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PROCEEDINGS B

Reduced thermal tolerance of massive coral species in a highly variable environment

C. N. Klepac and D. J. Barshis

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Original submission: 17 February 2020
1st revised submission: 11 June 2020
2nd revised submission: 21 July 2020
Final acceptance: 22 July 2020

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2020-0352.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Marginal

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

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Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
Yes

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
No

Is it clear?
N/A

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
This study tests the hypothesis that exposure to a more variable temperature regime increases coral thermal tolerance through mechanisms of acclimatization and/or adaptation. The results do not support this hypothesis and instead suggest that for the two focal species with massive morphologies, increased temperature variability reduces thermal tolerance. The study tests an important question in coral physiology and ecology, and it is well designed and executed. However, I have concerns that some of the conclusions drawn are too general and do not reflect the complexity of the results presented. Specifically, it seems that growth and thermal tolerance are not uniformly reduced in the HV pool as the stated conclusions imply, and that they depend on the timepoint, species, and pool of origin (e.g., during the first part of the study, growth was not different for some corals transplanted to the HV pool vs. their counterparts that remained in the pool of origin, and G. retiformis from the LV pool actually grew faster when transplanted into the HV pool for one of the timepoints). Moreover, the statistical tests do not show any significant differences in Fv/Fm or chlorophyll loss in corals that were transplanted into the HV pool vs. those that stayed in their native pools. Finally, additional discussion of how the natural thermal anomalies in the region may have impacted the specific results, and potential tradeoffs between thermal tolerance and growth, would help contextualize the results and address some of the additional hypotheses laid out in the introduction. I hope these and the specific comments below will help the authors in revising the manuscript.

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Discussion

- Some of the conclusions overstep what the data support – for example:
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- What about the 'tradeoffs' discussed in the introduction – what do these results say about the tradeoffs between growth and thermal tolerance? Can the data from the CBASS thermal challenges and the buoyant weight growth data be directly compared or correlated to evaluate the hypotheses regarding tradeoffs that are presented in the introduction?

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Acceptable

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
No

Is it clear?
No

Is it adequate?
No

Do you have any ethical concerns with this paper?
No

Comments to the Author
Klepac and Barshis examine the effects of natural temperature variability on growth and thermal tolerance of two massive coral species, Porites lobate and Goniastrea retiformis. In general, the vast majority of thermal tolerance studies in corals have been on Acroporids, potentially skewing our ideas of "general rules" of coral acclimation and adaptation. Indeed, the authors find unexpected patterns that are incongruent with previous findings that temperature variability leads to increased thermal tolerance. As such, this study represents an important addition to the literature. I do have some concerns regarding presentation and interpretation, which I have outlines below:

1) Perhaps the most striking result is not in the general patterns, but rather in the complexity. The two species react very differently to temporal (Jan/July) and spatial (LV/MV/HV) variation in temperature regime and both react differently than expected based on previous studies. I think the authors can acknowledge and highlight this complexity. At times, the attempts to generalize seem a little forced and can be misleading. For example, the abstract states "For both species, corals transplanted into the HV pool had reduced growth, decreased photosynthetic efficiency, and greater chlorophyll los following acute heat stress compared to native back-transplants…" However, according to Figure 3 it does not look like this was always the case. If I am interpreting the symbols correctly, there is no different between native and transplant G. retiformis for the Fv/Fm results. I understand that it was likely difficult to grapple with the complexity of this data, but generalizations that do not hold true made reading a little confusing.

2) Especially for the photophysiology results, I had trouble reconciling the model results presented in the text with the symbols on figure 3. For example, For G. retiformis July chlorophyll results the text says there is a treatment effect, but there are no asterisks. I think maybe the symbols represent post-hoc tests – are all the test statistics in the main text from the ANOVA? This should be clarified. In the section on coral growth, please include test statistics within the text where relevant.

3) I found the genetics data, especially of the coral host, pretty extraneous. For the host data, the data only exist for one of the two species and the implications are not discussed at all. For the symbiont, the patterns presented could be interesting, although a figure could really help with clarity. Again, these results were not discussed. I suggest the authors remove the coral data and either expand discussion of the symbiont data or remove it from the paper.

4) Finally, with results so complex it is impossible to attribute the results strictly to the influence of environmental variability. There are likely a number of factors that differ between these three pools. If we had the case where HV and LV were opposite ends of a spectrum with MV intermediate, it would build a stronger case for temperature variability driving the differences. But we do not see that pattern. I know it is really difficult to replicate natural experiments like this, so I just think the authors will need to be careful and caveat where necessary.

Minor comment:

Line 70: acclimatory, not acclamatory (this occurred in multiple locations)

Decision letter (RSPB-2020-0352.R0)

24-Mar-2020

Dear Miss Klepac:

I am writing to inform you that your manuscript RSPB-2020-0352 entitled "Reduced thermal tolerance of massive coral species in a high-frequency variable environment" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. While the Associate Editor has made a recommendation of Revise, I have decided that this is more in line with a reject and encourage resubmission. Either action would have required a second round of reviews, the difference is the time allowed for a revised manuscript to be submitted. A decision of revise allows you only 6 weeks to revise your manuscript, with a reject and resubmit allows you 6 months. Given the extensive nature of the revisions required I would prefer you take the necessary time to fully address the reviewers comments. With this in mind we encourage you resubmit you manuscript. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A ‘response to referees’ document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,
Dr Daniel Costa
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
16 March 2020

Dear Dr. Klepac,

As I had indicated in my earlier correspondence, I have had your manuscript entitled “Reduced thermal tolerance of massive coral species in a high-frequency variable environment” sent to peer review for the journal PRSB. I have now received two reviews and can proceed with a second Board Member recommendation: I am recommending revise.

Both of your reviewers are highly skilled in the subject area of your research, and I have strong respect for their opinions. I have read their reviews and revisited your manuscript and concur with their recommendations. Indeed it is most helpful that they articulate common issues, particularly ones that can be addressed quite easily with a revision.

Please can you consider these reviews, prepare a revision of your submission, and return your revised manuscript with a point-by-point response to the reviews. Overall, I think their suggestions are self-explanatory and you should be able to work through them with comparative ease. While preparing your revisions, and with consideration of the reviewer comments, it would be valuable to pay close attention to several issues:

1. Please consider the balance that is required between generalization, detail, and complexity. In several places your results are more complex than your summary statements indicate, and both reviewers suggest it would be valuable to embrace some of the diversities of responses. This task will also help you avoid over stepping what really can be supported with these data, which is another recommendation that has emerged in review.

2. The comment about the genetic data is very appropriate, and on reading your submission again, it is striking that this content does not feature in your discussion. As has been suggested, it would be valuable to use this material, or remove it from the manuscript. An compromise would be to present the data in supplementary material to recognize the limited role that it plays in your overall story, but even with this option, it would be prudent to make a bigger effort to use this content.

3. Finally, it would be valuable revisiting the graphical formatting of your data and ensuring that the presentations are as effective as is possible. I concur that the growth units in Fig. 2 appear to be incorrect, as your text suggests some kind of specific growth rate (weeks-1). Fig. 3 is a not as clear as it could be, as the legend is ineffective in clarifying the meaning of the faded symbols.

Thanks you for submitting your manuscript for consideration at PRSB. With two sets of reviews, supportive comments, and consensus opinions, you are now in a good position to prepare the revision. I shall look forward to hearing from you.

Yours sincerely,
Peter J. Edmunds PhD
PRSB Board Member

Reviewer(s)' Comments to Author:

Referee: 1

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Referee: 2

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Minor comment:

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Author's Response to Decision Letter for (RSPB-2020-0352.R0)

See Appendix A.

RSPB-2020-1379.R0

Review form: Reviewer 1

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
No

Is it adequate?
N/A

Do you have any ethical concerns with this paper?
No

Comments to the Author
I commend the authors for making significant improvements to the manuscript, particularly in embracing the complexity of the results. Most of my comments have been addressed sufficiently. I have a few remaining minor comments, mostly suggestions to help increase clarity.

Title/line 283/294/other places: The use of the phrase "high-frequency" to refer to the higher variation in temperature in the HV pool compared to LV/MV is problematic… Frequency implies timescale, so a "high-frequency" varying environment would vary faster than a lower frequency environment. (Of course, these pools ALL have higher frequency variability than offshore reefs). However, in comparing these pools to each other, it seems that the frequency of variability is the same (i.e., daily fluctuations), but that the magnitude of the variation differs among the pools. Make sure that all the language used correctly emphasizes the differences in the magnitude of this variability, NOT the frequency… Suggest removing "high-frequency" from title and other places in ms…

Line 24: Change "However" to "Moreover"
Line 26: Change "bleaching" to "heat stress"
Line 27: I don't think the 8 DHWs in 2015 are relevant here, as these occurred in Feb.-Jun. 2015, before this study began. Therefore, only the DHWs in 2016 occurred within the study period… Suggest removing the reference to/discussion of 2015 DHWs.

Line 100: Change "transplanted into" to "returned to"?

Figure 1C: Change x-axis to go from July to July rather than Jan to Jan, so that it is more comparable to the above panel 1B. This would make each color span two calendar years (e.g., 2015-16), but I think that would actually be better. Also, you could then add transparency to all the historical lines, leaving the 2015-2016 line fully opaque, so it is visually emphasized over the others.

Line 117: add "after transplantation" after "twelve months"

Line 215: was this 125 days where the daily maximum was over the bleaching threshold? If so add "in which the daily maximum exceeded…"

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Line 250-251: It is not entirely clear which values (points in Fig. 2C) are being compared in this statement, or which time point is being referred to.

Line 340: "similar Symbiodiniaceae communities within… G. retiformis across the back-reef" seems to contradict the results section, where it is stated that "G. retiformis community composition varied by native backreef pool…" (line 276).

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
Klepac and Barshis document growth and photosynthetic performance in two massive coral species transplanted across a gradient of temperature variability. As the vast majority of work on coral adaptation and acclimation is done in Acropora, this represents an important contribution to the field. That the story is complex I think only highlights the need to expand our investigations of coral thermal physiology to other species. In the revisions, I think the authors do a great job at dealing with and highlighting this complexity. I have only a few minor comments:

Abstract Lines 26-29: The relevance of the thermal anomaly is not clear here

The purpose for the comparison with the temperature during the Palumbi et al. paper is not totally clear. Is the intention to compare with a 'normal' year? It would be helpful to be explicit about this, maybe in the methods.

Why not normalize growth to starting weight? Was there any difference in starting weights of the different ramets?

Line 377-379: I think this sentence is a little bit of an overreach. I think the lack of evidence for tradeoff is interesting and important, but survival and fitness were not tested.

Decision letter (RSPB-2020-1379.R0)

13-Jul-2020

Dear Miss Klepac

I am pleased to inform you that your manuscript RSPB-2020-1379 entitled "Reduced thermal tolerance of massive coral species in a high-frequency variable environment" has been accepted for publication in Proceedings B.

The referee(s) have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee(s)' comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into https://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation
It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
• DNA sequences: Genbank accessions F234391-F234402
• Phylogenetic data: TreeBASE accession number S9123
• Final DNA sequence assembly uploaded as online supplemental material
• Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311
NB. From April 1 2013, peer reviewed articles based on research funded wholly or partly by RCUK must include, if applicable, a statement on how the underlying research materials – such as data, samples or models – can be accessed. This statement should be included in the data accessibility section.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available) which will take you to your unique entry in the Dryad repository. If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link. Please see https://royalsociety.org/journals/ethics-policies/data-sharing-mining/ for more details.

6) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit https://royalsociety.org/journals/authors/author-guidelines/.

Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,
Dr Daniel Costa
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member
Comments to Author:
11 July 2020

Dear Dr. Klepac,

Thank you for submitting your revised paper entitled "Reduced thermal tolerance of massive coral species in a high-frequency variable environment" for consideration as a research paper in PRSB. I appreciate you willingness to entertain the changes that have been suggested over the last few months, and the current two reviewers have returned very positive reviews.

Your submission contributes to an important aspect of contemporary marine research that seeks to understand how (or whether) marine organisms might find ways to reduce their susceptibility to the plethora of challenges associated with climate change. Some of the highest profile analyses in this area of research have come from coral reefs, where there are imminent threats to coral survival through thermal stress. Your analyses employ an elegant system of in situ experiment that exploits natural gradients of thermal conditions. This approach contrasts with the more standardized lab/mesocosm analyses that tend to produce (not unsurprisingly) results with more straightforward interpretations.

Your results make an important contribution to the field in revealing the complexity of ecologically relevant responses to complex signals. It is not possible to make this reality go away, and your study makes an effective case for why they need to be studied, and the complex set of real world results that are likely to be identified from such efforts. Your discoveries with the massive coral Porites provide a nice counterpoint to the results that have been obtained with other species using a variety of approaches, and I think the field of coral biology (and as well as the broader research community) will appreciate your contribution.

Reviewer(s)' Comments to Author:

Referee: 2

Comments to the Author(s).
Klepac and Barshis document growth and photosynthetic performance in two massive coral species transplanted across a gradient of temperature variability. As the vast majority of work on coral adaptation and acclimation is done in Acropora, this represents an important contribution to the field. That the story is complex I think only highlights the need to expand our investigations of coral thermal physiology to other species. In the revisions, I think the authors do a great job at dealing with and highlighting this complexity. I have only a few minor comments:

Abstract Lines 26-29: The relevance of the thermal anomaly is not clear here

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Line 377-379: I think this sentence is a little bit of an overreach. I think the lack of evidence for tradeoff is interesting and important, but survival and fitness were not tested.

Referee: 1

Comments to the Author(s).
I commend the authors for making significant improvements to the manuscript, particularly in embracing the complexity of the results. Most of my comments have been addressed sufficiently. I have a few remaining minor comments, mostly suggestions to help increase clarity.

Title/line 283/294/other places: The use of the phrase "high-frequency" to refer to the higher variation in temperature in the HV pool compared to LV/MV is problematic… Frequency implies timescale, so a "high-frequency" varying environment would vary faster than a lower frequency environment. (Of course, these pools ALL have higher frequency variability than offshore reefs). However, in comparing these pools to each other, it seems that the frequency of variability is the same (i.e., daily fluctuations), but that the magnitude of the variation differs among the pools. Make sure that all the language used correctly emphasizes the differences in the magnitude of this variability, NOT the frequency… Suggest removing "high-frequency" from title and other places in ms…

Line 24: Change "However" to "Moreover"
Line 26: Change "bleaching" to "heat stress"
Line 27: I don't think the 8 DHWs in 2015 are relevant here, as these occurred in Feb.-Jun. 2015, before this study began. Therefore, only the DHWs in 2016 occurred within the study period… Suggest removing the reference to/discussion of 2015 DHWs.

Line 100: Change "transplanted into" to "returned to"?

Figure 1C: Change x-axis to go from July to July rather than Jan to Jan, so that it is more comparable to the above panel 1B. This would make each color span two calendar years (e.g., 2015-16), but I think that would actually be better. Also, you could then add transparency to all the historical lines, leaving the 2015-2016 line fully opaque, so it is visually emphasized over the others.

Line 117: add "after transplantation" after "twelve months"

Line 215: was this 125 days where the daily maximum was over the bleaching threshold? If so add "in which the daily maximum exceeded…"

Line 223: Again the text here sort of implies that the 8 DHW in 2015 occurred during this study, but they did not… suggest changing this, and only focusing on the 2016 DHW's, which did occur during this study

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Author's Response to Decision Letter for (RSPB-2020-1379.R0)

See Appendix B.

Decision letter (RSPB-2020-1379.R1)

22-Jul-2020

Dear Miss Klepac

I am pleased to inform you that your manuscript entitled "Reduced thermal tolerance of massive coral species in a high-frequency variable environment" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

Your article has been estimated as being 10 pages long. Our Production Office will be able to confirm the exact length at proof stage.

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

You are allowed to post any version of your manuscript on a personal website, repository or preprint server. However, the work remains under media embargo and you should not discuss it with the press until the date of publication. Please visit https://royalsociety.org/journals/ethics-policies/media-embargo for more information.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

OLD DOMINION UNIVERSITY

COLLEGE OF SCIENCES
Department of Biological Sciences
Norfolk, Virginia 23529-0266
Phone: (757) 683-3595 Fax: (757) 683-5283

June 11, 2020

Dr. Edmunds,

We appreciate yours and the referees' feedback regarding our manuscript "Reduced thermal tolerance of massive coral species in a high-frequency variable environment." We were pleased to learn that both reviewers recognized the importance of the study and thought it worthy of publication following revision. All comments and concerns were taken into account, resulting in a greatly improved and substantially revised manuscript suitable for the wide PRSB readership. Overall, we believe we have fully addressed all comments in the revision, and have attached our point-by-point specific responses to each individual comment.

In this revision, we have extensively modified the Abstract, Results, and Discussion sections to clearly and honestly reflect the complexities of our study and avoid over generalizations (suggested by all reviewers). For both referees, we have updated and corrected the growth and photophysiological results and figures to effectively depict actual results. At the behest of Referee #2, we have removed coral host genetic data and elaborated further on Symbiodiniaceae community composition both in text and a supplemental figure. Referee #1 brought up constructive feedback regarding impacts of the natural thermal anomalies and potential tradeoffs mentioned in the Introduction but neglected during the Discussion. We have included additional discussion points to address these hypotheses in our Discussion, such as species-specific differences, potential tradeoffs between growth and thermal tolerance, and the timing of natural thermal anomalies relative to our experiments. We believe this revised version will make an important and valuable contribution to the broad field of thermal tolerance under variable environments and rapid climate change in addition to more coral-specific disciplines.

The revised manuscript contains 7,416 words of main text and 2 figures to fill approximately 10 pages when formatted for PRSB. There are 5 additional figures, 7 tables, and additional methods we would like to include as Supplementary Material. We would greatly appreciate your time and consideration of this revised manuscript for publication in PRSB.

Sincerely,

Courtney Klepac (corresponding author)
Department of Biological Sciences

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And

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Suggested Reviewers:
Verena Schoepf, Climate change impacts on coral reefs and naturally extreme coral reef environments, Assistant Professor, University of Amsterdam, v.schoepf@uva.nl

Emma Camp, Marine bio-geochemistry and naturally extreme coral reef environments, Postdoctoral Fellow, University of Technology Sydney, emma.camp@uts.edu.au

Carly Kenkel, Coral symbiosis biology, phenotypic plasticity and local adaptation, Assistant Professor, University of Southern California, ckenkel@usc.edu

Piero Calosi, Evolution of physiological systems, organismal biogeography and vulnerability to warming, Assistant Professor, University of Quebec, piero_calosi@uqar.ca

Rachael Bay, Evolutionary genomics under climate change, Assistant Professor, University of California at Davis, rachaelbay@gmail.com

Anne Cohen, Geochemistry of calcifying organisms under climate change, Associate Scientist, Woods Hole Oceanographic Institution, acohen@whoi.edu

Old Dominion University is an equal opportunity, affirmative action institution.

Dear Dr. Klepac,

As I had indicated in my earlier correspondence, I have had your manuscript entitled “Reduced thermal tolerance of massive coral species in a high-frequency variable environment” sent to peer review for the journal PRSB. I have now received two reviews and can proceed with a second Board Member recommendation: I am recommending revise.

Both of your reviewers are highly skilled in the subject area of your research, and I have strong respect for their opinions. I have read their reviews and revisited your manuscript and concur with their recommendations. Indeed it is most helpful that they articulate common issues, particularly ones that can be addressed quite easily with a revision.

Please can you consider these reviews, prepare a revision of your submission, and return your revised manuscript with a point-by-point response to the reviews. Overall, I think their suggestions are self-explanatory and you should be able to work through them with comparative ease. While preparing your revisions, and with consideration of the reviewer comments, it would be valuable to pay close attention to several issues:

1. Please consider the balance that is required between generalization, detail, and complexity. In several places your results are more complex than your summary statements indicate, and both reviewers suggest it would be valuable to embrace some of the diversities of responses. This task will also help you avoid over stepping what really can be supported with these data, which is another recommendation that has emerged in review.

2. The comment about the genetic data is very appropriate, and on reading your submission again, it is striking that this content does not feature in your discussion. As has been suggested, it would be valuable to use this material, or remove it from the manuscript. An compromise would be to present the data in supplementary material to recognize the limited role that it plays in your overall story, but even with this option, it would be prudent to make a bigger effort to use this content.

3. Finally, it would be valuable revisiting the graphical formatting of your data and ensuring that the presentations are as effective as is possible. I concur that the growth units in Fig. 2 appear to be incorrect, as your text suggests some kind of specific growth rate (weeks-1). Fig. 3 is a not as clear as it could be, as the legend is ineffective in clarifying the meaning of the faded symbols.

Thanks you for submitting your manuscript for consideration at PRSB. With two sets of reviews, supportive comments, and consensus opinions, you are now in a good position to prepare the revision. I shall look forward to hearing from you.

Yours sincerely,

Peter J. Edmunds PhD
PRSB Board Member

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
This study tests the hypothesis that exposure to a more variable temperature regime increases coral thermal tolerance through mechanisms of acclimatization and/or adaptation. The results do not support this hypothesis and instead suggest that for the two focal species with massive morphologies, increased temperature variability reduces thermal tolerance. The study tests an important question in coral physiology and ecology, and it is well designed and executed. However, I have concerns that some of the conclusions drawn are too general and do not reflect the complexity of the results presented. Specifically, it seems that growth and thermal tolerance are not uniformly reduced in the HV pool as the stated conclusions imply, and that they depend on the timepoint, species, and pool of origin (e.g., during the first part of the study, growth was not different for some corals transplanted to the HV pool vs. their counterparts that remained in the pool of origin, and G. retiformis from the LV pool actually grew faster when transplanted into the HV pool for one of the timepoints). Moreover, the statistical tests do not show any significant differences in Fv/Fm or chlorophyll loss in corals that were transplanted into the HV pool vs. those that stayed in their native pools. Finally, additional discussion of how the natural thermal anomalies in the region may have impacted the specific results, and potential tradeoffs between thermal tolerance and growth, would help contextualize the results and address some of the additional hypotheses laid out in the introduction. I hope these and the specific comments below will help the authors in revising the manuscript.
We thank the reviewer for their insightful and constructive feedback. We have substantially revised the manuscript throughout to include additional discussion of the complexity of the results, avoid over generalization, and discuss potential tradeoffs and impacts of the natural thermal anomalies to help better contextualize the results and improve clarity. Line by line responses are included below.

Abstract
- Line 22: were the ‘transplanted and native samples’ paired ramets of the same genets? If so, this may be worth indicating here!
This terminology has been added to the abstract:
Line 20 “Paired transplant and native ramets were exposed …”

- The language used to refer to corals that remained in their pools of origin is

inconsistent and slightly confusing: at various times, ‘native samples’ (line 22), ‘native back-transplants’ (line 26), ‘HV native corals’ (line 26), ‘native backreef’ (line 250)
The language has been revised throughout the manuscript to ‘SITE (i.e., HV, MV, or LV)’ + native/transplant corals or ramets.

- Lines 29-30: It looks like, based on Figure 1, that 2015 was the year with 8 DHW and 2016 with 5 – have the years been accidentally flipped in either the text or the figure?
This is correct and thank you for catching this typo. 2015 has 8 DHW and 2016 has 5. The text has been revised accordingly.
Line 27 “2015 had 8 Degree Heating Weeks (DHW) and 2016 had up to 5 DHW…”

- Line 31: what is meant by ‘exceeded the limits of corals in the most variable site’? What limit, and what was actually observed during this thermal stress event in the pools? Is this meant to imply that this limit may not have been exceeded in the less variable sites? When did the natural thermal stress event take place relative to the CBASS challenges involved in this study?
We are hypothesizing that the upper thermal limits of HV corals may have been exceeded during this study, based on greater thermal anomalies, increased bleaching susceptibility of HV native *P. lobata*, and the lack of response to heat treatment in *P. lobata* from the moderately variable (MV) site in July 2016. Degree Heating Weeks were just beginning to accumulate at the 6-month/Jan 2016 timepoint and had subsided by the July 2016 timepoint. We thus suggest that the decreased performance of HV native *P. lobata* in July 2016 could reflect accumulated stress due to the natural bleaching event.

- Line 32: what is meant by ‘during recent warming events’? As compared to less recent warming events? Or do you mean ‘in highly variable environments’ as compared to less variable environments?
This sentence has been modified to shorten the abstract as per journal guidelines.

Introduction
- Line 37: can you explain what is meant by the “duration of environmental variation”?
This wording has been removed from the text to improve clarity.

- Line 46: is it a certainty that ‘these populations have evolved the greatest thermal tolerance’? This seems like the hypothesis you are testing, and ultimately rejecting, in the present study.
Added in ‘likely’ to clarify we hypothesize this is a mechanism underlying enhanced tolerance in variable environments.

- There is some repetition between the first and second paragraphs of the introduction – would suggest cutting this down to streamline text

The first paragraph refers to marine organisms in general, while the second paragraph is coral specific and highlights coral-specific mechanisms. We think the inclusion of both as written is helpful for a general audience.

- Line 54: With 'heterogeneous' here, do you really mean 'extreme' or 'high variability'?

Line 54 Revised to "Resident coral populations in these environments are continuously exposed to high-frequency variability in abiotic conditions"

- Line 69: correct spelling for 'acclimatory'

Corrected to acclimatory in all cases.

- Line 87: ITS2 sequencing is not really 'population genetic structure' for Symbiodiniaceae

Line 87 Modified to "endosymbiont species assemblage (Symbiodiniaceae)".

Materials and Methods

- Could this 'dislodging event' in the LV pool in January 2016 have had any impact on the data collected in July 2016? (e.g., growth rates, if there was some recovery period after being re-attached?)

The grid itself was dislodged and wedged under a large *Porites lobata* colony (one of the sampled colonies in fact!) and likely lasted < 7 days. If impacts were to affect this grid, it would have been a change in light regime and flow for a week or so which we think is unlikely to have affected responses 6 months later.

- Figure 1: Consider adding symbols onto the timeseries in panels B and/or C to indicate when the experiment began and when data/measurements were collected

Great suggestion, we have included bars on the dates where sampling and data collection occurred.

- Line 138: Unclear exactly what is meant by 'four sets of head and sump tanks (42L volume per treatment)'. How many experimental tanks were there in total? How many replicate tanks per treatment, and how many treatments?

Each tank system is composed of a head and sump tank. The wording has been modified as follows:

Line 124 "… constructed from sets of head and sump tanks (42L volume per treatment), resulting in four experimental tank systems – two heat and two control."

- Line 143: So all the fragments of one species were assayed on one day, and all the fragments of the second species on the second day?

Correct. We have added the following for clarity:

Line 133 “All ramets from a single species were assayed in one day, with the second species assayed the following day.”

- Line 150: What is meant by ‘>50% bleaching response’? 50% of fragments appear bleached? Or all fragments have lost 50% of pigments on average? Or something else?

A > 50% bleaching response means visible paling in > 50% of the fragments (i.e., 50% of fragments appear bleached). The wording has been modified as follows:

Line 137 “The two maximum temperatures were chosen: based on preliminary trials to elicit a visible bleaching response in > 50% of fragments, to represent acute thermal exposures above the local bleaching threshold, and to be ~1°C above the HV pool’s mid-day low tide average maximum temperature.”

- Line 157: Should ‘21hrs’ actually say 22, as described in previous paragraph?

PAM measurements took one hour to complete, therefore, we began the ‘end’ measurements at 21hrs and they were completed by hour 22.

- Line 159: Using what liquid?

Text has been revised to:
Line 149 “… coral tissue was airbrushed from the skeleton using 35ppt artificial seawater”

- Line 168: When were biopsies collected for Symbiodiniaceae sequencing? Were these from all of the same genets as the experimental ramets? Why ‘less than or equal to’ 28 P. lobata?

We sampled for ITS2 genotyping from all genets at the beginning of the experiment and at all timepoints to characterize any potential changes in species assemblages either over time or following transplantation. The 28 *P. lobata* genets referred to a broader sample of *P. lobata* colonies for host genetics, though those data have now been removed in response to the editor’s suggestion as they were inconsequential. The text now reads:

Line 158 “A 1cm2 biopsy was sampled from each *G. retiformis* and *P. lobata* genet (n = 5 per species/site) at the beginning of the experiment and at each timepoint ... During both timepoints, similar sized biopsies were sampled from control ramets after acute experiments to characterize Symbiodiniaceae ITS2-level assemblages over time (0, 6 and 12 months).”

- Line 217: In this section it would be good to provide citations for the R packages used

Added in text and to the literature cited.

Results

- Line 235: ‘total number of days’ – during what period of time?

The text has been revised to:
Line 212 “… the total number of days during the experimental duration (July 2015 to July 2016)”

- Line 242: Again, relative to Fig. 1, it seems like there may be some mixup between years, as the figure shows 2015 having a greater max and min than 2016…

Correct, this was an error in the previous submission. The text has been modified accordingly to reflect the higher values for 2015.

- Line 250: does ‘native backreef’ mean pool of origin? Should use consistent language.

The wording has been revised to be more specific:
Line 227 “weekly growth rate was influenced by the three-way interaction among pool of origin, transplant destination, and time”

- Line 251: The stats presented in Figure 2 look like they reflect a two-way ANOVA with ‘origin_dest’ as one factor, time as a second factor, and their interaction. However, the text here implies that ‘native backreef’ (meaning pool of origin?), destination, and time are treated as three separate factors – please clarify

Correct the ANOVA was ~ origin_dest*time, utilizing a combined origin_destination variable due to the unbalanced design (i.e., not all origins were in each destination). The use of the combined origin_dest factor has been added to the statistic methods:

Lines 199-202 “Effects were tested using a mixed model ANoVA, where time, a combined origin_transplant site variable (due to the unbalanced design [i.e., not all origins in each destination]), and treatment were modeled as fixed factors, and colony identity was nested within experimental tank designation as a random factor. “

Additionally, We have reordered factors as they were tested in the figures and text. For any post hoc comparisons that indicated corals from a particular pool had greater growth and/or bleaching responses (irrespective of transplant site) than other coral origin_dest groups, we combined the two groups in text to simplify interpretations. I.e., Line 242-243: “F_v/F_m values were ~1.2-1.8 times higher in MV heated corals than heated HV and LV corals for both time points”, means both MV_MV and MV_HV corals had higher FvFm values than HV_HV or LV_LV.

- Figure 2: I find this figure difficult to interpret, and wonder whether presenting these data as boxplots (w/points) for each group of corals

(origin/destination/time) might be easier to digest visually? It is hard to quickly extract any clear take-home messages from this figure. If you do keep this design, I would make the x and y axes on each panel have equal extent, so that the 1:1 diagonal is at a 45° angle. There are also many overlapping points – use alpha to create some transparency.
This figure was originally similar to that of Figure 3, with points for each group of corals and two timepoint panels. An internal reviewer suggested depicting growth as an xy scatterplot since one of the hypotheses was whether growth is enhanced in the HV pool. We have now reverted back to our original figure as suggested where weekly growth, Fv/Fm and total chlorophyll are all in one large figure panel, split by coral species.

- Figure 2: If the change in mass was divided by initial mass then by weeks (as described in methods), shouldn't the units be week^-1, not g/week as indicated in axis titles? In the legend, don't points below the diagonal indicate lower growth in HV pool relative to the pool of origin (not 'relative to HV native corals')?
The change in mass has been updated in the new figure to g/week (i.e., weekly growth rate = growth (final-initial) divided by time (weeks)). Weekly growth rate (g/week) values were used in statistical analyses and figures.

- Line 272: '[Fv/Fm] of heat-treated MV corals was two times higher in January than July' – this does not look true based on Fig. 3B. (values are between 0.4 and 0.6…)
This is correct. The "two times higher" statement was based off of a previous calculation, and is no longer valid. Corrected to Line 246: "higher F_v/F_m values in January than July, but only for MV heated corals."

- Line 274: 'groups' – what groups?
Text has been modified for clarification. Line 243: "For *G. retiformis* there were no differences in F_v/F_m values among native and transplanted groups."

Discussion
- Some of the conclusions overstep what the data support – for example:
o Line 312 - "Corals transplanted for one year into the [HV pool] had reduced growth…" – assuming you mean relative to their counterparts that stayed in their native pools – this is not entirely consistent with the presented results. The statement seems true for P. lobata at the July 2016 timepoint, but not Jan. 2016. And for G. retiformis, growth also looks similar between transplants and natives in January 2016, while in July 2016 it is reduced for MV transplants, but it is actually higher in for LV transplants. These varying responses by timepoint and pool of origin do not entirely support the above conclusion – consider making this a bit more nuanced?
We have attempted to remove all generalizations in this revised manuscript in order to more accurately reflect and discuss the complexity inherent in the data set. This section is now written as:

Lines 283-287: “Corals transplanted for one year into the site with the Highest Variability (the HV pool common garden) did not increase growth or improve photophysiological responses following acute heat stress, as observed in previous studies [8]. Instead, growth and stress tolerance responded differently to spatial and temporal variation in temperature regimes, and differently in P. lobata and G. retiformis.”

o Line 313 - “…corals native to and transplanted into the HV pool had greater loss of photosynthetic efficiency and chlorophyll…”. Technically, the ‘loss of photosynthetic efficiency and chlorophyll’ (i.e., the difference between control and heated corals in each group) was not statistically compared. The reported tests use the Fv/Fm and chlorophyll values themselves as the response variable, and not the change in these values between control and heated. At the risk of being nitpicky, I think it is necessary to statistically compare the actual losses in each group in order to make this conclusion. However, the current comparisons of the heated values of Fv/Fm and chlorophyll still do not support the conclusion that corals transplanted into the HV corals performed worse than those that remained in their native pools. For P. lobata, the posthoc letters indicate no significant differences in Fv/Fm or chlorophyll between MV natives and transplants when heated, or between LV natives and transplants, at either timepoint. No differences are indicated for G. retiformis, either.
This text has now been revised (see response to the previous comment).

o “We also found highest growth in HV natives versus MV and LV corals transplanted into the HV pool” (line 368) – again, this does not seem to be true for all corals at all timepoints…
We have updated this section to clarify the species- and time-specific responses: Lines 356-361 “We also found highest growth in HV natives versus MV and LV corals transplanted into the HV pool, but only for *P. lobata* during July 2016 and no differences among their native environments. However, differences in stress tolerance between paired native versus transplanted ramets exist for both species: a non-significant then significant reduction in both F_v/F_m for MV *P. lobata* and total chlorophyll for MV and LV *G. retiformis* from January to July 2016, suggesting a potentially higher stress level in transplanted ramets.”

- Line 366-368: This sentence is very confusing…
Revised in response to above comment.

- Line 381: It is not entirely clear how the thermal stress in 2015 and 2016 may have impacted the experimental corals. How much bleaching was actually observed in American Samoa during these thermal anomalies, and specifically was bleaching observed in these pools or in these specific corals? Can you discuss the timing of the thermal anomalies relative to when the CBASS assays were performed, to give a more specific context of how these conditions may have influenced this particular study?

Additional text has been added to both the discussion and the methods section to clarify these points. Discussion currently states:

Lines 385-389 “Our experiments were a few months prior to or post maximal bleaching stress on Ofu Island (2015: February-June, 2016: March-June; Fig. 1C), however in January 2016, we observed sparse paling in some HV pool branching corals but not in our donor or transplanted corals (pers. obs.). Thus, the patterns observed herein could represent the initial stages of response to or accumulated after-effects of the thermal anomaly.”

- What about the ‘tradeoffs’ discussed in the introduction – what do these results say about the tradeoffs between growth and thermal tolerance? Can the data from the CBASS thermal challenges and the buoyant weight growth data be directly compared or correlated to evaluate the hypotheses regarding tradeoffs that are presented in the introduction?

A paragraph addressing the potential for tradeoffs in variable environments has been added to the discussion. We also ran correlations on HV coral growth and total chlorophyll (or F_v/F_m) and did find a negative, albeit non-significant, relationship between growth and chlorophyll of heat-treated samples, which will be added to the supplemental information.

The relevant additions are pasted below:

Lines 370-378 “For HV corals, increased growth but reduced stress tolerance could be evidence of tolerance trade-offs owing to specialization to highly variable habitats. Skeletal growth records of massive *Porites* colonies along the GBR illustrate progressive accretion rates associated with warming SST followed by precipitous declines following repeated mass bleaching events [75, but see 76]. We explored the relationship between HV *P. lobata* coral growth and response to acute thermal stress and found a negative, albeit non-significant, correlation between growth and total chlorophyll (Pearson’s R = -0.41; Fig. S6) and no correlation between growth and photochemical efficiency. Taken together, our results corroborate recent findings that coral growth is likely not a good predictor of survival (i.e., fitness) under extreme temperatures [77].”

Referee: 2

Comments to the Author(s)

Klepac and Barshis examine the effects of natural temperature variability on growth and thermal tolerance of two massive coral species, Porites lobate and Goniastrea retiformis. In general, the vast majority of thermal tolerance studies in corals have been on Acroporids, potentially skewing our ideas of “general rules” of coral acclimation and adaptation. Indeed, the authors find unexpected patterns that are incongruent with previous findings that temperature variability leads to increased thermal tolerance. As such, this study represents an important addition

to the literature. I do have some concerns regarding presentation and interpretation, which I have outlines below:
We appreciate the reviewer's recognition of the importance of studying non-Acroporid species as well as the inherent complexity in the dataset. We have made substantial revisions throughout the manuscript to better clarify and contextualize our results and avoid overgeneralizations.

1) Perhaps the most striking result is not in the general patterns, but rather in the complexity. The two species react very differently to temporal (Jan/July) and spatial (LV/MV/HV) variation in temperature regime and both react differently than expected based on previous studies. I think the authors can acknowledge and highlight this complexity. At times, the attempts to generalize seem a little forced and can be misleading. For example, the abstract states "For both species, corals transplanted into the HV pool had reduced growth, decreased photosynthetic efficiency, and greater chlorophyll los following acute heat stress compared to native back-transplants…" However, according to Figure 3 it does not look like this was always the case. If I am interpreting the symbols correctly, there is no different between native and transplant G. retiformis for the Fv/Fm results. I understand that it was likely difficult to grapple with the complexity of this data, but generalizations that do not hold true made reading a little confusing.
We appreciate and acknowledge the criticism of over-generalizing the complicated results of this study. As such, we have substantially revised the abstract, results, and discussion sections, including a species-specific differences discussion paragraph following the coral growth form/taxonomic differences to expand upon the complexities observed between the two massive species. Any generalizations in the text have been updated throughout to more accurately portray the observed results.

2) Especially for the photophysiology results, I had trouble reconciling the model results presented in the text with the symbols on figure 3. For example, For G. retiformis July chlorophyll results the text says there is a treatment effect, but there are no asterisks. I think maybe the symbols represent post-hoc tests – are all the test statistics in the main text from the ANOVA? This should be clarified. In the section on coral growth, please include test statistics within the text where relevant.
We have updated both Figure 2 & 3 as a combined physiology panel and have included all significant post-hoc comparisons such as treatment effect, differences among transplant groups, and differences in paired transplant ramets over time. In the main text, ANOVA main effects are reported first, followed by post hoc comparisons. Supplemental tables include all main effects and post hoc comparisons at each relevant level.

3) I found the genetics data, especially of the coral host, pretty extraneous. For the host data, the data only exist for one of the two species and the implications are not discussed at all. For the symbiont, the patterns presented

could be interesting, although a figure could really help with clarity. Again, these results were not discussed. I suggest the authors remove the coral data and either expand discussion of the symbiont data or remove it from the paper.
We have removed the coral host genetic data entirely, and added a supplemental figure of Symbiodiniaceae ASV proportions for each coral species. Additional discussion of the potential influence of the Symbiont data has been added in the new species-specific responses discussion paragraph.

Lines 330-344 “Although both *P. lobata* and *G. retiformis* are clustered into the stress-tolerant life-history strategy [67], species-specific responses are apparent under acute bleaching stress. For both photochemical efficiency (Fv/Fm) and total chlorophyll, we found opposing effects of time, where heat stress affected *P. lobata* in January but *G. retiformis* corals were more affected in July 2016. In addition, stronger effects of pool of origin were evident for *P. lobata* bleaching responses and July 2016 growth versus *G. retiformis*. Ofu backreef *Acropora* populations harbor pool-specific Symbiodiniaceae communities, where *Acropora spp.* in the HV pool predominantly host *D. trenchii*, while MV *Acropora spp.* host both *D. trenchii* and Cladocopium type C2 [25]. In contrast, we observed similar Symbiodiniaceae communities within *P. lobata* (type C15) and *G. retiformis* (type C40, C15, and C3) across the back-reef, though distinct assemblages between species. While it is unclear whether these different Symbiodiniaceae Cladocopium assemblages could be driving the observed species-specific seasonal variation in photophysiological responses to bleaching stress [71], both intra- and inter-specific host and symbiont variation is known to shape growth and thermal tolerance limits in corals [e.g. 37, 72, 73].”

4) Finally, with results so complex it is impossible to attribute the results strictly to the influence of environmental variability. There are likely a number of factors that differ between these three pools. If we had the case where HV and LV were opposite ends of a spectrum with MV intermediate, it would build a stronger case for temperature variability driving the differences. But we do not see that pattern. I know it is really difficult to replicate natural experiments like this, so I just think the authors will need to be careful and caveat where necessary.

We have modified the final discussion paragraph to dilute the emphasis placed on environmental variability driving the thermal tolerance differences observed. Also, we have included more information regarding our thermal experiments as analogues to the HV environment and discussed the natural bleaching timing with our experiments to clearly discuss the potential factors and caveats that contribute to our results.

Minor comment:
Line 70: acclimatory, not acclamatory (this occurred in multiple locations)
Corrected in all instances.

Appendix B

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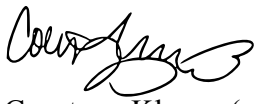
July 19, 2020

Dear Dr. Costa and Edmunds,

We sincerely appreciate yours and the referees' feedback regarding our manuscript "Reduced thermal tolerance of massive coral species in a highly variable environment." We are very pleased with the positive reviews on our revisions to the original manuscript, and are excited our study will make a valuable contribution to the coral biology field and wider audience of PRSB. We have fully addressed all comments in the revision, and have attached our final point-by-point specific responses to each individual comment (attached below). Many thanks for your time and consideration and we look forward to publication of our manuscript.

Sincerely,



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Reviewer(s)' Comments to Author:

Referee: 2
Comments to the Author(s).
Klepac and Barshis document growth and photosynthetic performance in two massive coral species transplanted across a gradient of temperature variability. As the vast majority of work on coral adaptation and acclimation is done in Acropora, this represents an important contribution to the field. That the story is complex I think only highlights the need to expand our investigations of coral thermal physiology to other species. In the revisions, I think the authors do a great job at dealing with and highlighting this complexity. I have only a few minor comments:

Abstract Lines 26-29: The relevance of the thermal anomaly is not clear here.
Although not definitive, we hypothesize that the anomalous temperatures experienced on Ofu during 2015-16 may have exceeded the upper thermal limits of HV native corals (the site with the greatest magnitude variability). Corals from this pool previously demonstrated increased tolerance, but we posit the environment could be reaching upper tolerance limits of the HV pool corals.

The purpose for the comparison with the temperature during the Palumbi et al. paper is not totally clear. Is the intention to compare with a 'normal' year? It would be helpful to be explicit about this, maybe in the methods.
Correct, additionally those were the years when increased tolerance was found in HV *Acropora* corals. Added in "These years were chosen to compare Ofu temperatures between previous 'normal' years - the Palumbi, Barshis [8] study (2010-2012) - and recent mass bleaching years." (Lines 178-180)

Why not normalize growth to starting weight? Was there any difference in starting weights of the different ramets?
Growth was normalized to starting/initial weight so any variance in starting weight of ramets is accounted for. Lines 109-110:
"Coral growth was calculated by subtracting initial weight from final weight and then divided by the number of weeks since transplantation to determine weekly growth rate."

Line 377-379: I think this sentence is a little bit of an overreach. I think the lack of evidence for tradeoff is interesting and important, but survival and fitness were not tested.
Updated text to reflect what was actually measured (i.e., bleaching response). Lines 360-361:
"Taken together, our results corroborate recent findings that coral growth is likely not a good predictor of bleaching responses under extreme temperatures"

Referee: 1
Comments to the Author(s).
I commend the authors for making significant improvements to the manuscript, particularly in embracing the complexity of the results. Most of my comments have been addressed sufficiently. I have a few remaining minor comments, mostly suggestions to help increase clarity.

Title/line 283/294/other places: The use of the phrase "high-frequency" to refer to the higher variation in temperature in the HV pool compared to LV/MV is problematic… Frequency

implies timescale, so a "high-frequency" varying environment would vary faster than a lower frequency environment. (Of course, these pools ALL have higher frequency variability than offshore reefs). However, in comparing these pools to each other, it seems that the frequency of variability is the same (i.e., daily fluctuations), but that the magnitude of the variation differs among the pools. Make sure that all the language used correctly emphasizes the differences in the magnitude of this variability, NOT the frequency… Suggest removing "high-frequency" from title and other places in ms…
After consideration, we agree with the referee and appreciate the clarification. Any instances of "high-frequency" have been altered to "highly variable environments" (title) or "high magnitudes of temperature variation."

Line 24: Change "However" to "Moreover"
Updated. (Line 22)

Line 26: Change "bleaching" to "heat stress"
Updated. (Line 23)

Line 27: I don't think the 8 DHWs in 2015 are relevant here, as these occurred in Feb.-Jun. 2015, before this study began. Therefore, only the DHWs in 2016 occurred within the study period… Suggest removing the reference to/discussion of 2015 DHWs.
Although the 2015 DHWs occurred before the experiment began, we think it is plausible that latent effects/delayed recovery following the 2015 anomaly (ended ~June 2015) could have influenced the physiological responses measured. Carryover effects/delayed recovery in multiple coral species have been found up to 12 months post bleaching for both physiological responses (e.g., Grottoli et al 2014) and gene expression patterns (e.g., Thomas and Palumbi 2017). The timing of the 2015 DHWs has been clarified in the text as pre-experiment (see response to comment below).

Grottoli AG, et al. 2014 The cumulative impact of annual coral bleaching can turn some coral species winners into losers. Global Change Biology 20.12: 3823-3833.
Thomas L, Palumbi SR. 2017 The genomics of recovery from coral bleaching. Proc. R. Soc. B 284: 20171790.

Line 100: Change "transplanted into" to "returned to"?
Updated. (Line 96)

Figure 1C: Change x-axis to go from July to July rather than Jan to Jan, so that it is more comparable to the above panel 1B. This would make each color span two calendar years (e.g., 2015-16), but I think that would actually be better. Also, you could then add transparency to all the historical lines, leaving the 2015-2016 line fully opaque, so it is visually emphasized over the others.
Done.

Line 117: add "after transplantation" after "twelve months"
Added. (Line 104-105)

Line 215: was this 125 days where the daily maximum was over the bleaching threshold? If so

add “in which the daily maximum exceeded…”
Correct, this was calculated as the number of days over which the daily maximum exceeded the bleaching threshold. Line 203:
“The HV pool had a total of 125 days in which the daily maximum exceeded the bleaching threshold…”

Line 223: Again the text here sort of implies that the 8 DHW in 2015 occurred during this study, but they did not… suggest changing this, and only focusing on the 2016 DHW’s, which did occur during this study
See response to comment above. We have clarified that these occurred prior to the first sampling timepoint. Lines 212-213:
“… 2015 had up to 8 DHW over five months (6 months prior to the first sampling point) …”

Line 228: According to your stats methods description, this is not a three-way interaction, but a two way interaction between the two predictors: orig_dest and time.
Correct. Text has been modified to state “two-way interaction between origin_destination transplant site and time” (Lines 217-218).

Line 230: “P. lobata from the HV pool grew ~2.4 times more than MV and LV corals”… what time point is this referring to? The posthoc letters in Figure 2A/Jan. show no difference between HV/MV/LV corals transplanted to HV?
This statement reflects the averaged effect of origin_destination on growth, where HV corals in January grew 2-2.5x more and 2-3x more in July than corals transplanted into the HV pool. Added in “Averaged across both time points, *P. lobata*…” to line 218.

Line 250-251: It is not entirely clear which values (points in Fig. 2C) are being compared in this statement, or which time point is being referred to.
The text has been corrected. Lines 239-2241:
“For *P. lobata*, native LV corals had ~2 times higher control than HV and MV corals during January (time*origin_dest*trt p = 0.047; Fig. 2C; Table S2, S7).”

Line 340: “similar Symbiodiniaceae communities within… G. retiformis across the back-reef” seems to contradict the results section, where it is stated that “G. retiformis community composition varied by native backreef pool…” (line 276).
Correct, this was an oversight and has been updated. Lines 321-323: we observed similar Symbiodiniaceae communities within *P. lobata* (type C15) across the back-reef, site-specific assemblages within *G. retiformis* (type C40, C15, and C3), and distinct species-specific assemblages.

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