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Coccolithophore surface distributions in the North Atlantic and their modulation of the air-sea flux of CO₂ from 10 years of satellite Earth observation data

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Abstract

Coccolithophores are the primary oceanic phytoplankton responsible for the production of calcium carbonate (CaCO_3). These climatically important plankton play a key role in the oceanic carbon cycle as a major contributor of carbon to the open ocean carbonate pump ($\sim 50\%$) and their formation can affect the atmosphere-to-ocean (air-sea) uptake of carbon dioxide (CO_2) through increasing the seawater partial pressure of CO_2 ($p\text{CO}_2$). Here we document variations in the areal extent of surface blooms of the globally important coccolithophore, *Emiliania huxleyi*, in the North Atlantic over a 10-year period (1998–2007), using Earth observation data from the Sea-viewing Wide Field of view Sensor (SeaWiFS). We calculate the annual mean surface areal coverage of *E. huxleyi* in the North Atlantic to be $474\,000 \pm 119\,000 \text{ km}^2 \text{ yr}^{-1}$, which results in a net CaCO_3 production of $0.62 \pm 0.15 \text{ Tg CaCO}_3$ carbon per year. However, this surface coverage and net production can fluctuate by $-54/+81\%$ about these mean values and are strongly correlated with the El Niño/Southern Oscillation (ENSO) climate oscillation index ($r = 0.75$, $p < 0.02$). Our analysis evaluates the spatial extent over which the *E. huxleyi* blooms in the North Atlantic can increase the $p\text{CO}_2$ and thus decrease the localised sink of atmospheric CO_2 . In regions where the blooms are prevalent, the average reduction in the monthly CO_2 sink can reach 12% . The maximum reduction of the monthly CO_2 sink in the time series is 32% . This work suggests that the high variability, frequency and distribution of these calcifying plankton and their impact on $p\text{CO}_2$ should be considered within modelling studies of the North Atlantic if we are to fully understand the variability of its air-to-sea CO_2 flux.

1 Introduction

Understanding the pathways, sources, sinks, and impact of CO_2 on the Earth's climate system is essential for monitoring climate and predicting future scenarios. The global oceans are considered the only true net sink of anthropogenic CO_2 , annually absorbing

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~30 % of emissions, with the North Atlantic accounting for ~23 % of this global uptake (Sabine et al., 2004). Despite this, it is currently not clear if the global oceanic sink is following the increasing atmospheric levels of CO₂ (Sabine et al., 2004). The North Atlantic sink in particular has been shown to be highly variable (Watson et al., 2009) and the mechanisms driving this variability are not well understood. Therefore, isolating and reducing the uncertainties in the estimates of the oceanic sink is a crucial goal of climate science (Le Quere et al., 2009).

Coccolithophores are an abundant and widely distributed group of marine phytoplankton that form external calcium carbonate (CaCO₃) scales or platelets, called coccoliths, during their life cycle. Coccolithophores are major calcifiers in the open ocean (Sabine et al., 2004), and play a key role in oceanic carbon cycles (Balch et al., 2005; Iglesias-Rodriguez et al., 2002). Coccoliths are generated through the calcification reaction:



This leads to a disequilibrium in the ocean carbonate system that can drive an outgassing of CO₂ to the atmosphere; calcification depletes surface CO₃²⁻, reduces alkalinity, and increases the seawater partial pressure of CO₂ (pCO₂). Within this process the deposition of 1 mol of calcium carbonate releases ~0.6 mol of CO₂ into seawater (Frankignoulle and Gattuso, 1994). In addition, production and sedimentation of coccoliths is a long-term carbon sink process. Of the numerous coccolithophores, the cosmopolitan species *Emiliania huxleyi*, when present at high concentrations (blooms) in the surface layer, profoundly impacts the optical properties of the upper ocean (Balch et al., 1991; Tyrrell et al., 1999; Holligan et al., 1993). The high reflectance spectral signature of *E. huxleyi* blooms allows the study of their frequency, distribution pattern, and areal extent by Earth observation (EO) from satellites (Brown and Yoder, 1994b; Cokacar et al., 2001; Smyth et al., 2004; Merico et al., 2003; Shutler et al., 2010; Iglesias-Rodriguez et al., 2002). It is known that there is a considerable amount of *E. huxleyi* activity in the North Atlantic. Based on EO data the *E. huxleyi* areal coverage

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in the North Atlantic has been estimated to account for 40–60 % of the global areal coverage (Brown and Yoder, 1994b), with single blooms covering areas of >100 000 km² (Brown and Yoder, 1994b). Similarly, the ability of calcification to alter the $p\text{CO}_2$ is well understood. However, the spatial and temporal impact that these blooms have on $p\text{CO}_2$ and the air-sea flux of CO_2 (F) across the whole of the North Atlantic has yet to be quantified. Furthermore, many ecosystem models used to generate short to medium term predictions of air-sea fluxes of CO_2 do not account for the impact that calcifying plankton can have on the $p\text{CO}_2$ e.g. Wakelin et al. (2012). This simplification may introduce a large source of uncertainty within the modelled air-sea fluxes.

In this paper we study the areal extent of *E. huxleyi* blooms in the open ocean (>200 m depth) in temperate to high latitudes of the North Atlantic (35° N–68° N, 75° W–11° E) (Fig. 1). We use Earth observation derived bloom surface areal coverage data collected over a 10-year period (1998–2007) to (i) study variability of the surface areal coverage, (ii) investigate linkages between surface coverage and leading climate oscillators, (iii) determine CaCO_3 standing stock calculations and (iv) estimate the effect that these surface distributions have on modulating $p\text{CO}_2$ and thus F in the North Atlantic.

2 Methods

E. huxleyi blooms were detected in ocean colour radiometry measurements acquired by the Sea Viewing Wide Field of View Sensor (SeaWiFS) from 1998 to 2007 by applying a recently developed technique (Shutler et al., 2010) to estimate their surface areal coverage. We restricted our examination of data to the months from April to August so that the minimum solar elevations were between 30° and 50°. This criterion helps reduce the uncertainties in the optical remote sensing data. It is also ecologically appropriate as low light levels and low temperatures inhibit coccolithophore growth during the Northern Hemisphere winter months (Tyrrell and Merico, 2004). A confusion matrix evaluation between the Earth observation data and a 10 year in situ dataset from the

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Continuous Plankton Recorder (CPR) (Reid et al., 2003) combined with analytical error propagation were used to determine error estimates in the Earth observation derived surface areal coverage. Net CaCO_3 production of *E. huxleyi* blooms was calculated following previous standing stock approaches (Balch et al., 1991, 1992; Brown and Yoder, 1994b). The estimates represent minimum yields due to the conservative assumptions used. The impact that the *E. huxleyi* distributions have on $p\text{CO}_2$ (and thus F) was then determined using the SeaWiFS data, the CaCO_3 production estimates, a carbonate system software toolbox (seacarb) and climatology data (Takahashi et al., 2009).

2.1 Datasets

The SeaWiFS level 2 quality controlled normalised water leaving radiance data covering the region of interest for all complete years (1998–2007) were obtained from the NASA ocean colour website (NASA, 2010). All SeaWiFS data were re-projected using generic tools (Shutler et al., 2005) to an equidistant cylindrical projection with an equatorial pixel size of 4 km. The SeaWiFS data archive also includes data for 2008–2009. However, these data were excluded from analysis due to prolonged gaps in data coverage during these years, as these prolonged gaps fail the requirements for the coccolithophore classification algorithm. The mean Multivariate El Niño/Southern Oscillation (ENSO) index data for each year were calculated using monthly data downloaded from (NOAA, 2011). The North Atlantic Oscillation (NAO) data used here are the result of Principal Component Analysis of sea-level pressure over the North Atlantic sector for months from December to March (Hurrell et al., 2001) and were obtained from Hurrell (2011). Correlations between the climate indices (ENSO and NAO) and the total season surface areal coverage were determined using the Pearson correlation coefficient in python using the SciPy (v0.7.1) toolbox. Climatological data of the partial pressures of CO_2 in seawater ($p\text{CO}_2$) and air, salinity and the gas transfer velocity (Takahashi et al., 2009) at $5^\circ \times 4^\circ$ global grid resolution were used as the basis to calculate F . Two grid cells south of Iceland were missing from the climatology data and this is a region of annual *E. huxleyi* activity, e.g. Raitsos et al. (2006). Therefore, to allow this area to

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be studied the climatology values within these cells were generated by linearly interpolating the data from the adjacent cells. In situ measurements of coccolithophore cell numbers for the same geographical region and temporal period as the SeaWiFS data were obtained from the CPR survey (Reid et al., 2003).

2.2 *Emiliana huxleyi* surface areal coverage

For each satellite pass in the time series a map of *E. huxleyi* surface areal coverage was generated (Shutler et al., 2010). The first stage of this algorithm exploits temporal correlation to remove the background signal (referred to as background subtraction and relies upon the data from proceeding months to characterize the region of interest).

This approach reduces the number of false positives caused by suspended sediment and allows the spectral classification stage to focus on just the areas of ocean that have recently changed (e.g. due to the formation of a bloom). The second stage of the algorithm uses a spectral algorithm (Brown and Yoder, 1994b) to classify the remaining data into areas that contain *E. huxleyi* and those that do not. The algorithm default parameters and data quality control thresholds followed those of Shutler et al. (2010). All maps of *E. huxleyi* surface coverage were masked based on bathymetry and only regions with depth >200 m were included in the analysis as these are considered open ocean waters. Additionally, the enclosed region of the Laurentian Channel (in the Gulf of St. Lawrence in the region of 48.0° N 61.5° W) was not included as this is only 290 m deep and was considered susceptible to influences from river run off. Monthly maps of counts of *E. huxleyi* elements (CC_{xy}) and cloud-free elements (CF_{xy}) at pixel position (x, y) were generated from the Earth observation data for all data for years 1998–2007. A cloud free element is defined as any pixel with a water leaving radiance >0 at any of the wavelengths of interest (443, 510 and 555 nm). For each month, m , the estimated area of *E. huxleyi* surface coverage, AC_{my} , at each latitudinal image line, y , is determined using:

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$$AC_{my} = \left(\frac{\sum_{x=1}^X CC_{xy}}{\sum_{x=1}^X CF_{xy}} \right) A_y NV_y \quad (2)$$

where x is the longitudinal grid point, NV_y is the number of valid ocean pixels in the longitudinal row and A_y is the pixel area at that latitude. The pixel area was determined by representing the Earth as an ellipsoid. The use of NV_y stops regions of land from consistently biasing the results and the normalisation using the cloud free element count (CF_{xy}) is done to make a first order correction for cloud cover by assuming that the proportion of *E. huxleyi* under the clouds is the same as that observed in cloud free areas. Summing this over all latitudes gives the monthly surface coverage; summing across all months gives the annual surface coverage (in km^2).

2.3 Standing stock and flux calculations

Following previous studies (Balch et al., 1992; Brown and Yoder, 1994b) the standing stock calculations represent minimum yields and are based on: a mixed layer depth of 20 m; 2000 cells ml^{-1} ; and a concentration of $0.065 \text{ g CaCO}_3\text{-C m}^{-3}$ (Brown and Yoder, 1994b). It was assumed that *E. huxleyi* blooms would be present in the water for an average of 1 month or ~ 30 days (Brown and Yoder, 1994a) (this period allows for time prior to and after detection), therefore a monthly surface coverage map represents the mean monthly conditions. The net fluxes in all cases were calculated for each year using the climatology dataset as perturbed by the *E. huxleyi* distributions (1998–2007) and following the methods in the original climatology publication (Takahashi et al., 2009) to produce F in teragrams of carbon per month (Tg C month^{-1}). The in-water and atmospheric partial pressures of CO_2 were increased linearly with year to account for the known underlying trend (Takahashi et al., 2009). We assume that the ratio of particulate inorganic carbon to particulate organic carbon (rain rate) remains the same

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between years. The change in $p\text{CO}_2$ within each climatology grid cell due to *E. huxleyi* bloom activity was modified using (i) the volume of water containing a bloom within each grid box; (ii) the standing stock calculations to determine the quantity of CaCO_3 produced within each grid box; (iii) the ratio (ψ) of CO_2 released ($\Delta[\text{CO}_2]$) to precipitated CO_3 as calculated using the methods in the seacarb software package (Lavigne and Gattuso, 2011; Dickson et al., 2007; DOE, 1994; Frankignoulle and Gattuso, 1994; Zeebe and Wolf-Gladrow, 2001) (Fig. 2) and (iv) the change in $p\text{CO}_2$ dissolved into the water due to calcification was calculated using $\Delta[\text{CO}_2]/k_0$, where k_0 is the temperature dependent CO_2 seawater constant. The modified $p\text{CO}_2$ was then used to determine F assuming also that the *E. huxleyi* blooms raise the temperature of the surface water within the bloom by 1°C (Holligan et al., 1993). This process was then repeated for all months and years and the average and maximum percentage differences in seawater $p\text{CO}_2$, the air-sea partial pressure difference ($\Delta p\text{CO}_2$) and F in each month (with respect to the original climatological values) were determined. The analysis was repeated excluding the years with strong mean multivariate ENSO index values (1998 and 1999). These additional analyses were conducted to determine if the impact on the air-sea fluxes is primarily driven by strong ENSO events.

3 Results

3.1 Uncertainties in *E. huxleyi* surface coverage estimates

The total uncertainty in the spectral classification algorithm due to the known uncertainties in the input spectral data was calculated to be 11 %. This analysis was performed by propagating the known uncertainties of the individual spectral channels and their ratios (Hooker et al., 2001) through the classification algorithm using standard error propagation approaches (Taylor, 1997). These known uncertainties are all random perturbations as the sensor spectral channels have been shown not to exhibit significant bias (Hooker et al., 2001). The accuracy of the coccolithophore (*E. huxleyi*) maps was

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analysed using the method of Shutler et al. (2010) and all available CPR (26 738 in situ data points) and SeaWiFS data for 1998–2007. This in situ database analysis resulted in $N = 2102$ coincident data points (265 bloom instances, 1837 no-bloom instances) and a correct classification rate (CCR) of 78 %. Following this the uncertainty of the surface coverage data is estimated as 22 % (100–CRR). The combined uncertainty (the uncertainty due to the input spectral data and the uncertainty in the accuracy of coccolithophore detection algorithm) in the *E. huxleyi* surface coverage, assuming all sources are independent, is estimated as 25 % (this is the square root of the sum of the individual sources of 11 % and 22 %).

3.2 Surface coverage, CaCO_3 production and correlation with climate indices

The mean annual surface areal coverage of the *E. huxleyi* blooms in the study area during the 10 years examined was $474\,000 \pm 119\,000 \text{ km}^2 \text{ yr}^{-1}$ with a highly variable inter-annual surface coverage, varying from –54 % to +81 % of the mean value in 2000 and 1998, respectively. Based on our standing stock calculations, these mean areal estimates represent a net CaCO_3 production of 0.62 ± 0.15 teragrams CaCO_3 carbon per year ($\text{Tg CaCO}_3\text{-C yr}^{-1}$), with an upper limit of net production $1.12 \pm 0.28 \text{ Tg CaCO}_3\text{-C yr}^{-1}$ in 1998. The monthly surface areal coverage and net CaCO_3 production for the months April to August for the study period are shown in Fig. 3a. Figure 3b shows the annual (April to August) net surface coverage for each year. The annual *E. huxleyi* surface areal coverage (1998–2007) was found to be strongly positively correlated with the mean multivariate El Niño/Southern Oscillation (ENSO) index ($r = 0.75$, $p < 0.02$) (Fig. 3d). A negative correlation with the winter North Atlantic Oscillation (NAO) was also observed ($r = -0.47$) (Fig. 3c) but the correlation was not statistically significant ($p = 0.17$).

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3.3 Modulation of the air-sea flux of CO₂

Our conservative calculations indicate that *E. huxleyi* blooms, through production of their calcareous coccoliths, have the ability (dependent upon the water temperature and salinity) to increase monthly mean $p\text{CO}_2$ by up to 23 μatm . We calculated values of $p\text{CO}_2$, $\Delta p\text{CO}_2$ and F in each year from 1998 to 2007 and each month from April to August. Figure 4 shows the average percentage change in these properties observed in each cell over all years and months. Figure 5 shows the maximum of the monthly values over the five months. In regions where *E. huxleyi* blooms are prevalent, monthly $p\text{CO}_2$ is increased on average by 3 % (Fig. 4a), reducing the monthly $\Delta p\text{CO}_2$ by 16 % (Fig. 4b), and consequently reducing F by 12 % (Fig. 4c). However, the monthly $p\text{CO}_2$ can be increased by a maximum of 8 % (Fig. 5a), reducing $\Delta p\text{CO}_2$ by 49 % (Fig. 5b) and consequently reducing F by 32 % (Fig. 5c). As can be seen from Figs. 4 and 5, the greatest impacts occur in the northeast (NE) sub-polar regions where bloom activity is greatest. The results from repeating the analysis excluding the years with strong ENSO values (1998 and 1999) are shown in Figs. 6 and 7. When these years are excluded the maximum impact on the monthly $\Delta p\text{CO}_2$ is slightly reduced to 45 % and the corresponding maximum reduction in F is 31 %. By comparing Figs. 4, 5, 6 and 7 it can be seen while the average and maximum impacts are very similar, the spatial regions that exhibit the maximum impacts vary.

4 Discussion

It has already been observed that $p\text{CO}_2$ in regions of the North Atlantic is highly variable (Watson et al., 2009; Schuster and Watson, 2007). However, within some regions of the N. Atlantic subpolar gyre $p\text{CO}_2$ has unexpectedly increased faster than atmospheric levels (Lefevre et al., 2004; Le Quere et al., 2009). Lefevre concluded that this unexpected increase was due to a decrease in biological activity as the trend was strongest during spring and summer (Lefevre et al., 2004). Similarly, in general

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E. huxleyi bloom activity in the N. Atlantic increases as spring progresses into summer, exhibiting a peak in bloom activity during late June and early July, with blooms still forming in the NE during August. Due to the slow equilibration time between the surface ocean and the atmosphere (6 months to a year) the increased $p\text{CO}_2$ due to calcification will remain in place long after a bloom has finished, blocking a large portion of the annual CO_2 sink cycle (Robertson et al., 1991). Therefore, our analysis suggests that annual *E. huxleyi* bloom activity at these higher latitudes could be partially responsible for the increase in $p\text{CO}_2$ observed.

The strong positive correlation found here between total *E. huxleyi* surface coverage and ENSO illustrates climate-driven variability, although the exact impact and processes of the ENSO acting on the *E. huxleyi* in the North Atlantic are unclear. Furthermore, this correlation also suggests a linkage between variations in $p\text{CO}_2$ and the ENSO. However, the large variation shown in Figs. 6 and 7 (results excluding the strong ENSO years) show that the *E. huxleyi* surface coverage (and thus the modulation of $p\text{CO}_2$) is not purely a function of ENSO variation. For example, previous work has shown that increased *E. huxleyi* abundance in the central North Atlantic is correlated with increased solar radiation, reduced mixed layer depth and increased water temperature (Raitso et al., 2006). It is apparent from Fig. 3a that *E. huxleyi* bloom surface distributions vary in extent between years and so their impact cannot be assumed to be identical each year. Furthermore, increased *E. huxleyi* bloom activity at higher latitudes has been reported in the polar Barents sea (Smyth et al., 2004), while an increasing (multi-decadal) trend in multi-taxa coccolithophore abundance has been identified (McQuatters-Gollop et al., 2010) for a sub-set of the NE Atlantic. However, it is the practice for air-sea exchange studies to exploit climatology datasets for values of $p\text{CO}_2$, under the assumption that $p\text{CO}_2$ is changing linearly with time. The high variability of *E. huxleyi* blooms between years, their correlation with the ENSO, their modulation of $p\text{CO}_2$ and the observed increase in *E. huxleyi* activity in some regions suggests that this assumption does not hold over large parts of the North Atlantic. *E. huxleyi* blooms are also known to form in other oceanic regions including the Pacific

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ocean (Beaufort et al., 2008), Bering sea (Merico et al., 2003), Barents sea (Smyth et al., 2004) and the Baltic and Black seas (Tyrell et al., 2008; Cokacar et al., 2001). The influence that these blooms can have upon $p\text{CO}_2$ and thus F in these regions will be dependent on the specific environmental conditions and the spatial extent and temporal variability of the blooms.

Previous studies have found a negative correlation between phytoplankton abundance and the NAO (Boyce et al., 2010; Fromentin and Planque, 1996). Therefore, we suggest that continued monitoring (i.e. to create a longer time series) will increase the significance of the negative correlation found here between the *E. huxleyi* surface coverage and the NAO. The SeaWiFS sensor is no longer in orbit, but alternative and equivalent optical sensors exist (including NASA's MODerate resolution Imaging Spectrometers, MODIS, and the European Space Agency MEdium Resolution Imaging Spectrometer, MERIS) which can be used to extend the time series analysis into the next decade.

It is important to note that calcification is not the only biological control on $p\text{CO}_2$. CO_2 uptake by photosynthesis and its release by respiration are major processes by which marine organisms and ecosystems can alter $p\text{CO}_2$ (Gattuso et al., 1995) and the interaction between photosynthesis, respiration and calcification in certain marine systems (e.g. coral reefs) can be tightly coupled (Gattuso et al., 1995). Therefore, any photosynthesising species of phytoplankton that develop within a body of water that holds or previously held an *E. huxleyi* bloom have the potential to further modulate $p\text{CO}_2$. Equally, the biogeochemical history of the body of water is also important. For example, a photosynthesising phytoplankton species could reduce $p\text{CO}_2$ through photosynthesis prior to the formation of any *E. huxleyi* bloom. However, many regional ecosystem models used to produce short to medium term predictions of air-sea CO_2 fluxes in the N. Atlantic do not include the effect that calcifying plankton can have on $p\text{CO}_2$ (e.g. ERSEM; Wakelin et al., 2012). Global biogeochemical/ecosystem models often represent calcification by a highly simplified parameterisation, for instance as a globally constant rain ratio (e.g. OCMIP-2; Najjar et al., 2007), a latitudinal function

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(e.g. MEDUSA; Yool et al., 2011) or as a function of the surface saturation state of calcite or aragonite (e.g. BioGEM; Ridgwell et al., 2007). The work presented here shows the high spatial and temporal variability that these calcifying plankton can exhibit and their modulation of the air-sea flux. Previous work has suggested that their latitudinal distribution could be changeable (Smyth et al., 2004; McQuatters-Gollop et al., 2010). Therefore, applying the simplifications detailed above when modelling the N. Atlantic (for short to medium term predictions) has the potential to introduce a large source of error within any estimated air-sea CO₂ fluxes. Reasons for such simplifications within models include a lack of knowledge about the biogeochemical and ecological factors that fundamentally govern calcification rates, disparate responses of different calcifying organisms to these factors, and also the lack of appropriate data to evaluate model output at the appropriate scale. Towards this last issue, the advantages of using Earth observation to evaluate ecosystem model output has recently been highlighted (Shutler et al., 2011) and the maps of *E. huxleyi* surface coverage generated within this study would provide a suitable dataset for model evaluation.

In the natural marine environment the *E. huxleyi* cell concentrations will generally gradually decrease at the edge of each bloom. However, as already discussed the Earth observation *E. huxleyi* detection algorithm (Shutler et al., 2010) classifies areas of ocean into bloom and non-bloom regions. The output is a binary classification defining clear boundaries between regions of bloom and non-bloom. Whilst the spatial component of the classification algorithm is able to detect regions of gradually varying concentrations (through a ramp detector – see Shutler et al., 2010), the spectral component of the algorithm consists of a series of spectral thresholds which are defined to minimise confusion between *E. huxleyi* and other spectrally similar particulates. These conditions set by the spectral model mean that the algorithm is more likely to miss regions of reduced concentrations of *E. huxleyi*, such as those that can exist around the edge of a bloom. Therefore, the estimates of *E. huxleyi* surface coverage and the resultant net CaCO₃ presented in this study are expected to be conservative.

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5 Conclusions

The results presented in this study show a 10-year time series study of *E. huxleyi* bloom surface distributions in the North Atlantic, estimated to a precision of ~25 %. There is a large inter-annual variation in surface area of satellite-detected *E. huxleyi* blooms in the North Atlantic and this variability is correlated with leading climate oscillation indices. Using climatology data, the time series of Earth observation data, and the seacarb package we have evaluated the impact that these *E. huxleyi* blooms can have on $p\text{CO}_2$ in the surface water. They have the ability to increase the $p\text{CO}_2$, which in turn reduces the air-sea flux; this reduction in the flux can exist for six or more months after the bloom has dispersed. The 10-year times series has illustrated the widespread impact that these calcifying plankton can have on the air-sea flux of CO_2 in the North Atlantic. The work has also shown that these effects are likely to be greater during years with a strong positive ENSO signal. Our analysis highlights the need for the continued study and monitoring of these plankton if we are to fully understand the North Atlantic sink of CO_2 and its inter-annual variability. The work also highlights the importance of including calcifying plankton within biogeochemical/ecosystem models used to study air-sea CO_2 fluxes in the North Atlantic.

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ysis Service (NEODAAS). The authors would like to thank the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) for providing the CPR data.

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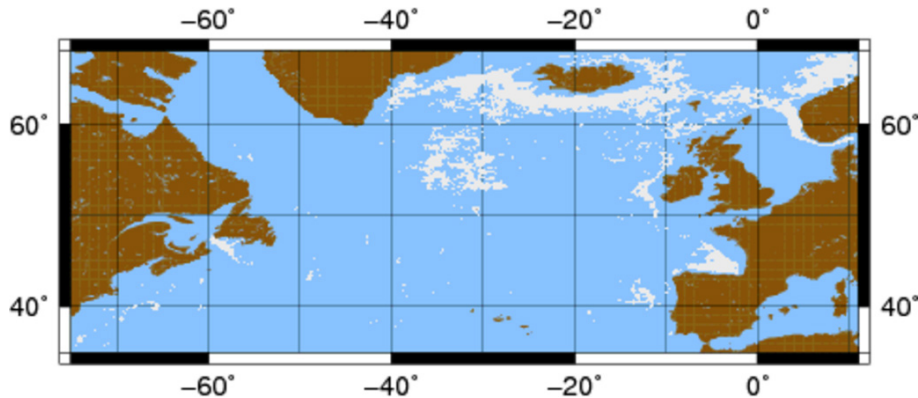


Fig. 1. The study region. The white regions show the spatial distribution of open ocean (>200 m) *Emiliana huxleyi* blooms during April to August as detected by the Earth observation data used in this study (1998–2007). Land is in brown.

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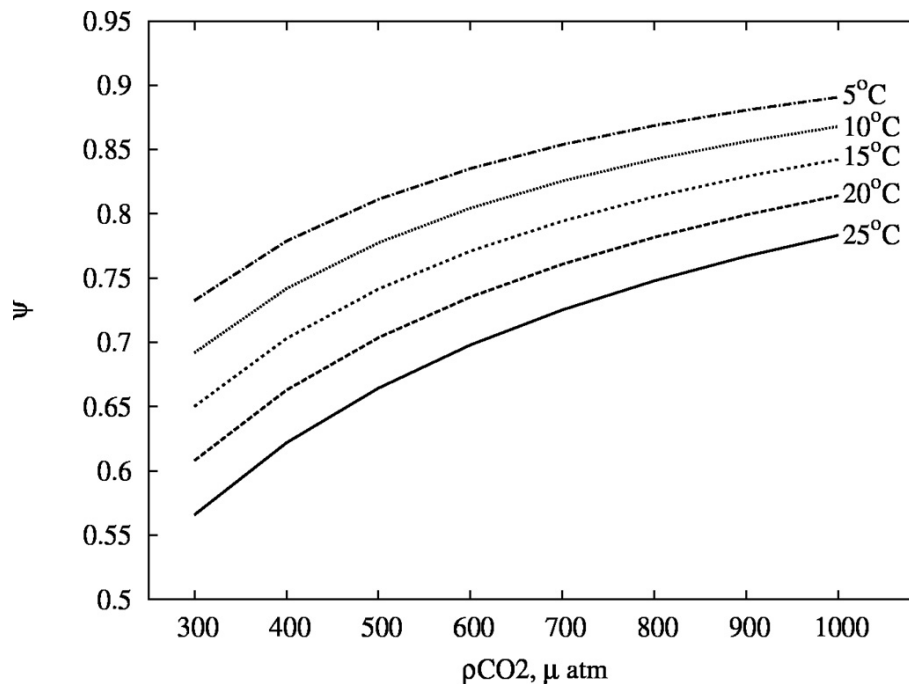


Fig. 2. Evolution of ψ (ratio of released CO_2 to precipitated CO_3) during the calcification process versus the dissolved CO_2 level in seawater (salinity = 35 PSU and total alkalinity $2400 \mu\text{eq kg}^{-1}$). This plot was generated using the seacarb package and is a reproduction of Fig. 2 from the original publication of Frankignoulle and Gattuso (1994).

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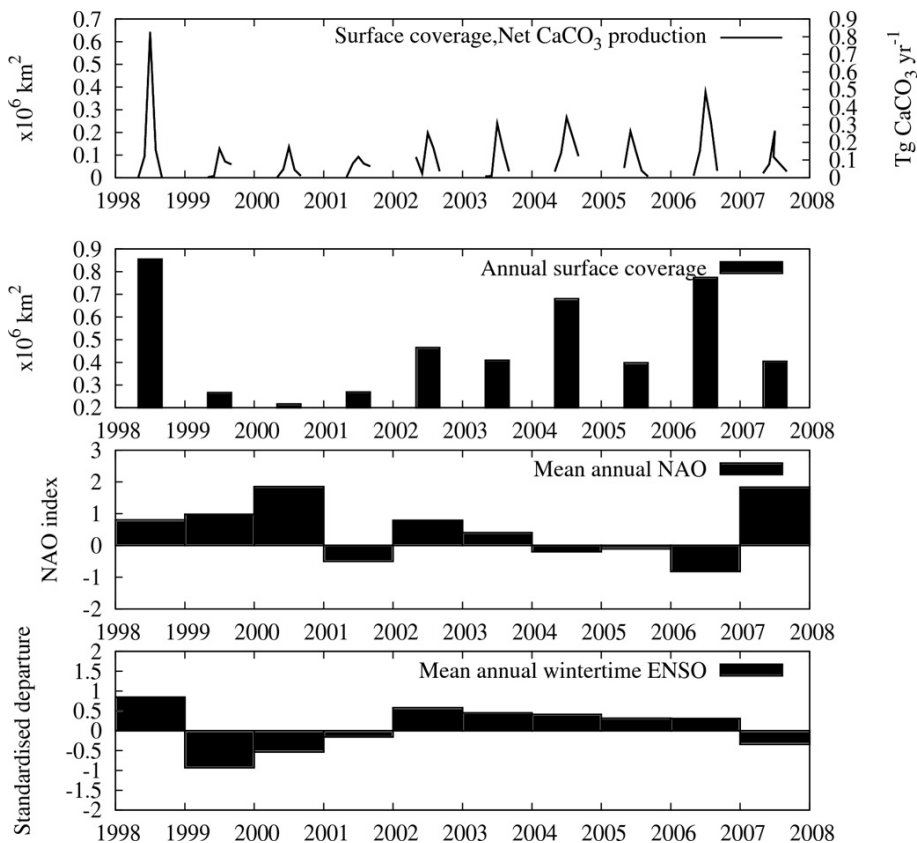


Fig. 3. Time series data (1998–2007). **(a)** Monthly *Emiliana huxleyi* surface coverage and CaCO₃ production for April to August of each year; **(b)** yearly total (April to August) of surface coverage for each year; **(c)** mean annual wintertime North Atlantic Oscillation (NAO) for each year and **(d)** mean annual ENSO for each year.

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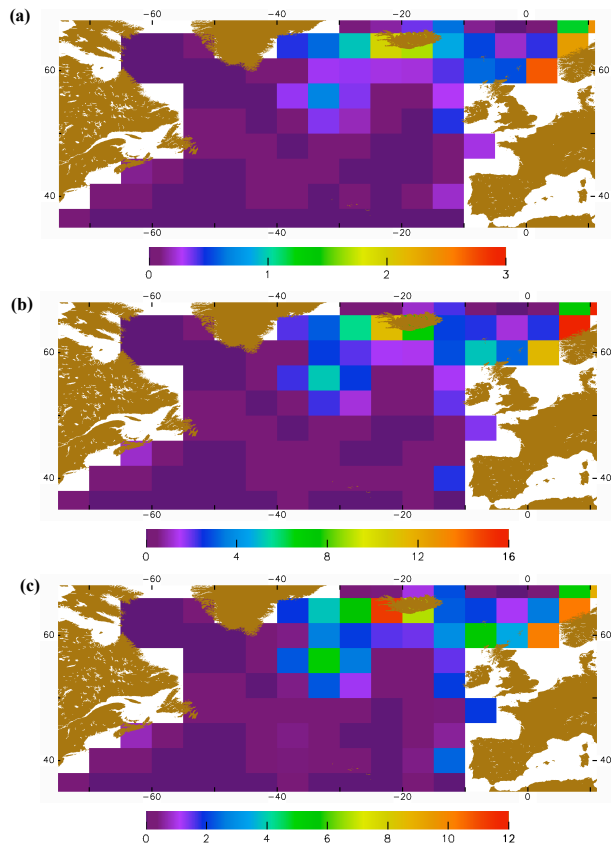


Fig. 4. Average impacts of *Emiliana huxleyi* spatial distributions on the monthly air-sea CO₂ flux for years 1998–2007. **(a)** Percentage decrease in water partial pressure $p\text{CO}_2$ (0–3 %); **(b)** percentage decrease in air-water partial pressure difference $\Delta p\text{CO}_2$ (0–16 %); **(c)** percentage decrease in air-sea CO₂ flux (0–12 %).

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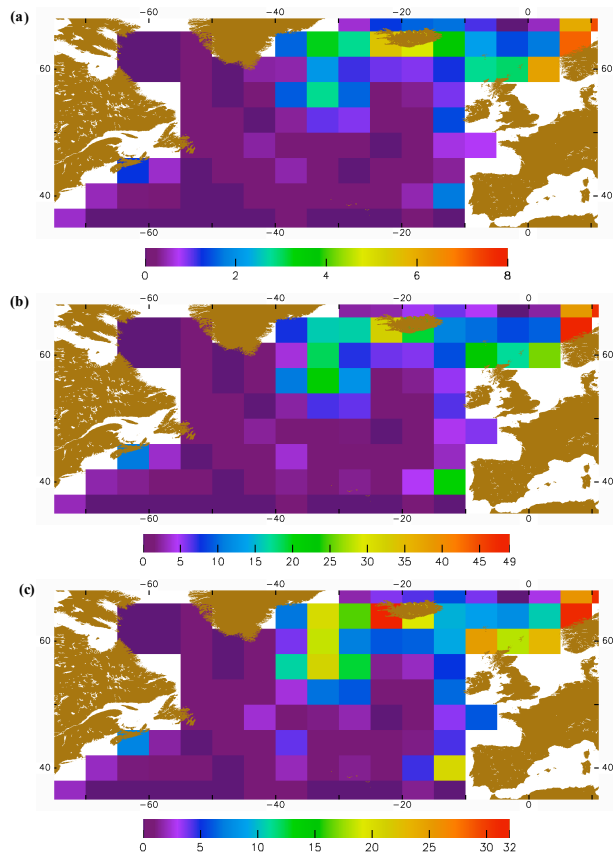


Fig. 5. Maximum impacts of *Emiliana huxleyi* spatial distributions on the monthly air-sea CO_2 flux for years 1998–2007. **(a)** Percentage decrease in water partial pressure $p\text{CO}_2$ (0–8%); **(b)** percentage decrease in air-water partial pressure difference $\Delta p\text{CO}_2$ (0–49%); **(c)** percentage decrease in air-sea CO_2 flux (0–32%).

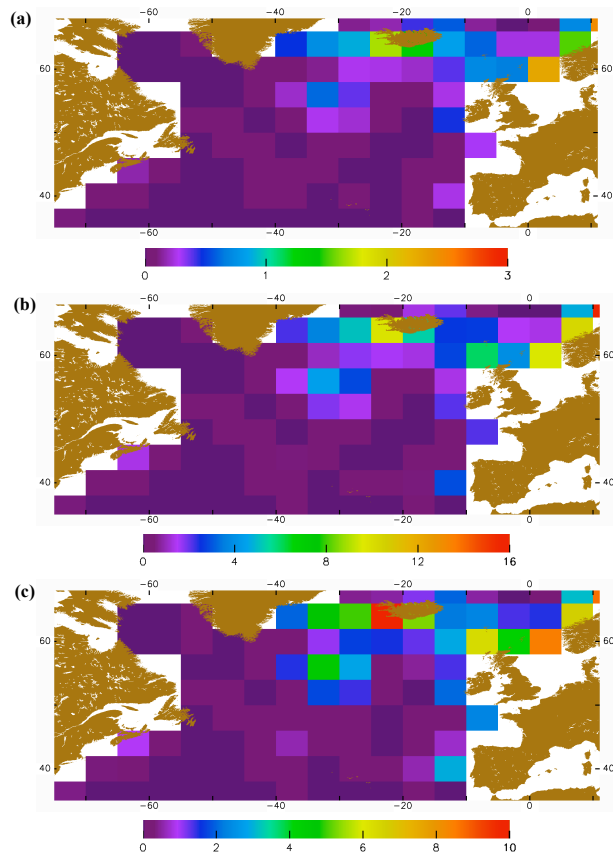


Fig. 6. Average impacts of *Emiliana huxleyi* spatial distributions on the monthly air-sea CO_2 flux for years 2000–2007. **(a)** Percentage decrease in water partial pressure $p\text{CO}_2$ (0–3%); **(b)** percentage decrease in air-water partial pressure difference $\Delta p\text{CO}_2$ (0–16%); **(c)** percentage decrease in air-sea CO_2 flux (0–10%).

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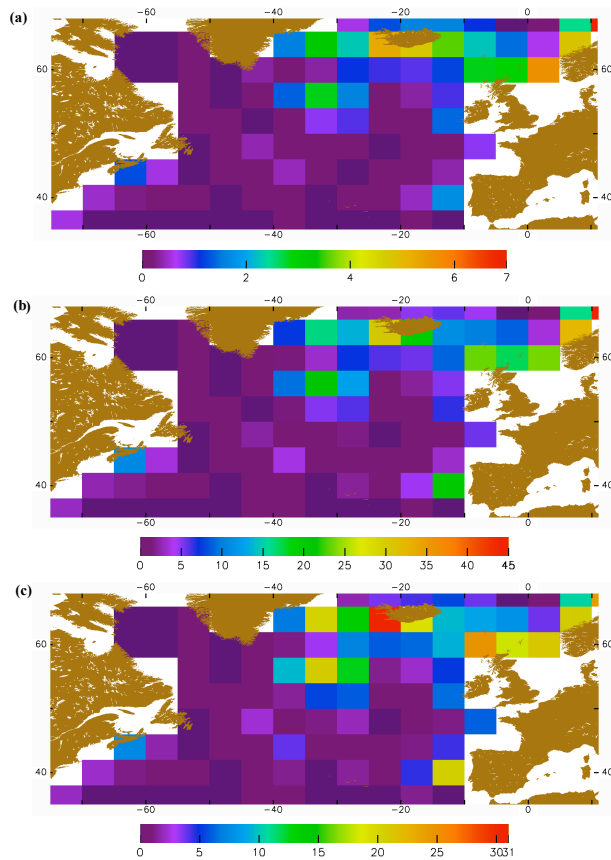


Fig. 7. Maximum impacts of *Emiliana huxleyi* spatial distributions on the monthly air-sea CO_2 flux for years 2000–2007. **(a)** Percentage decrease in water partial pressure $p\text{CO}_2$ (0–7%); **(b)** percentage decrease in air-water partial pressure difference $\Delta p\text{CO}_2$ (0–45%); **(c)** percentage decrease in air-sea CO_2 flux (0–31%).

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