

BGD

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Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

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Environmental controls on the *Emiliana huxleyi* calcite mass

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Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Abstract

Although ocean acidification is expected to impact (bio)calcification by decreasing the seawater carbonate ion concentration, $[\text{CO}_3^{2-}]$, there exists evidence of non-uniform response of marine calcifying plankton to low seawater $[\text{CO}_3^{2-}]$. This raises questions on the role of environmental factors other than acidification and on the complex physiological responses behind calcification. Here we investigate the synergistic effect of multiple environmental parameters, including temperature, nutrient (nitrate and phosphate) availability, and seawater carbonate chemistry on the coccolith calcite mass of the cosmopolitan coccolithophore *Emiliana huxleyi*, the most abundant species in the world ocean. We use a suite of surface (late Holocene) sediment samples from the South Atlantic and southwestern Indian Ocean taken from depths lying well above the modern lysocline. The coccolith calcite mass in our results presents a latitudinal distribution pattern that mimics the main oceanographic features, thereby pointing to the potential importance of phosphorus and temperature in determining coccolith mass by affecting primary calcification and possibly driving the *E. huxleyi* morphotype distribution. This evidence does not necessarily argue against the potentially important role of the rapidly changing seawater carbonate chemistry in the future, when unabated fossil fuel burning will likely perturb ocean chemistry beyond a critical point. Rather our study highlights the importance of evaluating the combined effect of several environmental stressors on calcifying organisms to project their physiological response(s) in a high CO_2 world and improve interpretation of paleorecords.

1 Introduction

Coccolithophores are an abundant marine phytoplankton group that plays a significant role in both the marine food web and the carbon cycle (Young, 1994), comprising an important sedimentary carbon reservoir (Berger, 1976; Ridgwell and Zeebe, 2005). They are responsible for the photosynthetic fixation of inorganic carbon, regulating the

BGD

10, 9285–9313, 2013

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

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

particulate inorganic–organic carbon ratio and a large portion of the calcium carbonate (CaCO_3) production (Raven et al., 2005). The relative strength of photosynthesis and calcification at the surface ocean determines the biologically mediated exchange of carbon dioxide (CO_2) between the oceanic and atmospheric carbon reservoirs (Sigman et al., 2010), making quantification of these two processes central to our understanding of the dynamics of the global carbon cycle. The export of carbon and CaCO_3 to the seafloor enhances the ocean's capability to buffer the rise of atmospheric CO_2 concentrations (Van Cappellen, 2003; Ploug et al., 2008; Doney et al., 2009). The coccolithophore calcite plates, so-called coccoliths, are in fact a major source of calcite to the calcareous deep-sea oozes that cover almost half of the global oceanic floor (Berger, 1976; Ridgwell and Zeebe, 2005).

Despite the role of coccolithophores in the marine carbon cycle, the environmental factors modulating their calcification remain debated. In order to investigate the controlling factors of coccolithophore calcification, research has centered on their variability in mass and size (Young and Ziveri, 2000) in different types of experimental and field observational settings. Several environmental parameters have been examined (Broerse et al., 2000; Beaufort et al., 2008; Henderiks et al., 2012), such as light (Paasche, 2002), nutrient availability (Winter et al., 1994; Båtvik et al., 1997; Paasche, 1998; Müller et al., 2012), calcification temperature (Bollmann et al., 2002; Ziveri et al., 2004; Boeckel et al., 2006), salinity (Bollmann and Herrle, 2007; Bollmann et al., 2009; Fielding et al., 2009), and carbonate chemistry (Iglesias-Rodriguez et al., 2008; Langer et al., 2009; de Bodt et al., 2010; Müller et al., 2010; Ramos et al., 2010; Beaufort et al., 2011; Bach et al., 2012).

Ongoing ocean acidification (due to the oceanic uptake of the anthropogenic carbon from the atmosphere) is expected to impact marine calcifying organisms such as coccolithophores (Van Cappellen, 2003; Feely et al., 2004; Delille et al., 2005; Fabry et al., 2008). The high concentration of CO_2 in the ocean leads to a $[\text{CO}_3^{2-}]$ reduction and to a decline of the calcite saturation state of the seawater (Zeebe and Wolf-Gladrow, 2001; Raven et al., 2005; Fabry et al., 2008), which has been proposed as an im-

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

portant factor in the reduction of coccolith mass (Riebesell et al., 2000; Delille et al., 2005; Langer et al., 2009; Beaufort et al., 2011). However, there is complementary evidence pointing to a non-uniform response of calcification to high CO₂ (cf. Langer et al., 2006; Iglesias-Rodriguez et al., 2008; Riebesell et al., 2008; Doney et al., 2009), casting doubts on the notion that [CO₃²⁻] is the prime (and sole) controlling factor of (bio)calcification.

In order to advance our understanding of the role played by different seawater physicochemical properties in coccolithophore calcification, we examined a widely distributed suite of surface sediment samples taken along oceanic transects characterized by steep surface ocean environmental gradients, such as the South Atlantic and South-western Indian Oceans, the Agulhas System, and the Subantarctic sector of the Southern Ocean. All samples were selected from coring sites lying well above the depth of modern lysocline (Boeckel and Baumann, 2008). This prevents post-depositional effects (dissolution) on the coccolith calcite preservation and diagenesis, thereby allowing unambiguous recognition of the surface ocean environmental factors influencing the coccolith mass. Hence, this dataset has the potential to elucidate the influence of multiple environmental parameters at the surface ocean (temperature, salinity, nutrients, pH, [CO₃²⁻], and partial pressure of CO₂), on the coccolith mass of the most common living, blooming coccolithophore species *Emiliana huxleyi*. The majority of studies emphasize culture experiments to test the response on the calcite mass of *E. huxleyi* to changing environmental parameters (Langer et al., 2006; Iglesias-Rodriguez et al., 2008; Riebesell et al., 2008; Bach et al., 2012; Müller et al., 2012). By focusing on modern surface sediments here, we address a number of environmental property gradients and their influence on coccolith mass. This dataset also provides new constraints on how paleoceanographic data can be interpreted, such as across glacial-interglacial transitions that are marked by substantial changes in atmospheric CO₂ concentrations (e.g., Monnin et al., 2001; Lüthi et al., 2008) and seawater carbonate chemistry (e.g., Hönisch and Hemming, 2005; Foster, 2008).

2 Oceanographic setting

The South Atlantic, the Agulhas System, and the Southern Ocean are characterized by strong gradients in surface water properties, such as temperature (Fig. 1), salinity, and nutrient concentration (Mizuki et al., 1994; Lutjeharms, 2006). This region is marked by the strongest physicochemical gradients in the entire global ocean, with approximately 13°C changes in temperature with 12° of latitude. The surface circulation is driven by the atmospheric pressure gradients (winds), with the subtropical regions controlled by an anticyclonic regime and the higher latitude portion governed by strong westerly winds and characterized by the eastward-directed Antarctic Circumpolar Current (ACC) (Toggweiler, 1999; Toggweiler et al., 2006; Toggweiler and Lea, 2010). The ACC is a complex structure with the demarcation of three main fronts, the Subtropical Front (STF), the Subantarctic Front (SAF) and the Polar Front (PF), each associated with an intense cross-stream gradient in temperature, salinity and other properties (Orsi et al., 1995; Rintoul, 2009).

The fronts of the ACC define thermal and biological boundaries, representing a wide latitudinal band ranging from subtropical nutrient-depleted water to nutrient-rich polar waters that enhance the productivity (Orsi et al., 1995; Banse, 1996). They create biogeographic zones with a dominance of coccolithophores and small zooplankton at the north of the SAF (Popp et al., 1999; Rintoul, 2009). The higher biological productivity near fronts is due to advection of nutrients by the currents and injection of nutrient-rich waters from below (Sokolov and Rintoul, 2007; Rintoul, 2009).

Other important features of the circulation system in the study area are the South Equatorial Current (SEC), a cross-equatorial surface current that transports waters from the South Atlantic Gyre, through the central region of the ocean up to the North Atlantic Ocean (Peterson and Stramma, 1991). The region also features the Agulhas Current, a strong western-boundary current reaching the southern tip of Africa. It transports warm and saline Indian water that is mostly retroflected back into the In-

BGD

10, 9285–9313, 2013

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

dian Ocean, while a portion of this leaks into the South Atlantic and is subsequently advected northward (Lutjeharms, 2006).

3 Materials and methods

Coccolith calcite plates of coccolithophores are formed in the upper photic zone and are eventually exported to the sea floor via macroaggregates and fecal pellets (Young, 1994). The studied region has up to 80% of the carbonate sediment originating from coccolith calcite (Baumann et al., 2004; Frenz et al., 2005) and is particularly significant in the global carbon cycle (Asmus et al., 1999) due to the relevant function of CO₂ sequestration through physical and biological processes (Takahashi et al., 2012), storing over half of the oceanic anthropogenic CO₂ (Sabine et al., 2004).

We assessed the carbonate mass and distal shield length of individual coccolith specimens of *Emiliana huxleyi* in 70 surface sediment samples taken in the South Atlantic and southwestern Indian Oceans from water depths ranging between ~ 1100 and ~ 3500 m, with a single sample taken at ~ 4400 m (Fig. 1). The samples were obtained during several cruises from 1989 to 2004, listed in Table 1. Generally, the uppermost centimeter of the sediment column was sampled, with the exception of two samples from the cruise CD154, for which the interval of 1–2 cm below the surface was selected. Ages of the samples range between modern and Late Holocene (Baumann et al., 2004), making the sedimentary data that we generated directly comparable with preindustrial surface ocean physicochemical properties. Accordingly, we corrected the modern values of the carbonate system parameters from the anthropogenic CO₂ footprint (Sabine et al., 2004) (see Sect. 3.2).

3.1 Calibration slides and coccolith mass estimation

It is possible to estimate the mass of a calcium carbonate particle based on the measure of its brightness when viewed in cross-polarized light, as long as this particle has

BGD

10, 9285–9313, 2013

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



a thickness of less than 1.5 μm (Beaufort, 2005). But in the first place, it is necessary to calibrate the brightness of such particles to its known mass. To this aim, we prepared calibration slides with known amounts of pure crystalline calcite (0.098; 0.157; 0.221; 0.342; 0.507; 0.651; 0.833; 1.299 and 2.075 mg of CaCO_3).

The calcite was weighed on a micro-balance, mixed in water and filtered on a cellulose acetate membrane (0.45 μm pore size and 47 mm diameter) filter, using a low pressure vacuum pump to obtain even distribution of the particles. After oven-drying the samples at 40 °C for 24 h, a small portion of the filters were mounted on glass slides following the methods described in Ziveri et al. (1999). For each calibration slide, 100 pictures were randomly taken and processed using a Leica DM6000B cross-polarized light microscope with $\times 1000$ magnification fitted with a Leica DDC12DMC camera.

The pictures are composed of 256 grey levels (GL) going from the white (GL = 0) to the black (GL = 255) and have a resolution of 832 \times 832 pixels. As (i) the mass of calcite on the picture can be estimated and (ii) the sum of the GL composing the picture is proportional to this amount of calcite, it is then possible to estimate the amount of calcite for one pixel and link it to its brightness, or in other words to its GL (Fig. 2a). On the basis of this calibration, it is then possible to calculate the mass of a single coccolith as follows:

$$M_{\text{coc.}} = \sum \text{GL}_{\text{coc.}} / 2275.14 \quad (1)$$

Where $M_{\text{coc.}}$ is the mass of a coccolith in pg and $\sum \text{GL}_{\text{coc.}}$ is the sum of the GL composing the picture of this coccolith.

Smear slides of surface sediment samples were prepared following standard procedures (Henderiks and Törner, 2006). For each sample, we took on average 50 pictures that were analyzed with SYRACO, an automated system of coccolith recognition (Système de Reconnaissance Automatique de COccolithes, Dollfus and Beaufort, 1999; Beaufort and Dollfus, 2004), which is able to make the distinction between the different species composing the assemblages. A morphological study was performed on the most ubiquitous and abundant species, *Emiliania huxleyi*, as well as on another

BGD

10, 9285–9313, 2013

Environmental controls on the *Emiliania huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



well studied common species, *Gephyrocapsa oceanica*. The coccolith surface, length and width in relation to the distal shield were converted from pixels to micrometers (1 pixel \sim 0.15 μ m). The masses were estimated as described above, converting GL into picograms (pg) of calcite. The high correlation between length and mass indicates the linearity of the measurements, reflecting a positive relation among size and mass (Fig. 2b).

3.2 Environmental parameters

The environmental parameters discussed in this study were extracted from existing databases. The temperature and salinity data were retrieved from the World Ocean Atlas (WOA) 2009 (http://www.nodc.noaa.gov/OC5/WOA09/pr_woa09.html). The concentrations of phosphate and nitrate were retrieved from the WOCE Global Hydrographic Climatology database (Gouretski and Koltermann, 2004). The modern total alkalinity and total dissolved carbon data were extracted from the Global Alkalinity and Total Dissolved Carbon Estimates database (Goyet et al., 2000). We used the Anthropogenic CO₂ dataset from the GLODAP website (<http://cdiac.esd.ornl.gov/oceans/glodap/index.html>) to correct the total dissolved carbon values from the anthropogenic footprint; the values of the anthropogenic CO₂ were removed from those of the total dissolved carbon. Finally, we used the total alkalinity and the corrected total dissolved carbon to calculate the pH, the [CO₃²⁻], and the p CO₂, using CO₂sys (Lewis and Wallace, 1998).

The datasets were processed with Ocean Data View (ODV, Schlitzer, 2009) and the values closest to the sample locations were extracted at different depths (0, 10, 20, 30, 40 and 50 m) and averaged between 0 and 50 m in order to characterize the upper water column. Finally, the mean annual data of chlorophyll *a* concentration were extracted from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) project. The Chl *a* data are distributed as a Level-3 Binned file product (BIN), reprocessing No. 5, October 2011 (Feldman and McClain, 2011). The annual composites were downloaded from the <http://oceancolor.gsfc.nasa.gov/> website in Hierarchical Data Format (HDF). The

BGD

10, 9285–9313, 2013

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



images have a resolution of 9 km² (4320"2160 pixels) and were analyzed using SeaWiFS Data Analysis System (SeaDAS, Baith et al., 2001). Information was extracted from the pixels closest to the location of the surface sediment sample sites. These parameters were selected since they are important in controlling coccolith ecology and calcification. Even if the coccolithophore production layer depth in the open ocean expands towards the equator, most *E. huxleyi* production occurs in the surface (Okada and Honjo, 1973; Okada and McIntyre, 1977). We therefore use environmental parameters extrapolated from the upper 50 m.

3.3 Statistical methods

In order to identify the environmental parameters that govern the mass of *E. huxleyi* coccoliths in the surface sediment samples, we first performed two hierarchical cluster analyses using the method between group linkage and squared Euclidian distance, on (i) *E. huxleyi* mass (see Supplement); and (ii) *E. huxleyi* mass and the environmental parameters (temperature and salinity; nitrate, phosphate and chlorophyll *a* concentrations; and pH, $p\text{CO}_2$ and $[\text{CO}_3^{2-}]$) (Fig. 3a). Then we performed Principal Component Analyses (PCA), which are based on a product-moment correlation matrix (Wold et al., 1987), on *E. huxleyi* mass and the environmental parameters. Following Sokal and Rohlf (1995), the environmental parameters were standardized by subtracting the mean and dividing by the standard deviation. Both analyses were performed using SPSS (version 10.1) statistical software. Analyses were carried out on the average of the parameters of each sample for each cluster.

4 Results

A total of 13 140 *E. huxleyi* coccoliths were analyzed from surface sediment samples retrieved from the South Atlantic, the Subantarctic, the Agulhas System, and the Southwestern Indian Oceans (Fig. 1). The measured morphometric parameters

BGD

10, 9285–9313, 2013

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

of each coccolith include the length (L), the width (W), the surface area of the distal shield, and the mass (M) of calcite. The mean coccolith calcite mass is 3.12 pg ($n = 13\,140$, $\sigma = 0.66$,) with values ranging between 1.73 pg ($n = 101$, $\sigma = 0.69$) in sample ANT2606-3 (53°22' S, 41°21' E, 2552 m water depth) and 4.85 pg ($n = 209$, $\sigma = 2.23$) in sample ANT2561-1 (42°26' S, 28°57' E, 4471 m water depth) (Fig. 1). Our results indicate that coccoliths with the largest calcite mass occur at the northernmost and southernmost margins of the Subantarctic Zone, i.e., across the STF and SAF (Fig. 1). This is corroborated by the results of the cluster analyses (Fig. 3a), which differentiates seven clusters (eight clusters if the analysis is on *E. huxleyi* mass only; see Supplement Fig. S2). We note that the sample clusters generally follow a latitudinal distribution, mimicking the main oceanographic features, such as the regional oceanic fronts and the Agulhas System. Three clusters that are spatially distinguished are located in the Subantarctic Zone. Although all are under the influence of Antarctic conditions, cluster #5 at 40° S is particularly influenced by the STF, marking the division between warmer-tropical and cold-polar waters. To the south, clusters #5 and #6 are highly associated with the SAF, with sharp decreases in salinity and temperature (cfr. González-Dávila et al., 2011). Besides, cluster #1 can be linked to the AGC and the Agulhas leakage that also combines with the SEC and can reach northern parts of the South Atlantic. The clusters #2, #3 and #4 are beneath equatorial and subtropical waters. The spatial distribution of #3 and #4 might be due to the location of the Mid Atlantic Ridge, which can cause a considerable discrepancy of depths in a relatively short distance. In the central region of the Atlantic Ocean, especially at the Mid Atlantic Ridge, the samples present lower coccolith calcite mass, in line with previous studies that showed lower abundances of *E. huxleyi* (Boeckel et al., 2006).

When we compare *E. huxleyi* mass to physico-chemical parameters (Fig. 3b), we show that even if clusters #5 and #6 have a restricted spatial distribution in comparison with the studied area (Fig. 3a), the variability of the physico-chemical parameters observed within these 2 clusters is of the same (or even higher) magnitude than the variability observed within the others clusters taken together (Fig. 3b). This is due to

BGD

10, 9285–9313, 2013

Environmental controls on the *Emiliania huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

the fact that the SAF region is marked by the strongest physicochemical gradients in the entire global ocean (Levitus and Boyer, 1994). For that reason, further PCA analyses were conducted on: 1. clusters 1–4 and #7, and 2. Clusters #5 and #6. The PCA analysis, performed on the samples of the clusters 1–4 and #7 (Fig. 3c), reveals that 83.48 % of the variance may be explained by two factors. The first component (F1) explains 54.75 % of the variance and is characterized by negative loadings of temperature, salinity, and $[\text{CO}_3^{2-}]$, with the positive loadings being mass, nitrate, phosphate, and Chl *a* concentrations. The second component explains 28.73 % of the variance and is characterized by a positive loading of the pH and a negative loading of the CO_2 (Fig. 3c). The PCA analysis of clusters #5 and #6 (Fig. 3d) reveals that 89.17 % of the variance may be explained by two factors. The first component (F1) explains 65.12 % of the variance and is characterized by a positive loading of mass, temperature, salinity, Chl *a* concentration, and $[\text{CO}_3^{2-}]$, while nitrate and phosphate concentrations are the negative ones. The second component explains 24.06 % of the variance and is characterized by a positive loading of the pH and a negative loading of the CO_2 (Fig. 3d).

5 Discussion

We tested the *E. huxleyi* morphometry and calcite mass in sediment samples deposited under non-anthropogenic conditions but similar to modern in the South Atlantic, Southern Ocean, Agulhas System, and Southwestern Indian Ocean. Notably, these areas were not considered in a recent study focussing on coccolith mass quantification in other domains of the global ocean (Beaufort et al., 2011). We provide information on the combined effects of environmental factors driving their distribution. Current knowledge of the factors that control the coccolith mass variability alludes to a prominent role of the seawater carbonate system (e.g., Riebesell et al., 2000; Beaufort et al., 2011; Riebesell and Tortell, 2011 and references therein). A reduction of ~ 25 % coccolith mass has been linked to an increase of 100 ppmv CO_2 (Beaufort et al., 2011), that is,

the amplitude of the change in atmospheric CO₂ concentrations seen across the Late Pleistocene glacial-interglacial transitions (Mönnin et al., 2001; Lüthi et al., 2008).

Emiliana huxleyi is present with numerous ecotypes that likely justify its dominance in the coccolith assemblages over the last ~ 80 000 yr (Thierstein et al., 1977). The process behind the calcification of its coccoliths appears strongly biologically regulated and genetic analyses may likely provide further insights into the mechanisms controlling the coccolith mass (Paashe, 2001). Indeed, *E. huxleyi* is known for its genetic and phenotypic plasticity (cf. Young and Westbroek, 1991; Langer et al., 2006, 2009; Riebesell et al., 2008) that can be reflected in different strain specific responses to high CO₂ carbonate chemistry conditions (Langer et al., 2011; Beaufort et al., 2011; Lohbeck et al., 2012). An open issue is to understand the combined environmental conditions that can prompt different feedbacks during calcification (e.g. Müller et al., 2012). The seawater carbonate chemistry impact on coccolith mass has been mainly studied in experimental culture settings and secondarily with in-situ observations. These studies highlight the uneven responses of coccolith calcification (Ridgwell et al., 2009). The seawater environmental conditions induce changes in coccolithophore cell division rate and calcification, and in the particulate organic and inorganic carbon production (Müller et al., 2008). Our results suggest that it is the combination and synergy of multiple environmental factors such as seawater nutrients (phosphate), temperature, and carbonate chemistry that control the *E. huxleyi* coccolith calcite mass.

The PCA performed on our dataset reveals that more than 83 % of the *E. huxleyi* calcite mass variance is explained by two factors (Fig. 3c and d). When we consider the results on the samples of the low to middle latitudes (clusters #1–4 and #7, Fig. 3c) or on the samples of the high latitudes (clusters #5 and #6, Fig. 3d), in both cases the first variance factor is clearly correlated to water mass physical features, mainly associated with the temperature and the nutrients (phosphate/nitrate concentrations). This is in line with previous studies showing that in the South Atlantic, the *E. huxleyi* export production is related to the thermocline and nutricline depths; higher *E. huxleyi* coccolith concentrations in the underlying surface sediments are observed when the

BGD

10, 9285–9313, 2013

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

1998), temperature (de Bodt et al., 2010; Hagino et al., 2005) and seawater carbonate chemistry (Iglesias-Rodriguez et al., 2008; Beaufort et al., 2011; Bach et al., 2012). In our dataset, the observed changes in *E. huxleyi* calcite mass distribution could be controlled by ecological preference of the different morphotypes. The observed mass variations of *E. huxleyi* could be strongly linked to the different *E. huxleyi* morphotypes as highlighted in a previous study in the South Atlantic where *E. huxleyi* morphotype composition changes from type A/corona to type C dominated assemblages (Boeckel and Baumann, 2008). The *E. huxleyi* mass distribution is linked to surface water phosphorus concentration and temperature where coccolithophores calcify. Phosphorus concentration interacts with coccolith calcification (Båtvik et al., 1997) with relatively low phosphate concentration (but not phosphorus limitation) being related to lighter *E. huxleyi* coccoliths, while temperature presents a negative relation (de Bodt et al., 2010).

Our study provides a picture of the *E. huxleyi* calcification response to changing seawater physicochemical properties under preindustrial conditions, i.e., when the carbonate chemistry forcing on the calcifying organisms was plausibly much weaker than today (Feely et al., 2004). The results emphasize the potential role of nutrients in determining *E. huxleyi* coccolith mass, in line with the impact of nutrients (namely phosphorous) on the calcification of other organisms (Aldridge et al., 2012). Besides, secondarily temperature and seawater carbonate chemistry are also linked to the coccolith mass distribution, although it is difficult to delineate which one plays the key role, as they are closely related to one another. The combined influence of different factors on calcification seems to be a more robust assumption than a sole parameter controlling marine calcification. In addition, the coccolith mass appears not to be a straightforward relation between cause and effect, in that it may reflect both calcification and growth rate, determining, respectively, the thickness and morphology (size) of the coccolith plates (cf. Müller et al., 2008).

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

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

6 Conclusions

There is currently much debate on the response of calcifying planktonic organisms (e.g., coccolithophores, foraminifera, pteropods) to the ongoing seawater acidification (Doney et al., 2009; Kroeker et al., 2013). By examining a suite of 70 surface sediment samples taken at depths lying well above the lysocline from the South Atlantic, the Agulhas System, and the Southern Ocean we found that the combined effects of nutrients, temperature, and secondarily seawater carbonate chemistry control coccolithophore calcification in conditions similar to present day, yet less “acidified”. Although it appears clear that combined these changes can have profound impact on coccolithophore calcification, the balance among various environmental factors makes singular cause-effect relations difficult to be conclusively determined. The ongoing anthropogenic climatic and environmental changes, such as global warming, increased stratification, and ocean acidification (Gruber, 2011) have important consequences on the calcification processes. Because of the ongoing rapid physicochemical alterations of the ocean, the evidence we report of multiple environmental factors affecting coccolithophore calcification provides important information for projecting the response of (bio)calcification in the near future. Finally, our study suggests that paleorecords of coccolith calcite mass should not be used in a straightforward manner to decipher the response of coccolithophore calcification to past atmospheric CO₂ fluctuations.

Supplementary material related to this article is available online at:
<http://www.biogeosciences-discuss.net/10/9285/2013/bgd-10-9285-2013-supplement.pdf>.

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**Environmental
controls on the
Emiliana huxleyi
calcite mass**

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



References

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Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome 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, 9285–9313, 2013

**Environmental
controls on the
Emiliania huxleyi
calcite mass**

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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Table 1. Sample information.

Sample	Cruise	Year	Latitude	Longitude	Depth (m)
1112-3	M9-4	1989	06°18' 23" S	11°14' 33" W	3128
1203-2	M12-1	1990	26°55' 00" S	05°02' 00" E	2395
1208-1	M12-1	1990	24°49' 00" S	07°11' 00" E	2971
1217-1	M12-1	1990	25°35' 00" S	07°13' 00" E	2007
1403-2	M16-1	1991	01°20' 23" S	12°11' 17" W	3692
1405-7	M16-1	1991	02°09' 00" N	11°13' 33" W	4393
1413-2	M16-1	1991	16°07' 50" S	09°46' 07" W	3785
1414-2	M16-1	1991	15°53' 23" S	11°13' 23" W	3605
1415-1	M16-1	1991	15°53' 00" S	11°58' 23" W	3116
1417-1	M16-1	1991	15°54' 00" S	13°11' 07" W	2845
1418-1	M16-1	1991	15°53' 33" S	15°28' 50" W	3524
1419-1	M16-1	1991	15°54' 23" S	17°07' 00" W	4024
1420-1	M16-1	1991	15°35' 33" S	19°09' 07" W	4587
1901-1	So84	1993	01°22' 07" S	16°24' 20" W	2879
1902-3	So84	1993	04°38' 17" S	12°20' 23" W	2744
1903-1	So84	1993	09°08' 05" S	12°24' 33" W	3161
1904-1	So84	1993	14°28' 33" S	14°21' 50" W	3041
1905-1	So84	1993	17°14' 33" S	14°39' 07" W	2972
1906-1	So84	1993	18°22' 00" S	14°15' 17" W	2843
1907-1	So84	1993	15°13' 07" S	09°09' 23" W	3382
2213-1	M23-2	1994	01°26' 50" S	24°15' 33" W	4323
5112-5	M41-3	1998	24°22' 50" S	16°26' 23" W	3841
5115-2	M41-3	1998	24°14' 33" S	14°04' 33" W	3291
5121-2	M41-3	1998	24°18' 33" S	12°02' 17" W	3486
5130-1	M41-3	1998	19°40' 33" S	09°46' 23" W	3166
5134-1	M41-3	1998	19°04' 50" S	11°08' 33" W	3411
5136-2	M41-3	1998	19°37' 00" S	13°07' 00" W	3227
5137-1	M41-3	1998	19°29' 17" S	13°45' 33" W	3502
5140-3	M41-3	1998	19°05' 17" S	17°01' 33" W	3660
6402-9	M46/4	2001	40°14' 27" S	23°16' 05" W	3878
6403-4	M46/4	2001	40°01' 33" S	23°36' 52" W	4226
6406-1	M46/4	2001	42°00' 03" S	21°18' 40" W	3514
6410-1	M46/4	2001	44°52' 08" S	21°30' 00" W	4038
6411-4	M46/4	2001	44°36' 33" S	18°35' 20" W	3893
6412-1	M46/4	2001	44°25' 40" S	18°05' 07" W	3475
6417-2	M46/4	2001	39°09' 33" S	21°04' 17" W	4024
6418-3	M46/4	2001	38°43' 05" S	21°53' 50" W	4126
6419-1	M46/4	2001	38°17' 40" S	22°26' 42" W	3568
6421-2	M46/4	2001	36°45' 23" S	22°44' 50" W	4220
6425-1	M46/4	2001	34°22' 00" S	23°59' 15" W	4352
6429-1	M46/4	2001	32°35' 00" S	24°25' 23" W	4335

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Table 1. Continued.

Sample	Cruise	Year	Latitude	Longitude	Depth (m)
ANT2557-2	ANTXI-4	1994	37°35′ 00″ S	22°18′ 00″ E	3371
ANT2558-1	ANTXI-4	1994	38°49′ 00″ S	24°06′ 00″ E	5262
ANT2560-3	ANTXI-4	1994	40°55′ 00″ S	25°57′ 00″ E	2641
ANT2561-1	ANTXI-4	1994	42°26′ 00″ S	28°57′ 00″ E	4471
ANT2563-3	ANTXI-4	1994	44°56′ 00″ S	35°19′ 00″ E	3515
ANT2565-2	ANTXI-4	1994	47°00′ 00″ S	35°21′ 00″ E	3682
ANT2568-3	ANTXI-4	1994	50°21′ 00″ S	06°16′ 00″ E	3791
ANT2569-1	ANTXI-4	1994	51°26′ 00″ S	03°59′ 00″ E	3333
ANT2570-1	ANTXI-4	1994	52°33′ 00″ S	01°28′ 00″ E	2575
ANT2606-3	ANTXI-4	1994	53°22′ 00″ S	41°27′ 00″ E	2552
ANT2610-1	ANTXI-4	1994	51°07′ 50″ S	40°12′ 00″ E	3584
ANT2611-2	ANTXI-4	1994	49°47′ 00″ S	39°20′ 00″ E	4449
CD154 01-01K	CD154	2003/04	29°29′ 10″ S	33°14′ 40″ E	1997
CD154 02-03K	CD154	2003/04	29°06′ 40″ S	33°17′ 30″ E	1626
CD154 03-05K	CD154	2003/04	29°12′ 10″ S	33°29′ 20″ E	1747
CD154 05-07K	CD154	2003/04	30°33′ 40″ S	34°21′ 50″ E	1850
CD154 07-07PK	CD154	2003/04	30°13′ 20″ S	32°10′ 10″ E	1017
CD154 09-09K	CD154	2003/04	31°23′ 50″ S	32°14′ 20″ E	2986
CD154 10-10K	CD154	2003/04	31°17′ 00″ S	32°15′ 00″ E	3074
CD154 04-06K	CD154	2003/04	29°59′ 00″ S	33°44′ 00″ E	2469
CD154 15-13K	CD154	2003/04	34°09′ 10″ S	28°25′ 10″ E	3145
CD154 15-14K	CD154	2003/04	34°13′ 10″ S	28°20′ 30″ E	3236
CD154 16-15K	CD154	2003/04	34°10′ 10″ S	28°24′ 30″ E	3166
CD154 17-17K	CD154	2003/04	33°27′ 30″ S	29°12′ 20″ E	3333
CD154 18-18K	CD154	2003/04	33°31′ 20″ S	28°25′ 00″ E	3037
CD154 20-20K	CD154	2003/04	34°45′ 00″ S	27°15′ 20″ E	3512
CD154 23-24K	CD154	2003/04	37°20′ 40″ S	22°01′ 00″ E	3173
CD154 24-25K	CD154	2003/04	37°36′ 20″ S	21°55′ 30″ E	3417
MD02-2594	MD128	2003	35°11′ 00″ S	17°34′ 00″ E	2440

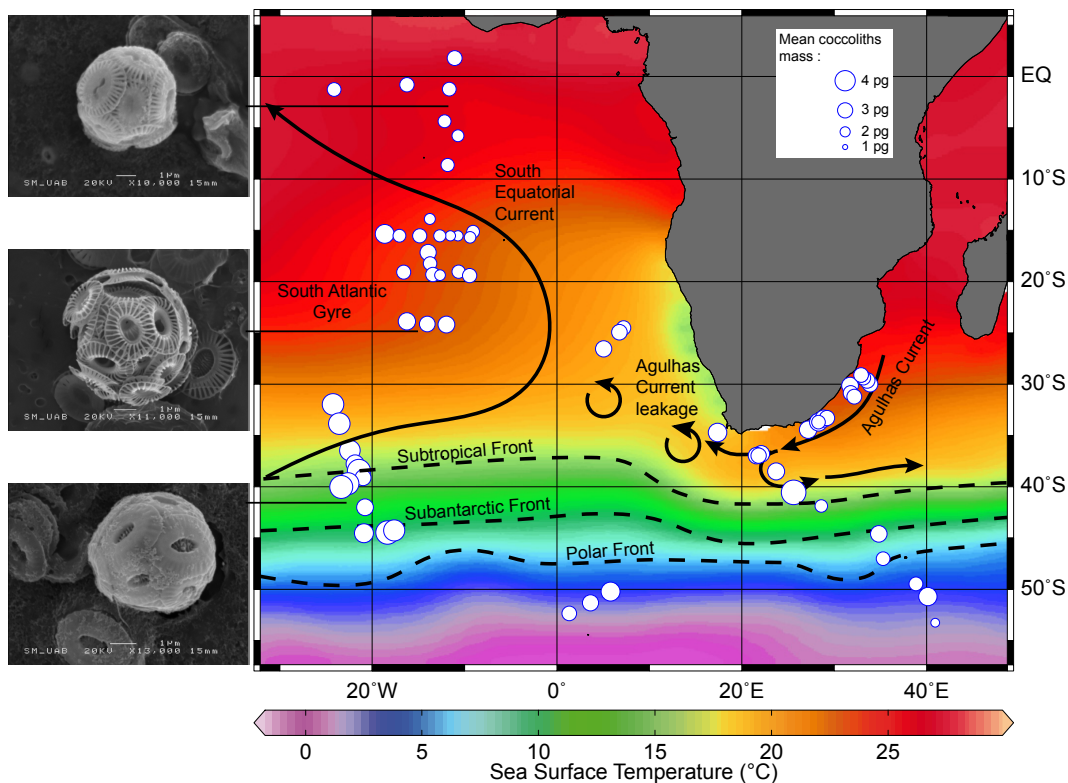


Fig. 1. Annual sea surface temperature map (data from World Ocean Database 2009), also indicating the subtropical front (STF), the location of the surface sediment samples, and the mass of *E. huxleyi*, represented by the size of the circles. Scanning electron microscope (SEM) images show typical *E. huxleyi* coccoliths from different latitudes.

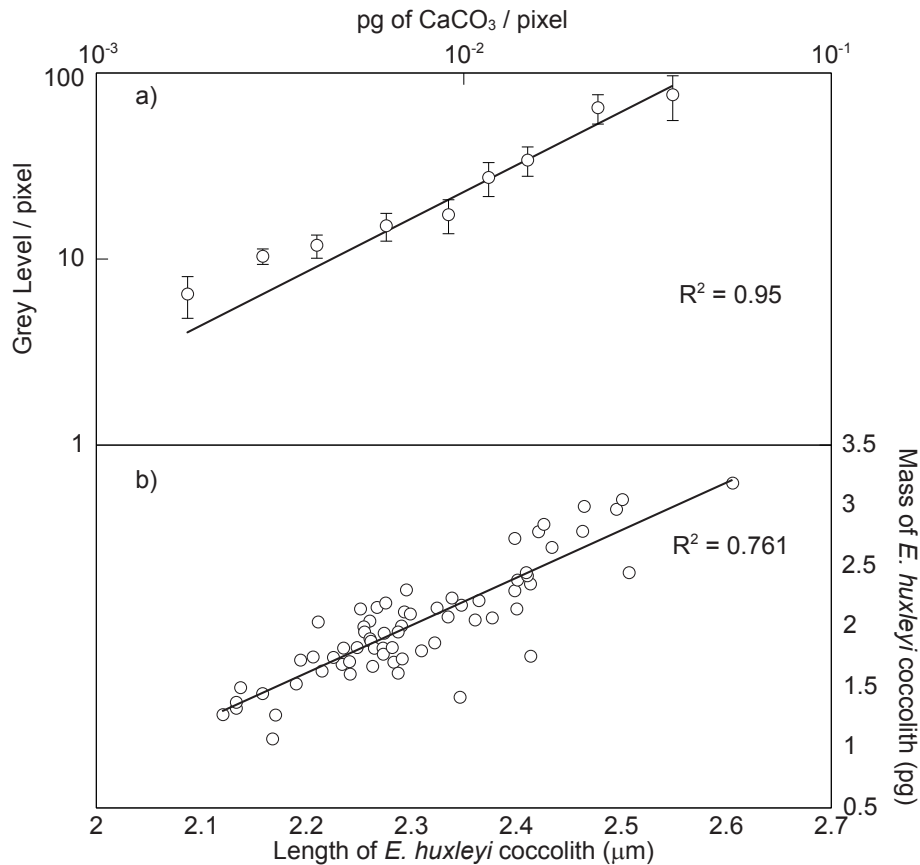


Fig. 2. Method calibration and validation. **(a)** Relation between the mass of calcite and the average Grey Levels (GL) values. The x- and y-axes are both on a logarithmic scale. The regression line (black) is forced to the axis origin. The vertical error bars give the 2 sigma standard deviation **(b)** *E. huxleyi* coccolith length versus mass, with black line indicating the linear regression.

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

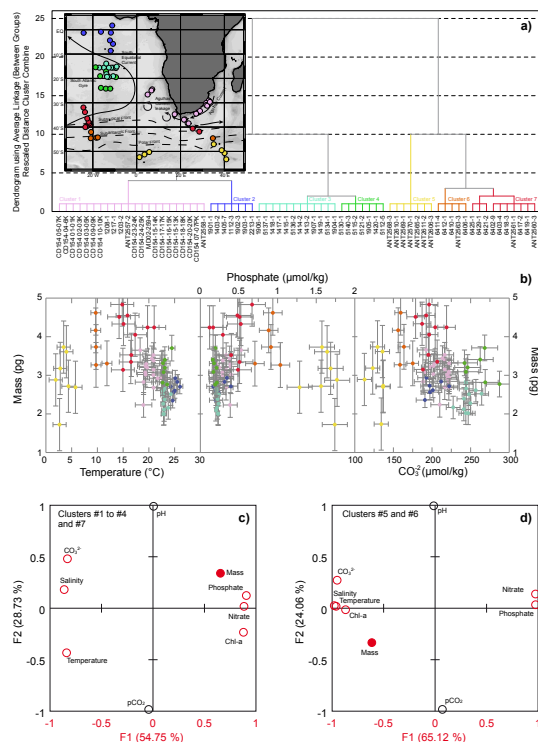


Fig. 3. Relation between coccolith mass and environmental parameters. **(a)** Cluster analysis performed on *E. huxleyi* mass and the environmental parameters. The map represents the distribution of the clusters. **(b)** Comparison of the mass with environmental parameters. From left to right: temperature, phosphate concentration, and carbonate ion concentration [CO_3^{2-}]. Each cluster is identified by the same color as in **(a)**. **(c)** Results of the PCA performed on clusters 1–4 and #7. In red, the parameters associated with the 1st factor and in black, the ones related to the 2nd factor. **(d)** Same as **(c)** but on clusters #5 and #6.

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

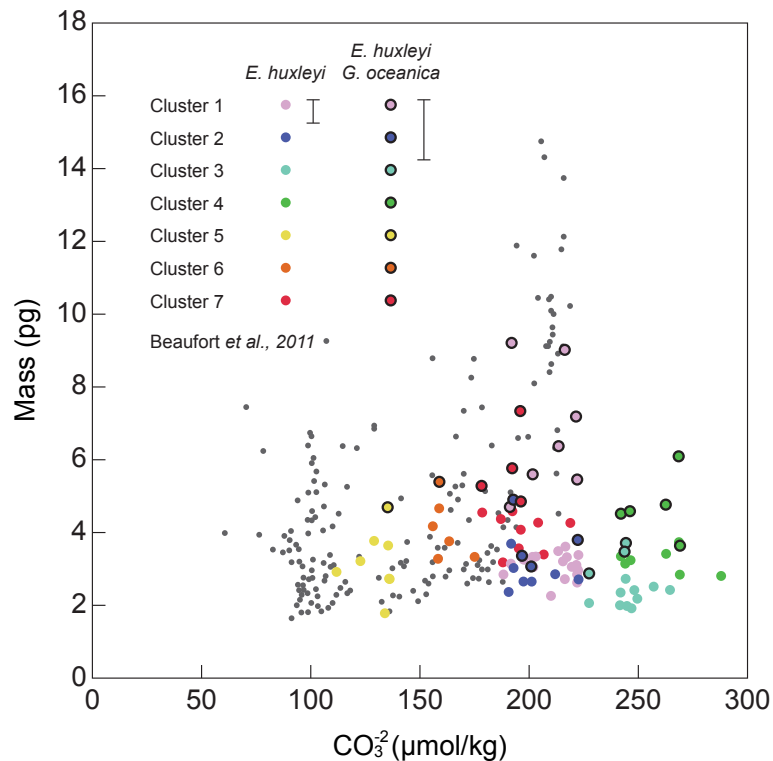


Fig. 4. Comparison of the relationship between coccolith mass to the carbonate ion concentrations ($[\text{CO}_3^{2-}]$) for this study (colored circles) and Beaufort et al. (2011) (grey dots). We present here results of *E. huxleyi* mass and *E. huxleyi* plus *G. oceanica* mass. The thin black bars give the 1 sigma error on the measurement.

Environmental controls on the *Emiliana huxleyi* calcite mass

M. T. Horigome et al.

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

