Influence of surface ocean density on planktonic foraminifera calcification

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This study provides evidence that ambient seawater density influences calcification and may account for the observed planktonic foraminifera shell mass increase during glacial times. Volumes of weighed fossil *Globigerina bulloides* shells were accurately determined using X-ray Computer Tomography and were combined with water density reconstructions from Mg/Ca and δ18O measurements to estimate the buoyancy force exerted on each shell. After assessment of dissolution effects, the resulting relationship between shell mass and buoyancy suggests that heavier shells would need to be precipitated in glacial climates in order for these organisms to remain at their optimum living depth, and counterbalance the increased buoyant force of a denser, glacial ocean. Furthermore, the reanalysis of bibliographic data allowed the determination of a relationship between *G. bulloides* shell mass and ocean density, which introduces implications of a negative feedback mechanism for the uptake of atmospheric CO2 by the oceans.

Planktonic foraminifera adjust to the dynamic behaviour of the fluid in which they are immersed1. As with other zooplankton, the precipitation of relatively heavy calcitic tests, with a specific gravity significantly greater than that of the ambient seawater, provides foraminifera a mechanism to counteract uplifting due to lighter cellular components and allows them to inhabit certain depths, which represent favourable ecological niches, by regulating their buoyancy at the expense of biochemical energy2. But little is known about how this behaviour may have varied through time as the density of seawater has evolved in response to changes in the temperature and salinity structure of the oceans. Therefore we explore the novel hypothesis that downcore shell mass variations may in part reflect a hydrostatic response to seawater density changes.

A number of authors have observed that planktonic foraminifera shell mass was higher during glacial stages and lower during interglacials3–7. The cause of this behaviour is debated. Since it was first shown in culture experiments that an increase in shell mass was induced by an increase in carbonate ion concentration8, a link between calcification efficiency and carbonate ion concentration ([CO32−]) has been found in the physical environment9. A number of authors have shown that glacial shell mass of some planktonic foraminifera species from different regions, is correlated with proxy records for carbonate ion concentration [CO32−], which increases in seawater due to the decrease of glacial atmospheric pCO23,4,7,10. This reasoning thus has been used to reconstruct past distributions of carbonate ion concentration from shell mass5,11,12.

Additional work has suggested that downcore variations in shell weight may not always be explained by [CO32−]. For example, a causal relation between shell mass variations and [CO32−] could not be verified for a number of down-core studies13,14 and contemporary biogenic material investigations from different localities. Some authors have suggested that such attempts should be considered with caution15. Calcification temperature has been suggested to not always play a major role on shell mass16.

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were performed with a constant gravitational acceleration (9.82 m/s²). We found that foraminifera shell mass of temporary shells and the results are shown in Fig. 2. Calculations of the weight of seawater displaced by the organism density. Average buoyancy values calculated for different time intervals were plotted against the mass of contemporaneous shells. The 1σ confidence interval for each plot is shown as solid grey area and bars, respectively.

σ minimal. The 1σ confidence interval for each plot is shown as solid grey area and bars, respectively. Increased BDX' values signify greater dissolution, with significant dissolution starting at values above 3. The results show no evidence for high dissolution, and also no systematic decrease in Mg/Ca values is observed with reduced preservation. Therefore any low-temperature bias to paleotemperature estimates from Mg/Ca due to preferential post-depositional dissolution of the Mg-rich portions of the foraminiferal calcite is likely to be minimal. The 1σ confidence interval for each plot is shown as solid grey area and bars, respectively.

Even for modern shells of the same species, in different sites almost identical in water [CO₃] and temperature, an offset in shell mass has been observed. Although the influence of nutrients has been hypothesized, yet another study excluded nutrient availability and instead called upon optimum growth conditions as the cause for the observed shell mass variations, although subsequently size-normalized weight was found not to respond to optimum growth conditions. Finally it has been suggested that changes in size-normalized shell weight of planktonic foraminifera reflect mainly abiotic forcing since heavier shells in the Mediterranean were associated with high salinity waters. Dissolution as the major parameter affecting recorded shell mass variation was excluded qualitatively in most of the studies above, while it was semi-quantitatively assessed only for a set of core-top samples.

Since planktonic foraminifera are major contributors of calcium carbonate (CaCO₃) to the sea floor, the identification of the processes that affect their biomineralization is relevant to testing hypotheses on the origin of glacial-interglacial pCO₂ variations and to predicting the future of marine calcifying organisms and ecosystems. Here, the state of shell preservation is evaluated by semi-quantitative means, and the role of ocean density variations on shell mass and the subsequent change in the intensity of ocean buoyancy force during glacial-interglacial intervals are examined.

At North Atlantic ODP Site 982 we measured Mg/Ca to reconstruct temperature. Furthermore we measured the volumes of weighed G. bulloides shells at different intervals and calculated the buoyancy force exerted to them by the ocean. Reconstructed temperature values were combined with available oxygen isotope data to calculate seawater salinities. The proxy derived salinity and temperature estimates were used in the equation of state of seawater to derive past surface ocean density changes. We also evaluate shell weight and density data from published geochemical datasets for a number of Atlantic and Southwest Pacific sites.

Results
Tests of G. bulloides from ODP Site 982 are very well preserved and exhibit evidence for only a minor increase in dissolution during glacial times (Fig. 1), in accordance with previous studies on dissolution impacts on planktic foraminifera from the Atlantic. Preservation events are recorded during stadials. No significant dissolution was inferred for the Mid-Brunhes interval (~200–600 ka). In particular the assessment of the X-ray imprint of a number of specimens (Table 1) suggests that calcite loss for most may be well below 15%.

The buoyancy force exerted on G. bulloides by surrounding seawater was estimated as a function of water density. Average buoyancy values calculated for different time intervals were plotted against the mass of contemporaneous shells and the results are shown in Fig. 2. Calculations of the weight of seawater displaced by the organism were performed with a constant gravitational acceleration (9.82 m/s²). We found that foraminifera shell mass correlates well (R² = 0.58, p < 0.005, n = 10) with the buoyant force exerted on them by the surrounding seawater suggesting that their shell mass increases with an increase in the force of buoyancy. The heavier shells are the most voluminous ones (Table 1; R² = 0.43, p < 0.05, n = 10).

There is evidence of a relationship between G. bulloides shell mass and ocean density from the reanalysis of data from core NEAP 8K which we used to calculate paleodensities. Paleodensity estimates were plotted against G. bulloides shell normalized mass, from the 300–355 μm size fraction, and the results are shown in Fig. 3. The measurements correlate significantly (R² = 0.56, p < 0.001, n = 79) supporting the hypothesis that heavier shells precipitated in denser waters. The correlation between size normalized weight to salinity was R² = 0.52 (p < 0.001, n = 79) and to temperature was R² = 0.07 (p > 0.1, n = 79), while temperature and salinity in this case were not correlated to each other (p > 0.05, n = 79). The significant correlation of shell mass with seawater salinity, in contrast to temperature, supports previous findings. This result implies that the salt concentration of ambient seawater greatly affects plankton shell mass, which could be due to the impact of salinity on density.
Figure 2. Evidence for a significant correlation between the shell mass of *G. bulloides* from Site 982 and buoyancy force estimates derived from X-ray microtomographic volumetry and combined Mg/Ca - δ\(^{18}\)O measurements of the same samples. Grey dots are values from interglacial or interstadial samples and black dots represent glacial or stadial samples (Table 1). The dashed lines around the regression line indicate the 95% level of confidence.

Table 1. Data summary of specimens used for buoyancy calculations. Cold climatic times (glacials, stadials) are shown in bold. MCD = Meters Composite Depth of ODP Site 982 samples, MIS = Marine Isotope Stage and XDX = X-ray Dissolution Index.

| MCD | MIS  | Age BP (ka) | Individual shell volume (μm\(^3\)) | Number of shells | Shell mass (μg) | Buoyancy \(\times 10^{-9}\) (N) | XDX index |
|-----|------|-------------|-------------------------------------|------------------|----------------|--------------------------------|------------|
| 1.13 | MIS 3b | 35.769 | 20,737,310 ± 14% | 16 | 18.9 | 209.3 ± 15% | 0.9 ± 0.4 |
| 1.37 | MIS 3b | 48.173 | 21,322,473 ± 13% | 16 | 17.7 | 215.2 ± 14% | 0.5 ± 0.3 |
| 1.57 | MIS 4 | 58.096 | 20,564,595 ± 12% | 15 | 18.5 | 207.6 ± 13% | 0.8 ± 0.3 |
| 1.73 | MIS 4b | 66.035 | 20,395,211 ± 11% | 16 | 19.0 | 205.7 ± 12% | 0.8 ± 0.2 |
| 2.07 | MIS 5b | 82.904 | 20,059,312 ± 7% | 16 | 17.2 | 201.6 ± 8% | 0.8 ± 0.2 |
| 5.63 | MIS 8e | 287.63 | 19,961,907 ± 14% | 16 | 15.9 | 184.7 ± 15% | 0.9 ± 0.4 |
| 5.68 | MIS 8d | 289.95 | 18,291,153 ± 15% | 16 | 17.0 | 187.2 ± 15% | 0.8 ± 0.3 |
| 5.87 | MIS 8e | 298.77 | 18,410,906 ± 11% | 16 | 14.4 | 193.7 ± 12% | 0.7 ± 0.3 |
| 6.02 | MIS 9 | 304.09 | 19,190,259 ± 14% | 16 | 15.1 | 190.4 ± 15% | 0.8 ± 0.2 |
| 6.07 | MIS 9 | 305.86 | 18,866,448 ± 10% | 16 | 14.6 | 180.5 ± 10% | 0.8 ± 0.3 |
| 6.17 | MIS 9 | 309.41 | 17,895,821 ± 7% | 15 | 16.4 | 190.9 ± 8% | 0.6 ± 0.3 |
| 6.23 | MIS 9 | 311.54 | 18,903,846 ± 13% | 16 | 16.9 | 189.0 ± 14% | 0.5 ± 0.3 |

Figure 3. Evidence for a significant correlation between the mass of *G. bulloides* shells from the Eastern Atlantic and seawater paleodensity within two different size classes. The upper right (in blue) data are based on size-normalized weight values for the 300–355 μm size fraction from core NEAP 8K in the Northeast Atlantic. The lower left data (in red) are values from the 250–315 μm sieve fraction for cores MD02-2594 and MD96-2080 in the Southeast Atlantic. Ambient seawater paleodensity values are estimated from Mg/Ca and carbonate δ\(^{18}\)O. Core top samples are denoted with bigger, black infilled symbols, while vertical lines represent modern in-situ annual average seawater density. The dashed lines around the regression line indicate the 95% level of confidence.
Bulloides Dissolution Index (BDX)30, and they were found to be mostly well preserved. Dissolution is not believed to have affected skeletal Mg2+
record other than biomineralization temperature.

The preservation state of tests was assessed by examining their ultrastructures under the SEM using the Bulliodes Dissolution Index (BDX)3, and in some cases internal structures with XMCT using the X-ray Dissolution Index (XDI)10, and they were found to be mostly well preserved. Dissolution is not believed to have altered the overall shell volume as any severe dissolution will initially affect the inner calcite layers31. In general the mass of the shells is inversely related with their preservation state. The shells were found to be relatively corroded during glacial periods, when their masses were found to be greater. The fact that the heavier shells were also the most corroded ones, together with the low BDX’ and XDI values, rule out dissolution as the primary controlling factor of the observed shell mass pattern.

For the paleotemperature reconstructions derived from Mg/Ca, the well preserved foraminiferal calcite and the insignificant change of late Pleistocene seawater Mg/Ca concentrations32 together with the nearly constant state of calcite saturation state of the ocean since the late Pliocene33 significantly rule out processes that have affected skeletal Mg2+ record other than biomineralization temperature.

Discussion
A relationship that equates the biogenically precipitated shell calcite, at different ontogenetic stages, with ambient seawater density was identified in Fig. 3. G. bulloides in its early life stages calcifies in shallower, lighter waters and by chamber addition during growth sinks into deeper and denser waters. Because the density and viscosity of sea water are on the order of 103 and 102 times greater than the density and viscosity of air, respectively, foraminifera are much more strongly influenced by buoyant and viscous forces than are comparably sized terrestrial organisms34.

The ability of planktonic foraminifera to inhabit specific depths in the surface ocean requires a means for species-specific buoyancy adjustments and calcification control. Test formation is not an inert and solid state but rather a dissolution and reprecipitation process35 that allows foraminifera to resorb and reallocate shell calcite during their life cycle36,37. The calcite shells provide foraminifera with the negative buoyancy needed to dive to
are, at present, supersaturated with respect to calcite51, as most surface ocean waters are52. In a glacial ocean, with CO$_3$ habitat as dictated by hydrography, competition, nutrient availability, and other factors. 

librium, they would need to increase shell mass, which in turn would allow them to sink back to their preferred depth range. The influence of density in depth habitat determination has been manifested elsewhere for most planktonic foraminifera48 since it was found that their calcification depths are tuned to particular density layers49 or isopycnals50.

Optimum habitat depth may be determined by carbonate ion concentration, nutrient availability, hydrography, and/or competition. It is possible to speculate in evolutionary terms, that planktonic calcifiers may have had the advantage of waters with increased [CO$_3$] at the times they needed them most. North Atlantic surface waters are, at present, supersaturated with respect to calcite31, as most surface ocean waters are52. In a glacial ocean, with increased carbonate ion concentration in the surroundings35, organisms may need to spend less energy to gather CO$_3$ for shell construction and can get heavier more quickly.

The data discussed above suggest that G. bulloides shell mass variations during glacial and interglacial times is related to the buoyant force exerted on organisms by surrounding seawater. During glacial times mean ocean density increases due to thermal contraction and storage of fresh water in ice sheets. Sea ice formation affects the salinity of the ocean, while continental ice deposition alters both ocean’s salinity and volume. A denser ocean, with increased salt concentration, will exert greater buoyancy force and thus will tend to buoy plankton towards the sea surface. In order for organisms to counteract this increased buoyant force and maintain hydrostatic equilibrium, they would need to increase shell mass, which in turn would allow them to sink back to their preferred habitat as dictated by hydrography, competition, nutrient availability, and other factors.

Since foraminifera are forced to increase carbonate precipitation during glacial times, then the excess carbonate precipitation alone will decrease the ocean's total alkalinity or pH and will increase its CO$_2$ concentration ([CO$_2$])34. On the contrary during terminations, when waters are fresher and lower in density, organisms would need to have a lower shell mass than their glacial form in order to maintain their optimal habitat depth within the water column. Such abiotically-driven reduction in planktonic calcification during terminations will decrease the [CO$_2$] in seawater, as a by-product of intracellular calcite formation and it may thus provide a mechanism for the ocean to counterbalance increased atmospheric pCO$_2$.

Conclusions
The analysis of well-preserved fossil G. bulloides shells from ODP Site 982 suggests a relationship between shell mass and ambient seawater density. We propose the hypothesis that this is driven by the need for buoyancy regulation. Changes in the density of waters in the upper water column, as a function of both temperature and salinity may explain some of the observed variation in planktonic foraminifera shell mass during glacial-interglacial transitions. This depth-regulating mechanism adds a new dimension to the debate over what causes downcore shell mass variations. Building on the carbonate ion hypothesis, we speculate these organisms would then have the advantage of heavier shells in glacial waters with higher [CO$_3$$^-$$]$. During terminations, abiotically-driven reduction in shell calcification promotes the mechanism of atmospheric CO$_2$ uptake by the ocean. Additional work will elucidate whether there are species-specific shell mass-seawater density equations.

Methods
The present study was conducted on G. bulloides specimens from ODP Site 982 that were previously studied3 and represent both cold and warm climatic phases. G. bulloides was investigated because it was present in all samples from Site 982, and due to the amount of published data already available for the species. Preservation of specimens was assessed via Scanning Electron Microscope (SEM) with the use of a semi-quantitative method, while the total volume of the shells during different time periods was determined with X-ray microcomputed tomography (XMCT) scannings. The determination of foraminifera test volume together with the ambient seawater density, reconstructed from bibliographic data, allowed, according to Archimedes’ principle, the calculation of the buoyancy force of the ocean on the foraminifera shells. The estimation of buoyancy force involved ambient paleo-seawater density calculations, which were based on published $^18$O data and new Mg/Ca measurements.
To further test the hypothesis, we examined all available published core datasets that include *G. bulloides* shell Mg/Ca, δ¹⁸O and mass measurements from different Atlantic and Pacific regions. Data were combined to reconstruct ambient seawater densities, and reanalysed to produce graphs of seawater density versus shell mass (Fig. 4). Two-tailed regression analyses were performed using the Reduced Major Axis model, at n-1 degrees of freedom. n represents sample size. Standard Bonferroni corrections to significance levels were applied to correct for multiple comparisons.

**Dissolution assessment.** The dissolution degree of the ODP 982 specimens that were used in buoyancy calculations (Table 1), for which XMCT scans exist, was assessed by applying the XDX, an empirical dissolution index that evaluates the appearance of dissolution features in the tomographs.". The XMCT appearance of their internal structure resembles that of almost intact specimens implying in most of the cases less than 15% of calcite loss.". In the absence of XMCT scans for the rest of the record, the carbonate preservation state of samples from ODP Site 982 for the first 1 My was examined, with higher resolution during the late Quaternary, by applying the Bulloides Dissolution Index (BDX)". In order for the evaluation to be representative of each time slice and the result to be statistically significant, 20 of the previously weighed *G. bulloides* specimens from each downcore sample were assessed. The spiral side of the ultimate chamber of each test was investigated using a ZEISS DSM 940 A Scanning Electron Microscope at the Department of Geosciences, University of Bremen. The BDX evaluates the corrosion of shell surface ultrastructure and thus provides a semi-quantitative measure of specimen dissolution.". These methods have the advantage of directly assessing the dissolution of the specimens rather than their general fragmentation, which is also affected by fragmentation through mechanical sieving or selective dissolution of the finer fragments. The results from the samples where overlapping in the dissolution assessment methods took place suggest that both methods are in good agreement.

**Determination of past seawater density.** The combination of Mg/Ca ratios of foraminiferal shell calcite with δ¹⁸O isotope measurements has been used here to reconstruct ambient water salinities 57–59. Mg/Ca thermometry for core ODP Site 982 was calculated using Anand et al. 60 equation, which is calibrated for temperatures lower than about 10 °C and thus more reliable for reconstructing glacial N. Atlantic temperatures. The use of the same equation is mentioned for the rest of published cores present here except from the temperate latitude cores MD02-2594 and MD96-2080 where temperature reconstructions were based on the Mashiothta et al. 61 equation because it yields more accurate results for core-top samples at warmer temperatures.

*G. bulloides* δ¹⁸O values were adjusted for a ‘vital effect’ using the published offset of 0.52‰ 62. δ¹⁸Osw was calculated using a published paleotemperature equation 63 and a VPDB-to-SMOW δ¹⁸O conversion of 0.27‰ 64. Salinity estimates were derived from δ¹⁸Osw values using the modern regional salinity-δ¹⁸O relationships 65, after correcting for global ocean salinity and ice volume changes 66,67, assuming that these relationships remain constant throughout time 68. **Error propagation in the conversion of Mg/Ca to temperature.** The data used in this study are mainly published data, from different laboratories, analysed after different cleaning procedures and precise replicate errors were not published in most cases. For samples from sites other than ODP Site 982 the replicate error (σMg/Ca = 0.7 °C) and the error of the calibration curve (σδw = 1.1 °C) gives a 1σ uncertainty in the temperature estimate of each sample of ±1.2 °C. NEAP 8K is quoted with a typical paleotemperature estimate error of ±1 °C and for cores ODP 1123, CHAT 1K, CHAT 16K the estimated error is on average ±1.3 °C. For ODP core 982 the replicate error based on two splits of eight samples is σMg/Ca = 0.08 mmol/mol.

**In-situ seawater densities for particular depths** were calculated using the equation of state of seawater 69 from the temperature and salinity estimates. The Mg/Ca ratios from the present study were combined with published δ¹⁸O isotope measurements 70 to calculate densities at ODP Site 982 for different time slices. Seawater densities were calculated from available Mg/Ca and δ¹⁸O measurements on foraminifera tests from the 300–355 μm size fraction for core NEAP 8K in the North Atlantic 6, ODP 1123, CHAT 1K, CHAT 16K in the Southwest Pacific 71 and from the 250–315 μm size fraction from combined nearby MD02-2594 and MD96-2080 core records in the South Atlantic 72. Together cores MD02-2594 and MD96-2080 yielded data for ~200 kys, while the NEAP 8K core covers the last deglaciation cycle 73. For the S. Atlantic shells of the 250–315 μm sieve fraction densities were calculated first for a depth of 75 m, to avoid forcing of the regression with a *a priori* lower densities when shallower water depths were used in the equation of state of seawater. Subsequently the regression was recalculated for a more realistic living depth of 25 m 74 for the smaller foraminifera, which gave a slightly better correlation and is more realistic living depth of 25 m 74 for the smaller foraminifera, which gave a slightly better correlation and is

"Propagation of errors in the calculation of in-situ density. The error in the δ¹⁸O of seawater (σδw) is a combination of the error in the measurement of δ¹⁸O of *G. bulloides* (σδ = 0.081‰) and the error in the Mg/Ca-derived pelagic temperature (σT = 0.192‰); σδw = √(σδ² + σT²), consequently σδw = 0.208‰. The total error in the ice-volume-corrected δ¹⁸O of seawater is σδv-ice = √(σδw² + σσT²) = 0.231‰. By assuming a linear relationship between σσT and salinity 66, the partial differential equations of ref. 75 yields an error for salinity δσ = 0.63 psu and for *in-situ* density σt = 1.73 Kg/m³.

**Determination of shell volume and buoyancy force.** In order to determine the foraminifera shell volume, X-ray computed tomography (CT) was used. The scannings were performed with a Skyscan 1072 desktop XMCT scanner at the Department of Earth Sciences, University of Cambridge. The scanner uses a point X-ray source to create a series of radiographs of a sample as it rotates. Cross-sectional slices ("tomographs") were reconstructed using Skyscan’s own software that uses the Feldkamp cone-beam algorithm 77. The reconstructed
tomographs were subsequently processed with CT data visualization software for entire shell volume determination \( (V_{\text{foram}}) \). In each tomograph the interior of the foraminifera imprint, together with the calcite imprint itself were segmented as a single object. By summing up all cross sections the data visualization software was able to calculate the overall volume (i.e. calcite and cavities) of each shell (Fig. 5).

The available CT data set consisted of scans for foraminifera from 12 different down-core time intervals representing (approximately equal) glacial and interglacial stages of the last three climatic cycles. All samples were scanned under the same conditions: anode voltage was set at 100 kV and the X-ray tube current at 0.98 μA. By processing 1024 images per sample a voxel size of \( \sim 1.8 \) μm was achieved. In total 191 shells were reconstructed from the 12 available down-core time interval samples. On average 16 tests from each sample were scanned and a mean \( G. \text{bulloides} \) shell volume \( V_{\text{foram}} \) was calculated for each time interval (Table 1). The total volume \( V_{\text{foram}} \) approximates the volume that a living foraminifer would occupy in the water column or the volume, \( V_{\text{dis.waters}} \), of seawater that it displaces. The buoyant force exerted on the shells was calculated from equation (1) using the estimated water density \( (\rho) \) and the results are shown in Table 1. The buoyant force (in Newton, N) exerted on a foraminifer \( (A) \) in equilibrium during floating at its optimum depth equals the weight of the water it displaces \( (W_{\text{displaced}}) \). The weight of the water that a single foraminifer (without spines) displaces equals its mass \( (m_{\text{dis.waters}}) \) times the acceleration of gravity \( g \) (m/s), or is the product of its volume times water density times \( g \). There is an underestimation of the shell volume, both because fossil spines usually break and also because their exact effect on buoyancy is not well understood, but the geochemical signal of the core shell will always reflect ambient seawater properties. Given that \( V_{\text{foram}} = V_{\text{dis.waters}} \), from above, we get:

\[
A = W_{\text{displaced}} = m_{\text{dis.waters}} * g = \rho g V_{\text{dis.waters}} = \rho g V_{\text{foram}} * g
\]

(1)

Error propagation in the determination of shell volume and buoyancy force. The error in the calculation of the buoyancy force of the ocean \( (\sigma_A) \) is a combination of the error in volume estimate of \( G. \text{bulloides} \) shells \( (\sigma_{V_{\text{foram}}} = 13.64\%) \) and the error of combined Mg/Ca - \(^{18}\)O derived in-situ density \( (\sigma_t = 6.27\%) \); \( \sigma_A = \sqrt{\sigma_{V_{\text{foram}}}^2 + \sigma_t^2} \), consequently \( \sigma_A = 15\% \), which is almost equal to the size interval of the sieve fraction used.

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Figure 5. 3D rendering of a \( G. \text{bulloides} \) test from the computed tomographic data illustrating (a) \( V_{\text{foram}} \) and (b) the equal action in seawater of the opposing forces of its weight \( (W) \) and the ocean’s buoyancy force \( (A) \) in order for hydrostatic equilibrium to be attained and for the organism to attain neutral buoyancy at a certain depth.
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Author Contributions

S.D.Z. conceived the project and the methodology. A.T. performed Mg/Ca data collection and M.G. performed Mg/Ca data collection and curation. S.D.Z. wrote the manuscript with the help of A.T., G.K., P.G.M. and M.G. under the supervision of A.A., P.G.M. and H.D.
