Response to Editor, bg-2014-100 (30 Jun 2014) by K. K. Yates et al.

Dear Dr. Kiessling,

Very many thanks for allowing us to submit a second revision. We believe that we have addressed all of your comments and requested revisions, and that the manuscript is greatly improved. However, if we have misinterpreted any of your requests or if you have further questions regarding our responses, please do not hesitate to let us know. We have provided a point-by-point account of specific changes that were made. Your text is in standard black print, our responses are in red italic text. The references to line and page numbers are from the annotated version that you sent with comments to authors. We greatly appreciate your consideration of the revised paper.

Kind Regards,

Kimberly Yates et al.

EDITOR COMMENTS AND AUTHOR RESPONSES:

You have provided a lengthy and convincing response to the reviewers' criticism. I am therefore inclined to accept your paper for publication in Biogeosciences. However, some arguments you raise in your response letter do not show clearly in the revised manuscript and the text is still not to the point and somewhat disorganized. I must therefore insist on another revision emphasizing the points listed below. Importantly, stay closer to the data at hand and be less speculative. To my understanding you have observed high a high-diversity and largely healthy coral assemblage at Hurricane Hole and measured some physico-chemical parameters and bleaching/non-bleaching in two coral species. Data and analyses are missing that would prove that your specific habitat may be classified as a refuge. The arguments in your paper are interesting but not iron-clad. You can only provide evidence that shading by mangroves helps the corals, but the effects of saturations state and temperature variability is quite speculative and should be condensed.

Please consider carefully the following points:

1. Change of title. I agree with you that a question would be a bad title, but the reviewers concerns suffice to raise serious concerns about generalizing the role of mangroves as refuges. So a change of your title is necessary. Either you change the title to a more neutral term (e.g., Diverse coral communities in mangrove habitats suggest a novel refuge from global warming) or you are more specific (e.g., Mangrove habitats as coral refuges in St. John, U.S. Virgin Islands).

We have now changed the title to "Diverse coral communities in mangrove habitats suggest a novel refuge from climate change".

2. The buffering effect of mangroves from ocean acidification is still not convincing.

In your rebuttal letter you agree that the shading effect may be prevalent but you keep discussing at length the acidification issue, for which the evidence is still meager.

We believe that our argument for a potential buffering affect from ocean acidification was strengthened by the addition of (and comparison to) the reef data. We also feel that our evidence and data are consistent with evidence and data that have been presented in other published work that we reference on potential ocean acidification refugia (e.g. Manzello et al., 2012; Kleypas et al., 2011; Semesi et al., 2009a and b). However, we think that strength was not apparent because of lack of clarity in discussion. We have rewritten our arguments to better clarify this point and reduce speculation. Specifically, we have:

- *modified the text on pages 16-17, lines 495-502 to clarify that aragonite saturation states on the reef were lower than in mangrove coral habitats and that reef saturation states surpassed critical threshold levels while those in mangrove coral habitats generally did not.*
- *rewritten the paragraph on page 10, lines 274-287 to streamline the text and to clarify the fact that mangrove coral sites showed higher aragonite saturation states and lower pCO_2 than mangrove sites without corals.*
- *shortened sections 3.2 and 3.3 by 30% and changed the language in the text to reduce speculation and better focus on the data that provides specific evidence for buffering from ocean acidification.*

Overall you seem to be arguing that the stress in mangrove habitats (temperature variability, storms, runoff etc.) makes corals more adaptive to even more stress. This should be perhaps be laid out more clearly and be supported by suitable references.

We are arguing that shading and variable temperatures in mangrove systems make corals more resistant to thermal/irradiance stress. We have added discussion of findings in Palumbi et al. (2014), van Woesik et al. (2012), Oliver and Palumbi (2011), Mumby et al. (2001) to Section 4 of the revised manuscript to clarify that point and as further support for the role of temperature variation and shading in reducing thermal stress.

Our reference to the detrimental effects of runoff associated with storms was in response to the request from the reviewer that we discuss mangrove systems that would not be suitable refuges or habitats for corals. We make the point that one reason corals are thriving in Otter Creek and Water Creek is that freshwater input/runoff is limited. We have revised lines 475 to 477 to reduce any confusion.

3. You report many numbers and tests in the main text that could be summarized in tables. At the same time some of your tests are not to the point. Importantly, you report at length (l. 402-422) the different bleaching sensitivity of the two coral species, when you should rather provide a rigorous test on the effect of shading by mangroves. So either perform standard medical tests such as log-odds ratios (not

possible individually for C. natans because there are zeros in one category) or a binomial test on the probability that the observed differences are due to chance. With your numbers in table 8 I get:
Unshaded shaded
bleached 121 16
unbleached 69 73

The odds ratio is thus 8.5 meaning unshaded corals are eight times more prone to bleaching than shaded corals. This is the sort of information that may help the reader to follow your argument that mangroves are refugia.

We have now calculated the odds ratio and 95% confidence interval to strengthen our argument for shading providing relief from coral bleaching. We have modified the methods section, and added results and discussion of this analysis to section 3.4. Our numbers were slightly different than those that you calculated, so we have included detail below for your review (however only the contingency table and results of the analysis were incorporated into the manuscript text). Table 8 was updated with the data used for the log-odds calculation.

The following 2x2 contingency table was used to calculate the OR:

	Bleached	*Not Bleached*
Shaded	*13*	*75*
Sun	*115*	*75*

The OR was calculated from the above table as follows:

	Bleached	*Not Bleached*
Shaded	*a*	*b*
Sun	*c*	*d*

OR = (a/b)/(c/d), using the notation in the above table.
OR = (Bleaching in sun/Bleaching in shade) = (115/75)/(13/75) = 1.53/0.173 = 8.84

The 95% confidence interval for the OR was calculated as follows:
1. The equation for calculating the 95% CI for the OR was:
ln(OR) = 1.96 [square root of (1/a + 1/b + 1/c + 1/d)],
where a,b,c & d were taken from the contingency table
2. ln(OR) = ln(8.84) = 2.1793
3. 95% CI: 2.1739 ± 1.96 [square root of (1/13 + 1/75 + 1/115 + 1/75)]
95% CI: 2.1739 ± 1.96 [0.3350]
95% CI: Upper limit: 2.8305 Lower limit: 1.5173
4. Convert the natural log values back to their original scale:
OR = 8.84

UL = 16.95
LL = 4.56
5. OR with 95% CI = 8.84 (4.56 – 16.95)
6. Interpretation: Since the 95% CI does NOT include the value 1.0 (which would indicate there is no difference between the occurrence of bleaching in shaded vs. direct sun exposed corals), the 95% CI indicates the odds or likelihood of coral bleaching occurring in coral exposed to direct sunlight are significantly greater (i.e., at the 0.05 significance level) than in those corals that are shaded from the sunlight.

If you have appropriate data, you could also compare bleaching between mangrove systems and open reefs (the latter could be from the literature).

Comparable data are not available for a rigorous comparison. The National Park Service documented bleaching on long-term transects , and we know that bleaching occurred in 2010 on reefs around St. John (National Park Service, 2012). However, although general trends on coral cover are available, data on bleaching of colonies of individual coral species are not. The National Park Service monitoring program is based on videos along permanent transects and calculation of the number of dots falling on different benthic components. Following the status (fate) of individual coral colonies in terms of bleaching and recovery is not possible. Data from the National Park Service long-term transects suggested more bleaching of D. labyrinthiformis than many other coral species, and more bleaching of C.natans than in the mangroves. We have now included general information on bleaching on the reefs relative to in the mangroves in Section 3.4.

4. Please omit all but one statement of "more research is needed"

We have omitted all but one statement of "more research is needed" and have moved that statement to the first paragraph of the introduction.

Specific comments: Sections 3.2 and 3.3 are especially hard to read as they report much data in a somewhat disorganized fashion. Please summarize important data in a table or refer to figures and condense the text by at least 30%.

We have reduced the text in these sections by approximately 30% (or 493 words). Specifically, we have:

- *reduced the discussion of nutrient results and refer to data availability at PANGAEA in section 3.2*
- *tightened and reduced the text regarding calcification/dissolution thresholds in section 3.2*
- *reduced the discussion of NEC:NEP ratios in section 3.3*
- *and generally streamlined text throughout both sections, referring to data in tables and supplemental files at Pangaea to improve readability*

Section 4 also requires reorganization. Please start with a succinct summary of previously identified refuges and then put your findings in this context. Avoid repetitions.

We have reorganized Section 4, starting with a summary of previously identified refuges from thermal stress and ocean acidification. We have added several references to further support the discussion and removed repetition of concepts.

Finally, I agree with referee 1 that the absence of species-abundance data is regrettable and your argument that the morphology hinders quantitative assessments is weak. There are methods (e.g. line-transect method) to deal with this. Please try to compare some of the semi-quantitative data from nearby reefs with those in your mangrove system. This is important to judge which corals are best suited to survive in the stressed mangrove habitats. Importantly absent from your mangrove systems are the two *Acropora* species which are (or were) important Caribbean reefs builders. You may want to hint to this observation more explicitly, because it means that some corals may survive in mangroves but not the ones that may save the reefs.

We have expertise with coral monitoring methods (for example, Rogers, C., Garrison, G., Grober, R., Hillis, Z-M., Franke, M.A. 1994, 2001. Coral Reef Monitoring Manual for the Caribbean and Western Atlantic. National Park Service. 100 pp. including photographs, and other journal papers) including line-transect methods. Such methods cannot be applied in a rigorous way in these mangrove systems primarily because the corals are so shallow and are growing on and even wrapped around densely packed prop roots that are completely inaccessible (see our Figure 2---We can provide another photograph to further illustrate this point as well as the abundance and diversity of the corals if desired). We have added text to Section 3.4 to clarify this point.

The morphology of some species makes it impossible to separate "colonies" into individual, distinct colonies. This is discussed in Rogers (2010) Diseases of Aquatic Organisms 91: 167-175 (see Figure 1). Because of their morphology and densely growing clusters, it is not possible to delineate and count individual colonies of some species such as those in the genera Agaricia, Orbicella (formerly called Montastraea) and Porites all of which are common in the mangroves and on the "true" coral reefs. However, based on photographs and observations, we can estimate relative abundance qualitatively. We added a paragraph to Section 3.4 of the revised manuscript discussing relative abundance of corals in mangroves versus on the reef based on newly released data from the National Park Service (Atkinson and Miller, 2014).

<u>Acropora palmata</u> is restricted to shallow zones around St. John (and everywhere else it occurs). The most abundant species on the reefs in the USVI from near the surface to over 20 m is <u>Orbicella annularis</u> (along with other species in the <u>O. annularis</u> complex) (see Rogers et al. 2008. Ecology of coral reefs in the US Virgin Islands. In Coral Reefs of the USA, edited by Riegl and Dodge 303-373.) Our study species are among the primary Caribbean reef builders. Therefore, although acroporids do not thrive in the

mangroves, all other major reef-building species were observed there. Over 40 species of scleractinian corals and 3 species of Millepora occur in the USVI (see Rogers et al. 2008 cited above), and 33 have been seen in the mangroves. We have also added this information to Section 3.4 of the revised manuscript.

Minor issues: No numbering of references please.

We have removed the numbers on the references.

Update references to tables and figures. These are often wrong.

We have corrected the references to tables and figures. Please note that Figures 6 and 7 have been renumbered to reflect reorganization of section 3.4.

Consider omitting Fig. 5. Very hard to read and only visualizing Table 7.

If at all possible, we very much prefer to keep figure 5. It is the centerpiece of the process heterogeneity discussion and highlights the most important factors that differentiate coastal water chemistry from open ocean chemistry. An additional main point is to show that MNC sites are heavily influenced by carbonate dissolution and respiration, are considerably different than MC and ROC sites, and can provide a source of alkalinity to MC and ROC sites to support calcification. This concept is important and even more difficult to visualize without seeing a graphical representation of the data. We have reformatted the figure to make it more readable. The NEC:NEP data provide secondary evidence of process heterogeneity and are of particular interest to the ocean acidification community. With hope of keeping the figure 5 data in the paper, we have streamlined and reduced discussion of the NEC:NEP data.

Non-public comments to the Author:
Please also note my specific comments in the annotated manuscript

Page 3, lines 76-78. We have now rephrased this sentence to clarify it. It now reads, "Qualitative surveys conducted in one bay in 1984 suggest that corals were present at that time, but neither diverse nor abundant (Beets et al., 1986). We considered that an increase in the diversity and abundance of corals in mangrove communities since that time (Rogers and Herlan, 2012) may be a response to climate change".

Page 4, line 81. Reference to remarkable abundance and diversity. We feel very strongly about leaving the words remarkable abundance with respect to corals in the mangroves because it is highly unusual to find corals in mangroves and major review papers do not even refer to this phenomenon (e.g. Kathirsan and Bingham, 2001; Nagelkerken et al., 2008). Our census data shows hundreds of colonies of the two species that we studied, and there are thousands of other colonies present.

Kathiresan, K. and Bingham, B. L.:Biology of mangroves and mangrove ecosystems, Adv.

Mar. Biol., 40, 81–251, 2001.

Nagelkerken, I., Blaber, S., Bouillon, S., Green, P., Haywood, M., Kirton, L., Meynecke, J.-O., Pawlik, J., Penrose, H., Sasekumar, A., and Somerfield, P.: The habitat function of mangroves for terrestrial and marine fauna: a review, Aquat. Bot., 89, 155–185, 2008.

Page 4, line 85. We define alternative refuges as non-reef refuges at first use on page 3, line 63 of the introduction and do not imply any other meaning throughout the paper.

Page 4, lines 109-110. We have listed the reef site locations in the footnote of Table 4. The latitude and longitude of mangrove and rock outcrop sites are listed in the supplemental data tables available at http://doi.pangaea.de/10.1594/PANGAEA.825752. We changed the text of figure caption 3 to read "Data and latitude/longitude of study sites are available at http://doi.pangaea.de/10.1594/PANGAEA.825752" to clarify to readers that the information is accessible there. We updated the map in figure 1 to reflect all of the study sites.

Page 4, lines 110-111. We changed the text to "The reef sites were…"

Page 4, line 111. We have removed "Orbicella annularis". It was initially separated from other members in the O. annularis complex because there are many colonies that are large enough that they can be identified reliably, but that detail is not necessary here.

Page 5, line 116. We removed the text "not from surface waters".

Page 5, line 125. We changed the word "measurements" to"values".

Page 8, line 216. We corrected the spelling of "dependent".

Page 10, lines 276-281. We have split this sentence into two sentences and these now read, "Aragonite saturation states fell considerably lower than calcification/dissolution threshold ranges of 3.0 to 3.2 and/or pCO_2 exceeded thresholds of 504 to 584 μatm (Langdon et al., 2003; Silverman et al., 2009; Yamamoto et al., 2012; Yates and Halley, 2006) at all MNC study sites in Princess Bay and Water Creek during both November and July. Thresholds in Otter Creek were exceeded only during July 2011."

Page 13, line 380. We have rounded the values and removed the decimal place.

Page 13, lines 383-384. Page 13, lines 383-384. We do prefer to use the term "major reef building species" to make it clear that we studied species that reach a large size and tend to persist for long periods of time on the reef and contribute to the reef *framework as opposed to "weedy" species with small colonies. (All are scleractinian corals but not all are reef-building species.)*

Page 13, line 387. Re: use of term cryptic. We have revised this sentence and changed the word "cryptic" to "shaded" to avoid confusion.

Page 14, line 405. Re: which statistics test was performed. The p values to which we refer in this section are from the Fisher's Exact test as described in the methods section on page 5, lines 192-193. We have added the following text to clarify: "Fisher's Exact Test results indicated that different proportions…"

Page 15, lines 433-436. We have deleted the following text from this section: "There is an urgent need to identify the characteristics of corals and other reef organisms that could enable them to adapt to the variety of stressors associated with climate change and ocean acidification. Research is needed on how these factors interact and how they will affect the overall biodiversity, function, and transition of these ecosystems". And added the following sentence to the first paragraph of the introduction on page 3: "Research is needed on how these factors interact and how they will affect the overall biodiversity, function, and transition of these ecosystems".

Page 15, lines 440-442. We have removed the sentence," The presence and increase in abundance and diversity of corals in the mangrove habitats of St. John could be a recent phenomenon (within the past several decades)."

Page 15, lines 444-448. We prefer to leave the following sentences in this section: "Evidence of onshore migrations of coral in response to past changes in sea level rise is well documented in the geologic record (e.g. Hopley et al., 1983; Neumann and Macintyre, 1985). However, evidence for co-location of live corals and mangroves is not." This is factual and referenced information that supports the suggestion that these mangrove coral habitats may be evidence of a recent ecosystem transition that has never before been documented. We feel that it is important to point this out to the research community to encourage searches for similar occurrences in other mangrove systems.

Page 15, line 452. We have removed the sentence, "More definitive research on reef refuges is needed."

*Page 16, line 465**.** We have clarified this sentence by revising it to read "Many coral species do not grow over an entire depth gradient---"*

Page 16, line 485. Re: alternative refuge. We defined the first use of "alternative" in the introduction. We have removed (non-reef) from this line to avoid confusion.

Page 16, line 488. We have removed the text "…that we have described…".

*Page 16, line 497. Re: Carbonate mineral saturation states in mangrove coral habitats versus the reef. We have revised the text to read as follows, "*Carbonate mineral saturation states and pH in the mangrove coral habitats are not as low as those on the reef. Furthermore, mineral saturation states and pCO_2 concentrations on the reef surpassed critical carbonate dissolution threshold ranges while those in mangrove coral habitats did not. We suggest that the ability of a refuge environment to consistently buffer declines in pH and carbonate saturation state to keep them from surpassing critical thresholds (as opposed to periodically elevating them) relative to reef environments is the most important factor for providing relief from ocean acidification".