

Interactive comment on “Size-dependent response of foraminiferal calcification to seawater carbonate chemistry” by Michael J. Henehan et al.

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Received and published: 10 February 2017

Reply to Referee comment 1 from R. Schiebel on “Size-dependent response of foraminiferal calcification to seawater carbonate chemistry” by Henehan, Evans et al.

We thank the reviewer for taking the time to review our manuscript, and for his positive and constructive comments. Below we detail the specific responses to the three points made.

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First comment: *"On page 8, lines 9-11, Henehan et al. note that 'logarithmic regression models were used because modelled CI through ontogeny approximates to a logarithmic relationship across the size range of our cultures (see Fig. 1b).' It should be made clear whether 'cultures' only include the size-to-calcite mass relationships of entire individuals of assemblages, or if data on the ontogenetic development (from cross-sections, or CT) of single specimens were also included here."*

Response: We fear that our writing was perhaps not clear enough here. What we mean to say is that we fit a logarithmic regression to the culture results (i.e. solely the results of our culture experiments, and nothing else) because the models that we have constructed indicate that the increase in calcification intensity with size over the size range of our cultures is approximately logarithmic. To illustrate this, in the attached figure 1 below we shade the range of sizes seen in culture (plots from Main text Fig. 4), to compare with the models (from Main text Fig. 2).

These models are built from our own measurements and published measurements from techniques such as synchrotron radiation X-ray tomographic microscopy (see Table 2), and are then screened by comparison with open-ocean Red Sea populations (see Section 2.4.2 and Appendix A). To reiterate, the objective here is only to describe the underlying size control on CI, so as to then determine the residual variability caused by pH change. We therefore use the shape of a relationship between CI and size (logarithmic over this size range) derived from our models (itself built on cross-sections, etc.), to inform as to the most appropriate fit. We will clarify the revised text, and also include clarification on the morphospecies used in cultures and in the construction of the model.

Second point (broken down for clarity): *"When comparing their data to the published data of others, Henehan et al. seem to have struggled with the classification of G. ruber morphotypes, and a general confusion concerning taxonomy of G. ruber*

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as presented in the literature. To my knowledge, Wang (2000) first described different water depth habitats of *G. ruber* s.s. and s.l. from the South China Sea (SCS). Wang (2000) knew all about the difference between the different morphotypes (*elongatus* and *pyramidalis*), but finally only used differentiated between the types with spherical final chambers (s.s.) and compressed final chambers. From Wang (2000): 'Initially the *Globigerinoides ruber* s.l. group was differentiated into tests with low and high trochospires. However, as these two sub-groups did not show significant differences in their isotopic signal, they were lumped again into one group.' The morphotype with the compressed final chamber is referred to as *platys* by some colleagues (see Numberger et al. 2009), and may just represent specimens with a *kummerform* final chamber. The concept of Wang (2000) was then largely adopted by Steinke et al. (2005) also working on the SCS and Indo-Pacific waters. Beer, Schiebel, Wilson (2009) did certainly distinguish between the different morphotypes, and did only use *G. ruber* (white), i.e. *G. ruber* s.s., in their analyses. *G. ruber*, *G. elongatus*, and *G. pyramidalis* were considered different species. However, tests with normal formed and *kummerform* final chamber were not distinguished, because the size-to-weight ratio of these tests was not significantly different in the samples from the Arabian Sea.

Response: We thank the reviewer for the comments regarding our use of species concepts with regards *G. ruber* in the published literature, and have reviewed the manuscript for locations where we could be clearer and more exact. We will clarify our taxonomy in multiple locations of the main text, including the caption to figure 4, to address this concern.

Please note: The ecological significance of different morphotypes, i.e. G. ruber s.l. in warmer waters, and G. elongatus and G. pyramidalis in colder waters as found by Steinke et al. (2005) may differ at the regional scale. Water temperature may just be one among many (more relevant?) parameters, which determine the ecological niche

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of a species.

Response: While we agree that there may be other controls on the relative abundance of *G. ruber* s.l., certainly the geographic range of these morphotypes may suggest temperature is a very important control. For instance, in core tops we have worked with characterised by mean annual surface water temperatures of 15-20 °C in the North Atlantic and Southwest Pacific, it is common to find *G. ruber* s.l., but none of the more tropical sensu stricto species. A paper published this week also indicates that sensu lato *ruber* is associated with colder waters than co-habiting sensu stricto in the East China Sea (A. Carter et al., Marine Micropalaeontology, doi:10.1016/j.marmicro.2017.01.001). In that sense it seems a reasonable null hypothesis that *G. ruber* s.l. either tolerates, or even prefers, colder temperatures, even if there may of course be other factors at work.

“To conclude, the statement on p. 10, lines 23-25, is wrong, and should be corrected: ‘Beer et al. did not differentiate between species, but it is likely they would have sampled an increasing proportion of higher-SNW sensu lato species (i.e. G. elongatus and G. pyramidalis) in lower-pH upwelling waters, given these species preference for colder waters (Steinke et al., 2005).’ I would have happily discussed this point with the authors before submission of your manuscript, and I might have even provided you with the original samples.”

Response: We agree that our communication could have been better, and apologise for this oversight. We will remove this passage from the revised discussion altogether, since we have no alternative explanation to offer for the disagreement between our data and those of Beer et al. (2010).

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Third point (broken down for clarity): “In Figure 5, Henehan et al. show present a schematic view of the factors affecting shell thickness, by comparing large modern planktic foraminifers and small Paleocene-Eocene benthic foraminifers. To my consideration, this is comparing apples and oranges, and is hence insignificant. Calcification in benthic foraminifers is possibly related to the nature and chemistry of the bulk sediment, and follow an entirely different systematics than in planktic foraminifers.”

Response: While we appreciate that benthic and planktic foraminifera have clear eco-physiological differences, we would argue that there is no reason to think that their mechanisms of calcification are fundamentally different. Much of our understanding about biomineralisation processes in foraminifera comes from laboratory studies in benthic foraminifera (e.g. ter Kuile and Erez 1988, 1989; Elderfield et al., 1996; Bentov and Erez, 2005; Bentov et al., 2009; de Nooijer et al., 2009; de Nooijer et al., 2014), and conclusions from these benthic foraminifera are extended often, if not always, to the rest of the non-porcelaneous calcareous foraminifera. In addition, observations from benthic foraminifera we discuss here are seen in both epifaunal (*N. truempyi*) and shallow-infaunal (*O. umbonatus*) taxa, suggesting porewater chemistry is not the driving factor here (Foster et al., PNAS 2013). Furthermore, it was recently observed that the proton flux associated with calcification in the shallow-dwelling benthic foraminifera *Ammonia* does not change as a function of seawater pH (Toyofuku et al., 2017 Nat. Comms.). This observation, from a very different benthic species, is in agreement with our model in that it also indicates a limited response of calcification to reduced pH in small species that probably lack an internal calcium or carbon pool.

We therefore do not think it unreasonable to posit a hypothetical model regarding commonality in calcification behaviour as we do, so that these ideas can be tested and falsified. However, we recognize the uncertainties associated with this comparison, and will add this caveat clearly to the revised text, while emphasising that this is as yet an untested hypothesis.

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“Natural and cultured specimens ‘pH reaction’ may just reflect the general health of individuals, which might be related to alimentation.”

Response: We stress that our cultured foraminifera were all offered food at the same rate between pH experiments, and so alimentation should not have a role in producing our observed pH effect in culture. Furthermore, we would suggest the findings of Aldridge et al. (2012) in *Globigerina bulloides* indicate food supply has no greater influence on shell weight than co-varying carbonate system parameters.

*“In addition, production and preservation may both affect wall thickness: Pores in the images (Fig. 5) of *G. ruber* are funnel shaped, which may indicate dissolution. I would suggest to change Fig. 5 and text on page 9 and 10.*

Response: We agree that preservation can be an issue when interpreting sediment records- a point we make firmly in the manuscript based on our analysis of core-tops. However, in the case of this figure, de Moel et al (2009) considered the possibility of dissolution, and regard it as unlikely: *“The shells in the sediment ... generally look well preserved, some with remnants of spines still present. Fragmentation and dissolution are known to change faunal assemblages (Berger, 1970; Anderson and Archer, 2002; Le and Thunell, 1996), and susceptibility for it is related to the thickness of the shell walls (Barker et al., 2007). However, Conan et al. (2002) showed that exactly at this site the abundance of dissolution-sensitive species in the surface sediment is high and there is a close similarity between foraminifera assemblages and skeletal group compositions in the surface sediment and in an on-site sediment trap. This implies a good preservation without selective removal of susceptible carbonate components (i.e. thin walled shells) in the sediment.”* From our experience in cultures, pores in

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foraminifera grown in low pH conditions can appear slightly larger (see e.g. images in Henehan et al. 2013, Fig. 4), and so there is the potential that widened pores such as those in de Moel et al.'s figure could conceivably be due to some influence of pH on pore size. However, our culture observations are by no means quantitative. The question of controls on porosity is an active research question amongst our group, however, and so we hope to address this question in due course.

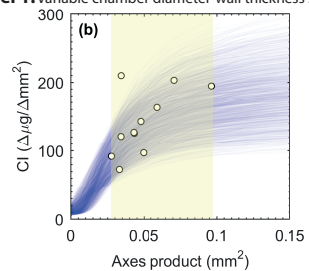
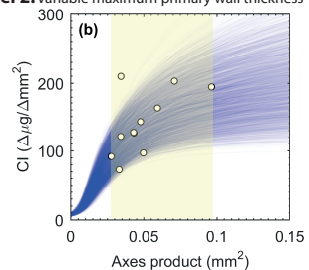
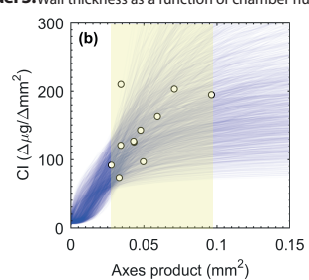
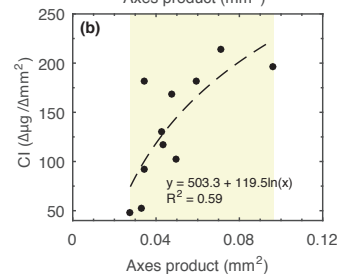
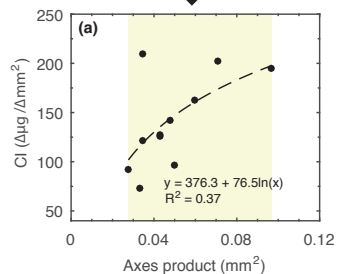
For these reasons, we respectfully prefer to retain the figures and text as presented, but with some rewording to the text and the explicit recognition that this remains a hypothetical model that should be tested by the community going forward.

“By the way: The expression ‘Larger Foraminifera’ signifies an informal group of large benthic foraminifers, and should not be used for planktic foraminifers and other benthic foraminifers, to avoid confusion.”

Response: We will change the wording in the revised manuscript to ‘bigger’ rather than ‘larger’ so as to avoid any possible confusion.

Interactive comment on Biogeosciences Discuss., doi:10.5194/bg-2016-459, 2016.

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Model 1: Variable chamber diameter-wall thickness slope**Model 2:** Variable maximum primary wall thickness**Model 3:** Wall thickness as a function of chamber numberCI from cultures, raw data
(from Fig. 4)CI from cultures, normalised
for chamber addition
(from Fig. 4)**Fig. 1.** Clarification of the 'size range seen in culture' that we refer to in the text.

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