

Controls of shell calcification in planktonic foraminifers

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Abstract

In order to better constrain the factors controlling the calcification rate in planktonic foraminifera, and to assess shell weight reliability as an atmospheric CO₂ proxy, changes in shell weight in *Globigerina bulloides*, *Neogloboquadrina pachyderma* (right coiling) and *Globigerinoides ruber* (white) have been studied in core samples from the Alboran Sea (Western Mediterranean) between 250 and 160 ka (Marine Isotopic stages 6 and 7). These results suggest that *G. bulloides* and *G. ruber* (white) calcification rate is mainly controlled by atmospheric CO₂ and water temperature, whereas *N. pachyderma* (right coiling) shell weight is directly related to optimum growth conditions, since heavier shell weights coincide with more relative abundance of this species due to optimum temperature conditions. Therefore, foraminifer shell weight should be used carefully as an atmospheric CO₂ proxy.

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1. Introduction

Carbonate-bearing organisms play a very important role in the global carbon cycle since they transfer and deposit huge amounts of calcium carbonate (CaCO₃) on the sea floor (Milliman, 1993; Archer and Maier-Reimer, 1994; Broecker and Clark, 2001). Over the past decade, several studies have focused on the quantification of the relationship between the calcification of marine calcium carbonate producers and water carbonate saturation (e.g. Riebesell et al., 2000; Barker and Elderfield, 2002) with a view to evaluating the possible negative effect of today's increasing atmospheric CO₂ levels on these organisms. Barker and Elderfield (2002) have recently suggested that water carbonate saturation is the main factor controlling the calcification rate in planktonic foraminifera (based on samples from a latitudinal transect in the North Atlantic), supported previously by culture studies (Spero et al., 1997). These authors proposed shell weight as a carbonate saturation and atmospheric CO₂ proxy. However, other studies have demonstrated that controls on the shell weight are not so simple, and that water carbonate saturation is not the only factor controlling the calcification rate in planktonic foraminifera (de Villiers, 2003, 2004). This

latter author suggested that the environmental factors and optimum growth conditions are very important for higher calcification rates and no relationship between water [CO₃²⁻] and calcification rate was detected in that work. Since conflicting results have emerged from different studies addressing the reliability of shell weight as an atmospheric CO₂ proxy, our aim here is to gain a better understanding of the control of calcification rate in different foraminifer species. We report that the main control factor is water temperature in the case of *Globigerina bulloides*, *Neogloboquadrina pachyderma* (right coiling) and *Globigerinoides ruber* (white).

2. Regional setting

The Mediterranean Sea is a semi-enclosed marginal basin with a negative water balance, which results in an anti-estuarine circulation and hence oligotrophic conditions (Béthoux, 1979). The Alboran Sea is the westernmost basin in the Mediterranean Sea and is connected to the Atlantic through the Strait of Gibraltar (Fig. 1). The Atlantic Water flows into the Alboran Sea at the surface (down to 220 m), whereas the Mediterranean Outflow Water (MOW) enters the Atlantic at depth (Millot, 1999). In the Alboran basin, the Atlantic Water flows eastwards and is gradually modified due to vertical water mixing and heat interchange with the atmosphere resulting in lower

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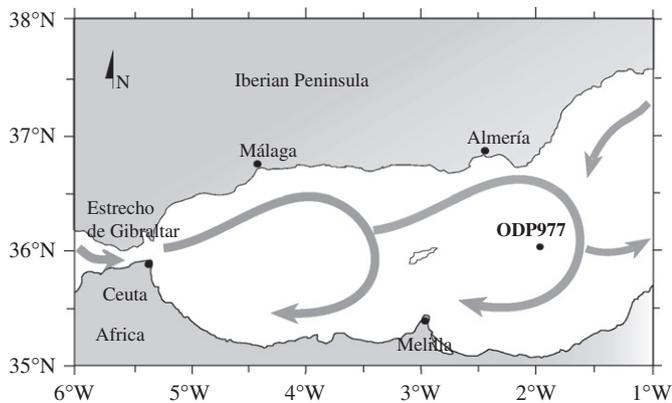


Fig. 1. Location of ODP site 977 (36°01.907'N, 1°57.319'W) in the Alboran Sea, Southern Spain, Western Mediterranean Sea. Arrows indicate the surface circulation pattern (Heburn and La Violette, 1990).

temperature and salinity. It is therefore known as the Modified Atlantic Water (MAW). Below it, there are three more water masses (Pierre, 1999): two intermediate waters (between 600 and 1000 m) and the Western Mediterranean Deep Water (WMDW, below 1000 m). Intermediate water comprises the Levantine Intermediate Water (LIW), slightly modified on its way westwards, and the Tyrrhenian Dense Water (TDW; Millot, 1999). Both are the main components of the MOW. The WMDW is formed in the Gulf of Lions and accounts for 10% of the Mediterranean Outflow.

The present-day climate in the Mediterranean area is strongly controlled by the position of the Inter Tropical Convergence Zone (ITCZ), its seasonal migration, and its influence upon pressure systems (Cramp and O'Sullivan, 1999). A stable high-pressure system dominates the region during summer months, causing excess evaporation in the basin. However, during winter the arrival of pressure depressions brings cooler and wetter weather.

3. Materials and methods

Cores from the ODP site 977 (Fig. 1) were recovered from the eastern basin of the Alboran Sea (36°01.907'N, 1°57.319'W; 1984 m water depth) during Leg 161 of the Ocean Drilling Program in 1996 (Comas et al., 1996). The core sediment consists of a bioturbated hemipelagic facies, composed of nannofossil-rich and calcareous silty clay and clay.

G. bulloides and *N. pachyderma* (right coiling) are subpolar species whereas *G. ruber* (white) is a subtropical–tropical species (Pujol and Vergnaud-Grazzini, 1989).

Systematic samplings were made in order to study the evolution of planktonic foraminifer shell weight. The average sampling resolution was 5 cm between 32 and 40 m depth and 10–20 cm between 29 and 32 m depth. From each sample, approximately 30 individuals of *G. bulloides*, *N. pachyderma* (right coiling) and *G. ruber* (white) were picked from pre-washed sediment sieved to 250–300 μm . Weight measurements were made using a

microbalance (0.1 μg) and the error associated with natural variations was about $\pm 0.5 \mu\text{g}$. Therefore, the values used in this work are the average weight of 30–50 individuals in each case.

For estimating the relative abundance of each species, the >150 μm size-fraction was studied, splitting the total residue to obtain an aliquot of 400 planktonic foraminifer specimens, which were identified and counted. The fragmentation index was calculated as the “number of foraminifer shell fragments/number of foraminifer shell fragments + number of complete foraminifer shells”, considering the >150 μm size-fraction.

Calcification temperatures are based on Mg/Ca paleothermometry in each species. Approximately 20 individuals of each species from the 250 to 300 μm fraction were picked to measure the Mg/Ca ratio on an ICP-AES (Varian Vista AX CCD simultaneous) in the University of Cambridge as described by de Villiers et al. (2002); the cleaning protocol was established by Barker et al. (2003). The calibration equations used for the different species were established by von Langen et al. (2005) for *N. pachyderma* (right coiling); for *G. bulloides*, the specific equation by Elderfield and Ganssen (2000), and the Anand et al. (2003) equation (constant A assumed, 250–350 μm) for *G. ruber* (white).

The age model used was that established by Martrat et al. (2004), based on a correlation between the SPECMAP stacked curve (Martinson et al., 1987) and the *G. bulloides* $\delta^{18}\text{O}$ curve from this site (ODP site 977). According to this age model, the interval studied here spans between 250 and 160 ka.

Blackman–Tukey spectral analyses were carried out using the AnalySeries 1.2 software (Paillard et al., 1996).

4. Results

Shell weights in *N. pachyderma* and *G. ruber* vary between 6 and 17 μg , whereas in *G. bulloides* they range between 6 and 13 μg (Fig. 2). *G. ruber* and *G. bulloides* weights show similar patterns although their ecological requirements are very different (Hemleben et al., 1989); however, *N. pachyderma* weight presents a very different pattern. In addition, there is no relationship to dissolution, based on the fragmentation index (Fig. 2).

G. bulloides shell weights show a close relationship with marine isotopic substages in stage 7 (Fig. 3). In general, during the warm periods, isotopic substages 7.5, 7.3 and 7.1, shell weights are lighter than during the cold periods, except for substage 7.2, in which shell weights are quite light. Also, during cold stage 6 the weights are very heavy. The main variations in shell weight are gradual and respond to astronomical cycles, although during the termination and the beginning of substage 7.5 several abrupt changes of up to 4 μg in 2 ka are seen.

The shell weights of *N. pachyderma* present more variability than those of *G. bulloides*. In this species, variations in shell weights are not related to cold or warm

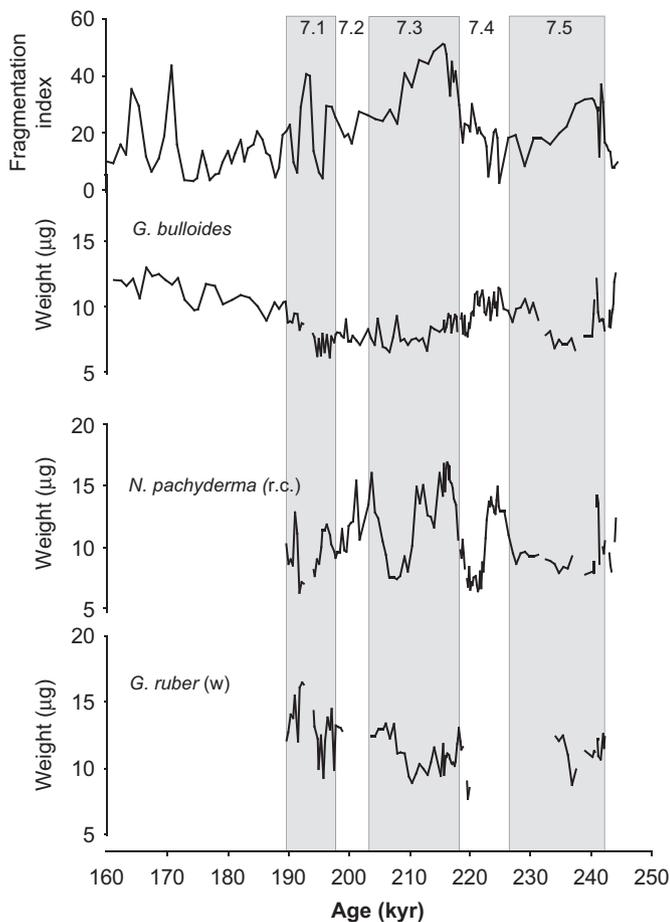


Fig. 2. *Globigerina bulloides*, *Neogloboquadrina pachyderma* (right coiling) and *Globigerinoides ruber* (white) shell weight (μg) variations between 250 and 160 ka compared with the fragmentation index. The shell weight trend in *Globigerina bulloides* is very similar to stadial/interstadial variations, whereas in *Neogloboquadrina pachyderma* (right coiling) and *Globigerinoides ruber* (white) shell weights are not governed by these astronomical variations. There is no correlation between weight and fragmentation, since high weight values coincide with periods of high fragmentation index in the three species. Dissolution may have existed, but it did not affect shell weight significantly.

substages (Fig. 4). They show more abrupt and frequent changes at the millennial time scale. The lightest values occur around the middle of the relatively warm substage 7.1 (192 ka) and in the second half of the relatively cold substage 7.4 (around 220 ka), whereas the heaviest are observed at the beginning and end of substage 7.3 (217 and 204 ka) and in the first half of 7.4 (around 225 ka).

The *G. ruber* shell weights also present a millennial variability within the warm substages, showing the lightest values at the middle of the substages (Fig. 5). There is no record of this tropical species within the cold substages since the amount of specimens during these periods was not enough for Mg/Ca analyses.

5. Discussion

The low correlation between shell weights and planktonic foraminifer fragmentation indicates that the dissolu-

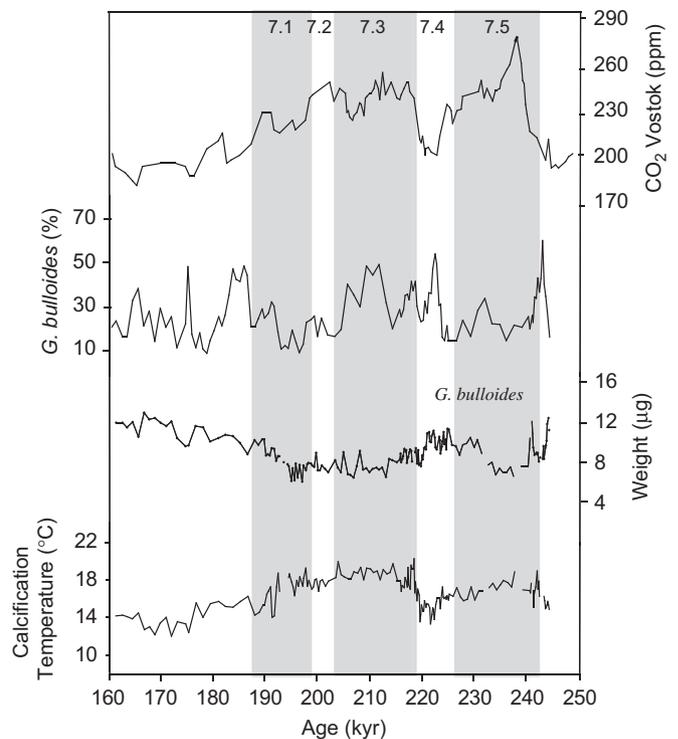


Fig. 3. *Globigerina bulloides* shell weight (μg) is compared with the species calcification temperature ($^{\circ}\text{C}$) based on Mg/Ca paleothermometry. Both curves are represented together with Vostok atmospheric CO_2 (Petit et al., 1999). The direct relationship between atmospheric CO_2 and shell weight implies that the calcification rate in this species is controlled by PCO_2 . The *Globigerina bulloides* relative abundance (%) is also represented for a comparison with the other parameters.

tion may have occurred but it was not the major factor controlling shell weight in the three species studied here (Fig. 2). Minor dissolution, not identified by the fragmentation index, could decrease both Mg/Ca ratio and shell weight (Brown and Elderfield, 1996). In that case, this should have affected *G. bulloides*, *N. pachyderma* and *G. ruber* in a similar manner; however, the fact that each species behave very differently argues against this possibility. Therefore, these shell weights can be used to infer sea surface conditions.

The idea that carbonate saturation is correlated with the calcification rate of marine organisms arose from several studies based on coral reefs and coccolithophores that demonstrated that these marine carbonate producers are sensitive to elevated atmospheric CO_2 pressure (Langdon et al., 2000; Riebesell et al., 2000). If foraminifer calcification is sensitive to atmospheric carbon dioxide concentrations, the shell weight record should be affected by glacial–interglacial variations in CO_2 pressure. However, CO_2 and carbonate ion concentrations in surface water also depend on sea surface temperature that controls CO_2 solubility in sea-water and therefore can potentially change the calcification rate of planktonic foraminifera. These different factors control the calcification rate in opposite directions.

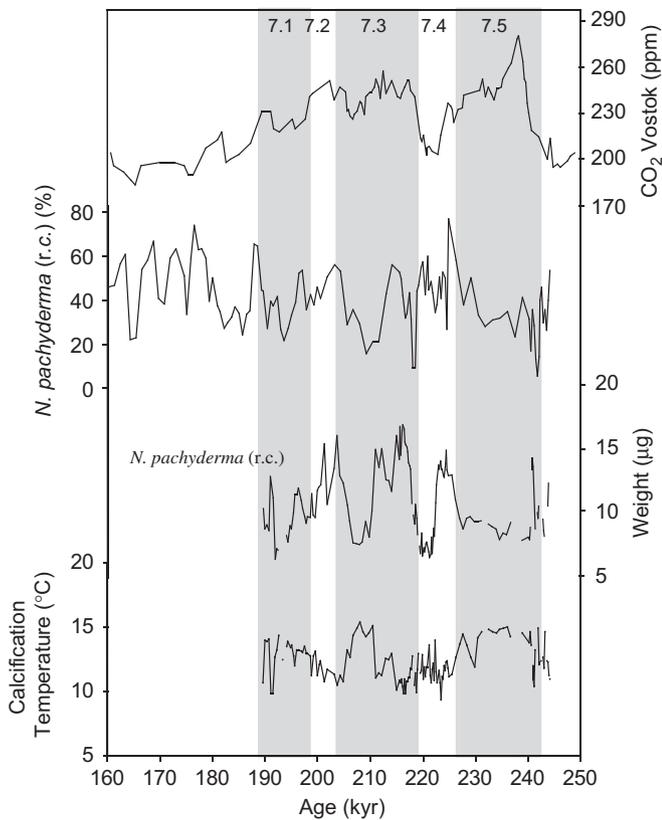


Fig. 4. *Neogloboquadrina pachyderma* (right coiling) shell weight (μg) is compared with the species calcification temperature ($^{\circ}\text{C}$) based on Mg/Ca paleothermometry. The *Neogloboquadrina pachyderma* (right coiling) relative abundance (%) and the Vostok atmospheric CO_2 (Petit et al., 1999) are also represented to make a comparison with the other parameters. It seems that calcification temperature controls the *Neogloboquadrina pachyderma* shell weight and relative abundance; that is, the lower the temperature, the higher the weight, and the greater the abundance (better growth conditions). Vostok atmospheric CO_2 (Petit et al., 1999) is also represented for comparison, although no relationship is observed with this species' shell weight.

If atmospheric CO_2 is indeed the factor controlling calcification, during cold stages (stage 6, substages 7.2 and 7.4) foraminifer shells should have been heavier, since in these periods surface water $[\text{CO}_3^{2-}]$ increased due to the decreases in atmospheric CO_2 . By contrast, a temperature control would produce the opposite trend, since during the cold periods CO_2 solubility increases and lower $[\text{CO}_3^{2-}]$ in surface waters and, as a result, shell calcification must be lower. In both cases, the main factor controlling foraminifer calcification would be carbonate saturation.

G. bulloides shell weights follow the opposite trend to Vostok CO_2 (Petit et al., 1999), that is, weights are heavier when atmospheric CO_2 is lower (Fig. 3). Shell weight maxima coincide with CO_2 minima during Termination III, at around 220 ka, and in stage 6, although there is a subtle CO_2 decrease centred at 205 ka, which is not very apparent in *G. bulloides* shell weights. In general, it seems that the calcification of this species could be controlled by calcium carbonate concentration in surface water, as suggested previously by Barker and Elderfield (2002) in their studies

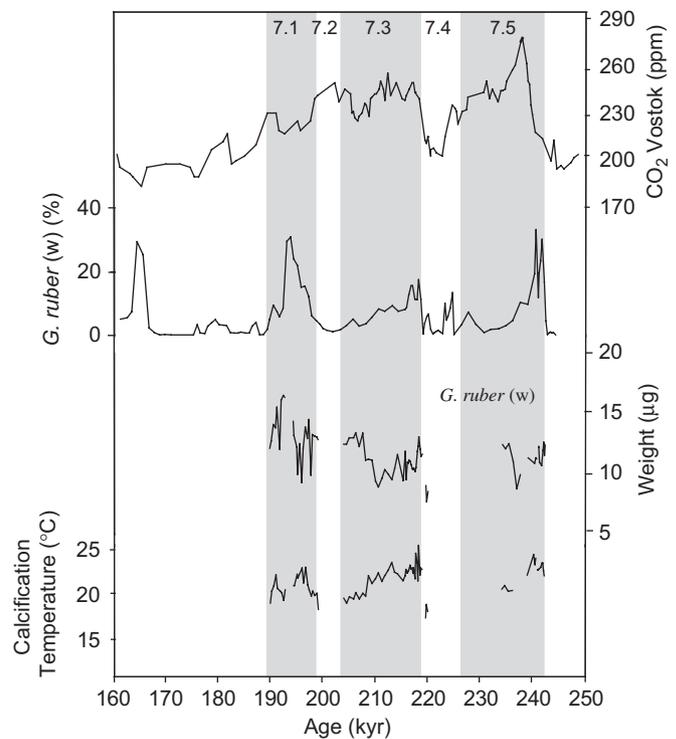


Fig. 5. *Globigerinoides ruber* (white) shell weight (μg) as compared with the species calcification temperature ($^{\circ}\text{C}$) based on Mg/Ca paleothermometry. The relative abundance (%) of *Globigerinoides ruber* (white) and the Vostok atmospheric CO_2 (Petit et al., 1999) are also represented for comparison with the other parameters.

of core tops from a latitudinal transect in the North Atlantic. Higher atmospheric CO_2 caused surface water acidification and a decrease in calcium carbonate saturation; the resulting $[\text{CO}_3^{2-}]$ was lower and produced a lower shell calcification rate. However, water $[\text{CO}_3^{2-}]$ could also be controlled by sea temperature. During colder periods with lower atmospheric CO_2 , attending to this effect there should be higher water $[\text{CO}_3^{2-}]$; however, the temperature effect on $[\text{CO}_3^{2-}]$ would lower calcium carbonate saturation, thus diminishing the shell calcification rate. Therefore, in our results we probably have an atmospheric CO_2 effect on carbonate saturation dampened by the temperature control. These simultaneous effects of temperature and CO_2 have resulted in the apparent anti-correlation observed between shell weight and calcification temperature (Fig. 3). *G. bulloides* cultures and core-top studies (de Villiers, 2004) have revealed that the optimum growth conditions result in higher shell weights, independent of the surface water $[\text{CO}_3^{2-}]$. This is not the case, however, since higher shell weights do not coincide with the maximum relative abundance of this species, although it could be considered a possible minor effect.

In *N. pachyderma*, there is no relationship between Vostok CO_2 (Petit et al., 1999) and shell weights (Fig. 4). This suggests that the calcification rate in this species is not driven by changes in atmospheric CO_2 concentration and the influence this has on surface water $[\text{CO}_3^{2-}]$. Moreover, shell weight and the calcification temperature based on

Mg/Ca analyses on *N. pachyderma* shells show opposite trends, and hence temperature-driven CO₂ solubility cannot be a major controlling factor. In our results, during warmer periods shell weight is lighter (Fig. 4), also in concordance with the lower relative abundance of *N. pachyderma* except at 220 ka (see discussion below). By contrast, when calcification temperatures are colder, shell weights are heavier and the abundance of this species increases. *N. pachyderma* is a temperature-dependent species (Bé, 1977; Hemleben et al., 1989) whose optimum conditions range from 12 to 14 °C (in winter) in the Mediterranean Sea (Kallel et al., 1997). It seems clear that temperature controls the relative abundance of this species in these samples, since the abundance of this species starts to decrease when temperature is higher than 13 °C, whereas it increases at lower temperatures. Our data suggest that in *N. pachyderma* (right coiling) optimum growth conditions (lower calcification temperature for this species) result in higher shell weights. However, although this seems to be the primary control on *N. pachyderma* calcification rate, we cannot dismiss a possible less-important [CO₃²⁻] control.

There is a special period at around 220 ka during which the calcification temperature was relatively cold, and *N. pachyderma* was quite abundant relative to *G. bulloides*, although its shell weight was very light. This interval coincides with a Heinrich-type event during which sea surface temperatures were especially cold in the North Atlantic and also in the Alboran Sea (Grousset et al., 1993; Lebreiro et al., 1996; Gonzalez-Mora et al., submitted). During this event, the total number of planktonic foraminifera was very low, suggesting adverse growth conditions for all foraminifer species. The high relative abundance recorded by *N. pachyderma* seems to respond to a statistical effect, since in absolute terms this species is not very abundant during this period. This could explain why *N. pachyderma* shell weight was very light during the Heinrich-type event when growth conditions were not so favourable. In fact, during this period the lightest weights of this species are recorded.

G. ruber (white) weight record is very discontinuous since the amount of specimens in many samples was not enough for Mg/Ca analyses. However, the pattern seems to be very similar to that of *G. bulloides*, although both species have different habitat controls (Fig. 5). Therefore, it seems that both atmospheric CO₂ and water temperature have controlled carbonate saturation and *G. ruber* calcification rate. Also in this case, the combination of their opposite effects has resulted in an apparent anti-correlation between shell weight and calcification temperature.

Regarding the spectral analysis of *N. pachyderma* shell weight (Fig. 6), a marked variability is observed. There is a dominant cycle of 12.7 ka controlling shell weight in this species. A period of around 13 ka results from the combination of two cycles: the precession cycle (19 ka) and the obliquity cycle (41 ka). Since *N. pachyderma* shell weight and temperature estimates reflect variations in the water masses where this species thrives (lower part of the

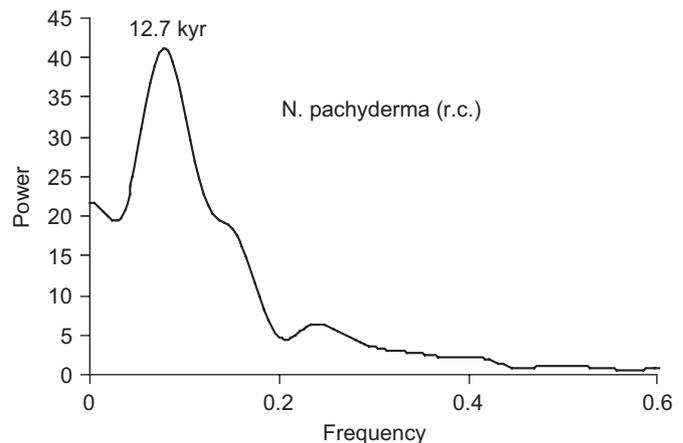


Fig. 6. Spectral analysis of *Neogloboquadrina pachyderma* (r.c.) shell weight. There is a dominant cycle of 12.7 ka that results from the combination of two cycles: precession (19 ka) and obliquity (41 ka).

surface layer, influenced by intermediate waters, which are partially originated in the Levantine Basin in the Eastern Mediterranean (Millot, 1999)), it seems that intermediate water formation in that area is strongly controlled by both astronomical cycles. Considering these results, it seems that we have to be careful with calcification rate (or weight) as atmospheric CO₂ proxy. Different species may have very different primary factors controlling the calcification rate.

6. Conclusions

With this work, we have attempted to better constrain which factors control planktonic foraminifer shell weight in order to assess its reliability as an atmospheric CO₂ proxy. *N. pachyderma* (right coiling), *G. bulloides* and *G. ruber* (white) shell weights and relative abundance have been studied in samples from core ODP site 977 recovered in the Alboran Sea (Western Mediterranean). The time interval studied is between 250 and 160 ka.

It seems that in planktonic foraminifers, regardless of whether they are subpolar (*G. bulloides*) or tropical (*G. ruber* (white)) species, calcification rate is mainly controlled by surface water [CO₃²⁻], resulting from the opposite effects of atmospheric CO₂ and water temperature. However, in *N. pachyderma* optimum growth conditions seem to be the primary factor controlling the calcification rate.

This study questions the use of foraminifer shell weight as a proxy of carbonate saturation and atmospheric CO₂ in surface waters and suggests that further studies are needed to better understand the processes behind shell calcification in planktonic foraminifera and to assess the control parameters in each species.

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References

- Anand, P., Elderfield, H., Conte, M.H., 2003. Calibration of Mg/Ca thermometry in planktonic foraminifera from a sediment trap time series. *Paleoceanography* 18 (2).
- Archer, D., Maier-Reimer, E., 1994. Effect of deep-sea sedimentary calcite preservation on atmospheric CO₂ concentration. *Nature* 367, 260–263.
- Barker, S., Elderfield, H., 2002. Foraminiferal calcification response to glacial–interglacial changes in atmospheric CO₂. *Science* 297, 833–836.
- Barker, S., Greaves, M., Elderfield, H., 2003. A study of cleaning procedures used for foraminiferal Mg/Ca Paleothermometry. *Geochemistry Geophysics Geosystems* 4 (9), 8407.
- Bé, A.W.H., 1977. An ecological, zoogeographic and taxonomic review of recent planktonic foraminifera. In: Ramsay, A.T.S. (Ed.), *Oceanic Micropaleontology*, vol. I. Academic Press, Wales, pp. 1–100.
- Béthoux, J.P., 1979. Budgets of the Mediterranean Sea. Their dependence on the local climate and on the characteristics of the atlantic waters. *Oceanology Acta* 2 (2), 157–163.
- Broecker, W.S., Clark, E., 2001. Glacial-to-Holocene redistribution of carbonate ion in the deep sea. *Science* 294, 2152–2154.
- Brown, S.J., Elderfield, H., 1996. Variations in Mg/Ca and Sr/Ca ratios of planktonic foraminifera caused by postdepositional dissolution: evidence of shallow Mg-dependent dissolution. *Paleoceanography* 11, 543–551.
- Comas, M.C., Zahn, R., Klaus, A., et al., 1996. Proceedings of the Ocean Drilling Program, Initial Reports, 161: College Station, TX (Ocean Drilling Program).
- Cramp, A., O'Sullivan, G., 1999. Neogene sapropels in the Mediterranean: a review. *Marine Geology* 153, 11–28.
- De Villiers, S., 2003. A 425 ka record of foraminiferal shell weight variability in the western Equatorial Pacific. *Paleoceanography* 18 (3), 1080.
- De Villiers, S., 2004. Occupation of an ecological niche as the fundamental control on the shell-weight of calcifying planktonic foraminifera. *Marine Biology* 144 (1), 45–50.
- Elderfield, H., Ganssen, G., 2000. Past temperature and N18O of surface ocean waters inferred from foraminiferal Mg/Ca ratios. *Nature* 405, 442–445.
- Gonzalez-Mora, B., Sierro, F.J., Flores, J.A. Paleoclimatographic and Paleoclimatic Variability in the Alboran Sea between 245–145 ka. *Marine Micropaleontology*, submitted for publication.
- Grousset, F.E., Labeyrie, L., Sinko, J.A., Cremer, M., Bond, G., Duprat, J., Cortijo, E., Huon, S., 1993. Patterns of ice-rafted detritus in the glacial North Atlantic (40°–55°N). *Paleoceanography* 8 (2), 175–192.
- Heburn, G.W., La Violette, P.E., 1990. Variations in the structure of the anticyclonic gyres found in the Alboran Sea. *Journal of Geophysics Research* 95, 1599–1613.
- Hemleben, C.H., Spindler, M., Anderson, O.R., 1989. *Modern Planktonic Foraminifera*. Springer, New York.
- Kallel, N., Paterne, M., Duplessy, J.C., Vergnaud-Grazzini, C., Pujol, C., Labeyrie, L., Arnold, M., Fontugne, M., Pierre, C., 1997. Enhanced rainfall in the Mediterranean region during the last sapropel event. *Oceanology Acta* 20, 697–712.
- Langdon, C., Takahashi, T., Sweeney, C., Chipman, D., Goddard, J., Marubini, F., Aceves, H., Barnett, H., Atkinson, M.J., 2000. Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles* 14, 639–654.
- Lebreiro, S.M., Moreno, J.C., McCave, I.N., Weaver, P.P.E., 1996. Evidence for Heinrich layers off Portugal (Tore Seamount: 39°N, 12°W). *Marine Geology* 131, 47–56.
- Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore, T.C., Shackleton, N.J., 1987. Age dating and the orbital theory of the ice ages: development of a high-resolution 0–300,000-year chronostratigraphy. *Quaternary Research* 27, 1–29.
- Martrat, B., Grimalt, J.O., Lopez-Martinez, C., Cacho, I., Sierro, F.J., Flores, J.A., Zahn, R., Canals, M., Curtis, J.H., Hodell, D.A., 2004. Abrupt temperature changes in the Western Mediterranean over the past 250,000 years. *Science* 306, 1762–1765.
- Milliman, J.D., 1993. Production and accumulation of calcium carbonate in the ocean: budget of a nonsteady state. *Global Biogeochemical Cycles* 7, 927–957.
- Millot, C., 1999. Circulation in the Western Mediterranean Sea. *Journal of Marine Systems* 20, 423–442.
- Paillard, D., Labeyrie, L., Yiou, P., 1996. Macintosh program performs time-series analysis. *EOS* 77, 379.
- Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.M., Basile, I., Bender, M., Chappellaz, J., Davis, J., Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M., Lipenkov, V., Lorius, C., Pépin, L., Ritz, C., Saltzman, E., Stievenard, M., 1999. Climate and atmospheric history of the Past 420,000 years from the Vostok Ice Core, Antarctica. *Nature* 399, 429–436.
- Pierre, C., 1999. The oxygen and carbon isotope distribution in the Mediterranean water masses. *Marine Geology* 153, 41–55.
- Pujol, C., Vergnaud-Grazzini, C., 1989. Paleoclimatography of the Last Deglaciation in the Alboran Sea (Western Mediterranean). Stable isotopes and planktonic foraminiferal records. *Marine Micropaleontology* 15, 153–179.
- Riebesell, U., Zondervan, I., Rost, B., Tortell, P.D., Zeebe, R.E., Morel, F.M.M., 2000. Reduced calcification in marine plankton in response to increased atmospheric CO₂. *Nature* 407, 364–367.
- Spero, H., Bijma, J., Lea, D.W., Bemis, B.E., 1997. Effect of seawater carbonate ion concentration on foraminiferal carbon and oxygen isotopes. *Nature* 390, 497–500.
- Von Langen, P., Pak, D.K., Spero, H.J., Lea, D.W., 2005. Effects of temperature on Mg/Ca in neogloboquadrinid shells determined by living culture. *Geochemistry Geophysics Geosystems* 6 (10), Q10P03.