

"Nutrients attenuate the negative effect of ocean acidification on reef coral calcification in the Arabian Sea upwelling zone (Masirah Island, Oman)"

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We would like to thank the reviewers for commenting on our manuscript. Their supporting comments and ideas have substantially improved the scientific significance of our work. In line with the reviewers' comments and the editor recommendations, major changes have been made to our revised manuscript. General modifications include:

- Improved statistical robustness of the mean annual calcification data through addition of three further specimens (Table 2, Fig.9).
- Discussion of the sub-annual growth patterns is made internally, i.e., by comparing the calcification performance during the upwelling and non-upwelling season (line 321-362).
- More extensive discussion of the geochemical data (289-312).
- Reorganisation of paragraphs into other chapters for reaching a clear separation between results and discussion as well as between introduction and methods.
- Omission of a quantitative comparison of our data with growth data from the Indo-Pacific. In the revised manuscript, this approach has been replaced by a qualitative comparison of our data with an extended data set on *Porites* calcification from various Pacific and Atlantic reef sites (Fig. 9).
- Adjustment of the Abstract and the Conclusion.
- Change of the working title to:

„Calcification response of reef corals to seasonal upwelling in the northern Arabian Sea (Masirah Island, Oman)“

Detailed responses to all comments made by the reviewers and the editor are described point-by-point in the section below.

1. Editor comments:

1.1. ... "the manuscript should be refocused on the geochemical proxy data instead of the calcification data"

The geochemical proxy data is discussed more extensively in the revised manuscript (line 289-312). However, geochemistry remains a tool for establishing sub-annual chronologies of the calcification records and for assessing the influence of temperature on skeletal calcification only. The *Porites* calcification data represents the very first contribution to this topic for the Arabian Sea and the north-western Indian Ocean. For this reason, we are of the opinion that the focus of the manuscript should be kept on the calcification data.

1.2. ... "you rely heavily on low average saturation states in this region, however, there is minimal data to back this up in any of your regressions and plots"

To back up the presence of a temporarily low seawater aragonite saturation state (Ω_{sw}) at the sampling site, we included monthly-modelled Ω_{sw} to Fig.2 (Takahashi et al., 2014).

2. Reviewer # 1 (RC1):

- 2.1. *“Three replicate cores is just not enough to have robust statistics...Actually, the only way I see forward for the authors (besides getting more corals) is to completely re-frame the study based on the geochemistry.”*

Statistical robustness of the mean annual calcification data has been reached through addition of three further specimens (Table 2; Fig.9). A total of six specimens for estimating mean calcification performance at a site is in line with other coral growth studies from the literature (e.g., Lough and Barnes, 2000; Manzello et al., 2014).

- 2.2. *“I had no idea there was going to be Li/Mg geochemistry in this study based on the title and abstract.”*

We have added information on the application of Li/Mg and Ba/Ca geochemistry to the abstract (line 18).

- 2.3. *“I don't think it makes sense to compare the growth rates to just the GBR.”*

We fully refrain from the quantitative comparison of our data with growth data from the Indo-Pacific (GBR and Hawaii). Instead, we show a more qualitative comparison of our data with published *Porites* growth data (Fig.9). In this way, we provide a more global perspective, by showing published *Porites* growth data from Thailand, Western Australia, the Gulf of Mexico plus three other regions affected by upwelling, in addition to the previously presented data from the GBR and Hawaii. This approach fully supports our finding of low skeletal density and high extension growth of *Porites* from upwelling zones.

3. Reviewer # 2 (RC2):

Concerns:

- 3.1. *“Overall, an n of 3 is fairly small to make these growth assumptions with... growth is highly variable across locations and genotypes and thus would require a higher n to make stronger predictions/estimates.”*

The statistical robustness of the mean annual calcification data is now sufficient through addition of three further specimens (Table 2). The total sample size of six corals for a site is in line with other coral growth studies from the literature (e.g., Lough and Barnes, 2000; Manzello et al., 2014).

- 3.2. *“Coral growth is reliant on a lot of different biological processes that are largely ignored throughout this text.”*

In the revised manuscript, we describe in detail that photosynthesis by algal symbionts provides most of the energy for the coral to grow (line 40-45, 341-344). This highlights the variety of biological processes controlling photosynthetic efficiency to also affect coral growth. Furthermore, we introduce and discuss the process of active pH and Ω_{Arag} upregulation within the corals' calcification fluid (line 47-52, 358-362, 391-395). We therefore do believe to have adequately addressed major controlling factors on coral calcification, i.e. SST, light, nutrients, pH and Ω_{Arag} (Courtney et al., 2017; Ross et al., 2019).

- 3.3. *„While calcifying fluid is discussed, the authors never actually make these measurements.”*

Indeed, we did not perform combined analyses of B/Ca and $\delta^{11}\text{B}$ on our specimens in order to estimate the Ω_{cf} of the calcification fluid. Recent publications, however, have led us to consider Ω_{cf} as a major parameter controlling skeletal density (Mollica et al., 2018). Considering this, it is essential for us to discuss the variability in skeletal density with regard to possible influences of Ω_{cf} . Systematic measurements of B/Ca and $\delta^{11}\text{B}$ are currently underway in the frame of a cooperation beyond the group of co-authors for this manuscript.

- 3.4. *“Further, the authors ignore how much variability in coral growth there is within a genus or even a species and over-estimate the reliance of growth on SST. Along these same lines, coral cores collected from the Pacific may not experience similar environmental conditions and may likely have different populations/species of Porites corals, thus comparison of the corals from this study with Pacific corals should be made with caution”*

In the revised version of the manuscript, we completely refrain from comparing our data with "theoretical values" based on temperature-calcification calibrations of *Porites* from the Indo-Pacific. Nonetheless, it should be noted that studies on Pacific *Porites* did explicitly make no difference between species (Lough et al., 2000)

- 3.5. *“While the satellite SST matched very well with in situ SST measurements, the other satellite phosphate and nitrate parameters were not similarly grounded in truth. Further, the lower resolution for these satellite products is concerning since nutrient values can be highly variable across a spatial gradient.”*

In the revised version of the manuscript we only present monthly resolved seawater nutrient data from Masirah Island (WOA18, Garcia et al., 2018) (Fig.2). Considering the excellent agreement to skeletal Ba/Ca records (line 209-211), we assume that the general pattern of monthly resolved WOA18 nutrient concentrations at the study site qualitatively reflect the intra-annual nutrient cycle of surface waters (Montaggioni et al., 2006). We are aware of temporal and spatial heterogeneities in nutrient distribution and discuss this based on variability between the Ba/Ca records across specimen (line 293-294).

- 3.6. *“Finally, because of the discussion of ocean acidification is a major component of this manuscript, it also may be valuable for the authors to also include carbonate parameters for the area (i.e., omega-aragonite, TA, pH, etc.).”*

In addition to the reference from Omer (2010) which gives information on the seawater Ω_{Arag} at Masirah Island in lines 98-100, we have added monthly-modelled data on seawater Ω_{Arag} in Fig.2 (Takahashi et al., 2014).

Minor edits:

Abstract

- 3.7. *“Lines 14-15: This statement is a bit of an overstatement. Calcification responses to changing environments is very well studied. If this is intended to be in terms of a specific type of environmental variation, then that needs to be clarified.”*

We have revised the sentence to read: “The calcification response of reef corals on rapid changes in Ω_{sw} and seawater nutrient concentrations is currently under discussion in coral science.”

Introduction

- 3.8. *“Line 29: Consider replacing ‘zooxanthellate’ with symbiotic.”*

We have replaced the word “zooxanthellate” by “symbiotic”.

- 3.9. *“Lines 36-37: This statement should be backed with the literature. Coral calcification is not highly debated; however, responses are highly variable. I recommend referencing several papers covering this here.”*

We have revised the sentence to read: “The responses of reef coral calcification on this rapidly changing environment are highly variable and remain contemporarily a matter of intense research.” and covered this statement with literature from Cornwall et al., (2021), Guan et al., (2020) and Hall et al., (2018).

- 3.10. *“Lines 50-52: This statement seems misplaced and should be incorporated better within the introduction. Additionally, recent reviews suggest different calcification responses in corals under global change (see Cornwall et al 2021, Global declines in coral reef calcium carbonate production under ocean acidification and warming, PNAS).”*

We have removed this sentence because variable responses in corals under global change are already addressed in the introduction where the reference to the work of Cornwall et al., (2021) is cited.

- 3.11. *“Line 54: savage disposal? Do you mean sewage?”*

We have revised the spelling mistake to “sewage”.

- 3.12. *“Lines 54-55: This is an incomplete statement.”*

We have revised the sentence to read: “Eutrophication can have both beneficial as well as detrimental effects on coral growth, however (Tomascik and Sander, 1985; Tomascik, 1990).”

- 3.13. *“Lines 55-56: Again, I suggest updating your language here to reflect more recent terminology of coral algal symbionts (see LaJeunesse et al. 2018, Systematic Revision of Symbiodiniaceae Highlights the Antiquity and Diversity of Coral Endosymbionts, Current Biology).”*

We have revised the sentence to read: “In general, reef corals are highly adapted to oligotrophic waters with micro-algae symbionts to allow an efficient use of essential nutrients and to outcompete other fast-growing biota on a reef whose growth is inhibited by the undersupply of nutrients (Barrot and Rohwer, 2012; LaJeunesse et al., 2018; Vermeij et al., 2010).”

- 3.14. *“Lines 66-68: These sentences could be a bit stronger to introduce this important topic in your introduction.”*

We have revised the sentence to read: “Understanding how coral calcification responds to rapid changes in seawater nutrient conditions and Ω_{sw} is critical for more accurate predictions on the persistence of reef habitats under the influence of global change.”

- 3.15. *“Lines 70-72: This statement would benefit from a clear connection of how calcification responses from upwelling locations can be applied to systems without upwelling.”*

We have revised the sentence to read: “This allows these regions to serve as natural laboratories to investigate the calcification response of reef corals to these multiple environmental stressors that are likely to affect global coral reefs in the near future (Camp et al., 2018; Wizemann et al., 2018).”

- 3.16. *“Lines 84-125: This section should be moved into the methods as a section describing the sites. A condensed version of this could be included in the previous paragraph to describe the sites if that is desired.”*

We have moved the chapter "Arabian Sea climate and oceanography" to the beginning of the methodology section in the revised version of the manuscript.

Methods

- 3.17. *“Lines 128-134: It sounds like these colonies were not collected in situ, rather collected as dead skeletons from the beach. What about differences in local conditions? If these corals were washed up on shore you don't really know what depth or location they came from? Also what years? How do you know when they washed up on the beach?”*

We have streamlined this text section in the revised manuscript to clarify that the specimens presented are collected as dead coral material from a storm deposit associated with cyclone Gonu in 2007 (Fritz et al., 2010) (line 120-122).

The original growth position of the specimens was 1-4 metres below sea surface, as coral growth at Masirah Island is limited to these very shallow waters (Glynn, 1993) (see line 116-117). Using colonies from shallow waters for estimating mean coral calcification for a site is in line with other growth studies in the literature, considering colonies grown in water depths of 1-6 metres (Lough and Barnes, 2000; Manzello et al., 2014; Mollica et al., 2018). Depth related variation in coral growth is generally not expected in this near surface zone (Schlager, 1992).

It should also be mentioned here that substantial discussion in the revised manuscript focusses on intra-annual variability of calcification with regard to seasonal environmental changes (line 321-362). Location factors are hereby to be neglected, as they remain uniform within a single specimen.

The detailed information about the calendar years represented in our records is marginal, as we establish generalized annual calcification records with monthly resolution from several years of the total record lengths (Multi-year monthly means). These generalised records represent the mean monthly calcification of *Porites* corals at Masirah Island during the more recent current era.

- 3.18. *“Lines 216-219: Unclear what these numbers and acronyms represent. Please rephrase in a clearer way.”*

We have revised the sentence to read: “A detailed chronological frame for the Li/Mg records was established with the aid of the generalized annual record of remote sensing SST data (JPL MUR, daily averaged 2003-2018) (Fig.2). Dates of seasonal SST extremes as well as dates of inflection points between consecutive seasons were assigned to corresponding data points of the Li/Mg records (see supplementary material, Fig.S2).” The newly appended supplementary Fig.S2 provides a detailed illustration on how the age model was developed.

- 3.19. *“Note on the standard corals: How do we know that the other corals are effective standards for comparison? Who is to say that they were not influenced by SST or OA? Or other factors?”*

We did not exclude the influence of environmental factors other than SST on the calcification of the Indo-Pacific reference corals (GBR and Hawaii) used for comparison in the preprint version of our manuscript at any point. Based on the highly convincing correlations with SST (bulk density: $r^2 = 0.49$, $p < 0.0001$; extension rate: $r^2 = 0.9$, $p < 0.0001$), we stated that calcification of these corals is “largely controlled” by water temperature (Lough and Barnes, 2000). However, we agree that our approach of applying the regressions from the Indo-Pacific reference dataset to predict calcification performance of *Porites* from the Arabian Sea possibly overstates the global validity of the causal relationship between SST and calcification. For this reason, we have omitted the use of “standard corals” in the revised manuscript and instead provide a qualitative comparison of our data to an extended dataset of *Porites* calcification reported in the literature from other reefs in the Atlantic and Pacific (Fig.9).

Results

- 3.20. *“Lines 248-249: Do these n refer to the number of transects for the measures?”*

These n referred to the number of years considered in the calculation of the mean annual and sub-annual (seasonally, monthly) calcification of individual specimens. In the revised manuscript, these numbers are presented in table form in order to provide a clear structure (Table 2).

Discussion

- 3.21. *“A lot of the current discussion is results. These should be moved to the results section and then the discussion can include more incorporation of implications/meaning of these results.”*

Thank you very much for this advice. We have moved several parts of the discussion (e.g., an updated version of Fig.9) to the results.

- 3.22. *“Lines 285-288: But don’t you expect biological variability?”*

This quantitative comparison of our data with data of *Porites* from the Indo-Pacific no longer appears in the revised version of our manuscript.

3.23. *“Lines 367-369: Split into two different sentences for easier reading.”*

We have revised the section to read: “This finding implies that there is no intensified upregulation of internal Ω_{cf} relative to Ω_{sw} during the non-upwelling seasons (McCulloch et al., 2017; DeCarlo et al., 2018; D’Olivo and McCulloch, 2017). As an explanation, we propose that internal upregulation processes of corals affected by seasonal upwelling are not capable to adapt completely to ocean chemistry change on a quarterly scale. As a consequence, a relatively low Ω_{cf} is maintained year-round so as to avoid high gradients to the external Ω_{sw} during southwest monsoonal upwelling.” (line 391-395)

3.24. *“Lines 414-433: This section is lacking incorporation of the current literature and needs some more grounding in terms of what is known and previous work.”*

This section underwent substantial reorganisation and is no longer available.

Figures

3.25. *“Figure 1: This is a really helpful figure to demonstrate this reef system, collection site, and the currents/upwelling, however, this figure could be made a bit clearer with a few updates as suggested here. There is a lot going on with colours so I recommend making your land either white or grey to make the focus of the map more on the reef locations. I also recommend selecting a different colour to represent the coral reef provinces with better contrast against the red and blue.”*

We have turned the colour of the land surface greyish to put more focus on the reef locations. The yellow colour of the coral reef provinces contrasts most strongly with the adjacent red and blue colours, which is why we consider it to be exceptionally suitable.

3.26. *“Figure 2/3: Please define NEM, SIM, SWM, and AIM in your figure captions.”*

We have defined the abbreviations in the figure captions.

3.27. *“Figure 3: please include what years were assessed in to calculate these monthly values.”*

The number of years included in calculating the monthly values (multi-year monthly means) are shown in Table 2 of the revised manuscript.

3.28. *“Figure 5: again, please include the years assessed in the monthly values.”*

The number of years included in calculating the monthly values (multi-year monthly means) are shown in Table 2 of the revised manuscript.

3. References

- Barrot, K.T., Rohwer, F.L.: Unseen players shape benthic competition on coral reefs. *Trends Microbiol.*, 20, 621-628, <http://doi.org/10.1016/j.tim.2012.08.004>, 2012.
- Camp, E.F., Schoepf, V., Mumby, P.J., Hardtke, L.A., Rodolfo-Metalpa, R., Smith, D.J., Suggett, D.J.: The future of coral reefs subject to rapid climate change: Lessons from natural extreme environments. *Front. Mar. Sci.*, 5, 1–21, <https://doi.org/10.3389/fmars.2018.00004>, 2018.
- Cornwall, C.E., Comeau, S., Kornder, N.A., Perry, C.T., van Hooidek, R., DeCarlo, T.M., Pratchett, M.S., Anderson, K.D., Browne, N., Carpenter, R., Diaz-Pulido, G., D’Olivo, J.P., Doo, S.S., Figueiredo, J., Fortunato, S.A.V., Kennedy, E., Lantz, C.A., McCulloch, M.T., González-Rivero, M., Schoepf, V., Smithers, S.G., Lowe, R.J.: Global declines in coral reef calcium carbonate production under ocean acidification and warming. *Proc. Natl. Acad. Sci. U. S. A.*, 118, 1-10, <https://doi.org/10.1073/pnas.2015265118>, 2021.

- Courtney, T.A., Lebrato, M., Bates, N.R., Collins, A., De Putron, S.J., Garley, R., Johnson, R., Molinero, J.C., Noyes, T.J., Sabine, C.L., Andersson, A.J.: Environmental controls on modern scleractinian coral and reef-scale calcification. *Sci. Adv.* 3, 1-9, <https://doi.org/10.1126/sciadv.1701356>, 2017.
- Garcia, H. E., Weathers, K., Paver, C. R., Smolyar, I., Boyer, T. P., Locarnini, R. A., Zweng, M. M., Mishonov, A. V., Baranova, O. K., Reagan, J. R.: World Ocean Atlas 2018, 4: Dissolved Inorganic Nutrients (phosphate, nitrate, silicate), 2019.
- Glynn, P.W.: Monsoonal upwelling and episodic *Acanthaster* predation as probable controls of coral reef distribution and community structure in Oman, Indian Ocean. *Atoll Res. Bull.*, 379, 1–66. <https://doi.org/10.5479/si.00775630.379.1>, 1993.
- Guan, Y., Hohn, S., Wild, C., Merico, A.: Vulnerability of global coral reef habitat suitability to ocean warming, acidification and eutrophication. *Glob. Chang. Biol.*, 26, 5646–5660, <https://doi.org/10.1111/gcb.15293>, 2020.
- Hall, E.R., Muller, E.M., Goulet, T., Bellworthy, J., Ritchie, K.B., Fine, M.: Eutrophication may compromise the resilience of the Red Sea coral *Stylophora pistillata* to global change. *Mar. Pollut. Bull.*, 131, 701–711, <https://doi.org/10.1016/j.marpolbul.2018.04.067>, 2018.
- LaJeunesse, T.C., Parkinson, J.E., Gabrielson, P.W., Jeong, H.J., Reimer, J.D., Voolstra, C.R., Santos, S.R.: Systematic Revision of Symbiodiniaceae Highlights the Antiquity and Diversity of Coral Endosymbionts. *Curr. Biol.*, 28, 2570-2580, <https://doi.org/10.1016/j.cub.2018.07.008>, 2018.
- Lough, J.M., Barnes, D.J.: Environmental controls on growth of the massive coral *Porites*. *J. Exp. Mar. Bio. Ecol.*, 245, 225-243, [http://doi.org/10.1016/s0022-0981\(99\)00168-9](http://doi.org/10.1016/s0022-0981(99)00168-9), 2000.
- Montaggioni, L.F., Le Cornec, F., Corrège, T., Cabioch, G.: Coral barium/calcium record of mid-Holocene upwelling activity in New Caledonia, South-West Pacific. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 273, 436-455, <https://doi.org/10.1016/j.palaeo.2005.12.018>, 2005.
- Ross, C.L., DeCarlo, T.M., McCulloch, M.T.: Environmental and physiochemical controls on coral calcification along a latitudinal temperature gradient in Western Australia. *Glob. Chang. Biol.*, 25, 431–447, <https://doi.org/10.1111/gcb.14488>, 2019.
- Schlager, W.: Sedimentology and sequence stratigraphy of reefs and carbonate platforms: A short course. *Am. AAPG Bulletin*, 34, <https://doi.org/10.1306/CE34551>, 1992.
- Tomascik, T., Sander, F.: Effects of eutrophication on reef-building corals. *Mar. Biol.*, 87, 143–155, [https://doi.org/10.1016/0198-0254\(87\)90298-6](https://doi.org/10.1016/0198-0254(87)90298-6), 1985.
- Tomascik, T.: Growth rates of two morphotypes of *Montastrea annularis* along a eutrophication gradient, Barbados, W.I. *Mar. Pollut. Bull.*, 21, 376–381, [https://doi.org/10.1016/0025-326X\(90\)90645-O](https://doi.org/10.1016/0025-326X(90)90645-O), 1990.
- Tudhope, A.W., Lea, D.W., Shimmield, G.B., Chilcott, C.P., Head, S.: Monsoon climate and Arabian Sea coastal upwelling recorded in massive corals from southern Oman. *Palaos*, 11, 347-361, <https://doi.org/10.2307/3515245>, 1996.
- Vermeij, M.J.A., van Moorselaar, I., Engelhard, S., Hörnlein, C., Vonk, S.M., Visser, P.M.: The effect of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. *PLoS One*, 5, 1-8, <https://doi.org/10.1371/journal.pone.0014312>, 2010.
- Wizemann, A., Nandini, S.D., Stuhldreier, I., Sánchez-Noguera, C., Wisshak, M., Westphal, H., Rixen, T., Wild, C., Reymond, C.E.: Rapid bioerosion in a tropical upwelling coral reef. *PLoS One*, 13, 1–22, <https://doi.org/10.1371/journal.pone.0202887>, 2018.