and Pleistocene at Site NEAP 8K of Barker and Elderfield (2002) were similar, while the temperature in the Caribbean during the Pliocene was very stable. The large glacial–interglacial temperature difference of ∼6 °C at Site 607 is plausibly 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

![Fig. 4. (a) SST with linear trend line (Naafs et al., 2010) and (b) SST (°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* (Groeneveld, 2005). For all panels red represents ODP Site 999 and blue DSDP Site 607 and (c) benthic Foraminifera oxygen isotope ($\delta^{18}O$ (%)) stack (LR04; Lisiecki and Raymo, 2005)](www.biogeosciences.net/10/6131/2013/)
test weight variability in the thermocline-dwelling *G. punc-
ticulata*, which is greater 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). Weight changes at
both sites could also be due to the presence of changing abun-
dances of cryptic species within established species, as
are known to exist for modern North Atlantic *G. bulloides* (Dar-
ling and Wade, 2008)

The overall reaction of coccolithophores to these environ-
mental 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.
Carbonate chemistry seems to influence the ecology of coc-
colithophores and alter species and morphotype abundance
in the ocean (Beaufort et al., 2011). Coccolith size may there-
fore reflect a complex interplay of extinction, migration and
size changes within the population.

In general, the Pliocene is an interval of relatively
high evolutionary turnover in coccolithophores (Bown,
2005). There are at least four *Discoaster* extinctions
(Gibbs et al., 2004) indicating significant changes within
the nanoplankton communities, but these do not di-
rectly impact our data, which solely represent the domi-
nant taxa, the reticulofenestrids. The different size trends
seen at the two sites represent different proportions of
species/genotypes/ecophenotypes in the reticulofenestrid
populations (e.g. as seen in Young and Westbroek, 1991;
Renaud, et al., 2002), but these are relatively subtle shifts,
which generally fall below the resolution of traditional taxo-
nomic groupings. Hence their relationship with environmen-
tal change is uncertain. It is likely that these trends reflect a
trend in turnover, not dissolution, because fragmentation is
relatively stable across the record at Site 607 and improves at
Site 999 when large liths, which are less prone to dissolution,
disappear (Fig. 2).

The overall trend towards smaller liths through the
Pliocene into the Quaternary has been previously docu-
mented and linked to species turnover and extinction events
(Young, 1990; Gibbs et al., 2005). A decline in the larger
reticulofenestrid coccoliths similar to that 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 Bra lower,
2000; Sato et al., 2002). This trend cannot be driven by the
extinction of the largest (> 7 µm) reticulofenestrids (*Reticu-
lofenastra 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 reticulofenestrid coc-
coliths > 5 µm (*Reticulofenastra amplus* of Sato et al.,
1991), are seen at Site 607 around ~ 2.7 Ma, and the global nature
of this trend suggests that these are widespread evolution-
ary changes. Evolution, changes in abundance, and extinc-
tions within large-sized genera, such as *Calcidiscus*, *Coc-
colithus*, *Helicosphaera*, and *Reticulofenastra*, and the rise
of small-coccolith-producing taxa, such as *Emiliania* and
*Gephyrocapsa*, have been linked to size changes in coccol-
ithophore assemblages (Herrmann et al., 2012). In contrast,
the size record at the Caribbean Site 999 is dominated by a
short-lived increase in larger liths (> 5 µm) between 2.8
and 3.0 Ma, and may represent a migration event into the
Caribbean. The predicted change in p*CO*₂ clearly does not
influence the lith size in reticulofenestrids, and the size dif-
ference between the Caribbean (smaller liths) and North At-

tlantic (larger liths) presumably reflects different ecological
preferences within the small- to medium-sized reticulofen-
estridds.

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*CO*₂. The fi-
nal closure of the CAS has been suggested to have occurred
at 2.7 Ma (Bartoli et al., 2005; Schmidt, 2007), which coin-
cides with the first major glaciation of the Plio-Pleistocene
at 2.73 Ma (Listiecki and Raymo, 2005) and a number of
changes in our biotic records. The loss of large reticulofen-
estrid coccolithophores in the North Atlantic, a relative in-
crease 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 At-

tlantic in general. The convergence of the lith records might
suggest that the environments at both sites became more simi-
lar and may be linked to an increase in warm-water transport
to the north due to the closure of the shallow-water through-
flow (Haug et al., 2001) or to increased vertical stratification
in high latitudes (Sigman et al., 2004).

One key difference that must be noted in any attempt to
compare these results from the Pliocene with modern oceans
is that the rate of p*CO*₂ change was much lower than at
present, a difference which could affect both any poten-
tial adaptive responses and the potential for decoupling of
pH and saturation state in the Pliocene. Thus, while proxy
records may clearly indicate both a greater than pre-industrial
atmospheric p*CO*₂ and lower pH, saturation state may not
have been significantly changed (Hönisch et al., 2012). This
latter parameter is especially important in the interpretation
of foraminiferal weight as it is the [CO³⁻] specifically that has
been implicated in driving changes in test weight.

5 Conclusions

The drop in p*CO*₂ at the end of the Pliocene had no ef-
fect on carbonate mass accumulation, reticulofenestrid coc-
colith size or foraminiferal weight. 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 $p$CO$_2$ alone during the Pliocene. While these environmental changes may not be forcing critical stress on either plankton group (in terms of evolution or extinction events), they may be causing organisms to adjust their biogeographical distribution to suit environmental tolerances (e.g. Renaud and Schmidt, 2003). Both groups of organisms adapted to the environmental changes during the Pliocene, including the higher $p$CO$_2$ levels that are comparable to those predicted for the next decades, as well as the onset of more intense glaciations. We suggest that rates of change, via a link to migration rates and generation time, rather than absolute $p$CO$_2$ values, might drive a calcification response in these groups.

Supplementary material related to this article is available online at http://www.biogeosciences.net/10/6131/2013/bg-10-6131-2013-supplement.pdf.

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