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Latitudinal Variation of Planktonic Foraminifera Shell Masses During Termination I

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Abstract. The oceans' surface layer holds large amounts of dissolved inorganic carbon that is exchanged rapidly with the atmosphere. Carbon enters the ocean mainly through the dissolution of atmospheric carbon dioxide (CO_2), and a part of it is converted into carbonate by marine organisms. Calcifying marine organisms include planktonic foraminifers that contribute to the marine carbon turnover by generating inorganic carbon production ($CaCO_3$ shells). Anthropogenic CO_2 acidifies the surface ocean, changes the carbonate chemistry and decreases the saturation state of carbonate minerals in sea water, thus affecting the biological precipitation of carbonate shells. Relative changes in average foraminiferal shell mass can be interpreted as variations in test thickness and the extent of calcification that subsequently impacts the global carbonate budgets. The response of calcifying marine organisms to elevated atmospheric pCO_2 is diverse and complex with studies reporting from reduced rates of net calcification to neutral receptivity or even increased calcification intensities. This diverse behavior implies that the concentration of dissolved inorganic carbon may not be the dominant factor controlling the amount of carbonate shell masses. Here we provide further evidence that glacial/interglacial variations of planktonic foraminifera shell masses are invariant to atmospheric pCO_2. We identify that differences in shell weights of several planktonic foraminiferal species from narrow size intervals, over the most recent deglaciation (Termination I) vary systematically as a function of latitude. Past intervals of abruptly changing pCO_2 and temperatures, such as the terminations, can offer a glimpse into the response of marine calcifying plankton to changes in surface oceans. We have compiled all the available bibliographic data of planktonic foraminifera shell weights from restricted sieve fractions of different species from the Atlantic, Pacific and Indian Oceans and we find that for the same pCO_2 conditions planktonic foraminifera from equatorial regions may alter their shell mass only as little as 8.2%, while towards higher latitudes changes in shell mass reach up to 54% during the transition from the last glacial to interglacial conditions. We attribute this low variability in the shell mass of planktonic foraminifera from the equator to the stability of the physical oceanographic conditions that characterize the equatorial zone.

1. Introduction

The climatological and ecological impacts of elevated atmospheric CO_2 partial pressures ($pCO2$) are two of the most pressing environmental concerns of the present. The anthropogenically emitted CO_2 is

absorbed by the surface ocean and causes significant changes in the pH and carbonate chemistry of surface and deep waters [1]. As it dissolves in seawater, it influences the dissolved inorganic carbon (DIC) species; $CO_{2(aq)}$, carbonic acid (H_2CO_3), bicarbonate (HCO_3^-), carbonate ($CO_3^=$) ions and thus the level of calcium carbonate saturation [2]. There is mounting concern over the impact that future CO_2-induced reductions in the calcium carbonate ($CaCO_3$) saturation state of seawater will have on marine organisms that construct their shells and skeletons from this mineral. It has been reported that decreased carbonate ion concentrations cause marine calcareous organisms to show reduced calcification rates [3-5]. Although many studies on modern shells identify a species-specific connection between shell mass and ambient seawater [$CO_3^=$], not all studies confirm this [6, 7] nor does the wider paleoceanographic record both for foraminifera [8] and coccolithophores [9]. This discrepancy between the different studies undermines shell mass as a reliable proxy of carbonate saturation or carbon dioxide levels and leaves the cause behind such behavior that affects the overall carbon cycle still under debate. Past intervals of abruptly changing pCO$_2$ and temperatures, such as the terminations, are ideal to study the response of marine calcifying plankton to changes in surface oceans. In the present study the change in the calcification intensity of different foraminifera species during the last glacial to interglacial transition was evaluated using the weights of ontogenically similar, adult foraminifera tests from different areas and their variation was compared to the atmospheric pCO$_2$ levels.

2. Background

Shell size and mass are central features of marine organisms, reflecting their physiology, ecology and evolutionary history. These two are easily measured morphological characteristics [10], comparable across taxa and extremely variable in time and space. Unlike size, shell mass has not drawn extensive micropaleontological attention although microplankton is a major contributor to the particulate inorganic carbonate in the ocean. Different planktonic foraminifera species shell mass has been found to vary systematically both spatially and temporally (Table 1) with an average intraspecific variation of ~34% during the last two Terminations. Planktonic foraminifera contribute 23-53% to the total global open-marine $CaCO_3$ production, with a total carbonate flux of ~1.3-3.2 Gt yr^{-1} [11]. Hence, shell mass changes in these organisms influence global biogeochemical cycles and carbonate budgets. A number of theories have been proposed to explain planktonic foraminifera shell mass changes across deglaciations, based mostly on ambient seawater chemistry and a brief overview of them is presented below.

Lohmann [12] made the case that the weight of foraminifera shells picked from a narrow size range provides a measure of the extent of dissolution, and it has been used to analyze deep-sea carbonate ion differences at the LGM [13]. However, recent data [14] indicated that the weight of foraminifera shells may be largely dependent upon conditions that prevailed at the sea surface during formation of the shells, such as the surface water [$CO_3^=$]. This dependency upon surface water conditions is expected to translate into biases when using the proxy to reconstruct deep-sea carbonate ion changes at the LGM [15]. On the other hand observations of several other authors do not support the relationship between shell weight and (pressure-corrected) carbonate ion concentration but attribute it to some other environmental factors [7, 16] and thus questions the use of shell weight as a reliable proxy of carbonate saturation and carbon dioxide levels.

Shell mass variation may not result from a single process but rather from a number of different, complex processes with the first, as for any paleontological record, being the degree of dissolution. Thus variability on any shell mass record may therefore be considered as a composite effect of preservation state superimposed upon initial shell weight variability. In the literature cited, the effect of dissolution on the reported shell masses of down-core records is acknowledged but only qualitatively assessed, except from work of Naik and Naidu [17] who used calcite crystallinity variations as a semi-quantitative measure of shell dissolution, though their investigation was confined

merely to core top samples. Once the degree of dissolution is assessed the cause of changes in the 'initial' shell mass can be considered. In general the number of records examined for the scope of the present study is not severely affected by dissolution and thus the observed initial shell mass variation is to be attributed to other environmental factors.

Table 1. Bibliographic data of shell mass variations in different planktonic foraminifera species, from different regions, covering the last Termination.

Species	Region	Sieve fraction	Termination I
G. bulloides	N. Atlantic [a]	300-355 μm	52.4%
	N. Atlantic [b]	300-355 μm	54.2%
	S. Atlantic [h]	300-355 μm	30%
	Agulhas [i]	250-315 μm	27%
	S.W. Pacific [j]	300-355 μm	22.6%
	S.W. Pacific [k]	300-355 μm	21%
	S.W. Pacific [l]	300-355 μm	28%
	S. Indian [m]	300-355 μm	19.5%
G. sacculifer	N. Indian [c]	350-420 μm	32.3%
	Caribbean [d]	355-420 μm	15.4%
	Caribbean [e]	355-420 μm	12.1%
	W. Eq. Pacific [f]	355-425 μm	9.0%
	W. Eq. Pacific [g]	355-425 μm	21.1%
G. ruber	W. Eq. Pacific [f]	355-425 μm	13.8%
	W. Eq. Pacific [g]	300-355 μm	8.5%
	W. Eq. Pacific [g]	215-250 μm	13.8%
	S. Atlantic [h]	300-355 μm	37.2%
N. dutertrei	Caribbean [d]	355-420 μm	8.2%
	Caribbean [e]	355-420 μm	9.0%
O. universa	S. Atlantic [h]	300-355 μm	16.2%
G. inflata	S. Atlantic [h]	300-355 μm	21.5%
	S.W. Pacific [l]	300-355 μm	20.9%
G. truncatulinoides	S. Atlantic [h]	300-355 μm	11.2%

[a] core NEAP 8K [14], [b] core ODP 982 [18], [c] core AAS9/21 [19], [d] core RC8-107 [20], [e] core V28-122 [20], [f] core RC10-140 [21], [g] core RC17-177 [21], [h] core RC13-228 [16], [i] core MD02-2594 [22], [j] CHAT 1K [23], [k] ODP 1123 [23], [l] CHAT 16K [23], [m] core GC17 [4].

Foraminifera shell mass is related to a component of the ocean-atmosphere carbonate system. The initial weight of foraminiferal shells has, so far, been shown to vary under the influence of different chemical properties of ambient seawater during growth [24-27]. It was initially shown by culture experiments of the planktic foraminifera *O. universa* that an increase in shell mass can be due to increased shell thickness as a result of higher ambient $[CO_3^=]$ [26]. Later it was demonstrated that shell mass of several planktic foraminifera species, from narrow size fractions from the north Atlantic varied systematically as a function of latitude. Measured mass of several planktonic foraminifera species from a North Atlantic latitudinal transect increase by a factor of 2 between 60° and 30°N being greater at 30°N [14]. In the same study, these findings were combined with a record of shell mass across glacial-interglacial Termination I to demonstrate that the changes are a result of ambient seawater $[CO_3^=]$ rather than calcification temperature and are consistent with known changes in atmospheric pCO$_2$. Nevertheless, the effect of changes in $[CO_3^{2-}]$ of seawater on δ^{18}O values and thus calcification was found to be small [28].

Foraminifera shell weights have been found heavier during glacial relative to interglacial periods [14-16, 18, 20, 29, 30]. This would be predicted from the proposed inverse relationship observed between initial shell weight and pCO$_2$ [14]. In the record of Barker et al. [18] it can be seen that prior to the Mid-Brunhes event, when pCO$_2$ was oscillating between ~ 200 to 250 ppm, *G. bulloides* shell

mass was oscillating between ~20 to 25 µg. After the release of ~10% more CO_2 in the atmosphere (and ever after the new $p CO_2$ maximum) these organisms decreased (~25%) their shell mass for one glacial-interglacial cycle and in total, it might have taken them two glacial-interglacial cycles to adopt to the new atmospheric $p CO_2$ and return back to their initial shell mass values (of 20 to 25 µg). Moy et al. [31] observed a 30-35% reduction in mass of modern *G. bulloides* shells relative to earlier Holocene shells. They also concluded that it is the maximum shell weights rather than the minimum ones that are driving changes in the average shell weights, so that the seasonal variations are not the cause of the differences. According to the above reasoning glacial-interglacial changes in foraminiferal shell mass are related to changes in ambient carbonate ion concentration through time in response to changing atmosphering $p CO_2$.

Nevertheless, shells from different species, regions, climates or $CO_{2(aq)}$ concentrations differ systematically in their shell weights, even when dissolution was found to be minor or before any dissolution has taken place. For example, *P. obliquiloculata* shells from the Pacific were found, for the same pressure normalized carbonate ion concentration, consistently 10 µg heavier than those from the Indian Ocean. Weights for *P. obliquiloculata* from the Atlantic lie in between these end members. On the other hand while *N. dutertrei* shells from the Pacific and Indian Oceans show no significant weight offset, those from the Atlantic average are 8 µg heavier [32]. The same authors later [20] noted that neither a significant $[CO_3^=]$ difference nor a significant temperature difference exists for the previously mentioned calibration sites and they concluded the same for the measured shell weight variability from different core-top locations, of the same depth, from the Ceara Rise. Thus, subsequent studies have shown that factors which control shell weights are more complex than previously thought [21] and might not respond strongly to $[CO_3^=]$, if at all [7, 15]. Inconsistency between $p CO_2$ and changes in plankton calcite production has also been reported for the high $p CO_2$ Pliocene between equatorial and higher northern latitudes in the Atlantic [8].

de Villiers [33] suggested that shell calcification is apparently a function of complex interplay of environmental parameters and that species optimum growth conditions are responsible for the observed shell mass variations. Her results, along with that of Naik and Naidu [19], showed that calcification temperature does not play a major roll on shell mass and she therefore concluded that neither $[CO_3^=]$ or nutrient levels can be invoked to explain the observed trends in the shell mass, while inorganic overgrowths have been ruled out both theoretically [12] and empirically [4]. Nevertheless, a study from the tropical Indian Ocean demonstrated that *Globigerinoides sacculifer* shell mass is indeed controlled by $[CO_3^=]$ of surface waters [17]. The conflicting results led to another study that employed different foraminifer species, i.e. *Globigerina bulloides*, *Globigerinoides ruber* and *Neogloboquadrina pachyderma* to gain a better understanding of the control of calcification rate [34]. It was shown that in general, $[CO_3^=]$ of surface waters controls shell weights in *G. bulloides* and *G. ruber*, but *N. pachyderma* thrives on optimum growth conditions. Yet Beer et al. [7] found that $[CO_3^{2-}]$ does not exert a dominant control on foraminiferal test mass, while foraminiferal abundance data do not support the assumption that shell mass responds to optimal growth conditions and concludes that further work is needed to determine those environmental factors that are simply correlated with shell mass and those that exert control.

The above analysis of previous investigations lends support to the hypothesis that neither $[CO_3^{2-}]$, temperature, nutrient availability nor optimal growth conditions are the causal factor of the observed foraminiferal intraspecific shell mass variation. Recently, Weinkauf et al. [27] concluded that changes in the precipitation of calcite mass in planktonic foraminifera shells should reflect mainly abiotic forcing and that foraminifera calcification intensity increases with seawater salinity. Since salinity influences ocean density, our present results agree with the previous findings and strengthens the hypothesis that foraminifera shell masses are related to ambient seawater densities [35], according to

which any temporal and spatial variation in ocean buoyancy forces planktonic calcifiers to regulate their shell mass towards the acquisition of a species specific optimum depth [36].

3. Methods

The difference in the mass (ΔMass) of the shells of several planktonic foraminifera species was studied between the last glacial to interglacial transition using available bibliographic down core shell weight records from different geographic locations. In the literature, although the word weight is commonly used the reported values are in (micro)grams (μg) which are essentially mass units and this is what the balance displays. As weight is a force and its units are Newtons we here more correctly use the word mass when referring to microbalance measurements. We considered only mass records obtained from foraminiferal tests of different sizes that prior to weighing were sieved using a narrow (~60 μm) size window. Tests from restricted size fractions yield some homogeneity and consistency within the sample that minimizes ontogenetic and growth rate offsets [37]. ΔMass signifies the mass of the glacial test, i.e. at the time of maximum mass minus its value at the interglacial time of minimum mass. Due to scarcity of records reporting planktonic foraminifera shell mass values over multiple climatic cycles we focus here on the percent loss in shell mass (ΔMass%) of foraminifera during the last deglaciation of Termination I (Table 1).

Terminations are periods of sharp climatic transitions from maximum glacial to maximum interglacial conditions [38]. The most recent of these periods was the transition from the Last Glacial Maximum (LGM) to the Holocene, during which CO_2 increased by ~40% (80 μatm) [39, 40]. Although terminations are considered nearly synchronous between the two hemispheres their magnitude and timing exhibit both regional intra- and inter-hemispheric variations. The last ice recession in the northern hemisphere began at about 20 ka, while in Antarctica and the Southern Ocean the last termination began about 2 ky later [41]. Since we compare time series from different latitudes and hemispheres, abrupt changes in shell masses are not always synchronous between records. We therefore consider as LGM counterparts the local maximum shell mass values that are recorded between 22 to 19 ka [42] and as post-termination subsequent local minimum values close to the beginning of the Holocene around 11 ka. Although LGM values in most cases were distinct local maxima and therefore easy to distinguish, the immediate interglacial values were not always straightforward to select. To this extent, instead of the absolute local minima as post-termination values we considered a three-point average around the local minimum values.

4. Results and discussions

Paleoceanographic archives from various geographic locations that record the shell mass variations of several planktonic foraminifera species during the last climatic cycle were investigated. The calculated percentages of mass loss between heavy glacial and lighter interglacial-early Holocene shells from different ocean basins were plotted against the archive's latitude and the results are shown in Figure 1. The analysis revealed a latitudinal control on the degree of differentiation between glacial and interglacial shell mass measurements that is species invariant and test size independent. Close to the equator the variation in mass loss percentage is the smallest ranging from ~10% to 20%, while in the subtropics loss maybe up to 37%. The highest differences in shell mass across the last climatic transition are recorded in two adjacent cores in the northern high-latitude Atlantic, where foraminifera calcification declines more than 50%. It becomes apparent that the increase in atmospheric pCO$_2$ does not result in an equal decrease in planktonic foraminifera calcification on a global scale. Thus, foraminifera calcification does not show a linear relationship to the atmospheric pCO$_2$ increase but responds to changes in pCO$_2$ zonally. Near the equator the ~40% increase in atmospheric pCO$_2$ during the termination only slightly (as little as 8.2%) perturbs foraminifera test mass, while closer to the polar region their masses are affected to a percent even greater than the atmospheric pCO$_2$ changes.
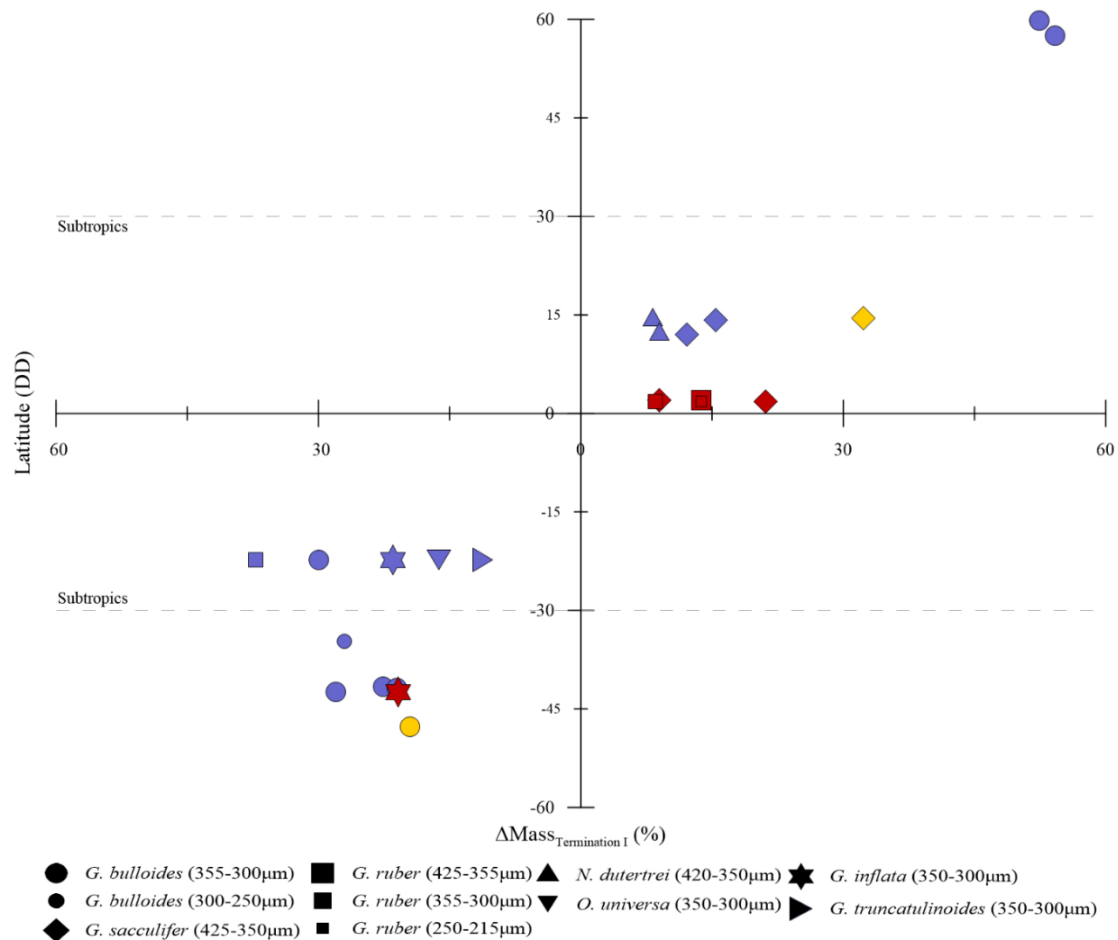
Figure 1. Changes in shell mass of different planktonic foraminifera species between the LGM and the onset of the Holocene as a function of geographic location. The ΔMass% is the percent reduction shell calcite mass. Note that for better illustration and in order to avoid overlapping between hemispheres the percentages were mirrored on the left x axis and are descending positive values. In blue are samples from the Atlantic including the Caribbean and the Agulhas regions; in yellow are samples from the Indian Ocean including the Arabian Sea at the north and the central subantarctic zone in the south, and in red samples from the western equatorial and the south-west Pacific. Symbol size denotes the size of the specimens and the grey dashed lines are the boundary between the Hadley cells at the subtropical zone.

As mentioned above, elsewhere latitudinal planktonic foraminifera shell mass variations have been attributed to the temperature dependence of CO_2 solubility in seawater [14] since a decrease in ocean temperature increases the solubility of CO_2 in the ocean [43]. During the LGM, average sea-surface temperatures were globally about 2.3°C lower than today with the greatest cooling in high latitudes, moderate cooling in the equatorial and boundary current regions, and minimal cooling in the central gyres [44]. Following the argument of a possible solubility effect on shell precipitation the greatest percent loss in shell masses should have occurred in high latitudes, which is in accordance with our results; the minimum loss should have been in the intermediate latitudes and the moderate at the Equator but overall this is not what we observe. Further considering a possible solubility effect on foraminifera shell mass in the hypothetical scenario in which we completely neglect the existing relationship between shell mass and $CO_3^=$ [15] based on the fact that oceanic $[CO_3^=]$ in total has not varied during the termination [45], at the Equator where climatic shifts are minimum due to constant solar forcing, let's assume that the on average 15% loss of shell mass in our record is due to CO_2

solubility decrease for a 2°C Holocene warming [46]. The above would yield a response of the organisms to solubility changes of 7.5% shell mass loss per °C. For an additional 4°C warming of the high latitudes at the onset of the Holocene [47] we would expect an additional 30% reduction in foraminifera shell mass, which is not exactly what we record. Since foraminifera from different oceanic basins demonstrate a diverse response in the amount of shell calcite precipitation for the given atmospheric pCO$_2$ alteration during Termination I, and this diverse pattern is not explained by basin to basin CO$_2$ solubility offsets in the lack of other possible chemical forcing behind their shell mass variations [48], we check for physical parameters. We find that this zonation in shell mass follows that of modern surface ocean mixed layer density and it may be explained by the variation in ocean density between maximum glacial and Holocene conditions.

According to the latest summary of global CTD data [49], today the minimum mixed layer density values are found in the tropics where salinity is lowest and also just north of the equator (beneath the Intertropical Convergence Zone; ITCZ) across the Pacific and Atlantic. Density increases toward the poles where temperatures are very cold or where salty water influence is strong, also under cold temperatures. Furthermore beneath the ITCZ seasonal density changes are weak because the temperature and salinity changes are small and possibly during the LGM since paleoclimatic evidence is generally interpreted to indicate only small variations in tropical temperatures as compared to those at high latitudes [50], which would support the hypothesis that tropical conditions may be relatively insensitive to changes in radiative forcing [51]. On the contrary density estimates suggest that the northern surface ocean density was higher during the LGM [52], due to high Equator-to-Pole temperature gradient [53], and may be sufficient to explain the reported offsets in planktonic foraminifera shell mass. If the density and thus the buoyancy force of the equatorial zone decreased only slightly during the climatic transition, then these almost passively floating organisms would need to decrease their shell mass only slightly in order to counterbalance and maintain a certain (optimum) water depth. On the other hand, the greater density differences between the glacial and the interglacial ocean, at higher northern latitudes would require greater shell mass losses to regulate their flotation. The Equator-to-Pole salinity profile alone does not match the reported shell mass loss pattern as salinity shows maxima in the subtropical regions, due to its dependency on evaporation and precipitation and decreases in the higher latitudes [49].

5. Conclusions
Well preserved, globally distributed, bibliographically available core records of weighed planktonic foraminifera shells of restricted size were compiled and their percent in mass loss during Termination I was calculated. The analysis revealed a shell mass loss latitudinal pattern with greater losses in the high latitudes, which minimizes equator-ward and is species- and size-invariant. This wide variability between locations cannot be explained by the globally uniform atmospheric pCO$_2$ increase during the last deglaciation and is attributed instead to the greater surface ocean mixed layer density changes of the higher latitudes compared to those of the tropics as part the foraminifera optimum depth acquisition mechanism.

Acknowledgments

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