

Interactive comment on “Multi-decadal changes in structural complexity following mass coral mortality on a Caribbean reef” by George Roff et al.

Anonymous Referee #1

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This study combines field measurements of *O. annularis* survival/mortality, erosion, and linear extension across two decades following the 1998 bleaching event with a model of how those changes affect colony complexity over time. These sorts of fine-scale measurements of how coral mortality affect reef structural complexity and habitat partitioning are rare and it is, therefore, an important contribution to the literature. The manuscript is well-written and worthy of publication, but I think it could benefit from a more nuanced discussion of several aspects of the results, the most significant of which I've outlined below.

First, I would like to see the authors discuss how unique their results are to the specific

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species of coral/habitat considered in the study. I suspect that the lack of change in colony-level rugosity is at least partially a result of the unique morphology and growth of *O. annularis* and the fact that the measurements were made continuously along the perimeter including the narrow gap between ramets (see my next comment). When most corals experience partial mortality (including other species of *Orbicella*), the majority of the regrowth by surviving ramets will be lateral, rather than vertical as in *O. annularis*. Therefore, the net positive growth of the corals in this study despite high levels of mortality, is not a result that would likely be observed in other species. The reef considered in this study is also fairly unique in its dominance by *O. annularis*. Although the authors are correct that *Orbicella* spp. have been dominant species on reefs throughout the Caribbean for more than a million years, many fore reefs have been dominated by *O. faveolata* rather than *O. annularis*, which is typically more common in lagoonal environments. While never stated outright, the manuscript implies from the very first sentence of the introduction that the reef considered in this study is typical of Caribbean reefs, but I would argue that the trajectories of erosion and complexity are likely very different elsewhere. I would like to see the authors more directly discuss how their observations from *O. annularis* at Long Cay may differ from what occurs for other species in other locations.

I would also like to see the authors put their rugosity estimates in the context of more traditional rugosity measurements that have been done on reefs and to discuss more explicitly what the observed changes in colony growth mean for the geometry of habitats within the colony. First, the rugosity estimates in this study are based on a theoretical continuous perimeter along the colony surface, whereas more traditional, chain-based methods of estimating rugosity vary based on the interval (chain link size) over which the measurements are made. In theory, the sort of continuous measurement estimated with the model in this study is a more accurate representation of overall rugosity, but from a practical standpoint it also gives a relatively high weight to the very narrow microhabitats between ramets. A traditional chain-based rugosity survey over the tops of these colonies would likely miss these microhabitats (which only have

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an average opening of 0.4 cm) and would put more weight on coarse-level rugosity, which is likely low on living *O. annularis* colonies. This is important because while this study did not find significant colony-level rugosity changes over time, with the continued divergence between live and dead ramets, there likely were significant changes (increases) in more coarse-level rugosity that would be picked up with a chain-based measurement. The scale over which rugosity is considered is critical when thinking about how habitats may be changing over time. I think this is what the authors may have been suggesting in relation to the changes in the urchin populations, but changes in the sizes of microhabitats is not considered/discussed explicitly by the authors. It may be beyond the scope of this study, but one way to try tease apart changes in habitat over different scales would be to use the model presented in this study to look at the rugosity changes with varying theoretical measurement intervals ("chain link sizes"). A more minor, but related point is that while the authors suggest that the colony-level measurements represent "reef-scale" rugosity in several places in the manuscript, to my understanding they are only based on the height of the ramets, rather than on total colony elevation from the reef surface. That information and information about colony spacing would be needed to accurately estimate reef-scale rugosity.

I also think that it is important for the authors emphasize early in the Results and Discussion section that only vertical erosion was quantified/considered in this study. Although it is briefly discussed towards the end of the manuscript, the modeled changes in complexity do not consider erosion on the sides of the ramets, which is significant based on the images of the colonies. This erosion could have a significant effect on the perimeter values used to estimate rugosity in the model. This should at least be discussed as an assumption/source of uncertainty in the model.

Finally, I have some concerns about the discussion of the changes in urchin populations, which seem somewhat in conflict with the major conclusion of the study: that there were no significant changes in colony-level complexity over time. The authors suggest in the discussion that the decline in *Eucidaris* populations was a result of "ob-

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served long-term changes in complexity among crevices" (Lines 155-157), but the is at odds with the conclusion that structural complexity was "remarkably stable" (Line 107) over the time period. Furthermore, they suggest that bioerosion caused reduced crevice depth (Line 162), but the increase in the height difference between live and dead ramets over time seems to suggest just the opposite. The increased aperture of the openings between ramets because of erosion on their sides seems to be the most likely reason for increased predator access, but as mentioned previously, these changes were not measured/considered explicitly in this study. I don't necessarily disagree with the conclusion that urchin populations decreased because of increased access by predators after the coral mortality event, but I don't see how this conclusion is supported by the data they present.

Specific comments:

Line 10: "Th" should be capitalized throughout

Lines 22-23: I don't think this is true on many (most?) reefs anymore and this statement is not directly supported by the study cited at the end of the sentence. Although *Orbicella* spp. were historically the most abundant coral in Caribbean fore-reef environments, its abundance has declined significantly in many locations and the relative abundance of other taxa is now higher (as highlighted in Alvarez-Filip's studies for the Mesoamerican reef, specifically). I would re-word this sentence. It might be worth mentioning that this is a species complex not just *O. annularis*. Are the corals in this study *O. annularis* specifically? It looks like it from Fig. 1, but it would be good to make that clear in the methods.

Line 40: add a hyphen after "micro"

Lines 70-71: I think it might be helpful to add a sentence describing how these complexity measures are different from more typical, transect-level complexity measurements. Before digging into the code, it wasn't clear to me, for example, that the colony-scale complexity estimates were only measured for the top surface of the colony (right?), not

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from its base.

Line 81/Figure 2c: The graph is labeled 2008, but the surveys were done in 2007, correct?

Line 82-84: This data should be summarized (means +/- SD) even if they were ns

Line 94: I would suggest changing “results in” to “resulted in” or perhaps just “drove”

Line 135-137: The colonies in the Keys were also 100% dead for the entire study period, so there was no potential for accretion. The two studies were also looking at different species of *Orbicella*, which have very different morphologies. Had there been surviving fragments of the *O. faveolata* colonies in the Keys, they would have likely expanded laterally before resuming any significant vertical growth.

Line 169-170: Is Long Caye a marine protected area? What is known about how invertivore populations have changed there over time?

Line 187: You are not looking at reef-scale complexity because your measurements are restricted to the top surfaces of the colonies. More broad-scale complexity relative to the seafloor is not considered.

Line 199: And 2003, correct? There are field photos from that year.

Line 204: A minimum distance?

Line 206: “it” should be “them”, correct?

Line 210: were there also random factors included in the model?

Line 215: Where were the heights measured from? Not the base of the colony based on the values in the code. I’m guessing that it is the “height (i.e., vertical depth) of the ramet that parrotfish can graze, based upon field measurements.” From Roff et al. 2015, but this is not clear in the text.

Line 235: *O. annularis* should be italicized Figure 1: Was there no bleaching in Belize

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after 2010? What about disease?

Line 37 in the R code: The comment says minimum colony height was set at 2, but the value is 2.5. Thank you for providing your code!

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