Biogeosciences
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Discussions

Biogeochemical implications of comparative growth rates of *Emiliania huxleyi* and *Coccolithus* species

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BGD

11, 10513–10536, 2014

Comparative growth rates of *Emiliania huxleyi* and *Coccolithus* species

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Abstract

Coccolithophores are a diverse and biogeochemically important group of phytoplankton in terms of the production and export of calcite, yet the comparative physiology and ecology of species other than the ubiquitous *Emiliania huxleyi* is poorly understood. Despite assumptions that *Emiliania huxleyi* is a fast growing species, we found it had comparable growth rates (0.16–$0.85\,\mathrm{d}^{-1}$) with strains of *Coccolithus pelagicus* and *Coccolithus braarudii* when grown under identical temperature and light conditions. A recently isolated Arctic strain of *C. pelagicus* (RCC4092) exhibited only a 12 % slower growth rate, on average, than a recently isolated Arctic strain of *E. huxleyi* (RCC3533), over a temperature range of 6–12 °C. Established temperate strains of *E. huxleyi* and *C. braarudii* (RCC1228 and RCC1198) exhibited a slightly larger difference in growth rates, with *E. huxleyi* growing 28 % faster on average than *C. braarudii* over a temperature range of 12–19 °C. Coupled with the 30–80 times higher cellular calcite content of *C. pelagicus* and *C. braarudii* compared to *E. huxleyi*, this suggests that *Coccolithus* species could be major calcite producers in mixed populations. The relative abundance of coccolithophore species is key for determining which species will dominate calcite production in mixed communities growing at similar rates. Field samples from the North Atlantic show that *C. pelagicus* is in a high enough relative abundance in 69 % of samples collected in the spring and summer of 2010 to be a larger source of calcite production than *E. huxleyi*.

1 Introduction

Coccolithophores are a diverse and biogeochemically important group of phytoplankton; through the production and subsequent export of their calcite coccoliths, they form a key component of the global carbon cycle (de Vargas et al., 2007). *Emiliania huxleyi* is considered the keystone species of the coccolithophores due to its global dominance, propensity to form large scale blooms and its perceived relatively fast

growth rates (Paasche, 2002). Assumptions on the comparative physiology and ecology of the other ∼ 200 extant species are often poorly addressed, although studies have examined intra- and inter-species differences in response to carbonate chemistry changes (Langer et al., 2006, 2009), photo-physiological differences between haploid and diploid life stages (Houdan et al., 2006), and patterns of coccosphere construction during reduced growth rate (Gibbs et al., 2013). However, the often stated (e.g., Tyrrell and Merico, 2004) assumption that *E. huxleyi* is a fast growing species relative to other coccolithophores has been largely un-tested.

Understanding whether different species grow at comparable or vastly different rates is key to understanding the relative calcification of these species within natural communities. *Emiliania huxleyi* has a relatively low cellular calcite content (~ 0.3–0.4 pmol C cell^{-1}; Table 1 and Fig. 1) compared with larger, more heavily calcified species such as *Coccolithus pelagicus* (~ 16.6 pmol C cell^{-1}; Table 1 and Fig. 1). With a similar growth rate (e.g., 0.7 d^{-1}), at a cellular level *C. pelagicus* would have a calcification rate approximately 40–50 times greater (11.6 pmol C cell^{-1} d^{-1}) than *E. huxleyi* (0.21–0.28 pmol C cell^{-1} d^{-1}). Alternatively, if *C. pelagicus* grew at only a tenth of the growth rate of *E. huxleyi* (e.g., 0.07 d^{-1}), then the difference in calcification between the two would be greatly reduced to around four times (although *C. pelagicus* would still represent ~ 80 % of the total calcite production).

Besides relative growth rates, the distribution and relative abundance of the different species are important factors in determining whether *Coccolithus* will dominate calcite production. While *E. huxleyi* is ubiquitously distributed throughout the oceans, the biogeography of *C. pelagicus* only covers the Arctic Ocean and the sub-polar Northern Hemisphere (McIntyre and Bé, 1967; McIntyre et al., 1970), with a particular prevalence in the sub-polar North Atlantic (Milliman, 1980; Tarran et al., 2001). As such, *C. pelagicus* has the potential to be a major oceanic calcite producer in this region. *Coccolithus braarudii*, a closely related taxa of *C. pelagicus* with an even greater cellular calcite content (39.1 pmol C cell^{-1}; Table 1 and Fig. 1), has a more limited range, restricted to coastal and upwelling areas (Giraudeau et al., 1993; Cachao and Moita,

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2000; Ziveri et al., 2004; Cubillos et al., 2012). However, where present, *C. braarudii* also has the potential to dominate calcite production.

Although studies concerning coccolithophore growth and calcite production have concentrated mainly on *E. huxleyi*, the potential for other species to be biogeochemically important has been previously highlighted in studies concerning coccolith export (Broerse et al., 2000; Ziveri et al., 2000; Baumann et al., 2004; Ziveri et al., 2007). *Coccolithus pelagicus* is a major contributor to the downwards flux of calcite in the northern North Atlantic (Ziveri et al., 2000), while other larger coccolithophore species such as *Calcidiscus leptoporus*, *Helicosphaera carteri* and *Gephyrocapsa oceanica* are significant contributors in other regions (Ziveri et al., 2007). The relative abundance of *C. pelagicus* in the downward flux has been shown to increase with depth, which is likely to be due to the disintegration and remineralisation of smaller coccospheres such as those of *E. huxleyi* (Ziveri et al., 2000). Therefore, *C. pelagicus* can dominate coccolith calcite export despite relatively low abundances in surface waters.

We set about to experimentally test the basic hypothesis that under identical growth conditions (light, nutrients, temperature) *E. huxleyi* would grow at a significantly faster rate (i.e., 2 times higher) than either of the *Coccolithus* species, *C. pelagicus* and *C. braarudii*. Furthermore, we also collected a number of ancillary cellular parameters (e.g., cell size, cell chlorophyll content) and examine these in a comparative sense between the different species. The biogeochemical implications of relative cell abundances are assessed using model and field data.

2 Materials and methods

2.1 Experimental design

Monoclonal cultures of *Coccolithus pelagicus* (RCC4092) and an Arctic strain of *Emiliania huxleyi* (RCC3533) were obtained in June 2012 through single cell isolations from surface water samples collected in the Greenland Sea (67.83° N, 16.42° W and

66.79° N, 25.14° W respectively) during the 2012 UK Ocean Acidification Arctic cruise (JR271). These cultures have been deposited into the Roscoff Culture Collection (RCC). North Atlantic Ocean strains of *Coccolithus braarudii* (RCC1198) and *E. huxleyi* (RCC1228) were obtained from the RCC.

Cultures were grown in sterile-filtered (0.2 μm) enriched seawater K/20 medium (modified from Keller et al., 1987), under a 12/12 h light/dark cycle. Experiments on parallel cultures of either the Arctic strains (*C. pelagicus* and *E. huxleyi* RCC3533) or the Atlantic strains (*C. braarudii* and *E. huxleyi* RCC1228) were carried out over a range of temperature and light conditions.

To reflect a realistic in situ environment, different experimental conditions were used for the Arctic and Atlantic cultures. The Arctic strain experiments were carried out at 6, 9 and 12 °C, with a daily photon flux ranging from 1.3–8.2 mol photons $m^{-2} d^{-1}$ (30–190 μmol photons $m^{-2} s^{-1}$) between experiments, while the Atlantic strain experiments were carried out at 12, 14, 16 and 19 °C, with a daily photon flux ranging from 1.9–10.5 mol photons $m^{-2} d^{-1}$ (45–244 μmol photons $m^{-2} s^{-1}$; Table 2). Cells were acclimated to experimental conditions for approximately 10 generations and grown in dilute batch cultures in duplicate. To avoid biological effects on the carbonate system, cultures were grown in ventilated flasks, to low cell densities and sampled during the mid-exponential phase.

For determination of cell density, samples were taken daily or every other day and counted immediately in triplicate using either a Sedgwick rafter cell for *C. braarudii* and *C. pelagicus* (Langer et al., 2006), or a Coulter Multisizer III (Beckman Coulter) for *E. huxleyi* (Langer et al., 2009). Cell density was plotted against time and growth rates (μ) were calculated by exponential regression (Langer et al., 2006).

Biometric measurements of coccolithophores were made on samples collected on cellulose nitrate (0.8 μm) and polycarbonate (0.8 μm) filters, and prepared following Poulton et al. (2010) and Daniels et al. (2012), respectively. Light microscopy was used for all biometric measurements of *Coccolithus* (Gibbs et al., 2013), while a combination of light microscopy and scanning electron microscopy (SEM) was used to study *E.*

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huxleyi. Measurements of coccolith size and the number of coccoliths per coccosphere were used to estimate cellular calcite content following the relationship of Young and Ziveri (2000). Cellular particulate organic carbon (POC) was estimated from measured internal cell diameters and cell biovolume following Menden-Deuer and Lessard (2000).

5 Samples for determination of cellular chlorophyll *a* (Chl *a*) were collected on Fisherbrand MF300 filters (effective pore size 0.7 µm), extracted in 8 mL of 90 % acetone (HPLC grade, Sigma) for 24 h and analysed on a Turner Designs Trilogy Fluorometer calibrated using a solid standard and a chlorophyll *a* extract.

2.2 Field samples

10 Samples for coccolithophore abundance were collected from three RRS *Discovery* cruises spanning the Irminger and Iceland Basins of the North Atlantic during the period of April to August 2010. Two cruises (D350, D354) were part of the (UK) Irminger Basin Iron Study (IBIS), while the third cruise (D351) occupied the Extended Ellett Line. In all three cruises, surface water samples (0.2–1 L) were filtered through cellulose nitrate

15 (0.8 µm) and polycarbonate (0.45 µm or 0.8 µm) filters, oven dried (30–40 °C, 6–12 h) and stored in Millipore PetriSlides. The filters were examined using a Leo 1450VP scanning electron microscope, with coccolithophores identified following Young et al. (2003), and enumerated from 225 fields of view (Daniels et al., 2012). The detection limit was estimated to be 0.2–1.1 cells mL^{-1}.

20 # 3   Results and discussion

3.1   Growth rates

Through manipulation of experimental conditions (temperature and irradiance), a wide range of growth rates was achieved, ranging from 0.16–0.85 d^{-1} (Fig. 2). While the maximum growth rates achieved here were lower than in other studies of *E. huxleyi*

25 (0.98–1.64 d^{-1}, Langer et al., 2009) and *C. braarudii* (0.73–0.99 d^{-1}, Langer et al.,

2006; Gibbs et al., 2013), the experimental design of this study intended to assess the relative growth rates between species under realistic in situ environmental conditions, not necessarily achieving maximal growth rates.

Emiliania huxleyi (0.50–0.85 d^{-1}) grew faster than *C. braarudii* (0.32–0.58 d^{-1}) in all experiments, while for the Arctic strains *E. huxleyi* (0.16–0.58 d^{-1}) grew faster than *C. pelagicus* (0.18–0.49 d^{-1}) in all but the experiment with the slowest growth rates (Fig. 2). However, the difference in these growth rates was relatively small with *E. huxleyi* growing on average only 12 % (−11 % to 26 %) faster than *C. pelagicus*. The difference was greater for the temperate strains, with *E. huxleyi* 28 % (12–49 %) faster than *C. braarudii*. This is significantly smaller than previously reported in a study by Buitenhuis et al. (2008) who found higher growth rates of *E. huxleyi* than *C. braarudii*. However, the strain of *E. huxleyi* used by Buitenhuis et al. (2008) was a non-calcifying mutant and thus is not directly comparable with our study.

Both temperature and irradiance had a measurable effect on growth rates (Table 1, Fig. S1). Temperature was the primary driver of growth rates for both *E. huxleyi* ($r^2 = 0.84$, $p < 0.001$, $n = 18$) and *Coccolithus* ($r^2 = 0.62$, $p < 0.001$, $n = 18$), while irradiance had a secondary, but significant effect, on both *E. huxleyi* ($r^2 = 0.33$, $p < 0.02$, $n = 18$) and *Coccolithus* ($r^2 = 0.23$, $p = 0.04$, $n = 18$). The growth rate of *C. braarudii* declined between 16 °C and 19 °C, suggesting that 19 °C was above the optimum temperature for *C. braarudii*. No such decline was observed in the temperature range experienced by *C. pelagicus* (6–12 °C). The lower maximal growth rates observed here are likely to be due to the lower daily irradiance relative to other laboratory studies (e.g., 20–23 mol photons $m^{-2} d^{-1}$, Langer et al., 2006, 2009), thus by increasing the daily irradiance we would expect the growth rates of both species to increase.

In general, a decrease in absolute growth rates was coupled with a smaller difference in the relative growth rates of *E. huxleyi* and *Coccolithus* (Fig. 2). As growth rate was primarily driven by temperature, this suggests that growth rates of *Coccolithus* and *E. huxleyi* may be most comparable in cold waters (< 10 °C), while the growth rate of *E. huxleyi* will become increasingly greater relative to *Coccolithus* in temperate waters.

As a cold water species (Winter et al., 1994), with a biogeography spanning the Arctic and sub-polar Northern Hemisphere (McIntyre and Bé, 1967; McIntyre et al., 1970), *C. pelagicus* could potentially dominate calcite production in this region. As a more temperate species, seemingly present only in coastal waters of the North Atlantic (Cachao and Moita, 2000; Daniels et al., 2012) and upwelling pockets (Giraudeau et al., 1993; Cubillos et al., 2012), we expect the difference in growth rate between *C. braarudii* and *E. huxleyi* to be greater in areas where they are both present. However, as a heavily calcified species with the coccosphere calcite of one cell equivalent to ∼ 78 cells of *E. huxleyi* (Table 1), *C. braarudii* still has the potential to dominate calcite production in these regions.

3.2 Modelling relative calcite production

The potential for *C. pelagicus* and *C. braarudii* to dominate calcite production in their respective environments is dependent on both their relative growth rates and the relative abundance of these species compared to other coccolithophores.

We can examine this potential by modelling a simplified community comprised of just *E. huxleyi* and either *C. pelagicus* or *C. braarudii*. Assuming steady state, calcite production for a given species is the product of its growth rate (μ), cellular calcite (C) and abundance (N) (Leynaert et al., 2001; Poulton et al., 2010). Therefore, we can calculate the percentage of calcite production by a specific species ($\%CP_{sp}$), such as *Coccolithus,* within a mixed community, using the following equation:

$$\%CP_{sp} = \frac{\sum_{i=1}^{n} \mu_i C_i N_i}{\mu_{sp} C_{sp} N_{sp}} \times 100 \tag{1}$$

In this model, we have used a range of relative growth rates spanning those measured in our culture experiments (Fig. 2, Table 2), and have varied the abundance ratio of *E. huxleyi* to *Coccolithus* from 0 to 80. Results are presented in Fig. 3 for *C. pelagicus* and *C. braarudii* relative to *E. huxleyi*.

Coccolithus braarudii is the major source (> 50 %) of calcite production in 88 % of the model scenario (Fig. 3a), and will dominate calcite production if the relative abundance of *E. huxleyi* to *C. braarudii* is less than 50 : 1, despite a growth rate only 50 % that of *E. huxleyi*. With simulated comparable growth rates, *C. braarudii* calcifies at a rate

5 equivalent to 99 cells of *E. huxleyi*, thus dominating the model across the entire range of relative abundance.

While *C. pelagicus* is less dominant in its model scenario when compared to the *C. braarudii* model due to its lower cellular calcite (16.6 and 38.7 pmol C cell^{-1} respectively, Table 1), it is still the major source of calcite production in 61 % of the model

10 (Fig. 3b). When compared to the observed relative growth rates (Fig. 2), *C. pelagicus* calcifies at a rate equivalent to 38 cells of *E. huxleyi* when growing slowest (74 % relative growth rate), while if *C. pelagicus* exceeds the growth rate of *E. huxleyi* (111 %), then it will dominate calcite production if the relative abundance of *E. huxleyi* to *C. pelagicus* is greater than 58 : 1.

15 Although we have modelled the effect of growth rate and relative abundance on the role of *Coccolithus* as a calcite producer, these models are dependent on the cellular calcite quotas attributed to both *E. huxleyi* and *Coccolithus*. As calcite production is the product of growth rate and cellular calcite, this initial condition will have a significant effect on the relative calcite production of the two species.

20 In this study, we have determined cellular calcite through biometric measurements of coccolithophores, rather than through bulk chemical measurements. This was done to achieve consistency between our cellular calcite estimates of *E. huxleyi*, *C. braarudii* and *C. pelagicus*. However, as with all methods of estimating cellular calcite, there is an associated error, and estimates of cellular calcite vary between studies (Langer et al.,

25 2006, 2009; Poulton et al., 2010). To address this and further illustrate the impact of cellular calcite on calcite production, we have varied the cellular calcite quotas in our model by concurrently increasing the calcite content of *E. huxleyi* and decreasing that of *Coccolithus*, by one standard deviation, or vice versa (Fig. 3c–f).

Reducing the calcite content of *C. pelagicus* ($12.7\,\mathrm{pmol\,C\,cell^{-1}}$) and *C. braarudii* ($32.5\,\mathrm{pmol\,C\,cell^{-1}}$) and increasing that of *E. huxleyi* (0.43–$0.49\,\mathrm{pmol\,C\,cell^{-1}}$) reduces the dominance of *Coccolithus* in the model (Fig. 3c and d). Thus, *C. braarudii* is the major calcite producer in only 62 % of the model (Fig. 3c), and calcifies at a rate equivalent to 66 cells of *E. huxleyi* when growth rates are the same. *Coccolithus pelagicus* is the major calcite producer in only 35 % of the model (Fig. 3d), but will produce more calcite than *E. huxleyi* if the relative abundance is less than 21 : 1.

An increase in the calcite content of *C. pelagicus* ($20.5\,\mathrm{pmol\,C\,cell^{-1}}$) and *C. braarudii* ($44.9\,\mathrm{pmol\,C\,cell^{-1}}$), coupled with a decrease in that of *E. huxleyi* (0.21–$0.29\,\mathrm{pmol\,C\,cell^{-1}}$) results in both *C. braarudii* (99.9 %, Fig. 3e) and *C. pelagicus* (98 %, Fig. 3f) dominating nearly all of the model scenario.

3.3 The importance of relative abundance

The model scenarios clearly highlight the importance of relative cellular calcite quotas, relative growth rates and relative abundances when determining the relative role of *E. huxleyi* and *Coccolithus* in calcite production. While cellular calcite and growth rates will affect relative calcite production at a cellular level, it is the relative abundance of *E. huxleyi* and *Coccolithus* within a population that will determine the proportion of calcite production that derives from *Coccolithus*. Using data from field populations we can examine whether populations exist where *C. pelagicus* has the potential to be a significant calcite producer.

Coccolithophore abundances were determined from samples collected on three cruises in the Irminger and Iceland Basins of the North Atlantic, a region in which both *E. huxleyi* and *C. pelagicus* are present (McIntyre and Bé, 1967). Although other species of coccolithophore were present, we have extracted only abundances of *E. huxleyi* and *C. pelagicus*, so that the data is comparable to our model scenarios in Sect. 3.2. Of the 37 samples analysed, *E. huxleyi* and *C. pelagicus* were observed in 29 samples, with *E. huxleyi* present in a further 6 samples in which *C. pelagicus* was ab-

sent (Fig. 4). When present, concentrations of *E. huxleyi* ranged from 2–980 cells mL^{-1}, while *C. pelagicus* ranged from 0.1–74 cells mL^{-1}. The relative abundance of *E. huxleyi* to *C. pelagicus* was generally low (0.7–85) and therefore comparable to our modelled range. However in 2 samples, the relative abundance was much higher (155–212) such that *C. pelagicus* was unlikely to be a significant calcite producer in these samples.

Assuming the original model scenario of measured cellular calcite (Table 1, Fig. 3a and b) and a relative growth rate for *C. pelagicus* of 74 %, the minimum relative abundance of *E. huxleyi* to *C. pelagicus* required for *E. huxleyi* to dominate calcite production (38 : 1) was exceeded in only 5 samples. Taking into account those samples in which *C. pelagicus* was absent, *C. pelagicus* is a greater calcite producer than *E. huxleyi* in 69 % of the samples. If equivalent growth rates are assumed, then C. pelagicus becomes the major calcite producer in 74 % of the samples.

Coccolithus pelagicus remains the major calcite producer in 57 % of the samples even under the more conservative model scenario (Fig. 3d) with a relative growth rate of 70 %, where a relative abundance of 21 : 1 or less is required for *C. pelagicus* to dominate calcite production. Using experimentally determined relative growth rates and cellular calcite quotas, in conjunction with relative abundances from field populations, we have shown that *C. pelagicus* is likely to be a major source of calcite in the sub-polar North Atlantic. Data on relative abundances of *E. huxleyi* and *C. braarudii* were not available for an equivalent comparison study.

3.4 Implications of cell size differences

While the difference in growth rates between *E. huxleyi* and *Coccolithus* is comparatively small, the difference in cell volume of *C. pelagicus* ($\sim 1100\,\mu m^3$) and *C. braarudii* ($\sim 2100\,\mu m^3$) compared to *E. huxleyi* ($\sim 50\,\mu m^3$) is relatively large. These differences are reflected in their cellular Chl *a* and cellular calcite : POC (Table 1), with the species having similar ratios of Carbon : Chl *a* (25–36 g g^{-1}) across the experimental conditions. Larger cells have a lower surface area to volume ratio which reduces the diffusive nu-

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trient uptake per unit volume of the cell (Lewis, 1976; Finkel et al., 2009), thus maximal growth rates generally increase with decreasing cell size (Sarthou et al., 2005). Hence, although we expect *E. huxleyi* maximal (optimal) growth rates to be higher than *Coccolithus*, the relatively small difference in growth rate (Fig. 2) compared to cell volume (Table 1) implies that *Coccolithus* must have efficient (competitive) nutrient uptake pathways, or that these experimental conditions are less optimal for *E. huxleyi* than *Coccolithus*.

As well as relative differences in cell size and surface area to volume, it is also worth considering what implications these have for nutrient requirements to support growth. From our estimates of cellular POC (Table 1), assuming Redfield stoichiometry (Redfield, 1958) we can also estimate the cellular particulate organic nitrogen (PON) and particulate organic phosphorus (POP) content of *E. huxleyi*, *C. pelagicus* and *C. braarudii*. The PON and POP content for *E. huxleyi*, *C. pelagicus* and *C. braarudii* estimated this way is 0.10, 2.0 and 3.6 pmol N cell^{-1}, and 0.01, 0.12 and 0.22 pmol P cell^{-1}, respectively. While there is a lack of comparable culture data for *C. braarudii* and *C. pelagicus*, our estimates of cellular quotas for *E. huxleyi* are similar to those found in other studies (Langer et al., 2013).

For culture media with a given nitrate concentration of 10 µmol N L^{-1}, the maximum cumulative cell concentration that could be supported would therefore be $\sim 1 \times 10^5$, $\sim$ 5000 and $\sim$ 2800 cells mL^{-1}, respectively for *E. huxleyi*, *C. pelagicus* and *C. braarudii*. This corresponds to cumulative calcite concentrations, using cellular calcite quotas from Table 1, of $\sim$ 50, $\sim$ 80 and $\sim$ 110 µmol C L^{-1}, such that for a given nutrient concentration, despite lower cell densities, a population of *C. pelagicus* and *C. braarudii* would be a greater source of calcite than *E. huxleyi*.

Emiliania huxleyi regularly forms seasonal blooms in excess of 1000 cells mL^{-1}, particularly in the high latitudes of the Northern and Southern Hemispheres (Tyrrell and Merico, 2004; Poulton et al., 2013). For a bloom with a magnitude of 1000 cells mL^{-1}, this would require a nitrate concentration of $\sim$ 0.1 µmol N L^{-1}. Comparatively, although rare, *C. pelagicus* has also been reported in concentrations exceeding 1000 cells mL^{-1}

in the high latitude North Atlantic (Milliman, 1980), thus requiring a much larger nitrate concentration of $2\,\mu\mathrm{mol\,N\,L^{-1}}$. The seasonal drawdown of nitrate in the North Atlantic is estimated be $\sim 10\,\mu\mathrm{mol\,N\,L^{-1}}$ (Sanders et al., 2005; Ryan-Keogh et al., 2013), and thus a *C. pelagicus* bloom of $1000\,\mathrm{cells\,mL^{-1}}$ requires around 20 times more nitrate than a *E. huxleyi* bloom, and represents a significant amount of the available nutrients. For a bloom of this magnitude to occur, we would expect *C. pelagicus* to be a significant portion of the total phytoplankton community with a relatively low mortality rate, as nutrient drawdown will be related to gross production by the total phytoplankton community. Reduced mortality has also been discussed as a possible factor in the formation and persistence of *E. huxleyi* blooms in the southeast Bering Sea (Olson and Strom, 2002).

The function of coccoliths is not well understood, but may have a significant role in reducing mortality by providing a certain level of protection from zooplankton grazing (Young, 1994; Tyrrell and Young, 2009). If this is the case then we would speculate that *C. pelagicus* has a relatively lower mortality then *E. huxleyi* due to both its larger cell size and it's much larger and heavier coccosphere. A lower mortality may explain how *C. pelagicus* is able to form high density populations, while the large nutrient requirement would restrict *C. pelagicus* blooms to populations where it heavily dominates the plankton community and this may explain the scarcity of reported *C. pelagicus* blooms.

4 Conclusions

The data we have presented shows that when grown in parallel under identical experimental conditions, the relative difference in growth rates between *E. huxleyi* and *Coccolithus* species was generally small (12 % and 28 % respectively for *C. pelagicus* and *C. braarudii*), although *E. huxleyi* generally grew faster than both *C. pelagicus* and *C. braarudii.* Using relative growth rates and estimates of cellular calcite to model relative calcite production we have shown that when in a suitable relative abundance to *E.*

huxleyi, both *C. pelagicus* and *C. braarudii* have the potential to dominate relative and absolute calcite production.

The relative abundance of *E. huxleyi* and *C. pelagicus* was determined from samples collected from the Irminger and Iceland Basins in the North Atlantic. This showed that using our standard model scenario with *C. pelagicus* growing at only 70 % of the growth rate of *E. huxleyi*, we would expect *C. pelagicus* to be the major calcite producer in 69 % of the field samples. Using a more conservative model reduced this to 57 %. Therefore, we would expect *C. pelagicus* to be a major source of calcite in the sub-polar North Atlantic. An investigation of calcite production in natural diverse communities would allow us to examine these results further.

Despite a small relative difference in growth rates, there were large differences in cell size. Estimates of the cellular nutrient requirements suggest that for a given nutrient concentration, despite a much smaller maximum cell density, both *C. pelagicus* and *C. braarudii* would be a greater source of calcite than *E. huxleyi*. These results have significant implications for how we view calcite production in natural coccolithophore communities, and which coccolithophores are key stone species for oceanic biogeochemical cycles.

The Supplement related to this article is available online at doi:10.5194/bgd-11-10513-2014-supplement.

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Discovery cruises in the North Atlantic; and finally, Richard Pearce, Elena Maher and Jonathan Hurst for assistance with coccolithophore cell counts.

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Table 1. Coccolithophore strain-specific values of cell diameter, cellular calcite, cellular particulate organic carbon (POC), cellular chlorophyll (Chl) and cellular calcite : POC. Values reported are averaged over experiments, with ±1 standard deviation. [a] Measured from light microscopy, calculated following Young and Ziveri (2000). [b] Measured from SEM, calculated following Young and Ziveri (2000). [c] Calculated following Menden-Deuer and Lessard (2000).

Species	Strain	Cell diameter (μm)	Cell calcite (pmol C cell^{-1})	Cell POC (pmol C cell^{-1})	Cell Chl (pg Chl cell^{-1})	Cell calcite : POC
C. pelagicus	RCC4092	12.9 (±1.8)	16.6[a] (±3.9)	13.8[c] (±5.1)	5.1 (±1.0)	1.2
E. huxleyi	RCC3533	4.47 (±0.52)	0.32[b] (±0.11)	0.67[c] (±0.24)	0.31 (±0.06)	0.48
C. braarudii	RCC1198	15.9 (±2.4)	38.7[a] (±6.2)	25.0[c] (±8.9)	7.8 (±1.4)	1.5
E. huxleyi	RCC1228	4.52 (±0.58)	0.39[b] (±0.10)	0.69[c] (±0.26)	0.32 (±0.07)	0.57

Table 2. Experiment culture strains, temperature, instantaneous irradiance, daily irradiance and growth rates, with ±1 standard deviation for the experiments. Atlantic = RCC1198 and RCC1228, Arctic = RCC4092 and RCC3533.

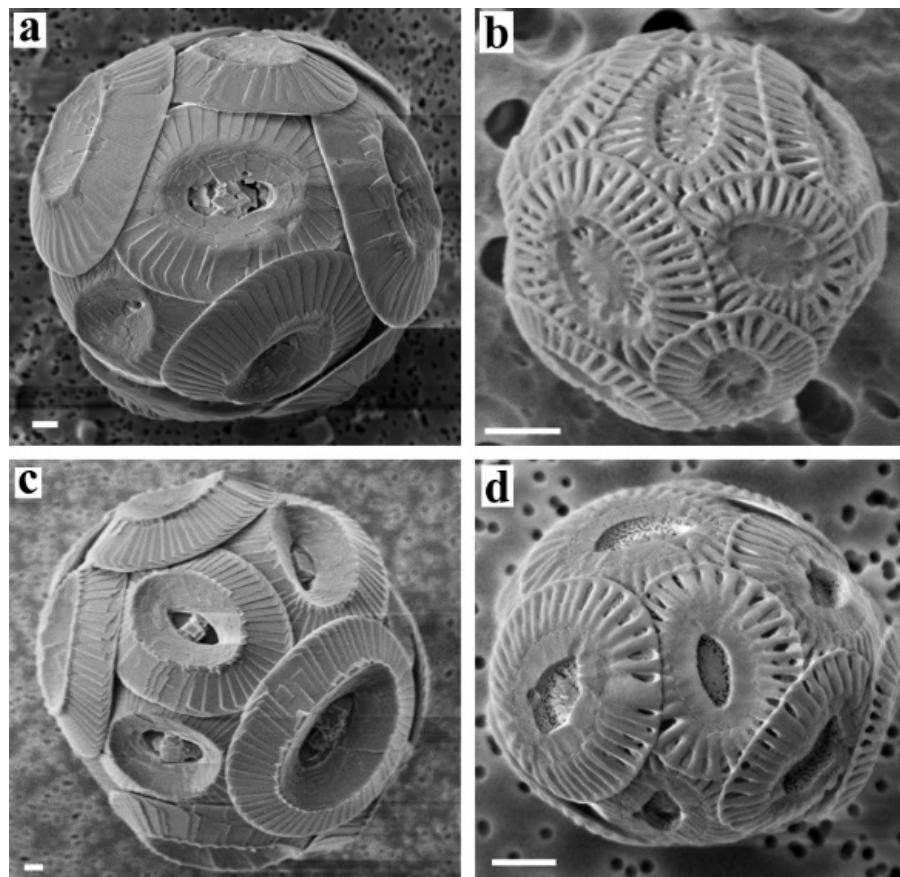| Experiment Strains	Temperature (°C)	Irradiance (µmol photons m^{-2} s^{-1})	Daily Irradiance (mol photons m^{-2} d^{-1})	Growth Rate (d^{-1})	
				E. huxleyi	*Coccolithus*
Atlantic	16	210	9.1	0.59 (±0.02)	0.52 (±0.02)
	16	200	8.6	0.72 (±0.03)	0.58 (±0.03)
	16	200	8.6	0.74 (±0.01)	0.54 (±0.02)
	16	115	5.0	0.62 (± < 0.01)	0.49 (±0.02)
	16	74	3.2	0.53 (±0.01)	0.42 (±0.03)
	14	200	8.6	0.62 (±0.01)	0.42 (±0.02)
	14	130	5.6	0.59 (±0.01)	0.43 (±0.02)
	12	190	8.2	0.50 (±0.01)	0.32 (±0.02)
	12	120	5.2	0.50 (±0.01)	0.32 (±0.02)
	19	244	10.5	0.85 (±0.02)	0.44 (±0.03)
	19	45	1.9	0.67 (± < 0.01)	0.48 (±0.01)
Arctic	6	90	3.9	0.27 (±0.01)	0.26 (±0.02)
	6	30	1.3	0.16 (± < 0.01)	0.18 (± < 0.01)
	12	190	8.2	0.58 (±0.02)	0.49 (±0.02)
	12	120	5.2	0.56 (±0.02)	0.48 (±0.02)
	9	190	8.2	0.47 (±0.02)	0.38 (±0.03)
	9	120	5.2	0.44 (±0.01)	0.36 (±0.02)
	6	140	6.0	0.29 (±0.01)	0.21 (±0.03)

Figure 1. SEM images. **(a)** *Coccolithus pelagicus* RCC4092. **(b)** *Emiliania huxleyi* RCC3533. **(c)** *Coccolithus braarudii* RCC1198. **(d)** *Emiliania huxleyi* RCC1228. Scale bars represent 1 μm in each image.
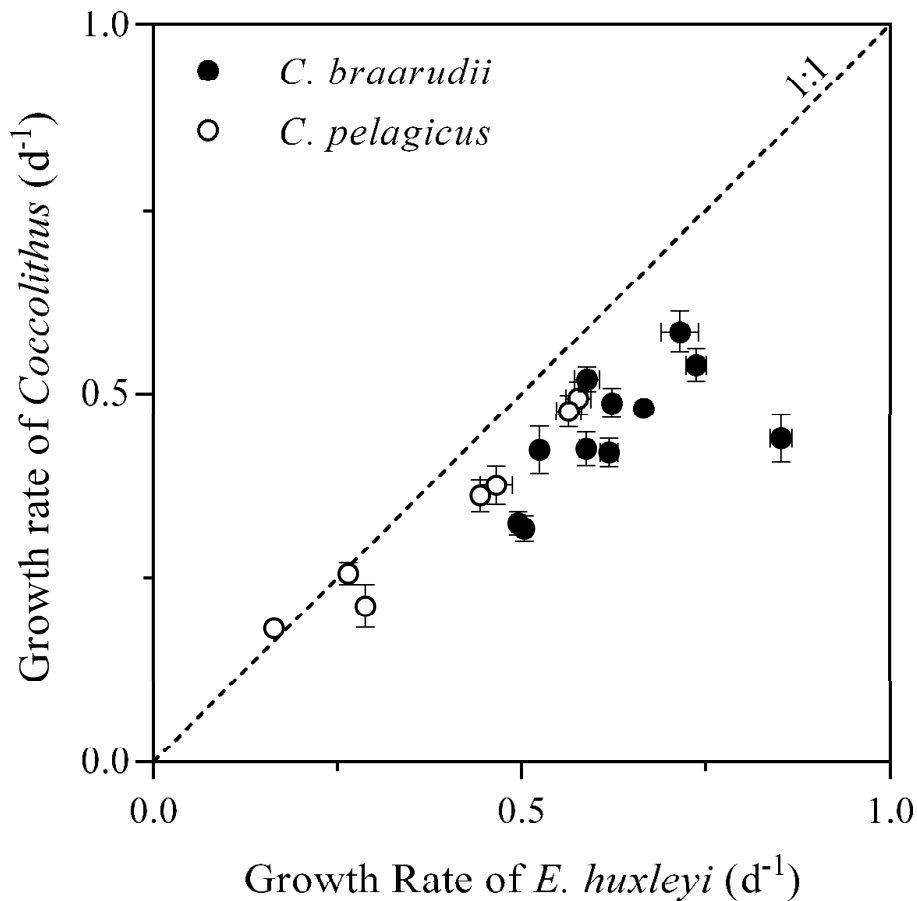
Figure 2. Growth rates (d^{-1}) of *Coccolithus pelagicus* RCC4092 and *Coccolithus braarudii* RCC1198 against corresponding growth rates of *Emiliania huxleyi* RCC3533 and RCC1228 respectively. Dashed line indicates a 1 : 1 ratio. Error bars are ±1 standard deviation.
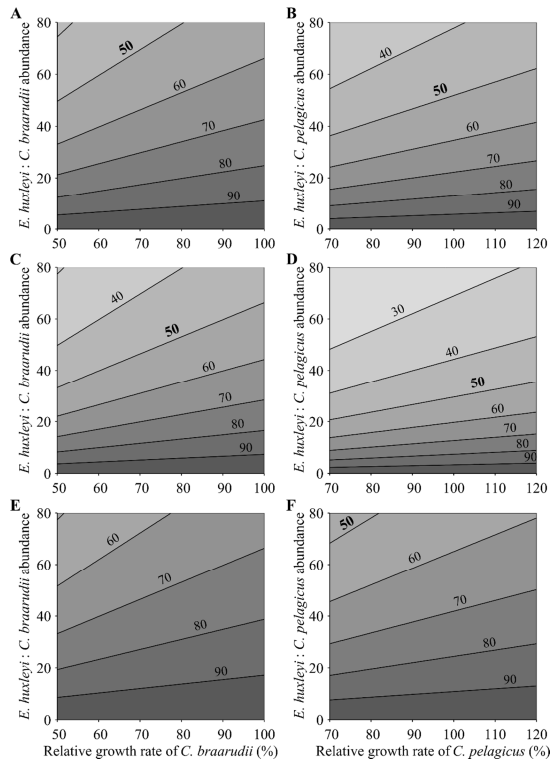
Figure 3. Contour plots of how percentage calcite production by *Coccolithus* varies with the abundance ratio of *Emiliania huxleyi* to *Coccolithus* and the growth rate of *Coccolithus* relative to *E. huxleyi*, for modelled communities of *Coccolithus braarudii* and *E. huxleyi* **(A, C, E)** and *Coccolithus pelagicus* and *E. huxleyi* **(B, D, F)**. **(A)** and **(B)** show model with input using calcite quotas from Table 1, **(C)** and **(D)** have increased *E. huxleyi* and decreased *Coccolithus* calcite content by one standard deviation from average values in Table 1, while **(E)** and **(F)** have decreased *E. huxleyi* and increased *Coccolithus* calcite by one standard deviation away from average values given in Table 1.

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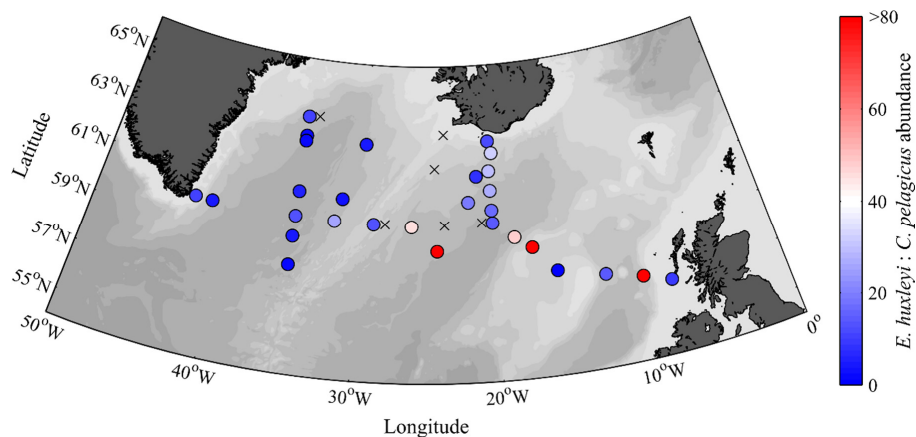
Interactive Discussion

Figure 4. Relative cellular abundance of *Emiliania huxleyi* to *Coccolithus pelagicus* in the North Atlantic in 2010 (April–August). Crossed symbols indicate samples where *C. pelagicus* was absent.