Dear Professor Lasker,

Please find attached the revised version of the manuscript CORE-D-15-00336 *“Environmental factors limiting fertilisation and larval success in corals.”* We greatly appreciated the constructive criticism of both the Topic Editor and the three reviewers. We have addressed each of their concerns as outlined below.

The most substantial change is to the discussion and the application of our model. Following the reviewers’ advice, the direction of the manuscript has substantially changed, where we have expanded sections about the application of the model as well as incorporated several real-world scenarios.

In addition, we have rewritten parts of the paper to provide more clarity (please see specific alterations outlined below).

We hope you agree that the manuscript is much improved. We look forward to your response.

Sincerely,

Rachael Woods

**Reviewer #1:**

The authors created a useful and informative model of coral fertilization and larval survival based on a meta-analysis/data compilation of published data on numerous environmental stressors. While their model will provide utility in this field, I have some concerns about the limited data used in their model and the way the authors described and interpreted their results. Specifically, the authors were too limiting in their search of the literature and missed studies from which additional data could have been used to generate a more robust model.

We searched the literature further and have added 2 more studies to our analysis, which have not changed the overall findings, but rather made them more robust. We have made significant changes concerning the interpretation of the results throughout the manuscript (Results section and Discussion section). Please see below for details.

I am also concerned by the circular reasoning that seems to be employed at times in the Discussion in which the authors state that their model agrees with previous findings in the literature, yet the data in their model was extracted from those very same studies (based on Supplemental Table 1). To ameliorate this issue, the authors should focus more directly on the outcomes of their model, such as the relative consequences of one environmental factor versus another, rather than dwelling on whether their model does or does not reflect the findings of past studies.

We have completely re-written the discussion based on this comment. We now focus on applications of the model rather than our previous rehashing of patterns already found by other studies (Discussion, page 17).

Introduction:

- Rather than solely summarizing the literature, it would be useful if the Introduction also discussed the use of meta-analyses in these endeavours and the potential for real-world application of their modeling.

We have re-written the introduction, which briefly introduces the literature and now focuses on combining past work to analyse multiple variables simultaneously as well as the application of such an approach for understanding success in early life stages of corals (Introduction, page 4 ).

Methods:

- I am concerned by the use of a limited set of search terms as the only way to identify papers for the meta-analysis. Given that the authors are targeting the effects of specific stressors on coral larvae, a more exhaustive search is possible and will not be particularly time-consuming. I identify two papers below on the effects of salinity on coral larval survivorship and I am certain there are papers on other stressors that could be included. Limiting meta-analyses to papers found by using specific search terms is often done to query consensuses in the literature, but this approach is too limiting for meta-analyses that seek to use as much data as possible to generate predictive models.

We have now conducted a more rigorous search of the literature as well as included the papers the reviewer suggests below. Please see Table S1 for overview of studies now included in our analysis.

- Line 137: An important component of seawater is the microbial fraction. Thus, to suggest that seawater in all the studies is ‘typical’ based on nutrients and abiotic characteristics alone ignores an extremely important characteristic of the seawater. More specifically, there likely were different levels of water filtration used in these studies and I suggest that the authors include the degree of water filtration (e.g., 45µm) as another variable identified from each study (perhaps as a column in Supplemental Table 1).

We agree that abiotic and nutrient variation may be a factor affecting the results within each study; however, the level of filtration within each experiment was rarely given. Instead, we have discussed this limitation in the discussion (page 19 line 493) and hope that this will prompt people to properly record water quality data in future experiments.

Results:

- The effect of salinity on fertilization and larval survivorship is a primary result of the study (abstract, modeled by itself in the Results (line 203), and addressed extensively in the Discussion). Yet, the data modeled for salinity and fertilization is based on two papers and larval survivorship is based on one paper. This seems very limiting, especially given that there are other papers examining the effect of salinity on coral larval survivorship. I am fairly certain that the data reported in both the papers listed below meet the authors’ criteria for inclusion and thus should be incorporated for a more robust conclusion:

Vermeij, M. J. A., Fogarty, N. D., & Miller, M. W. (2006). Pelagic conditions affect larval behavior, survival, and settlement patterns in the Caribbean coral Montastraea faveolata. Marine Ecology Progress Series, 310(11).

Hartmann, A. C., Marhaver, K. L., Chamberland, V. F., Sandin, S. A., & Vermeij, M. J. (2013). Large birth size does not reduce negative latent effects of harsh environments across life stages in two coral species. Ecology, 94(9), 1966-1976.

We have included the papers suggested above, and also searched the literature for further examples of the effect of salinity on larval development (Table S1).

- It would be interesting to model the degree of water filtration or presence vs. absence of microbes as another variable. Water filtration could be modeled as a continuous variable with an explanation of which microbial components are lost as the degree of filtration increases. Alternatively, water filtration could be modeled as a binary variable based upon whether the level of filtration removes bacteria or not.

We have addressed this in the comment above (Reviewer 1, Comment 5.)

Discussion:

- Again, much like in the Introduction, the authors focus on the results of specific studies, rather than the results they achieved from their model by combining data from multiple studies. Because of this approach to the writing, the Intro and Discussion read much like a review with a model in the middle. The meta-analysis and modeling approach is interesting and useful and should be more of the focus of the Intro and Discussion. Specifically, it would be useful to consider the relative or hierarchical strength/degree of harm from each factor as identified by the model. For example, there could be sentences such as “per unit change in nutrient x there is 50% greater change in survivorship that a per unit change in nutrient y.” These sorts of comparative conclusions would be informative, especially when applied to real-world situations.

We have re-focused the manuscript based on this comment. We now focus on the model we created rather than rehashing the patterns already found in other studies, and also demonstrate the application of the model using real-world seawater samples (Introduction page 4; Discussion page 17).

- Line 280: The sentence starting in this line seems to be very circular. As I read it, the authors state that conclusions from the literature agree with their model, but their model is based on data from these same articles in the literature (based on one being listed in Supplemental Table 1). This isn’t very informative and may be misleading to a casual reader by suggesting external verification of the model.

Similar comments have been made by the other reviewers, and so we have made extensive changes to the structure of the manuscript. We now focus on the application of our model rather than on re-stating previous findings (Discussion page 17).

- Line 280: In addition to the circular reasoning issue that I identified above, this sentence is also concerning because only one paper (Scott) was used in the modeling, while the other (Richmond) was not, yet both are suggested to confirm the results of the model. Why was Richmond not included? How are the results of the two studies different? This use of the literature is imprecise and confusing.

See previous comment (Reviewer 1, Comment 9). We have made changes to the focus of the manuscript and now focus on the application of our model rather than on re-stating previous findings (Discussion page 17).

- Line 285: It is not surprising that the model would reflect the results of the Chua study (because it was included in the model) but not necessarily reflect the results of the Albright study (which was not included in the model). I certainly would hope that the model reflects the data that went into it. Given that one study was used in the model and the other was not, it is misleading to draw the conclusion in this sentence that Chua is supported and Albright was not.

See previous comment (Reviewer 1, Comment 9, referring to Line 280).

- I appreciate that the authors identify some of the limitations of their model. This is rarely done and was useful and refreshing to read. While I fully understand their inability to compare across species, perhaps they could at least include reproductive differences (brooding or broadcasting) or another higher-order life history character as an effect in the model.

We attempted adding reproductive mode in our model. However, all species used for fertilisation experiments were broadcast spawners, and only one species used for survivorship experiments was a brooder. Therefore, we were unable to use reproductive mode in our analyses.

- The authors of many studies like this one suggest that their models can be used to establish environmental pollution limits and conservation priorities. Such an application is a very useful and noble pursuit, and thus I commend the authors for this. Yet, as with many other studies, the details of how the models can be used are buried in the methodological details. This way of describing the model may be informative enough for casual readers, but won’t be all that useful for someone trying to generate a useful prediction with the model based on a real-world situation. To allow others to use the model I suggest that the authors include a brief yet detailed supplemental describing how someone with e.g., phosphorous measurements from an MPA reef, can use the model to estimate the impact of phosphorous on coral fertilization and larval survival.

We have posted all data and analysis code in a Github repository, and referenced the repository in the supporting online information.

Minor comments:

- Line 56: “changes to alternative stable states” should be re-phrased.

We can see that this statement is poorly worded and have rephrased this sentence (Line 65).   
- Line 305: Consider re-phrasing “our study is significant because…”

This sentence has been re-phrased (Line 480).

**Reviewer #2:**

Overall comment: The difficulty of what is being attempted here is great. As noted in the conclusions the number of usable studies found is small and hence I think the uncertainty in any conclusions found is large. Hence I find many of the conclusions as to degree of effect unconvincing especially after examining the strength of the statistics as well as the range of concentrations causing effects. Overall I think many more caveats are needed in interpreting the analysis and unfortunately these will weaken the value of the conclusions from the study.  
  
Other comments:  
1. Very annoying that "phosphorus" is generally miss-spelt throughout.

These spelling errors have been corrected throughout the manuscript.

2. Line 49/50 - runoff MAY CAUSE eutrophication (a complex term to use anyhow) but not necessarily.

This sentence has seen re-phrased (Line 57).

3. Line 51/52. Separate "heavy metal" from "pollutants" - not automatically the same thing.

We have re-phrased this sentence (Line 59).

4. Line 52/53 - "higher trophic level" - higher than what?

We have changed this sentence (Line 60).

5. Line 55 - increased nutrient status can cause issues to coral reefs even in the absence of decreased herbivory.

This sentence has been changed (Line 63).

6. Line 60. - Not "leading to" but perhaps "associated with"

This change has been made (Line 69).

7. Line 86 - nutrient "concentrations" not nutrient "load"

This change has been made (Line 96).

8. Line 88/89 - The presence of copper and lead in ocean waters is not mainly the result of mining and manufacturing! Perhaps INCREASED concentrations above "natural" may be.

We have clarified this section of the introduction (Line 99).

9. Line 93. Rewrite this line as it is inaccurate as well as not making sense.

We have re-written this line to make it more accurate (Line 102).

10. Line 95 - "increased" freshwater fluxes?

We have made changes to clarify this sentence (Line 107).

11. Line 123 - What does "phosphor(o)us" mean here?? I'm assuming maybe "phosphate" or DIP - absolutely need to use an accurate term for what the levels or concentrations were actually of. As written it could be anything from TP, PP, DIP, DOP, TDP or some combination of these. This is totally unacceptable.

This change has been made throughout the entire manuscript.

12. Line 133 - Suspended sediment in experimental systems comes in many forms - with varying amounts of organic content, carbonate content, nutrient content etc and differing particle size. These will not all have the same toxic effect on the processes examined in this study.

While we agree with the Reviewer that suspended sediment can come in many forms, the studies used within our model did not specify the organic content, carbonate content or the nutrient content. While some the papers did suggest the particle size, it was not consistently stated across all papers used. We have added this concern to the list of issues raised in the caveats paragraph (Line 292).

13. Line 124 - By "acidification" you mean pH I think and you should say so.

This change has been made (Line 155).

14. Line 148 - Of the 18 studies how many included each of the parameters used in your analysis? i.e. how many studies included, for example, salinity as a test parameter. This is important to know.

We have created a table to show this information (Table 1).

15. Line 213/214 - However the results also show the resilience of the processes to changes in the other parameters.

We have made this point clearer in the Discussion (Line 491).

16. Line 216 - elevated copper often related to shipping and anti-fouling in coastal marine environments rather than just industrial activities

We have highlighted that copper is used in anti-fouling paint (Line 408).

17. Line 221 - No discussion here WRT the effects of "free" Cu ions versus organically bound copper in marine waters. Not a simple system.

We have made extensive changes to the discussion, which includes discussion about the complexities of copper in the marine environment (Discussion, paragraph 1, line 408).

18. Line 228 - Presumably what is meant here is reducing copper pollution NOT reducing copper presence in natural unpolluted systems. Needs to be made clear.

This section has been re-written (Line 408).

19. Line 230/231 - Incorrect - Cu is once again the main anti-foulant (in combination with herbicides) on new and current ships.

We agree and have clarified this point in the text (Line 408).

20. Line 231 - Most copper in marine environments DOES NOT originate from anti-fouling!!

We have clarified that this does not include naturally occurring within marine environments (Line 408).

21. Line 236 - I don't believe lead is likely to be a more serious pollutant than copper in nearshore environments because of its higher "levels". I note the references used here are very old and pre-date the reduced use of lead in petrol and the increasing use of Cu again in anti-fouling due to cessation of use of TBT.

We have made changes to clarify the statements regarding lead and copper pollutants (Line 413).

22. Line 250 - 100 mg/L is hardly a "low level" of suspended sediment!

We agree and have clarified this section to better reflect natural levels of sediment (Line 413).

Line 267 - wetlands to "fix-nitrogen" - I assume you mean to remove nitrogen as biomass or dinitrogen. I don't see how this affects phosphorus however the subject of this sentence.

This section has been re-written and this line removed (Line 415).

Line 276/277 - Why "especially in tropical waters"?

This section has been re-written and this line removed (Line 425).

Line Line 279 - There's no suggestion climate change will lead to the oceans or even coastal waters becoming GENERALLY less saline. Episodically perhaps in larger runoff events.

We have more clearly stated that these changes are episodic in nature and not general (Line 427).

Line 285/286 - pH effect depends on ranges of pHs tested in original studies. These are not shown so hard to comment.  
We have made extensive changes to the discussion with this section re-written (Discussion, paragraph 1).

Conclusions generally - More discussion of the effects of these parameters in episodic events would be good as this is when one gets the greatest range of many of the parameters tested.

We have attempted to show episodic results by re-focusing the paper onto our model and real-world scenarios (Discussion, paragraph 2).

Figure 2b - Huge concentrations of lead - unrealistic in the real world - amazing there is such a small effect given the toxicity of lead.  
Figure 2d - Not much affect until salinity is less than 25. i.e. all OK between 25 to 37.

Table 1. The references used for these "natural" concentrations in seawater are all inappropriate coming from aquarium sources etc. Please use well scientifically validated sources of which there are many. In particular assuming phosphorus means phosphate 0.446 (a strangely precise number!) uM is very high for "normal" tropical ocean waters.

We have now filled data gaps in two different ways for linear and quadratic factors (i.e., by either calculating one percent of the maximum pollutant treatment level reported across all studies for each factor or fitting a quadratic models and identifies peak probability; Methods, paragraph 2).

**Reviewer #3:**

Review of Wood's Environmental factors limiting fertilisation and larval success in corals  
This paper addresses for sure an interesting (i.e., publishable) topic, but several improvements are required before the ms (as a review paper) truly overviews the current state of the field the authors address in this ms:  
  
-     There are a lot of published papers missing from the analyses (e.g., the very famous review paper of Fabricius (2005)). Consequently, the paper simply reflects the "input", i.e., the limited number of papers used to generate the "model" rather than yielding new insights/ conclusions. Similarly, in the abstract the authors talk about the results of a combined "model", but after reading the ms, I am still not sure what was meant by this "combined model". Please clarify.

We have gone back to the literature and included a number of new papers to boost our analysis sample size. In the case of review papers – they could not be included in the analysis because they do not present original raw data. We did however read a number of review papers including Fabricius (2005) and included the papers used within their review.

-     Carry-over effects whereby planktonic experiences (partly) determine benthic performance should in my opinion be included to realistically reflect how stressors affect the ultimate benthic performance of recruits, especially since the authors set out to come up with a model linking various pelagic life stages.

While we agree that pelagic life-history can affect benthic performance we were not able to explore this process with the data we had for this study. Instead, we suggest in paragraph 4 of the discussion that our hope is that future meta-analyses will be able to focus on the transition to benthic stages of development, including settlement.

-     In the Abstract the authors mention that their findings can be used to define "recommended targets for water quality", but these appear to be missing in the text itself.

As suggested by all the reviewers, we have now focused our study on the applications of our model and hope that other researchers can utilise our models to recommend targets to Government bodies. For this reason, we will be making the data and code publicly available on Github.

-     I do not see how "a model" was constructed that includes all studies used. More so, it looks like the authors performed a meta-analysis of all datasets to draw conclusions on this larger dataset. This is confusing as one could interpret the use of the term "model" for some conceptual approach whereby all sorts of life-history aspects are combined to generate predictions on which species will be most successful in recruiting under what circumstances. This is not the case, and while the approach taken is not "wrong", I found it very confusing until later in the ms.

In retrospect, we can see that we did not adequately explain our approach in the original manuscript, and also agree that our Discussion was circular. We have spent substantial time expanding the explanation of the models and how the various data sets integrate into the same analysis (Line 206-260). We have also removed the circular Discussion and instead focus on real-world examples of using the statistical models we developed (Discussion, paragraph 2).

-     The use of "alternative stable states" (56-57) is inappropriate as these "states" should be able to exist under the same conditions whereas the states the authors refer to here exist under very different environmental conditions (e.g., altered herbivory and nutrient regimes). Check the original ecological texts on the appropriate use of these terms (I realize coral reef ecologists use these terms frequently in this manner, but it is still inappropriate).

We have rewritten this sentence to better reflect the wide-spread use of the terms (Line 64).

-     Clarify when you talk about larvae in the water column vs those crawling on the bottom… This will greatly aid to a better understanding of what factors affect what life stage.

We have made changes to the whole manuscript to better explain our use of the term larvae, as those within the plankton.

-     "experimental treatments tended to be large" (138)… Please clarify

This point has been clarified (Line 178).

-     While statistics are not my field of expertise, I noticed that values in your graphs often cluster around one value (often "0") with a few data points outside this range. The observed trends thus result from a very uneven distribution of data points along each axis of interest. Are corrections required for such data-distributions? Please clarify/ explain.

The reviewer is correct about the point clusters; these result from our assumption that unmeasured variables in published experiments were presumably close to levels in normal seawater (we explained how these were allocated in the Methods, page 6, line 172). Our analysis (GLMM) is robust to this kind of clustering in predictor variables, especially when considering multiple predictors. Clustering could potentially act to weaken modelled relationships, which therefore makes our analyses conservative.

-     Please quantify "relative importance" (211-212). Putting a value on "relative importance" would greatly contribute to a better understanding of the negative effects of all "stressors" considered in this study.

We have made extensive changes to the entire discussion section to better explain out model and show its applications as well as how different factors interact (Discussion Section).

-     Throughout the Discussion terms like "affected" are used a lot. Please provide "direction" (negative or positive) and "magnitude" (e.g., 3 times more) to explain how and to what degree stress factors affected the larvae.

We have made changes throughout the discussion to better describe our results (Discussion Section).

-     The results of the combined fertilisation x survivorship (FxS) model consist of only one example. This section needs elaboration. It appears that the model is a simple multiplication of independent factors whereby the joint probability is not surprisingly "less" than that of each factor individually (299-301). This section is unclear and needs to be better explained throughout the ms.

We have further explained the model within the methods and have included a new analysis to demonstrate our models use (Methods – Data analysis section).

-     Random factors were included in the model design, but results remain unreported. E.g., species choice could have affected the outcome of the analyses, but results are nowhere presented. Authors state that interaction effects or species choice did not affect the outcome of their analyses (309-319) but fail to support such claims by other studies.

We have included species as a random factor as discussed in the methods section (Methods, paragraph 1 in Data analysis section). We have also discussed this as a limitation within the discussion section (Discussion, paragraph 3).