

Response to review of “Mangrove habitats provide refuge from climate change for reef-building corals” (bg-2014-100) by K.K. Yates et al.

Reviewer comments are in italics, and our replies are in plain text. List of all relevant changes for the editor is in red text, bulleted lists.

Anonymous Reviewer 1

General comments

A climate change refugia is a location that is buffered from an extreme condition associated with climate change. For reef-building corals and coral reef ecosystems, more broadly, we are talking about increased temperature and ocean acidification. Thus, a refugia should limit or reduce exposure to these stressors. Presumably this would be a demonstrated lessening of high temperature exposure that directly reduces bleaching and/or mortality associated with bleaching, or possibly some factor that ‘shades’ corals as the bleaching response is due to the interaction of temperature and light. The latter has been reported for some time, primarily anecdotally. In respect to ocean acidification, this would be an elevation in carbonate saturation state relative to the prevailing conditions either offshore, or at the nearby reef environment. This study shows that the mangrove habitat is warmer than the nearby reefs, so it doesn’t meet that criteria.

Keppel et al. 2012 define refugia as “habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions”. We consider the mangrove habitat that we have described as a refuge because it provides relief from thermal and photo-oxidative stress through shading by mangroves and greater variability of sea water temperatures. The presence of such a remarkable abundance and species richness of corals, and their largely intact condition in contrast to severe declines of corals on nearby reefs following bleaching and a major disease outbreak, supports the concept of this as a refuge. We suggest that it is primarily shading that has allowed a diverse community of corals to retreat to this mangrove habitats and to persist at elevated temperatures, and that this is the first documentation of such a diverse suite of corals thriving in this unlikely environment. We also discuss that exposure to warmer and more variable conditions in the mangroves may facilitate adaptation of these corals to higher temperatures which may enhance resiliency for future expansion under changing environmental conditions. We have added reference to Keppel et al. 2012 and defined refuge in a revised version. Additionally, we have expanded the discussion to clarify how the definition applies to this case in the revised version of our paper.

With respect to ocean acidification, we provide discussion and additional, new data (see below) indicating that saturation states at depth where the corals are actually growing are, in fact, lower on a nearby reef environment than in the mangrove coral habitat. However, we would also argue that elevation of carbonate saturation state in the mangrove coral habitat is not a refuge criterion requirement. Rather the ability of the environment to buffer declines in pH and carbonate saturation state is the more important factor.

- **Section 1, we have added Keppel et al. (2012) definition of refugia and other supporting text regarding our intended definition of refugia.**

- Section 4, added discussion of factors that define the St. John mangrove habitat as a refuge from thermal and photo-oxidative stress, and from ocean acidification.

*What the authors do show is that the mangrove canopy shades corals and this was associated with less bleaching and mortality, but this was only significant for *Diploria labyrinthiformis* as only 2 colonies out of 67 monitored in the other species assessed, *Colpophylia natans*, bleached.*

We chose the two coral species that were the focus of our observations because they were the most abundant major reef-building species in Hurricane Hole. They are thriving in Hurricane Hole despite the fact that both species declined in relative and absolute abundance on St. John reefs as a result of the 2005/2006 bleaching/disease event (Whelan et al. 2007, Miller et al. 2009). The fact that *C. natans* occurred statistically more often in the shade and that few of these colonies bleached provides more support for the role of shading in providing refuge conditions. Both of these species occur in exposed (as opposed to cryptic) habitats on the reefs.

- Section 3.4, added discussion on choice of species for this study.
- Section 3.4, added comment “The fact that *C. natans* occurred statistically more often in the shade and that few of these colonies bleached provides more support for the role of shading in providing refuge conditions.”

The discussion of ocean acidification is a bit puzzling because the authors compare carbonate chemistry of mangrove sites with and without coral to nearby rocky outcrops. What is perplexing is that there is no measurement of carbonate chemistry on any of the nearby reef environments (where corals primarily live (at least historically) and accumulated framework), nor in the offshore waters. The aragonite saturation state values at the mangrove and rocky outcrop sites reach a maximum mean value of $\Omega_{3.6}$, based on Figure 3. I've seen CO₂ data, albeit unpublished but analyzed according to 'best practices', that show values on US Virgin islands Reefs from July, including St John, average approximately 3.9, with minimum value of 3.7 and a maximum value of 4.1. Therefore, with respect to acidification, these sites may be more impacted than the nearby reefs if cumulative exposure to aragonite saturation state levels $< 3 - 3.2$ (as discussed in paper) is what is important. This is the value when it has been hypothesized that coral reefs will become net dissolutional (i.e., rates of dissolution exceed calcification). Is this relevant to the non-reef setting studied? We know corals can grow just fine at low saturation states, but generally fail to accrete anything less than about 3. The paper is unfocused and incomplete as the real link to any possible refugia seems to be associated with shading from the mangrove canopy, yet there is much discussion about carbonate chemistry (e.g., sediment mineralogy and organic matter, rates of net ecosystem calcification [NEC] and net productivity [NCP] etc.). The affirmation that these site are buffered from acidification doesn't seem supported because there is no data from any reef environments. The authors rationale is that the general direction of the current is from the mangrove fringe out to Hurricane Hole to the open ocean, thus the low NEC/NCP ratio in the mangroves buffers the corals to acidification by raising

aragonite saturation values. The conclusion of net current flow is based on Lagrangian drifter studies from one point in time (one August) and a MS thesis. However, the bigger issue is that the authors don't talk about CO₂ on reefs, which seems to be lower on the reef vs this environment. It seems difficult to suggest that a site is buffered from acidification if CO₂ levels are naturally higher than the reef, right? This manuscript needs considerable work to tighten focus and narrative. A refugia from corals may be plausible on shaded mangrove prop roots, but this is a thermally related response with little to do with ocean acidification.

The primary focus of this study was, in fact, the Hurricane Hole mangrove habitat. The simple fact that a very diverse suite of reef building corals are thriving in a mangrove habitat (despite repeated exposure to elevated temperatures, extensive coral loss due to bleaching and disease on nearby reefs, and chronic exposure to episodic storm events) when corals on nearby reefs are not is first line evidence that this mangrove habitat is providing refuge for corals. The intent of this paper was to provide the first detailed characterization and documentation of a mangrove coral habitat and to identify characteristics for this and other mangrove environments that are potential resiliency factors for coral refuges (see Table 7 in the manuscript). The sampling schedule was very intensive in this area, and logistics and resources prevented concurrent measurements of the reefs and offshore waters outside of Hurricane Hole. Valid comparison of the reef data reported by the reviewer to our data depends upon whether or not these unpublished data were collected from surface waters or near the seafloor, the habitat composition, and at what time of day they were collected. Without access to the unpublished data that are being referred to by the reviewer we are unable to compare our data to the reviewer's data.

We do, however, have limited data from a nearby reef in Long Bay (approximately 2 km from the nearest mangrove coral study site) that we collected from July 16 to August 22, 2004. We originally considered including these data, and decided they might be too "dated" having been collected more than 6 years ago. However, in light of the reviewer's comments and general absence of published data for comparison, we have now included these data here and in the revised version of our paper. Figure 1 in the revised manuscript has been modified to include this study location.

Our data from Hurricane Hole and from the Long Bay reef were collected near the seafloor, not from surface waters. Many seawater-monitoring programs collect surface water measurements. Very few time series measurements at depth have been collected. We have also included (here and in the revised manuscript) vertical profile data of carbonate system parameters that we collected over a coral habitat at 6.5 m water depth near the mouth of Otter Creek at 7:00 am on July, 19, 2011 that show surface water to seafloor gradients in these parameters (Fig. 1). These data were collected at 1.5 m, 3.0 m, 4.6 m, and 6.0 meters water depth. Results showed considerable differences in aragonite saturation state (Δ 0.34), pH (Δ 0.04), and pCO₂ (Δ 40 μ atm) between surface and bottom water. These data demonstrate why one cannot assume that surface water measurements reflect bottom water conditions even in shallow water environments.

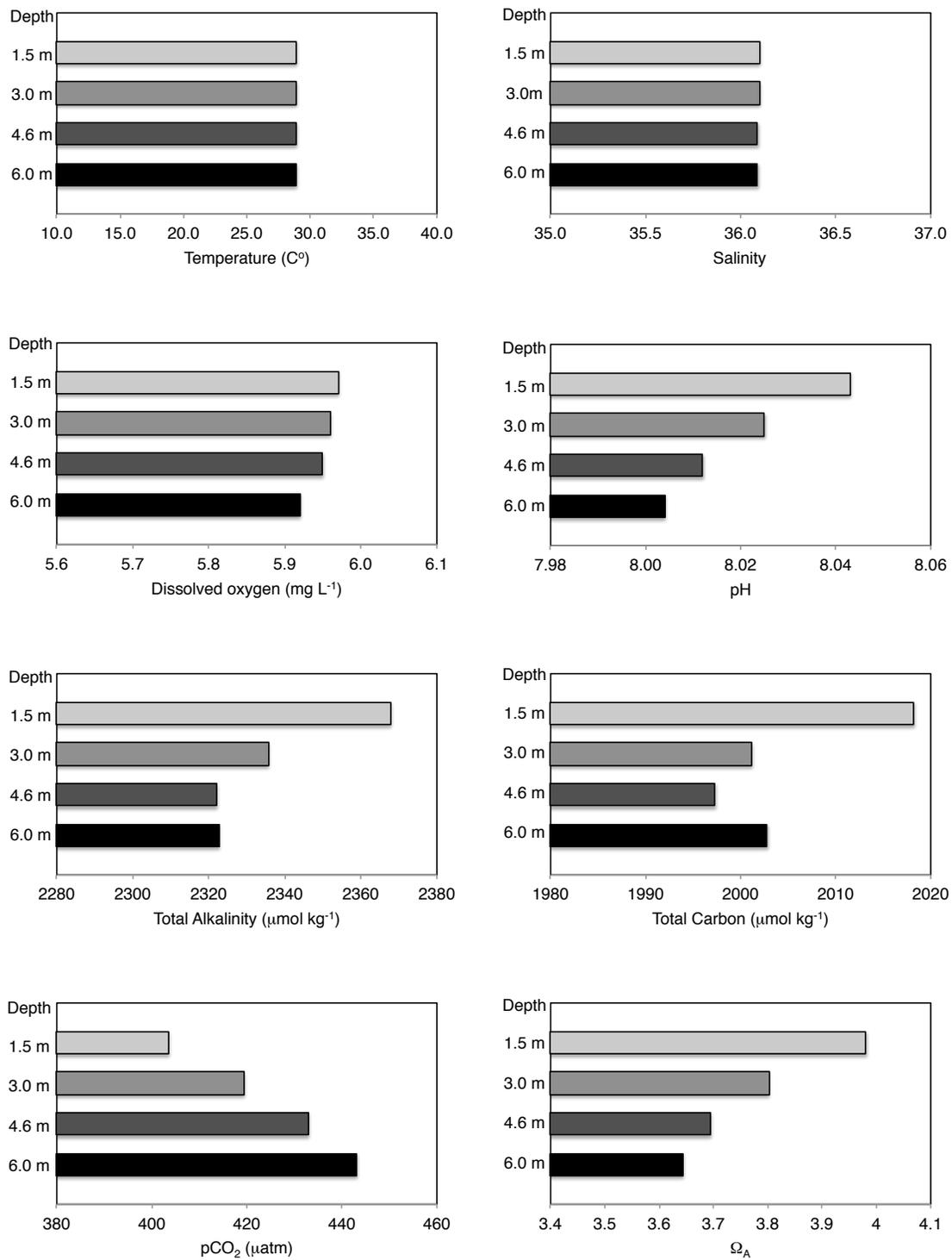


Fig. 1. Vertical profile data of seawater chemical parameters collected at 7:00 a.m. on July 19, 2011 over coral habitat at 6.5 m water depth. Vertical axis = depth below sea surface.

Measurement of diurnal variability in carbonate system parameters in Hurricane Hole indicates that lowest saturation states, pH, temperature, and DO, and highest TCO₂, pCO₂, and TA generally occur in the early morning and are reflected in our 7:00 am measurements (see <http://doi.pangaea.de/10.1594/PANGAEA.825752>). Our reef data from Long Bay were only collected at 7am and 11am. Therefore, only the minimum Ω_A , pH, temperature and DO data, and maximum values for TCO₂, pCO₂, and TA from our reef data are comparable to Hurricane Hole data. However, median data for all Long Bay reef parameters may be biased toward lower or higher values. We have excluded discussion of the November 2010 data that were collected in Hurricane Hole during tropical storm conditions and off-season from the July 2004 data, and have focused discussion on minimum and maximum values that are comparable from each study site.

The seawater chemistry data at Long Bay reef were collected using the same methods as described in the methods section of our manuscript, and samples were collected from less than 1m above the seafloor. We have modified figure 3 in the manuscript to include the reef data (and it is also presented here as Fig. 2) and have also included a table of the reef data. Long Bay reef aragonite saturation states showed a minimum value of 2.93 that was considerably lower than any other coral site in Hurricane Hole. This reef value is also lower than the reported range of dissolution thresholds. The lowest saturation state of 3.18 at Hurricane Hole coral sites occurred in Otter Creek during July 2011, and this was the only coral site that showed a saturation state that fell within the reported carbonate dissolution threshold ranges. All median and maximum values from Hurricane Hole coral sites in July 2011 and 2012 fell well above dissolution threshold ranges, and maximum values reached 4.2. Minimum pH observed at the Long Bay reef was 7.894, and was lower than the lowest pH (7.95, and also in Otter Creek during July 2011) recorded for any coral site in Hurricane Hole. Maximum pCO₂ values at Long Bay reef (626 μatm) were higher than any other coral site in Hurricane Hole (maximum = 550 μatm in Water Creek, July 2011) and fell above the reported dissolution threshold range. Reef data for DO, temperature, salinity, TA, and TCO₂ are also included and discussed in the revised manuscript. Our data indicate that maximum aragonite saturation states at the seafloor where corals are growing are not elevated in mangrove coral sites relative to the nearby reef. However, minimum values at mangrove coral sites are not as low as those at the reef site and in most locations remain above saturation state thresholds for carbonate dissolution unlike reef values. We would therefore argue that our data do, in fact, show that the mangrove coral habitat can potentially provide refuge from ocean acidification by buffering against low pH, high pCO₂ and low saturation state. The processes that may facilitate this buffering effect are discussed in sections 3.2 and 3.3 of the original manuscript.

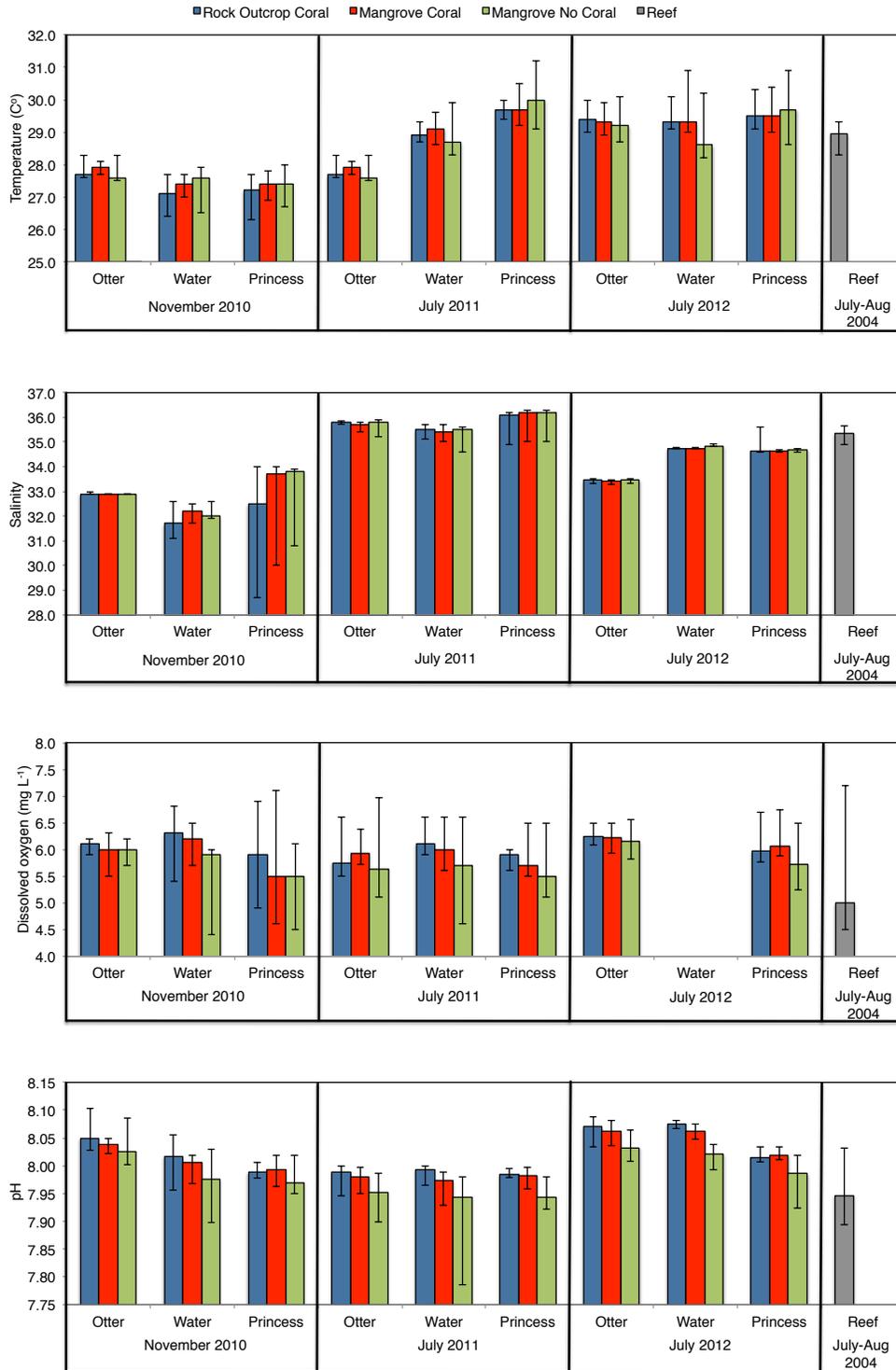


Fig. 2. Chemical and physical parameters. Median and range for chemical and physical parameters in Hurricane Hole bays during November 2010, and July 2011 and 2012 and for Long Bay reef during July and August 2004. Measurements were made every 4 h throughout a diurnal cycle ($n = 7$) at each study site during November 2010 and July 2011 and 2012, and for 3 consecutive days ($n = 19$) in Otter Creek during July 2012. Measurements at Long Bay reef were made at 7am and 11am ($n = 7$ and 3, respectively). No DO data were collected in Water Creek

during July 2012 due to DO sensor failure. Red shaded areas (3g and 3h) show reported ranges for $p\text{CO}_2$ and Ω_A thresholds for carbonate sediment calcification and dissolution. Data available at <http://doi.pangaea.de/10.1594/PANGAEA.825752>.

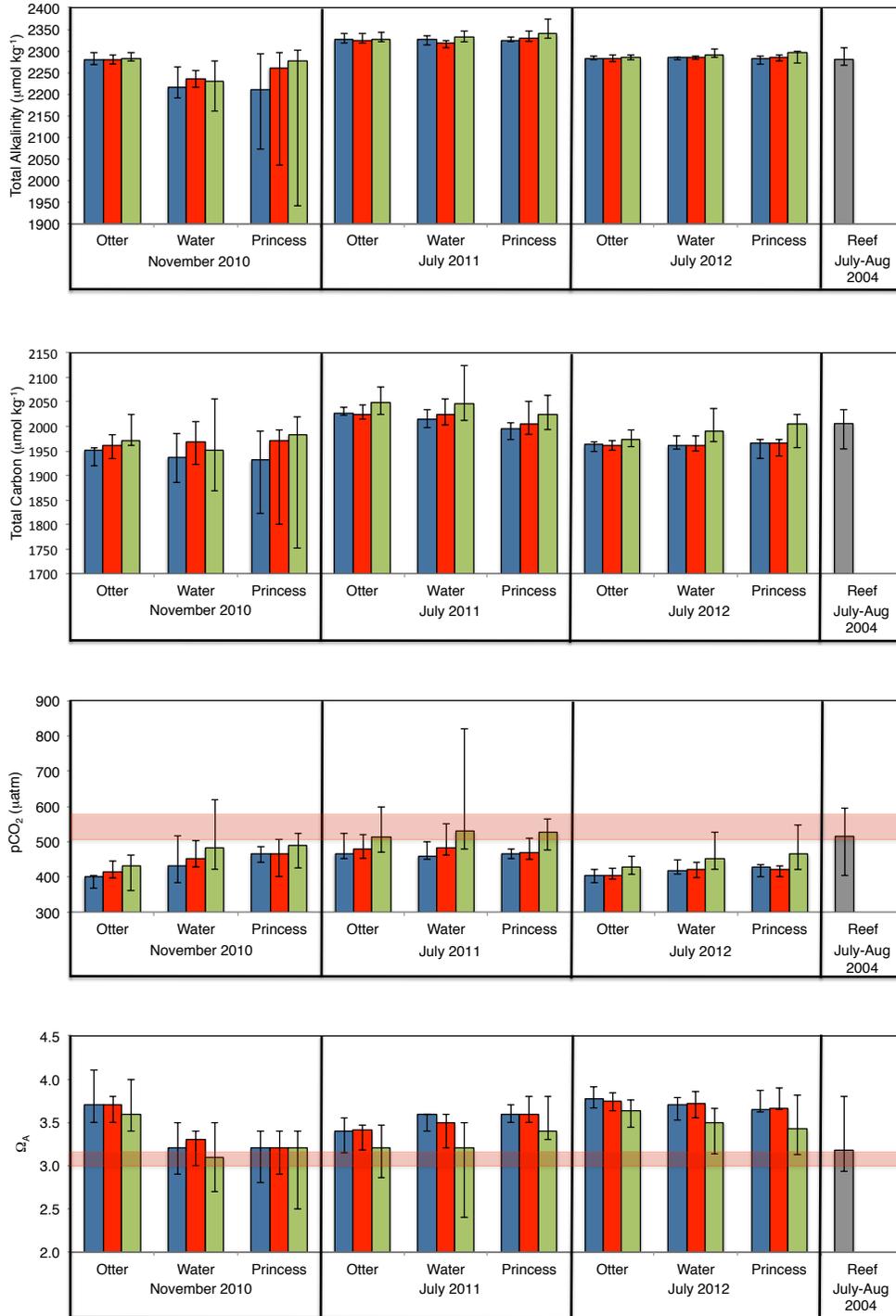


Fig. 2. Continued.

- We have added text to Section 2.0 and 2.1 to describe the methods we used for collection of reef data in Long Bay and vertical profile data near Otter Creek.
- We have added discussion of Long Bay reef and vertical profile data to section 3.2, modified figure 3 to include reef data, added a figure (now figure 4) for vertical profile data, and added tables (now tables 3 and 4 for vertical profile and reef data, respectively).

Also, I'd like to see a discussion about whether or not mangrove environments, different from this one, can serve as refugia. These shallow environments are associated with high thermal variability (as mentioned) and many can receive considerable runoff.

As noted in our Introduction, “mangrove communities are not thought of as having suitable conditions for coral recruitment and growth due to high sedimentation rates, lack of suitable substrate, and inadequate water quality”. Yet corals are thriving in the mangroves of Hurricane Hole. We have described the physical, chemical, and biological conditions that we believe are enabling corals to take refuge in this habitat. While many mainland coastal mangrove habitats do not share these characteristics, there are many more small island habitats that are potentially very similar to those on St. John for example where freshwater input is limited. However, we have found only two published references to corals growing in mangroves (Macintyre et al., 2000 and Rutzler et al., 2000, page 5056 of our paper), and no comprehensive multidisciplinary surveys of these habitats have been performed. There is also anecdotal evidence (online tourist photos) showing coral mangrove habitats in Raja ampat, Panama and Belize indicating that this is not an isolated case.

Our motivation for publishing resiliency factors for mangrove coral habitats is to provide the scientific community with baseline information to identify other potential mangrove coral refuges and perform these types of surveys in other locations. We believe these habitats have been largely overlooked because coral reef scientists don't typically look for corals in mangroves, and wetland scientists are usually focused on wetland vegetation and not corals. We stated on page 5067 in our discussion that “The unlikely association of corals with mangroves in many coastal ecosystems due to unsuitable growth conditions has dissuaded previous consideration of these habitats as potential coral refuges. However, numerous small tropical islands worldwide have physical characteristics similar to the US Virgin Islands and the potential for suitable mangrove–coral refuge conditions.”

- We have expanded the discussion in Section 4 regarding other potential mangrove habitats. However, no other mangrove coral refuges have been identified and no other data are available for comparison.
- With regard to the high thermal variability associated with some mangroves, corals subjected to variable water temperatures in some locations have shown higher resistance to thermal stress. As supporting information, we cited van Woessik et al. 2012 on page 5066 of our manuscript, and have added to our revised manuscript a citation to a paper that was just published by Palumbi et al. 2014 in Science on corals growing in shallow pools with high temperature variability in

American Samoa.

Specific comments

P5055, discussion of reef refugia. What about the deep reef refugia hypothesis (DRRH)? There was an entire issue of the journal Coral Reefs dedicated to this topic and this has garnered a lot of interest in recent years.

Our focus is on refuges for shallow-water corals. Although more research is needed, the potential for deep reefs (often defined as 30 m and below) to serve as refuges for corals and sources of replenishing larvae for shallower reef zones appears to be limited (Bongaerts et al. 2010). Such areas are not immune to major stressors including bleaching and disease (e.g., Menza et al. 2007, Smith et al. 2010). Many coral species are not found over an entire range of depths, many do not “broadcast” (spawn) larvae, and deep-water corals will not, therefore, provide larvae that can settle and survive in shallow waters.

- We have added this information to Section 4 of the revised paper.

P5056, no mention of depths of sites. Please list. You say 0 – 6m. What are the depths the corals are in etc.?

- The depths of the study sites are listed in the data tables of the supplementary data at <http://doi.pangaea.de/10.1594/PANGAEA.825752>.
- We have now revised the methods, Section 2, to include these data.

P5061, you discuss a storm event. You need to discuss importance of episodic events. For instance, if you get a significant storm event that causes high rainfall and lowers salinity, this could potentially kill a lot of corals. Need to discuss how this may impact mangrove prop roots as refugia.

Mangrove habitats with high input of freshwater runoff will not provide suitable habitat for corals. Some corals can, however, persist in mangroves if freshwater input is limited to infrequent storm events. At our study site, Princess Bay has a lower coral diversity and abundance perhaps because it receives more runoff than Otter Creek and Water Creek due to a larger sized watershed. However, large and numerous corals of many reef-building species have survived several storms in Hurricane Hole over decades.

- We have addressed episodic storm events along with potential effects of watershed size in Section 4.

P5063-4, discuss differences in CO₂ at different sites being driven by differing NEC/NCP ratio. Wouldn't a simpler explanation just be that sites with higher saturation state are likely more flushed and receive more water exchange with the open ocean?

We did a preliminary evaluation of flushing as a factor by performing a correlation analysis between tide and saturation state. We found no significant correlation between these parameters. The most notable correlations were between dissolved oxygen and pH,

TCO₂, or pCO₂, and between salinity normalized TA and TCO₂ indicating that photosynthesis, respiration, calcification, and dissolution were primary factors controlling the seawater chemistry and saturation states. The correlation analysis was beyond the scope of the paper; however, it was instrumental in leading us to calculation and discussion of the NEC/NCP ratios to examine the role of these processes in the mangrove habitat.

- We have not included this data because it did not add value and is beyond the scope of the paper.

Table 1, you present presence/absence data for multiple coral species. Why not any abundance data? It would be helpful to know how abundant the corals are in this environment relative to the reefs. Just cause corals are growing on the prop roots doesn't necessarily mean it's a refugia. Authors need to do a better job convincing the reader that this is a refugia 'effect' that is driving this trend.

It is possible to evaluate the relative abundance of some of the coral species in the mangroves and on the reefs qualitatively. However, a rigorous quantitative comparison of the relative and absolute abundance of all the species of corals in the mangroves versus on the coral reefs around St. John is not possible for a number of reasons. For example, 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. Additionally, the dense mangrove prop roots and shallow water make many coral colonies inaccessible. The National Park Service has long-term data on the cover of corals (not on density of colonies, or number per specified area of the bottom) that show one group of species, in the genus *Orbicella* consistently has the most cover. This group is abundant in the mangroves but not as abundant as the two major reef-building species that we focused on in our research.

The most abundant species in the mangroves are *Colpophyllia natans*, *Diploria labyrinthiformis*, *Orbicella* spp., *Porites* spp. and *Agaricia* spp. *Colpophyllia natans* and *Diploria labyrinthiformis*, the subject of the observations on bleaching and recovery reported here, have a higher relative and absolute abundance in some portions of Hurricane Hole than on the island's coral reefs based on data on coral cover from the National Park Service. Furthermore, these two species declined in relative and absolute abundance on the reefs as a result of bleaching and disease in 2005/2006. Several species in the mangroves have very few individuals---including *Scolymia* and *Mycetophyllia*. These coral species are more often found in deeper water (greater than 10 m) and are presumably able to survive because of the shading by the mangroves. The remaining species have an intermediate abundance. We suggest that this occurrence of such a high abundance and diversity of corals in the mangroves (along with other supporting information that we provide) does support the concept of this area as a refugium.

- Abundance data for coral species on St. John reefs are referenced on page 13, Section 3.4, lines 383 -388 of the revised manuscript.

- We have not included any additional abundance data in the revised manuscript because this information is based on personal observation.

Technical comments 1) Species names of corals aren't italicized 2) Fig 3 and 5 are hard to read

- We have corrected the species names
- We have changed the font size in figures 3 and 5 and formatted them to make them more clear
- We will work with the typeset editor to insure that the figures are easier to read.

Anonymous Reviewer 2

General Comments:

This clearly written paper describes an unusual (or possibly under-reported) habitat occupied by zooxanthellate corals among the prop roots of mid- and outer-bay mangroves of small tropical islands. The research team recorded observations of specimens or colonies representing more than 30 taxa of stony corals growing on or under mangrove prop roots in Hurricane Hole, St. John, US Virgin Islands. The authors measured a suite of physical and chemical parameters in inner-bay mangroves that lack associated corals, in mid- and outer bay mangroves with associated corals, and rock outcrops with unshaded corals.

The title of the paper might be more appropriately phrased as a question rather than as a statement. Moreover, while the authors measured a variety of chemical parameters, their observations support previous reports that shading is an extremely important factor in protecting corals from higher temperatures. Mangroves are consistent sources of colored dissolved organic matter (CDOM), which attenuates shorter, more damaging blue to ultraviolet wavelengths of light (see Zepp et al. 2008 or Ayoub et al. 2012 and references therein), and thereby can substantially reduce photo-oxidative stress that induces bleaching (e.g., Fitt and Warner, 1995). In this respect, corals living in proximity to mangroves are protected from the highest energy solar radiation by CDOM, just as mesophotic corals are protected by water depth. The major difference, which is critically important for the survival of shallow-dwelling coral species, is that many shallow-don't live in mesophotic habitats. So even if the author's data may not be particularly strong with respect to ocean acidification, their observations should be very useful to reef-resource management because they reinforce previous work concluding the critical importance of mangroves and CDOM. Although local management practices may not be able to protect coral reefs from ocean acidification, they can protect coral species from extinction by keeping mangrove shorelines intact.

- We have added reference to CDOM to the revised manuscript, and we have added new chemical data from nearby Long Bay reef to strengthen our conclusions regarding ocean acidification as discussed in the response to reviewer 1.
- Our discussion now includes the following information and references: "In addition to shading by mangrove trees, colored dissolved organic matter (CDOM) in the water near mangroves, especially where there is frequent freshwater input,

could also attenuate harmful visible and ultraviolet radiation and reduce the photo-oxidative stress on corals (Fitt and Warner, 1995, Shick et al., 1996, Zepp et al., 2008, Ayoub et al., 2012).” We do not think that CDOM is likely to be playing a major role in providing additional shading but it could be a contributing factor. The water clarity is generally very high particularly in shallow water near the mangrove prop roots in the bays we studied. Our PAR data in figure 5 shows that PAR at the rock outcrops which are in very close proximity to the mangroves is not considerably attenuated relative to PAR measured in air indicating that CDOM is likely not contributing much to attenuation of solar radiation.

- We believe that addition of the reef data, definition of refuge and clarification of the application of that definition to the mangrove habitats of St. John strengthens our argument that this habitat is, in fact a refuge for coral from climate change. We, therefore, prefer not to change the title of our paper.

Specific Issues:

a. What is the mineralogy of the rock outcrops? Are they limestone or igneous/metamorphic? That is important to understanding how the substrata can influence local seawater chemistry, as well as the texture and mineralogy of the sediments.

The rocks of St. John are all igneous and metamorphic. There is no limestone on the island (Rankin, 2002), so all of the carbonate sediments are modern, in situ, marine biogenic carbonates.

- We have now added this information and reference to Section 3.1 of the revised manuscript.
- Sediment grain size and mineralogical data from all of the study sites are in Tables 4 and 5 of the original manuscript.

b. Are there similar chemical and physical data available for reef sites in the general area? If so, this could contribute to understanding what environmental parameters associated with the mangrove habitat are particularly favorable to the corals.

- We have now included data from a nearby reef in Long Bay in the revised manuscript as is discussed in the response to reviewer 1.

Technical correction and suggestion:

Section 2.1 Seawater chemistry, line 10, fourth word should be “were” (not “was”).

Tables would be more readable if data were centered below headings (other than in the left column).

- These technical issues have been corrected in the revised manuscript
- We have also added reference to the Riegl and Piller (2003) and related text to Section 4, lines 453-460 of the revised manuscript

Reviewer References:

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