Size and Abundance of Late Pleistocene Reticulofenestrid Coccoliths from the Eastern Indian Ocean in Relation to Temperature and Aridity

Storlek och abundans av Pleistocen coccoliter från östra Indiska oceanen i förhållande till temperatur och torrhet

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Abstract

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Measurements on coccolith abundance and mass can be used as a signal of primary productivity and pelagic calcification in response to environmental change. The Leeuwin Current (LC) is known to transport warm and low-salinity waters from the Indo-Pacific Warm Pool (IPWP) southwards along the coast of West Australia. Along with the onset of continental aridity during late Neogene, increased strength of the LC may have played a role in reef expansion on the Northwest Shelf.

In this study the morphological variation in size and mass of reticulofenestrid coccoliths was assessed in material from IODP Site U1461 in the eastern Indian Ocean spanning the past 500 ka. Both the absolute abundance of all reticulofenestrid coccoliths (Emiliania huxleyi, Reticulofenestra spp., Gephyrocapsa spp. and Pseudoemiliania spp.) was determined, as well as the relative abundance of large versus small coccoliths. Coccolith size and mass were measured quantitatively under circularly polarized light. The data was compared to variations in sea surface temperatures (SST) of the LC, and to continental aridity of Australia. SST fluctuations could influence coccolithophore productivity by affecting their metabolic rate, whereas continental aridity may influence the influx of terrestrial matter by wind.

The investigated interval is dominated by small species of Gephyrocapsa. Peak values of absolute abundance and mass were observed during Marine Isotope Stage (MIS) 11, an interglacial period of extended warmth and humidity. These results coupled with high densities of aragonite needles in the same samples indicate the sediments were diluted by material overflowing from the adjacent shallow-water carbonate platform, analogous to the whiting events observed in the modern-day Bahamas. A decrease in abundance of Gephyrocapsa caribbiana at 240 ka can be linked to the timing of their last common occurrence (LCO), within MIS 7. The subsequent shift to Gephyrocapsa oceanica as the dominant large species may indicate an ecological replacement of G. caribbiana, or signify warm and low-salinity waters.

Keywords: coccoliths, abundance, biometry, circular polarized light microscopy, Late Pleistocene, Marine Isotope Stage 11

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Populärvetenskaplig sammanfattning

Storlek och abundans av Pleistocen coccoliter från östra Indiska oceanen i förhållande till temperatur och torrhet
Jeroen van Dijk

Mätningar av abundans och massa hos coccoliter kan användas som en signal för primärproduktion och pelagisk förkalkning som resultat av miljöförändringar. Leeuwin Current (LC) är känd för att transporterar varmt vatten och vatten med låg salthalt från Indo-Pacific Warm Pool (IPWP) söderut längs kusten i västra Australien. Tillsammans med början av kontinental torka under sen Neogen kan ökad styrka hos LC ha spelat en roll i expansionen av rev på nordvästsockeln. I denna studie bedömdes den morfologiska variationen i storlek och massa hos coccoliter i material från IODP plats U1461 i östra Indiska oceanen från de senaste 500 000 åren. Både den absoluta abundansen av alla reticulofenstridcoccoliter (Emiliania huxleyi, Reticulofenestra spp., Gephyrocapsa spp. och Pseudoemiliania spp.) bestämdes, liksom den relativa abundansen av stora jämfört med små coccoliter. Storlek och massa av coccoliter mättes kvantitativt under cirkulärt polariserat ljus. Uppgifterna jämfördes med variationer i havsytans temperatur (SST) hos LC, och med kontinental torrhet i Australien. SST-fluktuationer kan påverka produktiviteten hos coccolitoforider genom att påverka deras metabolism, medan kontinental torrhet kan påverka inflödet av markmaterial med vind. Det undersökte intervallet domineras av små arter av Gephyrocapsa. Toppvärden av absolut abundans och massa observerades under marinisotopsteget (MIS) 11, en interglacial period med förlängd värme och fuktighet. Dessa resultat kombinerat med hög densitet av aragonitnålar i samma prover indikerar att sedimenten späddes ut med material som svämmade över från den intilliggande grunda karbonatplattformen, vilket är jämförligt med de vitningshändelser som har observerats i dagens Bahamas. En minskning i abundans av Gephyrocapsa caribbeanica vid 240 ka kan kopplas till tidpunkten för deras senaste gemensamma förekomst (LCO) inom MIS 7. Den efterföljande övergången till Gephyrocapsa oceanica som den dominerande stora arten kan indikera en ekologisk ersättning av G. caribbeanica, eller indikera varmt vatten med låg salthalt.

Nyckelord: kokkoliter, mängder, biometri, cirkulär polariserat ljus, pleistocen, Marine Isotope Stage 11

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1. Introduction

Coccolithophores are unicellular calcifying phytoplankton, which have been present in Earth’s oceans since the late Triassic, 225 million years ago (Ma) (Bown et al., 2004). They require sunlight for photosynthesis and thus predominantly occur in the photic zone (the upper 200 m of the water column) in marine environments. Coccolithophores are most abundant in warm, low productivity waters, such as gyre centers and restricted areas of circulation (Winter & Siesser, 1994). In nutrient-rich environments, e.g. upwelling zones, they are usually outcompeted by diatoms (Margalef, 1978; Balch, 2004).

A calcareous exoskeleton, the coccosome, surrounds the cell and is composed of tiny interlocking plates known as coccoliths. New coccoliths are secreted inside the cell under influence of light, and once completed they are extruded through the membrane to cover the cell after division (Pienaar, 1994). Coccoliths commonly range in size from 3 to 15 µm, and vary in shape and ornamentation depending on the species. Consequently, their morphology is primarily used for taxonomic classification (Sáez et al., 2004). Together with other phytoplankton, coccolithophores form the basis of the marine food web, and are therefore often consumed by grazing zooplankton. Digestion has a minimal effect on coccoliths, and even complete coccosomes have been found in zooplankton fecal pellets (Winter & Siesser, 1994). In the fossil record however, the coccolithophores are mainly represented by single coccoliths found in the sediment. These coccoliths constitute a major part in the oceans’ carbonate burial and changes in morphology and abundance are therefore a good signal for paleoproductivity (Baumann et al., 2004).

This study mainly focuses on the genera Pseudoemiliania, Gephyrocapsa and Emiliania, which belong to the family of Noëlaerhabdaceae and are commonly referred to as reticulofenestrid coccoliths due to their comparable (Reticulofenestra-type) coccolith structure (Young et al., 1997; Young, 1998). Emiliania huxleyi, an extant species from this family of coccolithophores is at the present time the most dominant and globally distributed species. Cyclical variations of both size and distribution of Reticulofenestra specimens has been observed in the Miocene and through the Pliocene and these cycles appear to be typical of their evolutionary patterns (Kameo & Takayama, 1999).

Cell size is important for unicellular algal physiology as it determines transport rates of dissolved elements in and out of the cell (Raven, 1998). Small cells have greater surface area relative to volume compared to large cells, which facilitates incoming and outgoing fluxes of nutrients (Raven, 1998; Henderiks, 2008). Temperature, CO₂ concentration, and nutrient availability have an effect on cell growth and calcification (Henderiks, 2008; Sett et al., 2014). Coccolith size is linearly correlated to the coccosome size, and thus cell diameter of reticulofenstrids. It is therefore possible to infer coccolithophore cell size from size measurements of fossil coccoliths (Henderiks, 2008). Thickness and mass reflect the degree of calcification of coccoliths and these values can thus be used as indicators of productivity and ocean carbonate chemistry (Beaufort et al., 2008; Beaufort et al., 2014).
Coccolith size and mass can thus be used as indicators of current and past surface ocean dynamics and resource availability, through their response in size variation over time.
2. Aims

Abiotic factors, such as temperature, light and humidity versus aridity, are important drivers of evolutionary change and on a macroevolutionary scale, key changes in the physical environment lead to biodiversity and speciation. This study investigates the morphological variation in size and mass of reticulofenestrid coccoliths since 500 thousand years ago (ka). It also sheds light on the relative distribution of small species of *Gephyrocapsa* and *Emiliania huxleyi* grouped together into one category, and the two larger species of *Gephyrocapsa* that were present during this time. The studied samples were collected off the coast of Western Australia during International Ocean Discovery Program (IODP) Expedition 356. A quantitative, microscopy-based method has been applied that uses the property of calcite in cross-polarized light to measure the thickness of coccoliths, deduced from the birefringence of calcite (Beaufort *et al*., 2014). The degree of grey level (brightness) corresponds directly to the thickness of coccoliths, with thicker coccoliths appearing brighter in the image.

The objectives of this study were (1) to identify variations in absolute abundance, size and mass of reticulofenestrid coccoliths during the last 500 ka, (2) determine the relative abundance of two larger *Gephyrocapsa* species (*G. oceanica* and *G. caribbeanica*), and (3) compare the coccolith data to variations in paleoenvironment by using time series of sea surface temperatures (SST) and the variation in wind regimes (and continental aridity) derived from grain size distribution of terrestrial sediments (Spooner *et al*., 2011; Stuut *et al*., 2014).

Analyses were performed on core material from IODP Expedition 356 Site U1461, which documents the regional paleoclimate variability of Northwest Australia. This site is located on the edge of the Australian continental shelf in the proximity of the Leeuwin Current. Drowned reefs detected nearby may have affected carbonate ramp sediments at Site U1461. The outcome of this study could improve our understanding of the relationship between climate variability and the variation in size and abundance of reticulofenestrid coccoliths in the eastern Indian Ocean, with a special focus on paleoproductivity.
3. Background

3.1 Size variation in reticulofenestrid coccoliths

Coccoliths are a good signal of paleoproductivity as both their abundance and morphology can be used to track global environmental change (Hay, 2004). Coccolith abundance tends to be highest in interglacial stages (Baumann & Freitag, 2004), and appear to respond strongly to variation in insolation and ocean-atmosphere phenomena (Beaufort et al., 1997; Bordiga et al., 2013). The sensitivity of coccolithophores to climate change is also reflected in extinctions and appearances of new species, also called turnover events, which makes coccoliths a useful tool for biostratigraphy. Calcareous nannofossil assemblages from the Upper Eocene and younger have been dominated by the genus *Reticulofenestra* and subsequently its descendants *Pseudoemiliania*, *Gephyrocapsa* and *Emiliania* (Perch-Nielsen, 1985). Their coccoliths are placoliths with a *Reticulofenestra*-type structure, dominated by radially oriented calcite crystals (R-units) that form the proximal and distal shield elements and the inner and outer tube with central area structures (e.g. bridge) (Fig. 1A). They are strongly birefringent (Young et al., 2003). *Reticulofenestra* are lacking the distinguishing features observed in *Emiliania* with slits between shield elements, while *Gephyrocapsa* have a conjunct bridge across the central area (Samtleben, 1980; Young et al., 2003).

![Diagram of Gephyrocapsa morphotypes](image)

**Figure 1.** *Gephyrocapsa* morphotypes, with: (A) general *Reticulofenestra*-type structure of placolith, with R-units and *Gephyrocapsa* bridge. V-units indicated by circles. (B) Extant morphotypes of *Gephyrocapsa*, with ellipses depicting conventional species concepts. The six association-types identified by Bollmann (1997) indicate frequency maxima: Gephyrocapsa Minute (GM), Gephyrocapsa Transitional (GT), Gephyrocapsa Cold (GC), Gephyrocapsa Oligotrophic (GO), Gephyrocapsa Equatorial (GE), and Gephyrocapsa Larger (GL). Images adapted from Young et al. (2003).

Studies focused on reticulofenestrid coccolith evolution have identified cycles of size variation across time. *Reticulofenestra* coccoliths in Miocene and Pliocene nannofossil assemblages usually show a gradual increase of size and a sudden decreases of maximum size (Young, 1990; Kameo & Takayama, 1999). The disappearance of large *Reticulofenestra* (>7 µm) at the end of the Early
Pliocene was a global turnover event that is used in nannofossil biozonation (Young, 1998). The variation in diameter of coccoliths expressed as a ratio of size classes found in Late Miocene assemblages was shown to follow Earth’s precession cycles, indicating environmental forcing was at play (Beaufort, 1992). Towards the Late Pliocene, *Pseudoemiliania* generally dominates coccolith assemblages, but is replaced at the Plio-Pleistocene transition by *Gephyrocapsa* as the dominant reticulofenestrid genus (Young, 1998). *Gephyrocapsa* species are characterized by a bridge at various species-specific angles over the central area (Samtleben, 1980). Their variation in morphology is significantly correlated with environmental gradients, and six morphotypes could be identified in 70 globally distributed assemblages (Fig. 1B) (Bollmann, 1997). The morphological variation in *Gephyrocapsa* and their global dominance during the Late Pleistocene is most likely the result of evolutionary adaptation (Bollmann et al., 1998). Bridge angle and coccolith size are most closely linked to sea surface temperatures, which was adapted to a *Gephyrocapsa* transfer function for reconstructing paleotemperatures (Bollmann et al., 2002; Henderiks & Bollmann, 2004).

In modern day oceans *Emiliania huxleyi* and *Gephyrocapsa oceanica* are the two most abundant bloom-forming coccolithophores (Westbroek et al., 1993; Bendif et al., 2014), and they have been cultured extensively (Young et al., 2003; Probert & Houdan, 2004). They are studied in order to explain patterns in their ecology and evolution. Intraspecific variation in morphology has been observed in both species (Okada & McIntyre, 1977; Young & Westbroek, 1991; Bollmann & Klaas, 2008). Studies have found that size, and in particular calcification, are influenced by light, salinity, temperature and nutrients (Bollmann et al., 2002). The spatio-temporal distribution of differentially calcified species is in part influenced by carbonate chemistry (Beaufort et al., 2011). It has been suggested that decreasing CO₂ availability drove long-term trends towards smaller coccolith size over the past ~55 million years (Henderiks & Pagani, 2008; Hannisdal et al., 2012). A similar effect was observed for the degree of calcification, although this signal becomes unclear during the Pleistocene (Bolton et al., 2016), which seems to agree with laboratory and field observations (Hoppe et al., 2011; Young et al., 2014), indicating an intricate interplay of abiotic factors that is not yet fully understood.

3.2 Paleoenvironment of Northwest Australia

The Pleistocene is known for its glacial-interglacial cycles, periods of relative cool and warm climates, with the accompanying falling and rising of sea levels (Emiliani, 1955; Voris, 2000; Rohling et al., 2014). For Southeast Asia and Australia this meant dramatic changes to the coastline due to sea level changes related to glaciations (Voris, 2000). The change in sea level also strongly affected the ocean currents circulating Australia. Offshore along Northwest Australia, the Leeuwin Current (LC) flows southward transporting warm low-salinity water (Fig. 2).
Figure 2. Surface oceanography of the Indo-Pacific region, with 200 m shelf edge bathymetry contour. The red star marks the location of Site U1461 on the northwest shelf of Australia and the Leeuwin Current. Image adapted from Gallagher et al. (2009).

The Indonesian Throughflow (ITF) plays an important role in the transport of heat from low to high latitudes, and feeding the LC with warmth. Since its restriction it has strongly influenced the Indo-Pacific Warm Pool (IPWP) and the circulation in the Indian Ocean, becoming an important factor in the Asian monsoon systems (Wang et al., 2005). The large glacial/interglacial oscillations and continual uplift in the Indonesian Archipelago during the late Pleistocene have caused fluctuations in the restriction of the Indonesian seaway and influencing the strength of the LC (Gallagher et al., 2009). Glacial-interglacial sea levels fluctuated between -120 and 0 m (Voris, 2000; Rohling et al., 2009; Gallagher et al., 2014b). During interglacial periods with higher sea level there was a higher influx of warm tropical water from the ITF resulting in a stronger LC (Spooner et al., 2011), with a deeper thermocline which has been linked to low primary productivity (Molfino & McIntyre, 1990; Beaufort et al., 2001; Beaufort et al., 2003). On the other hand, during glacial periods the LC was weaker with a shallower and homogeneous mixed layer, and 6-9 °C lower SST (Spooner et al., 2011).

The changes between glacial-interglacial climates also caused variations in aridity, with generally arid glacial stages and humid interglacials (Stuut et al., 2014). Relative less rainfall led to a higher proportion of wind-blown sediment compared to fluvial sediment. An increase in size of aeolian particles also indicates higher trade-wind intensity during glacial stages (Stuut et al., 2014). These stronger winds may decrease the depth of the thermocline and therefore increase primary productivity (Beaufort et al., 1997; Beaufort et al., 2001). Glacial sea levels at Site U1461 may have been as shallow as 7.5 m, where the thermocline was not present, therefore effects of wind stress were more to
play role during highstands. The influx of wind-blown terrestrial dust carrying nutrients was likely of more importance to phytoplankton productivity, with diatoms outcompeting coccolithophores (Henderiks et al., 2002; Bordiga et al., 2013).

3.3 IODP Site U1461

The sediment samples used in this study are from drill cores collected during International Ocean Discovery Program (IODP) Expedition 356, at Site U1461 (20°12.84’S, 115°03.94’E). The expedition took place along the western continental margin of Australia from August 1 to September 30, 2015. Site U1461 (Fig. 3) is located in the Northern Carnarvon Basin on the edge of an outer shelf ramp, currently at ~127.5 m water depth, around 100 km northwest of Barrow Island (James et al., 2004; Gallagher et al., 2014a; Gallagher et al., 2017b). The general texture of seabed sediments is poorly sorted gravel, sand and aragonite carbonate mud (James et al., 2004). The four holes at Site U1461 were drilled through a 1 km thick layer of shelf to slope carbonate sediments. Due to basin-wide subsidence these sediments are an archive of the recent 4 Ma of climate change (Gallagher et al., 2017b). The main objectives of Expedition 356, and in extension Site U1461, were to determine the variability of the ITF and its influence on the LC, and to collect information through climate proxies on the Australian monsoonal history and the onset of continental aridity. The present study will focus on the upper ~70 m Pleistocene record that was recovered.
Figure 3. Northwest Australia and bathymetry of major basins, with the locations of the IODP Expedition 356 drilling sites (yellow stars), DSDP/ODP drill sites (green circles), industry well locations (yellow circles), and the locations of modern and drowned reef (Gallagher et al., 2017b). Site U1461 (this study) marked by the red box. SST data from Spooner et al. (2011) and aridity from Stuut et al. (2014) are based on material collected from Site MD002361, which is marked with the yellow box.

Site U1461 is downdip from a drowned reef further south near Barrow Island (Fig. 4). The LC has been instrumental in the expansion of reefs southwards along the coast of West Australia (Kendrick et al., 1991). The drowned reefs on the Northwest Shelf of Australia may have initiated in the Middle Pleistocene around 500 ka under influence of increased LC activity and a dry hinterland (Gallagher et al., 2014b). The expansion of reefs has been linked to glacial-interglacial sea-level cycles (Droxler & Jorry, 2013).
Figure 4. Seismic profile of Site U1461 with the locations of drowned reefs in light green (Gallagher et al., 2014b; Gallagher et al., 2017b). Reflector ages (0.5-4.0) are in millions of years.
4. Methodology

4.1 Sample collection and preparation

Four holes were drilled at Site U1461 between August 16 and August 25, 2015. Hole U1461A has a depth of 0–285 m CSF-A (core depth below sea floor), U1461B a depth of 0–880 m CSF-A, U1461C a depth of 0–445 m CSF-A, and U1461D reaches from 450–1085 m CSF-A. Biostratigraphy was determined from nannofossil assemblages in shipboard smear slides and used to establish a linear age model (Gallagher et al., 2017b). Overlapping cores from holes U1461A, U1461B and U1461C from the upper 0-285 m CSF-A were stratigraphically correlated to generate a splice. 80 samples in the range of 0-66.06 m CSF-A were subsequently selected from this splice for an initial sample request. Following the linear shipboard age model (Gallagher et al., 2017), the ages of these samples were determined based on their top depth CSF-A.

A subset of 20 out of 80 available samples was selected within the range of 0–500 ka. Selection was done systematically by picking the first of every four samples, starting at the very top of the splice. From the selected core samples a few lab spoons of sediment was collected and stored in 34x24 mm glass vials with plastic snap-cap. The vials were not fully closed and were left to dry for 24 hours in a 40° C oven. The selected samples were then prepared for absolute abundance counts and biometry following the “drop” technique (Bordiga et al., 2015). The next day 0.005 g of each sample was weighted on a microbalance and put into 50 ml falcon tubes. The samples were then mixed with distilled water buffered with 10% ammonia (NH₃) and dipped for 1 minute in an ultrasonic bath. More of the ammonia solution was added to create a 30 ml suspension. Two times 0.75 ml from the suspension was then carefully dropped and spread evenly onto a 24x32 mm cover glass (7.68×10⁸ µm²) with a high-precision micropipette as per Bordiga et al. (2015). Cover glasses were left to dry on a hotplate set to 50° C and afterwards glued onto microscope slides (UV-curing Norland Optical Adhesive).

4.2 Assemblage counts and biostratigraphy

An additional set of (denser) smear slides were made from the same 20 samples in order to refine the biostratigraphy by finding the first occurrence (FO) of *E. huxleyi* and the last occurrence (LO) *P. lacunosa*, and to gain robust estimates of the distribution of small and large specimens of reticulofenestrid coccoliths. Coccoliths were counted per field of view (FOV) until a minimum of 300 had been counted. Specimens were either classified as small reticulofenestrid (including *E. huxleyi, G. erisconii, G. muellerae*, and other unidentifiable small *Gephyrocapsa* species), *G. oceanica, G. caribbeicana*, or *P. lacunosa*. Presence of other types of coccoliths (beyond reticolofenestrids) was also counted.
4.3 Coccolith abundance and optical measurements

The drop samples were analyzed under a Leica DM6000B fully automated polarizing microscope and a SPOT Flex color camera. Samples were analyzed systematically by starting in the upper left corner and moving the FOV to the right with 2 mm each time. 10 FOV’s, with an area of $1.55 \times 10^4 \, \mu m^2$, were analyzed in one transect before moving down by 3 mm to start on a new row. This procedure was continued until a minimum of 50 coccoliths was measured.

Every whole and horizontally lying reticulofenestrid coccolith was photographed under circular polarization (Higgins, 2010; Bollmann, 2014; Fuertes et al., 2014), and was automatically measured by custom image processing software provided by Prof. Luc Beaufort, CEREGE Aix-en-Provence (Beaufort et al., 2014). The software determines the dimensions of the central and outer area, and uses the birefringence properties of calcite to accurately estimate the coccolith mass under circularly polarized light. Images were then saved in a predetermined folder and image data was written into a single text file. The microscope settings, light intensity (200), aperture (10) and “field” setting (20), were kept constant for all analyses. The trinocular tube was set to transmit 100% light to the camera for measurements. The threshold in the image processing software was set to 35, which worked best for filtering out most of the aragonite needles that were observed in high densities in several of the samples (see below).

The total number of reticulofenestrid coccoliths visible in each FOV was counted, as well as the number of FOV’s it took to collect and measure the minimum number of coccoliths. The amount of sediment in suspension that was pipetted onto cover glass is known, and therefore it is possible to calculate the absolute abundance of coccoliths per gram sediment of each sample. The absolute coccolith abundance was calculated using the following equation (Koch & Young, 2007; Bordiga et al., 2015):

$$X = \frac{N \times A}{f \times n \times W}$$  \hspace{1cm} (1)

where $X$ is the number of coccoliths per gram (N g$^{-1}$), $N$ is the total number of coccoliths counted per sample, $A$ is the area of the cover glass ($\mu m^2$), $f$ is the area of one FOV ($\mu m^2$), $n$ is the number of FOV’s counted, and $W$ is the weight of dry sediment on the cover glass (g). Since the weighted dry sediment was diluted in 30 ml suspension, from which 1.5 ml was pipetted onto the cover glass, the above equation can be modified to:

$$X = \frac{N \times A \times V_{tot}}{f \times n \times \omega \times V_{sus}}$$  \hspace{1cm} (2)

where $\omega$ is the weight of the initially dried sediment (g), $V_{tot}$ the total volume of the suspension (ml), and $V_{sus}$ the volume of the suspension that was pipetted onto the cover glass (ml).
Only coccoliths that were identified as reticulofenestrid were measured, and no further distinction was made between species. The reasoning behind this is that size definitions throughout the literature are not uniform and even taxon names have not been used consistently; reticulofenestrid coccoliths are a large intergradational group, which makes any division arbitrary (Young, 1998). To avoid bias in the sampling method, the coccoliths were not sorted initially in a pre-determined size category. The measured coccoliths were afterwards labeled small (S), medium (M) or large (L), by comparing the images within each sample and grouping them within these size classes.

4.4 Data handling

The size and thickness measurements were stored in text files and compiled into an excel table (Appendix 3). Depth, age, and counts were noted in a separate table. All data was also saved in CSV file format, in order to read the data in R. Graphical representations of data were created in R and compiled in Adobe Illustrator. Simple linear regression analyses were performed on the relationships between mass and size, and mass and thickness.
5. Results

5.1 Lithostratigraphy and sediment characteristics

Shipboard observations (Gallagher et al., 2017) and own inspection of the individual sediment samples, following Dunham classification (Dunham, 1962), from top to bottom indicate a change from unlithified homogeneous olive-gray to brown/greenish-gray packstone in the upper 11 m, to light colored grey unlithified mudstone to wackestone with few black particles (<0.5 mm) between 11 to ~40 m depth in core. Between 40 to ~60 m a gradual change is observed from unlithified greenish-grey packstone to wackestone to partially lithified white to cream wackestone (Fig. 5). Under the microscope there are two clear intervals with samples containing micrometer-scale aragonite needles (Fig. 6), which correspond to the grey intervals with black particles and the chalky light grey samples, respectively.
Figure 5. Lithostratigraphic summary of Site U1461, adapted from Gallagher et al. (2017). Descriptions are in text. Splice intervals are marked in red, with black pointers showing sample positions in splice. The deepest sample analysed in this study comes from core U1461B-9H3 at a depth of 63.05 m CSF-A.
Figure 6. Assemblage with various reticulofenestrid coccoliths and aragonite needles in sample U1461C-4H4 photographed in circular polarized light.

The aragonite needles appear in low density in Sample U1461B-5H4-25 cm. A peak density follows in the next three samples: U1461C-4H6-5 cm, U1461C-4H4-5 cm, and U1461B-4H5-5 cm. Above, slightly lower densities were observed in samples U1461B-4H3-5 cm, U1461A-5H3-85 cm, and U1461B-3H5-5 cm. A short hiatus without aragonite is observed in two samples before its reappearance in sample U1461C-2H3-5 cm, which is the youngest sample in the series and has similar aragonite density compared to the previous three aragonite-containing samples.

5.2 Biostratigraphy and age model

The shipboard biostratigraphic age model of Site U1461 was based on core-catcher samples, at 10 to 20 m intervals at Holes A, B and C (Gallagher et al., 2017). In this study, smear slides were prepared of all samples in order to verify, and possibly refine, this biostratigraphy for the upper ~70 m. Specimens of *P. lacunosa* were very rare, although one was identified in sample U1461B-5H4-25 cm, at a depth of 37.65 m CSF-A, which corresponds with shipboard observations. Its last occurrence defines the transition of Biozone NN19 to NN20 at 0.44 Ma (Gradstein *et al.*, 2012). The first specimens of *E. huxleyi* were found in sample U1461B-3H3-5 cm, at a depth of 16.95 m CSF-A, which marks the base of Biozone NN21 at 0.29 Ma. Based on these observations a linear age model was constructed by calculating the sedimentation rate for three stages: 37.65 m down to the last sample in the splice, 37.65–16.95 m and 16.95–0 m (see Fig. 7).
Figure 7. Age-depth model and linear sedimentation rates at Site U1461, used to determine sample ages. Shown are two biostratigraphic datums: the first occurrence (FO) of *Emiliania huxleyi* at 17.65 m and the last occurrence (LO) of *Pseudoemiliania lacunosa* at 37.06 m.

5.3 Coccolith assemblages

The majority (over 90%) of observed coccoliths belong to the genus *Gephyrocapsa*. Very few *Reticulofenestra* specimens were identified. In the top 290 ka *E. huxleyi* (Fig. 8A) is present although sometimes hard to distinguish in cross-polarized light from similar sized small *Gephyrocapsa* species. *Pseudoemiliania* was rarely observed, but its morphology is quite distinct with large open area and slits between distal shield elements (Fig. 8B). Small gephyrocapsids either have a very thin bridge or lost their bridge through damage (Fig. 8C-E). These specimens include the very small *G. ericsonii* with the characteristic thin bridge, and the small to medium sized *G. muellerae* with its bridge at low angle to the long axis (Bollmann, 1997). The large specimens in the samples were *G. oceanica* (Fig. 8F-H) with a thick inner tube and its bridge at high angle to the long axis, and *G. caribbeana* with an almost closed central area and the bridge at intermediate angle. Specimens of *G. oceanica* without bridge (Fig. 8F and I) were also observed. Overgrowth was most clearly observed in large species, which appear bigger and brighter (Fig. 8H).
Figure 8. Reticulofenestrid coccoliths from Site U1461. Images taken under cross-polarized light (left), and images taken under circularly polarized light (right). (A) *E. huxleyi*. (B) *P. lacunosa*. (C-D) small *Gephyrocapsa*. (E) *G. oceanica*. (F) *G. oceanica* without bridge. (G) *G. oceanica* with overgrowth.

5.4 Coccolith counts and measurements

The FOV of the SPOT Flex color camera on the Leica DM6000B has an area of $1.55 \times 10^4 \, \mu m^2$. The absolute coccolith abundance could be calculated from the drop samples using equation 2, and is shown as specimens per gram sediment at different depths in Fig. 9A. Absolute abundance varies between $1.07 \times 10^8$ and $2.85 \times 10^9 \, N \, g^{-1}$. Several peaks in abundance occur in the first interval with aragonite needles between 20 and 35 m CSF-A (300-440 ka), with values between $2.5 \times 10^9$–$3.0 \times 10^9 \, N \, g^{-1}$. Another peak occurs during the second interval with aragonite needles near 11.5 m CSF-A (160-210 ka) with $1.57 \times 10^9 \, N \, g^{-1}$.

The change by depth in relative abundance of these two species is shown in Fig. 9B. On the whole, small reticulofenestrids are the dominant species. Only one specimen of *P. lacunosa* was encountered in the deeper samples, which was in sample U1461B-5H4-25 cm. Below 20 m (>300 ka) there is a relative low abundance of both *G. oceanica* and *G. caribbeanica* at around 10% each. After the first *E. huxleyi* appear (~290 ka), there is a decrease in *G. caribbeanica* (~240 ka), which is followed by an increase in *G. oceanica*. After the upper aragonite-dominated interval *G. oceanica* maintains a high relative abundance between 30-50%, while *G. caribbeanica* disappeared. Other species sometimes encountered include *Calciscus leptoporpus*, *Coccolithus pelagicus*, and *Umbilicosphaera sp*.

The presence of the two large *Gephyrocapsa* species would strongly influence the outcome of the average mass, and the dataset was therefore split into two groups: one with the large specimens (L) and the other with the small and medium sized specimens (S + M), as defined during image analysis. Per sample, and for each variable, the mean, standard deviation (SD) and standard error of the mean (SE) are given in Table 1. Size and mass of small coccoliths vary by depth (Fig. 9E-F) and follow the same pattern as abundance, while large coccoliths (Fig. 9C-D) mainly show a drop in both size and mass after the last aragonite needle interval (160-210 ka).
Table 1. Summary of coccolith measurements per sample, with Depth CSF-A in m. N is number of specimens. Per gram is the number of specimens per gram sediment. % Large is the relative amount of large specimens per sample.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Depth CSF-A (m)</th>
<th>N</th>
<th>S+M</th>
<th>L</th>
<th>Per gram (N g⁻¹)</th>
<th>% Large</th>
<th>Size S+M (μm)</th>
<th>Size L (μm)</th>
<th>Mass S+M (pg)</th>
<th>Mass L (pg)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>SD</td>
<td>SE</td>
<td>Mean</td>
<td>SD</td>
<td>SE</td>
<td>Mean</td>
<td>SD</td>
<td>SE</td>
</tr>
<tr>
<td>U1461C-1H-1, 5 cm</td>
<td>0.05</td>
<td>50</td>
<td>46</td>
<td>4</td>
<td>5.18E+08</td>
<td>8.00</td>
<td>2.08</td>
<td>0.55</td>
<td>0.08</td>
<td>3.96</td>
</tr>
<tr>
<td>U1461C-1H-3, 5 cm</td>
<td>3.05</td>
<td>51</td>
<td>43</td>
<td>8</td>
<td>6.61E+08</td>
<td>15.69</td>
<td>2.13</td>
<td>0.49</td>
<td>0.08</td>
<td>3.83</td>
</tr>
<tr>
<td>U1461B-2H-2, 5 cm</td>
<td>5.95</td>
<td>51</td>
<td>48</td>
<td>3</td>
<td>6.90E+08</td>
<td>5.88</td>
<td>2.33</td>
<td>0.56</td>
<td>0.08</td>
<td>4.30</td>
</tr>
<tr>
<td>U1461B-2H-4, 5 cm</td>
<td>8.95</td>
<td>51</td>
<td>47</td>
<td>4</td>
<td>1.17E+09</td>
<td>7.84</td>
<td>2.33</td>
<td>0.59</td>
<td>0.09</td>
<td>4.08</td>
</tr>
<tr>
<td>U1461C-2H-3, 5 cm</td>
<td>11.45</td>
<td>52</td>
<td>26</td>
<td>26</td>
<td>1.57E+09</td>
<td>50.00</td>
<td>2.68</td>
<td>0.57</td>
<td>0.11</td>
<td>4.01</td>
</tr>
<tr>
<td>U1461C-2H-5, 5 cm</td>
<td>14.45</td>
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<td>43</td>
<td>8</td>
<td>1.85E+08</td>
<td>15.69</td>
<td>1.86</td>
<td>0.57</td>
<td>0.09</td>
<td>4.47</td>
</tr>
<tr>
<td>U1461B-3H-3, 5 cm</td>
<td>16.95</td>
<td>58</td>
<td>54</td>
<td>4</td>
<td>7.93E+08</td>
<td>6.90</td>
<td>1.88</td>
<td>0.53</td>
<td>0.07</td>
<td>4.87</td>
</tr>
<tr>
<td>U1461B-1H-5, 5 cm</td>
<td>19.95</td>
<td>54</td>
<td>51</td>
<td>3</td>
<td>2.79E+09</td>
<td>5.56</td>
<td>1.82</td>
<td>0.36</td>
<td>0.05</td>
<td>4.91</td>
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<tr>
<td>U1461A-5H-3, 85 cm</td>
<td>24.35</td>
<td>51</td>
<td>44</td>
<td>7</td>
<td>2.34E+09</td>
<td>13.73</td>
<td>1.82</td>
<td>0.39</td>
<td>0.06</td>
<td>4.71</td>
</tr>
<tr>
<td>U1461B-4H-3, 5 cm</td>
<td>26.45</td>
<td>53</td>
<td>48</td>
<td>5</td>
<td>2.85E+09</td>
<td>9.43</td>
<td>2.14</td>
<td>0.42</td>
<td>0.06</td>
<td>5.16</td>
</tr>
<tr>
<td>U1461B-4H-5, 5 cm</td>
<td>29.45</td>
<td>51</td>
<td>43</td>
<td>8</td>
<td>2.43E+09</td>
<td>15.69</td>
<td>2.05</td>
<td>0.35</td>
<td>0.05</td>
<td>4.62</td>
</tr>
<tr>
<td>U1461C-4H-4, 5 cm</td>
<td>31.89</td>
<td>52</td>
<td>45</td>
<td>7</td>
<td>2.71E+09</td>
<td>13.46</td>
<td>2.10</td>
<td>0.57</td>
<td>0.09</td>
<td>4.77</td>
</tr>
<tr>
<td>U1461C-4H-6, 5 cm</td>
<td>34.89</td>
<td>51</td>
<td>42</td>
<td>9</td>
<td>2.05E+09</td>
<td>17.65</td>
<td>2.31</td>
<td>0.38</td>
<td>0.06</td>
<td>4.75</td>
</tr>
<tr>
<td>U1461B-5H-4, 25 cm</td>
<td>37.65</td>
<td>52</td>
<td>43</td>
<td>9</td>
<td>1.23E+09</td>
<td>17.31</td>
<td>1.91</td>
<td>0.41</td>
<td>0.06</td>
<td>4.40</td>
</tr>
<tr>
<td>U1461A-7H-1, 100 cm</td>
<td>40.55</td>
<td>52</td>
<td>48</td>
<td>4</td>
<td>4.17E+08</td>
<td>7.69</td>
<td>1.81</td>
<td>0.32</td>
<td>0.05</td>
<td>4.45</td>
</tr>
<tr>
<td>U1461A-7H-3, 100 cm</td>
<td>43.55</td>
<td>52</td>
<td>48</td>
<td>4</td>
<td>5.09E+08</td>
<td>7.69</td>
<td>1.70</td>
<td>0.34</td>
<td>0.05</td>
<td>4.68</td>
</tr>
<tr>
<td>U1461A-7H-5, 25 cm</td>
<td>45.75</td>
<td>51</td>
<td>44</td>
<td>7</td>
<td>7.43E+08</td>
<td>13.73</td>
<td>1.70</td>
<td>0.36</td>
<td>0.05</td>
<td>4.25</td>
</tr>
<tr>
<td>U1461C-6H-5, 25 cm</td>
<td>52.65</td>
<td>53</td>
<td>48</td>
<td>4</td>
<td>1.17E+09</td>
<td>9.43</td>
<td>1.81</td>
<td>0.38</td>
<td>0.06</td>
<td>4.16</td>
</tr>
<tr>
<td>U1461C-7H-4, 25 cm</td>
<td>60.65</td>
<td>51</td>
<td>49</td>
<td>2</td>
<td>1.07E+08</td>
<td>3.92</td>
<td>1.94</td>
<td>0.40</td>
<td>0.06</td>
<td>4.37</td>
</tr>
<tr>
<td>U1461B-9H-3, 25 cm</td>
<td>63.05</td>
<td>51</td>
<td>46</td>
<td>5</td>
<td>6.14E+08</td>
<td>9.80</td>
<td>1.73</td>
<td>0.48</td>
<td>0.07</td>
<td>4.48</td>
</tr>
</tbody>
</table>
During the second aragonite interval between 10-13 m CSF-A (160-210 ka), concurrent peaks in small coccolith mass and size, and elevated absolute abundances are observed. 4 extra smear slides were prepared, 2 before and 2 after the observed peaks to investigate changes in relative abundance (Fig. 9B) and these additional results confirm that the patterns observed between 160 and 210 ka are real. Elevated values in relative abundance *G. oceanica* are observed during and extending above the second aragonite interval.
Figure 9. Counts and measurements from Site U1461 plotted on depth scale, with aragonite needles represented by the grey areas. (A) Absolute abundance per gram sediment calculated from number of specimens per FOV in drop samples. (B) Relative abundance of *G. oceanica* (green) and *G. caribbeanica* (blue), calculated from smear slide counts. (C) Mean mass of large coccoliths (*G. oceanica* and *G. caribbeanica* combined). (D) Mean size of large coccoliths. (E) Mean mass of small coccoliths (*E. huxleyi*, *G. ericsonii*, *G. muellerae* and *G. small*). (F) Mean size of small coccoliths. Graphs C-F include standard errors of mean represented by the dotted vertical lines.
6. Discussion

6.1 Coccolith mass: preservation or productivity?

Absolute abundance as well as small coccoliths mass show a similar pattern and both have peaks during the two intervals with aragonite needles. During the second interval, the relative abundances of *G. caribbeanica* and *G. oceanica* species are elevated in parallel with peaks in absolute abundance and small coccolith mass. Mass and size are considered to reflect the rate of calcification and thus represent a direct indication for productivity. Mass increases exponentially with larger coccolith size (Fig. 10A), and is strongly correlated with both size and thickness (Fig. 10B), which signifies that any change in mass is a direct result from a change in size. Nannofossil preservation was moderate to good, but corresponding peaks in *G. oceanica* and *G. caribbeanica* abundance and small reticulofenestrid mass might indicate preferential dissolution of the smallest and lightly calcified coccoliths. However, the presence of aragonite counters this, as it would have dissolved first (Hay, 2004). As will be discussed below, the aragonite needles could be related to an allochtonous origin of the sediments, which indicates that the sediment content during these intervals may have been diluted. A detailed study of sediment composition and calculate accumulation rates would shed more light on this possibility.

Some coccoliths appeared larger and thicker due to overgrowth; this is also visible in SEM images from shipboard samples (Gallagher et al., 2017a). Overgrowth occurs in super-saturated carbonate environments (Dedert et al., 2014), and may happen post-depositionally as early diagenesis. In other studies it was noted that overgrowth occurs on distal and proximal shield elements, making coccoliths grow both larger and thicker (cf. Fig 10C), as well as on tube elements resulting in a smaller central area (Crudeli et al., 2004; Lübke et al., 2015). The degree of overgrowth is difficult to quantify under polarized light, and would require analysis in SEM to determine how much coccoliths are affected by it. In this study the observed patterns in size and mass likely shows the effect of overgrowth, although it does not rule out an adaptive response to climate change nor a change in species composition among small reticulofenestrads. Moreover, the variation in size and mass, whether due to overgrowth or adaptive response, can still prove useful for paleoenvironmental interpretation.
Figure 10. Scatterplots of raw data and log transformed data for mass versus size. (A) Mass increases exponentially according to power function shown in the upper left of graph. Nonlinear Least Squares, p<0.001. (B) Linear regression of normalized data with the adjusted $R^2$ shown in upper left of graph. Ordinary Least Squares, p<0.001. (C) Figure adapted from Lübke et al. (2015) showing the primary areas affected by overgrowth on coccoliths.
6.2 Central area measurements: biostratigraphy?

Segmentation of the central area in large *Gephyrocapsa* specimens with a strongly calcified bridge leads to odd shaped central areas where only one part of the central area was measured. *E. huxleyi*, dominant in younger sediments, has no bridge and a relative large open central area. Some *Gephyrocapsa* coccoliths had their bridge broken off, while others like *G. ericssonii*, have only a very thin bridge that was not always detected by the software.

The *E. huxleyi* Acme base was dated at 70 ka (Gartner, 1977), but was not detected in this data set since all small reticulofenestrid coccoliths were grouped together. *E. huxleyi* in general has a more open central area than *Gephyrocapsa* species, which is a measurement included in the data. Fig. 8 shows the log-normalized data for the central area for both small and large coccoliths, which can serve as a measure for “openness”. The FO of *E. huxleyi* in the samples from Site U1461 was dated at 290 ka (cf. geological timescale of Gradstein et al. 2012). In the Fig. 11A there is a trend visible in small coccoliths towards more open species, which could indicate an increase in relative abundance of *E. huxleyi*. However, the openness in large species (Fig. 11B) does not follow a similar pattern as would expected from Fig. 11C. A clear reduction in the abundance of *G. caribbeanica* occurs during Marine Isotope Stage (MIS) 7, which corresponds with previous reports on the global synchronous event of last common occurrence of this species at the base of MIS 7 around 243 ka (Flores *et al.*, 2010).
Figure 11. Log transformed data of the central area in (A) small reticulofenestrid coccoliths, (B) large reticulofenestrid coccoliths. (C) Relative abundances of *G. oceanica* and *G. caribbeanica* as reference for the figures above, and at the bottom the MIS timescale.

### 6.3 Paleoenvironmental context

Samples from Site U1461 represent a coastal marine setting that changed from a shallow coastal marine environment to deeper outer shelf environments between glacial and interglacial periods; *P. lacunosa* is well known to have been an open marine species predominantly, which may explain why it occurs only sporadically in samples from this site. The presence of aragonite is commonly associated with tropical carbonate factories, with biotically controlled precipitates from autotrophic organisms (Schlager, 2005). This implies that the drowned reefs near Site U1461 were active during the last 500 ka, which is in line with what has been suggested in earlier studies (Gallagher *et al.*, 2014b).

Plotting the results against age (Fig. 12A-C), it is possible to compare the patterns observed in this study with paleoenvironmental parameters from Site MD002361, near the North West Cape of
Australia (Fig. 2). The total dust (Fig. 12D) represents the wind strength, and is based on two aeolian end members: the Log-ratios of Zr/Fe and Ti/Ca, which indicate a terrigenous origin, and the grain-size (Stuut et al., 2014). The Log (Fe/Ca) record (Stuut et al., 2014), which is used here (Fig. 12E), varies in parallel with the δ¹⁸O ratio (Spooner et al., 2011), and shows a clear pattern of glacial-interglacial changes: being high during clay-rich interglacial stages and low during CaCO₃-rich glacial stages. Included in the figure are the Marine Isotope Stages (MIS) which are based on the LR04 benthic δ¹⁸O stack (Lisiecki & Raymo, 2005).

A peak in small coccolith mass (Fig. 12B) can be observed during MIS 11, with elevated values sustained into MIS 10. Another increase in small coccolith mass occurs at the end of MIS 7, and matches the increase in relative abundance of G. oceanica, as well as the decline of G. caribbeanica (Fig. 12C). During both MIS 11 and MIS 7 there is also an increase in absolute abundance (Fig. 12A). The higher values in mass and an increase in relative abundance of G. oceanica in MIS 7 are linked to the high sea levels during interglacials, and may indicate higher primary productivity during this time.

During MIS 11 the absolute abundance increases while at the same time there is a decrease in wind strength (Fig. 12D). The abundance is much lower than in calcareous ooze sediments, even at the peaks it is still much lower (Bordiga et al., 2015). This could either be the result of lower productivity, or more importantly, a larger influx of sediment on the continental shelf as compared to the open ocean (Boeckel et al., 2006). Nevertheless, assuming linear sedimentation rates, the observed patterns in abundance and mass may well indicate fluctuations in primary productivity. Three samples around 400 ka (Samples U1461B-4H5-5 cm, U1461C-4H4-5 cm, and U1461C-4H6-5 cm) have the highest observed densities of aragonite needles, matching the warm and humid MIS 11. Other research groups involved in Expedition 356 will provide stable isotope stratigraphies that will further constrain the biostratigraphic age model and facilitate correlations with data from this study (Henderiks, pers. comm. 2017).
Figure 12. Absolute abundance, mean mass of small coccoliths and relative abundance of large coccoliths plotted on the age model (A-C) and paleoenvironment at the North West Cape (D-E), with aragonite needles represented by the grey areas. (A) Absolute abundance per gram sediment calculated from number of specimens per FOV in drop samples. (B) Mean mass of small coccoliths (\textit{E. huxleyi}, \textit{G. ericsonii}, \textit{G. muellerae} and \textit{G. small}), with standard error of mean represented by the vertical dotted lines. (C) Relative abundance of \textit{G. oceanica} (green) and \textit{G. caribbeanica} (blue), calculated from smear slide counts. (D) Total dust of sediment core MD00-2361 from Stuut \textit{et al.} (2014). (E) Log (Fe/Ca) from the XRF scan of sediment core MD00-2361 from Stuut \textit{et al.} (2014) plotted on age scale from Spooner \textit{et al.} (2011). Marine Isotope Stages (M.I.S.) indicated above log (Fe/Ca).
6.4 Marine Isotope Stage 11

MIS 11 was an unusually long and warm interglacial with temperatures comparable to the current interglacial, and has therefore been the focus of much interest (Lisiecki & Raymo, 2005; Raymo & Mitrovica, 2012; Candy et al., 2014). Spooner et al. (2011) reported average SST of 26.7–28.6 °C and a strong LC during MIS 11. Data from Stuut et al. (2014) indicate that average wind speed was low during this MIS 11, which indicates that the continental climate was more humid. With the collapse of ice sheet during this interval (Raymo & Mitrovica, 2012), sea level had risen up to 6-13 m above the present-day value in the second half of MIS 11.

White clouds of fine-grained aragonite in the water column are today observed on the Bahamian banks, Hawaii, Florida Bay and the Persian Gulf, and referred to as “whitings” (Larson & Mylroie, 2014). This phenomenon has received much attention but is still not yet fully understood, and several models for the cause of whitings have been proposed: re-suspension through fish or micro-turbulent bursts (tidal or wind driven), direct precipitation of aragonite due to high carbonate saturation, or biological mediation (green algae, e.g. Halimeda). Whitings normally occur in the same area indicating a point source (Robbins et al., 1997), and are known to originate and persist during long periods with weak winds (Boss & Neumann, 1993).

The Bahamian whitings are probably the result of the direct precipitation of aragonite covering the shallow and more limited areas (Fig. 13), and are consequently swept off the bank into deeper waters (Robbins & Blackwelder, 1992; Robbins et al., 1997; Kendall et al., 2007). This process may therefore be analogous to the observations in cores from Site U1461 on the Australian Northwest Shelf, which is a carbonate ramp comparable to the Great Bahama Bank (James et al., 2004). The sediment content was thus likely diluted by whiting material overflowing from the updip shallow-water platform.
6.5 Abundance of *Gephyrocapsa oceanica*

*Gephyrocapsa oceanica* abundance increases as *G. caribbeana* abundance declines. This could point to an ecological replacement of *G. caribbeana* by *G. oceanica*. The occurrence of “*G. oceanica*-enriched flora” is generally correlated with higher water temperature, lower salinity, and lower water density in the upper-photic zone community (Takahashi & Okada, 2000). The shift toward *G. oceanica* since MIS 7 (Fig. 12C) appears during an interglacial but could be related to: intensified aridity, or rising sea level and the subsequent drawing of the nearby reef. Both scenarios would require more core samples to be analysed to improve the resolution of *G. oceanica* abundance patterns during this time interval.
7. Conclusion

The primary goal of this study was to identify patterns in absolute abundance of reticulofenestrid coccoliths during the last 500 ka, and analyse their variation in size and mass. Overall, absolute abundance of coccoliths was low (varying between $1.07 \times 10^8$ and $2.85 \times 10^9$ N g$^{-1}$), indicating moderate fluxes or high dilution rates with other sediment components. Increased absolute abundance and small reticulofenestrid coccolith mass occur during the aragonite-dominated intervals. This is especially evident during MIS 11, which is considered the warmest and most humid interglacial in the last 500 ka.

It follows that the investigated site was possibly affected by whiting events originating from the nearby shallow lagoon up the slope. The aragonite needles were transported and deposited on the outer slope, thereby diluting the sediments recovered at Site U1461. As a result from global sea level changes, Site U1461 varied between a shallow coastal marine environment during glacial periods and deeper outer shelf environment during interglacials. The correspondence of data from this study with local events during MIS 11 indicate that the linear age model used in this study is a close approximation of the actual age of the sediment.

Another aim was to determine the variation in relative abundances of small reticulofenestrids, *G. oceanica* and *G. caribbeanica* over the last 500 ka. Small gephyrocapsids dominate samples from the investigated period. The decline of *G. caribbeanica* during MIS 7 corresponds to the timing of their global disappearance (around 243 ka), and occurs during the second interval of aragonite needles, pointing to the possible drowning of the upslope reef during MIS 7. The increase in relative abundance of *G. oceanica* within MIS 7 may indicate a favorable environment (warm and low-salinity water) for this species, or the available ecospace after the decline of *G. caribbeanica*. 
8. Acknowledgments

First and foremost, I wish to thank Jorijntje Henderiks for being a wonderful and inspiring supervisor. I would also like to thank Luka Šupraha for his supervision in the lab, helping out with sample preparation, and data handling. Many thanks go to Nicolás Campione for his useful advice with R, and the helpful discussions. Gratitude goes to Yves Gally at CERE GE Aix-en-Provence for his assistance with the SYRACO software. I also like to thank Miriam Heingård for the last minute help on translating my summary to Swedish.
9. References


Dunham, R.J. (1962). Classification of carbonate rocks according to depositional textures.


Appendix 1: taxonomic appendix

Calcareous nannofossils

*Emiliania huxleyi* (Lohmann, 1902) Hay and Mohler in Hay et al., 1967
*Gephyrocapsa caribbeana*ica Boudreaux and Hay, 1967
*Gephyrocapsa ericsonii* McIntyre and Bé, 1967
*Gephyrocapsa muellerae* Bréhéret, 1978
*Gephyrocapsa oceanica* Kamptner, 1943
*Pseudoemiliania lacunosa* (Kamptner, 1963) Gartner, 1969
Appendix 2: statistical analyses

Nonlinear least squares Mass versus Size

Formula: MASS ~ a * MajorAxeOUT^b

Parameters:

|      | Estimate | Std. Error | t value | Pr(>|t|) |
|------|----------|------------|---------|----------|
| a    | 0.241785 | 0.009154   | 26.41   | <2e-16   *** |
| b    | 2.849938 | 0.024848   | 114.69  | <2e-16   *** |

---

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.324 on 1036 degrees of freedom

Number of iterations to convergence: 6
Achieved convergence tolerance: 3.861e-07

Linear model fit Log Mass versus Log Size

Call:

```r
lm(formula = log.mass ~ log.size, data = log.data)
```

Residuals:

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<th></th>
<th>Min</th>
<th>1Q</th>
<th>Median</th>
<th>3Q</th>
<th>Max</th>
</tr>
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<td>0.04772</td>
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</table>

Coefficients:

|                | Estimate | Std. Error | t value | Pr(>|t|) |
|----------------|----------|------------|---------|----------|
| (Intercept)    | -1.37741 | 0.02513    | -54.81  | <2e-16   *** |
| log.size       | 2.784938 | 0.02988    | 93.22   | <2e-16   *** |

---

Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.3485 on 1036 degrees of freedom
Multiple R-squared:  0.8935,    Adjusted R-squared:  0.8934
F-statistic: 8689 on 1 and 1036 DF,  p-value: < 2.2e-16
Appendix 3: data tables
Table 2. (Continued on next page.) Summary of data collected from drop slides and smear slides. Size and mass were also shown in Table 1. Here: total specimens measured (N), small specimens (S), medium specimens (M), and large specimens (L).

<table>
<thead>
<tr>
<th>Sample</th>
<th>Depth CSF-A (m)</th>
<th>Age (ka)</th>
<th>N</th>
<th>S</th>
<th>M</th>
<th>L</th>
<th>Size S+M (µm)</th>
<th>Size L (µm)</th>
<th>Mass S+M (pg)</th>
<th>Mass L (pg)</th>
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<td>4</td>
<td>1.81</td>
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<td>0.07</td>
<td>4.48</td>
</tr>
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</table>
Table 3. (Continued.) Summary of data collected from drop slides and smear slides. Shown here: total counts from drop slides and specimens per gram sediment, followed by counts from smear slides.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Depth CSF-A (m)</th>
<th>Age (ka)</th>
<th>Count (Drop)</th>
<th>Per gram (N g⁻¹)</th>
<th>Small reticulo-fenestrid</th>
<th>G. oceanica</th>
<th>G. caribb.</th>
<th>P. lacunosa</th>
<th>Others (non-ret.)</th>
<th>Total reticulo-fenestrid</th>
<th>Count (Smear)</th>
</tr>
</thead>
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<td></td>
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