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Effect of carbonate ion concentration and irradiance on calcification in foraminifera

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Abstract

The effect of carbonate ion concentration ($[CO_3^{2-}]$) on calcification rates estimated from shell size and weight was investigated in the planktonic foraminifera *Orbulina universa* and *Globigerinoides sacculifer*. Experiments on *G. sacculifer* were conducted under two irradiance levels (35 and 335 μmol photons $m^{-2}\,s^{-1}$). Calcification was ca. 30% lower under low light than under high light, irrespective of the $[CO_3^{2-}]$. Both *O. universa* and *G. sacculifer* exhibited reduced final shell weight and calcification rate under low $[CO_3^{2-}]$. At the $[CO_3^{2-}]$ expected for the end of the century, the calcification rates of these two species are projected to be 6 to 13% lower than at present conditions, while the final shell weights are reduced by 20 to 27% for *O. universa* and by 4 to 6% for *G. sacculifer*. These results indicate that ocean acidification would impact calcite production by foraminifera and may decrease the calcite flux contribution from these organisms.

1 Introduction

Due mostly to human activities, the atmospheric carbon dioxide (CO_2) partial pressure is currently increasing and, depending on the socio-economic scenarios, will reach 490 to 1250 ppmv by 2100 (Prentice et al., 2001). About 25% of the total anthropogenic CO_2 emissions have been absorbed by the ocean (Sabine et al., 2004). However, absorption of large quantities of atmospheric carbon implies changes in the carbonate system equilibrium, notably a decrease in pH and carbonate ion concentration ($[CO_3^{2-}]$). pH has already decreased by 0.1 units compared to pre-industrial values and will further decrease by 0.3 to 0.4 unit by 2100 (Feely et al., 2004; Orr et al., 2005). Such changes may significantly influence the calcification rates of various organisms. Negative impact of ocean acidification on calcification have been reported in coccolithophores, pteropods, corals and commercial shellfish (e.g., Riebesell et al., 2000; Leclercq et al., 2000; Gazeau et al., 2007; Comeau et al., 2009) but some species or

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strains may be unaffected to elevated pCO_2 (e.g., Iglesias-Rodriguez et al., 2008). Reducing the calcification rate of planktonic organisms can have opposite effects on the carbon cycle. Firstly, it decreases the positive feedback of calcification on atmospheric CO_2 (Gattuso et al., 1999; Wolf-Gladrow et al., 1999). Secondly, ocean acidification will decrease the role of ballast that calcium carbonate has by facilitating the export of organic matter to the deep ocean (Armstrong et al., 2002; Klaas and Archer, 2002). Understanding the possible effect of ocean acidification therefore requires investigating the response of the major calcifying organisms.

Planktonic foraminifera are widespread calcifying protozoa, responsible for 32–80% of the global deep-ocean calcite fluxes (Schiebel, 2002). Moy et al. (2009) reported that the modern shell weight of *G. bulloides* is 30 to 35% lower than that measured from the sediments. They attributed the difference to reduced calcification in response to ocean acidification. Few experimental results also indicated that ocean acidification can impact planktonic foraminifera, notably by reducing their shell thickness and weight (Bijma et al., 1999; Russell et al., 2004). However, these results were obtained as a by-product of geochemical study focusing on shell composition and did not provide any quantitative estimates of calcification rates.

This article presents a re-analysis of results from different geochemical experiments, designed to provide quantitative estimates of the effect of ocean acidification on foraminifera’ calcification.

2 Material and methods

Data used originate from two previous studies: one performed on *Orbulina universa* during summer 2000 in Catalina Island, California (Russell et al., 2004) and the second one on *Globigerinoides sacculifer* in summer 2006 in Puerto Rico (R. da Rocha, A. Kuroyanagi, G.-J. Reichart, and J. Bijma, unpublished data). In both cases, individuals were collected by scuba-diving, and grown in the laboratory until gametogenesis. They were fed regularly (every third day, starting on the day of collection) and kept under a 12:12 h light:dark cycle. *O. universa* was cultured under high irradiance (300 to 400 μmol photons m^{-2} s^{-1}) whereas *G. sacculifer* was grown under high (HL) and low (LL) irradiances (335 and 35 μmol photons m^{-2} s^{-1}, respectively). $[CO_3^{2-}]$ was manipulated by adding NaOH or HCl to filtered sea water. Foraminifera were kept in this modified seawater in closed borosilicate glass culture vessels of 125 ml, with no headspace to prevent exchange with atmospheric CO_2.

The carbonate chemistry of the solutions was analysed by measuring alkalinity via Gran titration using a Metrohm open-cell autotitrator with a mean precision of 10 μEq kg^{-1}, calibrated against certified reference material provided by A. Dickson. Seawater pH and culture media pH were determined potentiometrically and calibrated with standard NIST buffers and are reported on the NBS scale. Alkalinity and pH were measured at the start and termination of the experiments and used to calculate initial and final carbonate chemistry using CO2SYS (Lewis and Wallace, 1998) and the dissociation constants of Mehrbach et al. (1973) refitted by Dickson and Millero (1987).

Globigerinoides sacculifer was grown at 26(±1)°C, 36.2(±0.2) salinity. Data include measurements of the initial and final size (μm), the survival time (Δt; days from collection to gametogenesis), and final weight of the shell (W_f; μg) of each specimen measured prior to isotopic analysis. Only individuals that underwent gametogenesis and grew at least one chamber were used for later analysis. The shell length vs. weight regression obtained under "ambient" $[CO_3^{2-}]$ (233 μmol kg^{-1}, Fig. 1, Table 1) was used to estimate the initial shell weight (W_i; μg) from the measured initial shell size. Initial and final organic carbon weight of each foraminifera were calculated using a conversion factor (0.089 pg C μm^{-3}; Michaels et al., 1995) assuming spherical shells. The geometric average weight (W_{org}; μg C) was then calculated. In order to estimate calcification rates independently from the individual size, it was normalized per unit of cytoplasmic carbon (C; μg μg C^{-1} d^{-1}):

$$C = \frac{W_f - W_i}{W_{org}\Delta t} \tag{1}$$

Data for *O. universa* were directly taken from Table A1 of Russell et al. (2004) and only the results obtained at 22°C were used. Results from their experiment I and II, even though similar, were kept separate because the numbers of specimens per sample were different. The average shell length (μm) and weight (μg) of mature specimens were used to estimate the length-weight relationship within each condition. Unfortunately, critical measurements, such as initial size or survival time were not reported. The survival time in the laboratory (Δt) was assumed to be 7.4 days as it was the mean survival time at 22°C observed in experiments carried out at the Catalina Island laboratory (Lombard et al., 2009). All specimens grew a spherical chamber that represented 95% of the final shell weight (Lea et al., 1995; Russell et al., 2004). The initial (pre-spherical) weight of the shell (W_i) was therefore estimated to represent 5% of the final weight. The organic carbon weight (W_{org}) was calculated from the final size of adult *O. universa* (spherical form) and the specific conversion factor of 0.018 pg C μm^{-3} reported by Michaels et al. (1995). The calcification rate was then calculated as described in Eq. (1).

3 Results

In the *G. sacculifer* experiments, the average initial size was 396(±92) μm with minimum size of 190 μm and maximum size 716 μm (Table 1). Irradiance had a strong effect on both Δt and final size. In LL condition the individuals reproduced on average two days sooner and at a smaller size (about 100 μm less) than under HL. The different [CO_3^{2-}] conditions had no or only little effect on Δt and the final size of the animals (Table 1). Only the final shell weight seemed to be influenced by [CO_3^{2-}], and individuals had generally heavier shells when grown under high [CO_3^{2-}] conditions (t-test, $P<0.001$ in all cases). This indicates that the shell thickness is influenced by [CO_3^{2-}] but not the general growth pattern. However, Δt and the initial and final shell sizes influenced the final shell weight and a better indicator of calcification, insensitive to these parameters must be used.

The relationships between shell size and weight (Fig. 1, Table 2) better represented the influence of [CO_3^{2-}] but were still influenced by Δt and the initial size of the individuals. Only under ambient [CO_3^{2-}] (233 μmol kg^{-1}) was the shell-length-weight relationship not significantly different between HL and LL. The HL and LL data at ambient [CO_3^{2-}] were therefore combined and used to estimate the initial shell weight of individuals based on the initial shell size. On average, the initial shell weight represented 35% of the final weight under HL and 61% under LL. Consequently, the shell size-weight differences observed between the various [CO_3^{2-}] conditions are larger under HL conditions (Fig. 1a) than under LL conditions (Fig. 1b). For *G. sacculifer*, for all conditions, the exponents *b* of the regressions was not significantly different at various [CO_3^{2-}] whereas *a* is significantly different (covariance analysis on log-transformed data; Table 2). Under HL, for a given size, *G. sacculifer* grown at low [CO_3^{2-}] (72, 124 and 139 μmol kg^{-1}), was lighter than at "ambient" (233 μmol kg^{-1}) and 504 μmol kg^{-1} conditions and heaviest at high [CO_3^{2-}] conditions (455 and 566 μmol kg^{-1}). Only two groups can be identified at LL with heavier shells at [CO_3^{2-}] of 233, 455, and 566 μmol kg^{-1} and lighter shells at concentrations of 72, 124, 139 and, surprisingly, for 504 μmol kg^{-1}. In both conditions, the difference in weight as a function of increasing [CO_3^{2-}] was larger for the largest specimens. Similar observations were made for *O. universa*: the exponents of all relationships were not significantly different and can be approximated by a mean exponent *b* of 3.42, but the parameter *a* is significantly different for the different relationships (Table 2). *O. universa* shell weights increased with increasing [CO_3^{2-}] (Fig. 1c).

Figure 2 shows the shell length and weight as a function of [CO_3^{2-}] (Table 2, Fig. 1) for different ranges of shell size. Since the initial weight of *G. sacculifer* accounts for a large part of the final weight, only a final size of 700 μm was considered in order to minimize the pre-culture (field-grown) contribution to shell mass. For a similar size, the final shell weight for both *G. sacculifer* and *O. universa* increased significantly with increasing [CO_3^{2-}]. However, due to their different modes of calcification (final sphere formation vs. consecutive chamber additions), the [CO_3^{2-}] effect was greater for *O. universa* compared to *G. sacculifer*, greater for large individuals of *O. universa* and also greater under HL than under LL for *G. sacculifer*. The final shell weight of *G. sacculifer* obtained in LL was 20 to 26% lower than under HL. From previous weights and survival time measurements, calcification rates normalized per unit biomass were calculated. The biomass-normalized rate of calcification significantly decreased with decreasing [CO_3^{2-}] for both species (Fig. 3). The relationships between calcification (C; $\mu g\, d^{-1}\, \mu gC^{-1}$) and [$CO_3^{2-}$] ($\mu mol\, kg^{-1}$) as well as the standard deviation of these relationships was:

$$C = 6.5\,(\pm 2.3) \cdot 10^{-4}[CO_3^{2-}] + 0.67\,(\pm 0.08) \tag{2}$$

R^2=0.07 for *G. sacculifer* (HL)

$$C = 3.4\,(\pm 2.7) \cdot 10^{-4}[CO_3^{2-}] + 0.47\,(\pm 0.08) \tag{3}$$

R^2=0.03 for *G. sacculifer* (LL)

$$C = 2.70\,(\pm 0.97) \cdot 10^{-3}[CO_3^{2-}] + 1.3\,(\pm 0.34) \tag{4}$$

R^2=0.04 for *O. universa* (exp. I)

$$C = 2.47\,(\pm 0.89) \cdot 10^{-3}[CO_3^{2-}] + 2.7\,(\pm 0.23) \tag{5}$$

R^2=0.04 for *O. universa* (exp. II)

Despite the large variability, which led to low R^2, the slopes of all relationships were significantly different from zero ($F_{1,89}$=7.48 ; P=0.0075 for *G. sacculifer* HL; $F_{1,102}$=6.36 ; P=0.0134 for *G. sacculifer* LL; $F_{1,25}$=34.2 ; P<0.0001 for *O. universa* experiment I and $F_{1,4}$=8.3 ; P=0.0045 for *O. universa* experiment II).

Due to the calcification of its large spherical chamber, the calcification rate of *O. universa* was 2.5 to 4 times larger than for *G. sacculifer* (HL). The calcification of *G. sacculifer* in LL conditions was reduced by 30% on average compared to HL without any strong influence of [CO_3^{2-}] conditions.

4 Discussion and conclusions

The observation that [CO_3^{2-}] has an effect on the shell weight of foraminifera is consistent with previous studies (Bijma et al., 1999, 2002; Russell et al., 2004). However, there is, up to now, no quantitative estimate of the response of foraminifera calcification to changes in the seawater carbonate chemistry. The final shell weight was impacted by both the initial shell weight and the time needed till gametogenesis (Δt). For *O. universa,* the weight of the initial shell, calcified in the field, was negligible (~5% of final weight), whereas for *G. sacculifer*, it was about half of the final weight. Δt also varies under the two different light conditions used for *G. sacculifer*, with gametogenesis occurring two days sooner under high irradiance than under low irradiance. In contrast to previous estimates, the rate of calcification normalized per unit biomass was either not influenced or only slightly influenced by the initial shell size and Δt. Hence, the [CO_3^{2-}] impact on the final weight was certainly biased in *G. sacculifer* and normalizing the mass increase by the time required to precipitate it, effectively calculating the rate calcification, should lead to a better approximation of the [CO_3^{2-}] effect on the calcite production. To our knowledge, this is the first report providing a first order estimate of the [CO_3^{2-}] effect on calcification rates of planktonic foraminifera.

Our estimate of the calcification rate was, however, not free of biases, particularly in the case of *O. universa*. The initial shell size and survival time of this species in culture were not available and were estimated from independent observations. Therefore, the organic weight could not be calculated as the average weight during the experiment, but only as a function of the final shell weight. This uncertainty influences the calcification estimates of *O. universa*, but does not affect the conclusion that calcification decreases as a function of decreasing [CO_3^{2-}] and the final weight observations. Such bias does not occur with *G. sacculifer* because all the required data were available.

Foraminifera calcify intermittently. They calcify new chambers every few days within only a few hours (e.g., Spero, 1988; Hemleben et al., 1989). They add an additional layer of so-called gametogenic calcite just before undergoing gametogenesis, which can account for 4 to 20% of the final weight of the shell of *O. universa* (Hamilton et al., 2008). Hence, foraminiferal calcification is not a constant process and our estimates are averages over the culture period involving primary, secondary and gametogenic calcite. *O. universa* produces a thin juvenile trochospiral test and, at the end of its life cycle, a large thick spherical chamber. This massive calcification is responsible for the high calcification rate calculated for this species (Fig. 3), which is not representative of the calcification rate when growing its trochospiral shell. It should be noted that *O. universa* produces this final spherical chamber over a period of several days of continued calcification.

Irradiance had a significant effect both on growth and calcification of *G. sacculifer*. At low irradiance, the time between collection and reproduction (Δt) was shorter and the final shell weight as well as the rates of calcification were lower compared to high irradiance (Figs. 1–3, Table 1). Calcification was 30% lower in LL than in HL. This is consistent with measurements made on *G. sacculifer* (Erez, 1983) and *O. universa* (Lea et al., 1995) which indicated rates of calcification 3 to 4 times higher in the light than in the dark, corresponding to a 66–75% decrease in dark conditions. Similar observations have also been made on other photosynthetic calcifying organisms such as zooxanthellate corals (Gattuso et al., 1999; Moya et al., 2006; Schutter et al., 2008), stressing the strong interactions between irradiance and calcification rate.

The final shell weight (Figs. 1 and 2) as well as the calcification rate (Fig. 3) clearly depended on [CO_3^{2-}]. Over the full range of [CO_3^{2-}] tested, calcification rates increased between 34 and 44% for *G. sacculifer* and 34 to 41% for *O. universa*, resulting in a shell weight increase between 24 to 34% for *G. sacculifer* and 64 to 87% for *O. universa*. Based on these results, the potential impact of ocean acidification on foraminifera calcite production can be estimated. For this, we assume that, in the surface ocean, the current global [CO_3^{2-}] is around 200 μmol kg^{-1} (corresponding to the year 2004), 225 μmol kg^{-1} for the preindustrial period, 279 μmol kg^{-1} for last glacial maximum (LGM) conditions, and 110 μmol kg^{-1} under the IS92a "business as usual" scenario defined by the Intergovernmental Panel on Climate Change (IPCC) projected for the year 2100 (Orr et al., 2005). Under these conditions, the present rate of calcification of *G. sacculifer* and *O. universa* would be 1.5 to 3.5% lower than preindustrial values and 5 to 10% lower than during the LGM. The present calcification would correspond to a decrease of the final shell weight of 1.1–1.6% (*G. sacculifer* LL and HL) to 5–7% (*O. universa*) compared to preindustrial conditions and 3.4–4.8% (*G. sacculifer* LL and HL) to 15–20% (*O. universa*) compared to LGM conditions. These estimated differences between present, preindustrial and LGM foraminifera weights are in the same range of values (but slightly lower) than observed in sediment cores. *Globigerinoides ruber* is presently 11% lighter than preindustrial specimens and 20% than LGM specimens (de Moel et al., 2009). Individuals of *Globigerina bulloides* sampled in sediment cores exhibit a 30 to 35% decrease in weight since the LGM (Barker and Elderfield, 2002; Moy et al., 2009). Our results suggested that in 2100, the rate of calcification of *G. sacculifer* and *O. universa* could be reduced by 6 to 13% compared to present rates, leading to shell weights reduction of 20 to 27% for *O. universa* and of 4 to 6% for *G. sacculifer*. The magnitude of this potential decrease is consistent with that projected for some zooxanthellate corals (Langdon and Atkinson, 2005) and oysters (Gazeau et al., 2007), and lower than other observations on corals (Langdon and Atkinson, 2005), mussels (Gazeau et al., 2007) or pteropods (Comeau et al., 2009). Other planktonic foraminifera may have a higher sensitivity to [CO_3^{2-}]. Indeed, *O. universa* and G. *sacculifer* have numerous symbiotic algae that facilitate their calcification, whereas numerous other species, notably temperate to cold water species that are naturally exposed to waters more depleted in CO_3^{2-}, are not symbiotic. Hence, it is possible that the decrease of [CO_3^{2-}] may have a larger effect on non-symbiotic species than on symbiotic species. This may explain the larger decrease of shell weight between LGM to modern conditions observed for the non-symbiotic species *G. bulloides* (Barker and Elderfield, 2002; Moy et al., 2009) compared to the symbiotic *G. ruber* (de Moel et al., 2009). Consequently, there is a need to assess the effect of [CO_3^{2-}] on the calcification rate of non-symbiotic species. Additionally, in order to estimate the influence of global environmental changes on calcite fluxes generated by foraminifera, there is a need to estimate the effect of reduced pH on shell dissolution during sedimentation, but also to estimate the combined effect of decreased pH and elevated temperature. Indeed, at higher temperatures, foraminifera are usually more abundant (Bé and Tolderlund, 1971), have higher growth rates (Lombard et al., 2009) and larger shell sizes (Schmidt et al., 2006). Hence, the predicted increase in temperature could increase the production of calcite by foraminifera, counteracting the negative impact of ocean acidification. The combined effect of temperature and [CO_3^{2-}] thus need to be investigated in order to estimate the impact of global environmental changes on foraminifera.

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References

Armstrong, R. A., Lee, C., Hedges, J. I., Honjo, S., and Wakeham, S. G.: A new, mechanistic model for organic carbon fluxes in the ocean based on the quantitative association of POC with ballast minerals, Deep-Sea Res. II, 49, 219–236, 2002. 8591

Barker, S. and Elderfield, H.: Foraminiferal calcification response to glacial-interglacial changes in atmospheric CO_2, Science, 297, 833–836, 2002. 8598

Bé, A. W. H. and Tolderlund, D. S.: Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and Indian Oceans, in: Micropaleontology of Oceans, edited by: Funnell, B. M. and Riedel, W. R., Cambridge University Press, London, 105–149, 1971. 8599

Bijma, J., Hönich, B., and Zeebe, R. E.: Impact of the ocean carbonate chemistry on living foraminiferal shell weight: Comment on “Carbonate ion concentration in glacial-age deep waters of the Caribbean Sea” by W. S. Broecker and E. Clark, Geochem. Geophy. Geosy., 3, 1064, doi:10.1029/2002GC000388, 2002. 8596

Bijma, J., Spero, H. J., and Lea, D. W.: Reassessing foraminiferal stable isotope geochemistery: Impact of the oceanic carbonate system (experimental results), in: Uses of Proxies in Paleoceanography: Examples from the South Atlantic, edited by: Fischer, G. and Wefer, G., Springer Verlag, Berlin-Heidelberg, 489–512, 1999. 8591, 8596

Comeau, S., Gorsky, G., Jeffree, R., Teyssié, J.-L., and Gattuso, J.-P.: Key Arctic pelagic mollusc (*Limacina helicina*) threatened by ocean acidification, Biogeosciences Discuss., 6, 2523–2537, 2009, http://www.biogeosciences-discuss.net/6/2523/2009/. 8590, 8598

de Moel, H., Ganssen, G. M., Peeters, F. J. C., Jung, S. J. A., Brummer, G. J. A., Kroon, D., and Zeebe, R. E.: Planktic foraminiferal shell thinning in the Arabian Sea due to anthropogenic ocean acidification?, Biogeosciences Discuss., 6, 1811–1835, 2009, http://www.biogeosciences-discuss.net/6/1811/2009/. 8598

Dickson, A. G. and Millero, F. J.: A comparison of the equilibrium constant s for the dissociation of carbonic acid in seawater media, Deep-Sea Res., 34, 1733–1743, 1987. 8592

Erez, J.: Calcification rates, photosynthesis and light in planktonic foraminifera, in: Biomineralization and biological metal accumulation, edited by: Westbroek, P. and de Jong, E. W., D. Reidel Publishing Company, Dodrecht, 307–312, 1983. 8597

Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., and Millero, F. J.:

Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans, Science, 305, 362–366, 2004. 8590

Gattuso, J. P., Allemand, D., and Frankignoulle, M.: Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry, Am. Zool., 39, 160–183, 1999. 8591, 8597

Gazeau, F., Quiblier, C., Jansen, J. M., Gattuso, J. P., Middelburg, J. J., and Heip, C. H. R.: Impact of elevated CO_2 on shellfish calcification, Geophys. Res. Lett., 34, L07603, doi:10.1029/2006GL028554, 2007. 8590, 8598

Hamilton, C. P., Spero, H. J., Bijma, J., and Lea, D. W.: Geochemical investigation of gametogenic calcite addition in the planktonic foraminifera *Orbulina universa*, Mar. Micropaleontol., 68, 256–267, 2008. 8597

Hemleben, C., Spindler, M., and Anderson, O. R.: Modern planktonic foraminifera, Springer-Verlag, New York, 363 pp., 1989. 8596

Iglesias-Rodriguez, M. D., Halloran, P. R., Rickaby, R. E. M., Hall, I. R., Colmenero-Hidalgo, E., Gittins, J. R., Green, D. R. H., Tyrrell, T., Gibbs, S. J., von Dassow, P., Rehm, E., Armbrust, E. V., and Boessenkool, K. P.: Phytoplankton calcification in a high-CO_2 world, Science, 320, 336–340, 2008. 8591

Klaas, C. and Archer, D. E.: Association of sinking organic matter with various types of mineral ballast in the deep sea: Implication for the rain ration, Global Biogeochem. Cy., 16, 63–61, doi:10.1029/2001GB001765, 2002. 8591

Langdon, C. and Atkinson, M. J.: Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment, J. Geophys. Res.-Oceans, 110, C09S07, doi:10.1029/2004JC002576, 2005. 8598

Lea, D. W., Martin, P. A., Chan, D. A., and Spero, H. J.: Calcium-uptake and calcification rate in the planktonic foraminifer *Orbulina universa*, J. Foraminifer. Res., 25, 14–23, 1995. 8593, 8597

Leclercq, N., Gattuso, J.-P., and Jaubert, J.: CO_2 partial pressure controls the calcification rate of a coral community, Glob. Change Biol., 6, 329–334, 2000. 8590

Lewis, E. and Wallace, D.: Program developed for CO_2 system calculations, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, 1998. 8592

Lombard, F., Labeyrie, L., Michel, E., Spero, H. J., and Lea, D. W.: Modelling the temperature dependent growth rates of planktic foraminifera, Mar. Micropaleontol., 70, 1–7, 2009. 8593, 8599

Mehrbach, C., Culberson, C. H., Hawley, J. E., and Pytkowicz, R. M.: Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure, Limnol. Oceanogr., 18, 897–907, 1973. 8592

Michaels, A. F., Caron, D. A., Swanberg, N. R., Howse, F. A., and Michaels, C. M.: Planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda: abundance, biomass and vertical flux., J. Plankton Res., 17, 131–163, 1995. 8592, 8593

Moy, A. D., Howard, W. R., Bray, S. G., and Trull, T. W.: Reduced calcification in modern Southern Ocean planktonic foraminifera, Nature Geoscience, 2, 276–280, 2009. 8591, 8598

Moya, A., Tambutte, S., Tambutte, E., Zoccola, D., Caminiti, N., and Allemand, D.: Study of calcification during a daily cycle of the coral Stylophora pistillata: implications for "light-enhanced calcification", J. Exp. Biol., 209, 3413–3419, 2006. 8597

Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R. M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R. G., Plattner, G. K., Rodgers, K. B., Sabine, C. L., Sarmiento, J. L., Schlitzer, R., Slater, R. D., Totterdell, I. J., Weirig, M. F., Yamanaka, Y., and Yool, A.: Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms, Nature, 437, 681–686, 2005. 8590, 8598

Prentice, C., Farquhar, G. D., Fasham, M. J. R., Goulden, M. L., Heimann, M., Jaramillo, V. J., Kheshgi, H. S., Le Quéré, C., Scholes, R. J., and Wallace, D. W. R.: The carbon cycle and atmospheric carbon dioxide, in: Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J., Dai, X., Maskell, K., and Johnson, C. A., Cambridge University Press, New York, 185–237, 2001. 8590

Riebesell, U., Zondervan, I., Rost, B., Tortell, P. D., Zeebe, R. E., and Morel, F. M. M.: Reduced calcification of marine plankton in response to increased atmospheric CO_2, Nature, 407, 364–367, 2000. 8590

Russell, A. D., Hönisch, B., Spero, H. J., and Lea, D. W.: Effects of seawater carbonate ion concentration and temperature on shell U, Mg, and Sr in cultured planktonic foraminifera, Geochim. Cosmochim. Ac., 68, 4347–4361, 2004. 8591, 8592, 8593, 8596

Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., Wanninkhof, R., Wong, C. S., Wallace, D. W. R., Tilbrook, B., Millero, F. J., Peng, T. H., Kozyr, A., Ono, T., and

Rios, A. F.: The oceanic sink for anthropogenic CO_2, Science, 305, 367–371, 2004. 8590

Schiebel, R.: Planktic foraminiferal sedimentation and the marine calcite budget, Global Biogeochem. Cy., 16, 1065, doi:1010.1029/2001GB001459, 2002. 8591

Schmidt, D. N., Lazarus, D., Young, J. R., and Kucera, M.: Biogeography and evolution of body size in marine plankton, Earth-Sci. Rev., 78, 239–266, 2006. 8599

Schutter, M., Van Velthoven, B., Janse, M., Osinga, R., Janssen, M., Wijffels, R., and Verreth, J.: The effect of irradiance on long-term skeletal growth and net photosynthesis in *Galaxea fascicularis* under four light conditions, J. Exp. Mar. Biol. Ecol., 367, 75–80, 2008. 8597

Spero, H. J.: Ultrastructural examination of chamber morphogenesis and biomineralization in the planktonic foraminifer *Orbulina universa*, Mar. Biol., 99, 9–20, 1988. 8596

Wolf-Gladrow, D. A., Riebesell, U., Burkhardt, S., and Bijma, J.: Direct effects of CO_2 concentration on growth and isotopic composition of marine plankton, Tellus B, 51, 461–476, 1999. 8591

Table 1. *G. sacculifer* initial and final mean size (Is and Fs), final weight (Fw) and estimated initial weight (I_ew), duration of the experiment from collection till gametogenesis (Δt) and mean weight increase (Δw) under the different [CO_3^{2-}], total alkalinity (TA), pH and irradiance levels. See Table A1 of Russel et al. (2004) for similar information on *O. universa*.

Light	[CO_3^{2-}] (μmol kg^{-1})	TA (μEq kg^{-1})	pH	Is (μm)	Fs (μm)	Fw (μg)	Δt (d)	I_ew (μg)	Δw (μg)
HL	71.9	2055	7.66	372	625	33.8	6.1	14.5	19.3
	124	2165	7.90	388	699	49.0	7.0	16.0	33.0
	139	2204	7.95	430	691	47.6	6.7	19.0	28.5
	233	2365	8.21	380	662	47.6	7.4	15.6	32.0
	455	2680	8.53	399	667	57.1	6.3	16.6	40.5
	504	2741	8.59	386	678	51.4	6.8	15.4	36.1
	566	2827	8.64	401	637	48.5	5.5	17.0	31.5
	Mean			393	664	48.2	6.6	16.2	31.9
LL	71.9	2055	7.66	384	509	20.1	4.3	15.0	5.1
	124	2165	7.90	366	507	20.3	4.2	14.3	6.0
	139	2204	7.95	446	601	26.4	3.7	21.0	5.4
	233	2365	8.21	403	585	37.9	5.2	17.5	20.5
	455	2680	8.53	397	541	29.2	4.5	16.3	12.9
	504	2741	8.59	379	503	20.8	3.9	14.7	6.0
	566	2827	8.64	406	528	28.7	4.1	16.9	11.8
	Mean			399	550	29.1	4.5	16.8	12.3
Combined HH+LL				396	603	38.0	5.5	16.5	21.4

Table 2. Parameters of relationships between length (L) and shell weight (W) obtained for the different species, under different [CO_3^{2-}] and light conditions for *G. sacculifer*. All the relationships are expressed as $W=aL^b$. Covariance analyses on log-transformed data were used to test the effect of [CO_3^{2-}] and irradiance on the final shell weight. *: $P<0.01$; **: $P<0.005$; ***: $P<0.0001$.

							Test HL≠LL	
Species	[CO_3^{2-}]	Light	a	b	R^2	n	a	b
G. sacculifer	71.9	HL	$1.67\ 10^{-2}$	1.18	0.81	11	*	ns
		LL	$1.44\ 10^{-4}$	1.89	0.85	7		
G. sacculifer	124	HL	$1.13\ 10^{-2}$	1.27	0.29	8	*	ns
		LL	$3.55\ 10^{-5}$	2.12	0.73	12		
G. sacculifer	139	HL	$1.56\ 10^{-3}$	1.58	0.54	11	***	ns
		LL	$4.95\ 10^{-4}$	1.70	0.89	18		
G. sacculifer	233	HL	$2.63\ 10^{-4}$	1.86	0.62	20	ns	ns
		LL	$1.66\ 10^{-5}$	2.29	0.91	34		
		HL+LL	$3.60\ 10^{-5}$	2.17	0.87	54		
G. sacculifer	455	HL	$6.71\ 10^{-4}$	1.74	0.56	13	***	ns
		LL	$1.87\ 10^{-4}$	1.90	0.86	13		
G. sacculifer	504	HL	$1.41\ 10^{-3}$	1.61	0.73	15	***	ns
		LL	$5.65\ 10^{-4}$	1.69	0.66	12		
G. sacculifer	566	HL	$1.41\ 10^{-5}$	2.33	0.9	13	**	ns
		LL	$5.57\ 10^{-4}$	1.73	0.84	20		
Test within LL			***	ns				
Test within HL			***	ns				
O. universa	212		$3.92\ 10^{-9}$	3.61	0.84	7		
O. universa	301		$5.44\ 10^{-8}$	3.22	0.93	8		
O. universa	399		$5.25\ 10^{-7}$	2.89	0.85	6		
O. universa	480		$1.17\ 10^{-10}$	4.25	0.98	6		
Test within *O. universa*			***	ns				

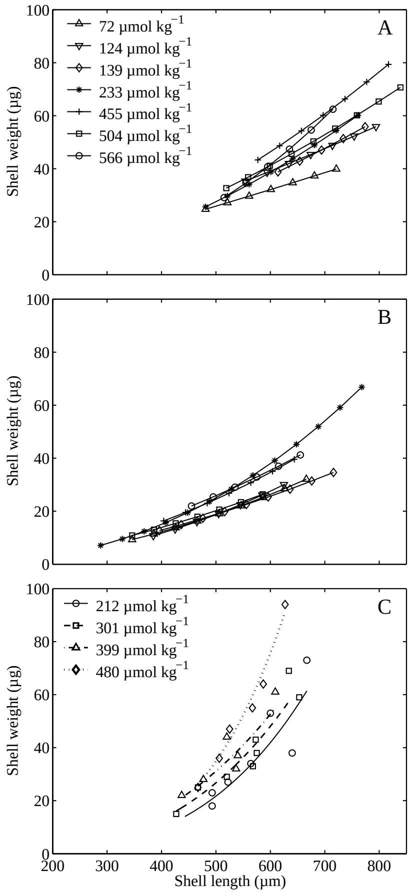

Fig. 1. Length-weight relationships obtained for different [CO_3^{2-}] conditions for *G. sacculifer* under HL **(A)** and LL **(B)** and *O. universa* **(C)**. For a better view, only regression lines are shown for *G. sacculifer*. Parameters of the regression lines are indicated in Table 2.

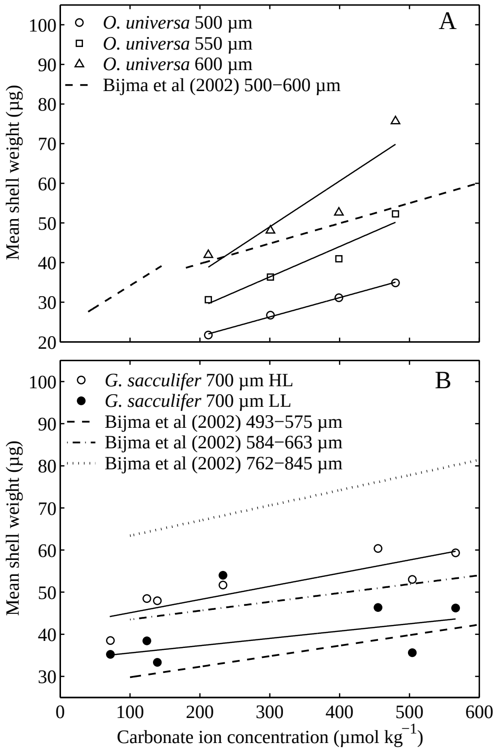

Fig. 2. Mean final shell weight (W_f) obtained for *O. universa* **(A)** and *G. sacculifer* **(B)** as a function of the carbonate ion concentration for different final shell sizes. The regression lines correspond to the following relationships with the corresponding confidence intervals: W_f=0.049(±0.002)[CO_3^{2-}]+11.67(±0.67), R^2=0.99 for 500 μm *O. universa*; W_f=0.077(±0.001)[CO_3^{2-}]+13.4(±4.8), R^2=0.94 for 550 μm *O. universa*; W_f=0.116(±0.04)[CO_3^{2-}]+14.3(±8.6), R^2=0.83 for 600 μm *O. universa*; W_f=0.031(±0.008)[CO_3^{2-}]+41.9(±2.9), R^2=0.73 for 700 μm *G. sacculifer* in HL and W_f=0.017(±0.009)[CO_3^{2-}]+33.8(±3.6), R^2=0.33 for 700 μm *G. sacculifer* in LL. All relationships have slopes significantly different from zero ($P<0.02$). The slopes are not significantly different (covariance analysis; $P>0.1$) whereas the intercepts are significantly different ($P<0.0001$). Similar relationships obtained for the same species (Bijma et al., 2002) were added for comparison.

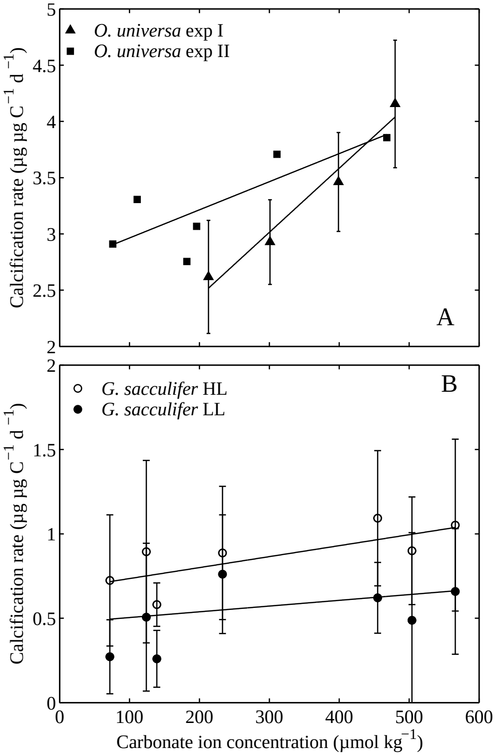

Fig. 3. Effect of the carbonate ion concentration on the biomass-normalized rates of calcification in *O. universa* **(A)** and *G. sacculifer* **(B)** calcification rates. Error bars indicate the standard deviation observed between the different foraminifera individuals within similar conditions.