Species-specific calcite production reveals *Coccolithus pelagicus* as the key calcifier in the Arctic Ocean

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Running Head: *Coccolithus pelagicus* dominates Arctic Ocean calcification

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Abstract

Through the production and export of their calcite coccoliths, coccolithophores form a key component of the global carbon cycle. Despite this key role, very little is known about the biogeochemical role of different coccolithophore species in terms of calcite production, and how these species will respond to future climate change and ocean acidification. Here we present the first study to determine species-specific calcite production, from samples collected in the Arctic Ocean and subarctic Iceland Basin in June 2012. We show that although the coccolithophorid *Coccolithus pelagicus* comprised only a small fraction of the total community in terms of abundance (2 %), it was the major calcite producer in the Arctic Ocean and Iceland Basin (57 % of total calcite production). In contrast, *Emiliania huxleyi* formed 27 % of the total abundance and was responsible for only 20 % of the calcite production. That *C. pelagicus* was able to dominate calcite production was due to its relatively high cellular calcite content compared with the other species present. Our results demonstrate for the first time the importance of considering the complete coccolithophore community when considering pelagic calcite production, as relatively rare but heavily calcified species such as *C. pelagicus* can be the key calcite producers in mixed communities. The response of *C. pelagicus* to ocean acidification and climate change is therefore likely to have a major impact on carbon cycling within the North Atlantic and Arctic Ocean.

Introduction

Coccolithophores are a major group of phytoplankton, comprising up to 10% of primary production (Poulton et al. 2007), dominating pelagic calcite production and export with their calcite coccoliths (Broecker & Clark 2009), and thus forming a key component of the global carbon cycle (de Vargas et al. 2007, Ziveri et al. 2007). Marine calcifiers, including coccolithophores, face an uncertain future, as they have to contend with the effects of global warming and ocean acidification (Royal Society 2005, Winter et al. 2013). Culture experiments considering the response of coccolithophores to ocean acidification have produced conflicting results (Iglesias-Rodriguez et al. 2008, Langer et al. 2009, Hoppe et al. 2011), with long term studies suggesting adaptive evolution could partly compensate for the effect of global warming and ocean acidification (Lohbeck et al. 2012, Schluter et al. 2014). Furthermore, more mechanistic understanding of coccolithophore responses to variable pH indicate that different species respond differently (Langer et al. 2009) and have different growth optimum conditions in terms of pH (Bach et al. 2015).

Many of the previous studies on coccolithophores, along with the majority of the current literature, consider only a single species of coccolithophore: *Emiliania huxleyi*. Although *E. huxleyi* is considered the keystone coccolithophore species due to its global dominance and ability to form large-scale highly visible blooms (Paasche 2002), there are ~ 200 extant species of coccolithophore, which vary considerably in cell size (2 to 20 μm), and cellular calcite quota (Young et al. 2003). In this context, *E. huxleyi* has a relatively small cell (~ 5 μm) with a relatively low cellular calcite content (0.2 – 1.1 μmol C cell^{-1}; Paasche 2002, Daniels et al. 2014) and hence relatively low calcification rates; other larger and more heavily calcified species, such as *Coccolithus pelagicus* with ~ 30 times more calcite per cell than *E. huxleyi* (Daniels et al. 2014), have the potential to be key species in terms of upper ocean calcite production and export (Ziveri et al. 2000, Bauman et al. 2004, Daniels et al. 2014).

The response of coccolithophores to ocean acidification in culture experiments appears to differ between species and strains (Langer et al. 2006, Langer et al. 2009), and culture experiments do not necessarily reflect the response of natural populations to environmental fluctuations (Smith et al. 2012). Therefore it is unlikely that *E. huxleyi*’s response to ocean acidification in culture can be applied to multi-species populations of coccolithophores (Bach et al. 2015). In natural communities the response to variability in pH is often secondary to effects of light, nutrient availability and growth rate (Zondervan 2007, Charalampopoulou et al. 2011, Poulton et al. 2014). To examine how a diverse coccolithophore community will respond to environmental changes, and to assess the relative biogeochemical importance of different coccolithophore species, field studies considering the whole coccolithophore community are required.

The effect of anthropogenic CO_2 emissions on the Arctic Ocean is expected to be among the largest and most rapid of any region on the globe (ACIA 2004), with the Arctic already experiencing rapid warming (ACIA 2004). Ocean acidification is also expected to be particularly enhanced at high latitudes because of the increased solubility of CO_2 at low temperatures. Within the Nordic Seas (Greenland Sea and Norwegian Sea) of the Arctic Ocean large natural gradients of environmental variables such as temperature and carbonate chemistry already exist; in the west, the East-Greenland Current transports cold (< 0 °C) Polar Water southwards through the Greenland Sea (Fig. 1), while in the east the Norwegian Current carries relatively warm (6 – 10 °C) Atlantic water into the Norwegian Sea (Johannessen 1986).

Coccolithophores are a key phytoplankton group within the Greenland and Norwegian Sea (Samtleben & Schröder 1992). The highest species diversities are found in the Norwegian Sea (Samtleben & Schröder 1992, Baumann et al. 2000), as the more diverse North Atlantic communities are transported northwards by the Norwegian Current. The Norwegian Sea coccolithophore community is generally dominated by *E. huxleyi* (Samtleben & Schröder 1992, Baumann et al. 2000, Charalampopoulou et al. 2011), with some species, such as *Calciopappus caudatus,* present throughout, while other species, such as *Syracosphaera spp.*, are limited to Atlantic surface waters. In contrast, coccolithophore diversity is lower in the Greenland Sea (Samtleben & Schröder 1992); *C. pelagicus* is commonly observed along with other polar species (e.g. *Papposphaera spp.*). The contrast in coccolithophore community structure and diversity, coupled with the strong natural environmental gradients of the Greenland and Norwegian Seas, means that this region is an ideal location to examine the influence of both the environment and the coccolithophore community structure on calcite production.

The aim of this study was to determine whether *E. huxleyi* was the major calcite producer in the Arctic Ocean, and if not, which coccolithophore species were. As only total community calcite production (CP) can be measured from mixed communities (e.g. Charalampopoulou et al. 2011, Poulton et al. 2014), a novel method was developed to determine species-specific calcite production (CP_{sp}) for each individual coccolithophore species. This method incorporates species-specific cellular calcite, growth rates and abundances to partition CP.

This is the first study to determine the calcite production rates of individual coccolithophore species within a natural multi-species community. Here we present results from 19 stations within the Arctic Ocean and the subarctic Iceland Basin (Fig. 1); calcite production (CP), coccolithophore cellular abundances, carbonate chemistry parameters and other environmental variables were measured, and CP_{sp} derived for each station.

Methods

Sampling

Sampling was carried out in the subarctic Iceland Basin, and the Greenland and Norwegian Seas within the Arctic Ocean (Fig. 1) between June 4th and 30th 2012 during the UK Ocean Acidification Arctic Cruise, aboard the RRS *James Clark Ross* (JR271). Water samples for rate measurements, coccolithophore community structure and ancillary measurements, were collected from a single depth within the middle of the mixed layer at 19 CTD stations. Temperature and salinity were obtained from the CTD. Incidental photosynthetically active radiation (PAR), measured with ship-mounted scalar irradiance sensors (Kipp & Zonen ParLite 0348900, Skye Instruments SK3), was integrated over the incubation periods to calculate daily incidental irradiance (mol photons m^{-2} d^{-1}). The vertical diffuse attenuation coefficient of PAR (K_d) in the water column was calculated from the CTD casts, with the depth of the euphotic zone (Z_{eup}) calculated as the depth of 1 % incident irradiance.

Calcite production

Daily rates of calcite production were measured using the micro-diffusion technique (Paasche & Brubak 1994, Balch et al. 2000) following Poulton et al. (2014). Water samples (70 mL, 3 light, 1 formalin-killed), collected from one depth within the middle of the mixed layer, were inoculated with 25 – 50 µCi ^{14}C labelled sodium bicarbonate. Samples were incubated for 24 hours in an on-deck incubator, chilled with surface seawater and the 55% incidental irradiance light depth was replicated using Misty-blue optical filters (LEE^{TM}). When the surface seawater supply was unavailable (at ice stations), samples were incubated in a constant temperature container laboratory (see Richier et al. 2014) with the temperature and photoperiod set to replicate the in situ environment. Formalin-killed blanks were prepared by addition of 1 mL of 0.2 µm triple-filtered and sodium-borate buffered formalin solution.

Incubations were terminated by filtration through 25 mm 0.45 µm polycarbonate filters (Nuclepore^{TM}). Filters were secured in glass scintillation vials with a gas-tight septum and a bucket containing a CO_2 trap (Whatman GFA filter soaked with 200 µl β-phenylethylamine), acidified with a weak acid (1 ml, 1% phosphoric acid), thus releasing the acid-labile inorganically fixed carbon (CP) as $^{14}CO_2$ to be absorbed by the CO_2 trap. After 24 hours, the GFA filters were removed to separate scintillation vials, and the activity of the filters was determined in Ultima Gold (Perkin-Elmer, UK) and their activity measured using a Tri-Carb 2100 Low Level Liquid Scintillation Counter. Spike activity was checked following Poulton et al. (2014).

The average coefficient of variation of the triplicate (light) CP measurements was 27 % (3 – 113 %), and the formalin-killed blank represented on average 26 % (7 – 60 %) of the CP signal, with generally higher contributions in lower CP signals. These are comparable to other studies using the same method (e.g. Poulton et al. 2010, Poulton et al. 2014).

Coccolithophore community structure

Water samples (100 – 250 mL) for the determination and enumeration of the coccolithophore community were collected following Poulton et al. (2014). Permanent slides were prepared on board using a low viscosity Norland Optical Adhesive (NOA 74) (Poulton et al. 2014). Coccolithophore cell counts and species identification were performed using a Leitz Ortholux polarizing microscope (x1000, oil immersion). A minimum of 54 fields of view were counted per filter for abundant species, with additional fields of view analysed for rarer species. The light microscopy species identification and enumeration were verified and supplemented using scanning electron microscopy (SEM) following Daniels et al. (2012).

Species-specific calcite production

The equation to determine species-specific calcite production (CP_{sp}) was adapted from Daniels et al. (2014). CP_{sp} is calculated as a product of the growth rate (μ), cellular calcite content (C) and abundance (N) of each species present (Eqn. 1). Species-specific calcite content was estimated from SEM images by combining derived estimates of coccolith calcite (Young & Ziveri 2000) with the number of coccoliths per cell (Table 1). The method of Young and Ziveri (2000) incorporates species-specific coccolith shape factors (k_s). Of the species observed here, only 4 (*E. huxleyi*, *C. pelagicus*, *A. quattrospina*, *Syracosphaera* spp.) had a pre-defined k_s. For those species with an undefined shape factor, shape factors were estimated from SEM images for *C. pelagicus* HOL and *C. caudatus* (Table 1), the k_s for *A. robusta* was adapted from *E. huxleyi* (Probert et al. 2007), and a “typical coccolith” k_s was used for *Ophiaster* sp. (Young & Ziveri 2000).

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

Species-specific growth rates cannot be directly determined from the measurements we made. However we can use relative growth rates to determine the fraction of calcite production per species, and multiply this by the measured total CP to obtain CP_{sp} (Eqn. 1). Initially we have made the simplifying assumption that all coccolithophores have the same growth rate as there is little data on relative growth rates of coccolithophores in the field or from laboratory experiments (Daniels et al. 2014, Daniels et al. 2015). The influence of variable growth rates for different species on the estimates of CP_{sp} will be examined in the discussion.

Macronutrients and carbonate chemistry

Macronutrients (nitrate + nitrite, NO_x; phosphate, PO_4; silicic acid, dSi) were determined following Sanders et al. (2007) on a Skalar autoanalyser. The relative concentration of NO_x to PO_4 (N*; $NO_x - 16 \times PO_4$ (Moore et al. 2009)) and the relative concentration of dSi to NO_x (Si*; dSi - NO_x (Bibby & Moore 2011)) were also determined.

Samples for total dissolved inorganic carbon (C_T) and total alkalinity (A_T) were collected into 250 mL borosilicate glass bottles and poisoned with 50 µL of saturated mercuric chloride solution following (Dickson et al. 2007). Using a VINDTA 3C instrument (Marianda, Germany), C_T was measured by coulometric titration, and A_T by potentiometric titration and calculated using a modified Gran technique (Bradshaw et al. 1981). The results were calibrated using certified reference material (batch 117) obtained from A.G. Dickson (Scripps Institution of Oceanography, USA). Measurement precision was ± 3.8 and ± 1.7 µmol kg^{-1} for C_T and A_T respectively. Calcite saturation state (Ω_c), pH on the Total scale (pH_T) and seawater partial pressure of CO_2 (pCO_2^{sw}) were calculated using version 1.1 of the CO_2SYS program for MATLAB (Van Heuven et al. 2011) using the carbonic acid dissociation constants of Lueker et al. (2000), the boric acid dissociation constant of Dickson (1990b), the bisulfate ion acidity constant of Dickson (1990a), and the boron:chlorinity of Lee et al. (2010).

Data availability and statistical analysis

All data included in the paper are available from the British Oceanographic Data Centre (BODC). Multivariate statistics were used to examine spatial variability in the coccolithophore species composition and CP_{sp} (biotic data) and the environment (abiotic data). Bray-Curtis similarity resemblance matrices were calculated from the standardised biotic data to determine changes in species composition and CP_{sp}. The abiotic data (temperature, salinity, Ω_C, pH_T, N*, Si*, daily PAR and Z_{eup}) were normalised, and a Euclidean distance resemblance matrix calculated to determine changes in the environmental variables. The species composition of samples via the Bray-Curtis similarity index was then used to cluster samples into groups using non-metric multi-dimensional scaling (NMDS). The species typical of each hydrographic region were identified using a breakdown of similarity percentages (SIMPER routine), calculated in E-PRIMER (Clarke 1993). Spearman's rank correlation (BEST routine) were calculated in E-PRIMER (Clarke 1993) to identify which environmental variables explained most of the variation in the coccolithophore community and CP_{sp}.

Principal component analysis (PCA) of normalised environmental variables was performed using MATLAB, and Pearson product-moment correlations were carried out between the calculated principal components (PC) and coccolithophore community composition and CP_{sp} to further examine the relationship between the biotic and abiotic data.

Results

General Oceanography

A wide variety of hydrographic environments were sampled during the cruise, throughout the Iceland Basin and the Nordic Seas (Greenland Sea and Norwegian Sea) of the Arctic Ocean (Fig. 1, Table 2), with two major fronts dividing the regions; the Norwegian Sea was separated from the Iceland Basin by the Iceland-Faroes Front, while the East Greenland Front separated the Greenland Sea from the Norwegian Sea (Cottier et al. 2014). The Iceland Basin was characterised by the warmest (10 – 10.6 °C) and most saline (35.2 – 35.3) waters of the study. The Greenland Sea, with the influence of the East Greenland Current, had the coldest (1 – 3.5 °C) and freshest (34.7 – 35.0) waters sampled. The Norwegian Sea lay between the two extremes of the Iceland Basin and the Greenland Sea, in terms of both temperature (3.1 – 7.8 °C) and salinity (34.8 – 35.2).

Macronutrient concentrations of NO_x (0.5 – 10.6 mmol N m^{-3}), PO_4 (0.11 – 0.77 mmol P m^{-3}) and dSi (1.3 – 6.1 mmol Si m^{-3}) were highly variable and no clear spatial patterns were observed (Table 2). The values of N* were negative at all sites (-3.0 to -0.3) indicating that, assuming Redfield stoichiometry (Redfield, 1958), NO_x was low relative to PO_4. The values of Si* ranged from -2.9 to 6.5. While generally positive, indicating high residual dSi concentrations, four stations exhibited a negative Si*, indicating depleted dSi relative to NO_x. No clear spatial patterns in N* or Si* were identified between sampling sites.

Euphotic zone depth (Z_{eup}) ranged from 15 to 50 m, and daily incidental PAR varied from 10 to 53 mol photons m^{-2} d^{-1}, with both showing variability within and between regions. As the cruise occurred in mid-summer, the stations in the Nordic Seas experienced a 24 hour photoperiod, while the Iceland Basin stations experienced a shorter photoperiod (~ 18 hours). The effect of this on daily PAR is not clear, suggesting a stronger influence through varying cloud cover. Values of pH_T varied from 8.07 to 8.29 and Ω_C varied from 2.65 to 4.46, with the low Ω_C particularly in the Greenland Sea.

Coccolithophore community structure

Total coccolithophore abundance was highly variable, ranging from 5 to 932 cells mL^{-1}. The most commonly observed coccolithophore species were *Emiliania huxleyi* (0 – 425 cells mL^{-1}), *Coccolithus pelagicus* (0 – 33 cells mL^{-1}) and the holococcolithophorid (HOL) life stage of *Coccolithus pelagicus* (0 – 223 cells mL^{-1}) (Fig. 2).

Other species present included *Acanthoica quattrospina, Algirosphaera robusta*, *Calciopappus caudatus*, *Ophiaster* sp. and *Syracosphaera* spp. (Fig. 2). While each species has been considered individually in determining CP_{sp} and in the environmental analysis, for the purpose of graphical representation, species other than *E. huxleyi*, *C. pelagicus* and *C. pelagicus* HOL were grouped into one category (termed ‘others’, Fig. S1) as they were minor contributors to regional calcite production. Scanning electron microscopy identified *Syracosphaera* spp. as including: *S. borealis, S. corolla*, *S. dilata*, *S. marginaporata* and *S. molischii*. The cellular calcite content of the *Syracosphaera* genus however are not well constrained (Young & Ziveri 2000), thus we have not considered these species individually and have used a “small *Syracosphaera*” coccolith calcite (Young & Ziveri 2000) estimate for calculating their cellular calcite. The different coccolithophore species had varying spatial distributions (Fig. S1, Table S1). *Emiliania huxleyi* was most abundant in the Iceland Basin and Norwegian Sea, *C. pelagicus* HOL was present in the highest latitude stations, while *Syracosphaera* spp. were restricted to the Iceland Basin.

To account for the large variability in coccolithophore abundances between stations, the stations were grouped into the three distinct regions (Iceland Basin, Greenland Sea and

Norwegian Sea, Fig. 1, Table S2), as defined from the characteristic hydrography of each station. Coccolithophore abundances, aggregated over these regions, and over the entire study area (Fig. 3A) showed that *E. huxleyi* represented 27 % of the total coccolithophore abundance, with a relatively consistent contribution across all regions (19 – 30 %, Fig. 3A). In contrast, *Coccolithus pelagicus* formed only a small component of the coccolithophore community in terms of abundance (1 – 4 %, Fig. 3A) in all regions sampled. The Iceland Basin community was dominated by *C. caudatus* (43 %) and *Syracosphaera* spp. (24 %), the Norwegian Sea by *C. caudatus* (43 %), and the Greenland Sea by *C. pelagicus* HOL (77 %, Fig. 3A).

Species-specific calcite production

The total community calcite production was highly variable throughout the study (from 2 to 202 µmol C m^{-3} d^{-1}), with rates similar to those measured previously in the North Sea and the Arctic Ocean (< 1 – 300 µmol C m^{-3} d^{-1}, Charalampopoulou et al. 2011), and in the subtropics (0.4 – 102 µmol C m-3 d-1, Poulton et al. 2006), but generally lower than those previously measured on the north-west European shelf (2 – 825 µmol C m^{-3} d^{-1}, Poulton et al. 2014). There were no clear spatial patterns in the distribution of calcite production; the largest calcite production (202 µmol C m^{-3} d^{-1}) was measured in the central Norwegian Sea (Fig. S2), with the lowest rates in the Greenland Sea (<10 µmol C m^{-3} d^{-1}).

At each individual station, the major calcite producers were *E. huxleyi* (0 – 100 %), *C. pelagicus* (0 – 98 %) and *C. pelagicus* HOL (0 – 100 %). However, there was significant variability between the stations (Table S3, Fig. S3), and when considering each station individually, *E. huxleyi* was the largest contributor at 6 stations, *C. pelagicus* at 10 stations and *C. pelagicus* HOL at 3 stations. Of the other species present, *Syracosphaera* spp. were also a significant source in the Iceland Basin (0 – 27 %), and *C. caudatus* was generally a small source (0 – 12 %) except at station 20 in the Norwegian Sea where it contributed 37 % of the total calcite production. When present, *A. robusta* was a minor contributor to calcite production in the Norwegian Sea (3 – 16 %).

Considering the percentage calcite production of each species on a per station basis however does not account for the high variability in the measured total calcite production. Incorporating total calcite production and aggregating over the three regions and the entire cruise reveals that *C. pelagicus* was the major calcifier, responsible for 57 % of the total calcite production (Fig. 3B), with a higher contribution in the Nordic Seas (59 – 61 %) than in the Iceland Basin (44 %). In contrast, *E. huxleyi* represented only 20 % of the total calcite production (Fig. 3B), with a much smaller contribution in the Greenland Sea (6 %) than in the Norwegian Sea (26 %) and Iceland Basin (25 %). *Coccolithus pelagicus* HOL was a significant calcite producer in the Greenland Sea (28 %), but less so in the other regions, resulting in a total contribution of only 12 % (Fig. 3B). The contribution of the other species to calcite production was greatest in the Iceland Basin (29 %), of which *Syracosphaera* spp. (19 %) and *C. caudatus* (7 %) were the major calcifiers. In the Arctic, *C. caudatus* (2 – 5 %) and *A. robusta* (0 – 7 %) were the largest calcite producers of the other coccolithophore species present.

Coccolithophore species composition, CP_{sp} and environmental variables

In order to explore the relationship between the environmental variables and the species composition of the coccolithophore community and their contribution to CP_{sp}, a PCA was carried out using normalised environmental variables (temperature, salinity, Ω_C, pH, N*, Si*, daily PAR and Z_{eup}). The first principal component (PC-1) explained 40.1 % of the variance between stations in terms of the environmental conditions, while the second principal component (PC-2) explained a further 33.3 % of the variance. Therefore, the combination of PC-1 and PC-2 explained 73.4 % of the total environmental variability.

Eigenvalues from the PCA (Table 5) indicate the relative weight of the environmental variables in influencing each of the PCs. Pearson moment correlations showed that PC-1 was strongly related to Ω_C, pH and Si* and Z_{eup} while PC-2 was related to temperature, salinity and N* (Table 5). Correlated with latitude ($r = 0.68$, $p < 0.005$, $n = 19$), PC-2 essentially describes the north-south environmental gradient, with warmer, more saline and high N* waters in the south. Correlations between PCs, coccolithophore composition and CP_{sp} found significant correlations ($p < 0.005$) between PC-1 and the contribution of *E. huxleyi* and *C. pelagicus* HOL to species composition, and between PC-1 and the percentage contribution to CP_{sp} by *E. huxleyi* ($p < 0.005$) and *C. pelagicus* HOL ($p < 0.05$). PC-2 was significantly correlated ($p < 0.005$) with the composition and percentage contribution to CP_{sp} of *Syracosphaera* spp., *A. quattrospina* and *Ophiaster* sp. These species were found only in the Iceland Basin samples, further demonstrating the link between PC-2 and the north-south environmental gradient.

To visualise the multivariate patterns in similarity between the individual stations in terms of community composition, non-metric multi-dimensional scaling (NMDS) analysis was applied to both species composition data (Fig. 6A) and CP_{sp} (Fig. 6B). The stress values of the 2-dimensional NMDS plots were low (< 0.08), thus indicating that they are a good representation of the high-dimensional patterns (Clarke 1993). The NMDS plots reveal different patterns of similarity between the stations whether species composition or CP_{sp} are considered. To examine the underlying factors driving the similarity between stations, individual species contributions to community composition (Fig. 6B-D) and CP_{sp} (Fig. 6F-H) where overlaid on to the NMDS plots. In terms of species composition, the spatial pattern was generally explained by the contributions of *E. huxleyi* (Fig. 6B) and *C. pelagicus* HOL (Fig. 6D) to community composition. The majority of Greenland Sea samples clustered distinctly away from other stations (Fig. 6A), with their coccolithophore communities comprised of a large contribution from *C. pelagicus* HOL and a small contribution from *E. huxleyi*.

The dissimilarities in species contribution to community composition between stations in the different hydrographic regions were tested statistically using a SIMPER analysis. The high dissimilarity between stations in the Greenland Sea and those in both the Iceland Basin (average dissimilarity = 85.6 %) and the Norwegian Sea (average dissimilarity = 82.3 %) was driven by *C. pelagicus* HOL (43 – 44 % of dissimilarity) and *E. huxleyi* (26 – 27 % of dissimilarity), as observed in the NMDS plots. The spatial patterns in the CP_{sp} NMDS plots contrasted that of species composition (Fig. 6E), being influenced by *E. huxleyi* (Fig. 6F), *C. pelagicus* (Fig. 6G) and *C. pelagicus* HOL (Fig. 6H). The Greenland Sea stations did not cluster separately in this case, as they did for analysis of their coccolithophore community composition; SIMPER analysis found that that the hydrographic regions were more similar in terms of CP_{sp} (average dissimilarity < 71 %) than in terms of species composition.

To determine which environmental variables best explain the patterns in species composition and CP_{sp}, Spearman's rank correlations (r_s) were calculated between resemblance matrices of abiotic and biotic data (Clarke 1993). The variability in species composition between stations was best explained by temperature, Ω_C, and N* ($r_s = 0.55$, $p < 0.01$, Table 6), while the single variable that explained most of the variability was Ω_C ($r_s = 0.55$, $p < 0.01$). The variability in CP_{sp} was best correlated with Ω_C (Table 6) though the relationship was slightly weaker (r_s = 0.37 $p < 0.01$) than for species composition.

Discussion

Coccolithus pelagicus as a key calcifier

Calculating CP_{sp} reveals that *C. pelagicus* is the major calcifier in this Arctic study, responsible for 57 % of the calcite production in the Arctic Ocean and sub-polar Iceland Basin, despite forming only 2 % of the total coccolithophore community abundance (Fig. 3). The influence of *C. pelagicus* on calcite production is further confirmed by a significant correlation between *C. pelagicus* abundance and total calcite production ($r = 0.55$, $p < 0.02$, $n = 19$); no other species correlated significantly with total calcite production. That *C. pelagicus* is able to dominate calcite production at such low relative abundances is due to its significantly higher cellular calcite quota compared to the rest of the coccolithophore species present in the community (Table 1). This potential to dominate community calcite production has been previously identified in a simplified two species model of *C. pelagicus* and *E. huxleyi* (Daniels et al. 2014). Although the natural communities in our samples are more complex and species-rich, *C. pelagicus* still has at least a 20 fold greater cellular calcite quota than the rest of the community (Table 1). Thus, when present *C. pelagicus* usually dominates coccolithophore calcite production.

The dominance of *C. pelagicus* in our study is not dependent on any single station. Removing the station (CTD 58) which has the highest rate of calcite production (202 µmol C m^{-3} d^{-1}), and therefore the largest influence over CP_{sp}, does not change the overall result. Although removing this station from the analysis results in a reduction of *C. pelagicus*-derived calcite production from 57 % to 43 %, *C. pelagicus* remained the single species with the largest source of calcite in the mixed communities of the Arctic Ocean and Iceland Basin. The effect of removing any other station from the analysis was minimal with *C. pelagicus* remaining the dominant calcifier.

Although *E. huxleyi* is often perceived to be the most abundant and the keystone coccolithophore species (Paasche 2002), we found that it was neither the most abundant (27 % total abundance, Fig. 3A), or the major calcifier (20 % of total calcite production, Fig. 3B), suggesting that it may not be the keystone species of coccolithophore in the North Atlantic and Arctic. However, previous studies have identified *E. huxleyi* as the most abundant coccolithophore in the Norwegian Sea (0 – 3000 cells mL^{-1}), although *C. pelagicus* was still an important component (0 – 30 cells mL^{-1}) of the communities studied (Baumann et al. 2000, Charalampopoulou et al. 2011). This change in dominance between studies is possibly due to seasonal (Baumann et al. 2000) or interannual variability occurring within the coccolithophore community. However, an increase in the abundance of *E. huxleyi*, coupled with a reduction in the abundance of other species such as *C. caudatus* and *A. robusta*, would be unlikely to change the overall result observed here, as *C. pelagicus* is the key calcifier (57 %) despite forming only a small fraction (2 %) of the coccolithophore community.

Despite dominating calcite production in this study, *C. pelagicus* is unlikely to be a globally dominant calcite producer, as its global distribution is constrained to the Arctic Ocean and sub-polar regions of the North Atlantic and North Pacific (McIntyre & Bé 1967, Ziveri et al. 2007). While other heavily calcified species (e.g. *Calcidiscus leptoporus*, *Helicosphaera carteri*) are more widely distributed (Ziveri et al. 2007) and thus have the potential to dominate calcite production (Daniels et al. 2014), here we show the biogeochemical importance of holococcolith bearing coccolithophores (i.e. *C. pelagicus* HOL) and relatively weakly calcified but highly abundant coccolithophore species (i.e. *C. caudatus*). Further research into these lesser-studied species is required in order to improve our understanding of the role of different species in calcite production.

A robust measure of species-specific calcite production?

As CP_{sp} cannot be directly determined, its calculation requires assumptions with associated potential errors. The two main sources of error are the estimates of both cellular calcite and growth rates. With the natural variability in coccolith size and shape, the error in determining cellular calcite is estimated to be ~30 to 50 % (Young & Ziveri 2000, Daniels et al. 2012). We have minimised this error by using species-specific shape factors together with measurements of coccolith length in SEM images, and our estimates of cellular calcite for *C. pelagicus* (15.2 pmol C $cell^{-1}$) and *E. huxleyi* (0.52 pmol C $cell^{-1}$) are comparable to literature values (16.6 pmol C $cell^{-1}$ and 0.22 – 1.1 pmol C $cell^{-1}$ respectively, (see Paasche 2002, Daniels et al. 2014)). Although *E. huxleyi* is perceived to be a fast growing coccolithophore species relative to other species (Paasche 2002, Tyrrell & Merico 2004), little data exists concerning relative *in situ* growth rates of coccolithophores in mixed communities. Furthermore, recent culture experiments (Daniels et al. 2014) and time series field data (Daniels et al. 2015) suggest that *E. huxleyi* may not be a relatively faster growing species *in situ*, with net growth rates of *C. pelagicus* similar to or higher than *E. huxleyi* in early spring North Atlantic communities.

To test the influence of these assumptions on species-specific calcite production, the growth rates of the three main calcifiers, *E. huxleyi* (Fig. 7A), *C. pelagicus* (Fig. 7B), and *C. pelagicus* HOL (Fig. 7C) were independently varied relative to the community growth rate, such that they had a growth rate between 10 and 200 % relative to the community. This is a similar approach to that used in Daniels et al. (2014) where growth rates and cellular calcite contents of *C. pelagicus* were varied to demonstrate that *C. pelagicus* was of potential biogeochemical importance when growing significantly slower and/or at lower relative abundances. In the resulting scenarios of our Arctic analysis, *C. pelagicus* remains the major calcifier except when its relative growth rate was less than 15 % of the rest of the community (Fig. 7B). In a further perturbation of the community, the relative growth rate of *E. huxleyi* was increased to 200 % before varying the relative growth rate of *C. pelagicus*. In this scenario, *C. pelagicus* did not dominate calcite production with a growth rate less than 30 % of the total community growth rate. Even in this extreme and potentially unrealistic scenario, *C. pelagicus* remained a significant single species calcifier (> 20 %). Although these scenarios demonstrate the potential influence of variable growth rates on CP_{sp}, and that further research is required to constrain both cellular calcite quotas and coccolithophore growth rates, *C. pelagicus* remained the dominant calcifier in the Arctic Ocean in all but the most extreme scenarios.

How does *Coccolithus pelagicus* dominate Arctic community CP?

It is well established that *C. pelagicus* is commonly found in the Arctic Ocean, but forms only a small component of the overall coccolithophore community (Samtleben & Schröder 1992, Baumann et al. 2000, Charalampopoulou et al. 2011), as observed here. Yet, the importance of *C. pelagicus* as a calcite producer has not previously been recognised. That *C. pelagicus* is a disproportionately larger contributor to calcite production than abundance is due to the significantly higher cellular calcite content of *C. pelagicus* than other coccolithophore species. However, how is it able to dominate calcite production - is it due to the absence of *E. huxleyi* or is it due to *C. pelagicus* being present in relatively high enough cellular abundances? Furthermore, what environmental characteristics determine these two factors?

To examine these competing factors we can compare and contrast the compositional analysis based on species composition in terms of cell abundances and in terms of species-specific calcite production. The NMDS plots of species composition show that the relative abundance of *E. huxleyi* in the community is a major driver of the variability in species composition between stations (Fig. 6B), whereas *C. pelagicus* has little influence (Fig. 6C). This is due to *C. pelagicus* being present in all most all samples but forming only a small fraction of the community. In contrast, *E. huxleyi* numerically dominates at some stations, but is totally absent from others (Table 3). This would suggest that as *C. pelagicus* dominates calcite production at stations where *E. huxleyi* is present and absent, it is the relative abundance of *C. pelagicus* that allows it to dominate calcite production.

The pattern in the NMDS plots of CP_{sp} however, with *E. huxleyi* (Fig. 6F) and *C. pelagicus* (Fig. 6G) both strongly influencing variability in CP_{sp}, suggest that *C. pelagicus* is responsible for a greater proportion of calcite production when the contribution of *E. huxleyi* is low. The difference between species composition and species contribution to calcite production between stations suggest that the dominance of *C. pelagicus* in terms of calcification is a combination of both the relative abundance of *C. pelagicus* compared to all other species of coccolithophore, and the relative absence of *E. huxleyi*, particularly from stations within the Greenland Sea (Fig. 6). Therefore species composition has a significant impact on calcite production and which species dominate calcification in the Arctic Ocean.

In terms of understanding variability in calcite production in the Arctic Ocean, it is then important to determine what drives the variability in species composition throughout the Arctic. Variability in the physicochemical environment is clearly recognised as influencing the biogeography of coccolithophores (e.g. Charalampopoulou et al. 2011, Poulton et al. 2013). However, the relationship between species composition and environmental variables is complex and difficult to directly elucidate. Other studies have linked variability in coccolithophore community composition and calcite production to carbonate chemistry (Charalampopoulou et al. 2011, Smith et al. 2012), irradiance (Poulton et al. 2010, Charalampopoulou et al. 2011, Poulton et al. 2014), and nutrient availability (Poulton et al. 2011, Poulton et al. 2014).

Using the same multivariate statistical approach as used by Charalampopoulou et al. (2011) on the data collected in this study, Spearman's rank correlations identified temperature, Ω_C, and N* as the environmental variables that could best explain species composition (Table 6). This contrasts with the results from Charalampopoulou et al. (2011) who found that pH and irradiance were the main drivers of coccolithophore species abundance along a transect from the North Sea to the Arctic Ocean. The influence of temperature and N* on species composition is likely to be due to the contrasting community composition in the warmer (> 10 °C) and less nitrate depleted (N* of -0.4 to -1.3) Iceland Basin compared to the colder (< 8 °C) and more nitrate depleted (N* of -1.2 to -3.0) Norwegian and Greenland Seas. That PC-2, which was related to temperature ($r = 0.87$, $p < 0.005$, $n = 19$) and N* ($r = 0.83$, $p < 0.005$, $n = 19$), and correlated with latitude ($r = 0.68$, $p < 0.005$, $n = 19$), correlated with those species found only in the Iceland Basin (*Syracosphaera* spp., *A. quattrospina* and *Ophiaster* sp.), further confirms the role of temperature in influencing species composition. However, temperature did not significantly affect CP_{sp}, with Ω_C alone best explaining the contribution of species to CP_{sp}. Those species limited only to the Iceland Basin, thus strongly influenced by temperature, were relatively minor contributors to calcite production (0 – 27 %) and had little impact on the variability in CP_{sp}.

That both species composition and CP_{sp} were affected by Ω_C can be further examined using the results from the PCA: PC-1, which is positively correlated to Ω_C ($r = 0.92$, $p < 0.005$, $n = 19$), is also positively correlated to the contribution of *E. huxleyi* to both species composition ($r = 0.85$, $p < 0.005$, $n = 19$) and CP_{sp} ($r = 0.67$, $p < 0.005$, $n = 19$), but is negatively correlated to the contribution of *C. pelagicus* HOL to both species composition ($r = -0.60$, $p < 0.01$, $n = 19$) and CP_{sp} ($r = -0.57$, $p < 0.05$, $n = 19$). This suggests that *E. huxleyi* represents a smaller fraction of the coccolithophore community in regions of lower saturation state, whereas *C. pelagicus* HOL represents a higher fraction in these conditions. This could be interpreted to suggest that the expected decline in saturation state in the future would reduce the abundance of *E. huxleyi*. However, our analysis does not allow us to conclude that Ω_C is directly affecting species composition, but rather that within the present day Arctic Ocean, *E. huxleyi* forms a smaller component of the coccolithophore community in regions of lower Ω_C. It should be noted that Ω_C was above the saturation point at all stations and that the gradient in saturation state was much lower (2.6 – 4.2) than other environmental variables, such as the gradient in temperature (1.0 – 10.6 °C) and NO_x (0.5 – 10.6 mmol N m^{-3}). Temperature is recognised to have a significant control on coccolithophore distributions, for example, there is a well recognised 2 °C limit to the range of *E. huxleyi* (Holligan et al. 2010), while *C. pelagicus* is able to persist in sub-zero temperatures (Braarud 1979).

The relationship between the environment, the coccolithophore community and calcite production is likely to be more complex than presented here; we found no significant environmental influence on total calcite production ($p = 0.09$), or the contribution of *C. pelagicus* to species-specific calcite production ($p = 0.1$), implying that other ecophysiological and environmental interactions exist and may influence species biogeography. Furthermore, correlations of individual environmental variables with abundance and CP_{sp} did not produce any significant results, further demonstrating the complexity of the interaction between coccolithophore abundance, calcite production, and environmental variables (Poulton et al. 2014). While the influence of some environmental variables (e.g. temperature) on coccolithophore physiology are well established, we are only beginning to get a mechanistic understanding of the influence of carbonate chemistry; for example, calcite production appears dependent on bicarbonate as its primary substrate, and is inhibited by protons (Bach et al. 2015), with Ω_C not directly affecting calcite formation (Bach 2015). However, we still have very little basic understanding of coccolithophore physiology; for example, until we understand why coccolithophores calcify, and the energetic costs associated with it, we cannot fully understand how cellular calcification will respond to a changing ocean, and the impact this will have on the coccolithophore community in terms of species composition or competitive fitness.

Wider Implications

Research into the effect of ocean acidification and climate change on coccolithophores has been dominated by studies of *E. huxleyi* as it is globally abundant and forms large-scale blooms of significant biogeochemical importance (Holligan et al. 1993, Poulton et al. 2013). However, *E. huxleyi* can be considered an atypical coccolithophore species in terms of its genetic lineage, physiology and ecology (de Vargas et al. 2007), and therefore the response of *E. huxleyi* to climate change and ocean acidification may not apply to other coccolithophore species. Few studies have examined the impact of ocean acidification on other species of coccolithophore (Langer et al. 2006, Fiorini et al. 2011, Krug et al. 2011), and very little is known about the Arctic species *C. pelagicus*. As a key calcifier in a region considered particularly vulnerable to ocean acidification and warming, the response of *C. pelagicus* to climate change and ocean acidification could have a major effect on calcite production in the Arctic and sub-polar Iceland Basin. Examination of the fossil record of *C. pelagicus* during the Palaeocene-Eocene Thermal Maximum (PETM), arguably the best geological equivalent of modern-day climate change, found that it was not able to maintain optimum growth during this period (Gibbs et al. 2013), and had reduced calcification rates (O'Dea et al. 2014). If *C. pelagicus* exhibits a similar response in the modern ocean to current perturbations, it could cause a significant reduction in calcite production within the Arctic Ocean and Iceland Basin, with a major impact on carbon cycling in the North Atlantic.

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Table 1: Coccolith shape factors, coccolith calcite, coccoliths per cell and cellular calcite for the individual coccolithophore species.

Species	Coccolith Shape Factor (k_s)	Coccolith Calcite (pmol)	Coccoliths per Cell	Cellular Calcite (pmol)
E. huxleyi	0.020	0.024	22	0.52
C. pelagicus	0.060	1.218	13	15.2
Syracosphaera spp.	0.015	0.012	35	0.40
A. quattrospina	0.030	0.008	36	0.27
C. caudatus	0.013	0.002	54	0.09
Ophiaster sp.	0.035	0.001	70	0.09
A. robusta	0.045	0.010	43	0.42
C. pelagicus HOL	0.036	0.008	100	0.78

Table 2: Physicochemical features: Z_{eup}, euphotic depth; Ω_C, calcite saturation state; NO_x, nitrate + nitrite; PO_4, phosphate; dSi, silicic acid; N*, excess NO_x relative to PO_4; Si*, excess dSi to NO_x.

										Carbonate Chemistry			Surface Macronutrients (mmol m^{-3})				
CTD	Location	Lat (°N)	Lon (°E)	Date	Depth (m)	Temperature (°C)	Salinity	Daily PAR (mol photons m^{-2} d^{-1})	Z_{eup} (m)	pCO_2 (µatm)	pH_T	Ω_C	NO_x	PO_4	dSi	N*	Si*
6	ICB	58.74	-0.86	04 Jun	9	10.0	35.3	45	40	277	8.2	4.2	0.5	0.11	1.7	-1.3	-1.2
8	ICB	60.13	-6.71	05 Jun	10	10.4	35.4	33	48	326	8.1	3.8	6.5	0.45	4.3	-0.7	2.3
10	ICB	59.97	-11.98	06 Jun	20	10.6	35.3	51	28	310	8.1	4.0	2.9	0.21	1.4	-0.4	1.5
12	ICB	60.00	-18.67	07 Jun	10	10.2	35.2	41	37	340	8.1	3.7	6.1	0.4	1.7	-0.3	4.4
17	ICB	60.59	-18.86	08 Jun	20	10.4	35.2	10	40	310	8.1	3.9	5.2	0.35	1.3	-0.4	3.9
19	NWS	65.98	-10.72	09 Jun	24	3.6	34.8	34	23	240	8.2	3.7	0.6	0.22	2.5	-3.0	-1.9
20	NWS	69.90	-7.58	10 Jun	15	3.1	35.0	53	36	363	8.1	2.7	9.1	0.64	6.1	-1.2	3.0
21	GS	74.12	-4.69	11 Jun	15	1.0	34.9	40	48	308	8.1	2.8	9.8	0.7	5.7	-1.4	4.0
27	GS	76.18	-2.55	12 Jun	20	1.5	34.9	42	50	319	8.1	2.7	9.3	0.67	4.7	-1.4	4.6
29	GS	78.72	0.00	13 Jun	10	3.5	35.0	51	15	209	8.3	4.1	2.6	0.31	5.5	-2.4	-2.9
40	GS	78.25	-5.55	14 Jun	15	3.1	34.9	20	25	309	8.1	3.0	8.7	0.62	5.6	-1.2	3.1
42	NWS	78.22	-6.00	15 Jun	15	6.0	35.1	28	22	208	8.3	4.5	4.0	0.38	4.3	-2.1	-0.4
45	NWS	77.82	-4.97	16 Jun	20	5.7	35.2	19	41	309	8.1	3.3	9.8	0.72	5.8	-1.8	4.0
54	NWS	77.85	-1.29	17 Jun	13	7.8	35.0	24	41	320	8.1	3.5	6.0	0.49	3.8	-1.8	2.2
56	NWS	78.99	7.98	18 Jun	15	6.7	35.2	33	31	305	8.1	3.5	6.8	0.5	5.2	-1.2	1.6
58	NWS	76.26	12.54	19 Jun	20	5.4	35.1	35	38	316	8.1	3.2	10.6	0.77	5.7	-1.7	4.9
60	GS	76.16	23.07	20 Jun	26	1.4	34.7	49	45	328	8.1	2.6	8.6	0.64	2.2	-1.6	6.5
63	NWS	72.89	26.00	22 Jun	20	3.8	34.8	40	32	318	8.1	3.0	8.9	0.65	2.6	-1.5	6.3
65	NWS	71.75	17.90	23 Jun	20	5.1	34.9	33	48	246	8.2	3.8	4.0	0.43	4.1	-2.8	0.0

Table 3: Coccolithophore abundances (cells mL^{-1})

		Coccolithophore abundance (cells mL^{-1})							
CTD	Location	*E. huxleyi*	*C. pelagicus*	*C. pelagicus* HOL	*Syracosphaera* spp.	*A. quattrospina*	*C. caudatus*	*Ophiaster* sp.	*A. robusta*
6	ICB	31.7	-	-	-	1.5	-	-	-
8	ICB	21.2	2.6	-	24.2	-	3.0	1.5	3.0
10	ICB	64.1	2.3	3.0	7.9	2.4	0.6	2.4	-
12	ICB	76.2	7.7	-	179.6	10.9	348.3	27.2	-
17	ICB	91.2	4.2	5.4	84.4	12.2	179.6	50.3	-
19	NWS	1.9	2.8	-	-	-	-	-	-
20	NWS	-	0.6	59.9	-	-	359.2	-	5.4
21	GS	-	0.4	3.8	-	-	-	-	-
27	GS	-	-	6.0	-	-	-	-	-
29	GS	17.0	0.4	0.9	-	-	-	-	0.9
40	GS	1.9	-	11.3	-	-	-	-	-
42	NWS	25.2	-	-	-	-	-	-	-
45	NWS	69.5	0.1	1.5	-	-	1.5	-	4.5
54	NWS	19.7	-	-	-	-	-	-	4.5
56	NWS	424.5	7.1	223.1	-	-	157.8	-	119.7
58	NWS	33.1	15.4	2.2	-	-	72.8	-	47.4
60	GS	-	2.8	54.8	-	-	-	-	-
63	NWS	20.8	32.7	-	-	-	274.0	-	-
65	NWS	2.8	2.9	-	-	-	-	-	-

Table 4: Total calcite production (µmol C m^{-3} d^{-1}) and species-specific calcite production (%)

			% Calcite Production							
CTD	Location	Total Calcite Production (µmol C m^{-3} d^{-1})	*E. huxleyi*	*C. pelagicus*	*C. pelagicus HOL*	*Syracosphaera spp.*	*A. quattrospina*	*C. caudatus*	*Ophiaster* sp.	*A. robusta*
6	ICB	7.25	97.6	-	-	-	2.4	-	-	-
8	ICB	21.65	17.7	64.1	-	15.5	-	0.5	0.2	2.0
10	ICB	7.06	44.4	47.1	3.1	4.2	0.9	0.1	0.3	-
12	ICB	42.51	14.9	43.9	-	27.0	1.1	12.3	0.9	-
17	ICB	13.56	27.2	37.0	2.4	19.3	1.9	9.7	2.5	-
19	NWS	11.31	2.3	97.7	-	-	-	-	-	-
20	NWS	17.45	-	9.8	50.8	-	-	36.8	-	2.5
21	GS	1.65	-	70.0	30.0	-	-	-	-	-
27	GS	3.54	-	-	100.0	-	-	-	-	-
29	GS	9.04	54.8	38.2	4.5	-	-	-	-	2.5
40	GS	29.64	10.0	-	90.0	-	-	-	-	-
42	NWS	18.96	100.0	-	-	-	-	-	-	-
45	NWS	16.69	88.6	3.5	2.9	-	-	0.3	-	4.7
54	NWS	8.61	84.2	-	-	-	-	-	-	15.8
56	NWS	63.93	38.9	19.0	30.5	-	-	2.6	-	8.9
58	NWS	201.55	6.2	83.6	0.6	-	-	2.4	-	7.1
60	GS	16.21	-	50.3	49.7	-	-	-	-	-
63	NWS	55.87	2.0	93.2	-	-	-	4.8	-	-
65	NWS	29.58	3.2	96.8	-	-	-	-	-	-

Table 5: Results of the principal component analysis (PCA), including eigenvectors and Pearson correlations coefficients for the relationships between PC scores, environmental variables and individual species contributions to both species composition and CP$_{sp}$. *** $p <$ 0.005, ** $p < 0.01$, * $p < 0.05$

Variables	Variables vs. principal components	
	PC-1 (40.1 %)	PC-2 (33.3 %)
Environmental		
Temperature	0.23 (0.41)	0.53 (**0.87*****)
Salinity	0.19 (0.34)	0.53 (**0.87*****)
Ω_C	0.51 (**0.92*****)	0.21 (0.34)
pH_T	0.48 (**0.87*****)	-0.26 (-0.42)
N*	-0.19 (-0.35)	0.51 (**0.83*****)
Si*	-0.50 (**-0.90*****)	0.12 (0.19)
PAR	-0.06 (-0.12)	-0.14 (-0.22)
Z_{eup}	-0.35 (**-0.62*****)	0.17 (0.27)
Latitude	-0.08	**-0.68*** **
Longitude	0.16	-0.12
Species Composition		
E. huxleyi	**0.85*** **	0.20
C. pelagicus	0.12	-0.43
C. pelagicus HOL	**-0.60** **	-0.32
Syracosphaera spp.	0.04	**0.78*** **
A. quattrospina	0.24	**0.66*** **
C. caudatus	-0.35	0.32
Ophiaster sp.	0.06	**0.75*** **
A. robusta	0.02	0.13
% CP$_{sp}$		
E. huxleyi	**0.67*** **	0.37
C. pelagicus	-0.08	-0.12
C. pelagicus HOL	**-0.57* **	-0.27
Syracosphaera spp.	0.02	**0.75*** **
A. quattrospina	0.22	**0.66*** **
C. caudatus	-0.32	0.31
Ophiaster sp.	0.04	**0.69*** **
A. robusta	-0.00	0.12

Table 6: Spearman's rank correlation (r_s) of environmental variables with coccolithophore species composition and species-specific calcite production (CP_{sp}).

Coccolithophore species composition		Species-specific calcite production (% CP_{sp})	
Environmental variables	r_s ($p < 0.01$)	Environmental variables	r_s ($p < 0.03$)
Temperature, Ω_C, N^*	0.553	Ω_C	0.368
Temperature, Ω_C	0.553	Temperature, Ω_C	0.308
Ω_C	0.546	$\Omega_{C,}$ PAR	0.256

Figure Captions

Fig. 1: Sampling locations in the Iceland Basin (triangles), the Norwegian Sea (black filled circles) and the Greenland Sea (white open circles). (A) Sea ice concentration (%) in June 2012, taken from www.nsidc.org. (B) MODIS sea surface temperature for June 2012, overlaid with the East Greenland Current (EGC) and the Norwegian Current (NC).

Fig. 2: SEM images. (A) *Emiliania huxleyi*. (B) *Coccolithus pelagicus*. (C) *Coccolithus pelagicus* HOL. (D) *Calciopappus caudatus*. (E) *Syracosphaera molischii*. (F) *Algirosphaera robusta.* Scale bars represent 1 µm.

Fig. 3: The distribution of total calcite production (µmol C m^{-3} d^{-1}).

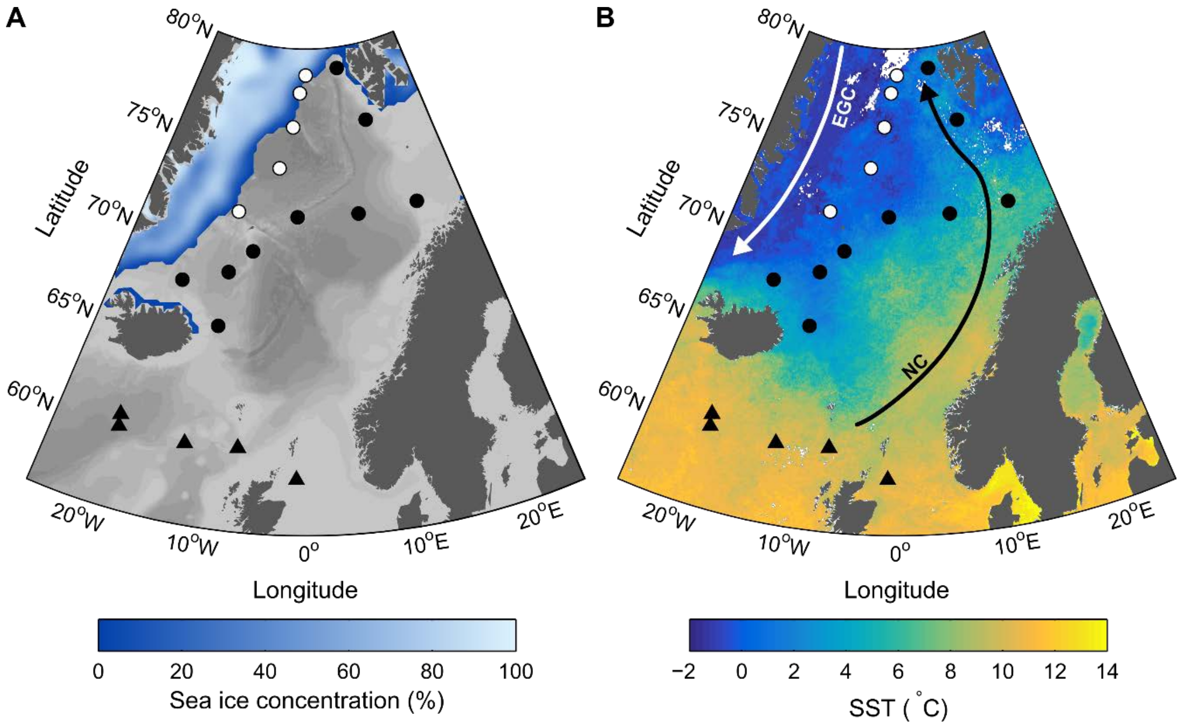
Fig. 4: The distribution of species-specific calcite production (µmol C m^{-3} d^{-1}). (A) *Emiliania huxleyi*. (B) *Coccolithus pelagicus* C) *Coccolithus pelagicus* HOL D) Other coccolithophore species.

Fig. 5: The percentage contribution of coccolithophore species to (A) abundance and (B) calcite production, aggregated over each hydrographic region and the entire study area.

Fig. 6: Non-metric multidimensional scaling (NMDS) ordination of (A, B, C and D) coccolithophore species composition and (E, F, G and H) species-specific calcite production based on Bray-Curtis similarity. Plots (A) and (E) are labelled according to the hydrographic province of the stations. Plots (B), (C) and (D) are overlaid with bubble plots of the composition of (B) *Emiliania huxleyi*, (C) *Coccolithus pelagicus*, and (D) *Coccolithus pelagicus* HOL. Plots (E), (F) and (G) are overlaid with bubble plots of the species-specific calcite production of (F) *Emiliania huxleyi*, (G) *Coccolithus pelagicus*, and (H) *Coccolithus pelagicus* HOL.

Fig. 7: The effect of varying the relative growth rate of one species on the species contribution to calcite production. The growth rates of (A) *Emiliania huxleyi*, (B) *Coccolithus pelagicus*, and (C) *Coccolithus pelagicus* HOL were singly varied whilst all other species had a relative growth rate of 100%. (D) The relative growth rate of *Coccolithus pelagicus* was varied, whilst *Emiliania huxleyi* had a relative growth rate of 200 % and other species 100 %.

776 **Fig. 1**



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778

Fig. 2

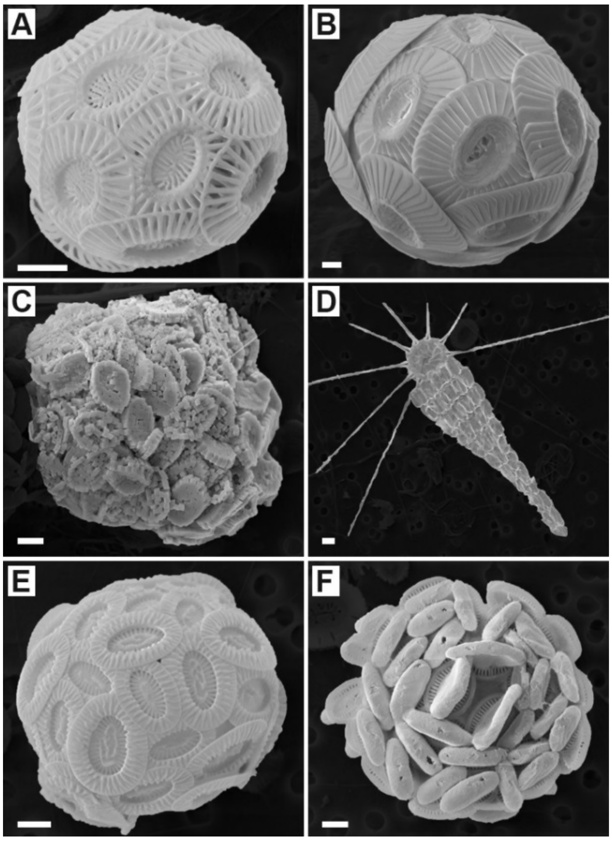


Fig. 3

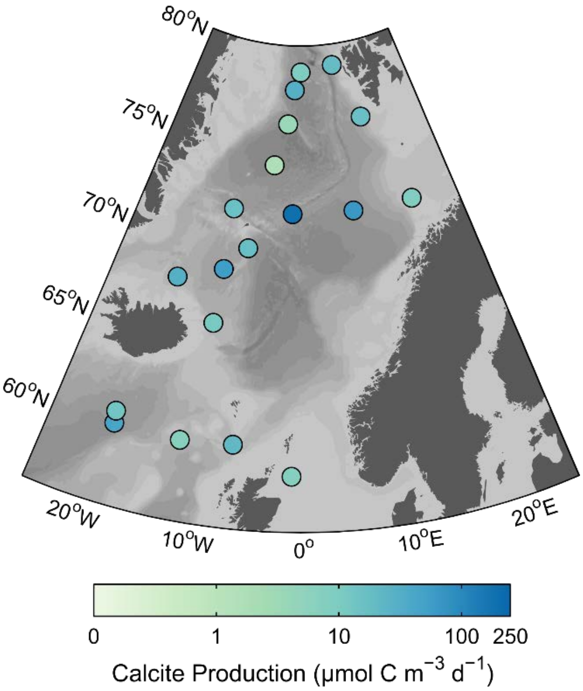

80°N
75°N
70°N
65°N
60°N
20°W
10°W
0°
10°E
20°E
0
1
10
100
250
Calcite Production (μmol C m^{-3} d^{-1})

Fig. 4

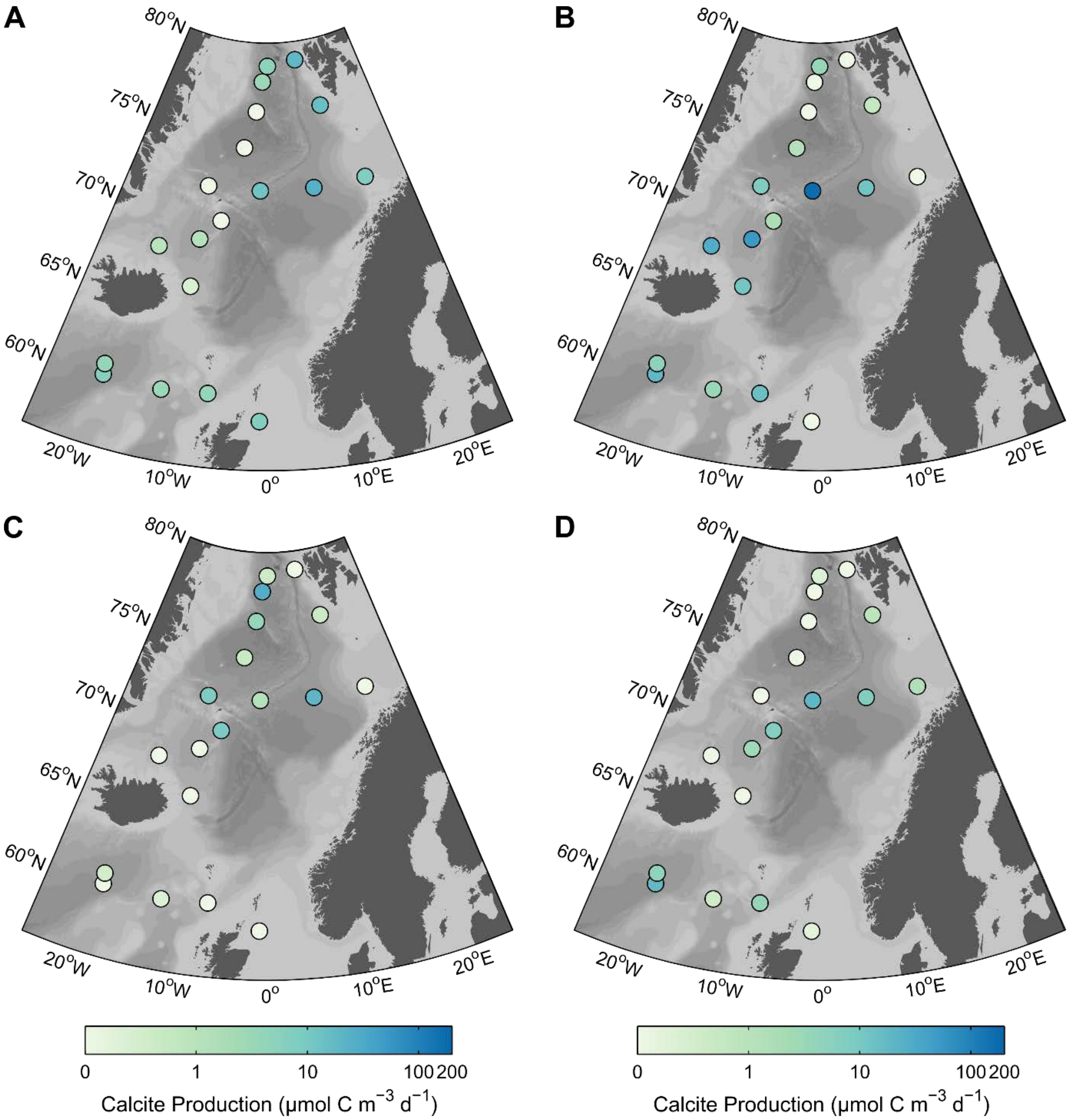

A
B
C
D
80°N
75°N
70°N
65°N
60°N
20°W
10°W
0°
10°E
20°E
0
1
10
100
200
Calcite Production (μmol C m^{-3} d^{-1})

Fig. 5

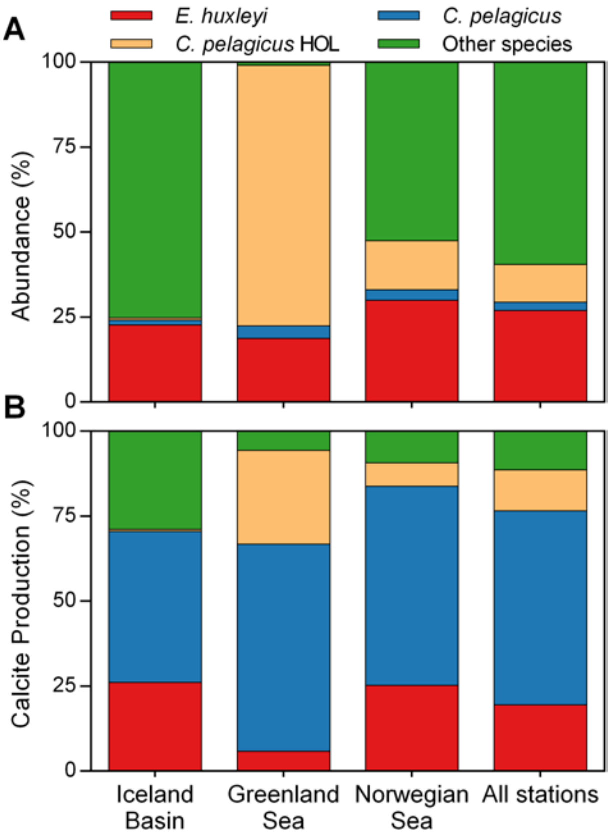

A
E. huxleyi
C. pelagicus
C. pelagicus HOL
Other species
Abundance (%)
100
75
50
25
0
B
Calcite Production (%)
100
75
50
25
0
Iceland Basin
Greenland Sea
Norwegian Sea
All stations

Fig. 6

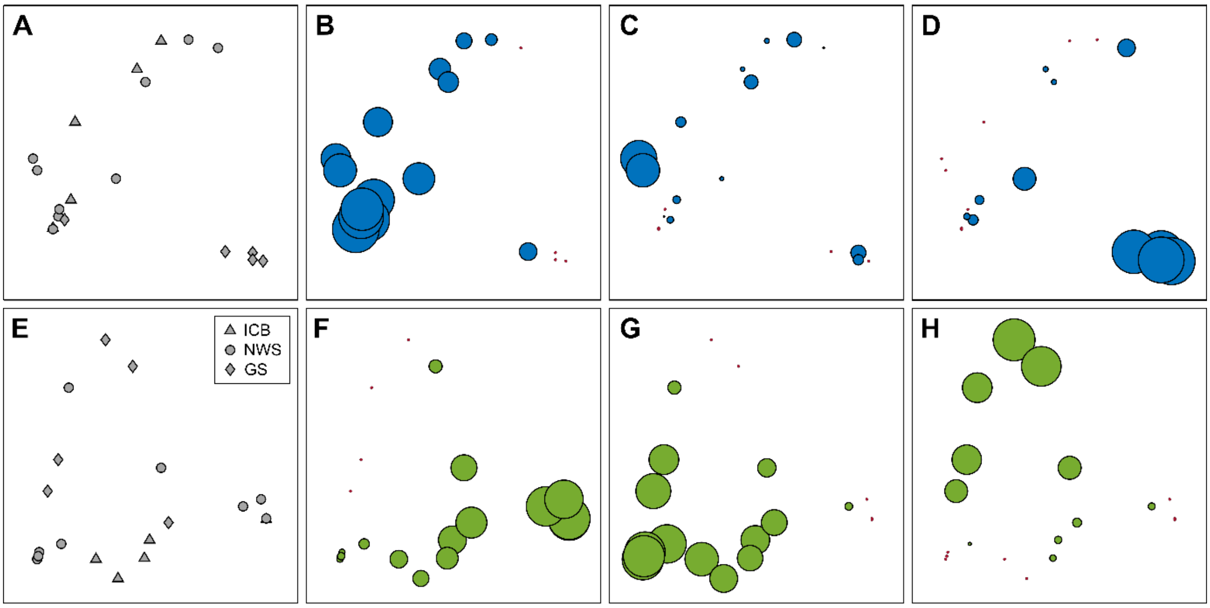
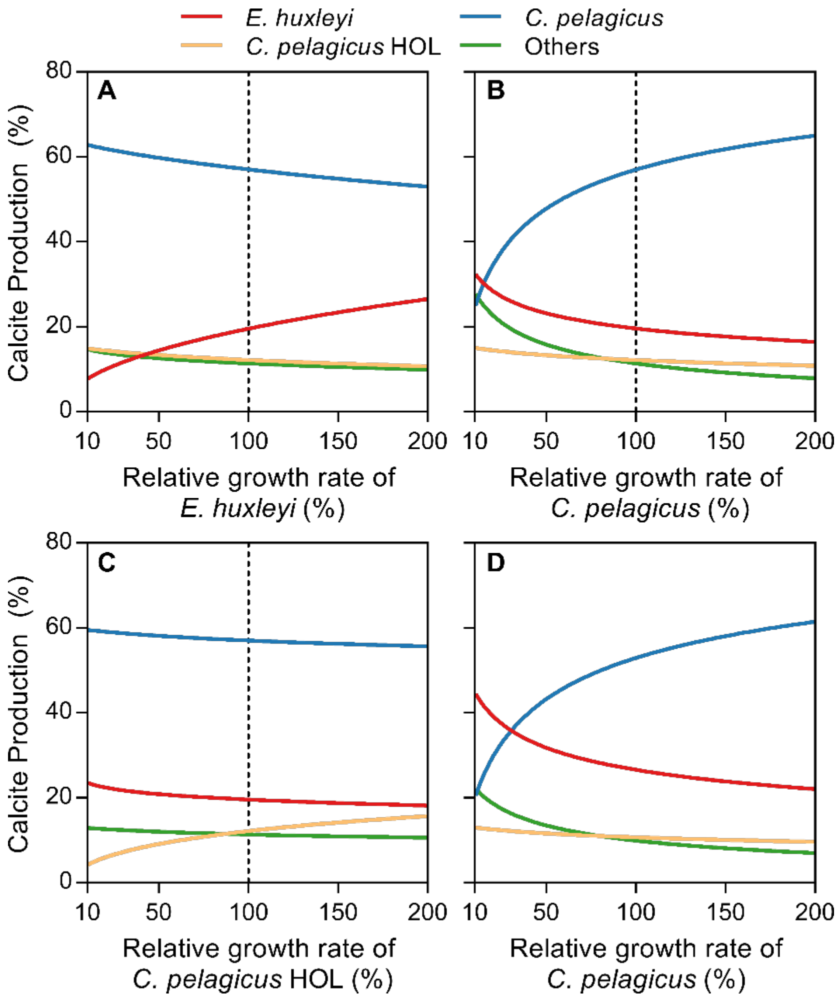


Fig. 7



E. huxleyi
C. pelagicus
C. pelagicus HOL
Others
A
B
C
D
Calcite Production (%)
0
20
40
60
80
10
50
100
150
200
Relative growth rate of E. huxleyi (%)
Relative growth rate of C. pelagicus (%)
Relative growth rate of C. pelagicus HOL (%)
Relative growth rate of C. pelagicus (%)