

Web links to the author's journal account have been redacted from the decision letters as indicated to maintain confidentiality.

21st Jul 20

Dear Dr Dove,

first of all, please allow me to apologise for the delay in sending a decision on your manuscript titled "Warming and acidification will drive the loss of carbonate reefs in the near future". It has now been seen by three reviewers, whose comments are appended below. You will see that they find your work of some potential interest. However, they have raised quite substantial concerns that must be addressed. In light of these comments, we cannot accept the manuscript for publication, but would be interested in considering a revised version that fully addresses these serious concerns.

We hope you will find the reviewers' comments useful as you decide how to proceed. Should additional work allow you to

- address these criticisms (that is, either to incorporate the suggestions or provide a compelling argument why the point made by the reviewer is not valid, or relevant to the editorial threshold as outlined below)

AND

- meet our editorial thresholds as outlined below,

then we would be happy to look at a substantially revised manuscript.

In the following, we list our main editorial concerns.

****Editorial threshold 1: present compelling novel insights into the effects of the individual and combined changes in temperature and carbon dioxide levels on an experimental coral reef over a period of 18 months.

****Editorial threshold 2: carefully consider and discuss the implications of these insights for natural coral reefs, taking into account the caveats and questions raised by the reviewers.

****Editorial threshold 3: analyse and clarify the reasons for any discrepancies between your study and earlier work in terms of the influence of CO₂ levels on net ecosystem calcification.

In addition, please address all the points raised by the reviewers.

However, please bear in mind that we will be reluctant to approach the reviewers again in the absence of substantial revisions.

If the revision process takes significantly longer than three months, we will be happy to reconsider your paper at a later date, as long as nothing similar has been accepted for publication at Communications Earth & Environment or published elsewhere in the meantime.

We understand that due to the current global situation, the time required for revision may be longer than usual. We would appreciate it if you could keep us informed about an estimated timescale for resubmission, to facilitate our planning. Of course, if you are unable to estimate, we are happy to accommodate necessary extensions nevertheless.

We are committed to providing a fair and constructive peer-review process. Please do not hesitate to contact us if you wish to discuss the revision in more detail.

Please use the following link to submit your revised manuscript, point-by-point response to the referees' comments (which should be in a separate document to any cover letter) and any completed checklist:

[link redacted]

** This url links to your confidential home page and associated information about manuscripts you may have submitted or be reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage first **

Please do not hesitate to contact me if you have any questions or would like to discuss the required revisions further. Thank you for the opportunity to review your work.

Best regards,

Heike Langenberg, PhD

Chief Editor
Communications Earth and Environment

On Twitter: @CommsEarth

EDITORIAL POLICIES AND FORMAT

If you decide to resubmit your paper, please ensure that your manuscript complies with our editorial policies and complete and upload the checklist below as a Related Manuscript file type with the revised article:

Editorial Policy Policy requirements

For your information, you can find some guidance regarding format requirements summarized on the following checklist:

Communications Earth &

Environment formatting checklist

REVIEWER COMMENTS:

Reviewer #1 (Remarks to the Author):

The results are based on long-term (> one year) culture of coral reef organisms, and would have interesting implications for coral reef community in the future. However, in terms of reef growth, I have to say I have major reservation on the paper.

The authors tried to mimic shallow-water coral reef systems to discuss the reef growth potential in the future. I, however, question if the system represents the shallow-water reef system correctly. The composition of sediment is particularly important as Mg-calcite tend to dissolve more than aragonite and could buffer the effect of ocean acidification (Yamamoto et al., 2012, Biogeosciences). What I suppose the authors should have mimicked was shallow reef crest or reef edge systems that includes abundant benthic foraminifers and coralline algae (often in algal-ridge form) that are composed of high Mg-calcite.

Because the authors neglected benthic foraminifers, I suggest the authors to investigate the behavior of coralline algae. They showed integrated data for calcifying macroalgae that include crustose coralline algae (high-Mg calcite) and Halimeda (aragonite) (Fig. 2d). Separating these might show the role of Mg-calcite in acidified seawater and have implications for shallow-water reef systems.

Perhaps I may be misunderstanding, but data in Figure 2 and 3 looked show contradictory results. In Figure 2a NEC showed the highest values for BAU pCO₂. But in Figure 3a daytime NEC showed the highest value for warm and low pCO₂ conditions, and in Figure 3c nighttime NEC showed the highest value for warm and high Omega (i.e., probably lower pCO₂) conditions. This means warm and low pCO₂ (BAU temperature) could show the highest NEC.

Finally, the title is less informative and may not help readers understand the contents at a glance. What the authors did should have more interesting scientific outcomes.

Reviewer #2 (Remarks to the Author):

The study tracks changes in net ecosystem calcification (NEC) and benthic cover by an experimental coral reef community over 18 months under projected future ocean temperatures and acidification. The treatments expose a mixed community to present day (PD) and elevated (BAU) T, elevated pCO₂ and combined elevated T and pCO₂. The experiments are carefully executed with a thorough statistical treatment of the data. Results are fascinating in that they are not entirely expected: for example, NEC is elevated under BAU pCO₂ conditions relative to PD conditions between June 2015

and Feb 2016, presumably as PAR increases over that time period. However, the combination of elevated pCO₂ with elevated temperature, a more realistic scenario than either variable alone, causes NEC to plummet. This is really the take home message of the paper: that interactive effects of pCO₂ and temperature are much more dramatic and concerning than the effect of pCO₂ (ocean acidification) alone.

Manipulation experiments are a valuable tool with which to test hypotheses. However extrapolation to reality is tricky and this is where the paper should err on the side of caution more than it does. In particular, the nature and timing of the connection between NEC and reef-building is assumed to be known. Consequently the authors extrapolate the finding of reduced NEC to an immediate reduction in reef growth, and thus inability of reefs to “keep up” with sea level rise. This is the main thrust of the paper, the title, the abstract and the conclusion. Yet, modern coral reefs make far more calcium carbonate than they actually need for reef growth and much more is either lost, or filling up lagoons than is actually used. Reefs grow from dead coral rubble, often piled up during storms, not from live actively growing corals. So the real question is: if reefs stop producing new calcium carbonate tomorrow, how long can they continue to grow? I don’t believe the answer is known but it is extremely relevant to the consequences of this study and deserves very careful consideration. At minimum the authors should scale back their assertion that reduced NEC means immediate and significant reduction in reef growth.

The timescale of the experiments is short and the trajectory very direct compared with the timescale and trajectory over which reef temperatures and pH will achieve BAU levels. This is one of the drawbacks of manipulation experiments for they do not allow for adaptation, acclimation or recovery, as has been noted on real reefs in the wild. A discussion on this aspect with reference to recent findings of acclimation and adaptation would go a long way toward strengthening the paper. My last comment relates to the impact of flow on NEC and benthic cover composition. The experiments do not include flow as a variable but in nature, flow is a critical determinant of benthic community composition of reefs and both modulates and exacerbates the community response to temperature and acidification. The effect is both physiological allowing for exchange of nutrients CO₂ and oxygen, and physical in that low flow exacerbates heating and pH changes, whereas high flow modulates them. A discussion on this aspect, again with reference to recent reports from field observations would strengthen the discussion.

A recent paper by Shamberger et al., in L&O reports low NEC values from a low pH coral reef environment with anomalously high coral cover, and may be relevant here.

Reviewer #3 (Remarks to the Author):

Overall

This is an impressively executed study looking at the impact of end-of-century, business-as-usual warming and ocean acidification on coral reef mesocosms using a unique, long-term (18 month) experiment. This manuscript will likely be acceptable for publication once the authors address my points below in a major revision.

Big points

1) This mesocosm study herein comes to essentially the same conclusion as the Perry et al. 2018 Nature paper that used in situ benthic cover and fish data from the Caribbean and Indian Ocean. Namely, future reefs will drown with sea level rise. The Perry study came to the conclusion that reefs will drown as a result of the ecological degradation and loss in live coral cover that has taken place over the past 30-40 years. The fact that differing studies using different approaches to assess reef CaCO_3 budgets (census-based vs TA flux) both predict a future of drowned reefs need to be highlighted and discussed.

2) The decline in NEC with ocean acidification is driven by an increase in dissolution. The authors gloss over the mechanism behind what may be driving this, but seem to attribute this to increased sediment dissolution. There is little discussion about the role of biologically-mediated dissolution versus abiotic dissolution. This is despite a prior paper by some of the authors (Reyes-Nivia et al. 2013 GCB) that claimed that dissolution of coral fragments was all biologically driven and that abiotic dissolution did not occur. As the authors are aware, one of the drawbacks of the TA flux techniques is that it is a black box as to what is actually causing increases in TA. What about the potential role of euendolithic algae or some other infauna that utilizes chemical means to dissolve reef carbonates? Please include a discussion of possible mechanisms behind the increased dissolution and what can cause this. There is little mention of the growing literature (aside from Schonberg review paper and Erye sand paper) of the growing literature focusing on OA effects on coral reef substrates (reef frameworks, coral heads, rubble, sediment etc).

3) Increased pCO_2 led to increased NEC. Unless I'm missing something, this is counter to what has been generally found – high CO_2 leads to depressed NEC. Please include a clearer, thorough discussion why your result differs from what has been observed in past studies.

4) One of the most impressive feats of this study is that the authors kept it going for 18 months. Since ocean acidification experiments started, it has been pointed out that experiments are not realistic because they are over such a short time period and thus do not consider adaptation/acclimatization. While 18 months certainly cannot truly answer the question of whether or not adaptation to acidification can occur, this work is an important step to addressing the issue of very short acidification experiments. You should explicitly discuss this and how you did not see any evidence of resistance or resilience to warming or CO_2 over a year and a half.

Specific comments

1) P1, L22. Please reword. This makes it seem like the onus of recovery rests with the corals. I.e., the corals need to act to save themselves and reverse trend

2) P4, L3. This is first mention of high-latitude reefs. Need a discussion on why this matters for climate and OA impacts. You should mention characteristics of high-lat reefs (reduced species, corals at environmental limits, more prone to climate impacts etc.). I suggest putting this in paragraph 3 of the intro

3) P4, L17. Insert “relative to controls.” at the end of the sentence.

4)P4 L28-30. Please explain this statement so the reader can follow your logic.

5)P5, L21. No Figure 4

6)P5, L24-25. I don't think Figure 2 supports this statement

7)P6, L3. Increased cover of what calcifiers? Corals and coralline algae? Or maybe just corals as you said the winter bloom of *Halimeda* did not raise NEC...

8)P6, L21. Suggest rewording to "...has the potential to increase the accretion-erosion threshold to ~50% coral cover."

9)P6, L23. Macroalgae misspelled

10)P6, L25. Canopy makes sense for a forest ecosystem, but I don't think this term translates to coral reef. The structure created by corals is much different than a canopy. I'd replace as "3D-structure"

11)P6, L26-27. How do these rates compare with Perry et al 2018 rates? I'm curious because this is an old study

12)P7, L9. Same comment about canopy as #10

13)P8, L1. Change erosion to dissolution. You measured dissolution, not erosion. The terms are not interchangeable.

14)P8, L9-13. Compare/contrast other studies. Need much more discussion about finding that NEC increased with increased pCO₂.

15)P8, L22-23. Not clear. Where is this shown?

16)The summary paragraph feels like it starts to devolve into boilerplate climate change jargon. I'd remove phrases like 'run-away climate change' and 'easy fixes'. I feel this takes away from the results of all the hard work you put in and dilutes it with these vague activist platitudes.

17)P9, methods. AS I'm sure you know, your study is pseudo-replicated sensu Cornwall and Hurd 2016 (REF 55) because you use one sump tank for CO₂ dosing and thus your individual mesocosms are technically not independent. Please include a sentence or two stating this caveat.

18)P10, L30. Total pH scale is the best practice and should be used

19)P11, L4. Said seawater scale, but now NBS. Should be using total scale

20)Figure 2 legend. Insert 'on' between warming and net in title. The 'and' between *Seriatopora* and *Stylophora* shouldn't be italicized

References

Perry C, et al (2018) Loss of coral reef growth capacity to track future increases in sea-level. *Nature* 558:396-400

Response to Reviewers

Reviewer number: 1

The authors tried to mimic shallow-water coral reef systems to discuss the reef growth potential in the future. I, however, question if the system represents the shallow-water reef system correctly. The composition of sediment is particularly important as Mg-calcite tend to dissolve more than aragonite and could buffer the effect of ocean acidification (Yamamoto et al., 2012, Biogeosciences). What I suppose the authors should have mimicked was shallow reef crest or reef edge systems that includes abundant benthic foraminifers and coralline algae (often in algal-ridge form) that are composed of high Mg-calcite.

We collected sediments at our reef location on the shallow reef slope (the outer margin of the reef facing into the Wistari Chanel). Those sediments include all the naturally occurring organisms found in the sediments, including foraminifers. According to Maxwell et al. (1964), “The sediments of Heron Island reef are derived mainly from *Lithothamnion*, *Halimeda*, corals, molluscs and foraminifer.”

Our initial grain sizes occurred in the following ratios: 2% (<0.250mm), <42% (<1mm), <42% (<2mm), and 14% (>4mm) (Dove et al. unpublished). In Maxwell et al. (1964), grain sizes of 0.250 to 2mm contain an abundance of foraminifera and *Lithothamnion*.

We have changed the text (p. 3, lines 1-5),

“Carbonate frameworks were allowed to be further built-up by the infilling of sediments created by a range of organisms including the calcifying alga, *Halimeda*^{17,18}, and organisms such as foraminifera and *Lithothamnion* that are abundant in the sediments collected from the shallow reef slope of Heron Island¹⁹”.

Because the authors neglected benthic foraminifers, I suggest the authors to investigate the behavior of coralline algae. They showed integrated data for calcifying macroalgae that include crustose coralline algae (high-Mg calcite) and *Halimeda* (aragonite) (Fig. 2d). Separating these might show the role of Mg-calcite in acidified seawater and have implications for shallow-water reef systems.

We did not neglect the benthic foraminifera within our experiment. Benthic foraminifera are included within the sediments that naturally occur at our location of interest —the shallow reef slope (~5m depth) of Heron Island (please see previous comment).

The principal goal of our study is to examine ecosystem responses to the dual impact of ocean warming and acidification on net ecosystem calcification. In this way, it was not our intention to disentangle the role of each individual organism and their specific responses. The response of these organisms (such as crustose coralline algae) are included in the collective net responses of the ecosystem, which include buffering of the acidification levels by dissolving CaCO₃ in whatever form it occurs and the uptake of CO₂ by photosynthetic organisms (e.g. Figure 2). We go beyond many experiments in so far as we do not fix the pCO₂ in the mesocosm tank, but only upstream to allow organisms within the ecosystem to buffer and alter observed pCO₂ levels.

Perhaps I may be misunderstanding, but data in Figure 2 and 3 looked show contradictory results. In Figure 2a NEC showed the highest values for BAU pCO₂. But in Figure 3a daytime NEC showed the highest value for warm and low pCO₂ conditions, and in Figure 3c nighttime NEC showed the highest value for warm and high Omega (i.e., probably lower pCO₂) conditions. This means warm and low pCO₂ (BAU temperature) could show the highest NEC.

The results presented in the three figures are not contradictory. Figure 2 (now Figure 3) defines the treatment as it is applied in the upstream sump, whereas Figure 3 (now Figure 4) details the conditions directly measured within the experimental tank. Figure 1 (now Figure 2) shows that large reductions (~50% decline) in pCO₂ occur under RCP8.5 acidification treatments at mid-day. This biotic mitigation of the pCO₂ conditions render values more similar to the present day control and result in comparatively high NEC. Notably, this reduction is not measured for the 7:00 daytime measurement, which result in high pCO₂ (e.g. 1000 ppm) and low NEC.

Please see the following statements within the manuscript that highlight these concepts,

“The typical age of water parcels in shallow seaward facing reef habitat is on the order of a few hours²⁶. To accommodate these retention times and allow reef organisms to influence the water chemistry²⁷, CO₂ was only controlled in large (8000L) upstream sumps with downstream tanks (300L) containing experimental reefs turned-over once per hour.” (p. 3, line 7)

“Ecosystem components (e.g., macroalgae, seagrass) may act as a buffer against acidification, with the suggestion that algal communities may benefit from increased seawater pCO₂, take up CO₂, and lessen the impact of ocean acidification on downstream organisms and structures²⁷.” (p. 3, line 21)

“Sump, as opposed to tank pCO₂, was controlled to allow organisms and their biology to influence in-tank pCO₂.” (p. 11, line 5)

Finally, the title is less informative and may not help readers understand the contents at a glance. What the authors did should have more interesting scientific outcomes.

We have changed our title so that it emphasizes what we have accomplished through our long-term experiment that cannot be accomplished in the field or via ecological modelling: “Uncoupling calcification from calcifier biomass leads to rapid reef decline”.

By experimentally collecting NEC over the long term, we are able to show that the cover (biomass) of calcifiers is uncoupled from rates of reef calcification under our scenario. The combined impact of acidification and temperature has an additional impact on daytime calcification that is separate to that associated with the loss of calcifying organisms on the reef. It is this relationship that demonstrates that the collective reef response to the synergistic impact of acidification and temperature is distinct to responses that can be modelled based on sum of parts assessments.

Reviewer number: 2

Manipulation experiments are a valuable tool with which to test hypotheses. However extrapolation to reality is tricky and this is where the paper should err on the side of caution more than it does. In particular, the nature and timing of the connection between NEC and reef-building is assumed to be known. Consequently the authors extrapolate the finding of reduced

NEC to an immediate reduction in reef growth, and thus inability of reefs to “keep up” with sea level rise. This is the main thrust of the paper, the title, the abstract and the conclusion. Yet, modern coral reefs make far more calcium carbonate than they actually need for reef growth and much more is either lost, or filling up lagoons than is actually used. Reefs grow from dead coral rubble, often piled up during storms, not from live actively growing corals. So the real question is: if reefs stop producing new calcium carbonate tomorrow, how long can they continue to grow? I don’t believe the answer is known but it is extremely relevant to the consequences of this study and deserves very careful consideration. At minimum the authors should scale back their assertion that reduced NEC means immediate and significant reduction in reef growth.

There are two balances at play in calcium carbonate accumulation at a given location:

1. net NEC (calcification – dissolution)
2. net import (import – export)

We measure the former, but we discuss how the latter can influence outcomes,

“Over the last 6000 years, modern coral reefs have been sustained under little ($<0.1\text{m } 100\text{yr}^{-1}$) to no sea-level rise⁶ because the net chemical balances of CaCO_3 (NEC) have been in equilibrium with net physical export of CaCO_3 from reefs⁷”. (p. 2 line 8)

“Biological agents of erosion, however, retain CaCO_3 within the reef infrastructure and operates as new foundation for reef construction²⁸, whereas, the chemical loss of CaCO_3 from reefs directly counters the production of CaCO_3 by key reef calcifiers”. (p.3 line 15)

Importantly, we do not dispute the claim that modern reefs can build-up at faster rates than we currently observe. We use this fact in our calculations. Our calculations begin with past maximum accretion of $\sim 10\text{mm yr}^{-1}$ offered in the literature for a reef with 50% porosity ($\sim$ density of 1300 kg m^{-3}), head-space to grow into, high coral cover $>80\%$, and imported substrates (See p.1 line 8, then argument on p.6 & 7). If we hadn’t begun with these maximum values, we would not have produced a positive growth rate of 2.3mm yr^{-1} under the RCP8.5 scenario that has a net negative NEC compared to our optimal control of 60% calcifier cover under long-term chronic RCP8.5. The failure to keep up with sea level rise is not overestimated.

The reviewer seems to be assuming that under future conditions, there will always be a ready upstream source of CaCO_3 to build-up reefs as the sea level rises. The reviewer is ignoring that in some reef locations: (i) wave energy and/or off-reef currents facilitate the net export of CaCO_3 preventing vertical accretion by otherwise thriving coral communities, and (ii) that some sheltered reefs are reduced to non-carbonate coral communities because abiotic change has had a negative impact on NEC (Kleypas et al. 1999). We are proposing that surrounding dead carbonates that can form reefs (inclusive of above sea level structures such as island) due to favorable hydrodynamics are themselves threatened by future warming and acidification. Both by day and night, we show that high temperature combined with acidification drives significant levels of dissolution for a reef with a fixed living calcifiers biomass. We are not sure as to why the reviewer believes that we view reef destruction as immediate. We explicitly argue for a phased response that extends to hundreds (maybe thousands) of years, the period over which end of century RCP8.5 conditions or worse are likely to persist (please see p. 7, and Supplementary Figure 8). We simply argue that the response

will be more rapid and drastic than illustrated by studies that dismiss the synergistic impact of acidification and warming on these reefs.

In response to the reviewer's issues, we have moderated the following statements:

1. Rewritten the end of the abstract:

"The approach demonstrates a decoupling of calcifier biomass and calcification under the synergistic impact of warming and acidification, that combined with increased night-time dissolution, leads to accelerated declines in carbonate stocks. The experiment demonstrates the potential for lost NEC to constrain the ability of coral reefs to keep-up with sea level rise, possibly for thousands of years. Consequentially, instead of simply transitioning to alternate states that are capable of buffering coastlines, reefs are at risk of drowning leading to significant loss in ecosystem functions." (p. 1 line 19)

2. We have added a reference to a recent paper that support a rapid loss of dead reef structure following current heatwaves:

"A recent study has demonstrated that following a thermal stress event, the rate of dissolution of exposed CaCO_3 framework can be significantly greater than the calcification rates of living coral⁵¹. Evidence for rapid structural loss following present day heatwaves emphasizes the potential for catastrophic loss of carbonate substrates under chronic future warming and acidification". (p. 9, line 5)

3. We have rewritten our concluding remarks to better define what we mean by rapid:

"Our study suggests that reefs will erode more rapidly, than under previous estimates³⁸, as they transition to alternate reef states under unmitigated climate change." (p. 10, line 1)

The timescale of the experiments is short and the trajectory very direct compared with the timescale and trajectory over which reef temperatures and pH will achieve BAU levels. This is one of the drawbacks of manipulation experiments for they do not allow for adaptation, acclimation or recovery, as has been noted on real reefs in the wild. A discussion on this aspect with reference to recent findings of acclimation and adaptation would go a long way toward strengthening the paper.

To respond to the comment, we have added the following paragraph to the discussion (p. 9, beginning line 11):

"Some studies propose that corals will adapt to the new conditions improving the outcomes for reefs in ways that cannot be captured by short-term experiments. Against this notion, it is argued that the life cycles and generation times may be too long to facilitate this change⁵²; or that any mechanisms of rapid adaptation is only sustainable under reduced emission scenarios⁵³. Others argue that this can be achieved via transcription changes occurring in response to epigenetic memory⁵⁴. In such studies, bleaching susceptibility is often tied to mortality; however, in the present study and in observations of reefs impacted by significant recent marine heatwave events, mortality was not correlated to bleaching susceptibility⁹. The focus on adaptations that prevent bleaching in the face of climate change obscure the potential costs on both primary (extension) and secondary (densification) calcification, even if they prove to facilitate coral survival. Our study argues for a decoupling of calcifier biomass and calcification rates under warming and acidification, and suggests that any adaption amongst key calcifiers would need to both increase survival potential and rates of

calcification substantially above maximal rates observed in the past. The likelihood of such an outcome is poor, but reduces even further with observations regarding the ephemeral status of CaCO_3 deposition by scleractinian corals, and their survival without fossil representation through 14 million year subsequent to the Permian extinction event⁵⁵.

My last comment relates to the impact of flow on NEC and benthic cover composition. The experiments do not include flow as a variable but in nature, flow is a critical determinant of benthic community composition of reefs and both modulates and exacerbates the community response to temperature and acidification. The effect is both physiological allowing for exchange of nutrients CO_2 and oxygen, and physical in that low flow exacerbates heating and pH changes, whereas high flow modulates them. A discussion on this aspect, again with reference to recent reports from field observations would strengthen the discussion.

In response, we do discuss flow in so far as we apply a wavemaker to maintain high flow rates within our system to minimize negative effects associated with boundary layer formation. It is true these flow rates are kept constant across treatment, as there are only so many parameters we can include as variables.

We have added the following to the methods (p. 11 line 25):

“Each tank was fitted with a powerful wavemaker (JVP-202B, SunSun, Zhoushan, China) to minimize boundary layer effects that can have significant negative influence on the exchange of nutrients, CO_2 and O_2 ⁶².”

A recent paper by Shamberger et al., in L&O reports low NEC values from a low pH coral reef environment with anomalously high coral cover, and may be relevant here.

We thank the reviewer for pointing out this relevant reference, and have now included reference to Shamberger et al. (p. 8, line10):

“Based on in-field responses of sediments to acidification, Eyre et al.²⁵ recently argued that coral reefs will transition to net dissolving reefs. Another in-field study by Shamberger et al.⁴⁷ showed that 26% coral cover barely maintained positive NEC under long-term acidification conditions. Similarly, in our experimental reefs under RCP8.5 acidification, NEC was reduced relative to present day over the first half of the experiment (~6 months), but increased significantly towards the end of the experiment.”

Reviewer number: 3

Big points

1) This mesocosm study herein comes to essentially the same conclusion as the Perry et al. 2018 Nature paper that used in situ benthic cover and fish data from the Caribbean and Indian Ocean. Namely, future reefs will drown with sea level rise. The Perry study came to the conclusion that reefs will drown as a result of the ecological degradation and loss in live coral cover that has taken place over the past 30-40 years. The fact that differing studies using different approaches to assess reef CaCO_3 budgets (census-based vs TA flux) both predict a future of drowned reefs need to be highlighted and discussed.

Our study is quite distinct to that of Perry et al (2018), and whilst we both conclude that reefs will submerge under sea-level rise, we base these conclusions on distinctive arguments. Both studies include the conclusion that coral cover contributes to the ability of reefs to keep up with sea-level rise. However, Perry et al. do not include the synergistic effect of acidification and temperature on carbonate dissolution within their study—an effect that we find to be significant and in addition to the effect of warming only on coral cover and reef calcification. Perry et al. however, includes bioerosion by organisms like parrotfish that are excluded from our assessment. We attempt to align the two methods by saying that adding our effect to Perry et al’s past calculations of accretion–erosion thresholds would shift the coral cover threshold from ~10% to ~50%.

Perry concludes that to keep up with sea-level rise under RCP8.5, coral cover would need to average 60-70%. Clearly, if our additional effect is equivalent to ~40% cover, this pushes requirements to 100-110% coral cover.

We have added the following statement to the discussion:

“Similarly, but excluding the synergistic effects of warming and acidification, Perry et al³⁸ conclude that reefs would have to maintain 60-70% coral cover to avoid submergence under RCP8.5. Again, adding our 40% cover equivalence for loss of NEC due to the synergistic impacts of warming and acidification, shifts Perry et al.³⁸ submergence threshold to ~100% cover. Our study demonstrates how studies that only include the effect of warming significantly underestimate the potential rate of reef decline”. (p 7. Line 13)

2) The decline in NEC with ocean acidification is driven by an increase in dissolution. The authors gloss over the mechanism behind what may be driving this, but seem to attribute this to increased sediment dissolution. There is little discussion about the role of biologically-mediated dissolution versus abiotic dissolution. This is despite a prior paper by some of the authors (Reyes-Nivia et al. 2013 GCB) that claimed that dissolution of coral fragments was all biologically driven and that abiotic dissolution did not occur. As the authors are aware, one of the drawbacks of the TA flux techniques is that it is a black box as to what is actually causing increases in TA. What about the potential role of euendolithic algae or some other infauna that utilizes chemical means to dissolve reef carbonates? Please include a discussion of possible mechanisms behind the increased dissolution and what can cause this. There is little mention of the growing literature (aside from Schonberg review paper and Erye sand paper) of the growing literature focusing on OA effects on coral reef substrates (reef frameworks, coral heads, rubble, sediment etc).

We have added the following to the paper (p. 9 line 1):

“Additional to observed night-time impacts, NEC declines relative to present day were observed under RCP8.5 acidification and warming during the day. These declines likely relate to previous observations of increased dissolution of dead coral substrates by endolithic algae and photosynthetic microbes^{49,50}, as well as potential reduction in the calcification rates of surviving calcifiers that may direct energy acquired to biomass production and maintenance, as opposed to calcification⁴¹. A recent study has demonstrated that following a thermal stress event, the rate of dissolution of exposed CaCO₃ framework can be significantly greater than the calcification rates of living coral⁵¹. Evidence for rapid

structural loss following present day heatwaves emphasizes the potential for catastrophic loss of carbonate substrates under chronic future warming and acidification.”

3) Increased pCO₂ led to increased NEC. Unless I’m missing something, this is counter to what has been generally found – high CO₂ leads to depressed NEC. Please include a clearer, thorough discussion why your result differs from what has been observed in past studies.

This relates back to comments made by reviewer 1, and misses the fact that we only control pCO₂ in upstream sumps allowing the downstream ecosystem to manipulate conditions. In this way, at mid-day, pCO₂ conditions in RCP8.5 acidification treatment are buffered by the increase in photosynthesis driven by calcifying algae that prospered (increased in biomass) over time in these conditions (Figure 3d).

In the results, we observe that (p4 line 14):

“The individual effect of RCP8.5 acidification had a positive effect on NEC by day, but a negative effect by night (Figure 2). By contrast, reefs experiencing the combination of RCP8.5 temperature and acidification responded negatively at all time points relative to present day treatments (Figure 2).

And we relate this to (p. 5 line 3):

“The abundance of macroalgae, turf algae and/or cyanobacteria was observed to increase significantly in any treatment that increased either temperature and/or acidification over PD values (Figure 3d–f). In RCP8.5 acidification treatments, average midday in-tank pCO₂ were significantly less than upstream sump pCO₂ values (Figure 2).”

Our responses are different because through the course of time, ocean acidification was dissipated in the middle of day by an increased biomass of photosynthetic organisms. We have altered the relevant paragraph in the discussion to (p. 8, line17):

“Based on in-field responses of sediments to acidification, Eyre et al.²⁵ recently argued that coral reefs will transition to net dissolving reefs. Another in-field study by Shamberger et al.⁴⁷ showed that 26% coral cover barely maintained positive NEC under long-term acidification conditions. Similarly, in our experimental reefs under RCP8.5 acidification, NEC was reduced relative to present day over the first half of the experiment (~6 months), but increased significantly towards the end of the experiment”

4) One of the most impressive feats of this study is that the authors kept it going for 18 months. Since ocean acidification experiments started, it has been pointed out that experiments are not realistic because they are over such a short time period and thus do not consider adaptation/acclimatization. While 18 months certainly cannot truly answer the question of whether or not adaptation to acidification can occur, this work is an important step to addressing the issue of very short acidification experiments. You should explicitly discuss this and how you did not see any evidence of resistance or resilience to warming or CO₂ over a year and a half.

Reviewer 2 had a similar comment (see above), and in response, we have we have added a paragraph to the discussion (p. 9, beginning line 11) where we discuss explicitly how we did not see any evidence of resistance or adaptation to ocean and warming over the year and a half long experiment.

Specific comments

1) P1, L22. Please reword. This makes it seem like the onus of recovery rests with the corals. I.e., the corals need to act to save themselves and reverse trend

We have replaced the statement (p.1, line 19):

“The approach demonstrates a decoupling of calcifier biomass and calcification under the synergistic impact of warming and acidification, that combined with increased night-time dissolution, leads to accelerated declines in carbonate stocks.”

2) P4, L3. This is first mention of high-latitude reefs. Need a discussion on why this matters for climate and OA impacts. You should mention characteristics of high-lat reefs (reduced species, corals at environmental limits, more prone to climate impacts etc.). I suggest putting this in paragraph 3 of the intro

We have removed the word “high latitude” and replaced with “diverse and complex” because Heron Island may not be considered a high latitude reef relatively speaking. Our study focussed on a reef system within the Great Barrier Reef that has high coral cover and diversity relative to many low latitude coral reefs outside of the Coral Triangle.

3) P4, L17. Insert “relative to controls.” at the end of the sentence.

Inserted statement as requested.

4) P4 L28-30. Please explain this statement so the reader can follow your logic.

We have added missing Figure reference for first sentence and explained the key observation using *Fungia* as an example of a coral that was visibly the first to bleach but amongst the long-term survivors: (p.4, line 26):

“Coral bleaching under the combination of RCP8.5 temperature and acidification occurred before the RCP8.5 temperature-only treatment (Figure 3c). However, greater sensitivity to bleaching amongst taxa was not found to be an indicator of coral thermal tolerance (e.g. *Fungia* is first to bleach but amongst survivors) (Figure 1, Supplementary Figures 1, 2, Supplementary Table 2)”.

5) P5, L21. No Figure 4

Corrected to appropriate Figure in new version.

6) P5, L24-25. I don’t think Figure 2 supports this statement

Figure reference corrected in new version.

7) P6, L3. Increased cover of what calcifiers? Corals and corraline algae? Or maybe just corals as you said the winter bloom of *Halimeda* did not raise NEC...

In our model, calcifiers include hard coral & calcifying macroalgae, as defined in the figure caption and the specification of the model parameters within the methods.

8) P6, L21. Suggest rewording to “...has the potential to increase the accretion-erosion threshold to ~50% coral cover.”

Reworded as requested.

9) P6, L23. Macroalgae misspelled

Corrected.

10) P6, L25. Canopy makes sense for a forest ecosystem, but I don't think this term translates to coral reef. The structure created by corals is much different than a canopy. I'd replace as “3D-structure”

Reworded as requested.

11)P6, L26-27. How do these rates compare with Perry et al 2018 rates? I'm curious because this is an old study

We believe the “old” reference the reviewer is referring to is Buddemeir & Smith (1988). Buddemeir & Smith (1988) propose the density of a 50% reef with diverse cover as $\sim 1300 \text{ kg m}^{-3}$, whereas Perry et al. (2018) appear to refer to the Smith & Kinsey (1976) estimate of $\sim 1000 \text{ kg m}^{-3}$. Our rates are not directly comparable to those of Perry et. al. because we measure different aspects of reef change (please see below).

The calculations of Perry et al. (2018) are quite different to ours. Perry et al. calculate max vertical accretion potential for reefs based on field studies of reef components (coral assemblages and bioeroding communities), converting % cover to $G (= \text{kgCaCO}_3 \text{m}^{-2} \text{yr}^{-1})$, then G to current vertical accretion based on estimates of reef porosity. They appear to follow Smith & Kinsey (1976), where $4 \text{ kgCaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ is deemed equivalent to 3–5 mm per year for a diverse reef given it a density of $\sim 1000 \text{ kg m}^{-3}$. They argue that, because they ignore the physical loss of carbonates, current vertical accretion rates are maximum potential rates of accretion for each reef. The maximal rates they give vary between locations, but range from -0.84 to 4 mm yr^{-1} for reef with variable coral cover that averages out at $\sim 20\%$.

Perry et al. (2018) then calculates future potential vertical accretion rates by varying coral cover and sea level rise (SLR) estimates under RCP4.5 and RCP8.5. Here, they basically calculate that under RCP8.5, coral cover would have to increase to 60–70% to prevent submergence.

Our study increases % cover estimate required to avoid submergence from Perry et al. (2018) estimates. We argue that if you add the dissolution driven by the synergistic impact of acidification and warming (Perry does not include this aspect in his calculation), then Perry's accretion–bioerosion threshold shifts from 10% cover to 50% without sea level rise, which would ultimately shift the estimates of percent cover required to avoid submergence under Perry's calculations.

Our calculations of risk of submergence are only based on the effects monitored in our experiment that exclude major bioeroders (e.g. parrotfish), which were the principle agent of erosion in Perry et. al. 2018.

We assume estimates of past maximal rates of 10 mm yr^{-1} for a 50% porous reef that is covered by $>80\%$ coral with head space to grow based on Buddemeier and Smith (1988). Based on Buddemeier

and Smith (1988), our optimal high diversity reef has a density of $\sim 1300 \text{ kg m}^{-3}$ which we use to covert lost $\text{kg m}^{-2} \text{ y}^{-1}$ to mm yr^{-1} (Table 1). We calculate the net dissolution associated with both the abiotic effect and the additional biotic effect of reducing cover from 60 (maximum cover observed in our system) to 10% to produce optimistic estimates of max vertical accretion of $\sim 2.3 \text{ mm yr}^{-1}$ under RCP8.5 (as a reductions from past 10 mm yr^{-1} estimates). Despite their optimistic nature and the fact that they do not include bioerosion attributable to parrotfish, they are nonetheless significantly lower than literature-based estimate of SLR (on the eastern seaboard of Australia) under RCP8.5 of $5\text{--}15 \text{ mm yr}^{-1,37}$.

See above for additions to text.

12)P7, L9. Same comment about canopy as #10

Reworded as requested.

13)P8, L1. Change erosion to dissolution. You measured dissolution, not erosion. The terms are not interchangeable.

Reworded as requested.

14)P8, L9-13. Compare/contrast other studies. Need much more discussion about finding that NEC increased with increased pCO_2 .

Please see previous comments above.

15) P8, L22-23. Not clear. Where is this shown?

Importantly, our calculations also include the potential mitigation of mid-day pCO_2 by an enriched macroalgal community²⁷ and we have clarified this point within the manuscript.

16) The summary paragraph feels like it starts to devolve into boilerplate climate change jargon. I'd remove phrases like 'run-away climate change' and 'easy fixes'. I feel this takes away from the results of all the hard work you put in and dilutes it with these vague activist platitudes

We have replaced "run-away" with "unmitigated" and have toned-down the final statement:

"The conclusions strengthen the call for achieving the goals of the Paris Climate Agreement as a matter of global emergency".

17)P9, methods. AS I'm sure you know, your study is pseudo-replicated sensu Cornwall and Hurd 2016 (REF 55) because you use one sump tank for CO_2 dosing and thus your individual mesocosms are technically not independent. Please include a sentence or two stating this caveat.

We have dealt with the pseudo-replicated caveat. Our sumps are very large (8000L), and the flow rates through these sumps are so great that interaction between the walls of the sump and the main body of water that passes through these sumps is very small. They are also kept in the dark to minimize any changes in conditions due to the differential growth of organisms as well as cleaned thoroughly. We therefore eliminate containment effects that are the main concern of Cornwall and Hurd 2016. We have argued this successfully and more forcefully in Achlatis et al. (2017), and have

amended the text as follows (p. 11, line 5):

“The flow-through rates ($>18\text{Lmin}^{-1}$), size (8000L) and the elimination of light from the sumps limited any containment effects and hence the potential for pseudoreplication⁶²

18)P10, L30. Total pH scale is the best practice and should be used

To prevent pH drift following movement from low ionic strength buffers to seawater, we used buffers made in synthetic seawater.

19)P11, L4. Said seawater scale, but now NBS. Should be using total scale

We agree, but we applied the NBS within CO₂Calc.

20)Figure 2 legend. Insert ‘on’ between warming and net in title. The ‘and’ between *Seriatopora* and *Stylophora* shouldn’t be italicized

Done.

References

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13th Oct 20

Dear Dr Dove,

Your manuscript titled "Uncoupling calcification from calcifier biomass leads to rapid reef decline" has now been seen by our reviewers, whose comments appear below. In light of their advice I am delighted to say that we are happy, in principle, to publish a suitably revised version in Communications Earth & Environment under the open access CC BY license (Creative Commons Attribution v4.0 International License).

We therefore invite you to revise your paper one last time to address the remaining concerns of our reviewers. At the same time we ask that you edit your manuscript to comply with our format requirements and to maximise the accessibility and therefore the impact of your work.

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REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

I find the manuscript was revised adequately.

One very minor correction: Lithothamanion (line 6, page 3) should be Lithothamnion.

Reviewer #3 (Remarks to the Author):

The authors have done a satisfactory job at addressing my comments.

My only two lingering issues are just semantics.

1) I feel the title is too vague and doesn't really tell the reader what the study is about. No mention of climate change, warming, ocean acidification etc.

2) the term carbonate 'stocks' in the abstract just doesn't sound right to me. I'd reword to ".....leads to accelerated degradation and loss of coral reef frameworks."

I suggest the authors make these changes, but it is up to them if they want to or not.

Response to Reviewers

Reviewer number: 1

I find the manuscript was revised adequately.

One very minor correction: Lithothamanion (line 6, page 3) should be Lithothamnion.

We have incorporated the requested changes.

Reviewer number: 3

The authors have done a satisfactory job at addressing my comments.

1) I feel the title is too vague and doesn't really tell the reader what the study is about. No mention of climate change, warming, ocean acidification etc.

We have changed the title at the request of the reviewer.

2) the term carbonate 'stocks' in the abstract just doesn't sound right to me. I'd reword to ".....leads to accelerated degradation and loss of coral reef frameworks."

We have incorporated the requested changes.