



Stockholm
University

Bachelor Thesis

Degree Project in
Marine Geology 15 hp

Pleistocene Planktonic Foraminifera Ecology: Insights from Oxygen and Carbon stable isotope analysis in North Atlantic deep sea sediment cores

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Stockholm 2024

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Abstract

Neogloboquadrina Pachyderma is a planktonic foraminifer that makes up more than 90% of the total planktonic foraminifera assemblage in the Arctic ocean, making it useful as a paleoceanographic proxy signal-carrier for obtaining information about past Arctic and North Atlantic Ocean conditions. Early in its evolutionary history the species used to be described as a bipolar cosmopolitan up until the early Pleistocene, when it started adapting to colder water and became a polar specialist, and this coincides with a genetic split between the genotypes of the species that took place at 1.8-1.3Ma. In order to use *N. pachyderma* for paleoceanographic proxy reconstructions it is important to understand the biology and ecology of the species through its evolutionary history and therefore the aim of this study is to find clues on how and when *N. pachyderma* became a polar specialist. By measuring the stable oxygen and carbon isotope ratio in the tests of *N. pachyderma* and 5 other arctic foraminifera species we can create a multi-species depth profile and see if the species has moved through the water column between the early and late Pleistocene. The results show that *N. pachyderma* has migrated down the water column in relation to the other species, which points to an adaptation to colder water in *N. pachyderma* rather than a global change in the isotopic composition of the seawater.

Table of contents

1. Introduction	3
2. Background	5
2.1 <i>Study area</i>	5
2.2 <i>North Atlantic Foraminifera</i>	6
2.3 <i>Stable Isotopes in Foraminifera tests</i>	7
2.4 <i>Glacial and Interglacial periods during the Pleistocene</i>	11
3. Method	12
3.1 <i>Picking foraminifera</i>	12
3.2 <i>Preparing samples for the mass spectrometer</i>	14
4. Results	15
5. Discussion	19
6. Conclusions	22
7. References	24
8. Appendices	27

1. Introduction

Planktonic foraminifera are single-celled marine protists with calcareous tests that live in the upper 500m of the oceanic water column and their preferred depth within that column depends on their season of growth, ecology and life stage. Their calcareous tests are widely used as a geochemical proxy for past ocean conditions since the stable isotopic composition of the tests are dependent on the isotopic ratio in the waters in which they calcify (Birch et al., 2013). The high-latitude North Atlantic and Nordic Seas are dominated by planktonic foraminifera belonging to the genus *Neogloboquadrina* throughout the late Neogene to Quaternary, in particular *Neogloboquadrina pachyderma* has been dominating these assemblages since the early Pleistocene (Berggren et al., 1995a). In the Arctic ocean it makes up more than 90% of the total planktonic foraminifera assemblage, making it useful as a paleoceanographic proxy for obtaining information about past Arctic and North Atlantic Ocean conditions (Greco et al., 2019). Because of the species domination in the Arctic and North Atlantic assemblages it is considered a high-latitude specialist, but this has not always been the case (Darling et al., 2004). Up until the early Quaternary, *N. pachyderma* could be described as a bipolar cosmopolitan but after the Earth had gone through a major cooling and expansion of ice sheets in the northern hemisphere, a divergence between the genotypes of the species occurred (Darling et al., 2007). The genotype that currently resides in the high latitudes (Type 1a, Morard et al., 2024), had a genetic split from the genotypes from the other ocean basins and this divergence is maintained to this day and the arctic specialist is both genetically and geographically isolated from genotypes in the Southern hemisphere. The genetic split leading to this bipolar isolation and assumed specialization to local environments is proposed to have occurred around 1.8-1.3 million years ago, coinciding with the intensification of Northern Hemisphere cooling and glaciation (Darling et al., 2004, 2007; Huber et al., 2000). According to paleorecords it seems *N. pachyderma* started dominating the polar waters at approximately the same time as this genetic split took place but as of today there are still no clear reason as to why this happened (Kucera and Kennett, 2002).

The aim of this study is to investigate how the paleoecology of early Pleistocene *N. pachyderma* compares to the modern species, and if that information provides any insight in how *N. pachyderma* could later become a polar specialist while many other species retreated

to lower latitudes as the high latitudes cooled during the Quaternary. More specifically this study will attempt to find answers to the following questions:

1. Why was *N. pachyderma* able to become a polar specialist?
2. Did the *N. pachyderma* genetic split at 1.8-1.3 Ma correspond to a change in ecology including a shift in preferred depth habitat?

The primary hypothesis to be tested is whether *N. pachyderma* was a deep dweller prior to the genetic split, preferring colder waters, which predisposed the species for migration into cooling surface waters, whereas temperate species were excluded by the cooling climate. There are currently no papers suggesting that *N. pachyderma* was a deep dweller before the Pleistocene which is why it is necessary to investigate this in this study. In order to optimize the applicability of *N. pachyderma* as a micropaleontological and geochemical proxy, such as for sea-ice extent, or as a tracer of a particular water mass, it is important to understand and define the ecology and biology of fossil *N. pachyderma*. So as to answer these questions, I will perform a multi-species isotopic depth profiling, where I will pick specimens of 5 planktonic foraminifera species, including *N. pachyderma*, *Neogloboquadrina incompta*, *Globigerina bulloides*, *Globigerinita glutinata* and *Turborotalita quinqueloba*, and one species of benthic foraminifera, collected from cores drilled at 3 different locations in the north Atlantic (Rockall Plateau, Reykjanes Ridge and Vøring Plateau). The benthic foraminifera are used to determine what the isotopic composition is at the seafloor, since we know that benthic species live either on top of the seafloor (epifaunal) or inside the seafloor (infaunal). These samples will then be put through a mass spectrometer in order to find out the isotopic composition of carbon and oxygen in the foraminifera tests. The time period of interest is the early and late Pleistocene, when the genetic split between the northern and southern genotypes occurred and *N. pachyderma* started dominating the north Atlantic. A useful way to investigate the paleoecology of planktonic foraminifera in the geological past is to compare the oxygen and carbon stable isotope signature of their calcitic shells (Birch et al., 2013). Samples are chosen from sites with established age models, allowing the targeted time interval to be identified. The study will shed light on if and how *N. pachyderma*'s depth habitat evolved over time, leading to its specialization as a true polar species.

2. Background

2.1 Study area

The study area is located in the North Atlantic Ocean and the foraminifera samples were collected at the Vøring Plateau, Reykjanes Ridge and the Rockall Plateau (figure 1). This region experienced a strong climate change during the transition into the ice ages, and a cooling trend that began about 1.8 Ma and intensified after 1.2 Ma lowered the sea surface temperature by 2-2.5°C (McClymont et al., 2013). The Vøring Plateau lies in the Norwegian sea at about 67°N and is therefore the most northern location (Eldholm et al., 1987). Here, the North Atlantic current (NAC) extends into the Norwegian current (NC) and carries warm water into the North Sea alongside the Norwegian coast (Schmitz and McCartney, 1993). South of the Vøring Plateau is the Rockall plateau which is a shallow platform located outside the Scottish continental margin and this location is also in the path of the NAC (Jansen, 1995). The water depth at the platform is about 1000m and it is overlying the continental crust (Roberts, 1971). Reykjanes ridge is located between Greenland and Iceland where the East Greenland current (EGC), carrying cold deep ocean water, meets the Norwegian current carrying warm surface water (Dickson et al., 1990).

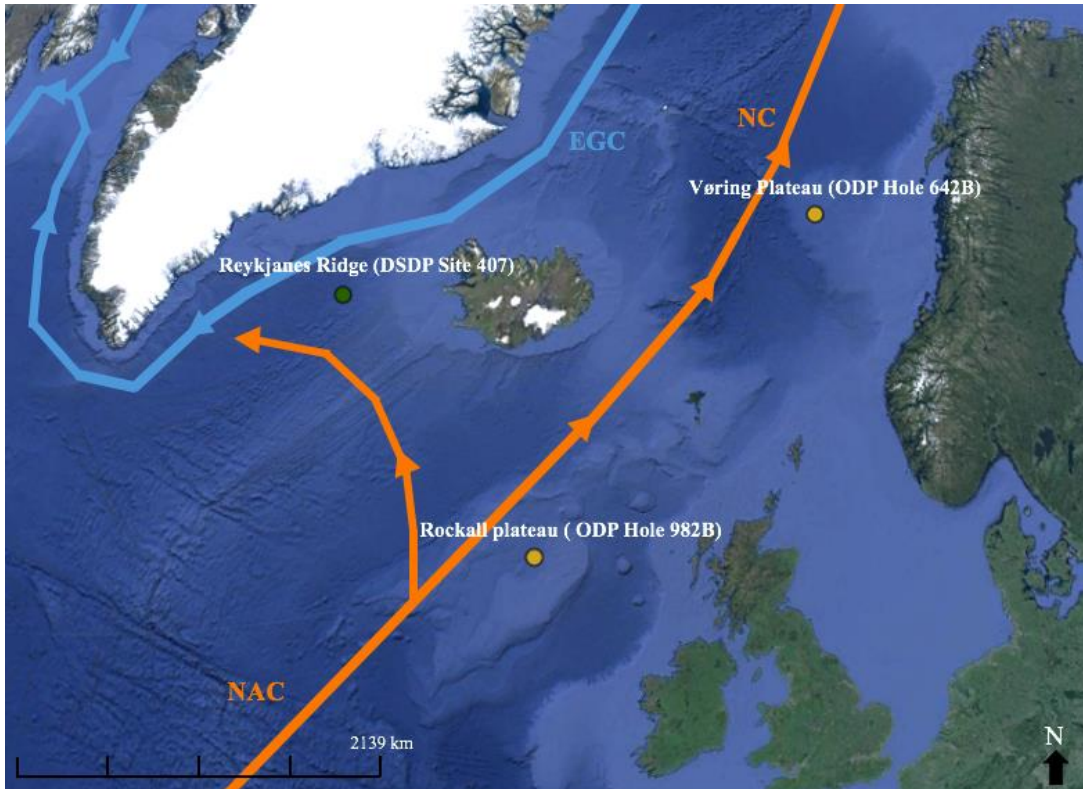


Figure 1. Map of the study area in the North Atlantic showing the locations of the cores used for the study (DSDP site 407, ODP hole 642B and ODP hole 982B) and the ocean currents that affect the area. The red arrows represent warm water currents, and the blue arrows represent cold water currents. The map is produced with google earth pro.

2.2 North Atlantic Foraminifera

Today, the foraminifera assemblages in the North Atlantic Ocean are dominated by *N. pachyderma*. The species originated about 9.3 Ma in the Southern Indian Ocean (Berggren et al., 1995a) and subsequently spread around the globe, however, its evolutionary history through the Neogene is not well documented. In present day, *N. pachyderma* thrives in cold waters with temperatures near freezing and salinities ranging from 32-35 PSU and thrives even under perennial sea ice in the Central Arctic Ocean (Carstens et al., 1997, Vermassen et al., in prep). Its preferred dwelling depth in the water column appears to be variable, with the mixed layer and upper thermocline being most densely populated (Kucera, 2007) and the depth is thought to be influenced by water temperature, chlorophyll concentrations and sea-ice cover (Carstens et al., 1997, Greco et al., 2019). Characteristic for *N. pachyderma* is that it goes through a secondary encrusting of its shell as it reaches full maturity (Spindler and Dieckmann, 1986). In the Antarctic ocean, *N. pachyderma* has been found living in sea-ice but this does not seem to be true for the Arctic genotype which is the focus of this study (Dieckmann et al., 1991). Although *N. pachyderma* is most dominant in the polar regions it can also be found in upwelling zones and subpolar regions and it can thrive in waters with temperatures ranging between -2 to +15°C although it seems to prefer the colder temperatures (Westgård et al., 2023).

Out of the 5 species of planktonic foraminifera that will be used for this study *N. pachyderma* is the only polar species while *Neogloboquadrina incompta*, *Turborotalita quinqueloba* and *Globigerina bulloides* are considered subpolar species. The habitat of *Globigerinita glutinata* also includes subpolar regions but their preferred habitat is in temperate waters and it stretches into tropical regions as well (Schiebel and Hemleben, 2017). Besides *N. pachyderma*, one of the most abundant planktonic foraminifera in cold water is *T. quinqueloba* which is a dominating species in the small-sizes planktonic foraminifera assemblages in the North Atlantic (Carstens et al., 1997). The distribution, depth habitat and recognizable characteristics of each species is summarized in table 1 and the depth habitat is based on studies of modern species.

Table 1. The distribution, depth habitat and recognizable characteristics of the planktonic foraminifera species used in this study based on existing studies on modern species.

Species	Distribution	Depth habitat	Recognizable Characteristics	References
<i>N. pachyderma</i>	Polar to subpolar regions. Temperature preference is -2 to +15°C	Mid-deep dweller (50-300 m depth)	4 chambers. Left coiling. Umbilical to slightly extra-umbilical. Thickened chamber walls in mature individuals.	Westgård et al., 2023; Schiebel and Hemleben, 2017; Greco et al., 2019; Carstens et al., 1997
<i>N. incompta</i>	Subpolar to temperate regions. Temperature preference is 10 to 14°C	Mid-deep dweller (60-150m depth)	4 chambers. Right coiling. Extra-umbilical. Umbilicus more open than <i>N. pachyderma</i>	Schiebel and Hemleben, 2017
<i>G. glutinata</i>	Subpolar to tropical regions.	Surface dweller (0-50m depth)	Umbilical aperture and can have characteristic bulla accessory. Small to medium sized.	Schiebel and Hemleben, 2017; Schiebel et al, 1995
<i>T. quinqueloba</i>	Subpolar to temperate regions. Temperature preference is where SST is 4 to 18°C	Mid-surface dweller (10-60m depth)	Small with 5 chambers. The umbilicus might be covered by an ampullate final chamber.	Carstens et al., 1997
<i>G. bulloides</i>	Subpolar to temperate regions. Temperature preference is where SST is 4 to 14°C	Surface dweller (0-50m depth)	Aperture is umbilical and wide open. Low trochospiral.	Schiebel and Hemleben, 2017

2.3 Stable Isotopes in Foraminifera tests

The majority of planktonic foraminifera species typically undergo vertical migration throughout their life cycle, with most secreting their calcitic tests within species specific depth ranges. The modern and ancient open ocean species can generally be categorized as calcifying in the mixed layer, thermocline, or subthermocline, and these environments can be identified in different species when their characteristic $\delta^{13}C$ and $\delta^{18}O$ signatures are compared relative to each other (Pearson et al., 1997, Pearson et al., 2001; Pearson and Wade., 2009; Birch et al., 2013) (figure 2). Since the isotopic composition of the foraminifera tests are dependent on the isotopic composition of the water in which they calcify, the controls of $\delta^{18}O$ and $\delta^{13}C$ in seawater is relevant for this study and will be discussed in this section.

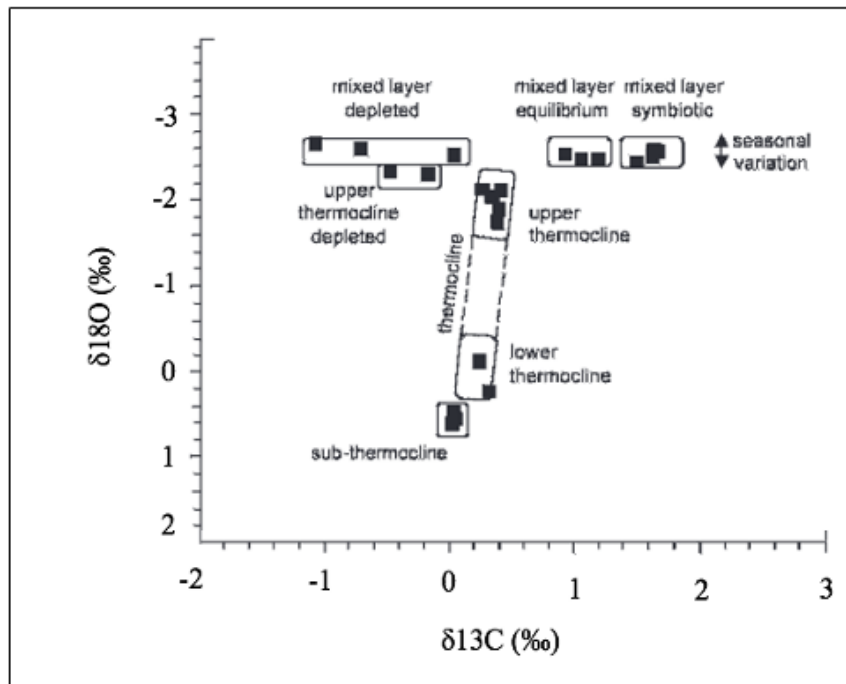


Figure 2. The different ecological niches for foraminifera based on their stable isotope composition (Pearson and Wade, 2009)

$\delta^{18}\text{O}$ in seawater can be influenced by processes that affect the seawater both globally and locally (Ravelo and Hillaire-Marcel, 2007) (figure 3). On a global scale, the main control on $\delta^{18}\text{O}$ is the amount of water stored as ice on land, known as the ice volume effect (Shackleton, 1967; Kucera, 2007). Since water molecules containing the lighter isotope ^{16}O is more easily evaporated, water vapor clouds will be enriched in ^{16}O which means that any precipitation from these clouds will also be enriched in ^{16}O . If the precipitation falls in the form of snow, it will not be returned to the ocean but instead be stored on land and thus the ocean will be depleted in ^{16}O and the foraminifera that are calcifying in these waters will have a relatively high $\delta^{18}\text{O}$ value. Once the sea ice melts ^{16}O will be released into the ocean again and $\delta^{18}\text{O}$ of the seawater will decrease (Ravelo and Hillaire-Marcel, 2007). Evaporation and precipitation also cause local changes in the seawater, as evaporation will cause the local $\delta^{18}\text{O}$ to increase and precipitation will cause the local $\delta^{18}\text{O}$ to decrease by returning H_2^{16}O molecules to the ocean. Local changes in $\delta^{18}\text{O}$ can also occur due to upwelling and advection that mixes the oxygen isotopes from different water depths (Kucera, 2007). How easily ^{18}O is incorporated into the foraminifera tests also depend on the water temperature, and tests that are calcified in cold water generally have a higher $\delta^{18}\text{O}$ value than the ones that calcify in warmer water and this is called the temperature effect.

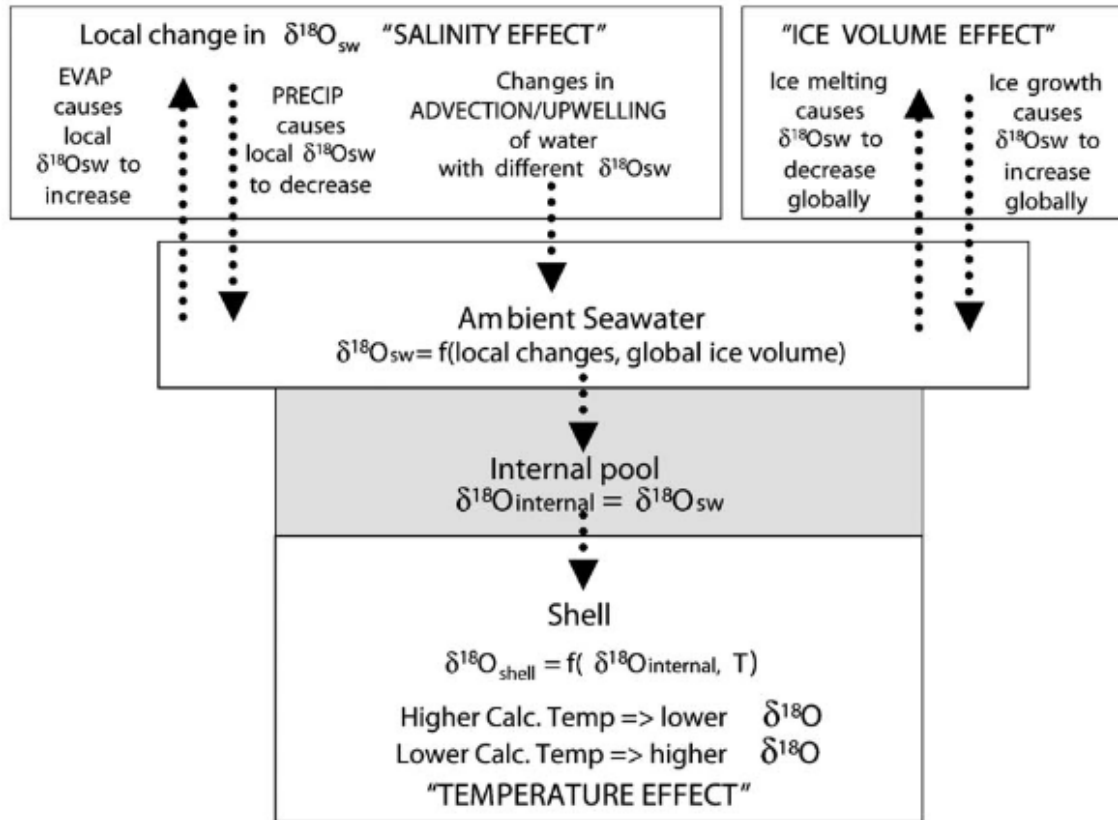


Figure 3. The global and local controls on $\delta^{18}\text{O}$ in foraminifera tests (Ravelo and Hillaire-Marcel, 2007).

The $\delta^{13}\text{C}$ of the foraminifera tests reflect the isotopic composition of the dissolved inorganic carbon (DIC) in the seawater in which they calcified and on a global scale, this is controlled by the carbon cycle and the exchange of carbon between the ocean, lithosphere, atmosphere and terrestrial biosphere (Kucera, 2007) (figure 4). Since vegetation and organic material favors ^{12}C during photosynthesis, a growing terrestrial biosphere will cause the atmosphere and the ocean to become enriched in ^{13}C and thus have a higher $\delta^{13}\text{C}$ value. As organic material dies ^{12}C will be returned to the other carbon reservoirs and $\delta^{13}\text{C}$ in the ocean will decrease. Photosynthesis can work both on a global and local scale and while terrestrial biosphere growth can affect the $\delta^{13}\text{C}$ of the global ocean, local photosynthesis and respiration can have an effect on the local seawater. The same upwelling and advections that affect $\delta^{18}\text{O}$ can also affect the local $\delta^{13}\text{C}$ in the same way and cause the isotopes to mix (Ravelo and Hillaire-Marcel, 2007).

Previous studies have shown that arctic foraminifera do not calcify in equilibrium with ambient seawater, but instead have a slight offset that is species specific and is called the vital

effect (Volkman and Mensch, 2001). One such vital effect is metabolic carbon isotope fractionation which affects most species with test sizes smaller than 300 μ m, including larger species in their juvenile stage. This effect favors the lighter isotope ^{12}C and creates a negative offset in $\delta^{13}\text{C}$ compared to the ambient water and since the effect is linked to test size it is important to use strict size fractions in order to make out isotopic differences between species caused by their biology (Birch et al., 2013).

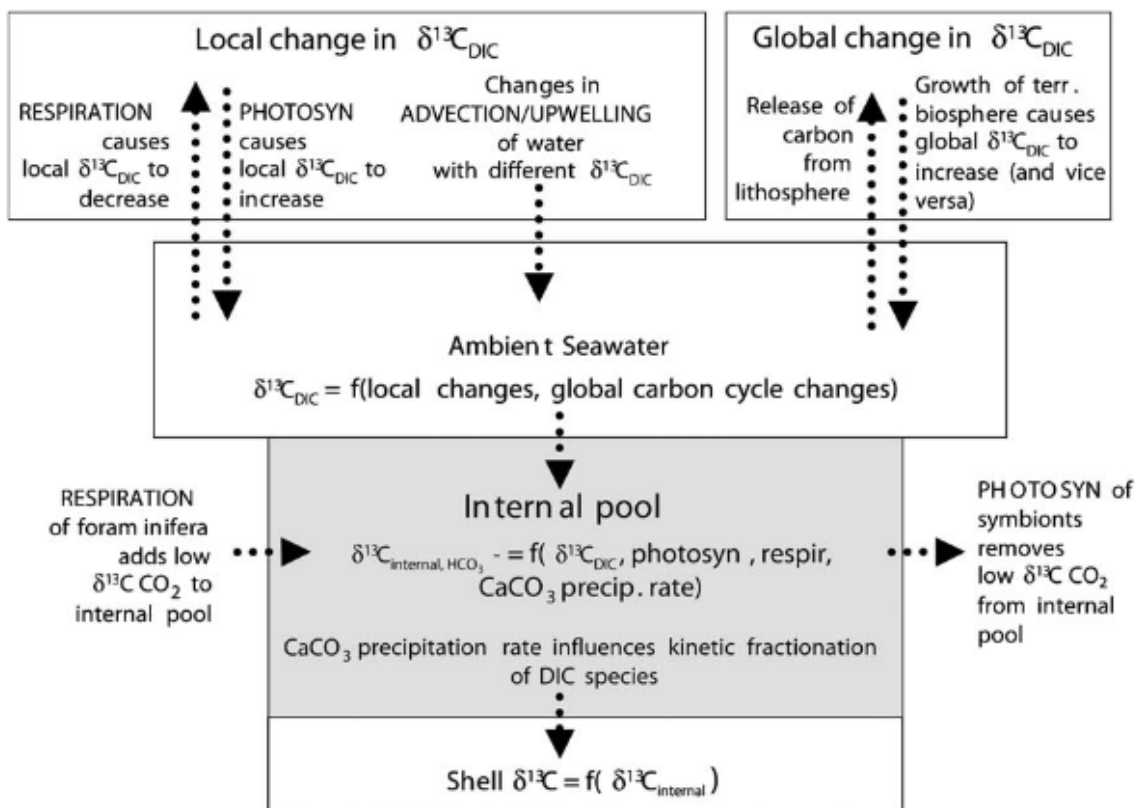


Figure 4. The global and local controls on $\delta^{13}\text{C}$ in foraminifera tests (Ravelo and Hillaire-Marcel, 2007).

2.4 Glacial and Interglacial periods during the Pleistocene

The Pleistocene epoch is known for its glacial and interglacial cycles and the initiation of the Northern hemisphere glaciation (Willeit et al., 2019). A glacial period is characterized by colder climate and extensive ice sheet growth and times in between the glacial periods, where ice sheets retreat, is known as interglacial periods. The cause of these glacial-interglacial cycles are variations in the earth's orbit known as Milankovitch cycles, and they affect the amount of solar radiation that earth receives. A higher amount of solar radiation results in a warmer climate, and shrinking ice sheets, while a lower amount of radiation results in an expansion of ice sheets (NOAA, 2021). As mentioned before, the global control of $\delta^{18}\text{O}$ in seawater is the amount of water stored on land as ice, and therefore we can trace the glacial-interglacial cycles by using the $\delta^{18}\text{O}$ of benthic and planktonic foraminifera as a paleoceanographic proxy. Higher $\delta^{18}\text{O}$ in foraminifera tests represent glacial periods and lower $\delta^{18}\text{O}$ represents interglacial periods and figure 5 shows glacial periods returning periodically in the last 1 million years with the last glacial maximum being at about 0.02Ma. During these glacial periods the Northern hemisphere ice sheet stretched all the way to the British Isles and thus covered the entire study area of this project (Clark et al., 2012).

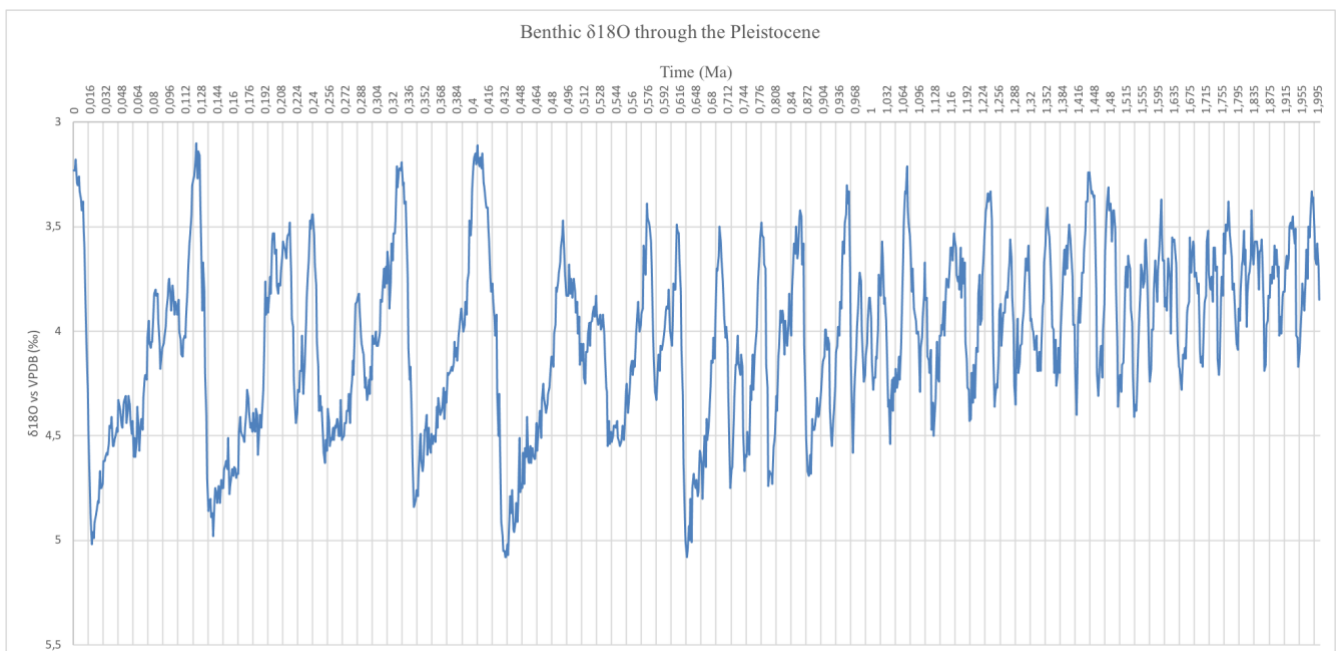


Figure 5. $\delta^{18}\text{O}$ for benthic foraminifera during the past 2 million years. The high peaks in $\delta^{18}\text{O}$ represent glacial periods and the low peaks represent interglacial periods. The Graph was produced with excel using data from Lisiecki and Raymo (2005).

3. Method

The cores with the samples were collected during ODP Leg 104 in 1989 (Vøring Plateau), ODP Leg 162 in 1999 (Rockall Plateau) and DSDP Leg 407 in 1979 (Reykjanes Ridge). In order to create an isotopic depth profile two samples were used from every site, one from the early pleistocene and one from the late pleistocene, which resulted in six samples being analyzed. The older samples spanned from 1.85-0.71Ma and the younger samples spanned 0.04-0.01Ma (table 2). Because the early Pleistocene sediments from core 642B was barren, this sample contains sediments from early to mid-Pleistocene.

Table 2. All cores and samples used in this study.

Site	Sample	Water depth (mbsl)	Depth (mbsf)	Age (Ma)	Dating method
Leg 104	1H-1, 102-104cm	1272	1.02	0.02	Paleomagnetism
Hole 642B	5H-5, 71-73cm		36.11	0.71	Bleil (1989)
Leg 162	1H-1, 52-54cm	1134	0.52	0.04	Orbitally tuned
Hole 982B	5H-2, 30-32cm		35.8	1.83	Diester-Haass et al. (2005)
Leg 407	1R-1, 57-60cm	2472	0.57	0.01	Planktonic foraminifera and calcareous nannofossil biostratigraphy
	6R-2, 56-58cm		46.06	1.85	Weitkamp et al. (in prep.)

3.1 Picking foraminifera

Before picking, all the samples were sieved and separated into the size fractions <63 μm , 63-125 μm , 125-150 μm , 150-212 μm and >212 μm and all fractions above 63 μm were used. We originally planned to only use size fraction 125-150 μm for every sample but because of an inadequate amount of some of the species we had to use the larger and smaller size fractions as well and these can be seen in table 3. The aim for the minimum weight for each species sample was 100 μg and about 50 specimens were picked for every sample in order to have the minimum amount. In the samples where they were present, *N. pachyderma* and *N. Incompta* could be found in sufficient amounts in all size fractions while *T. quinqueloba* and *G. glutinata* were more common in the two smallest size fractions. *G. bulloides* were most abundant in the largest size fraction and the number of specimens became fewer while moving down through the sizes. The benthic species followed the same pattern as *G.*

bulloides and were found in various amounts in all the samples. For *N. pachyderma* only the specimens that had gone through a secondary shell encrustation were used from all the samples. More than one species of benthic foraminifera were found in a majority of the samples and the most abundant one was chosen for the depth profile and sample 642B-5H-5, 71-73cm was the only sample that did not have enough benthic species. The aim was to use epifaunal species that are influenced by similar environmental factors as the planktonic species but due to a lack of epifaunal species in some samples, infaunal species were also used. The benthic species that were used for each site are in the last column of table 3.

Table 3. The planktonic and benthic foraminifera species found in each sample and from which size fractions they were picked from. More details on the size fraction used for each individual species in Appendix A.

Sample	Foraminifera species	No. of samples	No. of repeat samples	Size fractions used	Benthic species
ODP Hole 982B-1H-1, 52-54cm	NP., NI., GB., GG., TQ + Benthic	6	5	125-150µm 150-212µm >212µm	<i>Melonis barleeaanum</i>
ODP Hole 982B-5H-2, 30-32cm	NP., NI., GB., GG., TQ + Benthic	6	5	125-150µm 150-212µm >212µm	<i>Melonis barleeaanum</i>
DSDP Site 407-1R-1, 57-60cm	NP., NI., GB., GG., TQ + Benthic	6	1	63-125µm 125-150µm 150-212µm >212 µm	<i>Planulina wuellerstorfi</i>
DSDP Site 407-6R-2, 56-58cm	NP., NI., GB., GG., TQ + Benthic	6	1	63-125µm 125-150µm 150-212µm >212µm	<i>Oridorsalis umbonatus</i>
ODP Hole 642B-1H-1, 102-104cm	NP + Benthic	2	1	125-150µm 150-212µm	<i>Cassidulina neoteretis</i>
ODP Hole 642B-5H-5, 71-73cm	NP + Benthic	2	1	125-150µm 150-212µm	-

Because we wanted to test the replicability of this experiment we picked duplicates and triplicates for some of the species in each sample. Due to time constraints, Site 407-1R-1, 57-56cm and Site 407-6R-2, 56-58cm, only have duplicates of *N.pachyderma* and *N. Incompta*,

respectively, while site 982B has duplicates of all planktonic species. Both of the samples from site 642B have triplicates of *N. pachyderma*.

3.2 Preparing samples for the mass spectrometer

All the picked samples were transferred into semi-closed vials that were labeled with the site, species and time-period. They were placed in a predetermined pattern in a rack together with vials containing known standards. The two international standards, IAEA-CO-1 and NBS-18, as well as the working standard CaCo₃- *merck* weighed between 80-130µg. For the in-house standard Carm-2 we chose a lower weight-range in order to account for the lower weight of the foraminifera samples that had fewer specimens.

All the samples were put in the oven at 40°C and left overnight to remove any excess fluid and then 100µl of over 99% sulfuric acid was added to the vials at an angle to prevent it from touching the foraminifera tests at the bottom of the vial. The samples were flushed with helium for 10 minutes in order to remove any ambient air that would affect the reading of the isotopic composition and then the vials were tilted upright so the sulfuric acid could react with, and dissolve, the foraminifera overnight before they were put in a MAT 253 mass spectrometer connected to a gasbench II device that measured the isotopic composition.

4. Results

Microscope Images of all planktonic and benthic foraminifera species are displayed in figure 6 and 7, respectively. With the exception of a small hole in the test of *O. umbonatus* (figure 7), all specimens are well preserved and exhibit the typical characteristics of each species. The result of the stable isotope analysis is presented as 5 scatter plots of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ from each site and time-period (figure 8, 9 and 10). The cross plots were produced in excel and the data used for the plots can be found in appendix A. Of the 43 foraminifera samples that were analyzed, the samples containing *T. quinqueloba* and *G. glutinata* from site 407-6R-2, 56-58cm were both faulty, due to low weight, and has thus been excluded from the scatter plots.

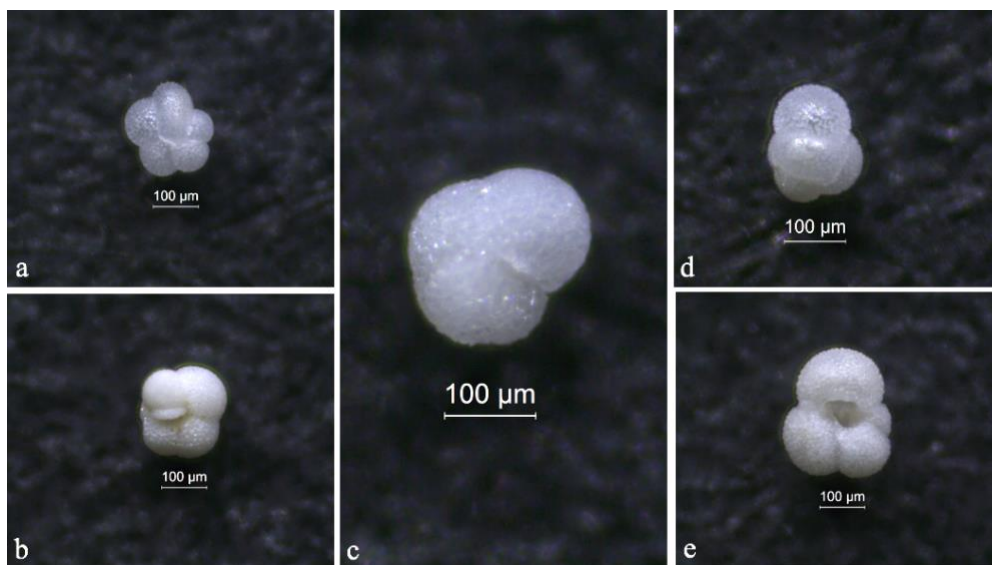


Figure 6. All planktonic species used for the study. **a)** *T. quinqueloba* from sample 982B-1H-1, 52-54cm. **b)** *N. incompta* from sample 407-6R-2, 56-58cm. **c)** *N. pachyderma* from sample 407-1R-1, 57-60cm. **d)** *G. glutinata* from sample 982B-1H-1, 52-54cm. **e)** *G. bulloides* from sample 982B-1H-1, 52-54cm.

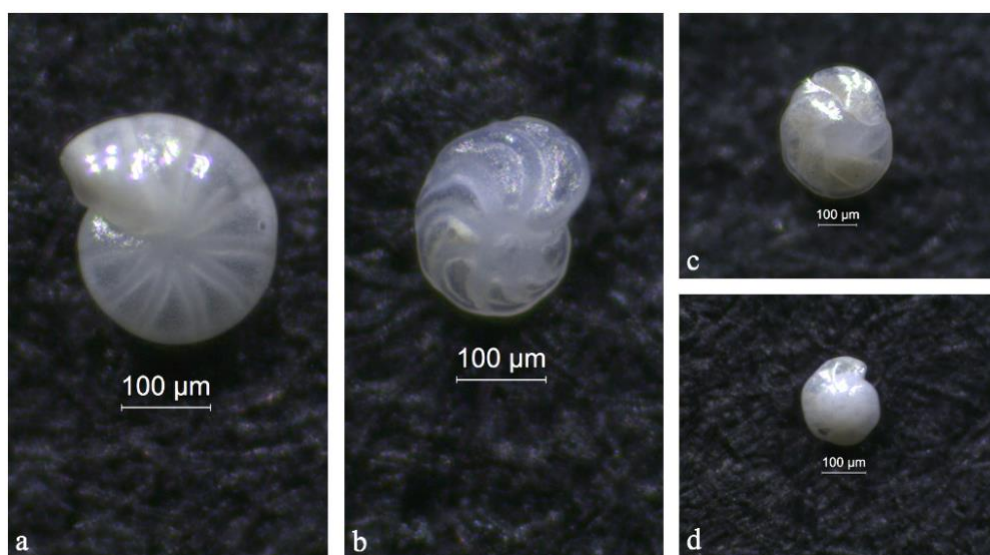


Figure 7. All benthic species used for this study. **a)** *M. barleeianum* from sample 982B-1H-1, 52-54cm. **b)** *P. wuellerstorfi* from sample 407-1R-1, 57-60cm. **c)** *C. neoteretis* from sample 642B-1H-1, 102-104cm. **d)** *O. umbonatus* from sample 407-6R-2, 56-58cm.

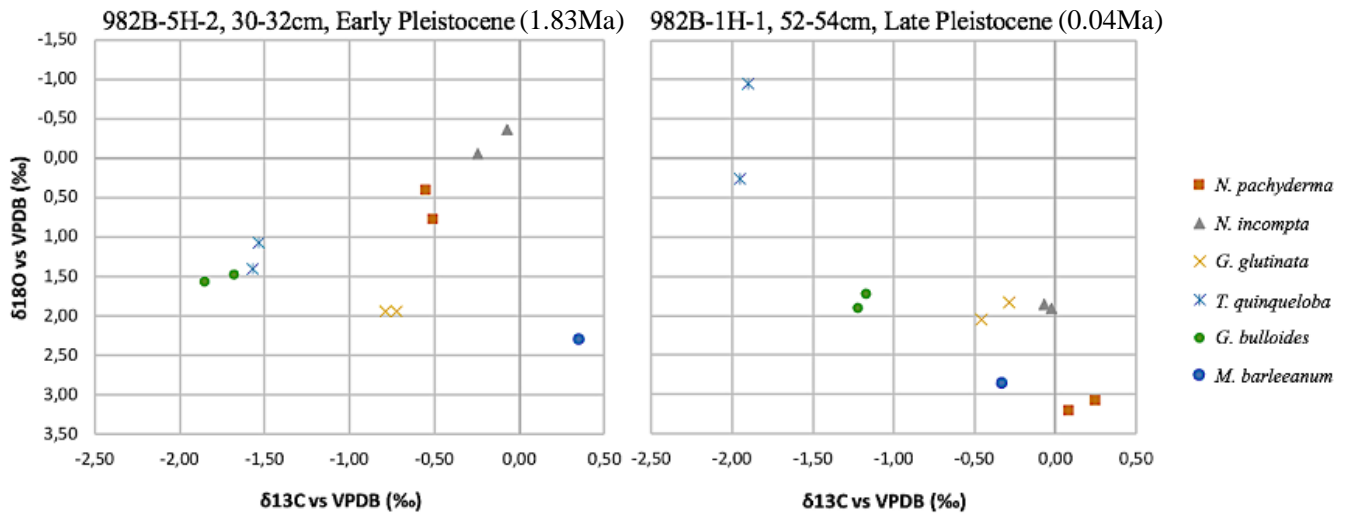


Figure 8. Scatterplots of the $\delta^{18}O$ and $\delta^{13}C$ values of all species from hole 982B. To the left is the early Pleistocene sample and to the right is the late Pleistocene sample. Scatterplots were produced with excel and include a legend.

In hole 982B, all species except *M. barleeaanum* have duplicates and with the exception of *T. quinqueloba*, all species have a higher $\delta^{18}O$ value in the late Pleistocene compared to the early Pleistocene (figure 8). The $\delta^{18}O$ value for *N. pachyderma* has increased the most, from an average of 0.59‰ in the early Pleistocene to an average of 3.14‰ in the late Pleistocene, and a similar change can be seen in *N. incompta*, which has increased from -0.21‰ to 1.89‰. The $\delta^{18}O$ values for *G. glutinata* and *G. bulloides* are relatively unchanged with the average value increasing by 0.01‰ for *G. glutinata* and 0.30‰ for *G. bulloides*. For *M. barleeaanum* the $\delta^{18}O$ value has increased from 2.29‰ to 2.85‰. The $\delta^{13}C$ value for *N. pachyderma*, *N. incompta*, *G. bulloides* and *G. glutinata* have all increased in the late Pleistocene but *N. pachyderma* increased the most by 0.7‰ while *N. incompta* increased the least by 0.11‰. Compared to the other species *N. pachyderma* has the most drastic change in $\delta^{18}O$ and has thus changed its position in relation to the other species. Despite being a bottom-dweller, *M. barleeaanum* unexpectedly has a very high $\delta^{13}C$ value, and it decreases by 0.68‰ from early to late Pleistocene.

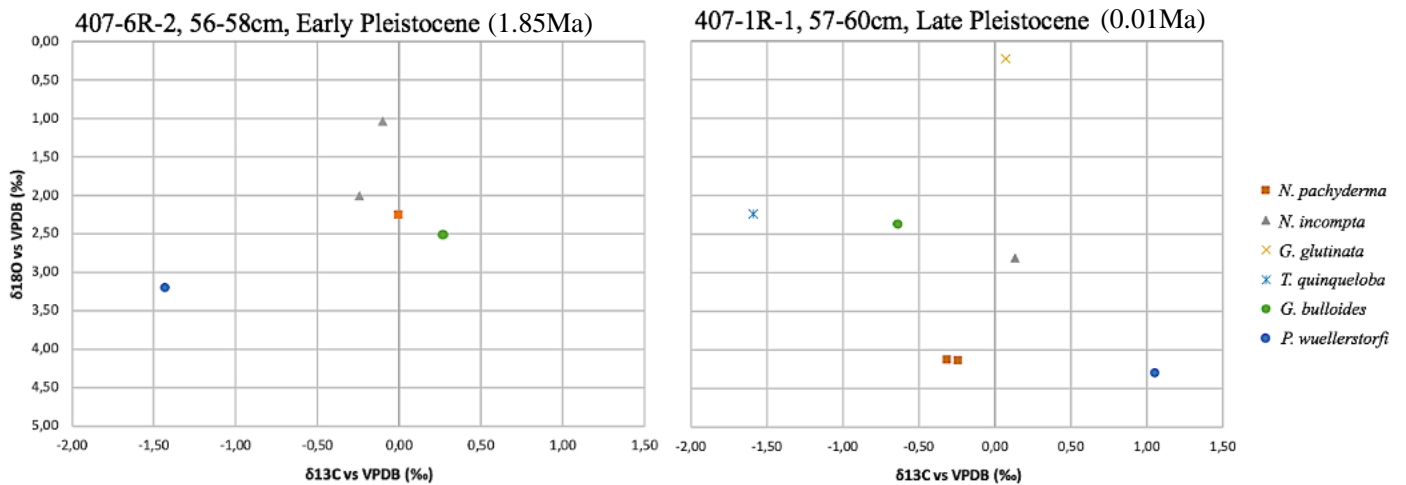


Figure 9. Scatterplots of the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of all species from site 407. To the left is the early Pleistocene sample and to the right is the late Pleistocene sample. Scatterplots were produced with excel and include a legend.

The foraminifera assemblage on Site 407 was dominated by *N. incompta* in the early Pleistocene and by *N. pachyderma* in the late Pleistocene and therefore these are the only species with a duplicate from their respective dominant time-period. There is no consistent pattern between the species from the early to late Pleistocene but the $\delta^{18}\text{O}$ value for *N. pachyderma* has increased the most by 1.87‰ and its relative shift in position is pronounced and its $\delta^{18}\text{O}$ is very similar to *P. wuellerstorfi* in the late Pleistocene. The duplicates of *N. incompta* in the early Pleistocene sample has very different $\delta^{18}\text{O}$ values compared to each other but the average value is 1.56‰ and has increases by 1.25‰ in the late Pleistocene. *P. wuellerstorfi* and *G. bulloides* show a decrease in their $\delta^{18}\text{O}$ values by 1.09‰ and 0.1‰, respectively and the $\delta^{13}\text{C}$ value for both species, especially *P. wuellerstorfi*, change drastically compared to *N. pachyderma* and *N. incompta*. For *P. wuellerstorfi*, the $\delta^{13}\text{C}$ value increases by 2.49‰ and for *G. bulloides* it decreases by 0.91‰ while for *N. pachyderma* the difference is 0.27‰ and for *N. incompta* it is 0.04‰. Relative to the other species *G. glutinata* has a very low $\delta^{18}\text{O}$ value.

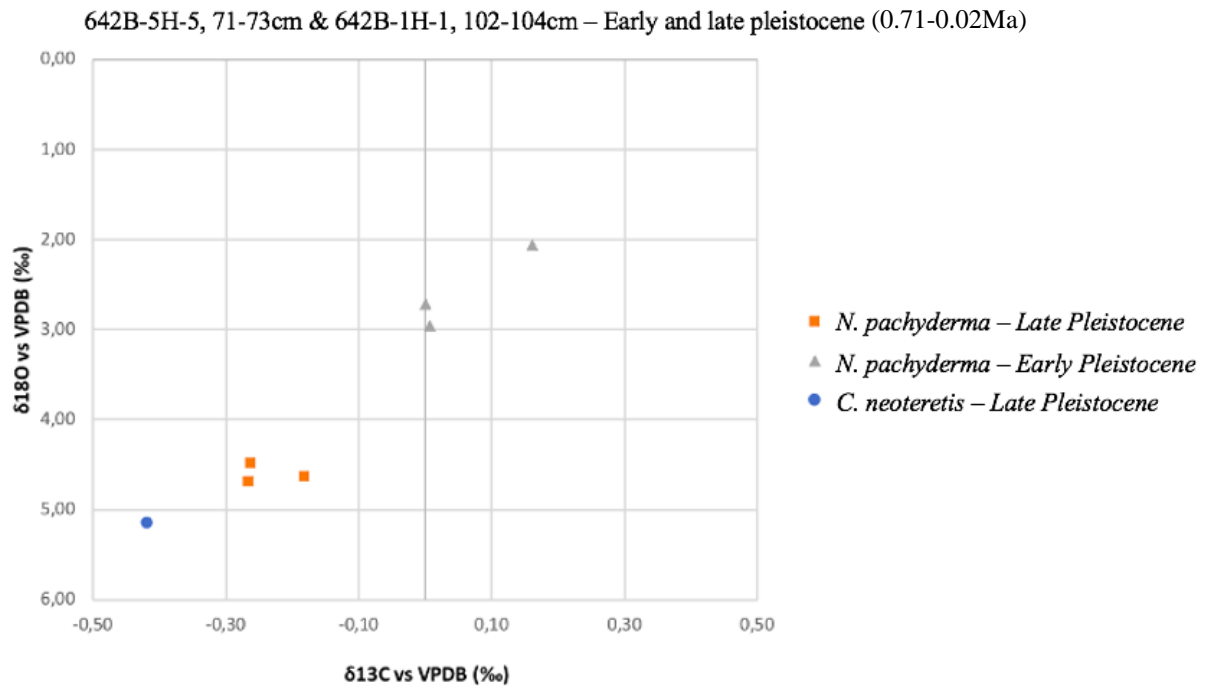


Figure 10. Scatterplot of the $\delta^{18}O$ and $\delta^{13}C$ values of *N. pachyderma* and *C. neoteretis* from hole 642B. Both the early and late Pleistocene sample are combined into one scatterplot that was produced with excel and include a legend.

The foraminifera assemblage in the samples from hole 642B were heavily dominated by *N. pachyderma*, with some *C. neoteretis* present in both early and late Pleistocene. A few *T. quinqueloba* were present in the late Pleistocene but there were not enough specimens to use in the mass spectrometer. *N. pachyderma* has triplicates from each sample and from early to late Pleistocene the $\delta^{18}O$ value for *N. pachyderma* has increased by 2.02‰ from an average of 2.58‰ to an average of 4.6‰ while the $\delta^{13}C$ value has decreased from an average of 0.06‰ to an average of 0.24‰. *C. neoteretis* only had enough specimens in the late Pleistocene sample and the $\delta^{18}O$ value is high at 5.14‰ and the $\delta^{13}C$ value is relatively low at -0.42‰.

5. Discussion

The isotopic data of this study show similar results to other studies made on foraminifera from the Pleistocene such as Lisiecki and Raymo (2005). Not surprisingly, species richness seems to decrease with increasing latitude and out of the planktonic species only *N. pachyderma* was found in adequate numbers in the most northern samples from hole 642B in the Norwegian sea. In the most southern sample, from hole 982B outside of Scotland, all species were common, and no species was particularly dominant compared to the others. Site 407 was clearly dominated by *N. incompta* in the early Pleistocene and by *N. pachyderma* in the late Pleistocene and this could have been explained by alternating interglacial and glacial periods favoring one of the species, but this is not what we see in figure 5. The ages of the samples are 0.01Ma and 1.85 Ma and at 0.01Ma, the last glacial maximum has just passed at 0.02Ma and a rapid change into an interglacial period is ongoing while at 1.85Ma the climate is relatively stable with no rapid shifts from longer glacial and interglacial periods. Another possible explanation is that a sudden infiltration of warm water from the NAC made the water temporarily warmer at site 407 so that the water conditions favored *N. incompta* but more research on Pleistocene samples are needed to confirm this. Besides the glacial cycles, the earth also experienced a global cooling trend and expansion of northern hemisphere ice sheets during the Pleistocene (Darling et al., 2007) and considering *N. pachyderma* is the dominating polar species today it is possible that it had out conquered *N. incompta* by adapting to colder waters before the late Pleistocene.

The common trend in the scatterplots (figures 8-10) is that the $\delta^{18}\text{O}$ value for *N. pachyderma* has increased drastically compared to the other species from early to late Pleistocene in all the samples. This is consistent with existing literature placing the start of *N. pachyderma*'s adaptation to colder waters at about 1.3Ma and in the samples from hole 982B and site 407 we can see that *N. pachyderma* has the largest increase in $\delta^{18}\text{O}$ out of all the species. If $\delta^{18}\text{O}$ would have moved in the same direction for all the species it would have suggested a collective shift in their preferred depth habitat caused by a change in the global or local seawater, but since *N. pachyderma* has a relatively dramatic increase compared to the other species there must be other factors causing this particular species to move through the water column. Huber et al. (2000) found that in 6 cores from the Norwegian-Greenland Sea there is a distinct net increase in the mean test size of *N. pachyderma* that has been ongoing since 1.3Ma and reached its maximum after 0.4Ma. A larger test size might have given *N.*

pachyderma certain advantages, such as a higher tolerance to varying environmental conditions, but the test size itself is most likely not the cause of the species adaptation to colder waters but rather a consequence of the adaptation. This is supported by a study by Malmgren and Kennett (1978) that found that the test size of *G. bulloides* increases with decreasing water temperatures. The same study also found that the number of specimens of *G. bulloides* was highest in colder water, so it is possible that the species grows larger if it is in its optimal environment, and assuming this is true for *N. pachyderma* as well, it might be further proof of how this species thrives in polar water temperatures. Another possible interpretation of the increased test size is that since we know *N. pachyderma* goes through a secondary encrusting of its test when it reaches full maturity and descends through the water column, it could be possible for the higher $\delta^{18}\text{O}$ value to be caused by this extra layer of crust. If additional calcite is added to the test as it sinks this might look like a migration to a deeper habitat when using stable isotopes. In order to minimize the error this might cause, only heavily encrusted *N. pachyderma* were used in this study, which also means the specimens had reached a similar level of maturity. *N. incompta* show similar patterns of increasing $\delta^{18}\text{O}$ as *N. pachyderma* in both samples, although it is not quite as drastic, and a possible explanation for this could be that they both belong to the same taxa and therefore have similar adaptive behaviors.

It is difficult to say with complete certainty where the ranges of the depth habitats fall on the scatterplots but based on what we know about the ecology of all the foraminifera species today, we can make some interpretations. Firstly, benthic species live in or on top of the seafloor which means they should reflect the isotopic composition of the bottom-water. Secondly, we know *G. glutinata* and *G. bulloides* prefers surface waters with depths of 0-60m so they might reflect the surface to mid surface waters (Schiebel et al, 1995; Schiebel and Hemleben, 2017; Carstens et al., 1997) and what is true in all scatterplots is that *N. pachyderma* has moved closer to the benthic species than what the other planktonic species have. This could mean that the species habitat has shifted to deeper waters in the late Pleistocene. If all samples in this study had duplicates or triplicates it would probably have been easier to interpret where the depth habitats are located on the scatterplots but due to time constraints this was unfortunately not possible.

The duplicates of *T. quinqueloba* in sample 982B-1H-1, 52-45cm have a $\delta^{18}\text{O}$ that differs by 1‰ which is relatively high which makes the reliability of this sample questionable. One possible cause of this could be that dirty specimens were used in one or both of the samples which skewed their isotopic composition.

Hole 642B was the most northern sample and it was heavily dominated by *N. pachyderma* with only a small amount of *T. quinqueloba* and *C. neoteretis*. Since the early Pleistocene sample only had *N. pachyderma* it is not possible to make any interpretations of how the species have moved through the water column in relation to other species. What we can see though, is that both *C. neoteretis* and *N. pachyderma* have very high $\delta^{18}\text{O}$ values in the late Pleistocene and according to figure 10 this coincides with the last glacial maximum at 0.02Ma, which is also the age of this sample (table 2). As mentioned before, during glacial periods ice will be trapped on land and result in an ocean that is depleted in ^{16}O and this is what we observe in the $\delta^{18}\text{O}$ profile of *C. neoteretis* and *N. pachyderma* in this sample.

A very surprising result is that *M. barleeaanum* has uncharacteristically high $\delta^{13}\text{C}$ values in the early Pleistocene sample from hole 982B and that *P. wuellerstorfi* has a very high value in the late Pleistocene sample from site 407. Typically, $\delta^{13}\text{C}$ decreases with increasing depth as organic material decomposes and release ^{12}C into the water, and therefore bottom-dwelling benthic species should have a low $\delta^{13}\text{C}$ compared to planktonic species (Ravelo and Hillaire-Marcel, 2007). According to Kroopnick (1985) the North Atlantic Deep water (NADW) has a $\delta^{13}\text{C}$ value of 1‰, which is similar to the $\delta^{13}\text{C}$ of *P. wuellerstorfi* in the late Pleistocene sample from site 407, and this location also has the deepest water depth so it could be possible for the $\delta^{13}\text{C}$ value to be affected by the NADW. Because the early and late Pleistocene samples from site 407 contain different benthic species it is difficult to compare the two samples in terms of benthic isotope values, since they probably differ between the species because of biological differences. In sample 982B, from the early Pleistocene, the $\delta^{13}\text{C}$ for all planktonic species is very low which might suggest a global or local seawater factor such as a low primary production, but that does not explain why *M. barleeaanum* has such a high $\delta^{13}\text{C}$. One thing to take into account is that *M. barleeaanum* is an infaunal species, meaning it lives in the topmost part of the seafloor and not in the water column (Caralp, 1989), which might affect the isotopic composition of the tests. The aim was to only use epifaunal species for this study, but in the 982B samples no such species could be found in

high enough numbers and *M. barleeanum* was the only species with a sufficient number of specimens in each sample. It is also worth noting that none of the benthic species have been corrected for vital effects, mainly due to lack of information about the species, and therefore the result of the isotopic composition reading could be misleading.

6. Conclusions

This study documents the stable isotopic composition of high-latitude North Atlantic foraminifera from the Pleistocene epoch. The focus of the study was the species *Neogloboquadrina Pachyderma* and in conclusion, the result of the study shows that *N. pachyderma* has travelled down through the water column in relation to the other species between the early and late Pleistocene in the samples from site 407 and hole 982B. It is clear that this shift was not caused by global or local variations in $\delta^{18}\text{O}$ because the scatterplots do not show a similar trend for the other species. It does not seem like *N. pachyderma* was a deep dweller prior to the genetic split, since $\delta^{18}\text{O}$ is similar or even lower than the other planktonic foraminifera species in the early Pleistocene, and this goes against the original hypothesis. In all three samples *N. pachyderma* has seemingly moved down in the water column in the late Pleistocene and is now closer to the benthic species than what all other planktonic species are, which suggest it now lives closer to the seafloor than it did before. This shift in depth habitat might coincide with the genetic split of the species at 1.8-1.3, Ma but further research is needed to determine exactly when the species started moving through the water column and whether it has moved up and down throughout the Pleistocene. The increased test size of *N. pachyderma* that started at 1.3 Ma and was ongoing until 0.4 M also speaks to a substantial adaptation to colder waters and could possibly mark the beginning of the depth habitat shift. Some uncertainties in this study include the possible effect that the glacial-interglacial cycles could have had on the foraminifera and their interpreted depth habitat and also the additional encrusting of *N. pachyderma* tests that might make the isotopic composition mirror a deeper habitat. Before *N. pachyderma* can be used as a reliable paleoceanographic proxy for the Pleistocene epoch, it is therefore necessary to do more detailed studies on its depth habitat throughout the entire Pleistocene.

Acknowledgements

Firstly, I would like to thank Professor Helen Coxall for introducing me to paleoceanography during my studies at Stockholm University which sparked my interest in microfossils. I would also like to thank both Helen and Tirza Weitkamp for giving me this project and for providing knowledge and guidance throughout this process. I especially want to thank Tirza for all the help with the practical parts of this project which helped me gain confidence in my work and I also want to thank Haoyi Yao for helping me in the lab. I also want to thank my parents for always supporting me and pretending to understand what this project was about even though they have no experience in the field of marine geology. Lastly, I want to thank all professors, teachers, PhD students and doctorates who unlocked the door to the microscope lab for me every morning, without you I would just have been standing in a corridor all spring looking at the foraminifera waiting to be sorted.

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8. Appendices

Appendix A: Data from isotopic analysis of foraminifera

Table A1: Table with all data from the isotopic analysis of the foraminifera, including number of specimens in each sample and the size fractions used for each species. The rows marked in yellow were faulty and have not been used for the scatterplots.

Foraminifera stable isotope $\delta^{18}O$, $\delta^{13}C$								
mätt 202405; med GB2014, SIL, Inst för geologiska vetenskaper, SU								
	Analysis number	Sample name	$\delta^{13}C$ vs VPDB, ‰	$\delta^{18}O$ vs VPDB ‰	$d^{13}C$ VPDB	d18O	no of individuals	Size fractions (μm)
	18658	Merck	-8,98	-18,10				
	18659	IAEA_603	2,50	-2,28	2,46	-2,37		
	18660	IAEA_603	2,50	-2,30	2,46	-2,37		
642B LP NP1	18661	NorthAtlantic1	-0,18	4,63			46	125-212
642B LP NP2	18662	NorthAtlantic2	-0,26	4,48			46	125-212
642B LP NP3	18663	NorthAtlantic3	-0,27	4,69			46	125-212
642B LP B	18664	NorthAtlantic4	-0,42	5,14			40	125-212
407 LP NP1	18665	NorthAtlantic5	-0,32	4,12			40	125-212
407 LP NP2	18666	NorthAtlantic6	-0,24	4,13			40	125-212
407 LP NI	18667	NorthAtlantic7	0,13	2,81			32	125-212
407 LP GG	18668	NorthAtlantic8	0,07	0,23			33	125-212
	18669	Carm2	2,64	-1,04				
	18670	Carm2	2,61	-1,10				
	18672	NBS18	-5,02	-23,17	-5,01	-23,2		
407 LP TQ	18673	NorthAtlantic9	-1,59	2,24			42	125-212
407 LP GB	18674	NorthAtlantic10	-0,64	2,37			20	>150
407 LP B	18675	NorthAtlantic11	1,05	4,29			40	>150
982B LP NP1	18676	NorthAtlantic12	0,09	3,21			44	125-212
982B LP NP2	18677	NorthAtlantic13	0,25	3,07			40	125-212
982B LP NI1	18678	NorthAtlantic14	-0,03	1,91			40	125-212
982B LP NI2	18679	NorthAtlantic15	-0,07	1,86			40	125-212
982B LP GG1	18680	NorthAtlantic16	-0,46	2,05			40	125-212
	18681	Merck	-8,98	-18,21				
	18682	Merck	-8,95	-18,42				
	18683	IAEA_603	2,50	-2,46	2,46	-2,37		
982B LP GG2	18684	NorthAtlantic17	-0,28	1,84			40	125-212
982B LP TQ1	18685	NorthAtlantic18	-1,90	-0,95			40	125-212
982B LP TQ2	18686	NorthAtlantic19	-1,95	0,26			40	125-212
982B LP GB1	18687	NorthAtlantic20	-1,17	1,73			32	125-212
982B LP GB2	18688	NorthAtlantic21	-1,22	1,91			30	125-212
982B LP B1	18689	NorthAtlantic22	-0,33	2,85			16	>150
642B EP NP1	18690	NorthAtlantic24	0,16	2,06			43	125-212
642B EP NP2	18691	NorthAtlantic25	0,01	2,96			43	125-212
	18692	Carm2	2,57	-1,10				
	18693	Carm2	2,49	-1,38				
642B EP NP3	18695	NorthAtlantic26	0,00	2,71			43	125-212
407 EP NP	18696	NorthAtlantic28	-0,01	2,26			35	125-212
407 EP NI1	18697	NorthAtlantic29	-0,10	1,04			40	125-212
407 EP NI2	18698	NorthAtlantic30	-0,24	2,01			38	125-212
407 EP GG	18699	NorthAtlantic31	-1,04	1,70			26	63-125
407 EP TQ	18700	NorthAtlantic32	-2,13	1,18			46	63-150
407 EP GB	18701	NorthAtlantic33	0,27	2,48			25	>150
407 EP B	18702	NorthAtlantic34	-1,44	3,20			13	>150
	18703	Merck	-9,04	-18,05				
	18704	Merck	-9,03	-18,02				
	18705	IAEA_603	2,39	-2,42	2,46	-2,37		
982B EP NP1	18706	NorthAtlantic35	-0,55	0,40			40	125-150
982B EP NP2	18707	NorthAtlantic36	-0,51	0,78			40	125-150
982B EP NI1	18708	NorthAtlantic37	-0,25	-0,06			40	125-212
982B EP NI2	18709	NorthAtlantic38	-0,07	-0,36			40	125-212
982B EP GG1	18710	NorthAtlantic39	-0,72	1,94			41	125-212
982B EP GG2	18711	NorthAtlantic40	-0,79	1,94			40	125-212
982B EP TQ1	18712	NorthAtlantic41	-1,57	1,41			40	125-150
982B EP TQ2	18713	NorthAtlantic42	-1,53	1,07			40	125-150
982B EP GB1	18714	NorthAtlantic43	-1,68	1,48			40	125, 150
	18717	NBS18	-4,95	-23,21	-5,01	-23,2		
982B EP GB2	18718	NorthAtlantic44	-1,85	1,57			40	125-212
982B EP B1	18719	NorthAtlantic45	0,35	2,29			14	>150