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

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Abstract.

Coccolithophores, a diverse group of phytoplankton, make important contributions to pelagic calcite production and export, yet the comparative biogeochemical role of species other than the ubiquitous *Emiliania huxleyi* is poorly understood. The contribution of different coccolithophore species to total calcite production is controlled by inter-species differences in cellular calcite, growth rate and relative abundance within a mixed community. In this study we examined the relative importance of *E. huxleyi* and two *Coccolithus* species in terms of daily calcite production. Culture experiments compared growth rates and cellular calcite content of *E. huxleyi* (Arctic and temperate strains), *Coccolithus pelagicus* (novel Arctic strain) and *Coccolithus braarudii* (temperate strain). Despite assumptions that *E. huxleyi* is a fast growing species, growth rates between the three species were broadly comparable (0.16-0.85 d^{-1}) under identical temperature and light conditions. *Emiliania huxleyi* grew only 12 % faster on average than *C. pelagicus*, and 28 % faster than *C. braarudii*. As the cellular calcite content of *C. pelagicus* and *C. braarudii* is typically 30-80 times greater than *E. huxleyi*, comparable growth rates suggest that *Coccolithus* species have the potential to be major calcite producers in mixed populations. To further explore these results we devised a simplistic model comparing daily calcite production from *Coccolithus* and *E. huxleyi* across a realistic range of relative abundances and a wide range of relative growth rates. Using the relative differences in growth rates from our culture studies we found that *C. pelagicus* would be a larger source of calcite if abundances of *E. huxleyi* to *C. pelagicus* were below 34:1. Relative abundance data collected from North Atlantic field samples (spring and summer 2010) suggest that with a relative growth rate of 88 %, *C. pelagicus* dominated calcite

production at 69 % of the sites sampled. With a more extreme difference in growth rates, where *C. pelagicus* grows at a tenth of the rate of *E. huxleyi*, *C. pelagicus* still dominated calcite production in 14 % of the field. These results demonstrate the necessity of considering interactions between inter-species differences in growth rates, cellular calcite and relative abundances when evaluating the contribution of different coccolithophores to pelagic calcite production. In the case of *C. pelagicus*, we find that there is strong potential for this species to make major contributions to calcite production in the North Atlantic, although estimates of relative growth rates from the field are needed to confirm our conclusions.

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; Langer et al., 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 (~ 0.4-0.5 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 30-40 times greater (11.6 pmol C cell^{-1} d^{-1}) than *E. huxleyi* (0.28-0.35 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 3-4 times (although *C. pelagicus* would still represent ~75 % of the total calcite production).

Besides relative growth rates (the growth rate of *Coccolithus* relative to *E. huxleyi*), 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, 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 greater susceptibility of smaller coccospheres, such as those of *E. huxleyi*, to disintegration and remineralisation (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 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. Lastly, the biogeochemical implications of growth rates and 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) modified K/20 medium (modified from Keller et al., 1987; following Gerecht et al., 2014); aged natural seawater was enriched with 28.8 µM nitrate and 1.8 µM phosphate. 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, under a 12/12 h light/dark cycle.

To reflect a realistic *in situ* environment (Poulton et al., 2010; Ryan-Keogh et al., 2013), 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 1.30-8.21 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 1.94-10.54 mol photons m^{-2} d^{-1} (45-244 µmol photons m^{-2} s^{-1}). Cells were acclimated to experimental conditions for approximately 10 generations and grown in dilute batch cultures in duplicate. Cultures were grown in ventilated flasks and to low cell densities to avoid biological effects on the carbonate system (150,000-470,000 cells mL^{-1}, 4,500-8,700 cells mL^{-1} and 5,300-16,000 cells mL^{-1}, for *E. huxleyi*, *C. braarudii* and *C. pelagicus* respectively) and sampled during the mid-exponential phase to avoid nutrient limitation (Langer et al., 2009; Hoffman et al., 2014).

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. 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). 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

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 (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}.

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). *Emiliania huxleyi* RCC1228 (0.50-0.85 d^{-1}) grew significantly faster (Student's t-test, $t = 6.8$, $df = 10$, $p < 0.001$) than *C. braarudii* (0.32-0.58 d^{-1}). For the Arctic strains, the growth rate of *E. huxleyi* (0.16-0.58 d^{-1}) was significantly different (Student's t-test, $t = 3.5$, $df = 6$, $p < 0.02$) to that of

C. pelagicus (0.18-0.49 d^{-1}), growing faster in all but the experiment with the slowest growth rates (Fig. 2).

Although *E. huxleyi* always grew faster than *C. braarudii*, and was generally faster than *C. pelagicus*, the differences in growth rates were smaller than previously reported, with *E. huxleyi* growing on average only 12 % (-11 % to 26 %) faster than *C. pelagicus*, and 28 % (12-49 %) faster than *C. braarudii*. In contrast, Buitenhuis et al. (2008) observed that when grown in conditions comparable to ours (12-15 °C, 14/10 L/D, 4.20 mol photons m^{-2} d^{-1}), the growth rate of *C. braarudii* was 42-51 % that of *E. huxleyi*, although the strain of *E. huxleyi* used by Buitenhuis et al. (2008) was a non-calcifying mutant, which have been observed to have higher growth rates (Paasche, 2002).

While our maximum growth rate of *E. huxleyi* (0.85 d^{-1}) was lower than in some recent studies (e.g., 0.98-1.64 d^{-1}, Langer et al., 2009), they are well within the range of reported growth rates (0.4-1.9 d^{-1}, Paasche, 2002). Strain-specific variability is likely to partly contribute to this large range in growth rates (e.g., Langer et al., 2009). However, it is also likely that our lower maximum growth rates are due to the effect of the day length used in our study (12 L/ 12 D), as day lengths shorter than 16 hours have been observed to reduce phytoplankton growth rates (Paasche, 1967). Although our *E. huxleyi* growth rates were lower than those obtained in 16 hour day length studies (e.g. Langer et al., 2009; Hoppe et al., 2011), they were similar to another 12 hour day length study (0.6-1 d^{-1}, Iglesias-Rodriguez et al., 2008). This is also the case for *C. braarudii* and *C. pelagicus*; the maximum growth rate of *C. braarudii* (0.58 d^{-1}) was below that observed in 16 hour day length studies (0.73-0.82 d^{-1}, Langer et al., 2006; Gibbs et al., 2013), but above both 12 hour (0.42-0.5 d^{-1}, Taylor et al., 2007; Gerecht et al., 2014) and 14 hour (0.4 d^{-1}, Buitenhuis et al., 2008) day length experiments. Although there are few studies of *C. pelagicus*, our maximum growth rate (0.49 d^{-1}) was greater than the 12 hour day length study (0.36 d^{-1}) by Gerecht et al. (2014) but lower than a 16 hour day length experiment (0.58 d^{-1}) by Gibbs et al. (2013). Given these differences between experiments, and no literature consensus on recommended day length (Probert and Houdan, 2004), we are therefore confident that our growth rates are representative of these coccolithophore species.

Both temperature and irradiance had a measurable effect on growth rates (Table 2, 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).

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 the variability in 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 therefore 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, where the coccosphere calcite of one cell is 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 cellular calcite inventories, as well as the relative abundance of these species compared to other coccolithophores. In the context of our study, we consider daily contributions to calcite production, as this is the minimal time-length over which we can realistically expect relative abundances to be least variable. Also, much of the work measuring calcite production by natural field communities is based on daily integrals (e.g., Poulton et al., 2010; Poulton et al., 2013).

We examine the potential relative daily calcite production by modelling a simplified community comprised of just *E. huxleyi* and either *C. pelagicus* or *C. braarudii*. Assuming steady state in terms of the cellular quota across a day, 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:

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

The model was parameterised using a range of relative growth rates that spans the range measured in our culture experiments (Fig. 2, Table 2), but has also been extended down to 10 % to investigate the effect of *Coccolithus* having a much lower relative growth rate. The relative abundance of *Coccolithus* and *E. huxleyi* in our simple model community is represented as the ratio of *E. huxleyi* to *Coccolithus* and was varied from 0 to 80. Cellular calcite values for each species were experimentally determined (Table 1). The percentage calcite production by *Coccolithus* is inversely related to its relative growth rate, cellular calcite and abundance, and linearly related to the ratio of *E. huxleyi* to *Coccolithus* (demonstrated in Fig. 3). As the ratio of *E. huxleyi* to *Coccolithus* increases, or the relative growth rate of *Coccolithus* decreases, a decrease in the percentage calcite production by *Coccolithus* is observed (Fig. 3).

Coccolithus braarudii is the major source (> 50 %) of calcite production in 56 % of the model, and 64 % of the model when considering only the range of relative growth rates of *C. braarudii* observed in this study (51-88 %, Fig. 3A). At its average relative growth rate (72 %), *C. braarudii* will dominate (> 50 %) calcite production if the ratio of *E. huxleyi* to *C. braarudii* is less than 53:1, whilst with the same growth rates, *C. braarudii* calcifies at a rate equivalent to 74 cells of *E. huxleyi*. However, if *C. braarudii* is only able to grow at a relative growth rate of 10 % that of *E. huxleyi*, its calcite production is reduced to only 7 times that of an *E. huxleyi* cell. Therefore, unless *C. braarudii* is both in a very low relative abundance and has a very low relative growth rate, we would expect *C. braarudii* to be a major source of calcite compared to *E. huxleyi*.

Coccolithus pelagicus has a lower cellular calcite content than *C. braarudii* (16.6 and 38.7 pmol C $cell^{-1}$ respectively, Table 1), thus only dominates 29 % of its total model, and 44 % of the model when constrained to observed relative growth rates (74-110 %). When growing at its average observed relative growth rate (88 %), *C. pelagicus* dominates calcite production when the ratio of *E. huxleyi* to *C. pelagicus* is less than 34:1 (Fig. 3B). Equivalent growth rates require a ratio less than 39:1 for *C. pelagicus* to dominate cellular calcite production,

whilst a growth rate of only 10 % that of *E. huxleyi* results in calcite production from *C. pelagicus* being only 3.5 times that of an *E. huxleyi* cell. Although a greater relative abundance of *C. pelagicus* is required to dominate calcite production compared to *C. braarudii*, we still find that it would also be a large source of calcite unless both relative growth rates and abundances are low.

Although we have modelled the effect of growth rate and relative abundance on the role of *Coccolithus* as a calcite producer, the relative calcite production of the two species in these models are highly dependent on the cellular calcite quotas attributed to both *E. huxleyi* and *Coccolithus* (Table 1), as calcite production is the product of growth rate and cellular calcite. Estimates of the cellular calcite content of *E. huxleyi* varies significantly between studies (Balch et al., 1996; Paasche, 2002; Langer et al., 2009; Poulton et al., 2010), which is likely due to both ecophysiological and methodological differences (Young and Ziveri, 2000; Poulton et al., 2010; Poulton et al., 2013; Hoffman et al., 2014). Our estimates of *E. huxleyi* cellular calcite (0.43-0.52 pmol C cell^{-1}) are similar to recent estimates based on similar biometric measurements (Hoffman et al., 2014), and are within the range of literature values (0.22-1.1 pmol C cell^{-1} Fritz and Balch, 1996; Paasche, 2002; Hoppe et al., 2011). Our value for *C. braarudii* cellular calcite is greater than previously measured (28 pmol C cell^{-1}, Langer et al., 2006; 17 pmol C cell^{-1}, Gerecht et al., 2014), while the value for *C. pelagicus* cellular calcite is lower (26 pmol C cell^{-1}, Gerecht et al., 2014).

To address the impact of variability in cellular calcite on calcite production we have varied the parameters of our model by concurrently increasing the calcite content of *E. huxleyi* and decreasing that of *Coccolithus*, by one standard deviation each (Table 1), or vice versa (Figs. 3C-F). In doing this, we capture most of the reported range of *E. huxleyi* calcite as it is the equivalent of varying *E. huxleyi* RCC3533 calcite by 0.23-0.75 pmol C cell^{-1} and RCC1228 by 0.33-0.79 pmol C cell^{-1}, while the value for *Coccolithus* is held constant.

Reducing the calcite content of *C. pelagicus* (12.7 pmol C cell^{-1}) and *C. braarudii* (32.5 pmol C cell^{-1}) and increasing that of *E. huxleyi* (0.57-0.66 pmol C cell^{-1}) reduces the dominance of *Coccolithus* in the model (Fig. 3C-D). Thus *C. braarudii* dominates only 37 % of the total model (Fig. 3C), 43 % of the model when constrained to observed relative growth rates, and calcifies at a rate equivalent to 49 cells of *E. huxleyi* when growth rates are the same. With the same reductions in cellular calcite content, *C. pelagicus* is the major calcite producer in only 17 % of the total model (Fig. 3D), 26 % of the model when constrained to observed

relative growth rates, and with the same growth rate will dominate calcite production if the ratio of *E. huxleyi* to *C. pelagicus* is less than 22:1.

An increase in the calcite content of *C. pelagicus* (20.5 pmol C cell^{-1}) and *C. braarudii* (44.9 pmol C cell^{-1}), coupled with a decrease in that of *E. huxleyi* (0.29-0.38 pmol C cell^{-1}), results unsurprisingly in an increased dominance of both *C. braarudii* (Fig. 3E) and *C. pelagicus* (Fig. 3F). *Coccolithus braarudii* dominates 75 % of the total model and 93 % of the observation-constrained model, while *C. pelagicus* dominates 53 % of the total model and 81 % of the observation-constrained model.

Cellular calcite clearly has a significant influence on our calculation of percentage calcite production, and therefore needs to be constrained more tightly, particularly in the case of *Coccolithus*. However, we still observe notable levels of calcite production deriving from *Coccolithus* rather than *E. huxleyi* in the models using even the lowest values of cellular calcite for *Coccolithus*.

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 communities 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). A physicochemical description of the region is available in Ryan-Keogh et al. (2013), which indicates nutrient replete conditions for the phytoplankton community in spring and nutrient depleted (iron and/or nitrate) conditions in summer. Although other species of coccolithophore were present, we have extracted only the abundances of *E. huxleyi* and *C. pelagicus*, so that the data is comparable to our model scenarios in Section 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 absent (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 (0.7-85) was generally comparable to our modelled range, with a relatively low median average of 12.7. However, in 2 samples (Supplementary Table S1), 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, Figs. 3A and 3B) and the average relative growth rate for *C. pelagicus* of 88 %, the minimum relative abundance of *E. huxleyi* to *C. pelagicus* required for *E. huxleyi* to dominate calcite production (34:1) was exceeded in only 5 out of 29 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* remains the major calcite producer in 69 % of the samples.

Under the more conservative model scenario (Fig. 3D), with a relative growth rate of 88 %, *C. pelagicus* remains the major calcite producer in 57 % of the samples, which is reduced to 51 % if the lowest measured relative growth rate (74 %) is used. If *C. pelagicus* has a higher nutrient requirement and lower nutrient affinity than *E. huxleyi*, then in low nutrient conditions, we would expect a lower relative growth rate. As we do not know the relative nutrient affinities, we have used an extreme in our original model where *C. pelagicus* has a relative growth rate of 10 %. Under this scenario, *C. pelagicus* is the major calcite producer in 14 % of the samples, although it would still form a significant component of the total calcite production (7-49%) in other samples when present.

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* in field communities 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* (~1100 μm^3) and *C. braarudii* (~2100 μm^3) compared to *E. huxleyi* (~50 μm^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 nutrient uptake per unit volume of

the cell (Lewis, 1976; Finkel et al., 2009) and 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*.

It is also worth considering the implications of relative differences in cell size and surface area to volume for nutrient requirements to support growth. From our estimates of cellular POC (Table 1) and assuming Redfield stoichiometry (Redfield, 1958), we can also estimate that the cellular particulate organic nitrogen (PON) and particulate organic phosphorus (POP) content of *E. huxleyi*, *C. pelagicus* and *C. braarudii* is respectively 0.10, 2.0 and 3.6 pmol N cell^{-1}, and 0.006, 0.12 and 0.22 pmol P cell^{-1}. Our estimates of cellular quotas for *E. huxleyi* are similar to Langer et al. (2013), who measured cellular quotas of 0.69 pmol C cell^{-1}, 0.12 pmol N cell^{-1}, and 0.003 pmol P cell^{-1}. Cellular quotas of both *C. pelagicus* and *C. braarudii* have recently been measured by Gerecht et al. (2014). While the cellular PON (1.9 pmol N cell^{-1}) and POP (0.19 pmol P cell^{-1}) of *C. pelagicus* were generally similar to our study, the value for cellular POC was slightly larger (20 pmol C cell^{-1}), suggesting a lower nutrient requirement per unit POC. However, Gerecht et al. (2014) report *C. braarudii* cellular quotas of POC (13 pmol C cell^{-1}) and PON (1.5 pmol N cell^{-1}) that are much lower than their values for *C. pelagicus*. This is unexpected, as it is generally accepted that *C. braarudii* is a larger species of coccolithophore than *C. pelagicus* (Geisen et al., 2004) and we would therefore expect a higher POC content for *C. braarudii* than *C. pelagicus* (Table 1) if POC scales with cell size. Clearly further cellular measurements of POC, PON and POP for different coccolithophore species are needed to fully examine cellular nutrient requirements.

For culture media with a given nitrate concentration of 10 µmol N L^{-1}, the maximum cumulative cell concentration that could be supported using our estimated cellular PON would therefore be ~ 1 x 10^5, ~ 5,000 and ~ 2,800 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 ~ 50, ~ 80 and ~ 110 µmol C L^{-1}. Therefore despite lower cell densities, for a given nutrient concentration, 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;

379 Poulton et al., 2013). For a bloom with a magnitude of 1000 cells mL^{-1}, this would require a
380 nitrate concentration of only ~ 0.1 µmol N L^{-1}. Comparatively, although rare, *C. pelagicus*
381 has also been reported in concentrations exceeding 1000 cells mL^{-1} in the high latitude North
382 Atlantic (Milliman, 1980), requiring a much larger nitrate concentration of 2 µmol N L^{-1}. The
383 seasonal drawdown of nitrate in the North Atlantic is estimated be ~ 10 µmol N L^{-1} (Sanders
384 et al., 2005; Ryan-Keogh et al., 2013), and thus a *C. pelagicus* bloom of 1000 cells mL^{-1}
385 represents the utilization of a significant amount of the available nutrients. For a bloom of
386 this magnitude to occur, we would expect *C. pelagicus* to be a significant proportion of the
387 total phytoplankton community with a relatively low mortality rate, as nutrient drawdown
388 will be related to gross production by the total phytoplankton community. Reduced mortality
389 has also been discussed as a possible factor in the formation and persistence of *E. huxleyi*
390 blooms in the southeast Bering Sea (Olson and Strom, 2002).

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

399 ## 4. Conclusion

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

408 The relative abundance of *E. huxleyi* and *C. pelagicus* was determined from samples
409 collected from the Irminger and Iceland Basins in the North Atlantic. This showed that using
410 our standard model scenario with *C. pelagicus* growing at 88 % of the growth rate of *E.*

411 *huxleyi*, we would expect *C. pelagicus* to be the major calcite producer in 69 % of the field
412 samples. Using a more conservative model reduced this to 57 %, while the scenario of an
413 extreme difference in growth rates led to *C. pelagicus* only dominating 14% of the samples.
414 Therefore, we would expect *C. pelagicus* to be a major source of calcite in the sub-polar
415 North Atlantic across a spectrum of relative growth rates. With a present-day distribution
416 constrained to the polar and sub-polar northern hemisphere, *C. pelagicus* is unlikely to be a
417 dominant calcite producer on a global scale. However, the fossil record of *C. pelagicus* shows
418 that it has remained a major contributor to sedimentary calcite for the last 65 million years
419 (Gibbs et al., 2013) and therefore there is the strong potential that it was also a major
420 producer in the surface ocean in the past. There are a number of other extant coccolithophore
421 species that have high cellular calcite content relative to *E. huxleyi* (e.g. *Calcidiscus*
422 *leptoporus*, *Helicosphaera carteri*) and are known to have high contributions to deep sea
423 calcite fluxes, and therefore may similarly make significant contributions to pelagic calcite
424 production. Further studies elucidating the relative growth rates of these species compared to
425 *E. huxleyi*, in culture and in the field, as well as their relative abundances in mixed
426 coccolithophore communities are therefore needed to fully examine their potential to
427 dominate calcite production. Lastly, investigations of community composition and
428 calcification rates are also needed to examine the contribution of different species to total
429 calcite production.

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

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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)	0.43[b] (± 0.14)	0.67[c] (± 0.24)	0.31 (± 0.06)	0.64
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)	0.52[b] (± 0.14)	0.69[c] (± 0.26)	0.32 (± 0.07)	0.75

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

Experiment Strains	Temperature (°C)	Daily Irradiance (mol photons m-2 d-1)	Growth Rate (d-1)	
			E. huxleyi	Coccolithus
Atlantic	16	9.07	0.59 (± 0.02)	0.52 (± 0.02)
	16	8.64	0.72 (± 0.03)	0.58 (± 0.03)
	16	8.64	0.74 (± 0.01)	0.54 (± 0.02)
	16	4.97	0.62 (± <0.01)	0.49 (± 0.02)
	16	3.20	0.53 (± 0.01)	0.42 (± 0.03)
	14	8.64	0.62 (± 0.01)	0.42 (± 0.02)
	14	5.62	0.59 (± 0.01)	0.43 (± 0.02)
	12	8.21	0.50 (± 0.01)	0.32 (± 0.02)
	12	5.18	0.50 (± 0.01)	0.32 (± 0.02)
	19	10.54	0.85 (± 0.02)	0.44 (± 0.03)
	19	1.94	0.67 (± <0.01)	0.48 (± 0.01)
Arctic	6	3.89	0.27 (± 0.01)	0.26 (± 0.02)
	6	1.30	0.16 (± <0.01)	0.18 (± <0.01)
	12	8.21	0.58 (± 0.02)	0.49 (± 0.02)
	12	5.18	0.56 (± 0.02)	0.48 (± 0.02)
	9	8.21	0.47 (± 0.02)	0.38 (± 0.03)
	9	5.18	0.44 (± 0.01)	0.36 (± 0.02)
	6	6.05	0.29 (± 0.01)	0.21 (± 0.03)

Figure Captions

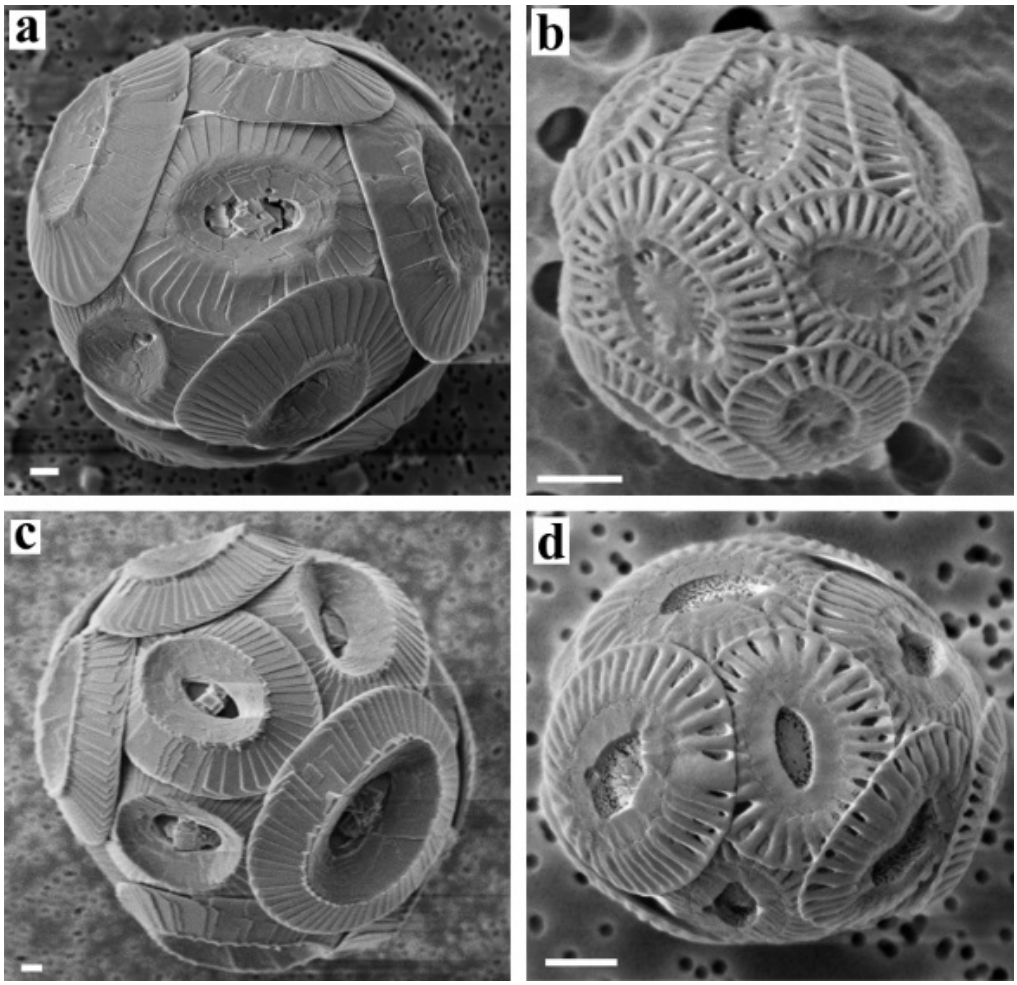
Fig. 1: SEM images. A) *Coccolithus pelagicus* RCC4092. B) *Emiliania huxleyi* RCC3533. C) *Coccolithus braarudii* RCC1198. D) *Emiliania huxleyi* RCC1228. Scale bars represent 1 µm in each image.

Fig. 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.

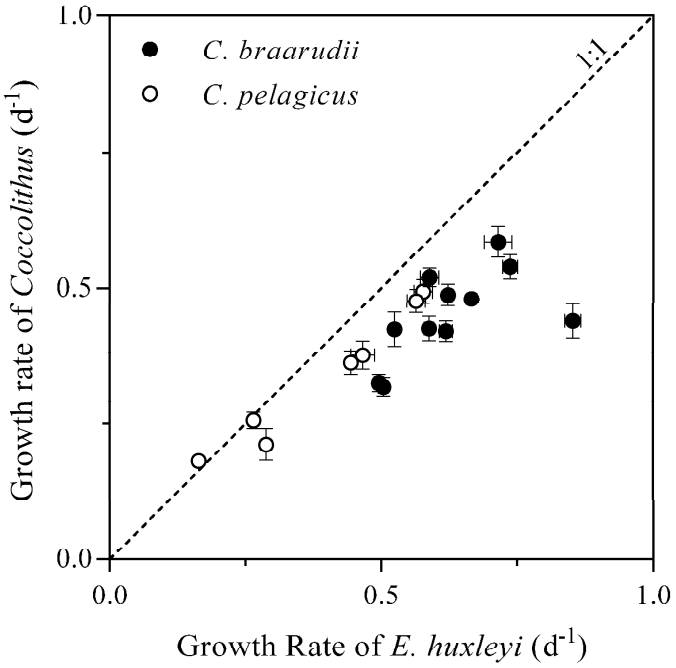
Fig. 3: Contour plots of how percentage calcite production by *Coccolithus* varies with the abundance ratio of *Emiliania huxleyi* to *Coccolithus* and the growth rate of *Coccolithus* relative to *E. huxleyi*, for modelled communities of *Coccolithus braarudii* and *E. huxleyi* (A, C, E) and *Coccolithus pelagicus* and *E. huxleyi* (B, D, F). Plots 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. Dotted lines indicate the average relative growth rate as determined from the culture experiments.

Fig. 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.

Fig. 1



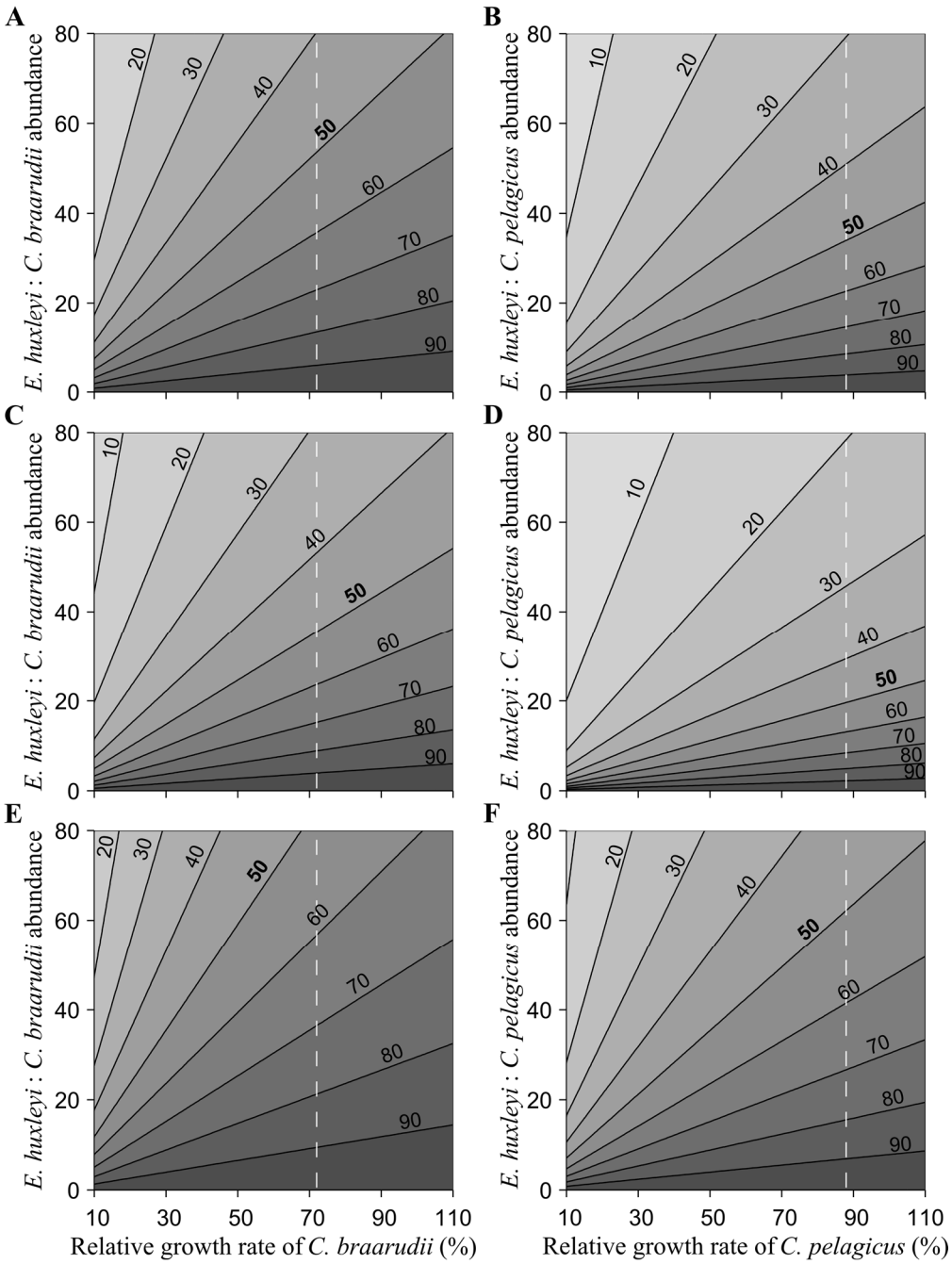
24 **Fig. 2**


1.0
0.5
0.0
0.0
0.5
1.0
C. braarudii
C. pelagicus
1:1
Growth rate of Coccolithus (d-1)
Growth Rate of E. huxleyi (d-1)

25

26

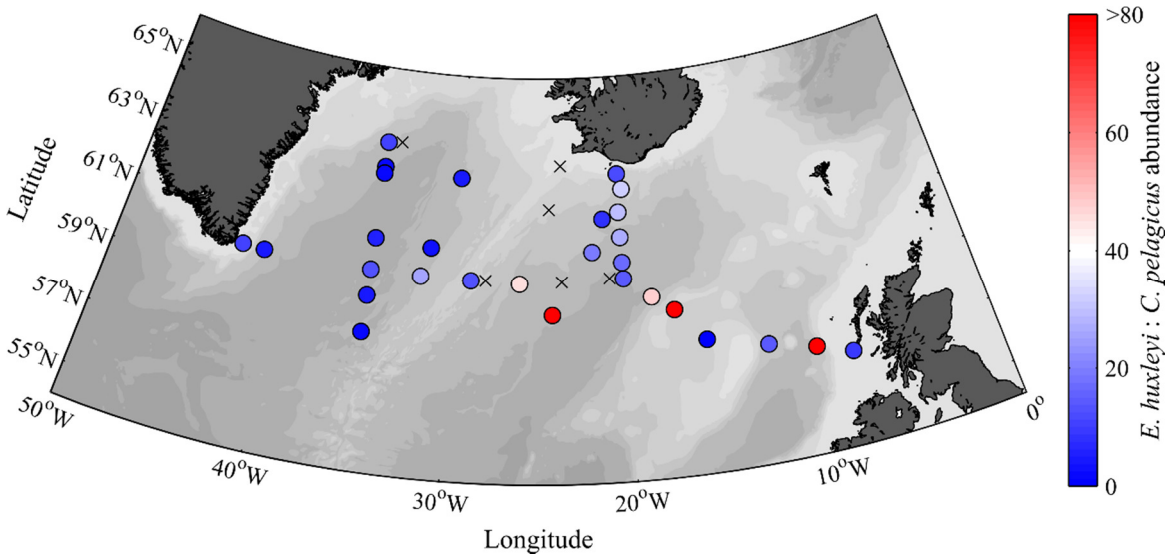
27 **Fig. 3**


A
B
C
D
E
F
E. huxleyi : C. braarudii abundance
E. huxleyi : C. pelagicus abundance
0
20
40
60
80
10
30
50
70
90
110
Relative growth rate of C. braarudii (%)
Relative growth rate of C. pelagicus (%)

28

29

Fig. 4


65°N
63°N
61°N
59°N
57°N
55°N
Latitude
50°W
40°W
30°W
20°W
10°W
0°
Longitude
>80
60
40
20
0
E. huxleyi : C. pelagicus abundance