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Comment

Interactive comment on “Modeling coral calcification accounting for the impacts of coral bleaching and ocean acidification” by C. Evenhuis et al.

C. Evenhuis et al.

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Response to reviewers for Modeling coral calcification accounting for the impacts of coral bleaching and ocean acidification by Evenhuis et al.

We thank the reviewers for their efforts in providing reviews for this manuscript. We have addressed the concerns of Reviewer #2 and Paul Jokiel. We acknowledge that while Reviewer #1 did not provide a complete review, and subsequently, this review was not posted we have nevertheless addressed their concerns. In the assessment of this paper we request that Reviewer #1 not be contacted again, given their inability to provide a complete review.

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Response to Reviewer Paul Jokiel (RC2132):

This Evenhuis et al. article presents an advanced model of coral calcification built on existing paradigms with a series of important new innovations. Parameter values used in the model are based on a synthesis of existing observational and experimental data. The resulting model improves our ability to mathematically describe and predict changes in coral calcification rate during a time of climate change. Their new model is an improvement over previous models that have been developed to show impact of future ocean acidification and temperature change, and sets the stage for future advancements in modeling. I agree with their conclusion that despite the implicit complexity of the coral reef environment a simple model based on temperature carbonate chemistry and different species can reproduce much of the observed response of corals to changes in temperature and ocean acidification. The model is “state of the art” and paves the way for future efforts.

Several simplifying assumptions that eventually will need to be addressed in future versions of this model.

Assumption 1. Coral reef calcification rate = Coral calcification rate.

This assumption has limits because corals can continue to grow relatively well at levels of ocean acidification that result in net dissolution of a coral reef (Andersson et al. 2009). Important reef calcifiers such as crustose coralline algae (CCA) are far more sensitive to OA condition than corals and can be eliminated from the reef at OA levels that still allow substantial coral growth (Kuffner et al. 2008). There are many reefs in the world that are dominated by CCA, with a very small component of live coral. Another related issue is that coral growth is generally measured directly by change in weight or linear extension while reef calcification is generally measured by the alkalinity depletion method (Kinsey 1978, Smith and Kinsey 1978). The alkalinity depletion method measures net calcification and includes the substantial alkalinity contribution of dissolving carbonate sediment and rocks (Murillo et al. 2014) as well as contribu-

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tions from other components such as macroalgae, crustose coralline algae, sediment diagenesis, etc. The authors recognize that Assumption 1 is necessary until we can produce enough data on the other components to refine the model. However, coral growth (weight change) cannot realistically be regarded as net reef calcification (alkalinity depletion method) although there must be a correlation. So the method will be useful in further defining and refining trends in coral reef response to global climate change, but with several caveats as mentioned above.

Assumption 2 is that calcification rate is driven by bulk water carbonate ion concentration.

Aragonite saturation state is a function of carbonate ion concentration. Assumption 2 is not correct (Jokiel et al. 2014). Carbonite ion concentration (and thus aragonite saturation state) of bulk water in laboratory incubations or in field flow metabolism experiments increases with increasing calcification rate, so carbonate ion concentration (or aragonite saturation state) cannot possibly be limiting (Jokiel 2014). Aragonite saturation state lags calcification by two hours (Shamberger et al. 2011, Jokiel et al. 2014) so cannot be driving calcification. However, there is a correlation between the two. The slope and intercept of the correlation varies from reef to reef. The calcification rate of reefs is driven primarily by photosynthetic rate of the calcifying component (available light) and limited by proton efflux from the corals (Jokiel 2014). A major issue here is that if G is measured using the alkalinity depletion method the result is greatly modified by dissolution rate of carbonates, changes in pH due to photosynthesis and other factors. Thus we find no consistent relationship. Many reefs with low aragonite saturation state show high rates of coral calcification (e.g. Shamberger et al. 2011, 2014).

The Evenhuis et al. model skilfully manipulates the aragonite saturation data that are presently available as a means of empirically describe the relationship between the aragonite saturation state of seawater and G . Eventually more data on response of various components to temperature and OA will become available and the model can be modified using the true drivers of net calcification. The use of irradiance (Q) as a

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major component of the equation resolves part of the issue because Pnet of the calcifying photosynthetic organisms drives Gnet (Jokiel et al. 2014) and these systems are very efficient at using all of the available irradiance through canopy development (Jokiel and Morrissey 1986) and other photo-adaptive processes. Use of these assumptions is appropriate due to the lack of data on the various other components of a calcifying reef system (e.g. impact of temperature and OA on sediment and coral rock dissolution, effects of crustose coralline algae). However, understanding the potential impact of these assumptions is critical to interpreting and applying the results to real world situations. More data will be developed on response of the calcifying organisms, bioeroding organisms, macroalgae, etc. as well as response to dissolution rates of carbonate sediments and rock to increased temperature and increased OA. More data will be needed on the actual biomass and reef areas involved.

This will be developed further in future studies.

According to this model the calcification rate (G) depends on five factors: 1. The level of light (Q) per day. This is an excellent feature. Q is easily calculated and drives Pnet which drives Gnet (Jokiel et al. 2014). Coral reef systems have evolved to efficiently use the photons that are available.

2. Sea surface temperature. There are existing data that allow linking temperature to coral growth and the use of fitting a second order polynomial to describe the growth response is well established (Buddemeier et al. 2008). It is more difficult to link degree heating metrics to the changes in growth and mortality that result from stress among the different species response or to account for thermal adaptation. The empirically derived relationship of mortality and reduced growth in relation to bleaching due to extreme temperatures has been modeled by the degree heating week or month metrics e.g. Their model shows the importance of annual temperature range as well as the bleaching threshold in determining the bleaching sensitivity and annual physiological performance of corals.

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3. Whether the species is fast or slow growing (Csp) Empirically derived.
4. The population of healthy corals (PH). Empirically derived.
5. The aragonite saturation state. The problem with use of omega is discussed above under the heading of Assumption 2. Although omega does not drive coral calcification it does show a correlation. omega is a dependent variable on G, pH, dissolution rate of the surrounding reef carbonates. Therefore the slope and intercept of the G vs. omega relationship varies widely over spatial and temporal scales. The authors have worked around this problem by using a mean of all observed values, which is appropriate for now. Correlation does not prove cause and effect, but can be used for a first approximation of the relationship until we can derive the needed data.

This paper shows creative innovations in the application of the Arrhenius equation to show enhancement of biological and chemical reactions with increasing temperature. The model takes into account thermal specialization among the different coral species adaption to local environment. The purpose of models is to synthesize available information in order to define relationships, predict and identify what data are needed to expand the model. The Evenhuis et al. model represents a great advancement in this area and should be published.

We thank Paul Jokiel for his very positive review, considered comments and recognition of work as both novel and state-of-the-art. To reflect the comments of Paul on the underlying assumptions of the model we included the suggested references to the manuscript to address concerns within Assumption 1, and the following text to the discussion to clarify that our model has been constructed to represent individual reef-building coral calcification rates and not community level coral reef net calcification dynamics:

In this study we simulate the calcification rate of individual reef-building corals to warming and ocean acidification. While the response of the coral reef maybe inferred from this response, as it is correlated, however we do not explicitly simulate coral reef cal-

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cification rate dynamics. This is the direction of future work as a better understanding emerges in order to link the response of individual coral colonies with community level ecological shifts in response to . Clearly the response of the entire coral reef to warming and ocean acidification is more complex, and capturing this requires inclusion of important species such as crustose coralline algae (CCA), which are more sensitive to OA condition than other reef building corals (Kuffner et al. 2008) and different dissolution processes, such as bio-erosion and mechanical damage (Silverman et al., 2009; Andersson and Gledhill, 2013). The consequently dissolution processes have not been included in our model and coral reefs will not dissolve until , while in reality net coral loss will likely occur much sooner (i.e. for values of). Clearly to confidently simulate and project the past and future response of the coral reef is beyond the scope of this study and remains an active area of research.

In response to Paul's comments on Assumption 2, "that calcification rate is driven by bulk water carbonate ion concentration," we have acknowledged (in the text) that given the variable observations of the correlation between calcification and saturation state (or by association CO_3 ion concentration) that exist, and that the possible drivers of calcification may include P_{net} and Ω_{arg} , we have chosen to use the average response in our model. We also acknowledge that a better understanding the relationship between P_{net} and Ω_{arg} is very important, and will require future experimental work.

Response to Anonymous Reviewer #2 (C2132)

Evenhuis et al. present a novel model of coral calcification taking into account bleaching and ocean acidification. The model accounts for healthy, pale, bleached and recovering coral states and is thoroughly confronted with data at multiple scales. The model is very simple and elegant in some aspects, detailed in others, while ignoring some other, perhaps essential factors. It reasonably reproduces literature observations and thus the conceptual model underlying the mathematical models makes sense. The topic is highly interesting for Biogeosciences audience and a revised version would therefore make a valuable contribution, but the present version needs significant mod-

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ification. One, the presentation of the model is not easy to follow. The notation might need attention for a biogeosciences audience. I also advice to clearly define units at an early stage. For instance, the population of healthy corals (P_{subH}) is presented in equation 1, but the units are not presented. At this stage it could be biomass, density, . . . There is quite some repetition of very similar equations (4, 5, 6) and (3, 7,10), this confuses the non-specialist reader.

We thank the reviewer for their positive comments. To address comments of readability and accessibility we have spent a substantial period of time rewriting parts of the manuscript, particularly the methods section, we have added a section on Energy Availability and included a table of the equations, variables, and determined and calculated values in the Appendix. We present the entire model and then proceed to explain the different parts of the model, we also believe that for a less mathematical audience the detail is sufficient that the equations prove inaccessible that the text will convey the necessary coral physiology background and how it relates to power and skill of the mathematics within this new model. We believe that this attention to detail will make the paper more accessible and easier for readers to follow. We have also consciously kept the detail in the text as this is a modeling paper and we are keen to demonstrate the steps, assumptions, and literature used to construct this model. While, we have not explicitly dealt with depth in this model, we also added a section on light and its treatment in the model, justifying our approach and highlighting the role depth may play in modulating SST ranges in the discussion. We have chosen also not to deal explicitly with depth as limited observations are available to include this given the complexity (see Discussion on the future use of RTMs and scales of variability associated with sea level over different timescales) and the desire to apply this model to future simulations for which current Earth System Models which are coarse resolution and don't resolve well the upper ocean at the reef scale.

Two, there are a number of miss references to figures and equations which confuse the reader. For instance, p. 200, line 27-28: Eq. 4.1 and 4.2 (these do not appear in the

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text) and the link with Figure 3 is unclear. Similarly, p. 202, line 1-3. Another example (there are more): p. 203: should Fig. 6 not be Fig. 5?; p. 211: should Fig. 11 not be Fig. 9.

Thank you. We have systematically worked through the text to ensure that all cross references are internally consistent.

Three, abbreviations are used without proper definition before: GBR (Great Barrier Reef) on p. 203; DHW (degree heating week?) on p. 190.

We have systematically worked through the text to ensure that all acronyms explicitly spelt out when introduced.

This paper needs to be carefully checked, rewritten for clarity and another round of evaluation before eventual publication. Strengths and weaknesses of your modeling approach could perhaps be stronger articulated

We have rewritten the paper for clarity and this has been carefully checked. We have also added additional text to the discussion to further discuss the strengths and weaknesses of our approach.

Response to Anonymous Reviewer #1 (non-published)

General: The description of the model is incomplete, confusing and contains errors (see below for details).

We have spent a substantial period of time rewriting and restructuring major parts of the manuscript to make it more accessible, and have added a section on Energy Availability and included a table of the equations, variables, and determined and calculated values in the Appendix to complete the description of the model.

Light and thus water depth has a major impact on the growth of corals. These two factors should be discussed in more detail.

Reviewer #1 is correct that depth plays a role in regulating energy to the corals. How-

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ever this effect is not very large as first maybe thought indeed studies have shown that corals acclimate quickly (<7-10 days) to changes in light conditions. For example, (Mass et al., 2007) reported constant rates of photosynthesis and calcification at 5m and 10m depths despite a 50% reduction in ambient light levels and Hennige et al. (2008) demonstrated that *Porites Lutea* from two sites and multiple depths regulate how much light is absorbed in order to maintain a constant load on their photosystem. Therefore in our model the assumption that corals are acclimated to their ambient light levels in order to saturate the photosystems to maximize photosynthetic efficiency and avoid photo-damage, and that this acclimation takes place rapidly, supports the published observations that net photosynthesis doesn't change significantly with decreasing light levels (see references the text below). This is not surprising given that corals have evolved efficiently use the photons available.

To address the concerns of the reviewer we have added a section on light to the methods section expanding on the comments above (below) we also acknowledge in the Discussion that our treatment of light could be further improved by the use of Radiation Transfer Model (RTM) but this a present is beyond the scope of this paper.

Added text: Irradiance () Our model assumes that corals are acclimated to their ambient light levels in order to avoid photo-damage, and that this acclimation takes place rapidly and the net photosynthesis doesn't change significantly with light levels. Consequently, in the model we assume that the energy available to the corals depends directly on the daily solar insolation, i.e. the amount of solar radiation (see equation in the Appendix).

Photosynthesis-Irradiance (P-I) curves for corals have been extensively studied and how their parameters change with local light environment has been well established (Anthony and Hoegh-Guldberg, 2003a; Chalker et al., 1983; Dubinsky et al., 1984; Mass et al., 2007; Porter et al., 1984). These studies show that there is a strong decrease in the saturation intensity as ambient light level decreases, which corresponds to an increase in the efficiency of photosynthesis. In addition, there are smaller de-

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creases in maximum photosynthesis and respiration. Laboratory experiments in which corals were transferred between different light levels have also shown that the response is very rapid i.e. it takes around a week for corals to adapt to a 10-fold change in light levels (Anthony and Hoegh-Guldberg, 2003a). The change in saturation intensity can be understood in terms of a trade-off between gains from photosynthetic capacity and losses from photo-damage. If the saturation intensity is much higher than the maximum ambient intensity the rate of photosynthesis is lower than it could be, and decreasing the saturation intensity will increase the overall energy budget available for growth. However, if an organism's saturation intensity is below the maximum ambient intensity the cell is damaged as the photosynthetic apparatus will experience long periods of saturation. Therefore, the optimum setting for the saturation intensity will be approximately the maximum ambient intensity. This line of reasoning has been used in models of phytoplankton (Geider et al., 1997).

These assumptions mean that in the model corals are never saturated (always on the linear part of the P-I curve) and that the net photosynthesis does not change with light levels. In other words, the exponential decrease in light that occurs with depth is offset by gains in efficiency from photo-acclimation. Clearly there are limits to this assumption as there will be a minimum level of light needed for photosynthesis. Nevertheless, there is evidence that this assumption holds when considering the community average of a coral living in typical reef conditions. For example, Mass et al. (2007) reported constant rates of photosynthesis and calcification at 5m and 10m depths despite a 50% reduction in ambient light levels and Hennige et al. (2008) demonstrated that *Porites lutea* from two sites and multiple depths regulate how much light is absorbed in order to maintain a constant load on their photosystem.

The English needs corrections here and there: this should be done by the co-authors (I guess native speakers!).

This concern has been addressed and the manuscript has been proof-read carefully to remove any glaring errors.

All remaining errors and typos have been addressed, further we have reorder the paper to start with the complete model and followed this by an explanation of the different parts that make up this equation.

Specific points: p.192, L8/9: the sea surface temperature (a, b) REMARKS: (1) sea surface temperature is denoted by T. (2) a and b are functions of T and other quantities. p.192, L9: the aragonite saturation state (g) REMARK: g is a function of the aragonite saturation state W p.194, L22: If $k = 0$ Eq.(2) simplifies to $W \approx 1 - 3.5 \approx 1$ REMARK: If $k = 0$ Eq.(2) simplifies to $W \approx 1 - (3.5 \approx 1)^2$ – or typo in Eq.(2)???

p.196 Eq.(3) REMARKS (1) d not explained (discussed only much later, p.215), (2) no value given for a_{max}

All of the above minor errors have been addressed

Three different sets of differential equations (Eqs. 4, 5, and 6) are presented for the same quantities (change in time of PH healthy, PR recovering, PP pale, and PB bleached corals). It is was not clear to me why different sets of equations are presented under headings 'Bleaching', 'Recovery from bleaching', and 'Growth constant'. The full model results from summing up the the three ride-hand-sides of Eqs. (4) to (6) and equate it to 1 left hand side. I find this presentation confusing and would prefer to present the complete model from the beginning and then discuss the parameterization of the various processes.

Remark: Given the model equations using matrix notation has its charm because the coupling between the equations is easy to recognize. However, four single equations might be easier to follow for less well mathematically trained readers.

While we respect the opinion of the reviewer, however we have continued to present the equations in their current form. But we have significantly reordered the text and added additional description to the manuscript to make it much easier for the reader to follow the concepts irrespective of the mathematics. p.200 Sentence does not make sense to me: 'As adapted range is the same for the three corals, T_{opt} the rates of the

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transition (healthy to pale, pale to bleached, bleached to dead) can be determined by fitting the model to the experimental observations for *P. damicornis*.'

Changed and clarified.

p.202: 'The coral growth term in the model has the highest uncertainty as it represents the combined effect of many processes.'

Changed to:

Coral population growth is the slowest of the population changes in the model and is very difficult to determine empirically; therefore it is associated with large uncertainty.

p.202: Eq.(6) gC should be the growth constant (not the bleaching constant). 'coral accumulation' might be a more appropriate term in this context. We agree that this was confusing and have renamed this term as the Population Growth Constant () as it is more than just accumulation; and have used in equation 1 only.

p.202 'In this work $K = 1$ (i.e. 100% carrying capacity).' This seems to imply that the various corals states (PH etc.) are measured in fraction of total coverage (%); this has to be properly explained.

Changed to:

In this work (i.e. 100% carrying capacity) assuming that the corals start at their maximum carrying capacity. However, there is scope to model external stressors that change the carrying capacity of a location, such as storm damage or sea-level rise, or the creation of habitat by allowing to vary temporally.

p.203 '... we selected the value of the growth constant (gC) to be 0.002 $d\text{A}\ddot{A}\ddot{A}1$, based on a synthesis of in situ published that report the return of coral coverage after a disturbance such as bleaching.'

We have added a reference to Table 2 to make it easier for the reader to follow.

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p.204 Eq.(7) is identical to Eq.(3): COPY & PASTE ERROR?

Fixed

Minor points: p.192, L5: from different from taxa -> from different taxa p.192, L8: The calcification rate is depends -> The calcification rate depends p.198, L3/4: correct: ' , and growth calcification are impaired' ' , and growth calcification is impaired' p.199 PB used in Eq.(4), however, symbol not properly explained p.200 'Collectively these recovery processes are modelled using the following set of 1st order differential equations (Eq. 5), which differ from Eq. (3) with the addition of an additional recovering state (PR).' You probably mean Eq. (4) and not Eq. (3). p.203, L16: GBR: explain abbreviation before using it

All minor issues have been addressed in the text

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