



Orbital-scale variability in the contribution of foraminifera and coccolithophores to pelagic carbonate production

Pauline Cornuault¹, Luc Beaufort², Heiko Pälike^{1,3}, Torsten Bickert¹, Karl-Heinz Baumann^{1,3}, Michal Kucera¹

¹University of Bremen, MARUM - Center for Marine Environmental Sciences, Leobener Straße 8, D-28359 Bremen, Germany

²Aix Marseille Univ, CNRS, IRD, INRAE, Coll France, CEREGE, Avenue Louis Philibert, F13090 Aix-en-Provence, France

³University of Bremen, Geoscience Department, Klagenfurter Straße, PO Box 330440, 28359 Bremen, Germany

Correspondence to: Pauline Cornuault (pauline.cornuault@gmail.com)

Abstract. Throughout the Cenozoic, calcareous nannoplankton and planktonic foraminifera have been the main producers of pelagic carbonate preserved on the seafloor. While past variability in pelagic carbonate production has been previously studied, relatively little is known about the variability in the relative contribution of the two components. This is important because the responses of the two groups to environmental forcing could be different such that they could amplify or reduce the magnitude of fluctuations in total carbonate production. Here we present new data from the tropical Atlantic that allow us to quantify changes in the relative contribution of the two groups to the total pelagic carbonate burial flux on orbital scales and between different climate states since the Miocene. We find that the composition of the deposited pelagic carbonate remained similar on long time scales, with foraminifera making up about 30% of the deposited carbonate, but varied by up to a factor of two on orbital time scales. We show that the relative contribution of planktonic foraminifera and coccoliths did not correlate with the total pelagic carbonate production, neither in the Pliocene, when its dominant cyclicity was in the precession band and in phase with orbital parameters modulations, nor in the Miocene, when its predominant cyclicity was in the eccentricity band and in antiphase with orbital parameters modulations. The observed variability in tropical pelagic carbonate productivity between foraminifera and coccolithophores suggests that the two main groups of pelagic calcifiers responded fundamentally differently to orbital forcing and associated oceanographic changes in the tropical ocean, but the resulting changes in their proportions did not drive changes in overall pelagic carbonate deposition neither on geological nor on orbital time scales.

1 Introduction

The biomineralisation of carbonate by pelagic calcifiers (planktonic foraminifera and calcareous nannofossils) is a key element of the marine carbon cycle, facilitating the long-term removal of carbon into the sedimentary reservoir (Landschützer et al., 2014). This reservoir interacts with the marine carbon cycle in various ways, such as chemical compensation, where sedimentary carbonate dissolution can compensate for changes in ocean carbonate chemistry, and biological compensation, which refers to changes in the amount of carbonate biomineralisation, removing dissolved carbonate and bicarbonate, thereby lowering oceanic alkalinity (Boudreau et al., 2018). Remarkably, modelling studies show that a change in carbonate production of only 10% on short (ka) to geological time scales would be sufficient to affect the marine carbon cycle. A global decrease in carbonate biomineralisation would lead to a higher alkalinity and, thus, to a higher capacity of the ocean to absorb dissolved CO₂ (Boudreau et al., 2018). Both biological and chemical compensation depend not only on the total amount of oceanic biomineralisation, but also on the composition of the deposited carbonate (Si and Rosenthal, 2019). This is because the main components of the pelagic calcite flux to the seafloor, planktonic foraminifera and calcareous nannoplanktons, produce skeletons of very different sizes and shapes and thus different sinking behaviour and susceptibility to dissolution. Calcareous nannoplanktons are up to two orders of magnitude smaller than foraminifera shells but can sink rapidly as they are often concentrated in faecal pellets (Fischer and Karakaş, 2009; Richardson and Jackson, 2007; Ziveri et al., 2007). The shells of



foraminifera are composed of nanoscale crystal units with a large surface-to-volume ratio, making their shells more susceptible
40 to dissolution (Honjo and Erez, 1978).

While total pelagic calcite production and burial and its changes on geological time scales have been intensively studied locally
and globally, the relative contribution of planktonic foraminifera and coccolithophores to the burial flux remains less well
constrained. Overall, coccolithophore calcite is considered to be the main component of deep sea pelagic carbonate, but
estimates of the contribution of coccoliths to the biogenic calcite exported from the photic zone vary substantially (20-80%),
45 reflecting differences among regions and methods used to quantify the mass of coccolithophore calcite (Baumann et al., 2004;
Frenz et al., 2005, 2006; Ramaswamy and Gaye, 2006; Schiebel, 2002), and there is strong evidence that the composition of
the pelagic carbonate flux varied on geological time scales (Chiu and Broecker, 2008; Si and Rosenthal, 2019). There are three
factors that can influence the bulk composition of pelagic carbonate arriving to the seafloor: the population size of the
producers, their mean cell size, and their investment in biomineralisation relative to cell size. Because coccolithophores and
50 planktonic foraminifera follow different lifestyles, have different metabolisms, and have different environmental preferences,
they may respond differently to environmental change with respect to each of the three factors, resulting in differences in the
pelagic calcite flux composition (Gehlen et al., 2007; Langer, 2008; Si and Rosenthal, 2019). Si and Rosenthal (2019) show
a long geological time scale shift towards more foraminifera and proportionally less coccoliths towards the Quaternary and
explain it to be due to long-term weathering alkalinity change towards a decrease related to the pCO₂ modulation. In our study
55 presented here, we investigate these variations at geological and orbital time scales. To understand to what degree the
composition of pelagic carbonate flux varied in the past and to qualify and quantify the changes in the differential contribution
of the two main pelagic calcifiers to the total pelagic carbonate production estimated from carbonate accumulation rate
(CaCO₃; AR) (Brummer and van Eijden, 1992; Liebrand et al., 2016), we generated new data for Leg 154 ODP Site 927, Ceará
Rise, where carbonate preservation was good during Quaternary interglacials and throughout the Neogene (Curry et al., 1995)
60 and where the site remained in a tropical setting throughout, while at the same time, well-recorded orbital cyclicity of sediment
properties allow the development of tuned age model and quantification of flux at orbital resolution. We made use of previously
analysed samples (Cornuault et al., 2023) and determined the contribution of coccoliths and foraminifera to the total carbonate
production using two independent methods to estimate the coccolith fraction. The sampling strategy allowed us to quantify
changes in the composition of the sedimentary carbonate at orbital time scale in the Pliocene and Miocene and among in four
65 time intervals known to be potential analogs for today's climate warming conditions: marine isotopic stage (MIS) 5 (88 to 150
ka, Clark and Huybers, 2009; Kopp et al., 2009), MIS 9 (276 to 370 ka, (Past Interglacials Working Group of PAGES, 2016;
Voelker et al., 2010), the Pliocene warm period (PWP, MIS KM5, 3096 to 3307 ka, Ravelo et al., 2004) and the Miocene
climatic optimum (MCO, 15.6 to 16 Ma, Foster et al., 2012; Pound et al., 2012; You et al., 2009; Zachos et al., 2008).

2 Material and methods

70 ODP Site 927 on the Ceará Rise in the western tropical Atlantic Ocean (5°27.77'N, 44°28.84'W, 3315 metres below sea level
(m.b.s.l.)) is located above the modern regional lysocline (4200 mbsl, Cullen and Curry, 1997; Curry et al., 1995; Frenz et al.,
2006). However, the depth of the lysocline has varied in the past, and some of the shoaling episodes has resulted in the site
being affected by carbonate dissolution. Such episodes are known from the glacial periods of the late Quaternary and are
related to the restructuring of the Atlantic Meridional Overturning Circulation (AMOC) and an increased influence of the more
75 corrosive Antarctic bottom waters (Gröger et al., 2003b). During the studied intervals of the Pliocene and Miocene, no such
events occurred at this site. The corresponding sediments from these intervals are rich in carbonate, show no relationship
between carbonate content and carbonate flux, and the preservation of planktonic foraminifera shells is always good, indicating
deposition above the regional lysocline (Curry et al., 1995; Gröger et al., 2003b). The location of this site is far from the high-
latitude climate changes and large-scale temperature variations at different time scales. From this site, we already have a set



80 of samples corresponding to these four time intervals, of which we already know the carbonate content and have a high resolution tuned age model (Cornuault et al., 2023). Thanks to their good state of preservation, their high carbonate content and sampling at orbital resolution, the data allow us to study both planktonic foraminifera and coccoliths in the same samples, preventing a possible bias on the relative changes between the two groups with respect to timing (and potential lags) of their response.

85 **2.1 Carbonate content of the different size classes and their relative contribution to the total pelagic carbonate production**

To characterise the contribution of the planktonic foraminifera and the coccoliths to the total carbonate, we have used two different and independent approaches. First, we assumed that most of the foraminifera shells and the coccoliths can be separated by size. At the studied location the carbonate is mainly composed of foraminifera and coccoliths (Curry et al., 1995).

90 Further, we assumed that most of the foraminifera calcite mass occurs in the size fraction above 63 μm and therefore, we assumed that the carbonate flux in the >63 μm size fraction represents foraminifera CaCO_3 flux (Si and Rosenthal, 2019). We are aware, however, that this does not represent 100% of the foraminifera carbonate production, but existing estimates indicate negligible contributions of small shells to the total foraminifera calcite mass (Kiss et al., 2021 and references therein).

The bulk sediment samples were disaggregated in tap water in centrifugation 15 mL falcons placed in rotating carousel
95 overnight and washed and sieved at 63 μm . Next, the dry bulk sediment weight (DBS) and the coarse fraction weight were used to calculate the proportion of the coarse fraction relative to the dry bulk sediment: $\text{Coarse fraction (>63 } \mu\text{m)}\% = (>63 \mu\text{m (g)} / \text{DBS (g)}) * 100$. Then, knowing the bulk carbonate content (Cornuault et al., 2023) and assuming the coarse fraction only consisted of carbonate (foraminifera shells), we calculated the percentage contribution of the <63 μm size fraction to the total carbonate content of the sediment. Following the approach by Si and Rosenthal (2019), we then calculated the contribution of
100 the coccoliths assuming it represents all the carbonate in the <63 μm size fraction. Finally, using the sedimentation rate (SR) and the dry bulk density (DBD), we derived the accumulation rate of both components as an estimate of their export production (Liebrand et al., 2016).

Second, because the <63 μm size fraction may contain non-coccolith carbonate particles, and to explore the effect of the simplification of using 63 μm as a size threshold, we generated an independent record of coccolith fraction CaCO_3 AR, based
105 on automated image analysis of the <32 μm size fraction of the sediment (Beaufort et al., 2014). To this end, we prepared microscope slides using a quantitative protocol to determine the amount of sediment <32 μm that was deposited on the slide and measured using optical microscopy the amount of carbonate <32 μm it contained. To assure a random and even distribution of the material on the slide, we followed the protocol presented by Beaufort et al. (2014). In this protocol, a tiny quantity of sediment is disaggregated in water in a vial and poured in a receiver containing a 12mm x 12 mm coverslip, over a <32 μm
110 mesh metal sieve. Specifically, we used $\sim 0.1 \text{ mm}^3$ of bulk sediment in 1 mL of low alkaline water in a 15 mL centrifugation falcon. The quantity of the deposited sediment was determined by weighing of the microslide using an ultra-microbalance with nominal precision of 0,1 μg . The resulting slides were analysed at CEREGE, France, using an automated microscope with the SYRACO device that automatically takes optical microscope pictures with polarised light (Beaufort et al., 2014; Beaufort and Dollfus, 2004) and provides an estimation of the weight of calcite per coccolith analysed and the total mass of calcite contained
115 in the analysed field of view (FOV). The version of SYRACO used in this study is the one described by Beaufort et al. (2022). Knowing the number of FOV analysed and the number of FOV on the whole slide, we can calculate the quantity of carbonate on the whole slide. As we know the quantity of bulk sediment on the slide, we can then calculate the coccolith carbonate content of the small fraction, as the ratio between the carbonate mass estimated by SYRACO and the mass of bulk sediment. We note that the resulting output is not directly comparable to the first method because of a different size fraction used and
120 because of an entirely different methodology that also depends on the accuracy of the scaling of the SYRACO procedure, but the method should provide a valid alternative estimate of the amount and nature of variation in the flux of coccolith calcite

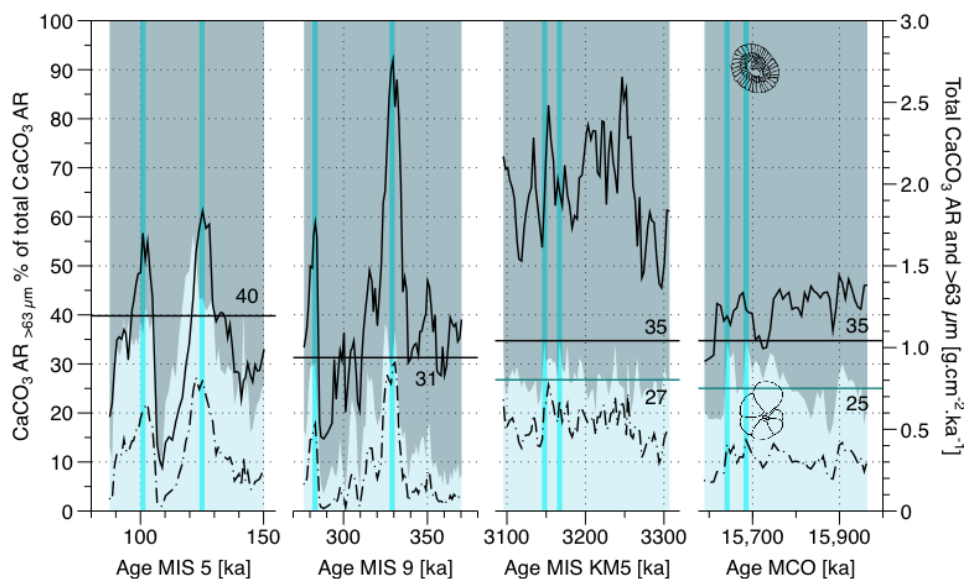


across the studied interval (Figures 2, S2 and S3). With regard to the absolute values of coccolith calcite flux, the estimate from SYRACO should be consistently lower than that of the first method, not only because of the smaller size fraction range used but also because SYRACO only analyses well-preserved, well-focused specimens that are not part of aggregates.

125 2.2 Spectral analysis

To see whether these changes are orbitally driven or not, we performed a Wavelet Transform (WT) spectral analysis (WaveletComp 1.1 package on R, Roesch and Schmidbauer, 2018) using R (4.1.2., R Core Team, 2021) for all parameters for the Pliocene and the Miocene intervals (not for the Quaternary, as these two time intervals are marked by strong precession-paced dissolution cycles, Harris et al., 1997). Additionally, to observe the actual relationship between the change in the relative contribution of the two size fractions and the environmental conditions at orbital time scale, we compared our results to an
130 E+T-P record (Laskar et al., 2004) that reflects the different orbital parameters.

3 Results



**Figure 1: Variability of the >63 μm carbonate contribution to the total CaCO_3 (background fill) and the CaCO_3 accumulation rate of the total sediment (black straight line) and of the >63 μm size fractions (black dashed line). Representative values (solid black lines with numbers) of the contribution of the coarse fraction to the bulk carbonate accumulation rate were calculated for each of the four time intervals as means of the two highest values (highlighted by vertical blue lines) in each interval. This was done to account for the effect of dissolution on the Quaternary samples. For MIS KM5 and MCO, where none of the samples were affected by dissolution, the overall averages per intervals
135
140 are shown by blue horizontal lines with numbers.**

The estimated contribution of foraminifera to the sedimentary carbonate based on particle size fractionation varies between 3.5% and 56.4% (Figure 1). The largest variations are observed in the Quaternary, which is related to the different susceptibility of foraminifera and coccoliths to carbonate dissolution, which affected the Ceara Rise sediments during Quaternary glacials.
145 However, a variability on orbital scales was also present during the Pliocene and Miocene (Figure 1) and is also evident in the record of coccolith fraction accumulation obtained by the SYRACO method (Figure S3). In contrast to the strong and consistent



variability on orbital time scales, the peak values of foraminifera fraction contribution for the four intervals studied were remarkably similar, ranging between 31.3% for MIS 9 and 39.8% for MIS 5 (Figure 1). This is consistent with the effect of dissolution on sediment composition during Quaternary glacials, and the strong positive correlation between foraminifera fraction contribution to the total CaCO_3 AR and bulk carbonate flux in the Quaternary intervals (Figure 2). In contrast, the composition of the carbonate flux shows no relationship with bulk carbonate flux during Pliocene and Miocene (Figure 2). During the Neogene, the contribution of the coarse fraction (foraminifera) to the CaCO_3 AR bulk and the CaCO_3 AR bulk do not co-vary, and they are in phase during the MIS KM5 and in antiphase during the MCO (Figure 1 and supplementary figures S4 to S14). Moreover, for the Miocene, the CaCO_3 AR bulk is showing lower amplitude changes than the contribution of the coarse fraction to it, whereas for the Pliocene, it is the reverse (Figure 1). During the Quaternary, the contribution of the coarse fraction (Figure 1) is driven by foraminifera dissolution (more sensitive than coccoliths, Frenz et al., 2005; Gröger et al., 2003a) due to deep ocean circulation changes (Curry et al., 1995; Harris et al., 1997). On a long geological time scale, we observe a 37% increase from the Miocene to the Pleistocene (taking in account maxima values average) but very similar average values between the Miocene and the Pleistocene (Figure 1). The variability within time intervals is larger than between the time intervals and the orbital scale variability within each time interval is the larger component of variability (63% and 78% amplitude, respectively for the Pliocene and the Miocene).

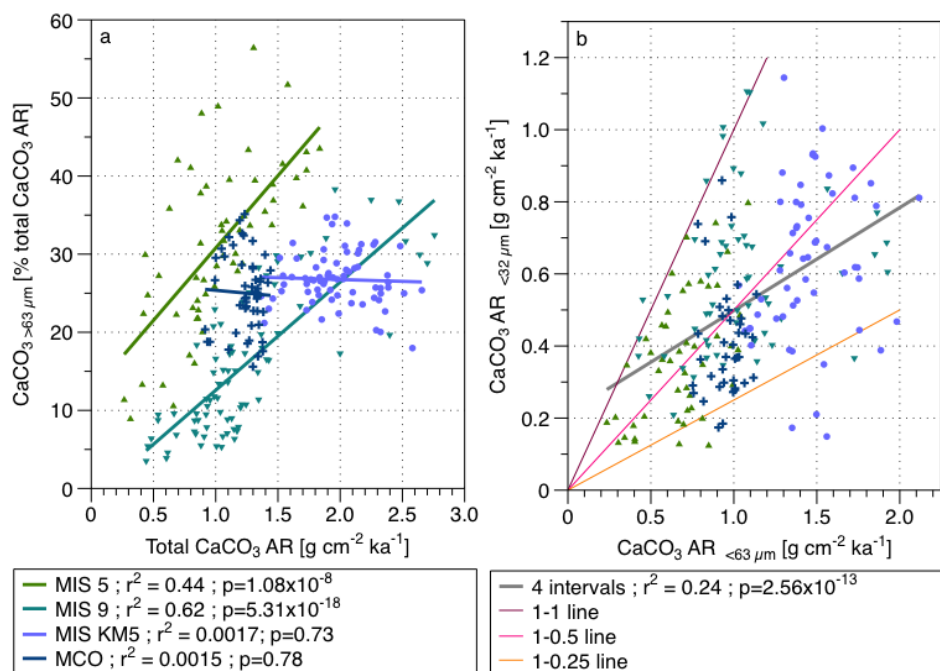


Figure 2: a) Contribution of the $>63 \mu\text{m}$ fraction to the total CaCO_3 AR versus total CaCO_3 AR for the four studied time intervals, with regression lines and b) the coccolith CaCO_3 determined by SYRACO versus the CaCO_3 AR of the $<63 \mu\text{m}$ fraction, with a common regression line of the four studies intervals and dotted lines showing the difference expressed as percentage underestimation by the SYRACO method MIS 5 values are green triangles, MIS 9 values the teal triangles, MIS KM5 are the purple dots and MCO the dark blue crosses.

To test whether the relative contribution of the two size fractions is related to the total CaCO_3 AR, we plotted the contribution of the coarse fraction to the bulk CaCO_3 AR vs the CaCO_3 AR bulk (Figure 2a). For the two intervals that were not affected



by carbonate dissolution, there is no correlation between the coarse fraction contribution to the total CaCO_3 AR and the bulk CaCO_3 AR (almost horizontal regression lines), indicating that the relative contribution of the two pelagic calcifiers was not driving the total bulk CaCO_3 AR (Figure 2a).

175 To test if the results may be affected by the way we estimated the percentage of coccolith carbonate in the samples, we plotted the CaCO_3 AR $<32 \mu\text{m}$ estimated using SYRACO device over the CaCO_3 AR $<63 \mu\text{m}$ estimated using the Si and Rosenthal (2019) approach (Figure 2b). If the values obtained from two different methods reflect the same underlying variability, we would expect that the values are correlated, that the SYRACO values are systematically lower and that there are no differences in the shape of the relationship among the four studied intervals. Indeed, we observe a strong positive relationship between the

180 CaCO_3 AR estimation of the small fraction of the two methods ($r^2 = 0.24$) which exists across the four studied intervals, as well as a systematically lower values given by the SYRACO method, as expected (Figure 2b).

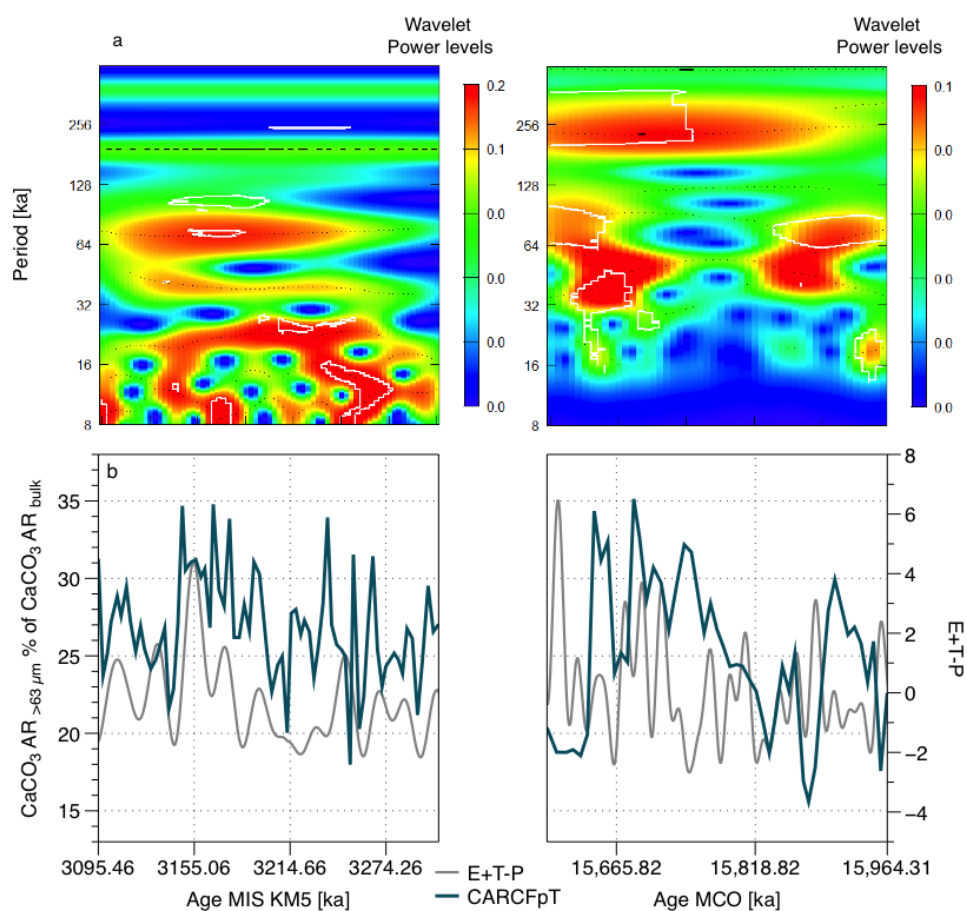


Figure 3: a) Wavelet transform coarse fraction percentage of bulk CaCO_3 AR for both MIS KM5 and MCO, 185 significance value on the figure = 0.1, b) coarse fraction contribution to bulk CaCO_3 AR and the actual E+T-P (Laskar et al., 2004).

For the MIS KM5, we observe a clear and continuous precession imprint around 20 ka periodicity from 3100 ka to 3270 ka which seems to be changing towards shorter cycles through time, an obliquity imprint (around 41 ka periodicity) and a distinct 190 100 ka eccentricity periodicity that is ranging from 3140 ka to 3230 ka more or less. Compared to an E+T-P curve, we see this



single 100 ka cycle by the naked eye, as well as the obliquity, playing a subordinate but not negligible role. Concerning the MCO, we see an indication of a 41 ka (obliquity) imprint from 15589 ka to 15900 ka. We cannot observe shorter periodicities as the sampling resolution wouldn't allow us to see it. The relative contribution of the $>63 \mu\text{m}$ to the bulk CaCO_3 AR is in phase with the E+T-P in the Pliocene and in antiphase with the E+T-P during the Miocene (as for the bulk CaCO_3 AR, 195 Cornuault et al., 2023) (Figure 3 and supplementary figures S4 to S14).

We found 100 ka (eccentricity) periodicities in the $>63 \mu\text{m}$ CaCO_3 AR and the $<32 \mu\text{m}$ CaCO_3 AR (MIS KM5 and MCO), and the $<32 \mu\text{m}$ CaCO_3 AR seems to be responding to 100 ka antiphased with a high AR when eccentricity is low and low AR when eccentricity is high (S1, S3). Additionally, we observe a 21 ka (precession) periodicity during the MIS KM5 and 41 ka (obliquity) periodicity during the MCO for the $>63 \mu\text{m}$ CaCO_3 AR and the $>63 \mu\text{m}$ CaCO_3 AR (S1, S2).

200 The $>63 \mu\text{m}$ CaCO_3 AR and $<32 \mu\text{m}$ CaCO_3 AR are in phase with E+T-P in the Pliocene, except during the peak of warmth of the PWP and antiphased during the MCO, suggesting that the coarse fraction (foraminifera) is responding in phase with E+T-P when the conditions are colder, and is in antiphase with E+T-P at a strong warm peak (PWP middle and all the Miocene interval chosen for this study). Even if the values are different, the variability is consistent between the $<63 \mu\text{m}$ CaCO_3 AR (direct approach) and the $<32 \mu\text{m}$ CaCO_3 AR (independent) SYRACO approach (Figure 2b).

205 4 Discussion

There is an increase of the relative contribution of foraminifera from Miocene to Quaternary (or decrease of the coccoliths contribution) coherent with what has been found by Si and Rosenthal (2019). Furthermore, we observe different variability of the relative contribution of foraminifera and coccoliths within the Pliocene and the Miocene so the two main carbonate producers are responding differently for those two periods, and the phase relationship between the CaCO_3 AR bulk and the 210 foraminifera contribution to it is changing between the Pliocene and the Miocene (Figure 1). For both time intervals, we do not observe any correlation between the contribution of the coarse fraction to the total pelagic carbonate production and the carbonate production itself (Figure 2), meaning that the changes in the relative contribution of the two main pelagic carbonate producers are not driving the changes in total CaCO_3 production (except concerning the Quaternary cold events, where the correlation is a proof of the preferential dissolution of the planktonic foraminifera in presence of dissolution). For the Pliocene 215 and the Miocene, we observe large changes in the correlations between the different size fractions and the bulk CaCO_3 AR, and in addition a large amplitude variability of the coarse fraction contribution to the bulk CaCO_3 AR within these two time intervals, highlighting that the relative contribution of the two main pelagic carbonate calcifiers, if remains similar on geological time scale, has changed a lot on shorter orbital time scale. For both the Pliocene and the Miocene, it isn't the coarse fraction CaCO_3 production which is driving the CaCO_3 AR bulk changes, but the $<63 \mu\text{m}$ CaCO_3 production. This means that 220 the two main pelagic carbonate producers responded differently, and that the coccolithophores relative contribution seems to be driving the overall changes. We found a coarse fraction contribution of about 20 to 30%, realistic and coherent with recent findings by Si and Rosenthal (2019), and Drury et al. (2021). The production within the two carbonate producers is changing synchronously and in the same direction, but with different amplitudes at both geological and orbital time scale, making their relative contribution to the CaCO_3 AR bulk to change.

225 According to the observations of the wavelet transform and CaCO_3 AR records vs time (Figures S1-S3), the foraminifera and the coccoliths are not responding to the same orbital parameter and not in the same way: the changes of CaCO_3 AR of the two groups do not seem to covary or being linked by any correlation, meaning that they are changing through the time, but 1) do not seem to be linked and 2) do not seem to be responding to the same forcing, which could also explain the different frequencies observed in the bulk CaCO_3 AR record (Cornuault et al., 2023): one frequency tracking coarse (foraminifera) and 230 one frequency tracking small (coccolithophores) fraction. There is an equilibrium on long time scales between the two groups, so when the CaCO_3 AR bulk is increasing, the two groups are increasing, but not necessarily the same amplitude (e.g. between



the Miocene and the Pliocene). We propose the idea of a stronger influence of the eccentricity changes on the nannoplankton. An increase of eccentricity corresponds to an increase of the mean annual solar insolation at all latitudes (Goosse, 2015) and modulates the precession and seasonal insolation contrast, which is higher when the eccentricity is high. Nannoplankton might be highly affected by these changes due to the dependence on light for photosynthesis as well as a greater diversity of ecological niches with higher seasonality (Longhurst, 2007), and so, a larger number of species (Beaufort et al., 2011; Henderiks and Bollmann, 2004). Furthermore, some studies are highlighting the high sensitivity of the coccoliths production to eccentricity changes (e.g. Beaufort et al., 1997, 2022; Drury et al., 2021). Their morphological diversity changes with the eccentricity modulation, as the results of coccoliths evolution being forced by eccentricity, and so, affect the carbonate accumulation rate and drive carbon cycle changes (Beaufort et al., 2022). The orbitally forced variability within the different time intervals has changed a lot and is different between the two groups. As the two main pelagic calcifiers do not seem to be responding to the same forcing within each time interval, we can expect that if the conditions are drastically changing, it can affect one of the two groups and not the other, affecting the ocean alkalinity and ocean capacity to absorb CO₂ (by biomineralisation processes, Boudreau et al., 2018). When the climate is warmer, we have more carbonate produced by the two groups, with a response of the coccoliths which seems to be stronger during the PWP than during the MCO. Furthermore, we observe an increase of the relative contribution of the coarse fraction, so if both the foraminifera and the coccoliths productivity is increasing, the foraminifera productivity seems to be responding with stronger amplitude, making its relative contribution to the total pelagic carbonate production higher. Can we expect a decrease in the role of the coccoliths in the surface ocean anthropogenic carbon absorption in the future with warmer climates? This would reduce the Ocean's carbon sink capacity. Our results are in line with those obtained by Schwab et al. (2013) and Stolz and Baumann (2010) who find a high coccolith productivity during the MIS 5e, even if during this interval, the coarse fraction increased that much that there is a relative increase of the foraminifera fraction in the sediment.

Our results are also in line with Holbourn et al. (2014), with a lower coarse fraction proportion centred in the MCO interval (corresponding to the lower d¹⁸O values). It is possible that above a certain temperature threshold (or CO₂ threshold) the response of the carbonate producers' changes: as the contribution of the coarse fraction is in phase during the Pliocene and in antiphase during the Miocene, we suggest that above a certain temperature (or more generally, in some extreme environmental condition) the pelagic carbonate production (especially that of the planktonic foraminifera) drops. This could be explained if the ecological optima of the planktonic foraminifera and the coccolithophores were systematically different in some aspect (Beaufort et al., 2011; Schmidt et al., 2006), and the tropical species remained highly sensitive to this ecological aspect (Schmidt et al., 2006).

5 Conclusion

Our results indicate that since the Miocene, in the tropical Atlantic, the contribution of coccoliths and planktonic foraminifera as the two important pelagic carbonate producers has varied on orbital time scales, but remained similar on average on longer time scales. We observe that the changes in the contribution of the coarse fraction to the total pelagic carbonate production followed mainly precession in the Pliocene, and obliquity and eccentricity in the Miocene and that the phase relationship to orbital forcing appears to have shifted between the two intervals. Individually, we show that the coarse fraction CaCO₃ AR was responding to precession and obliquity and the small fraction CaCO₃ AR was responding to eccentricity, indicating that the two pelagic carbonate calcifiers were responding to different orbital forcing, and following different phase relationships. It remains unknown whether the observed changes in their contribution to total carbonate reflect differences in population growth or changes in the size or calcification intensity of their skeletal elements. Either way, it appears that eccentricity not only modulates coccolithophore community assembly and evolution (Beaufort et al., 2022), but also their carbonate production, affecting the composition of pelagic carbonate deposited on the seafloor. In this way, the hitherto overlooked



variability in coccolithophore productivity and foraminifera productivity may play a role in the global carbon cycle. This is because the calcite skeletons of the two groups are associated with different amounts of organic carbon, they contain different amounts of trace elements and are sinking through the water column following different physics resulting in different ballasting effects on the biological carbon pump. Because coccolithophore and foraminifera calcite have different susceptibility to dissolution, a large change of the carbonate production by these two calcifiers could have an impact on the ocean capacity to regulate atmospheric CO₂ (Boudreau et al., 2018).

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6 Data availability

The datatable of this manuscript will be made available upon request to the main author until their online publication on PANGAEA (<https://pangaea.de>, last visit: 15th January 2025). This datatable contains the samples list, their ages and the mass of less than 32 μm sediment on the lamellas for coccoliths analyses, the mass of carbonate on these slides (measured with SYRACO automated device), the dry weight of the bulk sediment, the weight of the > 63 μm size fraction, the accumulation rate of the > 63 μm size fraction, and the accumulation rate of the < 32 μm size fraction.

285 7 Author contribution

Pauline Cornuault, the first author, is the main contributor to the manuscript. She prepared the research project, ran most of the experiments in MARUM (Bremen, Germany), interpreted the data, prepared all the figures, interpreted the data and wrote this manuscript.

Prof. Dr. Michal Kucera is the principal investigator, and helped a lot in the redaction of this manuscript. Prof. Dr. Heiko Pälke, Dr. Torsten Bickert and Dr. Karl-Heinz Baumann helped with the data interpretation and the redaction of this manuscript.

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Dr. Luc Beaufort ran the analysis of the small fraction samples in CEREGE (Aix-en-Provence, France) and helped with the data analysis and the redaction of the present manuscript.

8 Competing interest

295 All the authors declare no conflict of interest for this work.

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