Neogloboquadrina pachyderma
Anthropogenic warming is currently causing a pole-ward retreat of the global sea ice distribution (Stocker et al., 2013). Reduced summer sea ice allows for solar irradiation and wind mixing that promote ocean productivity and atmospheric CO₂ drawdown at elevated temperatures. Here we show that the past natural deglaciation was accompanied by punctuated shifts in the seasonal succession and species productivity of planktonic foraminifera now found in the modern polar, subpolar and temperate North Atlantic, respectively. We identify a similar succession in a single sediment core during the last glacial-interglacial transition using single shell oxygen isotopes of “polar” Neogloboquadrina pachyderma (left coiling) and “subpolar” Globigerina bulloides. Glacial productivity is limited to a single maximum in late summer and dominated by N. pachyderma, followed by melting icebergs and winter sea ice. Deglaciation shifted the main plankton bloom towards early summer, adding a second “warm” population of N. pachyderma with G. bulloides in between. At the end of the last deglaciation first “cold” then “warm” N. pachyderma become extinct by exceeding threshold temperatures while G. bulloides persists at the core location. We conclude that polar shifts in seasonal timing and productivity structure, resuming in response to the current Anthropogenic warming, are resolved by single shell $\delta^{18}O$ of planktonic foraminifera.
Deglaciation by global warming has strongly affected North Atlantic ventilation and overturning circulation which, in turn, impacted productivity and CO$_2$ exchange with the atmosphere. Decreasing sea ice cover enhances the nutrient supply to the photic zone that spurs primary productivity and thus the drawdown of atmospheric CO$_2$. Modern, Interglacial times exhibit stronger seasonality by increased solar insolation and foremost by deep, wind-driven winter mixing bringing nutrients to the surface before summer stratification sets in [Gruber et al., 2002]. How ocean seasonality changed in time, however, has remained unresolved. With the North Atlantic being the largest ocean carbon sink in the northern hemisphere [Gruber et al., 2002] changes in seasonal productivity have a global effect on anthropogenic CO$_2$ sequestration [Sabine et al., 2004].

Stable oxygen isotopes ($\delta^{18}$O) of marine carbonates allow for tracing water masses, sea level fluctuations and changes in productivity through glacial-interglacial cycles and are at the roots of international climate conventions (IPCC; Stocker et al. [2013]). The $\delta^{18}$O of foraminifera is mainly governed by that of the seawater and the temperature at which the carbonate shell is formed. Recent technical advances have facilitated routine isotope analysis of microgram amounts of calcium carbonate, i.e. single shells of foraminifera. Single Shell Analysis (SSA) allows for resolving seasonal conditions, whereas pooled specimens capture an averaged state of the system on longer time scales (e.g. Ganssen et al. [2011]). Insight into seasonal climate development during the last glacial-interglacial transition over the northern North Atlantic permits tracing the dynamical movement of the polar front (the boundary between Arctic and Atlantic water masses; Orvik and Niiler [2002]), estimated to have a retreat velocity of ~2 km/yr [Bard et al., 1987], which is strongly linked to the formation of North Atlantic Deep Water [Sarnthein et al., 2003], a major driver of the global ocean circulation [Broecker, 1987].

In order to resolve seasonal changes in the northern North Atlantic during the past deglaciation, we analysed single shells of the planktonic foraminifera Neogloboquadrina pachyderma (left coiling) and Globigerina bulloides in sediment core T88-3P from the Iceland Basin (56°N, 27°W) (Figs. 5.1 and 5.2 and suppl. info). In glacial times, both species show a clear unimodal distribution in $\delta^{18}$O (Figs. S5.1 and S5.2) until about 21 ka BP. Whilst G. bulloides remains unimodal throughout the entire record, $\delta^{18}$O values in N. pachyderma spread as a striking bimodality develops (Fig. 5.3) into a population high in $\delta^{18}$O persisting from the Glacial (P1) and a population low in $\delta^{18}$O appearing during the deglaciation (P2). All species show the typical decrease in $\delta^{18}$O during the glacial-interglacial transition, caused by the melting of land ice rich in $^{16}$O into a glacial ocean enriched in $^{18}$O. Subtraction of this ice volume effect [Bintanja et al., 2008] straightens out the long term isotope trend during deglaciation, but preserves the statistic bimodality in N. pachyderma with 0.9 ± 0.4 ‰ difference in $\delta^{18}$O between population P1 and P2 that persists for about 10 ka (Fig. 5.3 and S5.3). At the end of the last deglaciation by 11 ka BP, P1 disappears and N. pachyderma becomes unimodal again, now for P2, shortly before full extinction.
North Atlantic seasonality during Termination I

Figure 5.1. Map of North Atlantic study area. Core T88-3P (red dot) and the sediment trap locations (orange dots) of (a) and (c) Wolfteich [1994] and (b) Jonkers et al. [2010, 2013]. Modern maximum extent of sea ice cover (green line; March 2014, from http://nsidc.org/news/newsroom/2014_maximum_MA.html) and maximum winter sea ice extent for the LGM (dashed green line; Kucera et al. [2005]).

at the core site. Since bimodality is only seen in N. pachyderma but not in coeval G. bulloides abounding to the present day, bimodality does not result from sediment bioturbation mixing Holocene and Glacial shells. Rather, our findings down core equate with seasonal successions known from the modern North Atlantic in sediment traps deployed at three sites from polar 68°N [Wolfteich, 1994] to subpolar 59°N [Jonkers et al., 2010, 2013] to temperate 48°N [Wolfteich, 1994] (Fig. 5.1).

Modern conditions closest to glacial ones at our core site are found in the Greenland-Norwegian Sea where winter productivity is limited by low light conditions and occasional sea ice cover [Kucera et al., 2005]. At 68°N late summer
Figure 5.2. Core stratigraphy of T88-3P. (a) Image of core T88-3P with Log(Ca/Ti) ratio and calibrated 14C ages with correlation points to nearby core DS97-2P (italics; Fig. S5.5), (b) the percentage of ice rafted debris from particle counts (grey), (c) the δ18O of G. glutinata (red) and G. bulloides (blue) and (d) the abundance ratio (green) of N. pachyderma and G. bulloides (see methods). Note the absence of N. pachyderma in the upper 300 cm. Studied intervals indicated with green (deglaciation; see Fig. S5.1) and orange (glacial; see Fig. S5.2) boxes.
Figure 5.3. Ice volume corrected $\delta^{18}$O of *N. pachyderma* during the deglaciation. Single Shell $\delta^{18}$O corrected for ice volume [Bintanja et al., 2008]. Blue box indicates two standard deviations (2$\sigma$=1.14) around the mean (blue dashed line) for P1. Orange box indicates two standard deviations (2$\sigma$=0.54) around the mean (orange dashed line) for P2. The Glacial displays a unimodal distribution, the deglaciation a bimodal distribution with a dominance shift from P1 to P2 and the Holocene showing a unimodal P2 until *N. pachyderma* finally disappears from the core location (see also Fig. S5.1). Averages for both populations were calculated with mixture analysis in PAST [Hammer et al., 2001] and bimodality for the whole dataset was determined using Ashmans’ D test [Ashman et al., 1994] (D = 2.00).
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 [Wolfteich, 1994] at temperatures of 3-5 °C (Fig. 5.4), before the arrival of low salinity meltwater (Fig. S5.4). Further south, at 59°N in the subpolar Irminger Sea, modern N. pachyderma shows clear bimodal productivity, with an early ‘cold’ population in April-May (4-6 °C) and a late ‘warm’ population in August-September (7-9 °C) that are separated by a single pulse in G. bulloides [Jonkers et al., 2010, 2013]. By contrast, modern shell fluxes in the temperate North Atlantic at 48°N are completely devoid of N. pachyderma year around but have common G. bulloides, similar to the Holocene in our core, in a clear maximum during early summer at temperatures of 8-10 °C [Wolfteich, 1994].

The spatial succession observed in modern polar to temperate seasonality provides an interpretative frame work for the core record in terms of the seasonal development of the North Atlantic over the last deglaciation. During peak glacial times the northern North Atlantic is covered by sea ice down to 45°N [Kucera et al., 2005; Fig. 5.1] except for a brief interval in late summer allowing for a period of high productivity dominated by N. pachyderma (P1; Fig. 5.3) as seen in the Norwegian-Greenland Sea at 68°N [Wolfteich, 1994] (Fig. 5.4). As ice cover becomes shorter during deglacial warming, since 21 ka BP, also N. pachyderma starts appearing earlier in summer, at the same low temperature, following the shift of the plankton bloom. While ‘cold’ population (P1) persists from the Glacial, a second ‘warm’ population (P2) starts appearing in late summer with δ18O values 0.9 ± 0.4 ‰ lighter than P1. This difference in δ18O corresponds to a temperature offset of about 3 °C, the same as seen in present day temperatures at 59 °N [Jonkers et al., 2013]. This seasonal succession of P1 and P2 results in the bimodality we find in N. pachyderma during the deglaciation in our core record (Fig. 5.3). Such bimodality may well be an expression of two genetically different but morphologically identical “cryptic species” among N. pachyderma (e.g. Kucera and Darling [2002]). Indeed, morphologies are indistinguishable among our encrusted specimens from the 250-300 μm sediment as they are in several sizes for both seasonal maxima in modern N. pachyderma from time

Figure 5.4. (opposite page) Seasonality succession during North Atlantic deglaciation. Seasonal temperature-depth profiles for last glacial-interglacial transition with Glacial (top; 25 ka BP), the deglaciation (middle; 14 ka BP) and the interglacial (bottom; 10 ka BP) with fluxes of N. pachyderma (N.p.; blue, P1 and orange, P2) and G. bulloides (G.b.; green). Paleo-fluxes are calculated using modern flux data (> 150 μm fraction) from sediment traps in the Polar Greenland-Norwegian Sea (top; Wolfteich [1994]), subpolar Irminger Sea (middle; Jonkers et al. [2013]) and temperate North Atlantic (bottom, Wolfteich [1994]) scaled to relative abundance counts in core T88-3P with corresponding modern hydrography. Data for temperature-depth profiles from World Ocean Atlas [Levitus et al., 2013] and figures from Ocean Data View [Schlitzer, 2013].
series sediment traps [Jonkers et al. 2010, 2013]. Due to increasing temperatures first P1 disappears from the core location (10.5 ka BP) followed by P2 (9.5 ka BP) (Figs. 5.3 and 5.4) when Holocene temperatures at this latitude exceed \( N. \) pachyderma’s upper tolerance limit of 10 °C [Darling et al., 2006].

Despite the abundance of ice rafted debris (IRD) produced by melting ice bergs (Fig. 5.2), there is a contradictory lack of a clear concomitant meltwater effect on the \( \delta^{18}O \) of either \( N. \) pachyderma or \( G. \) bulloides, confirming previous regional studies (e.g. Straub et al. [2013]). Indeed, the seasonal contrast in glacial sea surface temperature remains minimal at the core site with only a brief ice free summer during which both species abound. The reason for the unexpected lack of a strong depletion in \( \delta^{18}O \) given the abundance of IRD would be a matter of seasonal timing in shell productivity occurring earlier than the melt water did from ice bergs that also delivered the IRD (Figs. 5.4 and S5.4). Furthermore, most of the freshwater input would have come from sea ice with a \( \delta^{18}O \) close to sea water, picked up by \( N. \) pachyderma (Fig. S5.3) forming immediately after the sea ice sheet retreated.

Given our results a similar succession should have occurred during earlier deglaciations and allow for tracing the movement of the sea ice sheet over glacial-interglacial transitions using high resolution SSA of planktonic foraminifera. Furthermore, Antarctic \( N. \) pachyderma is known to survive within the ice [Lipps and Krebs, 1974, Spindler and Dieckmann, 1986] and generate a single large pulse in productivity following summer melting [Wefer et al., 1988]. We expect a similar seasonal succession over the deglaciation can also be traced in sediment cores from the southern hemisphere. In line with our findings, we expect the current Anthropogenic deglaciation to cause a further poleward retreat of the sea ice cover increasing primary production in polar regions presently covered by sea ice.

Acknowledgements

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Methods

Piston core T88-3P (56˚438’ N / 27˚797’ W; length 937 cm; 2819 m water depth) was taken during the Actuomicropalaeontology Palaeoceanography North Atlantic Project (APNAP) II expedition in 1988. The age model for core T88-3P was constructed with six radiocarbon dates (Table 5.1) and correlation of the \( \delta^{13}C \) of \( G. \) bulloides to that of core DS97-2P (Fig. S5.5; age model for core DS97-2P was based on a combination of radiocarbon ages from Prins et al. [2001], Rasmussen et al. [2003], Jonkers et al. [2010] and Moros et al., [2012]).
Table 5.1. Calibrated $^{14}$C dates for core T88-3P.

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<tr>
<th>Lab-Code</th>
<th>Sample Code</th>
<th>Depth (cm)</th>
<th>Species</th>
<th>Cal. $^{14}$C BP</th>
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<td>110</td>
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<td>41900</td>
<td>470</td>
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Single shell stable isotope analysis of 20 $N. pachyderma$ (only left coiling) and $G. bulloides$ from the 250-300 μm size fraction was performed on a Thermo Finnigan Delta+ mass spectrometer equipped with a GASBENCH II preparation device. Samples were placed in a He-filled extainer vial and digested in concentrated $\text{H}_3\text{PO}_4$ at a temperature of 45 °C. Subsequently the $\text{CO}_2$-He gas mixture is transported to the GASBENCH II by use of a He flow through a flushing needle system where water is extracted from the gas using a NAFION tubing. The extracted $\text{CO}_2$ is analysed in the mass spectrometer after separation of other gases in a GC column. Isotope values are reported as the standards denotation $\delta^{13}$C and $\delta^{18}$O in per mil versus V-PDB. Reproducibility of routinely analysed lab CaCO$_3$ standards is within 0.12‰ (1 σ) for both $\delta^{18}$O and $\delta^{13}$C for quantities similar to single foraminifera (< 10 μg).

Abundance counts of planktonic foraminifera and terrigenous grains were performed on a minimum of 200 grains after splitting with an OTTO microsplitter. Abundance ratio of $N. pachyderma$ and $G. bulloides$ were calculated as $\% \text{N. pachyderma} / (\% \text{N. pachyderma} + \% \text{G. bulloides})$. XRF-scanning was at the NIOZ (Royal Netherlands Institute for Sea Research) with the NIOZ-AVAA TECH scanner [Jansen et al., 1998].

Supplementary information

Presently the main currents and water masses overlying the core location are the northward flowing North Atlantic Current at the surface [van Aken, 1995], Arctic Intermediate Water and Antarctic Intermediate Water flowing south- and northward, respectively, down to ~1 km depth [Pinet, 2009] and the southward flowing NADW [Charles and Fairbanks, 1992; Cai and Greatbatch, 1995]. During glacial times there was a strong retardation of the conveyor belt [Broecker, 1987; Ganopolski and Rahmstorf, 2001] caused by the replacement of NADW by Circumpolar Deep Water [Streeter and Shackleton, 1979].

Author contributions

G.M.G. collected the core. W.F., M.P. and G.M.G. designed the study. W.F. sampled the core. W.F. and J.v.‘t.H. performed stable isotope analysis. J.v.‘t.H. performed abundance counts. All authors contributed to data analysis and interpretation. W.F. and G.-J.B. wrote the manuscript with contributions from G.M.G. and M.P.
Figure S5.1. Raw single shell δ¹⁸O of *N. pachyderma* (grey) and *G. bulloides* (blue) during the deglaciation. Outliers were detected using Inter Quartile Range (IQR): Q1 - 1.5 * IQR and Q3 + 1.5 * IQR.
Figure S5.2. Raw single shell δ¹⁸O of glacial *N. pachyderma* (grey) and *G. bulloides* (blue) during the last Glacial. Outliers were detected using Inter Quartile Range (IQR): Q1 - 1.5 * IQR and Q3 + 1.5 * IQR.
Figure S5.3. Single shell δ¹⁸O of *N. pachyderma* during deglaciation. Blue box indicates two standard deviations (2σ=0.96) around the mean (blue dashed line) for P1. Orange box indicates two standard deviations (2σ=0.56) around the mean (orange dashed line) for P2. The Glacial displays a unimodal distribution, the deglaciation a bimodal distribution with a dominance shift from P1 to P2 and the Holocene showing a unimodal P2 until *N. pachyderma* finally disappears from the core location (see also Fig. S5.1). Averages for both populations were calculated with mixture analysis in PAST [Hammer et al., 2001] and bimodality for the whole dataset was determined using Ashmans’ D test [Ashman et al., 1994](D = 3.31).
Figure S5.4. Seasonal salinity-depth profiles. Seasonal salinity-depth profiles for modern sediment trap locations in the Polar Greenland-Norwegian Sea (top; Wolfteich [1994]), subpolar Irminger Sea (middle; Jonkers et al. [2013]) and temperate North Atlantic (bottom, Wolfteich [1994]) reflecting conditions during the Glacial (top; 25 ka BP), the deglaciation (middle; 14 ka BP) and the interglacial (bottom; 10 ka BP), respectively. Data for salinity-depth profiles from World Ocean Atlas [Levitus et al., 2013] and figures from Ocean Data View [Schlitzer, 2013].
Figure S5.5. Correlation of core T88-3P to core DS97-2P. Figure shows the correlation points of the δ^{13}C of G. bulloides from core T88-3P (red) to the δ^{13}C of G. bulloides from core DS97-2P (blue).