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Insolation forcing of coccolithophore productivity in the North Atlantic during the Middle Pleistocene

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Highlights (85 characters max. including spaces):

- Coccolithophore productivity is higher during glacials.
- Coccolithophores adjust their phenology in response to insolation forcing.
- Enhanced productivity occurs when summer/autumn insolation is at its maximum.
Abstract

Coccolithophores play a key role in the oceanic carbon cycle through the biological and carbonate pumps. Understanding controls on coccolithophore productivity is thus fundamental to quantify oceanic carbon cycling. We investigate changes in coccolithophore productivity over several Pleistocene glacial-interglacial cycles using a high-resolution coccolith Sr/Ca ratio record, which is an indicator of growth rate and thus a proxy for coccolithophore productivity. We use Middle Pleistocene sediments from the North Atlantic Integrated Ocean Drilling Program (IODP) Site U1313 (41.00’ N, 32.58’ W) spanning Marine Isotopic Stages 16 to 10 (638 to 356 kyr). The location of the record allows us to investigate processes affecting productivity in a mid-latitude setting and to unravel the effects of temperature and regional ocean circulation. Coccolithophore productivity shows a dominant glacial-interglacial cyclicity with higher productivity during glacials, which appears to reflect the southward migration of the North Atlantic high productivity zone currently located between 45º and 55º N. Spectral analysis of the productivity record reveals a suborbital variability consistent with forcing by insolation maxima superimposed on the front migration pattern. Similar to today, coccolithophore productivity during interglacials was enhanced when insolation was at its maximum in spring or in autumn, whereas during glacials, productivity was enhanced when summer/autumn insolation was at its maximum. We show that in the studied region, coccolithophore productivity was driven by processes reflecting regional insolation. Applying this information to model experiments is required to assess if coccolithophore productivity played a significant role in past changes of atmospheric CO₂.
1. Introduction

Coccolithophores are the main primary producers in temperate regions of the open ocean (Brand, 1994) producing biogenic calcite (Bolton et al., 2016) and mediating cycling, sequestration and export of organic and inorganic carbon (Rost and Riebesell, 2004; Baumann et al., 2005). Coccoliths, the minute calcite plates that cover coccolithophore cell, are very abundant in seafloor sediments and have been extensively used as paleoenvironmental tracers providing information on paleoceanographic conditions and composition of the overlying photic zone’s communities (e.g., Flores et al., 2003; Baumann et al., 2005; Marino et al., 2014; Emanuele et al., 2015; Maiorano et al., 2015). Enhanced coccolithophore calcification during glacial and terminations has been suggested to drive a decrease in the availability of the carbonate ion in the ocean and trigger the deglacial rise in atmospheric carbon dioxide ($pCO_2$) (Rickaby et al., 2010; Omta et al., 2013). Reconstructing past variations in the production and accumulation of sedimentary carbonate is thus important for understanding changes in $pCO_2$ (Sigman et al., 1998; Sigman and Boyle, 2000).

In well-preserved sediments, coccolithophore productivity has commonly been inferred from the total coccolith abundance (e.g., Emanuele et al., 2015) and the nannofossil accumulation rate (NAR) (e.g., Flores and Sierro, 2007; Cabarcos et al., 2014), but also from the relative abundance of small placoliths and *Florisphaera profunda* (e.g., Marino et al., 2008). In addition, other primary production indicators, such as alkenones (organic molecules mostly produced by certain species of coccolithophores) are also used (e.g., Villanueva et al., 2001; Emanuele et al., 2015). The accumulation of organic matter, including total organic carbon (TOC) and alkenones, represents the most direct record of general and coccolithophore productivity, respectively (Schoepfer et al., 2015). Both have been used as paleo-productivity
proxies (e.g., Rühlemann et al., 1999; Stein et al., 2009) by assuming that changes in organic carbon content of sediment can be interpreted as changes in the surface productivity through time (Wefer et al., 1999). However, all of these proxies depend not only on supply but also on dilution (by minerals or other sediment constituents), sedimentation or accumulation rates, and preservation conditions (Rullkötter, 2006).

The coccolith fraction (CF) Sr/Ca ratio has been suggested as an alternative productivity proxy that is independent of accumulation rate. Coccolithophores construct coccoliths internally within their cell and several studies suggest that Sr/Ca of the coccolith is directly proportional to the coccolith calcification rate, which is a function of growth rate (e.g., Stoll and Schrag, 2000; Rickaby et al., 2007; Mejía et al., 2014). The faster coccolithophores grow, the faster they calcify and the more Sr is incorporated into the calcite lattice of their coccoliths (Stoll and Schrag, 2000; Stoll et al., 2002a).

The amount of Sr introduced into the calcite (Sr partitioning) varies among genera and species, with larger and more heavily calcified coccoliths generally having higher Sr content than smaller and lighter coccoliths (Stoll et al., 2007; Fink et al., 2010). Dissolution intensity and changes in coccolith assemblage appear to exert only a minor influence on CF Sr/Ca in the modern ocean (Stoll and Schrag, 2000). However, significant downcore changes in coccolith assemblages, including due to intensive or selective dissolution (Stoll et al., 2002b), should be evaluated when applying this proxy to the past.

In laboratory cultures, coccolith Sr/Ca also correlates with temperature. Stoll et al. (2002a) cultured different coccolithophore species strains at different temperatures, with results for several strains of *Gephyrocapsa oceanica* indicating that increasing temperature can increase Sr partitioning. This suggests that there is a temperature-controlled change in Sr partitioning
coefficients ($D_{Sr}$) in calcite, analogous to that observed in abiogenic dolomite-calcite and
aragonite-calcite transformation experiments (Malone and Baker, 1999). If this interpretation is
correct, then the temperature effect should be removed from coccolith Sr/Ca records to identify
the component of variation due to growth rate. If the temperature effect on $D_{Sr}$ is the dominant
source of temperature dependence on coccolith Sr/Ca in culture experiments (Stoll et al., 2002a;
Müller et al., 2014), then the relationship from cultures coupled with an independent temperature
measurement (e.g., Mg/Ca-based sea-surface temperature (SST) from foraminifers) can be used
to correct for this effect, as has been done in previous studies (e.g., Mejia et al., 2014). With
temperature and assemblage effects considered, the SST corrected CF Sr/Ca curve should mostly
reflect qualitatively coccolithophore growth rate and therefore their productivity (Stoll et al.,
2002a; Müller et al., 2014). The validity of the CF Sr/Ca productivity proxy has been established
in previous studies in oceanographic regions where SST variations over glacial-interglacial
cycles were relatively small (~4 - 6ºC) (Mejia et al., 2014; Tangunan et al., 2017) as well as in
the Southern Ocean where SSTs are significantly lower (varying between 6 ºC - 12 ºC)
(Saavedra-Pellitero et al., 2017).

Here, we reconstruct the paleoproductivity of coccolithophores, the most significant
component of the phytoplankton community in the central North Atlantic, based on the CF Sr/Ca
ratio. We used a carbonate-rich sediment archive that contains well-preserved coccolithophores
from the mid-latitude North Atlantic (IODP Site U1313), spanning the mid-Brunhes dissolution
interval and the *Gephyrocapsa caribbeanica* acme (e.g., Baumann and Freitag, 2004; Barker et
al., 2006). The location of IODP Site U1313 (Fig. 1) allows the assessment of coccolithophore
productivity changes in a transitional productivity area particularly sensitive to basin-scale
forcing changes, such as changes in temperature and circulation (Barton et al., 2003).
Fig. 1 - Study area: (a) Schematic surface ocean circulation of the North Atlantic, in the vicinity of IODP Site U1313. Major currents and oceanic fronts: Gulf Stream (GS, in red), North Atlantic Current (NAC, in dark orange), Azores Current (AC, in light orange); and associated fronts: Subpolar Front (SPF) and Azores Front (AzF) – both as black lines. Black stars evidence sediment data: IODP Site U1313 (this study), IODP Site U1314 (Alonso-Garcia et al. 2011), ODP Site 980 and 984 (Oppo et al., 2011).
1998 and Ortiz et al., 1999, respectively), cores SU90-08 and MD95-2037 (Villanueva et al., 2001). Map template made with Ocean Data View (Schlitzer, 2015). Note different scales of the monthly chlorophyll a concentration represented in (b), (c) and (d) for the different production regimes, respectively: (b) subpolar (represented by the blue square located at 55 - 57° N, 31 - 33° W), (c) for the mid-latitude (black star at the location of IODP Site U1313, 40 - 42° N, 31 - 33° W) and (d) for the subtropical production regimes (red square located at 30 - 32° N, 41 - 43° W). Blue, yellow and red heavy lines indicate an average of ten years for each regime, respectively, whereas grey lines are individual years (2003 to 2013). Chlorophyll a concentration derived from MODIS and SeaWiFS satellite data available at http://disc.sci.gsfc.nasa.gov/giovanni).

The key motivation for this study is to understand the climate drivers of North Atlantic coccolithophore production dynamics across Pleistocene glacial/interglacial cycles. We investigate how atmospheric and hydrographic changes influence coccolithophore productivity, at both orbital and suborbital time scales. We emphasize that our research focuses on the qualitative characteristics of the paleoproductivity record, namely the inherent orbital and suborbital periodicities, rather than quantitatively estimating the coccolithophore productivity. Thus, we reconstruct the CF Sr/Ca component of coccolithophore productivity and not quantitative production.

We analyze changes in the ocean surface circulation and its relationship to nutrient availability, as well as changes in the insolation as a potential forcing mechanism. To do this we reconstructed coccolithophore productivity qualitatively based on the CF Sr/Ca at IODP Site U1313 over the interval between 638 and 356 ka. This is the first time that the Sr/Ca proxy has been used in a temperate region that experienced significant SST oscillations associated with glacial ice-rafting events (Stein et al., 2009; Naafs et al., 2011) and we address potential caveats accordingly. The studied interval covers a wide range of climatic conditions from Marine Isotopic Stages (MIS) 15 to MIS 11, including the late and early phases of MIS 16 and MIS 10, respectively. MIS 11 is acknowledged as an analogue for the present interglacial (e.g., Loutre and Berger, 2003) and MIS 12 was one of the harshest glacia...
On the other hand, MIS 15 and MIS 13, on the other hand, were relatively milder interglacial stages than MIS 11 (Jouzel et al., 2007).

It is worth noting that coccolithophore communities evolved and changed throughout this interval (e.g. Bollmann et al., 1998). Our 300 kyr-long sedimentary record falls mostly within the Gephyrocapsa caribbeana acme between MIS 14/MIS 13 and MIS 8 when this species dominated (≥ 50 %) coccolithophore communities worldwide. The interval also includes the extinction of Pseudoemiliania lacunosa in MIS 12 (Raffi et al., 2006). Neither species are found in modern assemblages and their behavior cannot be assessed through cultured studies. Additionally, our mid-Brunhes record precedes the first occurrence of Emiliania huxleyi (290 ka; Raffi et al., 2006), the cosmopolitan and dominating species in the modern ocean.

2. Regional setting

2.1. Hydrography

The North Atlantic constitutes a vigorous overturning circulation of the modern ocean (Toggweiler, 2009). It is characterized by the central anticyclonic subtropical gyre, the northern cyclonic subpolar gyre, and continuous poleward transport of warm and salty surface waters in between (Fig. 1a). This transport contributes to the Atlantic Meridional Overturning Circulation (AMOC) whose strength affects regional and global climate (Rahmstorf, 2002).

The northern edge of the North Atlantic Current (NAC) defines the Subpolar Front, which separates colder sub-arctic waters to the north from the warmer subtropical waters to the south (Rossby, 1999; Priede et al., 2013). Today IODP Site U1313 is located on the southern edge of the NAC. Surface waters near IODP Site U1313 are subjected to seasonal changes and are influenced by eddy formation both from NAC recirculation off the Grand Banks (Fratantoni,
and the nearby formation of the Azores Current and its associated front (Fasham et al., 1985; Schwab et al., 2012). The frontal system changes seasonally but also on geological time scales. During past glacials, fronts migrated south, reaching their southernmost limit at glacial maxima and during Heinrich events (e.g., McIntyre et al., 1972; Maslin et al., 1995, Alonso-Garcia et al., 2011).

2.2. Present productivity regime in the study area

The North Atlantic shows a distinctive latitudinal increase in primary productivity from the subtropical gyre to the north (Antoine et al., 1996a, b; Henson et al., 2009). Generally, the subpolar gyre area records the higher chlorophyll $a$ concentrations with maxima during the summer months (Fig. 1b). The area characterized by transitional waters (mid-latitudes) displays intermediate levels of chlorophyll $a$ concentrations (Fig. 1c), whereas the subtropical gyre exhibits lower chlorophyll $a$ concentrations with maxima during winter months (Fig. 1d; note the different chlorophyll $a$ scales for the respective productive regimes). In situ measurements, surface sediments and satellite images indicate chlorophyll and phytoplankton productivity maxima between 45º and 55º N, associated with the convergence zone between the subpolar and subtropical gyres (e.g., McIntyre et al., 1972; Weeks et al., 1993; Antoine et al., 1996a, b; Henson et al., 2009) and the meandering of the NAC (Rossby, 1999), which is characterized by higher occurrence of eddies and resultant mixing (Falkowski et al., 1991; Oschlies and Garçon, 1998; Oschlies, 2002).

Henson et al. (2009) described three areas with distinct productivity regimes in the North Atlantic. A positive correlation between chlorophyll concentration and mixed-layer depth characterizes the subtropical area, reflecting phytoplankton growth limited by nutrient availability. The subpolar area is characterized by a negative correlation reflecting light
limitation (Longhurst, 1995, 2007). IODP Site U1313 is located in the transition zone (40º to 45º N), where chlorophyll responds to changes in the mixed-layer depth and the blooms may either have subpolar or subtropical characteristics. This regime is the most variable in bloom timing and duration (Lévy, 2005; Henson et al., 2009). During summer, high SST indicates influence of subtropical, oligotrophic and stratified surface waters with a deep nutricline, resulting in low productivity. In autumn, the SST decreases and the nutricline shoals, allowing phytoplankton to bloom when sunlight is still available. Further cooling and light limitation in winter are associated with low productivity despite abundant nutrients. As soon as the duration of sunlight increases again in spring, phytoplankton (especially the opportunistic species that can grow rapidly) take advantage of the abundant nutrient availability and multiply quickly, reaching their productivity maxima during the spring bloom. At this time, the species capable of the highest growth rates, such as the coccolithophores *Emiliania huxleyi* and some species of the *Gephyrocapsa* genus, are the most abundant phytoplankton in the studied area (Broerse et al., 2000; Tyrrell and Young, 2009).

### 3. Material and methods

3.1. Sediment sampling and coccoliths separation

IODP Site U1313, located at 41.00º N; 32.58º W (3426 m water depth, Fig. 1), constitutes a reoccupation of Deep Sea Drilling Project (DSDP) Site 607, a reference site for Quaternary paleoceanography (Ruddiman et al., 1989; Channell et al., 2006). Four holes (U1313A to U1313D) were cored on the upper middle western flank of the Mid-Atlantic ridge, ~386 km northwest of the Azores (Fig. 1). The recovered sediment is composed of nannofossil ooze with varying amounts of foraminifers and clay- to gravel-sized terrigenous components.
(Channell et al., 2006; Stein et al., 2006). For the CF Sr/Ca record a total of 409 samples were collected from ~15 meters of the secondary stratigraphic splice (15.82 to 31.15 adjusted meters composite depth (amcd) from Holes U1313A and U1313D, see Supporting Information) at 4 cm spacing using a 1 cm-wide scoop (5 cm³). This resulted in a temporal resolution of ~700 years. Approximately 250 mg of each sample was collected and suspended in 2% ammonia to avoid carbonate dissolution, and then sieved through a 20 µm mesh to separate the coccolith fraction (<20 µm) from mostly foraminifer tests and fragments, as well as other larger microfossils and sediment components. All sieves were carefully washed with running tap water and rinsed with distilled water between samples to avoid cross contamination.

3.2. Sample preparation and Sr/Ca ratio analysis

Samples were cleaned following a three-step procedure based on Stoll and Ziveri (2002). First, 15 mL of MNX reagent (75 mg of hydroxylamine hydrochloride, 6 mL of concentrated ammonia and 9 mL of ultrapure water) was added and mixture was mechanically shaken for 12 hours. This step reduces Fe and Mn oxyhydroxides that scavenge metals from seawater and contain non-carbonate Sr. Then 2% ammonia was added to remove any non-carbonate Sr (e.g. from clays) by exchanging cations (Sr²⁺) with the excess of NH₄⁺. Finally, the mixture was rinsed with ultrapure water to extract any remaining ammonia. Initially, the procedure included a step to oxidize organic matter. However, after test results were identical with or without oxidation (Cavaleiro, 2011), possibly because of low TOC content (min=0.05 wt%; max=0.54 wt%; standard deviation=0.08 %) and high CaCO₃ content (min=36 wt%; max=91 wt%; mean=77 %; standard deviation=11 %), this step was removed. A weak buffered acid (6 g glacial acetic acid, 7 g ammonium acetate in 1 L of Milli-Q water) was used to dissolve the coccoliths over 12 hours to minimize the contribution of ions from non-carbonates phases. The solution was
then centrifuged, extracted and kept in acid-cleaned centrifuge tubes. A first inductively coupled plasma-atomic emission spectroscopy (ICP-AES) measurement of Ca was performed by diluting 100 µL of the original sample (2 mL) into 2 mL of ultrapure Millipore water. The samples were subsequently diluted to Ca concentrations similar to the standard solutions. Calibration was conducted following the method described by de Villiers et al. (2002) using standards with constant Ca concentrations and different Sr concentrations to give Sr/Ca ratios ranging from 0.75 to 4 mmol/mol. All measurements were conducted using the ICP-AES (Thermo ICAP DUO 6300) in the Geology Department at the University of Oviedo with reproducibility better than 0.02 mmol/mol. To infer any possible contamination other metals (such as Fe and Mg) were also measured together with Sr.

3.3. Coccolith assemblage

As previously mentioned, the CF Sr/Ca record can be affected by changes in the composition of the analyzed coccolith fraction. To investigate significant changes in the coccolith assemblage, coccolith counts were performed in 24 samples selected based on their CF Sr/Ca levels (8 low/ 8 intermediate/ 8 high, see Supporting Information). Samples were processed following Andruleit (1996). About 0.05 g of freeze-dried sample was diluted in about 50 mL of buffered water, ultrasonicated for 10 s and wet-split with a rotary sample divider. One one-hundredth of the solution was filtered through a polycarbonate membranes (47 mm diameter, 0.4 µm pore size) with a low-pressure vacuum pump. The filters were dried in an oven at 40 °C for at least 12 hours. A randomly chosen filter area (~1 cm²) was cut and fixed onto an aluminum stub and sputtercoated with gold/palladium. At least 500 coccoliths were counted in random transects using a Zeiss DMS 940A Scanning Electron Microscope at the Geosciences Department, University of Bremen, using 3000× or 5000× magnification. Scanning areas varied
between 0.53 and 1.86 mm$^2$. Taxonomy followed Young et al. (2003), Su (1996) and Nannotax 3
(http://www.mikrotax.org/Nannotax3/index.html). Calculation of the number of coccoliths per
gram of dry sediment (C) followed Andrulait (1996): $C = (F \times c \times S) / (A \times W)$, where $F$ is the
effective filtration area (1214 mm$^2$), $c$ the number of counted coccoliths, $S$ the split factor
(1/100), $A$ the investigated area (mm$^2$), and $W$ the mass of the sample (g). To aid the
visualization of contributions from different species of coccolithophores, the amount of
carbonate from each of the species or species group was calculated using species-specific
estimates given by Young and Ziveri (2000).

3.4. Calculation of residual CF Sr/Ca

As previously mentioned, to use the CF Sr/Ca ratio as a reliable productivity indicator,
the downcore CF should not be significantly biased by variations in temperature or changes in
the species assemblage composition. We therefore evaluate potential temperature effects as well
as coccolith assemblage changes through time that could have affected our CF Sr/Ca ratios.
Potential impacts of dissolution/preservation of coccoliths are elaborated in the Results and
Discussion sections as these parameters can also be used as water-mass tracers not just
influencing the CF Sr/Ca ratios.

To correct our CF Sr/Ca data for temperature changes, we use the $U^{K-37}$-based SST for
our site (Stein et al., 2009; Naafs et al., 2011). The alkenones in the sediment were mostly
produced by coccolithophores and therefore the $U^{K-37}$-based SST is the best estimate of
temperature of the coccolithophores’ habitat. The temperature correction of the CF Sr/Ca
consisted of subtracting the SST-predicted Sr/Ca curve from the CF Sr/Ca curve:

$$\text{CF Sr/Ca} - \text{SST-predicted Sr/Ca} = \text{Sr/Ca residual}$$
To obtain the SST-predicted Sr/Ca values most representative for our record, we compare the CF Sr/Ca anomalies (Fig. 2) from three temperature dependence equations for different species or species groups and show a sensitive analysis of these anomalies on our CF Sr/Ca curve (Fig. 3).

Fig. 2 - Predicted CF Sr/Ca ratio anomalies according to $\text{U}^{\text{K}}_{\text{SST}}$. Each curve represent the CF Sr/Ca anomaly according to the temperature dependence of different species or group of species: a) $G.\text{ oceanica}$ (dark blue), b) multi-species linear regression (orange), c) $E.\text{ huxleyi}$ (red). The Sr/Ca deviation to negative values is a consequence of colder temperatures, while deviation to positive values reflect higher temperatures. We added the $\text{U}^{\text{K}}_{\text{SST}}$ record (green) for IODP Site U1313 and highlight a 5 °C SST change to visualize that most of the SST record falls inside this range. MIS stands for Marine Isotopic Stage and each of the Terminations (T) are also identified from TV to TVII.
Fig. 3 - Sensitive analysis of the CF Sr/Ca anomalies caused by in SST changes on the CF Sr/Ca record. After extracting the temperature effect, each CF Sr/Ca curve shows a different amplitude according to the temperature dependence of different species or group of species: a) *G. oceanica* (dark blue), b) multi-species linear regression (orange), c) *E. huxleyi* (red). The dashed line represents the mean of the CF Sr/Ca ratio record. MIS and T as in Fig. 2.

We use the dependence of (1) *Gephyrocapsa oceanica* (Fig. 2a), a species morphologically similar to *Gephyrocapsa caribbeanica* that dominates our sediments, and compare it with (2) a multi-species dependence that combines *G. oceanica, Calcidiscus leptoporus, Helicosphaera carteri* and *Coccolithus pelagicus* (Fig. 2b). Finally, the dependence of (3) *Emiliania huxleyi* is also shown (Fig. 2c) on the rationale that this species and *G. caribbeanica* share a cosmopolitan and dominant presence in deep-sea sediments, albeit at different times. Whereas *E. huxleyi* rose to dominance at ~80 ka (*Raffi et al.*, 2006) and is still extant, *G. caribbeanica* had a similar distribution and dominance during the Mid-Brunhes interval (*Bollmann et al.*, 1998). The three respective equations are shown here:

1. \( y = (0.0636x) + 1.3944 \) (Stoll et al., 2002b)
2. \( y = (0.0501x) + 1.7053 \) (Mejía et al., 2014)
3. \( y = (0.0272x) + 2.4238 \) (Stoll et al., 2002b)
where \( y \) is the predicted coccolith Sr/Ca value according to a given temperature \( x \).

Anomalies based on \( G. \) oceanica (Fig. 2a) and the multi-species group (Fig. 2b) are similar, as are the CF Sr/Ca ratios of the sensitivity analysis (Fig. 3a and b). To decide which equation to use, we looked at the coccolith assemblage changes. Although the continuous presence of \( G. \) oceanica in our sediments and its similarities to \( G. \) caribbeanica favor the use of its temperature dependence (1), the beginning of our record contains a substantial number of non-gephyrocapsids (Fig. 4). From MIS 14 to MIS 10, our sedimentary record is dominated by \( G. \) caribbeanica, which constitutes 50 to 80 % of the assemblage (Fig. 4a). The assemblages from late MIS 16 until mid MIS 14 contain, however, higher abundances of larger and more heavily calcified coccoliths, such as \( Calcidiscus \) leptoporus and \( Helicosphaera \) carteri. This becomes even clearer when the numbers of coccoliths are converted into species-specific contribution to the CaCO\(_3\) content (Young and Ziveri, 2000) (Fig. 4b).
Fig. 4 - Coccolith assemblage results: a) coccolith relative abundance (%); b) coccolith abundance converted to relative carbonate contribution (%). Please note that the samples are not evenly spaced in time.

Based on these observations and the absence of *E. huxleyi* in our sediments, we rejected the species-specific curves and use the Sr/Ca residual resultant from the multi-species temperature dependence (Fig. 5a). We refer to this residual from here on as coccolithophore productivity, because after correcting for temperature changes, we expect the curve to mostly reflect coccolithophore growth rate and thus paleoproductivity variations. The coccolithophore
productivity record reflects relative productivity change, representing the productivity deviation around the average productivity of the time series.

Fig. 5 - Sr/Ca results: a) CF Sr/Ca residual record (black curve) with confidence interval (grey area; Monte Carlo 20 to 80% interval), b) coccolith fraction Sr/Ca results (dark blue curve), and c) SST-predicted Sr/Ca ratio curve (orange curve). The CF Sr/Ca residual curve corresponds to the reconstructed coccolithophore productivity with the dashed line indicating the mean: values above the mean represent higher coccolithophore productivity and below the mean lower coccolithophore productivity. MIS and T as in Fig. 2.

Finally, to accommodate for potential biases caused by short intervals of large amplitude SST changes not present in previous studies, we determined an uncertainty envelope/confidence interval (shown as a grey envelope in figures) for the CF Sr/Ca residual. Using Astrochron (Meyers, 2014) we ran 100 Monte Carlo simulations for each of the 409 data points and carried out propagation of errors accounting for measurement uncertainties of temperature (with $\sigma =$...
1.5°C) and Sr concentration (with $\sigma = 0.01$ mmol/mol), and the linear regression of temperature versus Sr ($\sigma = 0.12$ mmol/mol). All figures showing the paleoproductivity record are accompanied with a grey envelope whose upper and lower limits correspond to Monte Carlo 20 and 80% confidence intervals (following Mejía et al., 2014).

3.5. Additional proxy data

The residual Sr/Ca curve is compared to carbonate content, carbon and oxygen isotopes and coccolith assemblages and preservation data to infer the likelihood and severity of dissolution. A coccolith dissolution index (CDI) based on the differential dissolution behavior of different coccoliths was adapted from Dittert et al. (1999) to estimate the effect of carbonate dissolution on the coccolith assemblages. We calculate the ratio between small *Gephyrocapsa*, which are relatively fragile and more susceptible to dissolution, and *Calcidiscus leptoporus*, a larger and more robust placolith. We used small *Gephyrocapsa* because *E. huxleyi* (suggested as the fragile placolith by Dittert et al. (1999)) is not present in our sediments. The CDI is calculated as follows: $\text{CDI} = (\text{small } Gephyrocapsa \%) / (\text{small } Gephyrocapsa \% + \text{Calcidiscus leptoporus } \%)$.

The U$^{137}$-based SST record for Site U1313 is already published (Stein et al., 2009; Naafs et al., 2011), whereas some of the TOC and total alkenone concentration data are being published here for the first time. Methods for TOC and alkenone concentration analysis and methodology are described in Stein et al. (2009).

The methods used to generate the benthic foraminifer stable isotope data is presented in Voelker et al. (2010), whereas calculation of the polar planktonic foraminifer *Neogloboquadrina pachyderma* (formerly *N. pachyderma* (s)) percent in the fraction >150\(\mu\)m fraction follows
standard micropaleontological procedure (e.g., Voelker et al., 2009). Sediment carbonate content was estimated from the X-ray fluorescence (XRF) Ca data (see Grützner and Higgins (2010) for details on XRF measurements). The Ca intensity counts obtained by XRF scanning were calibrated through correlation ($r^2 = 0.84$) with 517 quantitative carbonate analyses on discrete samples (Stein et al., 2009) using a power function.

3.6. Age model

Voelker et al. (2010) constructed the age model for Site U1313 by correlating the benthic foraminifer oxygen isotope record ($\delta^{18}O_b$) with the LR04 stack (Lisiecki and Raymo, 2005) with most correlation points being isotopic maxima (Fig. S1). Both $\delta^{18}O_b$ and CF Sr/Ca were measured in samples from the secondary splice (Holes U1313A and U1313D), whereas the $U^{K, 37}$-based SST data, used to correct the CF Sr/Ca initial curve, were obtained from primary splice samples (Holes U1313 B and U1313C). We used linear interpolation to match the resolution of the CF Sr/Ca record. Both alkenone and TOC samples were collected from the primary splice, at 2 cm spacing. Using data from both splices was possible because the lightness ($L^*$) records of the four holes (U1313A to U1313D) were visually correlated to create a common adjusted meter composite depth (amcd) (Naafs et al., 2012). Using the amcd depths, the age model of Voelker et al. (2010) could then be applied to both the primary and secondary splice.

3.7. Time-series analysis

Spectral analysis was conducted to test for statistically significant periodicities in the coccolithophore productivity record. The harmonic analysis of SPECTRUM was used to filter the time series for specific frequencies (see Supporting Information). Because the CF Sr/Ca (coccolithophore productivity) record is an unevenly spaced time series (i.e., the time between
samples varies), we decided to use the SPECTRUM and REDFIT packages for the time series analysis (Schulz and Stattegger, 1997; Schulz and Mudelsee, 2002), the only packages able to execute time series analysis without interpolation of the real data to produce an evenly spaced time series. A band-pass filtered Gaussian curve of the coccolithophore productivity record was computed with the Analyseries software package (Paillard et al., 1996) to allow visual alignment with the monthly insolation curves for the same time period. To test the hypothesis of changing coccolithophore phenology through time, we used time series analysis to look for orbital and suborbital periodicities in the coccolithophore productivity record (see Supporting Information).

4. Results

4.1. CF Sr/Ca results and other productivity proxies

The CF Sr/Ca values range from 1.85 to 2.67 mmol/mol (Fig. 5b), with 85% of the data within the range of 2.1 to 2.5 mmol/mol. This represents 49% of the whole sampling variation, with a total sampling range of 0.82 mmol/mol. The CF Sr/Ca values vary between ± 10% with an average variation of 1.6%. Higher variability is present in the beginning of the record (MIS 16 and MIS 15) with distinct minima at 439, 428 and 427 ka (MIS 12), while maxima values are found at 613, 603 and 587 ka (during MIS 15). The Sr/Ca residual data, referred to as the coccolithophore productivity record, show maxima coincident with the CF Sr/Ca record during MIS 15, several intermediate peaks during MIS 14, maxima similar to those found in MIS 15 during MIS 12 (at 457, 443 and 433 ka) and slightly lower values in early MIS10 (390 kyr). Minima occurred in late MIS 16 (625 ka), during MIS 15 (605 and 594 ka), around Termination (T) V (428 ka), and during MIS 11 (416 and 408 ka).
Both the CF Sr/Ca ratios and coccolithophore productivity record reveal an abrupt increase from MIS 16 to MIS 15 and a general decreasing trend from early MIS 15 to late MIS 13 (~610 ka until ~490 ka), although with higher amplitude variability in MIS 16 and MIS 15 than within the rest of the record (Fig. 5). From mid-MIS 13 until TV the records show opposite trends: coccolithophore productivity increases, whereas the CF Sr/Ca shows a decreasing trend. TV marks a very abrupt change in coccolithophore productivity, from high values to the lowest of the record. From that point to the end of the record in MIS10, coccolithophore productivity increases. Noteworthy are the higher CF Sr/Ca rations in MIS 12 (from ~470 to 440 ka) relative to those in the MIS 11 interglacial period (from TV until ~400 ka), despite the lower SST (~13 °C in MIS 12 compared to ~18 °C during interglacial MIS 11).

The glacial-interglacial pacing of the coccolithophore productivity record is usually characterized by an increase during glaciation, with higher variability and amplitude than during interglacial. Maxima occur in MIS 12 and, exceptionally, the beginning of MIS 15. Glacial MIS 14 and MIS 12 show higher average values in comparison with interglacial MIS 15, MIS 13 and MIS 11. Abrupt decreases occur found at TVI and TV, even though the amplitude of TVI is less than half that of TV. Lower values are found in MIS 15 and MIS 11 interglacials (Fig. 5a).

Coccolithophore productivity thus shows variability at both orbital and suborbital time scales with generally higher values during glacials (except during late MIS 16) and lower values during interglacials.

The TOC and total alkenones concentration records (Fig. 6a and b) reveal similar patterns, with low values and low amplitude oscillations in MIS 15, MIS 13 and MIS 9 contrasting with higher levels and higher amplitude oscillations in MIS 16, MIS 14 and MIS 12.

The CaCO₃ content (Fig. 6c) records lower values in MIS 16 (including a minimum of almost 30
and a steady and rapid increase at TVII. High values and a slight increasing trend are present from TVII to the beginning of MIS 12. The CaCO$_3$ content decreases steadily in MIS 12, with large oscillations and several decreases to almost 50\%.
Fig. 6 - Primary productivity proxies: a) total organic carbon (TOC) weight % (Stein et al., 2009; this study), b) total alkenones concentration (ng/g of sediment) (Stein et al., 2009; this study) c) calcium carbonate (CaCO$_3$) content based on XRF measurements (this study), d) Coccolith Dissolution Index (CDI) (this study): the closest to 1, the lower the likelihood of dissolution/ the better the preservation, e) nannofossil accumulation rate (NAR) (nannofossils cm$^{-2}$ kyr$^{-1}$) (Kulhanek, 2009), f) reconstructed coccolithophore productivity (and confidence interval) based on coccolith Sr/Ca ratios (this study). MIS and T as in Fig. 2.

4.2. Coccolith preservation and dissolution

Coccolith preservation is moderate to good in MIS 12 to MIS 10 (Kulhanek, 2009) and the calculated CDI indicates good preservation throughout the examined record to MIS 16 (Fig. 6d). CDI shows no correlation with the CF Sr/Ca or residual record, even in MIS 12, when corrosive southern sourced waters invaded the deep glacial North Atlantic (Thunell et al., 2002; Voelker et al., 2010) as suggested by the lower benthic carbon isotopic values at Site U1313 in MIS 12 and MIS 16 (Fig. 7a).
Fig. 7 - Ventilation and water mass time series: a) benthic foraminifera carbon isotope data ($\delta^{13}\text{C}_b$) (Voelker et al., 2010 and this study), b) benthic foraminifera oxygen isotope data ($\delta^{18}\text{O}_b$) (Stein et al., 2009; Voelker et al., 2010), c) and d) correspond to the relative abundance of $N. \text{pachyderma}$ at IODP Site U1313 (this study) and IODP Site U1314 (Alonso-Garcia et al., 2011), respectively, e) reconstructed coccolithophore productivity (and confidence interval) based on coccolith Sr/Ca ratios (this study).
4.3. Time-series analysis

We applied spectral analysis to look for statistically significant periodicities in the coccolithophore productivity record and found a robust precessional signal and two additional significant periodicities that are ~15 kyr for the CF Sr/Ca record (Fig. 8a) and ~9 kyr for coccolithophore productivity (Fig. 8b). The two significant periodicities, ~15 kyr and ~9 kyr, are consistently found despite applying different filtering and smoothing methodologies, which gives robustness to our findings (see Supporting Information). The periodicities detected in the coccolithophore productivity time series are not observed in the U$^{K, 37}$-based SST record (Fig. 8c), whereas the total alkenone concentration record exhibits periodicities close to 9 kyr but with lower significance (see Supporting Information). Additionally, all methodologies consistently reveal a small but significant peak at 2.6 kyr. This cyclicity has been found in other North Atlantic time series (e.g., Pisias et al., 1973). However, since it is near the lower detection limit (sample resolution is 700 years) and below the age model uncertainties (4 kyr), (Lisiecki and Raymo, 2005)), it is not discussed further.
Fig. 8 - Spectral power results in REDFIT: (a) for the coccolith Sr/Ca ratio time series and (b) for the coccolithophore productivity record. We also present the spectral power results for the $^{137}$SST (c), for comparison. All records were filtered in SPECTRUM to extract significant frequencies above 1/40kyr and 1/23 kyr, respectively. Bandwidth for all spectral power results is $1.12 \times 10^{-2}$. The red lines represent the significance level of 90% $\chi^2$ (peaks below this line correspondent to periodicities which are not significant).
5. Discussion

5.1. Coccolithophore productivity record

Culture studies have found that coccolith Sr/Ca may increase by 0.03 mmol/mol per °C rise in temperature (Stoll et al., 2002a; Müller et al., 2014). Given the modest variation of the CF Sr/Ca ratios for most of our record (Fig. 5b) and the consistent temperature variations in the range of 5 °C, the temperature-induced Sr/Ca variation could be about 0.15 mmol/mol. Moreover, during TV, temperature rose by almost 10 °C. Therefore, SST must be considered as a potential contributor to the CF Sr/Ca ratios. We removed the temperature effect (see 3.4 Calculation of residual Sr/Ca) and the resulting curve, the Sr/Ca residual (Fig. 5c), reveals a persistent temporal pattern not evident in the CF Sr/Ca ratios that we interpret to be dominated by coccolithophore calcification/growth rate and thus paleoproductivity.

Changes in the coccolithophore assemblage may also have an effect on the CF Sr/Ca. In our record there is a change in dominance from larger, more calcified species in MIS 16 – MIS 15 to abundant *Gephyrocapsa caribbeanica* in the rest of the record. However, coccolith assemblage appears to exert a minor influence on CF Sr/Ca in the modern ocean (Stoll and Schrag, 2000) and the specific coccolith carbonate estimations, shown in Fig. 4b, have inevitable but substantial errors associated (±50%) (Young and Ziveri, 2000). It seems thus unlikely that the coccolith assemblage changes affected significantly our proxy, but to address the possibility of the existence of a caveat (if any) the coccolithophore productivity record for MIS 16 – MIS 15 should be interpreted more carefully and regarded as a conservative estimate of coccolithophore productivity. Noteworthy is the fact that the *Gephyrocapsa caribbeanica* acme spans the studied interval and constitutes an advantage as it minimizes the CF Sr/Ca ratio bias due to coccolith assemblage changes.
5.2. Effect of the southernmost position of the frontal system on coccolithophore productivity at Site U1313

The positions of ocean frontal systems around Site U1313 change not only seasonally, but also throughout geological time. During glacial periods, the North Atlantic Polar and Arctic/subpolar Fronts migrated southward and several authors have suggested an almost east-west position of the Arctic Front (Wright and Flower, 2002; Alonso-Garcia et al., 2011; Rodrigues et al., 2017). The high coccolithophorid productivity belt also migrated southward (McIntyre et al., 1972; Villanueva et al., 2001) in pace with changes in the positions of these hydrographic fronts. This belt, currently located between 45º and 55º N, is associated with the convergence zone between the subpolar and subtropical gyres (Weeks et al., 1993), and may have moved as far south as 42º N during glacials (McIntyre et al., 1972; Villanueva et al., 2001).

These large migrations of the frontal systems and high productivity band likely impacted Site U1313 during glacial periods. During the most severe glacial periods, evidenced by the highest benthic oxygen isotopic values in the record (e.g., MIS 12; Fig. 7b), or the Heinrich events, Site U1313 might have seasonally shifted into the subpolar region, outside of the coccolithophore habitat.

If subpolar/polar surface waters reached Site U1313 during glacial periods, the extremely low temperatures could lead to the reduction or disappearance of the coccolithophore community due to loss of habitat (McIntyre et al., 1972). Today, coccoliths in surface sediments of the Norwegian-Greenland Sea (i.e. in the polar domain) are mainly restricted to areas beneath subpolar surface waters, whereas very low coccolith concentrations are found in sediments underlying the sea-ice covered Arctic and polar waters (Baumann et al., 2000). To test whether subpolar/polar surface waters reached our study site we use the percentage N. pachyderma record (Fig. 7c). N. pachyderma is the most abundant planktonic foraminifer species in polar
(perennially covered by sea ice) and Arctic (seasonally ice covered) waters (Johannessen et al., 1994; Kucera et al., 2005; Alonso-Garcia et al., 2011). Today, relative abundances of *N. pachyderma* higher than 65% are indicative of the Arctic Front (Johannessen et al., 1994), which separates Arctic surface waters from the subpolar surface waters. Except for one instance with 68% *N. pachyderma* at 433 ka (MIS 12), the relative abundance of *N. pachyderma* is lower than 65% at Site U1313. If we compare the relative abundance of *N. pachyderma* at Site U1313 (our study; Fig. 7c) to Site U1314 (Alonso-Garcia et al., 2011; Fig. 7d), located at 56° N, the northern site was under greater influence of Arctic and even polar waters for longer periods than Site U1313. Based on these observations, we conclude that the coccolithophore community was not heavily affected by the loss of habitat during the studied time period because the Arctic front did not reach as far south as Site U1313 (41° N), at least not within the temporal resolution of this study. However, there were periods when subpolar surface waters (% *N. pachyderma* ≥ 20%) influenced Site U1313.

5.3. Drivers of coccolithophore productivity

All phytoplankton productivity is controlled by a combination of variables, of which light intensity and nutrient availability are considered the most relevant (Barbosa, 2009). We investigated these controlling factors focusing first on the hydrographical changes affecting coccolithophore productivity at our study site.

5.3.1. Nutrient supply

Coccolithophore productivity is linked to nutrient availability (Brand, 1994; Balch, 2004; Marinov et al., 2010; Müller et al., 2017), which in the open ocean reflects circulation (Herbert and Sarmiento, 1991). Therefore, we first hypothesized that the observed periods of high
Coccolithophore productivity in our record reflect changes in regional hydrography that increased nutrient availability. This process could indeed explain the glacial – interglacial productivity pattern. In this scenario, the North Atlantic atmospheric and oceanic frontal systems shifted southward during cold periods (e.g., Alonso-García et al., 2011; Frank et al., 2011) and, as proposed by McIntyre et al. (1972), the nutrient-driven “high productivity band”, also shifted southward. Villanueva et al. (2001) examined productivity based on alkenone content at two North Atlantic sites located at 37º N and 43º N (Fig. 1). They explained the time discrepancy in several of the productivity events as a consequence of this high productivity band migration. This is consistent with our findings that suggest that Site U1313 (41º N) was under the influence of this “high productivity band” during glacials, enhancing coccolithophore productivity.

Dust delivery has also been suggested as a fertilization mechanism for oceanic productivity (e.g., Martin et al., 1990). Naafs et al. (2012) reconstructed aeolian input at Site U1313 based on the concentrations of long-chain n-alkanes and terrestrial plant waxes, which indicate increased North American dust input during cold periods as a consequence of the waxing and waning of continental ice sheets and increased westerly wind strength. Stronger winds over the surface ocean during colder periods could also increase mixing depth (Barton et al., 2003), enhancing nutrient replenishment to the surface.

In addition to the dominant pattern of higher productivity during glacials, our coccolithophore productivity record indicates substantial variability at higher frequencies (Fig. 8). Thus, despite the effect of frontal migrations, there must have been other processes, such as changes in insolation, modulating coccolithophore productivity at the studied site.
5.3.2. Insolation

Insolation intensity, which changes cyclically through geological time, is a result of the combined changes in Earth’s orbital parameters (eccentricity, obliquity and precession) (e.g., Berger, 1988; Laskar et al., 2004). It directly influences the amount of light and temperature conditions at the surface of the ocean, which in turn affect organisms behavior (Vallina and Simó, 2007). Since both light and temperature enhance photosynthesis, the modulation of insolation could affect coccolithophore productivity. This could be a direct effect or it could act by modulating the phenology of the phytoplankton at the studied site. Coccolithophores require light to photosynthesize. Therefore, increases in insolation should enhance coccolithophore productivity (Nimer and Merrett, 1993; Zhang, 2015).

Site U1313 is currently located in a transitional area (Fig. 1a) with a mid-latitude productivity regime generally characterized by two productivity peaks per year, one in spring and the other in autumn (Fig. 1c) (Lévy, 2005). If coccolithophores living in this area were to experience higher productivity in spring and autumn (6 months apart) throughout the Pleistocene, these higher production periods would have coincided with insolation peaks for those two seasons. As a result, we would expect the record to show a precessional (~23 kyr) and semi-precessional (~11.5 kyr) enhancement of productivity would be expected in the productivity record (Fig. 9a and b). However, in addition to the precessional signal, the coccolithophore productivity record contains significant periodicities at “unusual” frequencies of ~15 kyr and ~9 kyr (Fig. 8).
Fig. 9 - Theoretical coccolithophore community response to insolation forcing. Expected theoretical cyclicity for coccolithophore productivity: a) precessional (23 kyr), b) semi-precessional (11.5 kyr). Theoretical cyclicity found for coccolithophore productivity: c and f) 17.3 kyr, d) 17.3 kyr, e) 11.5 kyr, f) 11.5 kyr or g) 5.8 kyr. Season abbreviations: Sp = spring, Su = summer, Au = autumn. Each sine wave represents a theoretical curve of insolation for each season: red corresponds to spring, blue to summer and grey to autumn.

We then examine whether these periodicities could be an artifact of the age model. The age model was based on visual correlation of the Site U1313 benthic oxygen isotope record (Voelker et al., 2010) with the LR04 stack (Lisiecki and Raymo, 2005). The resolution of the benthic oxygen isotope record is higher than our coccolithophore productivity record and because both records are from the same archive, the age model should be free of artifacts due to
phase shifts or resolution. Due to the lag in propagation of the oxygen isotope signal throughout
the ocean, this age model contains an uncertainty of about 4 kyr (Lisiecki and Raymo, 2005), but
the dating of glacial cycles is robust and the uncertainty is less when considering durations.
Therefore, the inferred duration of our record (~310 kyr) is relatively robust. If the observed
productivity peaks in the high-frequency part of the spectrum reflect semi-precession, we should
observe about 30 such peaks throughout the record. However, we find 22 productivity peaks
(Fig. 10), implying that the identified periodicities cannot be reconciled with semi-precessional
forcing.

The $^{14}C$-based SST and the total alkenone concentration record do not reveal a 15 kyr
periodicity (Fig. 8c and Supporting Information). This unusual frequency is thus exclusive to the
coccolithophore productivity record. There is some evidence for similar high-frequency
variability in the TOC and total alkenone data (Fig. 6a and b), but this is only manifested during
glacials. During interglacials, both TOC and alkenone concentration are low and reflect poor
preservation of organic matter in the sediments, precluding a meaningful spectral analysis of the
records. Since there is no evidence for migration of the frontal systems around the studied site at
these high frequencies especially during the interglacials, we instead look at insolation forcing.
To better visualize these periodic components in the coccolithophore productivity, the record
was filtered at a 14 kyr band pass with a 20 kyr bandwidth to produce a Gaussian smoothed
curve (pink line in Fig. 10e). This facilitated a visual inspection of the position of the individual
productivity peaks with respect to monthly insolation (Laskar et al., 2004) over the studied
interval (Fig. 10).
Fig. 10 - Direct comparison between the coccolithophore productivity record (this study) with confidence interval (grey) and a Gaussian bandpass filter (magenta; frequency of 0.07 c/kyr and a bandwidth of 0.05 c/kyr), in comparison to the monthly insolation curves (at 41ºN) from Laskar et al. (2004). Each group of three curves represent a season and each letter the respective month, for example, dark green is March (M), green is April (A) and light green is May (M). Spring is in green tones, Summer in red tones and Autumn in purple tones. Winter insolation curves were not drawn because low insolation and low temperatures would not allow high coccolithophore production.
As mentioned above, the southward migration of the hydrographic fronts drove a
southward migration of the high coccolithophorid productivity belt (McIntyre et al., 1972;
Villanueva et al., 2001). We therefore hypothesize that the phenology of coccolithophore
productivity changed through time and depending on the productive months the resulting
coccolithophore productivity record resonated with insolation at different times of the year. In
Fig. 10, a color code identifies the season of each production peak to better visualize that during
warmer periods, such as MIS 15, MIS 13 and most of MIS 11 the peaks coincided with either
spring or autumn, whereas during cold periods, such as in MIS 14 and MIS 12, peaks coincided
with summer or autumn.

A comparison of the timing of productivity peaks to insolation reveals that during MIS
15, MIS 13 and MIS 11, productivity peaks coincided either with spring or autumn insolation
maxima. This is comparable to the present day, when coccolithophores are most productive in
spring and/or autumn (Fig. 1c). On orbital time scales, these productivity peaks are enhanced by
insolation, generating an approximate semi-precessional pacing pattern during interglacials. On
the other hand, we observe that during MIS 14 and MIS 12, coccolithophore productivity peaks
only coincided with summer/autumn insolation maxima (Fig. 10). This fundamental shift in the
productivity regime, from interglacial to glacial conditions, breaks the regularity in the
precessional forcing and induces non-intuitive unusual periodicities at 15 kyr and 9 kyr (similar
to the non-intuitive examples given in Fig. 8c to f). These glacial periodicities provide insight to
the origin of the regime shift. It reflects the southward migration of the frontal system, which
forces coccolithophores at Site U1313 to change their phenology such that they only bloom once
a year during the warm season, similar to what happens today in the subpolar North Atlantic
(Fig. 1b). The productivity regime at Site U1313 would thus change from a mid-latitude regime
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(similar to Fig. 1c) during interglacials to a subpolar regime (similar to Fig. 1b) during glacial periods. Such a model with variable phenology would result in two annual productivity peaks approximately 6 months apart, in spring/early-summer and late-summer/autumn during interglacials, whereas during colder periods, and especially during MIS 14 and MIS 12, only one growth season occurred during summer/autumn and the high nutrients/high insolation window for rapid phytoplankton growth was narrower than today.

In all scenarios, productivity peaked whenever insolation was at maximum for the appropriate growth season(s). Productivity peaks during interglacials are thus ~23 kyr and ~11.5 kyr apart, reflecting precession and semi-precession signals associated with the rapid growth seasons of spring and autumn. On the other hand, during glacial periods peaks are only ~23 kyr apart but shifted in phase by ~6 kyr from the interglacial pattern because the rapid growth season happens later in the year, in summer/autumn (Fig. 10). The studied interval spans a series of successive events (interglacial, glaciation, glacial, termination, etc.) and Fig. 10 demonstrates a phenology shift through time, with higher coccolithophore productivity matching insolation maxima during different seasons. It is this continuous phase shift that results in the observed apparent 15 kyr and 9 kyr periodicities. The continuous adaptation to the best conditions leads to changes in phenology as the timing between peak-growth months changed.

5.4. Comparison with other productivity proxies

Our inference that coccolithophore productivity was generally higher during glacial periods compared to interglacials is in line with evidence from other primary productivity proxies. Both TOC and total alkenone concentration data from the same site support enhanced primary productivity during glacial periods, recording higher values during MIS 16, MIS 14 and MIS 12 (Fig. 6a and b). This pattern of increased TOC accumulation during MIS 12 (and MIS 10) and low
accumulation during interglacial MIS 11 and MIS 13 was also observed further south at Ocean Drilling Program (ODP) Site 1063 on Bermuda Rise (Poli et al., 2012). At that site, δ¹³C of organic matter and benthic foraminifer assemblage data support enhanced glacial marine productivity and constant organic matter flux, partially through delivery of phytodetritus, to the seafloor (Poli et al., 2012). In contrast to the CF Sr/Ca and organic matter evidence, the NAR at Site U1313, spanning MIS 12 to MIS 11 (Fig. 6f; Kulhanek, 2009), reveals higher coccolith accumulation rates during MIS 11 than MIS 12, suggesting that coccolithophore productivity was higher during warmer MIS 11 than during glacial MIS 12. Similar observations based on high coccolith numbers during interglacials were made for the North Atlantic and Norwegian-Greenland Sea (e.g., McIntyre et al., 1972; Henrich and Baumann, 1999; Emanuele et al., 2015).

Conditions for both calcium carbonate and organic matter preservation are known to have changed significantly on glacial-interglacial time scales in the North Atlantic basin. The deep North Atlantic was filled by southern sourced waters during glacial periods (Raymo et al., 2004; Curry and Oppo, 2005; Voelker et al., 2010; Poirier and Billups, 2014) as deduced by very low benthic carbon isotopic values in the record from MIS 12 and MIS 16 (Fig. 7a). These southern sourced water masses are poorer in oxygen and richer in CO₂ and thus enhance the preservation of organic matter (Rullkötter, 2006) whilst promoting dissolution of calcium carbonate shells, such as coccoliths. Although there is a consistent decrease in carbonate (and coccolith) accumulation during glacial periods, our observations indicate that coccolith preservation was good to moderate throughout the studied period. This could explain the seemingly contradictory trends of TOC (and alkenone) concentration and CaCO₃ (and NAR) at the studied site (Fig. 6a, b, c, f).

Results from the Site 1063 study (Poli et al., 2012) shows that the increased TOC content in the glacial sediments is not purely due to enhanced preservation, but also indicates higher
productivity, supporting our CF Sr/Ca productivity record. Moreover, increased phytoplankton (dinoflagellates) productivity at DSDP Site 607/IODP Site U1313 during the glacial periods around the Plio/Pleistocene transition was also attributed to increased nutrient availability following changes in atmospheric circulation (Versteegh et al., 1996; Hennissen et al., 2017).

The varying extent of southern source water masses would have acted to enhance the preservation of organic matter during times of high productivity, whilst decreasing the preservation of coccolithophore carbonate. We explain the discrepancy between the TOC and NAR proxies at Site U1313 by the relatively small change in carbonate content, which implies that the site remained above the regional lysocline. Indeed, other sites in the North Atlantic, such as ODP Sites 980 and 984 and IODP Site U1314 (Ortiz et al., 1999; Channell and Raymo, 2003; Grützner and Higgins, 2010), at 2180 m, 1660 m and 2820 m water depth, respectively, registered up to 20% reduction in calcium carbonate content during glacial MIS 12. The lower amplitude of change in carbonate signal at Site U1313 (3426 m depth) must therefore also include a component of enhanced carbonate productivity, which was in reality much higher during the glacial at this site and buffered the effect of the more corrosive nature of the bottom water.

6. Conclusions

We use the CF Sr/Ca ratio as a proxy for coccolithophore growth rate and productivity to show that the North Atlantic transitional area was characterized by high-frequency variability in productivity. The dominant glacial-interglacial pattern is explained by changes in circulation and frontal system position that allow enhanced replenishment of nutrients to the surface ocean during glaciations and culminating during glacial maxima. High-frequency suborbital shifts show periodicities of 15 kyr and 9 kyr that are not consistent with orbital forcing. However, a
different pattern appears when glacials and interglacials are viewed separately, which reveals a dominant insolation forcing for each, but resonating with different phenology patterns. Thus, we conclude that coccolithophore productivity responded to the interplay between oceanic circulation and insolation. It is important to integrate this into model experiments to assess possible scenarios where coccolithophores may have played a significant role on orbital and suborbital changes in $p\text{CO}_2$. 
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Supporting Information for

Insolation forcing of coccolithophore productivity in the North Atlantic during the middle Pleistocene

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This Supporting Information provides supplementary figures 1 and 2 (Fig. S1 and Fig. S2). Fig. S1 shows the IODP Site U1313 core photos along the primary and secondary splice, respectively, and information on the age model and sedimentation rates for the studied interval. Fig. S2 illustrates the location of samples for the coccolith assemblage counts relative to the Sr/Ca ratio and Sr/Ca residual curves.

Additional Text S1 and S2 containing Fig. S3 to S7 focus on the validity of the time-series analysis and on the methodology and reasoning for use of specific software, respectively. Supplementary Fig. S3 to Fig. S7 contain relevant spectral power results that support the main scientific conclusions of the paper but are not essential to the conclusions.
**Figure S1.** IODP Site U1313 splices and age model: a) primary and b) secondary splices (core photos), c) Site U1313 δ¹⁸Oš (blue line; adjusted to Uvigerina δ¹⁸O level; Stein et al., 2009; Voelker et al., 2010) and d) LR04 δ¹⁸Oš (grey line; adjusted to Uvigerina δ¹⁸O level) (Lisiecki and Raymo, 2005), e) linear sedimentation rate (LSR, red line) and f) insolation at 41ºN (orange line) (Laskar et al., 2004). Red dashed lines indicate tie points between the Site U1313 record and the LR04 stack.
Figure S2. Location of coccolith assemblage samples: a) coccolith fraction Sr/Ca ratio results (mmol/mol), b) Sr/Ca residual curve; Red, orange and green dots indicate samples with high, intermediate and low Sr/Ca values, respectively; used for coccolith assemblage analyses.
Text S1. Time-series analysis validity

We here present the first coccolithophore paleoproductivity reconstruction for a mid-latitude area based on the coccolith fraction Sr/Ca ratio. Our record has the distinction of being from a geographical area that experienced abrupt temperature and ocean circulation changes. For example, the abrupt SST shift of approximately 10 °C during Termination V (MIS 12 to MIS 11) or the shifts in deep-water mass fluctuations from North Atlantic Deep Water to the more carbonate-corrosive Antarctic Bottom Water during glacial MIS 12.

Despite the abrupt climatic changes, the following arguments convinced us that the reconstructed relative coccolithophore paleoproductivity variations are neither an artifact nor an over-correction of the temperature changes, and hence the time-series analysis is valid.

1) We aim to reconstruct coccolithophore productivity qualitatively in order to investigate the factors controlling it. For that we needed a continuous proxy to run time-series analysis. We investigated periodicities in the paleoproductivity data related to different climate system forcing. The TOC or the alkenone records are not constant throughout the record; during warmer periods, the organic matter content is almost negligible. Thus, we started by analyzing the CF Sr/Ca data and the coccolithophore productivity. We found significant periodicities at approximately 23 kyr and 15 kyr in both records. We then analyzed the U$^{137}$-based SST record and the alkenone content (despite not being continuous) to look for periodicities similar to the periodicities found in the coccolithophore productivity record. This was to determine if the dominant periodicities were an artifact of the temperature correction. In fact, neither the U$^{137}$-based SST record nor the total alkenone concentration time-series analysis (Fig. S7a and b) show the 15 kyr periodicity found in the coccolithophore paleoproductivity data.

2) The alkenone content downcore can be used as a coccolithophore paleoproductivity proxy if there are no significant changes in the preservation/degradation of the organic matter through time, in the water column and in the sediment. However, a multiproxy approach is much more advisable than individual proxy analysis when reconstructing past conditions. Therefore, we also examined other commonly used productivity proxies, such as the nannofossil accumulation rate, total organic carbon, and total alkenone concentration and accumulation in the sediments. As stated in section 5.4 of the Discussion we combined the alkenone concentration, coccolith
preservation, coccolithophore paleoproductivity and carbonate content to conclude that coccolithophore productivity was relatively higher during glacials and lower during interglacials.

Therefore, despite similarities between the coccolithophore productivity curve and the $U^{137}K$-based SST record, there is no evidence that it inherited its periodic characteristics due to temperature correction. Also, the coccolithophore paleoproductivity record still carries the same strong signals for the same periodicities as the original curve. Therefore, we assume that the coccolithophore productivity is not an artifact of the temperature correction and has its own periodic characteristics, worthy of being analyzed and discussed.

Text S2. Time-series analysis results and reasoning

The time series analysis tested for statistically significant periodicities in the coccolithophore productivity record. First, harmonic analyses were used to look for orbital periodicities in the coccolithophore productivity record. To further emphasize the suborbital scale variability (namely, precession and semi-precession signals) and to reduce the signal-to-noise ratio of coccolithophore productivity, several smoothing and filtering techniques were used. We then extracted the longer orbital periodicities (eccentricity and obliquity signals) using SPECTRUM and we further used a Gaussian bandpass filter with a central frequency of 0.01 cycles/kyr (10 kyr) and a bandwidth of 0.067 cycles/kyr (14 kyr) and Kernel smooth estimates (Mudelsee, 2014) centered at 23, 19 and 14 kyr, respectively, for comparison. Both Gaussian and Kernel curves were subtracted from the coccolithophore productivity time series and the resultant curves analyzed in REDFIT (the resultant filtered time series are shown in Fig. S3 and S4).

In detail, to reduce the signal-to-noise ratio of coccolithophore productivity, several smoothing and filtering techniques, using different available software, were performed prior to the time series analysis:

a) the Analyseries package was used for smoothing and filtering with the that it will only analyze evenly spaced time-series; so the record was first re-calculated to an evenly spaced resolution;

b) SPECTRUM was used for preliminary analyses, such as harmonic analysis, smoothing and filtering;

c) the Kernel package (Mudelsee, 2014) was used for smoothing and filtering;

d) the REDFIT package was used for spectral analysis of all original and resultant time series.

SPECTRUM was also used to perform cross-spectral analysis of the coccolithophore productivity record and the atmospheric carbon dioxide reconstruction by Lüthi et al. (2008).
Figure S3. Original and filtered time series:

top) CF Sr/Ca ratio time series (grey) and smoothed curve (a) – b) (blue);
bottom) CF Sr/Ca ratio filtered time series with SPECTRUM through harmonic analysis at 189, 103, 70.7, 56.6, 40.4, 35.4 and 32.3 kyr (red).
Figure S4. Original and filtered time series:

a) Coccolithophore productivity (CPP) time series (grey) and smoothed curve (CPP – b)) (blue);
b) CPP filtered time series with SPECTRUM through harmonic analysis at 126, 94.3 and 70.55 kyr (red);
c) CPP time series (grey) and smoothed curve (CPP – d)) (blue);
d) CPP filtered time series with SPECTRUM through harmonic analysis at 189, 126, 94.3, 70.55, 62.9, 51.4, 43.6, 36.5, 32.3 and 29.8 kyr (red);
e) CPP time series (grey) and Gaussian curve produced in Analyseries (blue). The Gaussian bandpass filter used had a frequency of 0.01 c/kyr (10 kyr) and a bandwidth of 0.067 c/kyr (14 kyr);
f) CPP filtered time series (CPP – Gaussian curve) (red);
g) CPP time series (grey) and Kernel estimate smooth (dark blue) and correspondent lower and upper standard deviation (light blue lines) with a bandwidth of 14 kyr;
h) CPP filtered time series (CPP – Kernel estimate for 14 kyr) (red);
i) CPP time series (grey) and Kernel estimate smooth (dark blue) and correspondent lower and upper standard deviation (light blue lines) with a bandwidth of 19 kyr;
j) CPP filtered time series (CPP – Kernel estimate for 19 kyr) (red);
k) CPP time series (grey) and Kernel estimate smooth (dark blue) and correspondent lower and upper standard deviation (light blue lines) with a bandwidth of 23 kyr;
l) CPP filtered time series (CPP – Kernel estimate for 23 kyr) (red).
Figure S5. REDFIT spectral power results with 3 segments (50 % overlap) for each of the following time series:

a) CF Sr/Ca ratio (mmol/mol);

b) CF Sr/Ca ratio (mmol/mol) filtered with SPECTRUM through harmonic analysis at 103, 70.7, 40.4, 56.6, 332.3 and 35.4 kyr;
c) CPP;
d) CPP filtered with SPECTRUM through harmonic analysis at 126, 94.3 and 70.55 kyr;
e) CPP filtered with SPECTRUM through harmonic analysis at 189, 126, 94.3, 70.55, 62.9, 51.4, 43.6, 36.5, 32.3 and 29.8 kyr;
f) CPP filtered with Analyseries by a Gaussian smoothing with a central frequency of 0.01 c/kyr and a bandwidth of 0.067 c/kyr;
g) CPP filtered with Kernel package by a Kernel smoothing for a cyclicity of 14 kyr;
h) CPP filtered with Kernel package by a Kernel smoothing for a cyclicity of 19 kyr;
i) CPP filtered with Kernel package by a Kernel smoothing for a cyclicity of 23 kyr.
The red line defines the significance level of 90% Chi2 (the peaks below this line correspond to cyclicities that are not significant). Bandwidth for the results with time series divided in 3 segments is 0.010.
Figure S6. REDFIT spectral power results with 6 segments (50 % overlap) for each of the following time series:

a) CF Sr/Ca ratio (mmol/mol);

b) CF Sr/Ca ratio (mmol/mol) filtered with SPECTRUM through harmonic analysis at 103, 70.7, 40.4, 56.6, 332.3 and 35.4 kyr;

c) CPP;

d) CPP filtered with SPECTRUM through harmonic analysis at 126, 94.3 and 70.55 kyr;

e) CPP filtered with SPECTRUM through harmonic analysis at 189, 126, 94.3, 70.55, 62.9, 51.4, 43.6, 36.5, 32.3, and 29.8 kyr;

f) CPP filtered with Analyseries by a Gaussian smoothing with a central frequency of 0.01 c/kyr and a bandwidth of 0.067 c/kyr;

g) CPP filtered with Kernel package by a Kernel smoothing for a cyclicity of 14 kyr;

h) CPP filtered with Kernel package by a Kernel smoothing for a cyclicity of 19 kyr;

i) CPP filtered with Kernel package by a Kernel smoothing for a cyclicity of 23 kyr.

The red line defines the significance level of 90% Chi2 (the peaks below this line correspond to cyclicities that are not significant). Bandwidth for the results with time series divided in 6 segments is 0.020.
**Figure S7.** REDFIT spectral power results for the alkenone based sea-surface temperature curve ($U^\text{37}_{\text{alk}}$-based SST) and alkenone content records: a) $U^\text{37}_{\text{alk}}$-based SST record filtered with SPECTRUM through harmonic analysis (at 103, 162, 80, 38.7, and 46.5 kyr) with 3 segments (50% overlap); b) alkenone content record filtered with SPECTRUM through harmonic analysis (at 103, 232, 54.7, 77.4, 33.2, 61.9, 38.7 and 46.5 kyr) with 3 segments (50% overlap). The red line defines the significance level of 90% Chi2 (peaks below this line correspond to cyclicities that are not significant). Bandwidth for the results with time series divided in 3 segments is 0.01. The quasi-periodicities found are written on top of each spectral peak.