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Algal constraints on the Cenozoic history of atmospheric CO₂?

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BGD

4, 1–11, 2007

Algal constraints on palaeo-pCO₂

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

EGU

Abstract

An urgent question for future climate, in light of increased burning of fossil fuels, is the temperature sensitivity of the climate system to atmospheric carbon dioxide ($p\text{CO}_2$). To date, no direct proxy for past levels of $p\text{CO}_2$ exists beyond the reach of the polar ice core records. We propose a new methodology for placing an upper constraint on $p\text{CO}_2$ over the Cenozoic based on the living geological record. Specifically, our premise is that the contrasting calcification tolerance of various extant species of coccolithophore to raised $p\text{CO}_2$ reflects an “evolutionary memory” of past atmospheric composition. The different times of first emergence of each morphospecies allows an upper constraint of past $p\text{CO}_2$ to be placed on Cenozoic timeslices. Further, our hypothesis has implications for the response of marine calcifiers to ocean acidification. Geologically “ancient” species, which have survived large changes in ocean chemistry, are likely more resilient to predicted acidification.

1 Introduction

Anthropogenic $p\text{CO}_2$ is absorbed largely by the oceans, causing acidification of the biologically productive surface waters (The Royal Society, 2005; Kleypas et al., 2006). Corals, foraminifera and pteropods decrease their calcification in response to increased acidification (Gattuso et al., 1999; Kleypas et al., 1999; Bijma et al., 1999; Orr et al., 2005). Despite the intracellular nature of coccolithophore calcification, culture experiments confirm that *Emiliania huxleyi* and its close relative *Gephyrocapsa oceanica* also decrease calcification as $p\text{CO}_2$ increases (Riebesell et al., 2000; Zondervan et al., 2001). Decreased calcification is a negative feedback to acidification on the short term (Zondervan et al., 2001) but poses a serious threat to the sensitive ecologic balance. Ultimately, the rate at which populations acclimatise or adapt to changing ocean chemistry will determine the operation of feedback mechanisms on future climate.

Long-term patterns in coccolithophorid evolution and success seem, however, coun-

BGD

4, 1–11, 2007

Algal constraints on palaeo- $p\text{CO}_2$

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

EGU

terintuitive to this paradigm of low calcification under high pCO₂. Coccolithophore diversity and abundance peaked during the greenhouse Cretaceous world and have since declined (Bown, 2005). In addition, and by contrast to the tests on *E. huxleyi* and *G. oceanica* (Riebesell et al., 2000; Zondervan et al., 2001), recent acidification experiments testing the environmental tolerance of different extant coccolithophore species reveal that the calcification response is species-specific (Langer et al., 2006). Calcification ability in the species *Coccolithus pelagicus* is unaffected by values of pCO₂ up to at least 920 ppmV, and even though calcification ability declines, coccoliths are still produced up to much higher levels (S. Krug, personal communication). *Calcidiscus leptoporus* shows an “optimum” calcification ability close to modern day pCO₂ (Langer et al., 2006). Species-specific effects must be considered when evaluating whole ecosystem response to elevated pCO₂. Although representative of few algal strains, these culture results raise a major question: why do different species respond differently to pCO₂?

2 Methodology and Hypothesis

With a geological perspective, the ability of different coccolithophore species to calcify in culture under a range of ocean acidity correlates with likely levels of atmospheric pCO₂ since the emergence of their corresponding morphospecies during the Cenozoic (Fig. 1a). Modern *E. huxleyi* and *G. oceanica* are distinct genetic outliers to most other extant coccolithophore (Fujiwara et al., 1994; Sáez et al., 2003), and group together with other alkenone-producing haptophytes such as the non-coccolith bearing species *Isochrysis galbana*. The morphospecies *E. huxleyi* had a first occurrence ~291-268 ka and has risen to global dominance since 85 ka, while *G. oceanica* evolved at 1.7 Ma (Thierstein et al., 1977; Raffi et al., 2007). In contrast, the morphospecies *Calcidiscus leptoporus* originated at 23 Ma (Knappertsbusch, 2000) and *Coccolithus pelagicus* in the Palaeocene, ~63 Ma (Haq and Lohmann, 1976). At face value, the levels of pCO₂ tolerated in cultures of the different coccolithophorid morphospecies coincide with the

BGD

4, 1–11, 2007

Algal constraints on palaeo-pCO₂

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

EGU

5 levels of $p\text{CO}_2$ from proxy reconstructions at the time of their emergence (Pagani et al., 2005; Pearson and Palmer, 2000). This evolutionary view of the culture results places an upper constraint on $p\text{CO}_2$ of at most 920 ppmV (and likely higher) since 63 Ma, and 360 ppmV since 23 Ma. Our novel proxy validates the accuracy of the indirect alkenone proxy for $p\text{CO}_2$ (Pagani et al., 2005), and concurs with an emerging view of different climate sensitivities before and after the marked draw-down of $p\text{CO}_2$ at the early Oligocene (Lowenstein and Demicco, 2006). We predict, with further experiments to push the calcification tolerance of *C. pelagicus* and additional modern representatives of ancient morphospecies, a tight bracketing of palaeo- $p\text{CO}_2$ estimates for the Palaeogene, especially in combination with a fixed minimum early Eocene $p\text{CO}_2$ of 1125 ppmV, as reconstructed by stability fields of sodium carbonates (Fig. 1a; Lowenstein and Demicco, 2006).

3 Discussion

15 Our statement that genetically “older” extant species are able to calcify at higher $p\text{CO}_2$ in these culture experiments, and that this envelope of ability may constrain past $p\text{CO}_2$ estimates, requires detailed consideration.

Which of the carbonate system parameters dictates the calcification ability of different coccolithophore species? To date, this remains unclear. Calcification and photosynthesis are intricately coupled due to the energy requirement for the transport of Ca^{2+} and CO_3^{2-} into the coccolithophore cells, and control of intracellular pH. In the culture experiments, as in the modern ocean, the carbonate saturation state and pH are inversely proportional to $p\text{CO}_2$, with coherence between lower energetic requirement for calcification at high saturation and pH, and lower photosynthetic energy available from low $p\text{CO}_2$. Rather than a calcification dependency on saturation state, pH or $[\text{CO}_3^{2-}]$ alone, the critical factor determining the calcification tolerance of different species may be the photosynthetic capacity to harvest energy from CO_2 . In the geological past, carbonate saturation state and $p\text{CO}_2$ were likely decoupled (Tyrrell and Zeebe, 2004).

BGD

4, 1–11, 2007

Algal constraints on palaeo- $p\text{CO}_2$

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

EGU

But in culture, *C. pelagicus* tolerates conditions (Krug pers. comm.) beyond the limit of modern surface waters (Orr et al., 2005) and indicative of a different past carbonate system or pH.

Is evolutionary capability preserved without degradation? The modern species *Cru-*
5 *ciplacolithus neohelis* produces coccoliths that are highly similar to its Palaeogene
counterpart, and persistently secretes low Mg-calcite in the high Mg/Ca modern ocean
and in culture manipulations (Stanley et al., 2005). This evidence implies that calci-
fication ability can be determined, in an “ancient” species, by the chemical composi-
tion of seawater at the time of origin and conserved for many millions of years. The
10 preservation of calcification tolerance may occur through genetic redundancy (Wag-
ner, 1999), variance in genetic expression or ecological generalism versus specialism
(Richmond et al., 2005). Our proposed evolutionary perspective requires that the cou-
pled photosynthetic and calcification potential of the various taxa is optimised for ocean
carbonate chemistry at their time of origin and has been locked into genetic make-up
15 since pCO₂ declined. Currently, little is known about genetic controls on calcification
(e.g. Marsh, 2003; Nguyen et al., 2005), or the detailed photosynthetic mechanism
of coccolithophores. Cells optimise their photosynthesis by increasing surface area
to volume, maximizing light acquisition, increasing Rubisco specificity (Tortell, 2000),
and carbon concentrating mechanisms (Giordano et al., 2005). Coupling of calcifica-
20 tion with species-specific Rubisco specificity provides a tangible means to preserve
the CO₂/O₂ composition at the time of origin of photosynthetic phyla (Giordano et al.,
2005; Tcherkez et al., 2006).

Using cell size as an indicator of photosynthetic capacity, today, *E. huxleyi* stands out
as one of the smallest coccolithophores alive, and is best adapted to low pCO₂ values,
25 whereas *C. pelagicus* represents one of the largest. Further, the morphological tem-
plate and the mean coccolith size, linearly related to cell size, have remained largely
constant for *Coccolithus* during the Cenozoic decline of pCO₂ (Fig. 1b; Henderiks, un-
published data¹). In contrast, the Cenozoic ancestors of *Gephyrocapsa* and *Emiliania*,

¹Coccolith morphometric data on 99 deep-sea sediment samples, ranging in age 2.2 ka–

BGD

4, 1–11, 2007

Algal constraints on palaeo-pCO₂

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

EGU

within the *Reticulofenestra* genus, have greatly varied in coccolith size, with largest morphospecies (14–20 μm) occurring during the late Eocene (Backman and Hermelin, 1986). The presence of large, heavily calcified *C. pelagicus* since the Palaeogene, and recent origination of small, lightly calcified *E. huxleyi* corroborates our hypothesis that the photosynthetic potential or calcification ability is set by the conditions at the time of emergence and can be preserved over millions of years despite large changes in pCO_2 . Indeed the preservation of *C. pelagicus*' calcification ability may be enhanced because this species prefers a high pCO_2 niche. *C. pelagicus* prevailed in Palaeocene equatorial regions (Haq and Lohmann, 1977), and was only restricted to high pCO_2 subpolar and upwelling niches since the late Pliocene (Sato et al., 2004).

4 Concluding remarks

A direction for future research is to diversify, with more ancient species, investigation into calcification and photosynthesis under a range of ocean carbonate conditions, nutrient levels and temperatures. Nonetheless, our ideas have implications for the future ocean. With fossil fuel burning and a predicted decrease in pH of ~ 0.3 over the next 100 years (The Royal Society, 2005), the larger species will likely have an advantage over the now prosperous *E. huxleyi*, as the carbonate system of the ocean reverses towards the acidity of the past. *C. pelagicus* has weathered large and abrupt changes in conditions in the geological past, e.g. the Palaeocene-Eocene thermal maximum (Gibbs et al., 2006), with no apparent impact on physiology, but the adaptive speed of newcomer *E. huxleyi* may not suffice. If anything, large coccolithophores will be more successful calcifiers, and could act to release CO_2 to the atmosphere with positive feedback on global warming.

57.3 Ma. Mean coccolith size was determined from 100–200 individual coccolith measurements per sample using 4 replicate sprayed slides under polarised light microscopy (Henderiks and Törner, 2006)

BGD

4, 1–11, 2007

Algal constraints on palaeo- pCO_2

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

EGU

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- 30

BGD

4, 1–11, 2007

Algal constraints on palaeo-pCO₂

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

EGU

Kleypas, J. A., Feely, R. A., Fabry, V. J., Langdon, C., Sabine, C. L., and Robbins, L. L.: Impacts of Ocean Acidification on Coral Reefs and Other Marine Calcifiers: A Guide for Future Research, 88 pp., sponsored by NSF, NOAA, and the U.S. Geological Survey, St. Petersburg, USA, 2006.

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BGD

4, 1–11, 2007

Algal constraints on palaeo-pCO₂

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

EGU

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BGD

4, 1–11, 2007

Algal constraints on palaeo-pCO₂

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

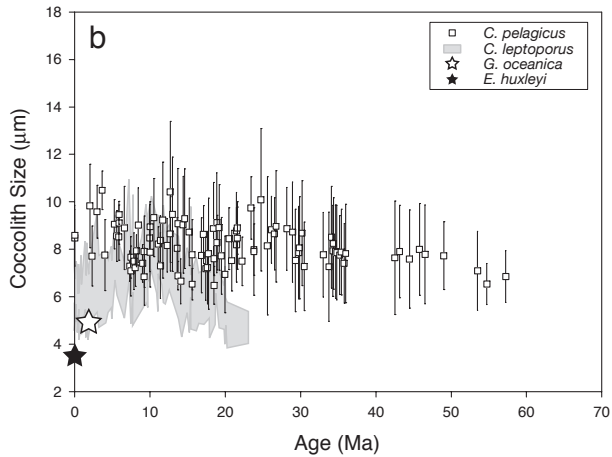
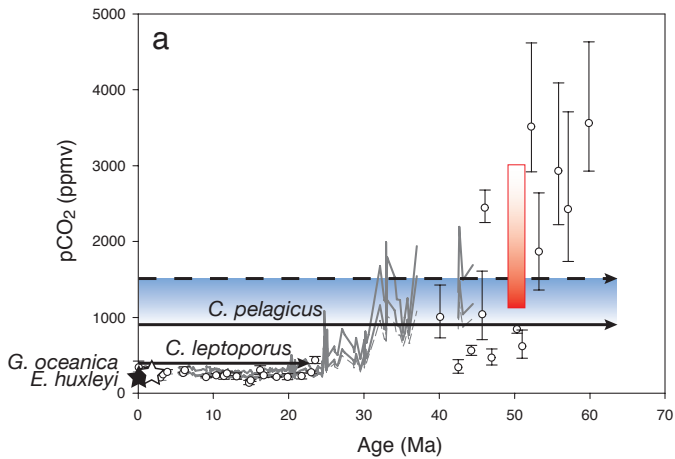


Fig. 1.

BGD

4, 1–11, 2007

**Algal constraints on
palaeo-pCO₂**

J. Henderiks and
R. E. M. Rickaby

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

EGU

Algal constraints on palaeo-pCO₂

J. Henderiks and
R. E. M. Rickaby

Fig. 1. (a) At face value, the levels of pCO₂ tolerated by different coccolithophore species for calcification in culture experiments (Riebesell et al., 2000; Langer et al., 2006) coincide with levels of pCO₂ from marine proxy reconstructions, based on alkenones (solid and dashed lines; Pagani et al., 2005) and boron isotopes in planktic foraminifera (open circles; Pearson and Palmer, 2000), at the time of emergence of each respective morphospecies; marked by a star for *E. huxleyi* (291–268 ka; closed star) and *G. oceanica* (1.7 Ma; open star), and solid arrows for *C. leptoporus* (23 Ma) and *C. pelagicus* (~63 Ma). The upper pCO₂ tolerance range for *C. pelagicus* is indicated by the blue box with a solid arrow at the maximum pCO₂ at which its calcification remains unaffected (Langer et al., 2006), and dashed arrow showing the potential for this species to determine the Palaeogene maximum pCO₂. The red box depicts the pCO₂ range in which the sodium carbonate nahcolite precipitates (Lowenstein and Demicco, 2006), fixing minimum early Eocene pCO₂ at 1125 ppmV.

(b) Mean coccolith size, a proxy for coccolithophore cell size, has remained largely constant for *Coccolithus* during the Cenozoic decline of pCO₂ (open squares ±1 stdev; Henderiks, unpubl. data), and for *Calcidiscus* (grey envelope ±1 stdev; Knappertsbusch, 2000) since the Miocene. Both genera are significantly larger than *E. huxleyi* (closed star), which stands out as one of the smallest, but most prolific calcifying coccolithophore alive today and represents the youngest evolutionary addition (291–268 ka) to the fossil record of calcifying haptophytes.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion