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**Changes in coccolith calcification under stable atmospheric CO<sub>2</sub>**

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# Changes in coccolith calcification under stable atmospheric CO<sub>2</sub>

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## Abstract

Coccolith calcification is known to respond to ocean acidification in culture experiments as well as in present and past oceans. Previous studies basically focus on changes in coccolith weight due to increasing CO<sub>2</sub> and the resulting changes in the carbonate system but pay little attention to the influence of other environmental factors. In order to untangle changes in coccolithophore calcification due to environmental factors such as temperature and/or productivity from changes caused by increasing pCO<sub>2</sub> and carbonate ion concentration we here present a study on coccolith calcification from the Holocene North Atlantic Ocean. The pre-industrial Holocene with its predominantly stable carbonate system provides the conditions for such a comprehensive analysis. For a realistic analysis on changes in major components of Holocene coccolithophores, the family Noelaerhabdaceae was selected, which constitutes the main part of the assemblage in the North Atlantic. Records of average coccolith weights from three Holocene sediment cores along a North–South transect in the North Atlantic were analysed. During the Holocene mean weight (and therefore calcification) of Noelaerhabdaceae (*E. huxleyi* and *Gephyrocapsa*) coccoliths decreases at the Azores (Geofar KF 16) from around 7 to 5.5 pg, but increases at the Rockall Plateau (ODP Site 980) from around 6 to 8 pg and at the Vøring Plateau (MD08-3192) from 7 to 10.5 pg. This amplitude of average weight variability is within the range of glacial/interglacial changes that were interpreted to be an effect of decreasing carbonate ion concentration. By comparison with SEM assemblage counts, we show that weight changes are partly due to variations in the coccolithophore assemblage, but also an effect of a change in calcification and/or morphotype variability within single species. Our results indicate that there is no single key factor responsible for the observed changes in coccolith weight. A major increase in coccolith weight occurs during a slight decrease in carbonate ion concentration in the Late Holocene at the Rockall Plateau and Vøring Plateau. Here, more favourable productivity conditions apparently lead to an increase in coccolith weight, either due to the capability of coccolithophore species, especially *E. huxleyi*, to adapt

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to decreasing carbonate ion concentration, or due to a shift towards heavier calcifying morphotypes.

## 1 Introduction

With the increasing anthropogenic influence on the carbon cycle by CO<sub>2</sub> emissions into the atmosphere over the past 250 yr, seawater carbonate chemistry changed due to the uptake of atmospheric CO<sub>2</sub> into the ocean (Doney et al., 2009). One result of the uptake is a decrease in seawater pH, a process known as ocean acidification (Raven et al., 2005). The impact of ocean acidification on calcifying organisms e.g. corals, molluscs and calcifying plankton, is one of the most actively followed marine research topics in recent years (e.g.: Gattuso et al., 1998; Riebesell et al., 2000; Fabry et al., 2008). A special focus lies on organisms that interact with the global carbon cycle. Among other calcifying plankton groups, particularly interesting are coccolithophores, which are one of the main producers of calcite in the oceans. Their small calcite scales, the coccoliths, form a large part of the carbonate flux from the surface to the deep ocean (Westbroek et al., 1993). As they can act as ballast in sinking organic aggregates, coccoliths enhance the vertical mass transfer of organic carbon and therefore have an influence on the biological carbon pump (Ploug et al., 2008). Variations in coccolith calcification change their weight and size, which affect the sinking velocity of the aggregates (Beaufort et al., 2007; Ziveri et al., 2007). This has an influence on the downward carbon and carbonate flux and consequently on the global carbon cycle (Rickaby et al., 2007). It is known that changing seawater carbonate chemistry influences coccolith calcification (Riebesell et al., 2000; Beaufort et al., 2011). Previous culture studies on different coccolithophore taxa reveal both species specific and strain specific optimum curve responses to changing carbonate chemistry (Langer et al., 2006; Krug et al., 2011). However, the most frequent response in recently conducted experiments is a decrease in coccolith calcification under future *p*CO<sub>2</sub> levels (Zondervan et al., 2002; De Bodt et al., 2010; Bach et al., 2012). A recent study on sediment sam-

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ples supports these findings by presenting the influence of changing CO<sub>2</sub> on coccolith calcification over the last 40 000 yr (Beaufort et al., 2011). The authors detected a decrease in calcification with declining carbonate ion concentration driven by the glacial to interglacial rise in CO<sub>2</sub> in different ocean basins. Interestingly in the same study, the authors observed a morphotype of the extant species *E. huxleyi* in Patagonian-shelf and Chilean upwelling waters that is able to calcify heavily in waters characterised by low carbonate ion concentrations. These findings were recently supported by the findings of Smith et al. (2012), who detected a seasonal dominance of a heavily calcified *E. huxleyi* morphotype in the Bay of Biscay under elevated CO<sub>2</sub> conditions. These results indicate that this morphotype may be adapted to a lower pH calcification optimum. Apart from seawater carbonate chemistry, other factors also have an effect on coccolithophore calcification. Environmental factors such as temperature (Grelaud et al., 2009), coccolithophore productivity (Beaufort et al., 2007; Flores et al., 2012) and salinity (Bollmann and Herrle, 2007) are suggested to have an influence on coccolith weight and size too. However, according to Beaufort et al. (2011) these factors play a minor role for coccolith calcification when the carbonate chemistry changes notably. Thus it can be expected, that during times of rather stable atmospheric CO<sub>2</sub> the influence of other environmental factors will be more prominent than the carbonate chemistry of the sea water. The scale of variability in coccolith calcification in an environment with only minor changes in the carbonate system is still unknown, as well as the consequences for the mean calcite mass of a coccolithophore community. For reliable predictions of future coccolith calcification under elevated CO<sub>2</sub> conditions predicted for the end of the century (Raven et al., 2005) it is necessary to study them in a natural environment with relatively constant CO<sub>2</sub> conditions. The minor changes in the carbonate system over the last 10 000 yr allow testing the influence of environmental conditions (temperature, coccolithophore productivity) on coccolithophore calcification. In our study, we focus on the coccolithophore family Noelaerhabdaceae as it dominates the coccolithophore assemblage in the Holocene North Atlantic and represents up to 84 % of the assemblage (e.g. Andruleit, 1995; Andruleit and Baumann, 1998; Schwab et al., 2012). The vari-

ability of single Noelaerhabdaceae coccolith weight was measured in three Holocene sediment cores along a North–South transect in the North Atlantic. The diverse trends and gradients of temperature, carbonate ion concentration and coccolithophore productivity in the three studied cores allow to assess which of the factors are reflected in coccolith weight and therefore in their calcification.

## 2 Material and methods

### 2.1 Material

Holocene sediment samples from three sediment cores from the North Atlantic areas were analysed. Piston core GEOFAR KF 16 was retrieved southwest of the Azores islands (37°99.90' N, 31°12.83' W) from a water depth of 3050 m (GEOFAR cruise; Richter, 1998). Additionally, a surface sediment sample from the same location (box-core GEOFAR KG 14) was analysed. OPD Site 980 (55°12.90' N, 14°14.20' W, 2179 m water depth) is located in the eastern North Atlantic at the Rockall Plateau and was taken during ODP Leg 162 (Jansen et al., 1996). The Calypso Square Core MD08-3192 was taken at 66°55.86' N, 007°33.92' E in 1010 m water depth in the eastern Norwegian Sea (Kissel et al., 2009) (Fig. 1).

### 2.2 Age models

The age model for core GEOFAR KF 16 was published by Schwab et al. (2012). The Holocene part of the age model of this core is based on accelerator mass spectrometer (AMS) data of planktonic foraminifera (*Globigerina bulloides*, *Globigerinoides ruber*). In addition, an alkenone SST record and a planktonic oxygen isotope record were correlated with the NGRIP oxygen isotope record. The age model for ODP Site 980 relies on AMS measurements of the benthic foraminifera *C. wuellerstorfi* (Oppo et al., 2006). We established an age model for MD08-3192 by graphically tuning red-green colour-scan data to the nearby core MD95-2011, using the software package Analyseries (Paillard

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et al., 1996). Significant peaks in the colorscan data at the end of the Younger Dryas, during the Mid-Holocene and Late Holocene were used as tie points. The age model of core MD95-2011 is based on AMS  $^{14}\text{C}$  dates of the foraminifera *Neogloboquadrina pachyderma* (Risebrobakken et al., 2003).

## 2.3 Methods

### 2.3.1 Sample preparation (smear slides), imaging and SYRACO weight measurements

A few milligram of sediment were taken with a toothpick, mixed with a drop of water on a glass microscope slide and smeared homogeneously on the slide. After drying quickly on a hot plate the sediment was fixed with 3–4 drops of the resin EUKIT and a cover slip. For scanning the smear slides a polarised light microscope (Leica DM6000B) with 1000x magnification was used. The microscope was equipped with a SPOT Insight black and white camera. Between 200 and 400 pictures of every sample were taken. The light of the Microscope bulb was continuously controlled to avoid a decrease in light intensity over time.

The automated recognition software for coccolithophores SYRACO (Beaufort and Dollfus, 2004) was used to identify and measure coccoliths. The software identifies and classifies coccoliths in the image files and returns output files containing coccoliths of a single species. In the output files, coccolith length and the grey level of every component pixel were measured. The sum of grey levels of a coccolith image was used to estimate coccolith weight. The brightness of coccolith calcite depends on its thickness, which can be expressed in an equation. After calibration to a known calcite standard (method after Beaufort et al., 2005) the summation of grey level of every single coccolith can be converted with an equation ( $\text{weight} = \text{grey level} \cdot 0.0016$ ) into the estimated weight of the coccolith in picogram. For each sample roughly between 100 and 3500 Noelaerhabdaceae coccoliths were measured, in total 89 160 single

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coccoliths. For a more detailed description of SYRACO see Beaufort et al. (2004 and 2005).

### 2.3.2 Carbonate chemistry, salinity, temperature and coccolithophore productivity

Alkenone Sea Surface Temperature data at the Azores is available from Schwab et al. (2012) and Repschläger et al. (in prep.). At the Rockall Plateau no published SST data were available for ODP Site 980, instead alkenone temperature data from site MD95-2015 (Marchal et al., 2002) were used as an indication. The SST data of MD95-2015 were compared to SST data from ODP Site 980 (Holtvoeth, unpublished) which confirm the general trend (with a difference of around 3 °C upwards) but slightly differ after 4 kaBP. Furthermore no SST data were obtainable for core MD08-3192, alkenone temperature from nearby site MD95-2011 were used (Calvo et al., 2002).

Coccolith accumulation rate has been successfully used to trace palaeoproductivity dynamics (Lototskaya et al., 1998; Stolz and Baumann, 2010; Schwab et al., 2012). Coccolith accumulation rates are available for the Azores from Schwab et al. (2012). Rockall Plateau coccolith concentrations base on SEM counts and were calculated into coccolith accumulation rates by using the bulk density (Jansen et al., 2005) and sedimentation rate of ODP Site 980 using the equation of Van Kreveld et al. (1996). Vøring Plateau coccolith concentrations were provided by Giraudeau (MD95-2011, unpublished) and calculated into coccolith accumulation rates by using the sedimentation rate and bulk density of sediment core MD95-2011 (Bassinot and Labeyrie, 1996). Carbonate ion concentrations at the coring sites were calculated with the program CO2Sys (Lewis and Wallace, 1998). Salinity, temperature, total alkalinity and  $p\text{CO}_2$  were used as input parameters. Taylor Dome Ice Core data were used for atmospheric  $\text{CO}_2$  (Indermühle et al., 1999), total alkalinity was calculated using the equation of Lee et al. (2006). Salinity was reconstructed from  $\Delta\delta^{18}\text{O}$ , using the equation of Duplessy et al. (1991). For the calculation of  $\Delta\delta^{18}\text{O}$ ,  $\Delta\delta^{18}\text{O}_{\text{seawater}}$  was derived to correct the

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global sea level effect, and  $\delta^{18}\text{O}_{\text{ice volume}}$  was calculated after Waelbroeck et al. (2002). At the Rockall Plateau, salinity estimates from the adjacent core NA87-22 (Duplessy et al., 2005) were used. At the Azores and the Vøring Plateau salinity was calculated from  $\Delta\delta^{18}\text{O}$ , which bases on the data Geofar KF 16 from Schwab et al. (2012) and Repschläger et al. (in prep.) and MD95-2011 from Risebrobakken et al. (2003).

### 3 Palaeoceanographic changes during the Holocene

Sediment core Geofar KF 16 is positioned southwest of the Azores Islands, at the northern rim of the subtropical gyre (Richter, 1998). The northeastern boundary of the subtropical gyre is defined by the Azores Current System with the corresponding Azores Front (Klein and Siedler, 1989; Rogerson et al., 2004). The Azores Front separates two different productivity regimes: low primary production in the subtropical gyre in the south, and nutrient rich conditions in the north (Schwab et al., 2012). At the coring site, enhanced productivity during the early Holocene is followed by a shift to modern oligotrophic conditions around 6 kaBP. The productivity changes due to a northward shift of the Azores Front in the late Holocene (Schwab et al., 2012). Sea surface temperature (SST) at the coring site is around 20 °C in the early Holocene, decreases to 17.8 °C at 8.2 kaBP and stabilises after 8 kaBP to modern conditions of 18.5–19.5 °C.

OPD Site 980 is located in the North Atlantic at the eastern edge of Rockall Plateau, in the high accumulation area of the Feni Drift, which is deposited along the northwestern flank of the Rockall Trough (Jansen et al., 1996). The Rockall Plateau is mainly influenced by Western North Atlantic water of the North Atlantic Current and its local northerly flowing Rockall–Hatton Branch, carrying warm and salty water. Eastward of the Rockall Plateau, the warmer, more saline and less stratified Slope Current flows into the Rockall Trough (Hansen and Østerhus, 2000; Pollard et al., 2004). This current belongs to East North Atlantic Water and origins in the Bay of Biscay (Read, 2001). Between 7 and 5.4 kaBP, a reorganisation of surface circulation patterns in the northeastern North Atlantic occurred due to decreasing summer insolation and the end of

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meltwater influence. The reorganisation resulted in a weaker North Atlantic current and a stronger influence of the Slope Current after 5–6 kaBP (Solignac et al., 2008). These regional changes are reflected in an increase of alkenone SST at ODP Site 980 between 3.5 ka and 2 ka and a following decrease (J. Holtvoeth, unpublished data, personal communication, 2013) and explain the opposing SST trend to site MD95-2015 after 3.5 kaBP. The coccolithophore productivity at ODP Site 980 is highly fluctuating over the entire Holocene with highest rates in the early and late Holocene.

Core MD08-3192, taken from the Vøring Plateau in the eastern Norwegian Sea is influenced by the Norwegian Atlantic Current, an extension of the North Atlantic Current (Andersson et al., 2010). Most of this water inflow originates from the slope current, carrying warm and saline water into higher latitudes (Blindheim and Østerhus, 2005). During the early Holocene, the North Atlantic current increased in strength (Birks and Koç, 2002), warmest sea surface conditions during the Holocene occurred in the early Holocene until approximately 6 kaBP (Berner et al., 2011). During the middle and late Holocene SST decreased to present-day conditions, synchronous to decreasing summer insolation (Calvo et al., 2002). Coccolithophore productivity rates at the Vøring Plateau increased during the entire Holocene and reached a maximum peak between 3 and 4 kaBP (Giraudeau et al., 2010).

#### 4 Coccolithophore family Noelaerhabdaceae

In our examined sites the coccolithophore family Noelaerhabdaceae includes *Emiliana huxleyi* and *Gephyrocapsa*. Both coccolithophore taxa in our study can be classified into different morphotypes and species. The Holocene *Gephyrocapsa* complex consists of a number of different species with frequencies dependent on the location. *Gephyrocapsa muelleriae* is highly abundant in the North Atlantic, in a preferred temperature range of 12–18 °C (Giraudeau et al., 2010) and often used as a cold water indicator (Weaver and Pujol, 1988).

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The small species *Gephyrocapsa ericsonii* and *Gephyrocapsa ornata* have a preference for high nutrient contents and less saline surface water conditions (Boeckel et al., 2006), but are less abundant in our examined sites, especially in the two northernmost. *Gephyrocapsa oceanica* favours high nutrient concentrations and warmer waters (Kleijne et al., 1989; Bollmann et al., 1997). It is a minor taxa in our sites due to its distribution in lower latitudes (Ziveri et al., 2004). The cosmopolitan coccolithophore species *E. huxleyi* has an extensive genetic and morphologic diversity with diverse environmental tolerances (Medlin et al., 1996; Young, 2003) and dominates the assemblage in our examined sites. In the Holocene North Atlantic, *E. huxleyi* can be separated into different types, regarding coccolith size and weight. Coccoliths < 4 μm are highly abundant in Holocene samples while coccoliths > 4 μm, which serve as a cold water indicator, are more common in glacial sediments and decrease during the deglaciation (Termination I) (Colmenero-Hidalgo et al., 2002; Flores et al., 2010). Recently, Smith et al. (2012) report on increasing abundance of a heavily calcified *E. huxleyi* morphotype in the North Atlantic (Bay of Biscay) during winter, when pH and CaCO<sub>3</sub> saturation are lowest. These findings support the results of Beaufort et al. (2011), who observed a highly calcified *E. huxleyi* morphotype (R-type), adapted to waters with low pH.

Regarding the mean coccolith weight of Noelaerhabdaceae, the different response of coccolithophore species and their morphotypes to environmental factors should be taken into account. A major abundance shift of one species or morphotypes can have an influence on the mean weight of Noelaerhabdaceae coccoliths.

## 5 Results

### 5.1 Holocene Noelaerhabdaceae weight trends

Mean Noelaerhabdaceae coccolith weight in sediment core Geofar KF 16 (Azores) shows a two-part trend during the Holocene (Fig. 2a). Characterised by significant oscillations over the entire Holocene, the mean coccolith weight record fluctuates around

7 pg in the early and middle Holocene until 6 kaBP, and subsequently decreases to values of less than 6 pg in the late Holocene. The same change can be observed in the relative abundance of Noelaerhabdaceae coccolith weight classes (Fig. 2a). During the early and middle Holocene a relatively broad weight range reaches high relative abundance. In the late Holocene the range narrows and a distinct maximum between 2 and 3 pg is observed.

At the Rockall Plateau mean Noelaerhabdaceae coccolith weight fluctuates around 6 pg during the early, middle and the beginning of the late Holocene, followed by an increase to 8 pg after 3.5 kaBP in the late Holocene (Fig. 2b). The relative abundance of Noelaerhabdaceae coccolith weight classes shows a maximum of light coccoliths between 3 and 5 pg in the early and middle Holocene (Fig. 2b). In the late Holocene the maximum of light coccoliths is less pronounced and narrows to 2.5 and 4 pg, paralleled by an increase in the abundance of heavier weight classes. From 1 kaBP onwards, the maximum of light coccoliths further flattens, and simultaneously the weight classes extend to heavier values.

At the Vøring Plateau mean Noelaerhabdaceae coccolith weight increases with a range of fluctuations during the entire Holocene from around 7 to more than 10 pg. The weight increase is rather slight until 3 kaBP and notably stronger afterwards (Fig. 2c). The relative abundance of Noelaerhabdaceae weight classes shows a narrowing maximum of light coccoliths from 2–4.5 pg in the early Holocene to 2–3.5 pg in the late Holocene (Fig. 2c). From 1.2 kaBP onwards, the maximum of light coccoliths is less pronounced. The relative abundance of heavier weight classes is high over the entire Holocene.

## 5.2 Carbonate ion concentration

Despite the rather stable atmospheric CO<sub>2</sub> conditions, the carbonate ion concentration in all studied cores decreases over the Holocene (Fig. 3). At the Azores carbonate ion concentration is highest. It decreases by about 30 μmol kg<sup>-1</sup> SW over the Holocene, from more than 260 to 230 μmol kg<sup>-1</sup> SW. At the Rockall Plateau the carbon-

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ate ion concentration is strikingly lower and decreases by  $15 \mu\text{mol kg}^{-1}$  SW from 200 to  $185 \mu\text{mol kg}^{-1}$  SW. The carbonate ion concentration at the Vøring Plateau represents the highest decrease of  $45 \mu\text{mol kg}^{-1}$  SW from 225 to  $180 \mu\text{mol kg}^{-1}$  SW from the early to the late Holocene, with a slight increase from 2.5 kaBP onwards to  $190 \mu\text{mol kg}^{-1}$  SW.

## 6 Discussion

### 6.1 Comparison with previous studies

The decreasing coccolith weight trend of Noelaerhabdaceae observed at the Azores is in line with results from previous studies (Beaufort et al., 2011), see Fig. 4. In one site of the data set of Beaufort et al. (2011, Supplement), the authors studied a core near the Azores (SU09-08) covering the Holocene, and recognised a decrease in coccolith mass of the family Noelaerhabdaceae of around 0.5 pg. Our own data from the Azores (Geofar KF 16) confirms this trend and shows a decrease of about 1 pg for Noelaerhabdaceae coccolith mean weight (Fig. 4). It should be mentioned that the Noelaerhabdaceae weight of Beaufort et al. (2011) is represented by five data points and is therefore able to reflect the mean trend but not the short-term changes of coccolith weight. Therefore the mean coccolith weights of sediment core SU09-08 and Geofar KF 16 are not exactly the same but reflect the same decreasing trend.

The studied sites from Rockall and Vøring Plateau show some different developments of Noelaerhabdaceae coccolith weights (Fig. 4). At both sites the weight and the general variation in weight is rather comparable in the early and middle Holocene and increases during the late Holocene.

According to Beaufort et al. (2011) decreasing carbonate ion concentration affects coccolithophore calcification and explains the decrease in coccolith weight in their results. In our studied sites and in the results of Beaufort et al. (2011) the carbonate ion concentration decreases between 10 and  $45 \mu\text{mol kg}^{-1}$  sea water (Fig. 3). Despite

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the decreasing trend in all sites, the coccolith weight reacts differently and leads to the assumption that other factors have a stronger influence on mean Noelaerhabdaceae coccolith weight in the Holocene North Atlantic. Possible factors that have an influence on the mean weight are other environmental factors as the sea surface temperature and coccolithophore productivity or changes within the assemblage of Noelaerhabdaceae.

## 6.2 The influence of assemblage shifts within the Noelaerhabdaceae

Weight changes of Noelaerhabdaceae due to assemblage shifts could be either result from changes in the relative abundance of differently calcifying species and/or their individual morphotypes within Noelaerhabdaceae or changes in the weight of species and/or their morphotypes within the Noelaerhabdaceae.

To improve the identification and quantification of our results we compared the Noelaerhabdaceae mean weights to given SEM counts of our studied cores or nearby cores. According to SEM counts of Schwab et al. (2012), the family Noelaerhabdaceae at the Azores consists of coccoliths from the species *E. huxleyi*, *G. muelleriae*, few *G. ericsonii* and *G. ornata* and a very small number of *G. oceanica* (Fig. 5). At the Rockall Plateau, Noelaerhabdaceae counts from ODP Site 980 include primarily *E. huxleyi* and *G. muelleriae* and few *G. oceanica* and *G. ericsonii* (Fig. 6). At the Vøring Plateau, no SEM counts for the entire Holocene were available for MD08-3192, therefore a comparison to coccolith counts of Andruleit (1995) from a nearby core (GIK 23071) is used as an indication (Fig. 7). At this site the family Noelaerhabdaceae consist of *E. huxleyi* and *G. muelleriae*, other coccolithophores of this family are not mentioned, and in all probability their number is less than 1 % and not worth considering.

In all three SEM counts of Noelaerhabdaceae, the assemblage considerably changes over the Holocene. In general, related to the main part of the assemblage, the relative abundance of the lighter species *E. huxleyi* increases by around 30 %, while the heavier *G. muelleriae* decreases in the same order. Interestingly, these changes are not reflected in the mean weight of the studied sites, not even the strong decrease of *G. muelleriae* at the Vøring Plateau between 7–8 ka BP. Therefore it seems very likely that

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the species itself change their weight. This could be caused by changes in the weight of *E. huxleyi* or *G. muelleriae* or both. Another explanation is a shift in the abundance of e.g. a heavily calcifying morphotype of *E. huxleyi* or *G. muelleriae* or both.

As verification we examined the uppermost sediment sample of the Vøring Plateau, with the highest Noelaerhabdaceae mean weight of all cores, under the SEM. Almost all coccoliths belong to the species *E. huxleyi* and a considerable number is heavily calcified. At this site it is very likely that the heavily calcifying morphotype increases the mean Noelaerhabdaceae weight. Our results do not support the high number of *G. muelleriae* reported in light-microscopic counts of Giraudeau et al. (2010), which show an increase of *G. muelleriae* at the Vøring Plateau after 2 kaBP. In our SEM counts we detected a very low abundance of around 1 % *G. muelleriae*.

### 6.3 Environmental factors

Based on our results, the individual response of single coccolithophore species and most likely their morphotypes is primarily responsible for changes in Noelaerhabdaceae weight. Hence, it is necessary to consider the factors that have an influence on species weight or changes in the abundance of their morphotypes. It is known that different coccolithophore species or morphotypes are adapted to individual environmental conditions (Bollmann, 1997; Henderiks et al., 2012). This might explain the implication of Beaufort et al. (2011) that coccolith weight in the North Atlantic and South Indian Ocean differ from tropical settings, especially during the Last Glacial Maximum, where coccolith weight displays a broad weight range but is not in line with the trend of coccolith weight from the tropical stack. Therefore it is not as simple as proposed to consider one main factor as for instance the carbonate system as the key factor for changes in coccolith weight especially not for the North Atlantic that deviates from the tropical or global trend. In the data set of Beaufort et al. (2011), temperature, productivity and salinity are also correlated to coccolith calcification, but weaker than CO<sub>2</sub> or carbonate ion concentration. This already indicates that other factors than carbonate ion concentration are important for coccolith calcification.

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### 6.3.1 Temperature

Sea surface temperature (SST) in our examined sites decreases over the entire Holocene less than 2 °C (Figs. 8c, 9c, 10c) and is unlikely to have a strong influence on Noelaerhabdaceae mean coccolith weight. Previous studies present indications for an influence on changes in SST on the abundance of coccolithophore species and their morphotypes or on their calcification, but with considerably higher temperature gradients (Hagino et al., 2005; Henderiks et al., 2012; Bach et al., 2012). In addition, studies on correlations between temperature and calcification rates of *E. huxleyi* showed different results (Langer et al., 2007; de Bodt et al., 2010). Beaufort et al. (2007) concluded that there is no global relationship between SST and the degree of *E. huxleyi* calcification. The influence of SST on *E. huxleyi* morphotypes is even more confusing due to its high morphologic and genetic diversity with different temperature tolerances (Young et al., 2003; Hagino et al., 2011) and it seems that the same morphotype can react differently. A heavily calcified *E. huxleyi* morphotype is reported to increase in abundance when SST is higher (Beaufort and Heussner, 2001; Grelaud et al., 2009), contrary to the results of Smith et al. (2012) where this morphotype increases during winter in the Bay of Biscay. For *Gephyrocapsa* only little is known about changes in calcification rate induced by temperature variability. Admittedly, the distribution of the different *Gephyrocapsa* morphotypes in the Holocene is longitudinal, the larger type (*G. oceanica*) occurs in warmer waters (Bollmann, 1997).

Due to the different response of species and morphotypes to SST, it is difficult to make a general statement for the coccolithophore family Noelaerhabdaceae to changes in SST. The slight decrease in temperature in our sites over the Holocene is unlikely to influence the calcification of coccoliths. More likely is the influence of morphotypes, which are adapted to different temperature conditions and therefore occur in different abundances in our sites. As detected by Flores et al. (2010), the abundance of the *E. huxleyi* cold water type with coccoliths > 4 µm increases with higher latitudes and reaches a number of 1–5 % at Vøring Plateau. The opposite trend is found in the

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distribution of *G. oceanica* of our studied sites. The abundance record decreases from less than 5 % at the Azores to around 1 % at Rockall Plateau and is probably absent at Vøring Plateau. Both coccolithophores could have an influence on the mean Noelaerhabdaceae coccolith weight, but the low number of 1–5 % might be too small to have significant effects on the average weight.

### 6.3.2 Carbonate ion concentration

The atmospheric CO<sub>2</sub> concentration is rather stable with a slight increase in the Holocene. Despite these stable atmospheric CO<sub>2</sub> conditions, the rate of CO<sub>2</sub> uptake into the ocean depends on parameters e.g. SST and salinity. As a result, the carbonate system in the oceans differs regionally (Zeebe & Wolf-Gladrow, 2001) and can show a strong decrease as in our results at Vøring Plateau within rather stable CO<sub>2</sub> conditions.

The decrease in carbonate ion concentration of around 30 μmol kg<sup>-1</sup> in our results at the Azores might have an influence on coccolith mean weight (Fig. 8b), but here the carbonate ion concentration presents the highest values of all three studied sites, therefore the basic conditions for coccolithophores should be more favourable than at the Rockall or Vøring Plateau. At the Rockall Plateau the decreasing trend in carbonate ion concentration of around 10 μmol kg<sup>-1</sup> sea water over the Holocene might be too small to have a large influence on coccolith calcification (Fig. 9b). At the Vøring Plateau, the decrease in Holocene carbonate ion concentration is relatively prominent (about 45 μmol, Fig. 10b) and is even stronger than at the Azores, but the increasing coccolith weight does not confirm the negative influence of carbonate ion concentration on the weight. Therefore there is no uniform trend of Noelaerhabdaceae weight at the three different sites, and a general influence of decreasing carbonate ion concentration in the range of 10–45 μmol on coccolith weight cannot be observed. This indicates that the carbonate system can not be the main factor having influence on the mean coccolith weight in the Holocene North Atlantic.

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### 6.3.3 Coccolithophore productivity

The coccolithophore productivity decreases northwards in our examined sites in absolute numbers. The relative trends are different between the sites over the Holocene (Figs. 8c, 9c, 10c). At the Azores, coccolithophore productivity is highest. Beginning with the onset of a northward shift of the Azores Front and the following oligotrophic conditions after 6 kaBP (Schwab et al., 2012) the mean coccolith weight starts decreasing, suggesting a possible coupling between coccolithophore productivity and coccolith calcification. Similarly, at the Vøring Plateau, where absolute coccolithophore productivity is 2 to 3 orders of magnitude lower, an overall increase in coccolithophore productivity over the entire Holocene is paralleled by the increasing Noelaerhabdaceae coccolith weight. At the Rockall Plateau the coccolithophore productivity is on the same level as at the Vøring Plateau, but relatively stable. Here, only a slight increase in coccolith productivity is observed during the Late Holocene when coccolith weight is increasing markedly, and coccolithophore productivity peaks are only slightly reflected in the mean weight. This may be caused by undersampling of the mean coccolith weight data, which could exclude short-term fluctuations from being detected.

Previous studies have shown the influence of enhanced coccolithophore productivity on coccolith weight. The weight of *E. huxleyi* increased during blooms and accordingly during times with high coccolithophore production (Beaufort et al., 2007). In addition Engel et al. (2005) observed an increase in *E. huxleyi* coccolith weight by 25 to 50% during blooms in mesocosm experiments after adding nutrients. Therefore, productivity plays a major role in coccolith calcification and is probably rather prominent in our study because CO<sub>2</sub> variability is low during the Holocene. Considering the environmental factors in all three sites, the main trends of temperature and carbonate ion concentration are rather similar. The only distinct difference of the studied environmental factors is the coccolithophore productivity, which seems to have an influence on mean Noelaerhabdaceae coccolith weight. As the absolute values in coccolithophore productivity are extremely different between the Azores and the two northern sites, it is

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have a large influence on the total coccolithophore carbonate production. Therefore, future studies should focus on assemblage and morphotype response to carbonate system changes.

## 7 Conclusions

5 The dominant coccolithophore family Noelaerhabdaceae shows a strong variability in mean coccolith weight during rather stable CO<sub>2</sub> conditions of the pre-industrial Holocene in the North Atlantic. The recently debated negative influence of decreasing carbonate ion concentration on coccolithophore calcification could not be detected for a small decrease of 10 to 45 μmol kg<sup>-1</sup> SW. Our results show weight changes during  
10 the Holocene of the same amplitude than previously reported for the CO<sub>2</sub> increase of the last glacial to interglacial change. Variability in Holocene Noelaerhabdaceae coccolith weight in a natural system of the North Atlantic is hardly driven by the carbonate system as a main reason. We show that in the absence of strong CO<sub>2</sub> variability in the North Atlantic coccolithophore productivity has a substantial influence on Noelaerhabdaceae coccolith weight. Favourable environmental conditions such as high coccolithophore productivity lead to increasing weight, either due to increasing calcification or an abundance shift to heavily calcifying morphotypes, even during times of decreasing carbonate ion concentration of 45 μmol kg<sup>-1</sup> SW over the Holocene. Differences in nutrient or productivity settings between the sites are likely influencing the response of  
15 Noelaerhabdaceae coccolith weight. The high natural variability of coccolith weight during the Holocene raises the question, whether future changes in the carbonate system of the oceans will have a positive or negative effect on coccolithophore calcification.

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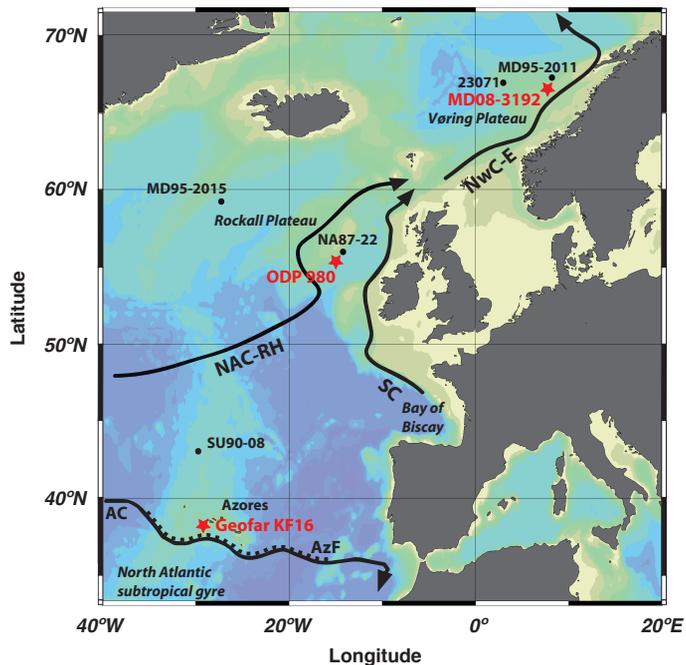
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**Fig. 1.** Core position and main oceanographic features: red stars mark the location of the studied sediment cores, black dots mark the position of other locations providing data for calculations of the carbonate system or coccolith counts discussed in the text. Black arrows show major ocean surface currents: North Atlantic Current Rockall–Hatton branch (NAC-RH), Slope Current (SC), eastern branch of the Norwegian Current (NwC-E), Azores Current (AC) with the corresponding Azores Front (AzF) figured as black dashed line. The map was designed with the ODV software by R. Schlitzer (Ocean Data View software, 2010, <http://odv.awi.de>).

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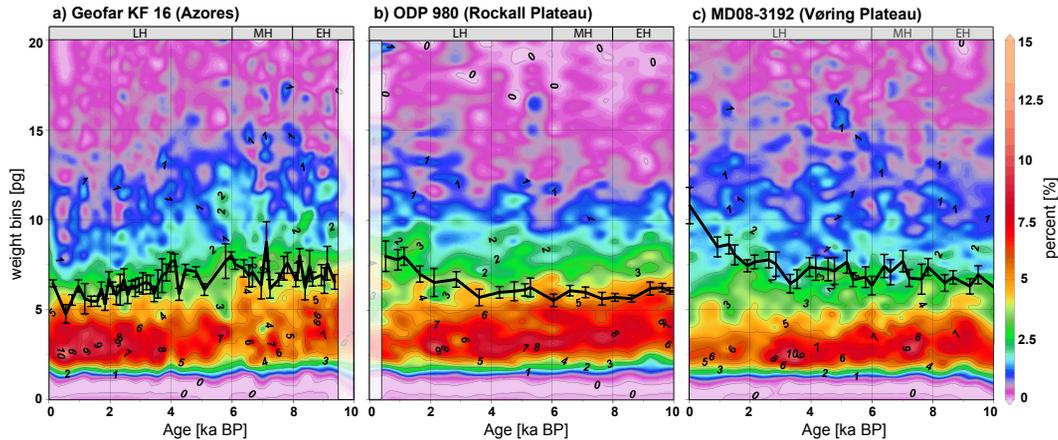
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**Fig. 2.** (a) Azores, core Geofar KF 16 (b) Rockall Plateau, ODP Site 980 (c) Vøring Plateau, core MD08-3192. Abundance of Noelaerhabdaceae coccoliths within weight bins (colours) and Noelaerhabdaceae mean coccolith weight (black line). Error bars indicate 95 % confidence intervals of the mean weight. Abbreviations: early Holocene (EH), middle Holocene (MH), late Holocene (LH).

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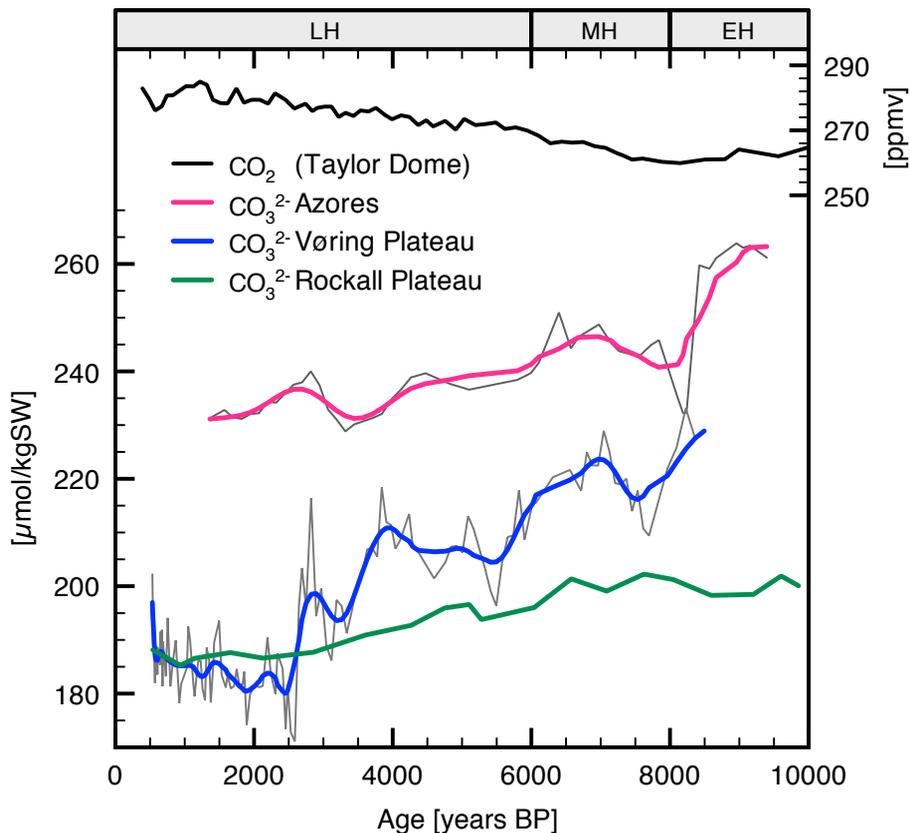
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**Fig. 3.** Holocene carbon dioxide concentration (black line), Holocene carbonate ion concentration of Azores (red line), Rockall Plateau (green line) and Vøring Plateau (blue line). Bold lines are smoothed (by factor 4), grey thin lines original data.

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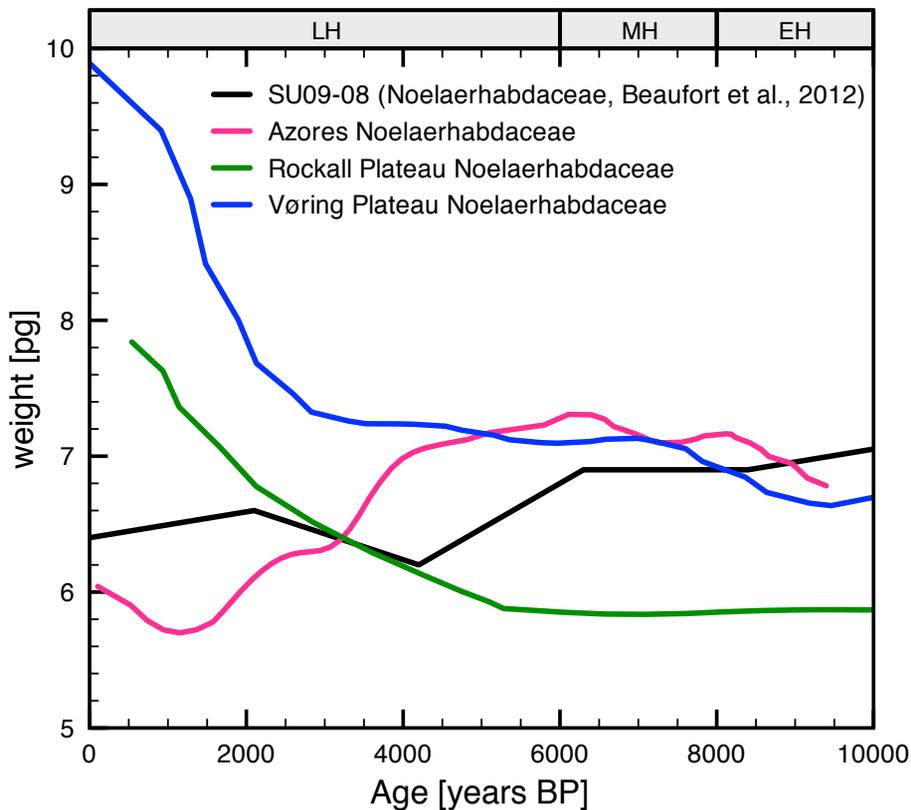
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**Fig. 4.** Noelaerhabdaceae coccolith weights from core SU09-08 (black line, Beaufort et al., 2012) in comparison to Noelaerhabdaceae smoothed mean weight record from the Azores (red line), Rockall Plateau (green line) and Vøring Plateau (blue line).

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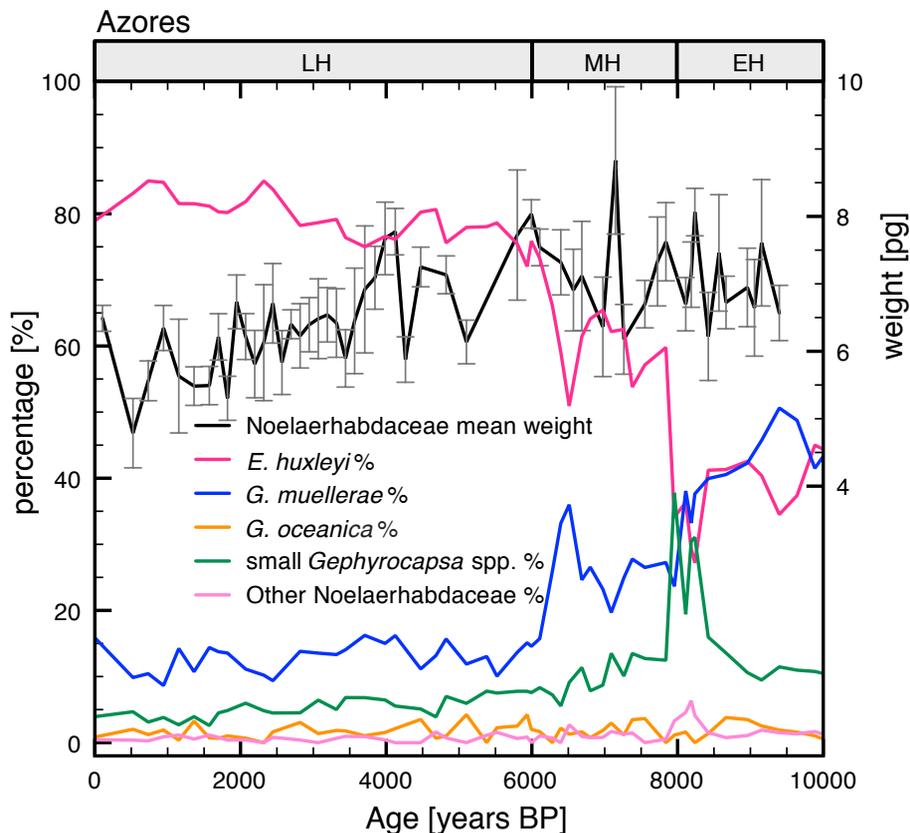
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**Fig. 5.** Relative abundance of Noelaerhabdaceae species at the Azores from sediment core Geofar KF 16 over the Holocene (Schwab et al., 2012): *E. huxleyi* (red line), *G. muellerae* (blue line), *G. oceanica* (orange line), small *Gephyrocapsa* (green line) and other Noelaerhabdaceae (light red line) in comparison to the Noelaerhabdaceae mean coccolith weight (black line).

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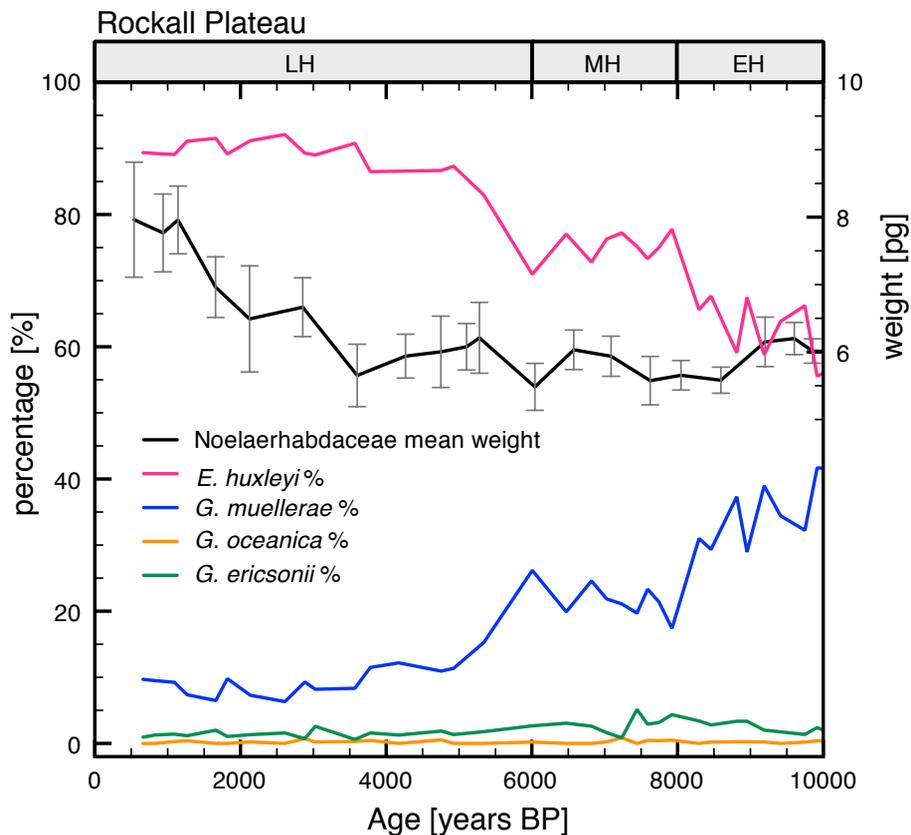
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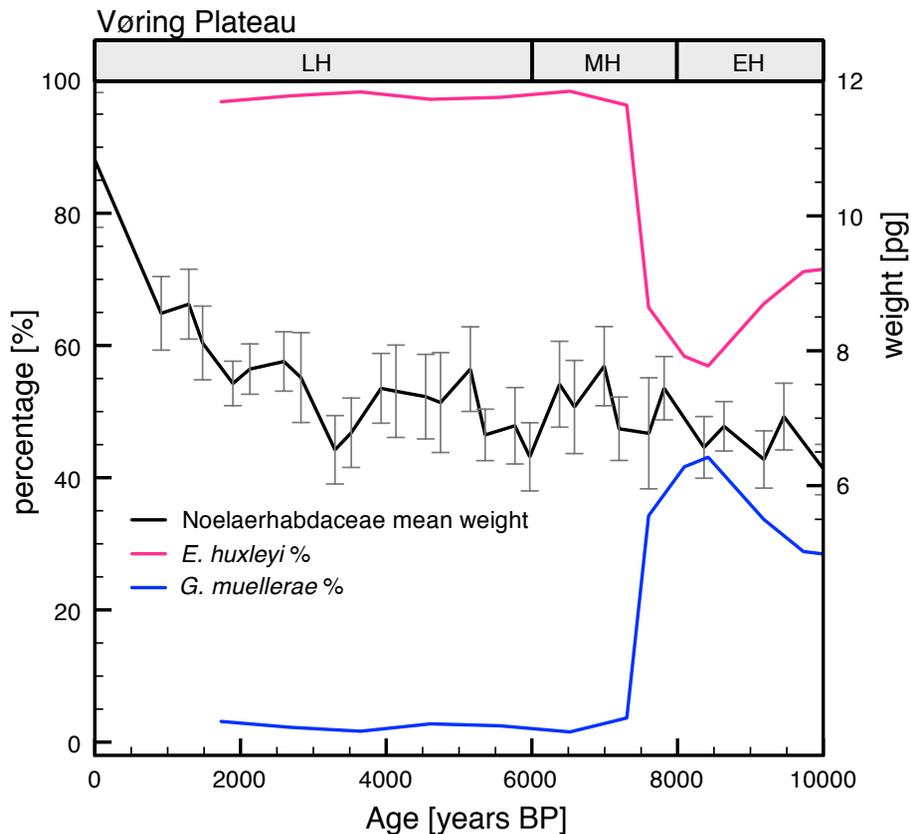
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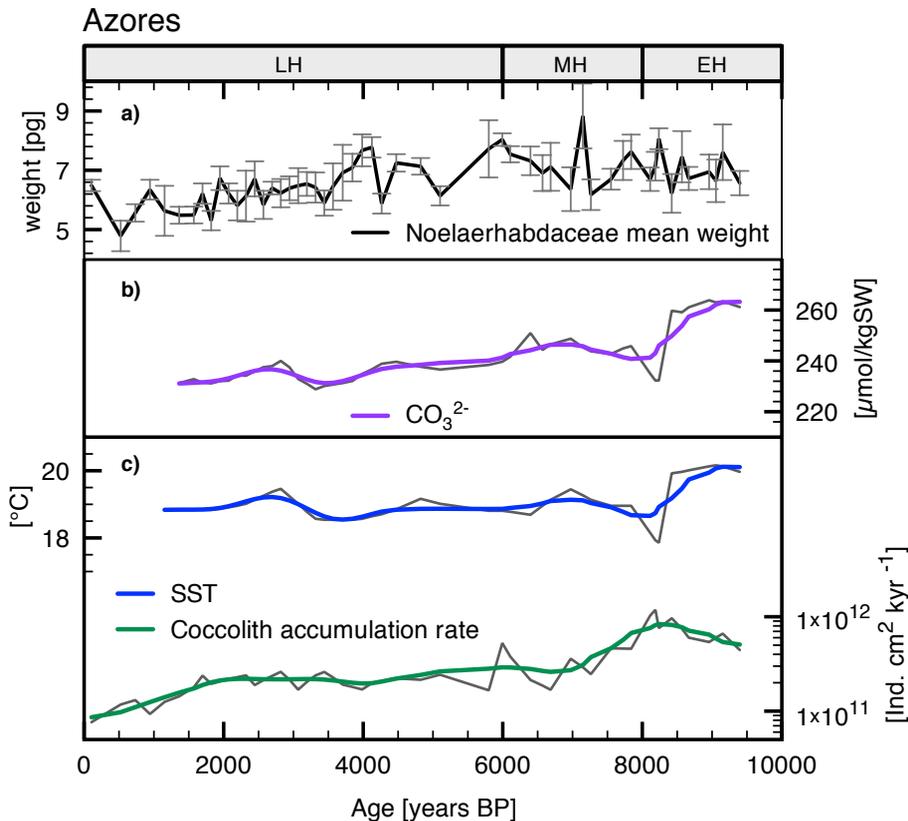
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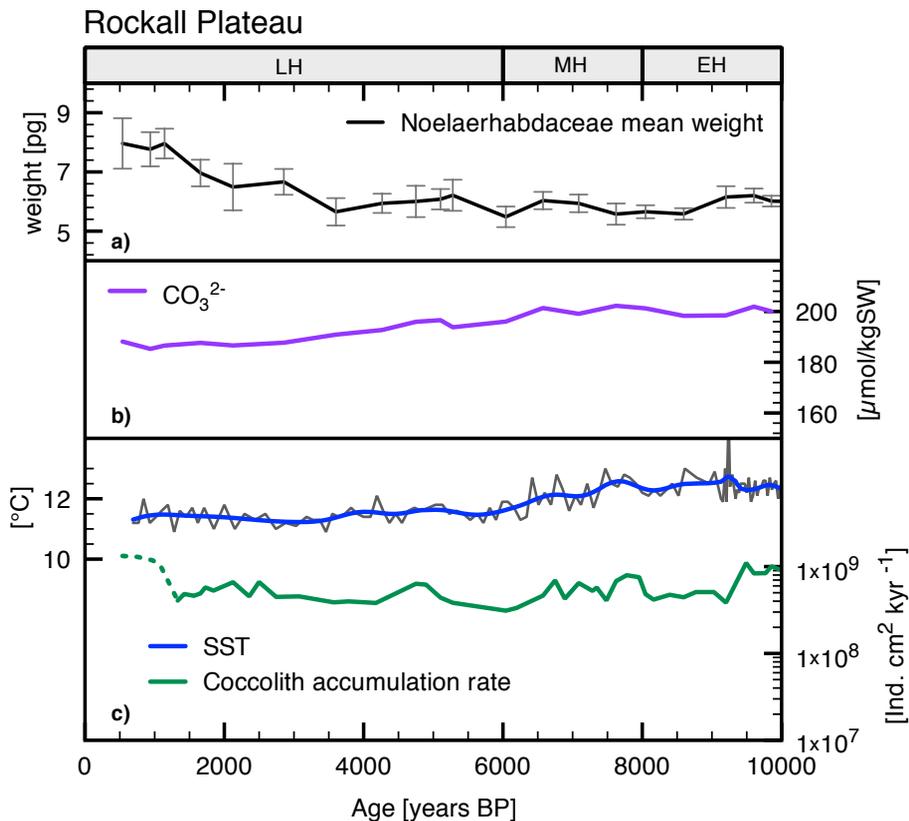
**Fig. 6.** Relative abundance of Noelaerhabdaceae species at Rockall Plateau from ODP Site 980 over the Holocene (Baumann, previously unpublished): *E. huxleyi* (red line), *G. muelleriae* (blue line), *G. oceanica* (orange line), *G. ericsonii* (green line) in comparison to the Noelaerhabdaceae mean coccolith weight (black line).



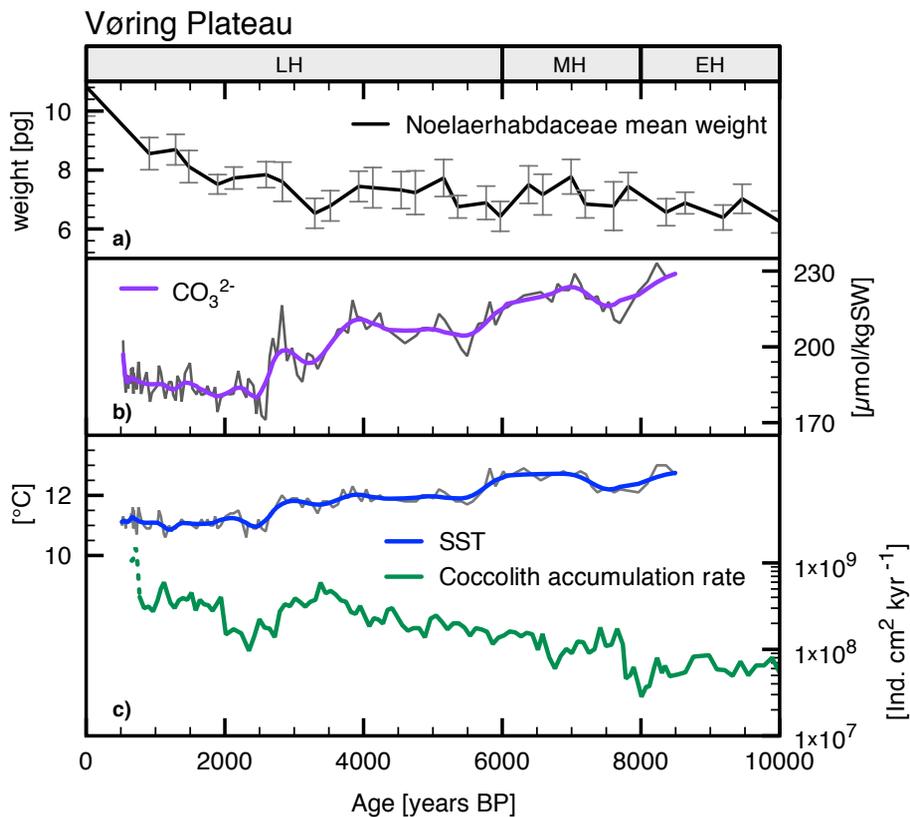
**Fig. 7.** Relative abundance of Noelaerhabdaceae species at Vøring Plateau from sediment core GIK 23071 over the Holocene (Andrulleit, 1995): *E. huxleyi* (red line), *G. muellerae* (blue line), in comparison to the Noelaerhabdaceae mean coccolith weight (black line).



**Fig. 8.** Azores, core Geofar KF 16. **(a)** Noelaerhabdaceae mean coccolith weight (black line), error bars indicate 95 % confidence intervals of the mean weight. **(b)** Carbonate ion concentration (purple line) **(c)** SST (blue line) and coccolith accumulation rate (green line). Bold lines are smoothed (by factor 4), grey thin lines original data.



**Fig. 9.** Rockall Plateau, ODP Site 980. **(a)** Noelaerhabdaceae mean coccolith weight (black line). Error bars indicate 95% confidence intervals of the mean weight. **(b)** Carbonate ion concentration (purple line) **(c)** SST (blue line) and coccolith accumulation rate (green line). Bold lines are smoothed (by factor 4), grey thin lines original data.



**Fig. 10.** Vøring Plateau, core MD08-3192. **(a)** Noelaerhabdaceae mean coccolith weight (black line). Error bars indicate 95 % confidence intervals of the mean weight. **(b)** Carbonate ion concentration (purple line) **(c)** SST (blue line) and coccolith accumulation rate (green line). Bold lines are smoothed (by factor 4), grey thin lines original data.