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Biogeosciences Discussions

Interactive comment on "Effects of seawater pCO₂ changes on the calcifying fluid of scleractinian corals" *by* S. Hohn and A. Merico

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General reply

The reviews that we received were very constructive and will help us to strengthen our manuscript both scientifically and in terms of clarity of meaning. Thus we propose a number of revisions. Please find enclosed detailed responses to reviewer concerns and descriptions of the changes we propose and their scientific justification.

Anonymous Referee 2

This paper, 'Effects of seawater pCO2 changes on the calcifying fluid of scleractinian

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Interactive Discussion

Discussion Paper

corals' by Hohn and Merico presents one of the first attempts at producing a kinetic model for the coral calcification process. Although such a model is much needed for improving our understanding of the calcification process, the model presented seems unrealistic and has failed to take into account much of the literature.

Re-reading our original submission in light of the comments received it is clear that we were too terse in our introduction of the topic so we are keen to consider a number of improvements.

We agree for example to include more details concerning coral physiology in the introductory section of our manuscript. However, many articles in the coral literature present single data points that show differences between control conditions and treatments. Even though these works give valuable insights in coral responses to certain treatments, they are usually insufficient to derive parameterizations for modelling studies. To develop a dynamical model, more comprehensive data are required that can help to identify functional responses. Therefore some articles in the literature have not been considered because the data do not offer an appropriate constraint for the development of the model.

The model produces a continuous increase in tissue alkalinity and calcium – both of which should be tightly regulated. Cycling of these values in the tissue layer could be expected, but a continuous increase seems highly unlikely. Although the data may not come from the same experiment which Hohn and Merico seem to focus exclusively upon, there are a number of useful measurements which should be considered in constructing the model.

We discussed and explained the continuous increase in tissue alkalinity and calcium concentrations in the submitted manuscript. We also mentioned that this pattern is rather unlikely as one could expect the import of calcium into the tissue to equal calcium export into to the calcifying fluid. However, in light of the comments received also by reviewer 1, we have refined our model runs (see below) to obtain more realistic tis-

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sue pH. We also ensured that the input rates of calcium into the tissue equal the active calcium transport from the tissue into the calcifying fluid. As a result, the intracellular calcium and tissue alkalinity do not increase over integration time in the new simulations (see Figure 1). While the adjusted fluxes from the coelenteron into the tissue are now in accordance to the strongly controlled calcium concentration in the tissue (see Figure 1B), they are too small to induce appreciable changes between light and dark phases in the calcium concentration and the pH of the coelenteron (see Figure 1C and 2C).

I suggest looking at Marshall et al 2007 (and references there in) and Tambutte et al 1996. Further the tissue pH values used are unrealistic, please see Venn et al 2009 and 2011.

The study by Marshall et al. 2007 is indeed interesting and we will certainly cite it in the revised introduction of our manuscript. However, the experimental conditions of Marshall et al. (2007) are very different from the experimental conditions of Al-Horani et al (2003), therefore the work of Marshall et al. (2007) is not directly comparable to our model system. The concentrations of calcium that are measured by Marshall et al. (2007) in the different tissue compartments, for example, are very high and represent total calcium content. These data do not necessarily reflect the free calcium concentrations in the cytoplasm, which would be the relevant information needed by our model to determine chemical reactions and transport potentials. The study of Tambutte et al. (1996) regards Stylophora pistillata, a coral species with much smaller polyps than Galaxea fascicularis, which is the coral species used by Al-Horani et al. (2003). Although Tambutte et al (1996) could determine the different compartment sizes and the exchange rates for Stylophora pistillata, these data cannot be used by our model which is set up for a much bigger polyp organism. However, from Tambutte et al (1996) we could use the general identification of different compartments as the basis for developing the structure of our model.

other comments: Methods are nowhere detailed enough – not even the software pack-

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age for the simulations is given, some parameters are missing while others lack details as to how the values were assigned and whether or not they are close to any estimates based on the literature.

There is no such "software package" used in this study. The model was written in a text editor from scratch using the programming language python. Python is platform independent and open source. The mathematical equations representing our polyp model were indeed presented in the appendix of our original manuscript. Typically, numerical codes are not attached to manuscripts because of their length. Given the mathematical equations, any experienced modeller would be able to code the model into any desired programming language. We are keen, however, to make our numerical code available on request. We will also improve the presentation of parameter values in the revised manuscript and provide the literature source.

Throughout the paper please use terminology consistent with the literature eg sub-calicoblastic = beneath the calicoblastic cell layer, calcification occurs in the sub-calicoblastic environment, not in the calicoblastic layer see Tambutte et al., 2011

Good point, thank you. We will correct the terminology concerning the "subcalicoblastic layer". To avoid any confusion with the "calicoblastic epithelium" we will use the term "calcifying fluid" throughout the manuscript.

intro line 15 there is considerable variation between studies and between conditions in a given study in the response to CO2 – eg Reynaud et al 2003, Holcomb et al 2011

The reviewer is correct to reason that different species react differently to same treatments or that a change in nutrient concentrations (or light, or temperature) might compensate for the response to CO2. However, the general response of coral calcification to ocean acidification is a reduction in calcification rates (cf. Figure 3b in McCulloch et al. 2012).

intro line 20 or at least spontaneous precipitation is not a rapid process see Morse et

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al., 2003

We agree. We will change the respective sentence on page 2657 lines 18-20 to: "However, despite oversaturation with respect to aragonite and calcite, spontaneous precipitation of CaCO3 rarely occurs in the ocean."

concentrations of phosphate are not generally very high - see Burton and Walter 1987, 1990 for the effects of Mg and PO4 on the precipitation of different species

Phosphate concentrations are generally very low in the oligotrophic tropical surface waters but not in the rest of the global ocean. Compared to other nutrients phosphate concentrations might be low although they could still be high enough to inhibit aragonite crystallization. We will revise our original statement in the revised manuscript and will add the references suggested by the reviewer.

clarify what is meant by growth medium when first used

With "growth medium" we mean the seawater in which the corals grow. To avoid a misunderstanding, we will write "water in which the corals grow" on page 2658, line 2, and then explain what we mean with "growth medium" in the next sentence, line 5.

Why has seawater entry to the subcalicoblastic medium been ignored?

The possibility of seawater entering the subcalicoblastic medium refers to the hypothesis of a paracellular pathway, which is based on the observation that a CaCO3 staining dye (calcein) makes its way from the outer growth medium to the extracellular calcifying fluid, staining the freshly precipitated aragonite (Tambutte et al 2012, Proc R Soc B, 279, pages 19-27). Since this dye is known to be membrane impermeable (because of its hydrophilic properties), its appearance in the calcifying fluid is explained by a flux through the intercellular space. We agree to introduce the description of this pathway in the introductory part of our manuscript to present a complete description of the current understanding of coral calcification. There are, however, at least two reasons why we did not include the paracellular pathway in our model. First, as acknowledged by

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Tambutte et al. 2011 (page 65): "Whether the ECM '(extracellular calcifying medium)' is closed to the outside environment or open to it is still debated." Given the uncertainties, we decided to exclude this pathway and investigated if the model is still able to produce the observed changes in the calcifying fluid. Second, if the intercellular space is permeable to dissolved ions, then the flux between the calcifying fluid and the seawater (or the coelenteron) should be described either by diffusive transport or by advective transport. In both cases, the model would require the rate of the transports, but unfortunately these rates are presently unknown. As suggested by reviewer 1, we will describe the paracellular pathway in the introduction and we will explain the reasons for excluding this process from our model.

references: Burton, E.A., Walter, L.M., 1987. Relative precipitation rates of aragonite and Mg calcite from seawater: Temperature or carbonate ion control? Geology. 15, 111-114.

Burton, E.A., Walter, L.M., 1990. The role of pH in phosphate inhibition of calcite and aragonite precipitation rates in seawater. Geochim Cosmochim Acta. 54, 797-808.

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Marshall, A.T., Clode, P.L., Russell, R., Prince, K., Stern, R., 2007. Electron and ion microprobe analysis of calcium distribution and transport in coral tissues. J Exp Biol. 210, 2453-2463.

Morse, J.W., Gledhill, D.K., Millero, F.J., 2003. CaCO3 precipitation kinetics in waters from the Great Bahama Bank: implications for the relationship between Bank hydrochemistry and whitings. Geochim Cosmochim Acta. 67, 2819-2826.

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Venn, A.A., Tambutte, E., Lotto, S., Zoccola, D., Allemand, D., Tambutte, S., 2009. Imaging intracellular pH in a reef coral and symbiotic anemone. PNAS.

Venn, A., Tambutte, E., Holcomb, M., Allemand, D., Tambutte, S., 2011. Live tissue imaging shows reef corals elevate pH under their calcifying tissue relative to seawater. PloS one. 6, e20013.

We thank the reviewer for providing this list of literature. We already knew, though not all, most of the mentioned articles.

Interactive comment on Biogeosciences Discuss., 9, 2655, 2012.

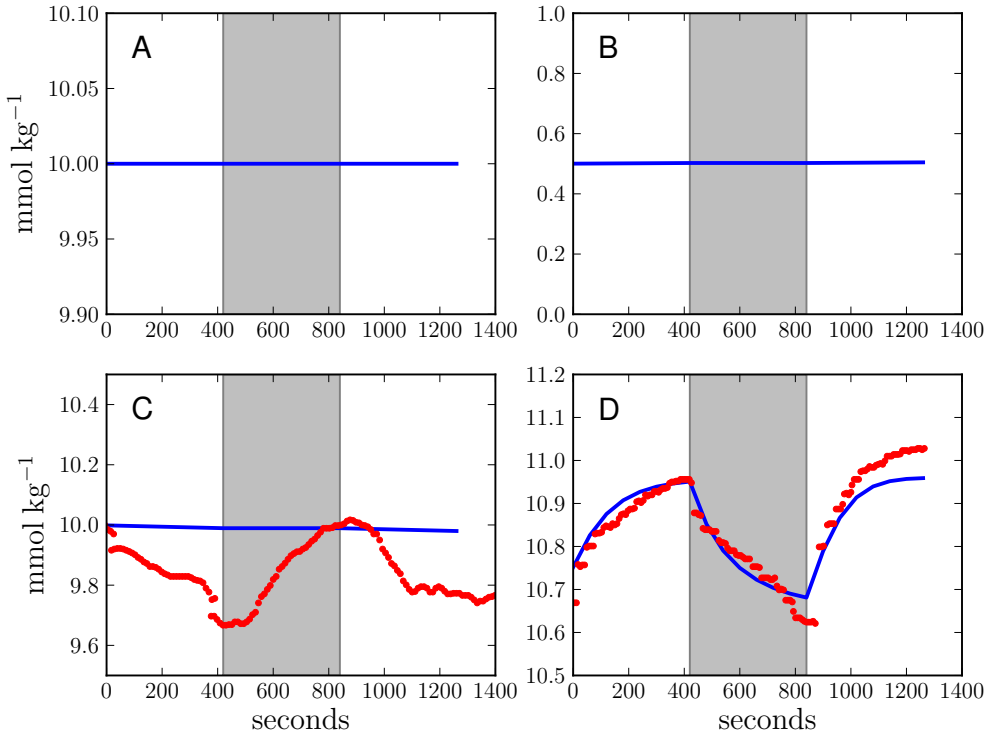

Fig. 1. Calcium ion concentrations in the four model compartments over time (A=seawater; B=tissue; C=coelenteron; D=calicoblastic layer).

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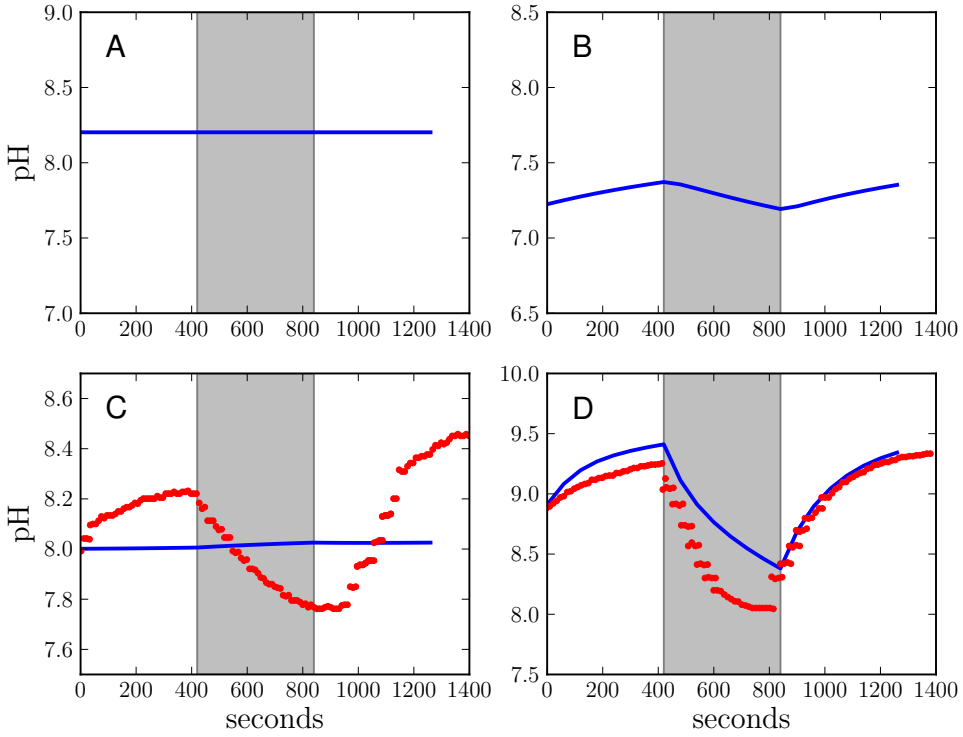

Fig. 2. pH in the four model compartments over time (A=seawater; B=tissue; C=coelenteron; D=calicoblastic layer).

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