Modal shift in North Atlantic seasonality during the last deglaciation

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Abstract. Change-over from a glacial to an interglacial climate is considered as transitional between two stable modes. Palaeoceanographic reconstructions using the polar foraminifera *Neogloboquadrina pachyderma* highlight the retreat of the polar front during the last deglaciation in terms of both its decreasing abundance and stable oxygen isotope values ($\delta^{18}O$) in sediment cores. While conventional isotope analysis of pooled *N. pachyderma* shells show a warming trend concurrent with the retreating ice, new single shell measurements reveal that this trend is composed of two isotopically different populations that are morphologically indistinguishable. Using modern time-series as analogues for interpreting down-core data, glacial productivity in the mid North Atlantic appears limited to a single maximum in late summer, followed by the melting of drifting icebergs and winter sea ice. Despite collapsing ice sheets and global warming during the deglaciation a second 'warm' population of *N. pachyderma* appears in a bimodal seasonal succession separated by the subpolar *G. bulloides*. This represents a shift in the timing of the main plankton bloom from late to early summer in a deglacial intermediate mode that persisted for ca. 10,000 years until the last deglaciation ended. When seawater temperatures exceeded the threshold values, first the "cold" (glacial) then the "warm" (deglacial) population of *N. pachyderma* disappeared, whilst *G. bulloides* with a greater tolerance to higher temperatures persisted throughout the Holocene to the present day in the mid-latitude North Atlantic. Single specimen $\delta^{18}O$ of polar *N. pachyderma* reveal a steeper rate of ocean warming during the last deglaciation than appears from conventional pooled $\delta^{18}O$ average values.

1. Introduction

1.1 Seasonality and single specimen isotope analysis of foraminifera

Recent technical advances now allow for the routine analysis of the stable isotopic composition of single microscopic shells of foraminifera (Feldmeijer et al., 2015; Lougheed et al., 2018; Metcalfe et al., 2015; Pracht et al., 2018) permitting the resolution of (sub-)seasonal contrasts in seawater temperature (Ganssen et al., 2011; Wit et al., 2010), in lieu of pooled specimens that capture an averaged state of the system on longer time scales. Stable oxygen isotopes ($\delta^{18}O$) of pooled foraminifera have been used as key tracers of water masses, ice-volume and sea-level fluctuations over glacial-interglacial cycles (e.g., Pearson, 2012; Waelbroeck et al., 2005). The use of single shell oxygen isotope analysis allows for moving beyond the "average" state of the climate system as expressed in pooled specimen analysis to observe the inter-specimen variance that includes seasonal differences (Feldmeijer et al., 2015; Ganssen et al., 2011; Metcalfe et al., 2015; Wit et al.,

2010). Seasonal changes during these glacial-interglacial cycles have rarely been addressed although resolving seasonal contrasts would significantly improve our understanding of past climate change (Huybers, 2006; Schmittner et al., 2011).

1.2 Aims and Objectives

As the largest ocean carbon sink in the northern hemisphere, the North Atlantic Ocean (Gruber et al., 2002) exhibits strongly seasonal productivity in the Present-Day. Deep wind-driven mixing in winter resupplies the photic zone with nutrients brought up from subsurface depths leading to phytoplankton blooms and maxima in the abundance of zooplankton including planktonic foraminifera during the onset of summer stratification, followed by a decrease as oligotrophic summer conditions develop. Present day temperature conditions in the mid-latitude North Atlantic (Fig. 1) preclude the occurrence of *Neogloboquadrina pachyderma* (Kretschmer et al., 2016), the species being restricted to the (sub)polar water masses in the high-latitude North Atlantic. With the southward shift of the polar front that accompanied the last glacial, more favourable conditions developed, whereas *Globigerina bulloides* (Ganssen and Kroon, 2000) existed throughout (Fig. 2). Here we analyse single shell stable oxygen and carbon isotopes (Feldmeijer et al., 2015; Ganssen et al., 2011; Metcalfe et al., 2015; Pracht et al., 2018) of the planktonic foraminifera *N. pachyderma* (left coiling) and *G. bulloides* in a sediment core from the Iceland Basin in the mid-latitude Atlantic. Given that present conditions in the mid North Atlantic are an anathema to the polar species *N. pachyderma*, as well as the direction of mean annual temperature change, we address seasonal changes during the past deglaciation.

2. Methodology

Piston core T88-3P (56.49˚N, 27.80˚W; Figs. 1 and 2) was taken on the eastern flank of the Mid-Atlantic Ridge during the 1988 RV *Tyro* expedition of the Actuomicropalaeontology Palaeoceanography North Atlantic Project (APNAP). Piston core T88-3P measures 937 cm in length (Figs. 1, 2) and was retrieved from above both the modern and glacial CCD (core water depth: 2819 m) ensuring minimal bias by carbonate dissolution. Core sections were manually split into a working half and an archive half.

2.1 X-Ray fluorescence core scanning and composite images

Archive halves of each section of the entire piston core were analysed at 1-cm down-core resolution using the Avaatech XRF core scanner (Richter et al., 2006), at the Royal NIOZ (Fig. 2). Optical line-scanning was first performed on the split halves allowing a detailed and accurate description of visual and chromatic changes in core texture (Fig. 2e). Prior to XRF-analysis the surface of the archive halves was scraped cleaned and each section was covered in SPEXCerti Ultralene® ultra-thin (4 μm) film. Bulk chemical composition was measured using energy dispersive fluorescence radiation, as elemental intensities in counts per second (CPS) at 10 kV and (for 10 seconds) and at 50 kV (for 40 seconds). Despite limitations upon the accuracy and precision (Weltje and Tjallingii, 2008) by matrix effects, sediment (e.g., water content; grain-size) and measurement properties (e.g. surface irregularities) as well as machines settings used (outlined above), the reliability for the elements Ca and Ti used herein is well established (Weltje and Tjallingii, 2008). To further minimize error, counts are expressed as log-ratios of two elements (Weltje and Tjallingii, 2008). Herein the Log (Ca/Ti) is used as a proxy for two end-members: marine productivity ([Ca]) and detrital terrestrial material ([Ti]) with minor contribution to [Ca] via detrital carbonate, which directly relates to ice rafted debris (IRD; Fig. 2d).

2.2 Abundance counts

Core sections of the entire working half were cut into 1 cm slices. Sediment slices were processed every 4 cm intervals and washed over a 63 µm sieve mesh, dried overnight at ~75°C and subsequently size fractionated into 63-150 µm and >150 µm. Abundance counts of planktonic foraminifera were performed on *G. bulloides* and *N. pachyderma* in the >150 µm size

5 fraction whilst all other specimens were pooled into '*other foraminifera*', terrigenous grains considered to be ice rafted detritus were also counted and identified (i.e., Stained-Quartz; Cloudy-Quartz; Bright-Quartz; Quartz; Sandstone, Igneous, Obsidian-glass; Rhyolitic-glass and '*Other*'), on a minimum of 200 grains after splitting with an OTTO-microsplitter. The ratio of *N. pachyderma* to *G. bulloides* (Fig. 2c) is expressed as:

$$Ratio\ of\ NPS = \frac{N.pachyderma}{(N.pachyderma + G.bulloides)}, (1)$$

10 ### 2.3 Stable isotope geochemistry ($\delta^{18}O$; $\delta^{13}C$)

For single shell stable isotope analysis, a continuous flow isotope ratio mass spectrometer was used (Feldmeijer et al., 2015; Metcalfe et al., 2015) based upon modifications (Breitenbach and Bernasconi, 2011) to the microvolume set-up (Spötl and Vennemann, 2003). For each sample 20 shells of both left coiling *N. pachyderma* and *G. bulloides* were picked at random from the 250 - 300 µm size fraction (Figs. 2-4). No morphological differences were observed among the picked

15 left coiling *N. pachyderma*. Each specimen was placed into a 4.5 ml exetainer vial, and the ambient air was replaced by He and subsequently digested in concentrated H_3PO_4 (45 °C for 160 minutes). The resultant CO_2-He gas mixture is transported to the GasBench II using a He flow through a flushing needle system where water is extracted from the gas using a Nafion tubing. The purified CO_2 is analysed in a Thermo Finnigan Delta$^+$ mass spectrometer after separation from other gases in a GC column. Isotope values are reported in the standard δ denotation with the ratio of heavy to light isotopes ($\delta^{18}O$) in per

20 mil (‰) versus Vienna-Peedee Belemnite (V-PDB). The reproducibility of an international carbonate standard analysed is <0.12‰ (1 σ) for both $\delta^{18}O$ and $\delta^{13}C$, measured within the same run and at similar quantities to a single foraminifer (> 10 µg).

2.4 Core stratigraphy and Age Model

For radiocarbon dating of core T88-3P pristine specimens of *G. bulloides* and *N. pachyderma* were picked from six samples

25 of core T88-3P and analysed by Accelerated Mass Spectrometry (AMS) at the AMS laboratories of Beta Analytic (Table 1; Fig. 2). The open source MatCal (version 1.0) function for Mathworks MatLab® (Lougheed and Obrochta, 2016) was used to calibrate conventional radiocarbon age to a calendar age, using the Marine13 Calibration curve (Reimer et al., 2013) and a reservoir age of 400 ^{14}C years with an error of 200 ^{14}C years, expressed mathematically as ΔR: 0 ± 200 ^{14}C yr. The 95% confidence limits for the calendar age, in kyr BP, of each sample is given in Table 1. A single date was excluded

30 because of the limitations of the calibration curve >35 kyr. For a down-core $\delta^{18}O$ stratigraphy, the cosmopolitan upper ocean dweller *G. glutinata* and the subpolar-temperate upper ocean dweller *G. bulloides* were measured for $\delta^{18}O$ and $\delta^{13}C$ using pooled specimens picked from the 250 - 300 µm size fraction, which were placed in mono-specific groups within a 15 ml exetainer vial. Analyses followed the same procedures as for single shell analysis, but with considerably better reproducibility of international standards for the larger sample mass (~100 µg). For samples between AMS dates, the $\delta^{18}O$

35 of *G. bulloides* was tuned to North Greenland Ice Core Project (NGRIP) (Rasmussen et al., 2008). Whilst the background sedimentation rate varies, with approximately 100 yr per cm during glacial periods and a much faster ~30 yr per cm during the Holocene (Interglacial). During intervals of high ice rafted debris (IRD) input the sedimentation rate noticeably varoes.

Using the maximum likely calendar age (in cal. yr. BP) from Table 1, the age model consisting of independent age markers places the deglacial period between ~410 and ~290 cm down core. For further details on age model construction, see the Supplementary Information.

2.5 Statistical analysis: End member modelling of IFA

5   Marine sediments reflect an averaged record over time, ranging from months to multiple centuries. However, if the individual components have distinct markers such as different $\delta^{18}O$ values, then the original distributions can be statistically unmixed into two or more univariate normally distributed populations using an un-mixing function (e.g. (Hammer et al., 2001; Weltje, 1997; Weltje and Prins, 2003; Wit et al., 2013). Mixture analysis was carried out using the open source PAST (version 3.10) palaeontological statistics software (Dempster et al., 1977; Hammer et al., 2001). Using the end member

10   modeling algorithm of Dempster et al. (1977), PAST estimates the mean, standard deviation and proportion of each population (see Hammer et al. (2001) for a discussion of the assumptions of the mixing model). These solutions can be tested by two methods: the log likelihood value in which a 'better' result produces a less negative value, and a minimum in Akaike Information Criterion (AIC) value indicating that the chosen number of groups has a good fit without subsequent overfitting. An additional output of this mixture analysis is to assign each individual to the most probable population (Table

15   2).

2.6 Modern Sediment trap record and Ocean reanalysis

As the modern analogue of our distinct isotopic 'end-members', we used seasonally resolved sediment trap time-series representing the modern polar, subpolar and temperate North Atlantic (Fig. 1). Three such sediment trap records are available (Fig. 5) from (a) the polar Greenland-Norwegian Sea over the Iceland Plateau (IP – Wolfteich, 1994), (b) the

20   subpolar Irminger Sea (IRM; Jonkers et al., 2010; Jonkers et al., 2013; Jonkers and Kučera) and (c) the temperate mid North Atlantic (NABE48 from the North Atlantic Bloom Experiment; Wolfteich, 1994). Ocean reanalysis S4 (Balmaseda et al., 2013) was used to complete the temperature and salinity profiles associated with each sediment trap time-series, both with respect to time and depth (Fig. 5). Ocean reanalysis data was converted from date into sediment trap cup number using a Mathworks MatLab® function: the monthly temperature and salinity data was first interpolated to one day resolution,

25   using the interp1 function, the opening and closing dates of successive cups were then found, temperature and/or salinity presented in figures represent the opening and therefore the closing of the previous cup used. Since the IRM time-series represents several years we generate both a time averaged flux record as well as an average profile for both temperature and salinity. The time averaged flux is calculated by finding corresponding bimonthly (cup opening interval: 14 days) trap opening and closing days and averaging the resultant flux.

30   ## 3. Results

3.1 IRD, Abundance

The upper ~290 cm of core T88-3P is Holocene in age as evidenced by near uniform values of $\delta^{18}O$, Log(Ca/Ti), IRD and the ratio NPS (Fig. 2). Between 290 and 410 cm, the deglacial interval, the ratio NPS approaches 1.0, IRD 20% and a minimum Log(Ca/Ti) of 0.9. The minimum in Log(Ca/Ti) occurs prior to the increase in IRD though coeval with the

35   increase in the ratio of NPS. Between 425 and 937 cm the ratio NPS and percentage of IRD appear to covary whilst the Log(Ca/Ti) shows an inverse, with a minimum in Log(Ca/Ti) at IRD events.

3.2 Single shell δ^{18}O

Our results show that δ^{18}O values of both *G. bulloides* and *N. pachyderma* are unimodally distributed during the last Glacial until about 21 ka BP (Fig. 3). Whilst the distribution of *G. bulloides* δ^{18}O values remains unimodal throughout, the δ^{18}O values of *N. pachyderma* develops striking bimodality (Fig. 4). For *N. pachyderma* the distributions can be

5 statistically unmixed into two discrete populations (Hammer et al., 2001) in varying numbers of specimens (Table 2): one high in δ^{18}O persisting from the Glacial (population P1) and a second population low in δ^{18}O appearing at the onset of the deglaciation (population P2). The difference in δ^{18}O between population P1 and P2 amounts to 0.9 ± 0.4 ‰ and persists for about 10 ka while absolute values gradually decrease by 1.6‰ (Figs. 3-4). At the end of the last deglaciation (11 ka BP), P1 disappears and the δ^{18}O values of *N. pachyderma* become once more unimodal, now for P2, shortly before

10 disappearing entirely until the present day. Carbon isotope values (δ^{13}C) measured on the same shells of *N. pachyderma* do not show this bimodal distribution (Fig. 3), precluding the possibility that the two populations in δ^{18}O represent a similar season but grew their shells at different depths given the enrichment and depletion with depth in seawater ^{13}C associated with phytoplankton growth and decay. Since the δ^{18}O values of *N. pachyderma* exhibit bimodality while coeval *G. bulloides* does not (Fig. 3), the observed bimodality in *N. pachyderma* cannot have resulted from sediment mixing of Holocene and

15 Glacial shells by bioturbation. Rather, our findings down core equate with seasonal gradients and species successions as observed in modern time-series from sediment traps deployed in the modern North Atlantic (Fig. 1) at 48°N (temperate), 59°N (subpolar) and 68°N (polar).

4. Discussion

4.1 Modern analogue

20 Modern conditions that mimic Glacial times down core are presently found in the polar Greenland-Norwegian Sea where productivity is limited by low light conditions, deep mixing and intermittent sea ice cover (Kučera et al., 2005). At 68°N, late summer insolation and thermal stratification spur a plankton bloom (August-September). At the same time planktonic foraminifera produce a single high maximum in the shell flux of *N. pachyderma* with few *G. bulloides* (Jonkers and Kučera, 2015) at temperatures of 3-5 °C, before the arrival of meltwater (Fig. 5a). Further south, at 59°N in the subpolar Irminger

25 Sea, the flux of *N. pachyderma* is bimodal, with an early 'cold' population being produced in April-May (4-6 °C) and a late 'warm' population occurring in August-September (7-9 °C) that are separated by a single pulse in *G. bulloides* (Jonkers et al., 2010; Jonkers et al., 2013) (Fig. 5b). Neither of the *N. pachyderma* populations from IRM display significant morphological differences (Jonkers et al., 2010; Jonkers et al., 2013). By contrast, modern shell fluxes in the temperate North Atlantic at 48°N, close to our core site, are dominated by *G. bulloides* in early summer yet completely devoid of *N.*

30 *pachyderma* year around (Wolfteich, 1994) (Fig. 5c).

Spatial differences in modern seasonality observed in the polar to temperate North Atlantic provide modern analogues for interpreting temporal changes in the sediment record in terms of the seasonal modes developing since the last Glacial. During peak glacial times the northern North Atlantic is covered by sea ice down to 45°N (Kučera et al., 2005) (Fig. 1) except for a short interval in late summer allowing for a period of high productivity dominated by *N. pachyderma* (P1) as

35 seen in the modern Norwegian-Greenland Sea at 68°N (Jonkers and Kučera, 2015) (Fig. 5a). With the reduction in (sea-)ice cover during the initial deglaciation *N. pachyderma* starts occurring earlier in summer, persisting at the same low temperatures. As the deglaciation progresses the 'cold' population (P1), with a similar unimodal distribution as in the Glacial, is joined by a second 'warm' population (P2) that starts appearing in late summer. The isotopic difference between

P1 and P2 (0.9 ± 0.4 ‰) corresponds to a temperature offset of about ~4 °C, the same as observed today at 59 °N (Jonkers et al., 2013).

The modern seasonal succession of P1 and P2 generates the same bimodality we observe in the δ^{18}O of the mixed *N. pachyderma* populations during the deglaciation in our core record (Fig. 4). Such bimodality may well be an expression of

5 two genetically different but morphologically identical "cryptic species" among *N. pachyderma* (Bauch et al., 2003; Darling et al., 2000; Kučera and Darling, 2002). Indeed, morphologies are indistinguishable among our encrusted specimens from the 250-300 μm both in our cored sediment and in modern *N. pachyderma* from the time-series sediment traps at 59°N during both seasonal maxima, regardless of the size fractions used (Jonkers et al., 2010; Jonkers et al., 2013). At our core site, increasing temperatures would have first caused the disappearance of the "cold" water population P1 (~9.5

10 ka BP) followed shortly after by the disappearance of "warm" population P2 (Fig. 4) when Holocene temperatures at this latitude exceed *N. pachyderma*'s upper tolerance limit of ca. 10 °C (Darling et al., 2006).

4.2 Alternative mechanisms and scenarios

Single specimen isotope analysis permits unravelling of mixed sedimentary assemblages into their constituent components. Here we show that the warming trend within the average δ^{18}O of pooled *N. pachyderma* is directly caused by the emergence

15 of a "warm" population (P2) shifting the mean isotopic value toward a warmer signal, concealing the continued existence of the original "cold" (P1) population. Within the northern North Atlantic an abrupt change occurs from a single peak in production during the LGM to two populations that remain approximately 4°C apart throughout the deglaciation, inferring that the difference in δ^{18}O is temperature driven, consistent with present day observations from subpolar sediment trap time-series. However, alternative scenarios that give the same or a similar solution for the existence of two populations can

20 be envisaged. Below, we discuss other causal mechanisms that might be inferred from the data, including a low salinity meltwater effect (Duplessy et al., 1991), bioturbation (Lougheed et al., 2018) and/or population dynamics (Mix, 1987; Roche et al., 2018).

4.2.1 Warming trend or Meltwater pulse?

Reconstructions of the $\Delta\delta^{18}O_{sw}$ anomaly between the LGM and Modern (Duplessy et al., 1991) suggest a series of regions

25 above the southerly displaced Polar Front where freshwater and meltwater entered the North Atlantic in sufficient volumes to perturb the system, from continental ice meltwater and/or riverine input. Throughout the deglacial period, advances in the subtropical watermasses and retreats of the Polar Front occurred. Repeated invasion of high temperature and salinity waters into the Nordic Seas have shown that the deglacial period was inherently highly dynamic and thus unstable compared to the LGM as evidenced by isotopic (Duplessy et al., 1992; Kroon et al., 1997) and radiocarbon (Waelbroeck

30 et al., 2001) measurements. Meltwater released into the northern North Atlantic during this time would have led to an increase in stratification and thus a decrease in SST altering the E-P balance that drives the poleward advection of subtropical water high in both temperature and salinity (Duplessy et al., 1992). The two populations found in our core during the deglaciation might have resulted from one seasonal population experiencing meltwater and a second seasonal population occurring before or after a meltwater event. The presence of continental ice-rafted debris (IRD) down core in

35 T88-3P, yet a lack of a clear concomitant meltwater 'spike' in the δ^{18}O of either *N. pachyderma* or *G. bulloides* (Fig. 2) would suggest that the difference in δ^{18}O between the two populations is dominated by temperature, consistent with previous studies showing no meltwater spike (Duplessy et al., 1996; Straub et al., 2013). Indeed, the presence of both foraminifera and IRD together down core does not necessarily imply cohabitation of the same environment, as the modern

seasonal maximum in polar shell productivity occurs prior to the arrival of melt water from ice bergs (Fig. 5). The extremely low values of continental ice (δ^{18}O: -30 to -40 ‰) should lead to δ^{18}O and salinity anomalies in surface waters, but sea-ice formed from ocean water will have little impact on δ^{18}O despite an impact upon salinity. Therefore, a concordial meltwater δ^{18}O signal and the presence of IRD is not compulsory (Duplessy et al., 1996) with increased sea-ice formation

5   predicted to occur during periods of increased freshwater and extended Arctic Ocean area (Duplessy et al., 1996).

4.2.2 Spatial rather than temporal populations: Shallow or deep?

Differences in depth habitat rather than timing might account for our observations. Depending on the structure of the water column, i.e. the depth of the surface mixed layer and the degree of stratification (see (Metcalfe et al., 2015) for a discussion), the populations could represent one shallower and one deeper population that are not divided temporally but vertically

10   within the water column (Fig. 5). Observations from the subpolar IRM time-series sediment traps show that the first maximum occurs at an early time when the water column is well mixed, so that two vertically divided populations, i.e. one shallow and one deep would have a similar δ^{18}O signature. The second maximum in IRM occurs at a later time of increased water column stratification, i.e. a shallow and deep population's δ^{18}O would diverge. Therefore, only when the water column is stratified would it be possible to produce two theoretical populations different in δ^{18}O, in much the same way as

15   discrete species calcifying at different depths acquire an isotopic offset, enabling the use of $\Delta\delta^{18}$O as a proxy for past ocean stratification (Emiliani, 1954; Lototskaya and Ganssen, 1999; Mulitza et al., 1997). Following this line of reasoning, our results would suggest that the water column was more stratified during the deglaciation and well-mixed during the LGM and Holocene. One approach to further differentiate between depths is the carbon isotope (δ^{13}C) signal, as seawater δ^{13}C has a distinct signature, due in part to photosynthetic fractionation in the surface ocean enriching the euphotic zone in ^{13}C,

20   exported organic matter may become remineralised at the base of the deep chlorophyll maximum enriching the euphotic zone in ^{12}C at greater depth. Thus, the δ^{13}C of foraminifera that have grown at different depths in these water masses should also have different values for each subpopulation, notwithstanding species specific vital effects.

By contrast, our results show no differences in δ^{13}C signature between the two populations of *N. pachyderma*, notwithstanding inter-specimen variance. What is directly observable however, is that the IRM shows that there are two

25   populations occurring seasonally. Second, there are no morphological differences observed between the specimens of *N. pachyderma* that isotopically belong to different populations in our core record, nor between the early and late summer maxima in *N. pachyderma* with a similarly distinct isotope composition in the modern sediment trap time-series. Most species undergo wall thickening with depth (Brummer et al., 1987, 1986; Hemleben et al., 1985; Reynolds et al., 2018; Steinhardt et al., 2015) whilst some, including *N. pachyderma* add a thick calcite crust with a different δ^{18}O signature

30   overprinting previous layers of the shell (Kozdon et al., 2009). This crust however is an ontogenetic feature (Brummer et al., 1987, 1986; Steinhardt et al., 2015). that is present in both seasons at IRM (Jonkers et al., 2010; Jonkers et al., 2013).

4.2.3 Sedimentary processes: Dissolution and Bioturbation

Seafloor processes such as dissolution and bioturbation may alter sediment populations in both isotope composition (Bard et al., 1987; Lougheed et al., 2017; Wit et al., 2013) and faunal composition (Bard, 2001; Löwemark, 2007; Löwemark et

35   al., 2008). Dissolution not only removes 'time' from the sediment but also leads to specimens being found together that have once been separated by centimetres of sedimentary material, as younger shells are deposited next to freshly exposed older shells (Lougheed et al., 2018). Similarly, depending on the oxygen content of sediments and the type and abundance of bottom fauna, bioturbation by benthic organisms can alter the sequence of cause and causality (Lougheed et al., 2017).

Thus, the two populations found in *N. pachyderma* δ¹⁸O could reflect relict specimens displaced in core-depth, and therefore in time, given there is a shift in the sedimentation rate of core T88-3P between 290 cm and 410 cm. Similarly, Löwemark et al. (2007; 2008) have shown that it is possible to have apparent differences due to the original abundance of the bioturbated species (Bard et al., 1987; Löwemark and Grootes, 2004). The lack of two populations in *G. bulloides*

5   demonstrates that bioturbation did not contribute to any measure because of the implausibility of species-specific bioturbation for specimens of the same size. Similarly, particle grain size distributions may also change by bioturbation (Bard, 2001) so that two differently sized species may show distinct isotope differences given species-specific size distributions (Brummer et al., 1986; Peeters et al., 1999). However, such sorting effects can be excluded here since both *N. pachyderma* populations and *G. bulloides* come from the same > 250 μm size fraction.

10   Bioturbation is more easily detected at a climatic change. As the resultant single specimen δ¹⁸O distribution is a product of species-specific temperature tolerances (Mix, 1987; Roche et al., 2018), the visibility of bioturbation is especially enhanced at periods of sharp climatic transition. If the climatic signal crosses through a species temperature tolerance then two separate warm and cold populations should exist separated in time, bioturbation will then mix these populations together. However, we exclude this particular scenario because sedimentary features (Fig. 2) indicate a lack of discernible mixing,

15   i.e. the sharpness of the IRD percentage, the Log(Ca/Ti) and the percentage of NPS all indicate that bioturbation is at a minimum.

4.3 Palaeoceanographic implications: Probability of drawing from either population I or II

The implications for the climate of the past are twofold. Firstly, our results suggest that there is more than one population of the polar *N. pachyderma* during the deglaciation and that its continued presence throughout much of this time period

20   puts doubt to two discrete modes. The presence of both a colder population and warmer population suggests that this period is characterised by heightened seasonality, given that the climate conditions prevalent at ~56°N supported two populations of *N. pachyderma*. The second implication is that this causal mechanism (i.e., seasonally distinct populations occurring during a climate transition) may not be captured using a pooled sample approach, given two distinct reactions to the same climate transition. Since *N. pachyderma* has two populations while the cosmopolitan species *G. bulloides* has only a single

25   population at the core site, we chose to investigate how multiple populations would impact pooled analysis. The un-mixing algorithm used in this paper gives the probability of each distinct population, using each population and their calculated mean and standard deviation to generate a normal distribution for the populations determined via statistical un-mixing (Hammer et al., 2001; Wit et al., 2013). Using this data it is possible to model the theoretical effect of sample size upon the resultant stable isotope measurements (Morard et al., 2016). For simplicity we assume, that each specimen contributes

30   an equal weighting to the overall pooled stable isotope value, of course in reality each specimen will contribute an amount of CO_2 equal to its weight. This assumption will result in some error associated with our prediction of pooled specimen δ¹⁸O values due to kinetic fractionation during conversion from $CaCO_3$ to CO_2 (and H_2O). The theoretical specimens were picked from either population, or for those samples in which only a single population exists (at either limits of our sampling), using the rand function of MatLab. The function rand is statistically uniform throughout the range 0 to 1 and

35   therefore can be used to construct a random number generator to define which population each theoretical specimen would have belonged to, using the following equations:

$$r = rand(N_{pool}, 1) \geq p(\delta^{18}O_{pop. \, II}) , (2)$$

$$R1 = normrnd(\delta^{18}O_{\mu \, pop. \, I}, \delta^{18}O_{\sigma \, pop. \, I}, N_{pool}, 1) , (3)$$

$$R2 = normrnd(\delta^{18}O_{\mu \, pop. \, II}, \delta^{18}O_{\sigma \, pop. \, II}, N_{pool}, 1) , (4)$$

$$S = (1-r). * R1 + r. * R2, \quad (5)$$

The number of pooled specimens (in-group analysis; N_{pool}) were varied between iterations of the model, so that 5, 6, 7, 8, 9, 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100 draws/specimens were used for each subsequent iteration. For each depth 10,000 redraws were performed, because we use a large number for resampling (N = 10,000), and due to the central limit theorem, the average δ^{18}O between the different iterations (variable number of pooled specimens) remains near constant. Therefore, the 2.5th, 25th, 75th and 97.5th quantiles were used to visually compare the spread of the data between different numbers of pooled specimens (Fig. 6). The results of the model indicate that for a foraminiferal fossil population composed of more than one discrete subpopulation, caution should be applied when using a small number of specimens for pooled analysis to ascertain an average state of the climate. Whilst the spread between the 25th and 75th quantile is narrower for some intervals, a number of down core samples have a spread of 1 to 1.5 ‰.

The fact that one species may have a single population (i.e., *G. bulloides*) and another having intermittently two populations (i.e., *N. pachyderma*) further complicates species comparison (e.g. $\Delta\delta^{18}$O). The emergence of a second population within *N. pachyderma* during the last deglaciation at the species southerly boundary, indicates that other species with multiple abundance or size maxima (Schmidt et al., 2004a; Schmidt et al., 2004b) may have a similarly hidden seasonal complexity within the stable isotope composition of pooled specimens. If these populations do not represent ecophenotypes, but instead are analogous to cryptic speciation in which populations are indistinguishable morphologically (Kučera and Darling, 2002; Morard et al., 2016), then pooled isotope measurement of such a sample will accidentally 'pick' from multiple populations. Therefore, the wide use of *N. pachyderma* isotopes as a measure of sea-level rise, rate of deglaciation or ice volume change based upon the δ^{18}O of pooled specimens may be unduly skewed.

5. Conclusions

Our findings expose and resolve the seasonal complexity that exists hidden in the δ^{18}O produced within pooled specimens whilst highlighting the usefulness of integrating down core studies with modern time-series observation in the interpretation of species ecology for palaeoceanographic research. Using sediment trap time-series data as modern keys to past climate conditions our results imply that conditions existing today within the subpolar Irminger Sea prevailed at significantly more southerly latitudes throughout the last deglaciation. The remarkable difference between the transition (Deglaciation) and the two climatic modes (Glacial and Interglacial), suggests that the mid North Atlantic has an intermediate "deglacial" stable mode that persisted for ~10 kyr, rather than gradually shifting from Glacial to Interglacial. Our observation of a distinct bimodality throughout the deglaciation has important implications for how δ^{18}O records can be interpreted given present-day seasonality, however the interpretation of *N. pachyderma* as two populations instead of one is consistent with previous studies. Therefore, the common use of this species as a measure of sea-level rise, rate of deglaciation or ice volume change, or ocean warming and stratification based upon the δ^{18}O of pooled specimens may be unduly skewed.

Data availability

Upon publication the data of APNAP II T88-3P will be uploaded to a data repository.

Sample availability

Access to APNAP II T88-3P material should be done via request to Gerald Ganssen (VUA).

Author Contributions

G.M.G. was Chief Scientist of APNAP II (RV *Tyro*) during core retrieval, initiated and supervised the study, together with
5   G.-J.B. W.F. conducted the investigation. J.v.'t. H. performed abundance counts. G.-J.B, W.F., B.M. and G.M.G. contributed to data analysis and interpretation. B.M. made the figures and performed statistics. G.-J.B. and B.M. wrote the manuscript with contributions from all authors.

Competing Interests

The authors declare no competing interests.

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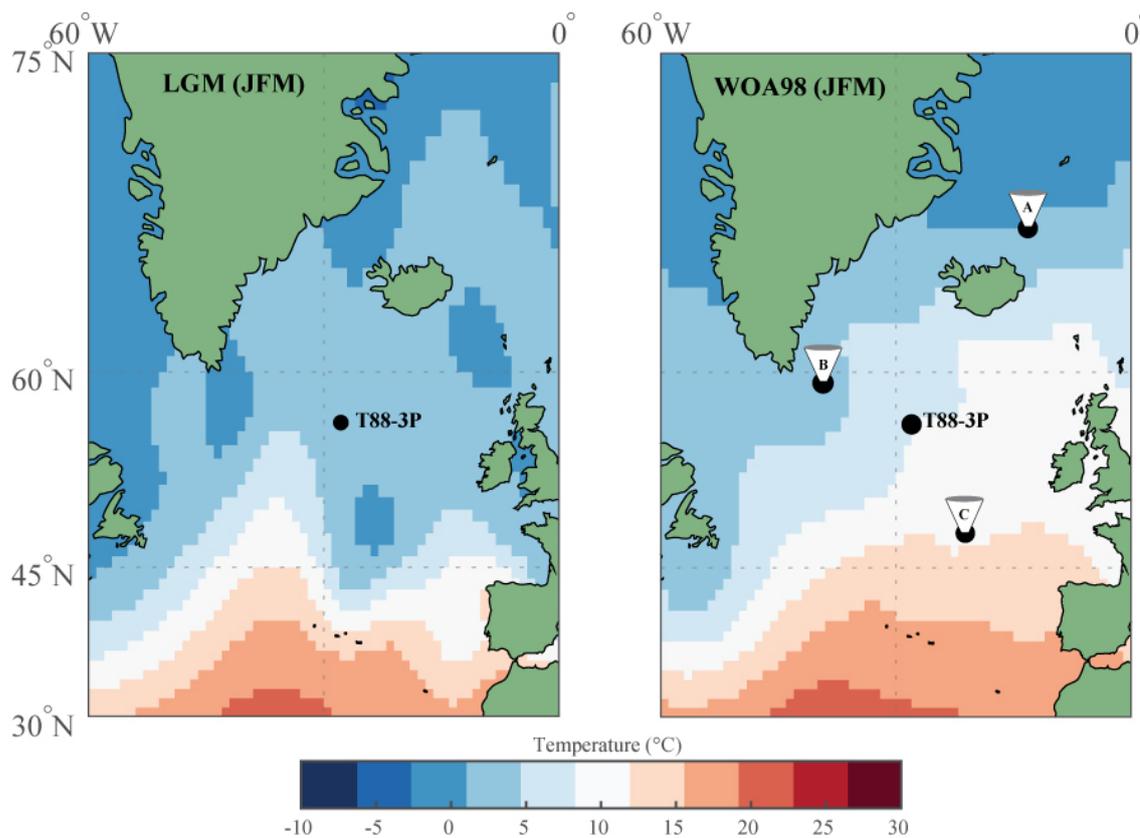
Figures

5   **Figure 1: Map of North Atlantic study area with location of core T88-3P and the position of the sediment trap time series from (A) Iceland Plateau (IP), (B) Irminger Sea (IRM) and (C) North Atlantic Bloom Experiment (NABE). Base maps represent the sea surface temperature for January-February-March of the Last Glacial Maximum based upon the MARGO database (Kučera et al., 2005) and the modern ocean, based upon World Ocean Atlas 1998 (as used by MARGO).**

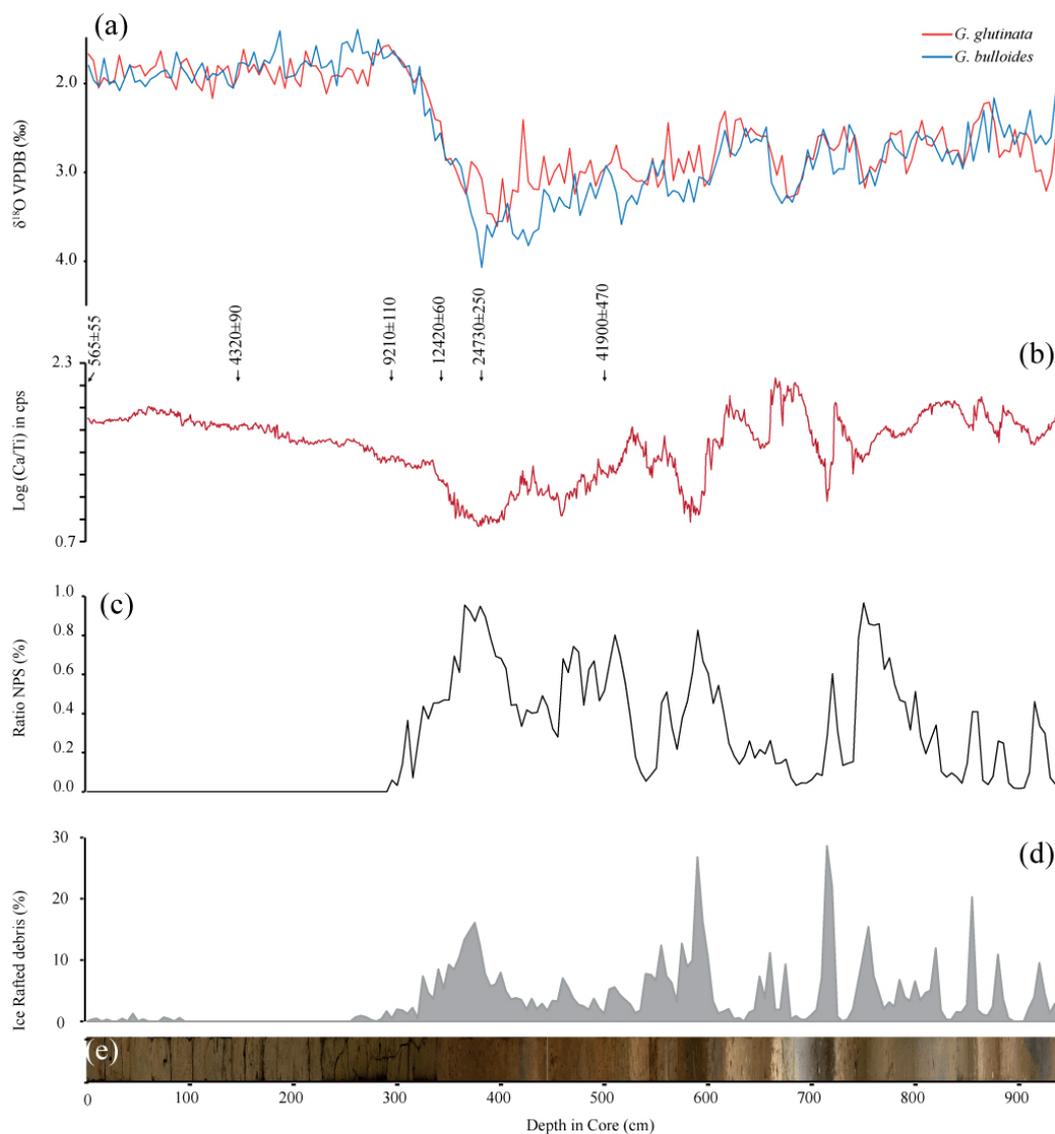
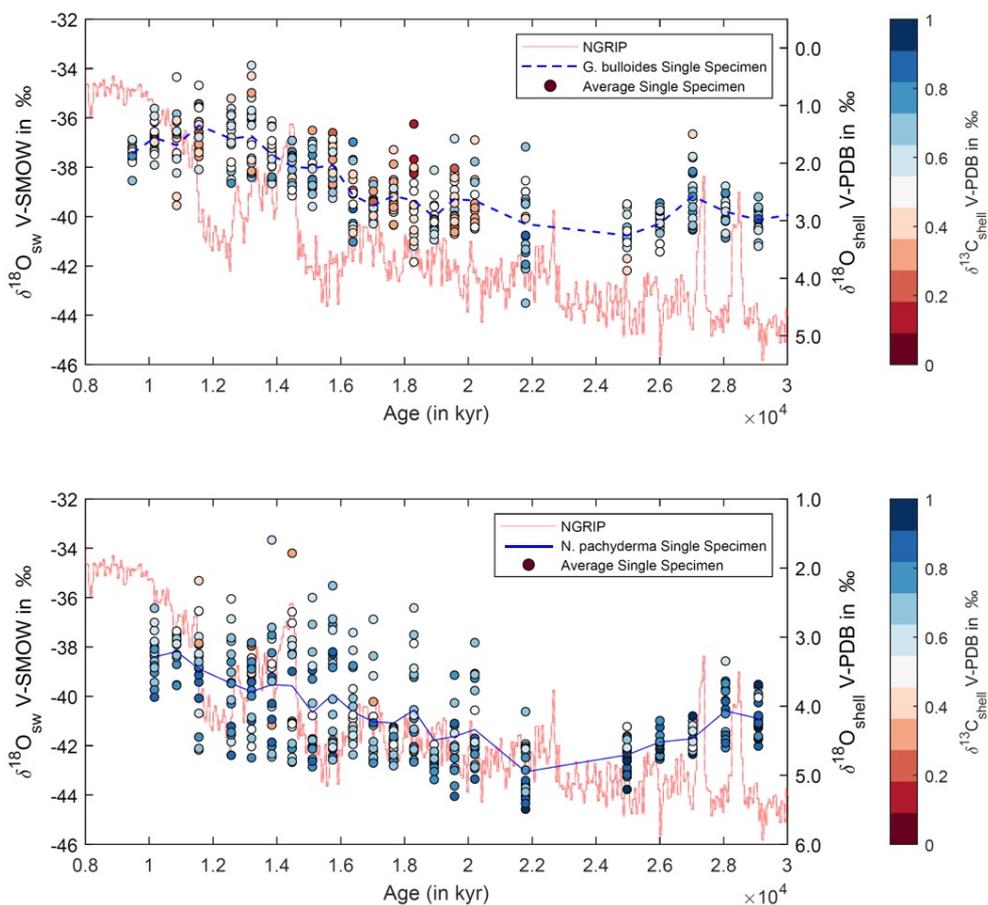



Figure 2: Core stratigraphy of T88-3P with (a) δ¹⁸O of *G. glutinata* (red) and *G. bulloides* (blue), (b) Log(Ca/Ti) ratio with calibrated ¹⁴C ages age-control correlation points, (c) abundance ratio (green) of *N. pachyderma* and *G. bulloides* (see methods), (d) percentage of ice rafted debris from particle counts (grey), and (e) Image of core T88-3P. Note the absence of *N. pachyderma* and IRD in the upper 300 cm.

5 **Figure 3: Raw single shell δ¹⁸O and δ¹³C value of single shell populations for specimens of *N. pachyderma* and *G. bulloides* in core T88-3P. The raw δ¹⁸O data of (top) *G. bulloides* and (bottom) *N. pachyderma* plotted against age, colours represent the δ¹³C value, alongside the NGRIP Ice core δ¹⁸O$_{sw}$ (red line). Blue line connects the average of the single specimen δ¹⁸O values for each sample.**

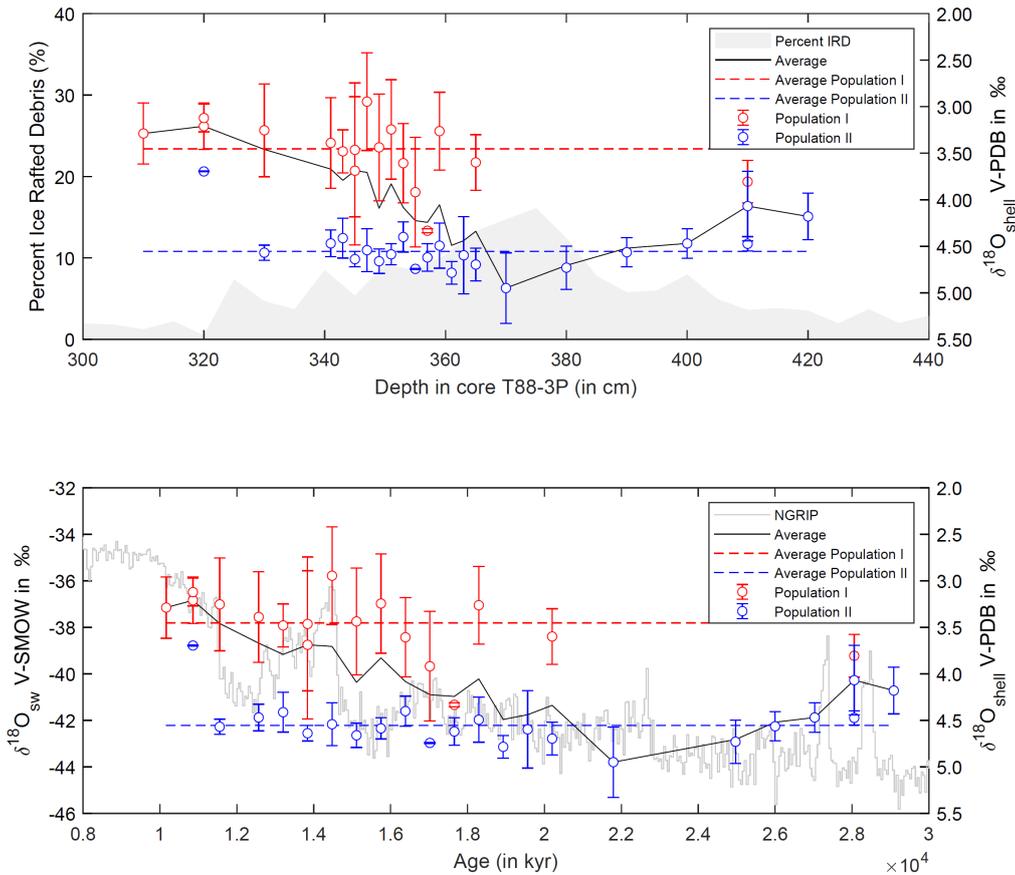



Figure 4: Average δ¹⁸O value of single shell populations for specimens of *N. pachyderma* across the deglaciation. (Top) Mean and standard deviation of distinct populations vs. ice rafted debris (IRD) plotted along core depth. (Bottom) Mean and standard
5 **deviation of distinct populations vs. NGRIP ice core values (δ¹⁸O$_{SW}$ in ‰ V-SMOW) plotted along age scale. Calculated values for Population I and II, as determined from mixture analysis (Hammer et al., 2001). Vertical bars represent the standard deviation for each population, depths where multiple symbols are present are where it is not possible to distinguish statistically either one or more populations, these thus represent a single population of the sample to the left. Horizontal dashed lines represent the averages for population I and II, black line is the total population average as would be reconstructed from pooled**
10 **shell analysis. Above 300 cm (< ~10 kya), the Holocene, *N. pachyderma* has disappeared from the site.**

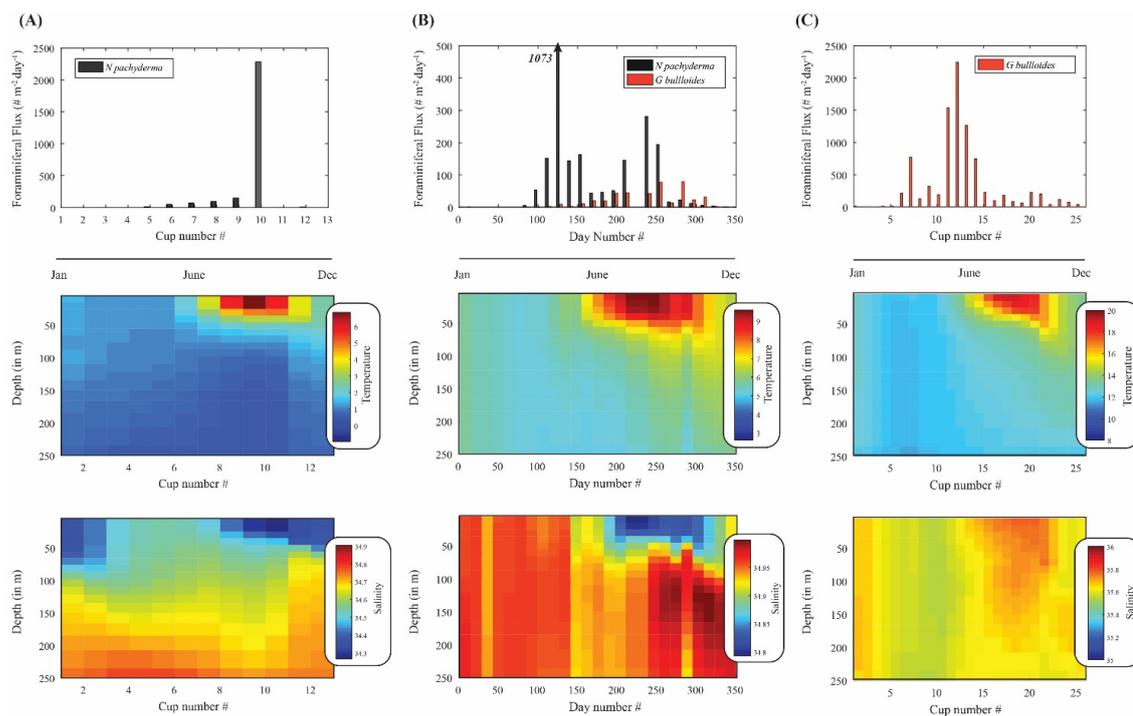



Figure 5: Seasonal succession in the modern North Atlantic. Top panel, fluxes of *N. pachyderma* (grey) and *G. bulloides* (blue) from sediment traps in (A) the polar Greenland-Norwegian Sea (Wolfteich, 1994), (B) subpolar Irminger Sea (Jonkers et al., 2010; Jonkers et al., 2013; Jonkers and Kučera, 2015) and (C) temperate mid North Atlantic (Wolfteich, 1994), same labels as in Fig. 1. Middle and Bottom panels represent the temperature and salinity from ocean reanalysis ORAS S4 (Balmaseda et al., 2013). For (A) and (C) cups have been rearranged to progress from January – December. The fluxes, temperature and salinity given represent an averaging over the trap deployment period.

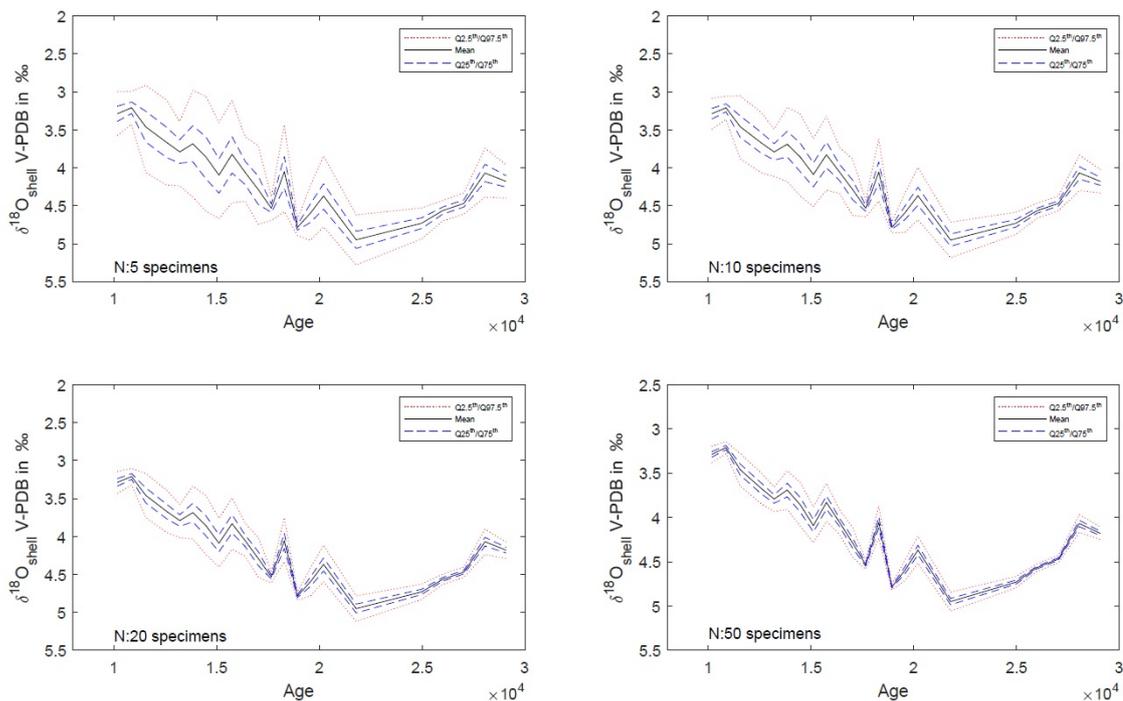



Figure 6: Output of estimate of pooled specimen variance for T88-3P. Using the unmixed populations of *N. pachyderma*, based the upon single shell measurements presented here, a pooled synthetic measurement was created using the probability of each population, and a synthesised normal distribution with the same mean and standard deviation. Estimates were made for 5, 10, 20, and 50 specimens. For each sample 10,000 replicates were produced, the mean (black line) of these pooled specimens remains near constant as a by-product of the number of replicates and therefore the purpose of comparison the quantiles are plotted for each sample against age. Four quantiles are used, the 2.5[th] and 97.5[th] quantiles (red dotted line) and the 25th and 75th (blue dashed line), which highlight the spread in the synthesised pooled specimen data.

Lab Code		Sample ID	Depth in core (cm)	Species	Measured Age (in BP)	δ13C	Conventional Age (in 14C yr BP)	±	Cal Age (in cal. Yr BP)	Cal Age (in cal. Yr BP)
Beta	343133	T883P001BULL	1	*G. bulloides*	570	-0.98	970	30	939	182
Beta	343134	T883P150BULL	150	*G. bulloides*	3830	-0.68	4230	30	4841	3783
Beta	343135	T883P295BULL	295	*G. bulloides*	8180	-0.76	8570	40	9637	8603
Beta	343136	T883P340BULL	340	*G. bulloides*	10590	-1.07	10990	40	12909	11803
Beta	343137	T883P380PACH	380	*N. pachyderma*	20750	-0.5	21150	90	25547	24396
Beta	343138	T883P500BULL	500	*G. bulloides*	37080	-0.41	37470	370	42233	40807

Table 1: Raw and calibrated radiocarbon ages.

Depth in core	Log likelihood	AIC	No. of groups	Prob 1	Mean 1	St dev 1	Prob 2	Mean 2	St dev 2	N in group 1	N in group 2
1	10.98	-17.16	1	1	3.2877	0.32952					
2	11.61	-18.03	1	1	3.2098	0.24822					
2	19.79	-26.58	2	0.84618	3.1215	0.14861	0.15382	3.6957	0.0042961	11	2
3	1.416	8.244	2	0.84353	3.2532	0.49936	0.15647	4.5686	0.081738	3	15
4	1.148	9.038	2	0.26023	4.469	0.14348	0.73977	3.3891	0.48657	5	12
5	6.971	-2.865	2	0.66587	3.4795	0.23115	0.33413	4.4121	0.21443	6	12
6	-4.62	14.1	1	1	3.6879	0.79594				17	
6^	-2.315	15.96	2	0.19105	4.6383	0.083236	0.80895	3.4635	0.71959	4	13
7	-0.6488	12.15	2	0.57144	4.5416	0.23083	0.42856	2.9452	0.52502	11	8
8	4.373	2.331	2	0.53459	4.6606	0.13057	0.46541	3.4368	0.57366	10	8
9	3.456	3.754	2	0.56458	3.2442	0.5345	0.43542	4.5863	0.11314	11	9
10	7.585	-4.092	2	0.56409	4.4003	0.16144	0.43591	3.6069	0.42575	11	7
11	7.927	-4.217	2	0.55355	3.9185	0.58911	0.44645	4.7425	0.0062485	8	8
12	22.23	-32.45	2	0.69344	4.6199	0.14852	0.30656	4.3331	0.021007	10	4
13	2.672	5.733	2	0.64344	4.4932	0.24184	0.35656	3.2622	0.41755	12	6
14	24.07	-43.13	1	1	4.7842	0.12192				15	
14*^	26.16	-40.31	2	0.93472	4.7648	0.1007	0.065283	5.0619	0.0003575	14	1
15^	6.413	-7.968	1	1	4.5964	0.41594				17	
16	9.593	-8.519	2	0.30027	3.5986	0.29849	0.69973	4.6963	0.17603	6	14
17	8.004	-11.15	1	1	4.9491	0.37877					
18	17.26	-29.71	1	1	4.7299	0.23255					
19	20.35	-35.69	1	1	4.5638	0.15624					
20	22.86	-40.86	1	1	4.4694	0.15808					
21	7.221	-9.442	1	1	4.068	0.37479					
21†	11.48	-10.96	2	0.39292	4.4734	0.07702	0.60708	3.8056	0.22872	6	9
22	17.7	-30.69	1	1	4.1795	0.25037					

Table 2: Results of Mixture analysis; * indicates potentially one population; ^ error distribution too far from model.