

Reviewer #1

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.

We appreciate the reviewer's thoughtful and detailed comments which have substantially improved the manuscript. We have included all revisions as suggested, and have outlined our responses and amendments below:

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

Done. We appreciate the reviewer's point. First, we have amended the methods to clarify the monospecific stands of *O. annularis* in the present study and outline the *O. annularis* species complex to avoid confusion. Additionally we have included a broader description of the *O. annularis* species complex to highlight ecological differentiation among taxa within the complex:

The study was conducted in Long Cay (Glovers Reef, Belize, Figure 1a). The reef framework at Long Cay is formed primarily from **monospecific stands of *Orbicella annularis* (Ellis and Solander, 1786)**, which experienced widespread mortality following anomalously high water temperatures (29–32 °C) between early September and mid-November 1998 and hurricane Mitch which occurred simultaneously (Mumby, 1999). Field data were collected in 1998, 2003, 2007 and 2018 from an area of **monospecific *O. annularis* dominated framework of approximately 400 m² at a depth of 6-12m. *O. annularis* forms part of a species complex (the "*Orbicella annularis* species complex") along with *O. faveolata* and *O. franksi*. Each species within the complex exhibits a preferred depth zone, with *O. faveolata* dominating shallow reef habitats, *O. annularis* mid-depth habitats, and *O. franksi* in deeper depths (Pandolfi and Budd, 2008).** (Lines 229-236)

Secondly, we appreciate the reviewer's point that trajectories of erosion and complexity will likely differ in other locations and among other closely related taxa. To highlight this point we have amended the results and discussion section to discuss the uniqueness of *O. annularis* frameworks more explicitly:

"High levels of genotypic diversity in *O. annularis* at Long Caye (Foster et al., 2013) and population connectivity to other reefs throughout the western Caribbean (Foster et al., 2012) implies that Long Caye is not unique, and differential growth of surviving ramets may lead to similar changes in **structural complexity for *O. annularis* dominated frameworks**

elsewhere in the Caribbean (e.g. Idjadi and Edmunds, 2006; Edmunds and Elahi, 2007) where growth rates exceed erosion. At colony scales, changes in microhabitat complexity do not appear to have translated into changes in reef complexity, as the erosion of dead ramets is offset by growth of surviving ramets. **This apparent stability in reef complexity at Long Caye is intrinsically linked to the columnar growth form of *O. annularis* colonies (Figure 2), and trajectories of erosion and structural complexity will likely vary among other Caribbean coral species with different morphologies (e.g. *O. faveolata*)**". (Lines 140-147)

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, chainbased 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 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").

We appreciate the reviewers concern regarding the over-estimation of rugosity. The reviewer states that "*A traditional chain-based rugosity survey over the tops of these colonies would likely miss these microhabitats (which only have an average opening of 0.4 cm)*", but we highlight here that **0.4cm** represents the minimum ramet spacing, not the average ramet spacing. To determine ramet spacing, we measured 50 colonies of *Orbicella annularis* at Long Cay in 1998. The spacing between ramets was **4.7cm** (see the nSpacing parameter in the supplementary model). A typical chain link of 0.7cm (e.g. Alvarez-Filip et al 2011) or nylon line as previously used in measurements of rugosity at Glovers Atoll (McClanahan 1999) would sufficiently capture such small-scale microhabitat complexity.

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.

Done. We appreciate the reviewers point and have amended "reef-scale" to "colony-scale" throughout the manuscript for consistency.

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.

Done. To emphasize the reliance on vertical erosion rates in the model we have included the following sentence in the first paragraph of the Results and Discussion:

“Prior to the 1998 mortality event, ramet heights within colonies were consistent, resulting in an even hemispherical colony appearance (Figure 1b). Surveys in 2018 revealed that surviving colonies exhibited a characteristic “serrated” topography, in that the isolated surviving ramets protruded above the remaining dead colony (Figure 2a, Figure S1). **As grazing parrotfish exhibit a strong tendency to erode the surfaces rather than sides of ramets (Roff et al., 2015), we focused on vertical erosion on the upper surfaces of dead ramets.** We hypothesised that differences in growth among surviving ramets and the erosion of dead ramets would result in changes to microhabitat complexity” (Lines 85-90)

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.

Done. We appreciate the reviewers point. While our observations indicate that parrotfish (particularly *Scarus*) prefer to graze on upper surfaces over the sides of dead colonies (Roff et al 2015), bioerosion on the sides of ramets would likely weaken ramets and threaten structural integrity over long periods of time. To highlight this point we have included the following sentence in the discussion:

“While not explicitly incorporated in our erosion model, slower rates of external bioerosion on the sides of ramets and ongoing bioerosion from micro and macroborers over decadal scales (Roff et al., 2015) will likely weaken skeletal structural integrity in *O. annularis* (Highsmith et al., 1983), facilitating mechanical breakage and storm-driven loss of now protruding surviving ramets (Figure S1), likely resulting in non-linear increases of framework loss over longer timescales (2050 and beyond)” (lines 223-227)

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 “long-term changes in complexity among crevices” (Lines 155-157), but this 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.

Done. We appreciate the reviewer’s point. We note that the “long-term changes in microhabitat complexity among crevices” (Lines 155-157) is in agreement with the conclusion that structural complexity was “remarkably stable” (Line 107). We agree with the reviewer that increased aperture of openings is likely to have facilitated access by predators, and have expanded the discussion to include preferential feeding of parrotfish on the edges of dead coral substrates and widening of crevice apertures as follows:

“While further experimental work is needed to quantify size thresholds of refugia by which urchins escape predation, these observations are consistent with the hypothesis that bioerosion of reef frameworks results in reduced crevice depth for refuge, which in turn affects *E. viridis* densities by allowing for increased access for invertivorous fish, resulting in higher urchin mortality. Declines in the minimum ramet depth from 6.6 ± 3.9 cm in 2007 to 4.8 ± 2.1 cm (Figure 2c) are consistent with our previous U-Th estimates of bioerosion at Long Cay (Roff et al 2015). **We hypothesise that as *O. annularis* ramets erode, the loss of the upper ramet lobes results in increased ramet spacing and a wider aperture of the crevices.** As parrotfish preferentially target convex surfaces of dead coral substrates (Roff et al 2015), bioerosion of ramet edges **can further widen** the aperture of crevices, further facilitating access to invertivores and diminishing refuge potential” (line 182-189)

Specific comments:

Line 10: “Th” should be capitalized throughout

Done.

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.

Done. We appreciate the reviewer's point and have reworded the sentence as follows:

“As an ecosystem engineer, *Orbicella.annularis* (Ellis and Solander, 1786) plays a critical ecosystem role as a framework building coral in the Caribbean (Geister, 1977) providing reef-scale structural complexity that supports a diverse range of fish (Alvarez-Filip et al., 2011) and invertebrate (Idjadi and Edmunds, 2006) assemblages” (Lines 22-24)

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.

Done. We have included the following ecological description of the *O. annularis* species complex in the methods:

“*O. annularis* forms part of a species complex (the “*Orbicella annularis* species complex”) along with *O. faveolata* and *O. franksi*. Each species within the complex exhibits a preferred depth zone, with *O. faveolata* dominating shallow reef habitats, *O. annularis* mid-depth habitats, and *O. franksi* in deeper depths (Pandolfi and Budd, 2008)” (Lines 234-236)

And have included mention of monospecific stands of *annularis* in the present study to avoid confusion:

“The reef framework at Long Cay is formed primarily from **monospecific stands of *Orbicella annularis* (Ellis and Solander, 1786), which experienced widespread mortality following anomalously high water temperatures (29–32 °C) between early September and mid-November 1998 and hurricane Mitch which occurred simultaneously (Mumby, 1999). Field data were collected in 1998, 2003, 2007 and 2018 from an area of **monospecific *O. annularis*** dominated framework of approximately 400 m² at a depth of 6-12m” (Lines 229-234)**

Line 40: add a hyphen after “micro”

Done.

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 from its base.

Done. We have added a sentence in the introduction to clarify the differences between typical complexity measurements:

“To determine changes in *O. annularis* frameworks at different scales, we calculated two metrics of habitat complexity: i) microhabitat complexity at the scale of individual ramets (centimetres), and ii) structural complexity at the scale of whole colonies (metres). **These metrics consider the upper surfaces of *O. annularis* colonies, and differ from traditional transect-chain measurements of reef rugosity that assess structural complexity across multiple colonies (e.g. Alvarez-Filip et al., 2011).**” (Lines 77-80)

and included a sentence in the methods to highlight how colony-scale estimates were included:

“To assess changes in rugosity at a colony scale in the two decades following the mass mortality, we created a structural model of *O. annularis* colonies parameterised using field data collected at Long Cay (see Supplementary code). **The surface structural complexity of *O. annularis* colonies were modelled using a simple cross-sectional topography of ramets and colony widths** (Figure 4a, see Supplementary R code).” (Lines 253-255)

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

Done. Corrected Figure 2c to 2007

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

Done. Included means as follows:

“No significant difference in height ($p > 0.05$) was observed between “live-live” or “dead-dead” ramet pairings in either 2007 (**0.5 ± 1.0 cm, 1.2 ± 0.9 cm**) or 2018 (**0.1 ± 1.2 cm, 0.6 ± 1.4 cm**), implying that processes of growth and/or erosion occur evenly among living and dead ramets (Figure S1)” (Lines 93-95)

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

Done. Changed to “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.

Done. Agreed - we have specified that the framework in the Keys study was dead *O. faveolata*:

“Long-term records of bioerosion over ecologically meaningful timescales are rare, yet a recent study (Kuffner et al., 2019) reporting exceptionally rapid rates of erosion of **dead *O. faveolata*** reef frameworks (maximum 1.63 cm yr⁻¹) in the Florida Keys” (Lines 152-153)

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

Done. Long Caye was designated a marine reserve in 1993 and enforced since 1996. Invertivores were never heavily exploited prior to the reserve, and our survey data indicate no change in invertivore populations through time. We have expanded this section to include further discussion as follows:

“Higher biomass of invertivores inside of marine protected areas can substantially increase predation pressure on urchins (Harborne et al., 2009), and may explain the rapid decline in *E. viridis* at Long Caye following diminished refuge potential between surveys. **As Long Cay has been an enforced marine reserve since 1996, an alternative explanation to our observed data could be that urchin numbers have declined in response to increased**

predation pressure following recovery of invertivore fish assemblages. While plausible, we discount this hypothesis as invertivores were not heavily exploited prior to 1996 when the reserve was established, and surveys of fish assemblages indicate no change in invertivores over time (Mumby pers.obs.).” (Lines 190-196)

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.

Done – amended to “colony scales”

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

Done - corrected

Line 204: A minimum distance?

Done – corrected to “minimum distance”

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

Done - corrected

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

Done. Included “**and “colony” as a random factor**” at line 250

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.

Done. Ramet heights were measured from within colonies (i.e. the top to base of ramets). We have amended this as follows in the text:

“*O. annularis* colonies were modelled using a simple cross-sectional topography of ramets (Figure 4a, **see Supplementary R code**). Colony widths were determined from in-situ measurements of 95 colonies at Long Cay in 2000, and ramet heights (**from the top to the base of the ramet within colonies**) and widths measured from 30 ramets within colonies in 2000”

Line 235: *O. annularis* should be italicized Figure 1: Was there no bleaching in Belize after 2010? What about disease?

Done. As far as we are aware there are no reports bleaching or disease at Long Cay between 2010 and our survey in 2018, although minor bleaching was observed in 2019 after our study.

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!

Done – corrected!

Reviewer #2

Overall, I found this manuscript to be very well written with the methodology easy to follow. The rationale for the study was well justified and the results are compellingly robust and well interpreted. On these grounds I would recommend acceptance after minor revision. I see two areas where revisions may improve the quality of the interpretations:

We thank the reviewer for their careful and detailed comments.

1) Echinometra decline: the hypothesis of decline is compelling and supported by the observations. I feel it would improve the manuscript however to include any alternative hypotheses (if the authors can think of any) that might explain the decrease.

As Long Caye was designated a marine reserve in 1993 and enforced since 1996, a plausible hypothesis would be that recovery in invertivore densities following enforcement may have placed increase predation pressure on urchins. However, invertivores were never heavily exploited prior to the reserve, and our survey data indicate no change in invertivore populations through time. We have expanded this section to include further discussion as follows:

“Higher biomass of invertivores inside of marine protected areas can substantially increase predation pressure on urchins (Harborne et al., 2009), and may explain the rapid decline in *E. viridis* at Long Caye following diminished refuge potential between surveys. **As Long Cay has been an enforced marine reserve since 1996 an alternative explanation to our observed data could be that urchin numbers have declined in response to increased predation pressure following recovery of invertivore fish assemblages. While plausible, we discount this hypothesis as invertivores were not heavily exploited prior to 1996 when the reserve was established, and surveys of fish assemblages indicate no change in invertivores over time (Mumby pers.obs.)**” (Lines 190-196)

2) Only one coral species was studied (albeit importantly the major reef building species), but how well do the authors think the general results reflect patterns playing out in other major reef building corals, such as those growing laterally rather than vertically?

Following comments from Review #1, amended the methods to clarify the monospecific stands of *O. annularis* in the present study and outline the *O. annularis* species complex to avoid confusion.

The study was conducted in Long Cay (Glovers Reef, Belize, Figure 1a). The reef framework at Long Cay is formed primarily from **monospecific stands of *Orbicella annularis* (Ellis and Solander, 1786)**, which experienced widespread mortality following anomalously high water temperatures (29–32 °C) between early September and mid-November 1998 and hurricane Mitch which occurred simultaneously (Mumby, 1999). Field data were collected in 1998, 2003, 2007 and 2018 from an area of **monospecific *O. annularis* dominated framework of approximately 400 m² at a depth of 6-12m. *O. annularis* forms part of a species complex (the “*Orbicella annularis* species complex”) along with *O. faveolata* and *O. franksi*. Each species within the complex exhibits a preferred depth zone, with *O. faveolata* dominating shallow reef habitats, *O. annularis* mid-depth habitats, and *O. franksi* in deeper depths (Pandolfi and Budd, 2008).**

Secondly, we appreciate the reviewer’s point that trajectories of erosion and complexity will likely differ in other locations and among other closely related taxa. To highlight this point we have amended the results and discussion section to discuss the uniqueness of *O. annularis* frameworks more explicitly:

“High levels of genotypic diversity in *O. annularis* at Long Caye (Foster et al., 2013) and population connectivity to other reefs throughout the western Caribbean (Foster et al., 2012) implies that Long Caye is not unique, and differential growth of surviving ramets may lead to similar changes in **structural complexity for *O. annularis* dominated frameworks**

elsewhere in the Caribbean (e.g. Idjadi and Edmunds, 2006; Edmunds and Elahi, 2007) where growth rates exceed erosion. At colony scales, changes in microhabitat complexity do not appear to have translated into changes in reef complexity, as the erosion of dead ramets is offset by growth of surviving ramets. **This apparent stability in reef complexity at Long Caye is intrinsically linked to the columnar growth form of *O. annularis* colonies (Figure 2), and trajectories of erosion and structural complexity will likely vary among other Caribbean coral species with different morphologies (e.g. *O. faveolata*)”.**

Multi-decadal changes in structural complexity following mass coral mortality on a Caribbean reef

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Abstract. In recent decades, extensive mortality of reef-building corals throughout the Caribbean region has led to erosion of reef frameworks and declines in biodiversity. Using field observations, structural models and high-precision ^{U-Th} dating methods, we quantify changes in structural complexity in the major framework building coral *Orbicella annularis* over a 20-year period at Long Cay (Belize). Despite extensive mortality following the mass coral bleaching event of 1998, structural complexity of frameworks remained largely unchanged between 1998 (rugosity index = 2.35 ± 0.1) and 2018 (2.29 ± 0.1). Colony-scale structural complexity was maintained through rapid growth of surviving ramets (0.69 ± 0.1 cm yr⁻¹) offsetting slower bioerosion of dead ramets (-0.11 ± 0.16 cm yr⁻¹). Despite apparent stability of structural complexity at colony-scales, bioerosion of individual dead ramets over two decades led to declines in microhabitat complexity, with an overall reduction of the depth of microhabitats within frameworks. Altered microhabitat complexity appears to have negative effects for cryptic fauna, with the grazing urchin *Echinometra viridis* declining from 1.5 ± 0.4 per m² in 1998 to 0.02 ± 0.02 per m² in 2018. Changes in microhabitat complexity have the potential to alter ecological interactions that can impact recovery dynamics on coral reefs in ways that are undetectable using traditional rugosity metrics of structural complexity.

1. Introduction

As an ecosystem engineer, *Orbicella annularis* (Ellis and Solander, 1786) plays a critical ecosystem role as a framework building coral in the Caribbean (Geister, 1977) providing reef-scale structural complexity that supports a diverse range of fish (Alvarez-Filip et al., 2011) and invertebrate (Idjadi and Edmunds, 2006) assemblages. From a geological perspective, *O. annularis* first appeared in the late Pliocene to early Pleistocene (~2 - 1.5 million years ago, (Budd and Klaus, 2001)) and linear extension of ~10 mm yr⁻¹ resulted in the accretion of modern day Caribbean coral reefs at a rate of ~3.3 m kyr⁻¹ (Gischler, 2008). Accretion of reef frameworks is a key ecosystem function, providing critical habitat for reef organisms and physical coastline protection from wave erosion (Moberg and Folke, 1999).

While Caribbean coral reefs have exhibited remarkable ecological persistence over geological timeframes (Pandolfi and Jackson, 2006), reefs throughout the region have declined over the past century due to climate change, overfishing and poor

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water quality ([Knowlton and Jackson, 2008](#)). In recent decades, populations of *O. annularis* have been decimated by recurrent coral bleaching events ([Szmant and Gassman, 1990](#)), disease outbreaks ([Pantos et al., 2003](#); [Bruno et al., 2003](#)), and increasing negative interactions with macroalgae ([Ferrari et al., 2012](#)) resulting in region-wide declines of *O. annularis* and shifts in population structure to higher densities of smaller colonies ([Nugues, 2002](#); [Bruckner and Bruckner, 2006](#); [Edmunds, 2015](#)). Following the loss of living coral tissue, the exposed coral skeleton is subjected to a gradual process of bioerosion – the biologically induced weakening and breaking down of coral skeletons ([Glynn and Manzello, 2015](#)).

On modern-day coral reefs, grazing parrotfish are the primary bioeroders, contributing between 79 - 84% of total bioerosion ([Perry et al., 2014](#)). Parrotfish scrape and excavate the external surfaces of coral reef frameworks ([Clements et al., 2017](#)), producing large volumes of carbonate sediments. Colonisation of exposed framework substrates by a broad range of micro- and macro-boring organisms, including sponges, endolithic algae, fungi, and boring invertebrates further weakens coral skeletons, making them more susceptible to physical erosion ([Hutchings, 1986](#)). The erosion of reef frameworks in the Caribbean over the past decades has resulted in a loss of reef-scale structural complexity, a process described as “flattening” ([Alvarez-Filip et al., 2009](#)). This region-wide loss of structural complexity has led to substantial declines in ecosystem functioning, including reductions in biodiversity ([Newman et al., 2015](#)) and losses of fisheries productivity ([Rogers et al., 2018](#)).

As the processes of accretion and erosion of coral reef frameworks occur over decadal to centennial time frames ([Glynn and Manzello, 2015](#)), few long-term in-situ studies of bioerosion exist (but see [Kuffner et al., 2019](#)). Here, we return to a multi-decadal study of Caribbean coral frameworks in Glovers Reef, Belize ([Roff et al., 2015](#); [Mumby, 1999](#)). In 1998, extreme thermal stress and the impact of hurricane Mitch resulted in extensive coral mortality throughout the Mesoamerican Barrier Reef ([Mumby, 1999](#); [Aronson et al., 2002](#); [Mumby et al., 2005](#)). Projections of future thermal stress events indicate that such mass bleaching events may become an annual occurrence by 2040 ([van Hooidonk et al., 2015](#)). These events are predicted to have a strong negative impact on carbonate budgets and reef accretion ([Kennedy et al., 2013](#); [Perry et al., 2013](#)), yet the landscape-scale impacts on the structure and function of coral frameworks are not well understood. Here we quantify multidecadal changes in *O. annularis* frameworks at Long Cay (Glovers Reef) and quantify long-term changes in structural complexity and microhabitat complexity.

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2. Results and discussion

Prior to the 1998 mass bleaching event, frameworks at Long Cay (Glovers Reef, Figure 1a) were dominated by large long-lived *O. annularis* colonies (Figure 1b). Surveys at Long Cay in June 1998 (10 m depth) revealed high levels of healthy *O. annularis* cover ($68 \pm 14\%$). Major coral bleaching occurred in September 1998 following a period of calm weather and elevated water temperatures, with 70 to 90% of *O. annularis* colonies exhibiting full or partial bleaching ([Roff et al., 2015](#)). Extensive wave damage from Hurricane Mitch in November 1998 compounded the impacts of bleaching, with ~85% of *O.*

annularis colonies exhibiting partial mortality (Roff et al., 2015). By June 2000, cover of *O. annularis* had declined to 20 ± 5 %, and remained at ~ 15 % in the decades following the mass bleaching event despite repeat minor hurricane disturbance (Figure 1c). Genetic analysis of these surviving *O. annularis* colonies at Long Cay indicates high levels of genotypic diversity compared to other reefs around the Caribbean (Foster et al., 2013). Field surveys in 2018 revealed high levels of macroalgal cover and extensive partial mortality within *O. annularis* colonies (Figure 2a), with low survival of *O. annularis* ramets within colonies (averaging 14.1 ± 11 % SD).

To determine changes in *O. annularis* frameworks at different scales, we calculated two metrics of habitat complexity: i) microhabitat complexity at the scale of individual ramets (centimetres), and ii) structural complexity at the scale of whole colonies (metres). ~~These metrics consider the upper surfaces of *O. annularis* colonies, and differ from traditional transect-chain measurements of reef rugosity that assess structural complexity across multiple colonies (e.g. Alvarez-Filip et al., 2011).~~ Microhabitat complexity of *O. annularis* provides critical permanent refugia for small reef-fish and cryptic invertebrates among ramets (Almany, 2004; Sammarco, 1982), and structural complexity at colony scales can reduce the foraging efficiency of predators and limit prey detection (Beukers and Jones, 1998).

2.1 Multi-decadal changes in microhabitat complexity

Prior to the 1998 mortality event, ramet heights within colonies were consistent, resulting in an even hemispherical colony appearance (Figure 1b). Surveys in 2018 revealed that surviving colonies exhibited a characteristic “serrated” topography, in that the isolated surviving ramets protruded above the remaining dead colony (Figure 2a, Figure S1). ~~As grazing parrotfish exhibit a strong tendency to erode the surfaces rather than sides of ramets (Roff et al., 2015), we focused on vertical erosion on the upper surfaces of dead ramets.~~ We hypothesised that differences in growth among surviving ramets and the erosion of dead ramets would result in changes to microhabitat complexity. To test this hypothesis, we measured height differences between live and dead ramet pairings from *O. annularis* colonies at Long Cay in successive decades, 2007 and 2018 (Figure 2b). Measurements of ramet pairings in 2007 indicated a significant difference in height between “live” and “dead” ramets of 3.1 ± 2.9 cm ($p < 0.01$, Figure 2c), a trend that had increased to 15.5 ± 3.8 cm in 2018 ($p < 0.01$, Figure 2c). No significant difference in height ($p > 0.05$) was observed between “live-live” or “dead-dead” ramet pairings in either 2007 (0.5 ± 1.0 cm, 1.2 ± 0.9 cm) or 2018 (0.1 ± 1.2 cm, 0.6 ± 1.4 cm), implying that processes of growth and/or erosion occur evenly among living and dead ramets (Figure S1).

Using high-precision U-Th dating methods and CT scan reconstructions, we previously quantified annual rates of external bioerosion and growth (linear extension) of *O. annularis* colonies at Long Cay between 1998 and 2011 (Roff et al., 2015). Estimates from U-Th dates indicated an average erosion rate of -0.11 ± 0.16 cm yr⁻¹, which was in close agreement with model predictions of external erosion by excavating parrotfish (Roff et al., 2015). Within the same time frame, linear extension (growth) of *O. annularis* ramets (as quantified by density banding of skeletons) was more than sixfold higher (0.69 ± 0.1 cm

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105 yr⁻¹) than surface bioerosion (Roff et al., 2015). Based upon these parameters, an estimate of ramet height difference between
1998 and 2018 would indicate a $\sim 13.8 \pm 2$ cm vertical growth of surviving *O. annularis* ramets, while bioerosion drove $\sim -$
2.2 \pm 1 cm loss of ramet height. The modelled net outcome of erosion and growth of ramets of $\Delta 16$ cm between 1998 – 2018
(Figure 2d) is in close agreement to the observed differences between live and dead ramets in 2018 of 15.4 ± 1.1 cm, indicating
that the six-fold higher growth of surviving ramets results in the observed “serrated” pattern of *O. annularis* colonies (Figure
110 2b).

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2.2 Multi-decadal changes in structural complexity

To determine changes in structural complexity at colony scales, we created a structural model of *O. annularis* colonies (Fig
3a) parameterised using field data collected at Long Cay (see methods for full details and model code). Briefly, the model
simulates annual changes in structural complexity of 1000 *O. annularis* colonies between 1998 – 2018 through growth of
115 surviving ramets and erosion of dead ramets (Figure 3a). Structural complexity within each simulated colony was measured
using the rugosity index (*R*, Figure 3), a common index of rugosity on coral reefs where a flat surface has an *R* of 1, and larger
numbers reflect a greater degree of structural complexity (Alvarez-Filip et al., 2009). Prior to the bleaching event in 1998,
uniform growth of living *O. annularis* ramets resulted in *R* values of 2.36 (95% CI: 2.3 - 2.4). Following the bleaching event,
extensive partial mortality resulted in erosion of dead ramets and growth of surviving ramets. Hindcasting long-term changes
120 in structural complexity between 1998-2018 revealed high variability among colony trajectories, with 58% exhibiting declining
rugosity, 41% exhibiting increases in rugosity, and 1% exhibiting no change. Despite such variance, overall structural
complexity was remarkably stable (Fig 3b), and average values of *R* in 2018 were within the range of pre-mortality levels (*R*
= 2.31, 95% CI: 2.28 - 2.34). Sensitivity analysis of the model indicates that changes in structural complexity between 1998
and 2018 (ΔR) was weakly correlated to colony size ($\rho = 0.1$, 95% CI: 0.04 – 0.15) in that smaller colonies experienced declines
125 in structural complexity (Figure 3c). Post-disturbance survival was a key driver of change in rugosity ($\rho = 0.79$, 95% CI: 0.75
– 0.8), in that colonies that experienced high levels of within colony mortality (>80%) experienced declines in structural
complexity (Figure 3d), whereas colonies that experienced higher survival rates (>20% surviving ramets within colonies)
exhibited increases in structural complexity (Figure 3d). Comparisons of structural complexity reconstructed from paired
photographs of *O. annularis* colonies at Long Cay in 2003 and 2018 (Figure 4a,b) validate model predictions, and support
130 wider field observations at Glovers Reef in 2018 of surviving ramets protrude above dead *O. annularis* frameworks (Figure
S1).

Losses of structural complexity following disturbance are primarily thought to be driven by processes of erosion (Alvarez-
Filip et al., 2009; Sheppard et al., 2002; Glynn, 1988), in that physical disturbance and chemical dissolution, combined with
135 intense internal and external bioerosion flattens structurally complex coral reef structure. If processes of bioconstruction from
coral growth are weak, reefs remain in a degraded and flattened state, as has occurred in several areas of the Caribbean to
varying extents (Alvarez-Filip et al., 2009). Here, we document changes in microhabitat complexity following mass coral

140 mortality that appear to be driven primarily by growth of surviving ramets of *O. annularis* rather than through processes of bioerosion. High levels of genotypic diversity in *O. annularis* at Long Caye (Foster et al., 2013) and population connectivity to other reefs throughout the western Caribbean (Foster et al., 2012) implies that Long Caye is not unique, and differential growth of surviving ramets may lead to similar changes in structural complexity for *O. annularis* dominated frameworks elsewhere in the Caribbean (e.g. Idjadi and Edmunds, 2006; Edmunds and Elahi, 2007) where growth rates exceed erosion. At colony scales, changes in microhabitat complexity do not appear to have translated into changes in reef complexity, as the erosion of dead ramets is offset by growth of surviving ramets. This apparent stability in reef complexity at Long Caye is intrinsically linked to the columnar growth form of *O. annularis* colonies (Figure 2), and trajectories of erosion and structural complexity will likely vary among other Caribbean coral species with different morphologies (e.g. *O. faveolata*). In colonies of *O. annularis* that experienced partial mortality, the wide spacing among surviving ramets (Figure 2c) allows access to previously protected skeleton by grazing parrotfish (see initial phase *Sparisoma viride*, Figure 1c). Such increased access to parrotfish appears to have accelerated erosion rates on the sides of surviving ramets, resulting in a narrowing of ramets (Figure S1) which increases susceptibility to physical breakage (Hein and Risk, 1975).

Long-term records of bioerosion over ecologically meaningful timescales are rare, yet a recent study (Kuffner et al., 2019) reporting exceptionally rapid rates of erosion of dead *O. faveolata* reef frameworks (maximum 1.63 cm yr⁻¹) in the Florida Keys provides important insight into heterogeneity of framework erosion throughout the wider Caribbean. The low rates of *O. annularis* bioerosion at Long Cay reported in the present study (-2.2 ± 1 cm over 20 years) compared to the Florida Keys (9.4 ± 5.6 cm over 17 years) is likely due to differences in skeletal density (1.9 g cm³, (Roff et al., 2015) vs 1.12 g cm³, (Halley et al., 1994)) driven by the highly productive windward location of Glovers Reef, but may also reflect regional differences in the structure of bioeroding herbivore assemblages. These two studies likely reflect the extremes of the bioerosionary spectrum on Caribbean reefs, and future research should focus on understanding factors that render some frameworks more resilient than others. While secondary cementation played an important role in hardening Holocene reef frameworks (Gischler and Hudson, 2004), the geochemical evidence (consistent initial uranium concentrations) within modern *O. annularis* skeletons from Long Cay (Roff et al., 2015) suggests that secondary cementation may not necessarily play an important reinforcing role in modern corals over at least decadal time frames.

2.3 Changing functional roles of structural complexity

165 At reef scales, *O. annularis* forms structurally complex frameworks that underpin species richness on Caribbean coral reefs (Newman et al., 2015). Prior to the 1998 disturbance events, the narrow crevices between *O. annularis* ramets provided critical refuge for scleractinian coral recruits (Mumby, 1999), juvenile and small-bodied Caribbean reef fish (Nemeth, 1998; Alvarez-Filip et al., 2011), and the eroding echinoids *Echinometra viridis* ((Sammarco, 1982), Figure 5a) and juvenile *Diadema antillarum* (Lessios, 1998). *E. viridis* are highly abundant in patch reefs and lagoonal reefs throughout Belize (Brown-Saracino et al., 2007), yet are historically less common on deeper, exposed fore-reef habitats such as Long Cay (PJM pers. obs.). *D.*

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175 *antillarum* have been historically rare on the windward reef slope at Glovers Reef (PJM pers. obs.) following the Caribbean-wide die-off in the early 1980's (Lessios, 1988), surveys prior to the mass bleaching event in 1998 indicate that *O. annularis* frameworks supported a population of the smaller urchin *E. viridis* at densities of 1.1 ± 0.6 individuals per m^2 (Figure 5b). As *E. viridis* are largely limited to crevice microhabitats due to high rates of predation (McClanahan, 1999), we hypothesise that the observed long-term changes in microhabitat complexity among crevices at Long Cay allows for increased access for predatory fish such as triggerfish (Balistidae) and porgies (Sparidae). In 2007, *E. viridis* was observed among *O. annularis* microhabitats at a comparable density to 1998 surveys, averaging 1.5 ± 0.4 individuals per m^2 to a maximum of 14.3 individuals per m^2 (Figure 4b). Ten years later, in 2018, we repeated surveys across the same study area at Long Cay, and only a single *E. viridis* was recorded in 40 colonies, resulting in an average density of just 0.02 ± 0.02 individuals per m^2 (Figure 5b).

185 While further experimental work is needed to quantify size thresholds of refugia by which urchins escape predation, these observations are consistent with the hypothesis that bioerosion of reef frameworks results in reduced crevice depth for refuge, which in turn affects *E. viridis* densities by allowing for increased access for invertivorous fish, resulting in higher urchin mortality. Declines in the minimum ramet depth from 6.6 ± 3.9 cm in 2007 to 4.8 ± 2.1 cm (Figure 2c) are consistent with our previous U-Th estimates of bioerosion at Long Cay (Roff et al., 2015). We hypothesise that as *O. annularis* ramets erode, the loss of the upper ramet lobes results in increased ramet spacing and a wider aperture of the crevices. As parrotfish preferentially target convex surfaces of dead coral substrates (Roff et al., 2011), bioerosion of ramet edges can further widen the aperture of crevices, further facilitating access to invertivores and diminishing refuge potential. Population dynamics of urchins are complex, and result from complex interactions between top-down and bottom-up factors (Tebbett and Bellwood, 2018). Higher biomass of invertivores inside of marine protected areas can substantially increase predation pressure on urchins (Harborne et al., 2009), and may explain the rapid decline in *E. viridis* at Long Cay following diminished refuge potential between surveys. As Long Cay has been an enforced marine reserve since 1996, an alternative explanation to our observed data could be that urchin numbers have declined in response to increased predation pressure following recovery of invertivore fish assemblages. While plausible, we discount this hypothesis as invertivores were not heavily exploited prior to 1996 when the reserve was established, and surveys of fish assemblages indicate no change in invertivores over time (Mumby pers.obs.).

200 Densities of *E. viridis* at the deeper exposed fore-reef habitat at Long Cay are substantially lower than reported for other shallow patch reef and lagoonal reef habitats in Belize (as high as 40 ± 7 individuals per m^2 , (Brown-Saracino et al., 2007)). Yet even at low densities (< 2 individuals per m^2) *E. viridis* density is positively related to coral cover (Bologna et al., 2012), implying a functional link. As *E. viridis* can play an important role in structuring reef communities by maintaining algal free space within ramet crevices (Figure 5a), in turn facilitating coral recruitment (Sammarco, 1982), losses of these urchins may have resulted in small-scale increases in macroalgal cover within *O. annularis* framework microhabitats – notably *Lobophora* spp. (Figure 1c) – which can reduce coral recruitment and impede future recovery potential (Mumby et al., 2007). As an ecosystem engineer, the structural complexity constructed by *O. annularis* provides critical refuge for a diverse range of

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210 invertebrate fauna (Buss and Jackson, 1979; Idjadi and Edmunds, 2006). As diversity is positively related to structural complexity and not coral cover (Idjadi and Edmunds, 2006), we expect to see similar declines in other motile and sessile invertebrate taxa that seek refuge in *O. annularis* microhabitats.

3. Structural complexity and decline of reef frameworks in the 21st century

215 In recent decades, declines in coral cover and losses of keystone species have resulted in region-wide reductions of structural complexity throughout the Caribbean (Alvarez-Filip et al., 2009). Here we highlight how small-scale changes in microhabitat complexity have the potential to alter ecological interactions that can impact recovery dynamics in ways that are undetectable using standardised metrics of structural complexity.

220 While losses of key microhabitat complexity may have cascading effects on diversity and ecosystem function, our results indicate that structural complexity at colony scales can be remarkably robust. Given the recent widespread recruitment failure of Caribbean corals (Hughes and Tanner, 2000) and low recruitment rates of *O. annularis* in general (Edmunds, 2002), the potential for recovery and long-term future of *O. annularis* frameworks at Long Cay in the 21st century is unclear. However, two decades after mass mortality at Long Cay, levels of coral cover in 2018 remain above the threshold of live coral cover of ~10% needed to maintain a positive state of reef accretion (Roff et al., 2015; Perry et al., 2013). While not explicitly incorporated in our erosion model, slower rates of external bioerosion on the sides of ramets and ongoing bioerosion from 225 micro and macroborers over decadal scales (Roff et al., 2015) will likely weaken skeletal structural integrity in *O. annularis* (Highsmith et al., 1983), facilitating mechanical breakage and storm-driven loss of now protruding surviving ramets (Figure S1), likely resulting in non-linear increases of framework loss over longer timescales (2050 and beyond).

4. Methods

230 The study was conducted in Long Cay (Glovers Reef, Belize, Figure 1a). The reef framework at Long Cay is formed primarily from monospecific stands of *Orbicella annularis* (Ellis and Solander, 1786), which experienced widespread mortality following anomalously high water temperatures (29–32 °C) between early September and mid-November 1998 and hurricane Mitch which occurred simultaneously (Mumby, 1999). Field data were collected in 1998, 2003, 2007 and 2018 from an area of monospecific *O. annularis* dominated framework of approximately 400 m² at a depth of 6–12m. *O. annularis* forms part of a species complex (the “*Orbicella annularis* species complex”) along with *O. faveolata* and *O. franksi*. Each species within 235 the complex exhibits a preferred depth zone, with *O. faveolata* dominating shallow reef habitats, *O. annularis* mid-depth habitats, and *O. franksi* in deeper depths (Pandolfi and Budd, 2008).

4.1 Microhabitat complexity

Surveys and measurements of *O. annularis* colonies were conducted at 6–12 m depth at Long Cay in March 2007 and May 2018. At both time points, colonies of *O. annularis* were selected among the framework at random using a system of fin-kicks

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245 and compass bearings. A [minimum](#) distance of ~5m was maintained between measured colonies, and ramets with signs of recent death were avoided. For each colony, we selected neighbouring ramet pairs from the central part of the colony ($n = 2-3$ per colony) and assigned [them](#) to one of three states: either “live-live” pairing, “live-dead” pairing or “dead-dead” pairing ($n = 20$ ramet pair measurements for each state in 2007, $n = 30$ in 2018). The difference in height between each neighbouring ramet pair was quantified using a ruler or calipers to determine differences in the microhabitat complexity within *O. annularis* colonies. Differences between 2007 and 2018 were tested with a linear mixed effects model in R software ([R Development Core Team, 2019](#)), with “year” and “state” as fixed factors [and “colony” as a random factor](#).

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4.2 Structural complexity

To assess changes in rugosity at a colony scale in the two decades following the mass mortality, we created a structural model of *O. annularis* colonies parameterised using field data collected at Long Cay (see Supplementary code). [The surface structural complexity of *O. annularis* colonies](#) were modelled using a simple cross-sectional topography of ramets [and colony widths](#) (Figure 4a, [see Supplementary R code](#)). Colony widths were determined from in-situ measurements of 95 colonies at Long Cay in 2000, and ramet heights [\(from the top to the base of the ramet within colonies\)](#) and widths measured from 30 ramets within colonies in 2000 ([Roff et al., 2015](#)). The model simulates 1000 colonies of *O. annularis* randomly sampling from colony width measurements and uses measurements of ramet diameter and ramet spacing to determine the number of ramets within colonies. Prior to the 1998 mortality event, the ratio of live to dead ramets within colonies was determined from surveys of pre-disturbance *O. annularis* in 1998, where 97.8% of *O. annularis* ramets were alive ([Roff et al., 2015](#)). The ratio of live to dead ramets twenty years after the 1998 mortality event was determined from surveys of 25 colonies of *O. annularis* at Long Cay in 2018. Surviving ramets were subject to annual linear extension (sampled at random from CT scan derived skeletal growth measurements at Long Cay between 2006-2011, ([Roff et al., 2015](#))), while dead ramets underwent annual external linear bioerosion (sampled at random from [U-Th](#) derived measurements of *O. annularis* at Long Cay between 1998-2011, ([Roff et al., 2015](#))). Annual changes in structural complexity within each simulated colony between 1998-2018 was measured using the rugosity index (R , ([Alvarez-Filip et al., 2009](#))), a ratio between the width of the colony and the external surface (i.e. sum of ramet heights, ramet width and inter-ramet spacing). Correlations between changes in rugosity (1998-2018) and colony width, post-bleaching survival, and both number of live and dead ramets within simulated colonies was determined using Pearson's product moment correlation coefficient (ρ) with the `cor.test` function ('stats' package) in R software ([R Development Core Team, 2019](#)).

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4.3 Urchin densities

To examine local ecological impacts of changes in ramet size distribution, we censused the density of the urchin *Echinometra viridis*, which occupies the interstitial space between ramets. Surveys of at Long Cay in 1998 were conducted using five 10×0.5 m transects, and found that urchins were dominated by *E. viridis* within ramets of *O. annularis* framework ([Mumby et al., 2005](#)). In subsequent survey years (2007 and 2018), urchin surveys were conducted on a per colony basis, and the number

of urchins within each *O. annularis* colony was standardised to the colony area to give individuals per m² ($n = 50$ colonies, 280 2018: $n = 40$ colonies).

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Data availability

Complete R code for structural model is provided in the supplementary, and underlying survey data will be made available on Dryad Digital Repository.

Supplement

285 Figure S1 Characteristic “serrated” topography of *O. annularis* colonies at Long Caye in 2018 with isolated surviving ramets protruded above the remaining dead colony.

Author contributions

Survey data: PJM, GR, JJ; structural complexity model: GR; writing – original draft: GR; writing – review and editing: GR, PJM

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Competing interests.

The authors declare that they have no conflict of interest.

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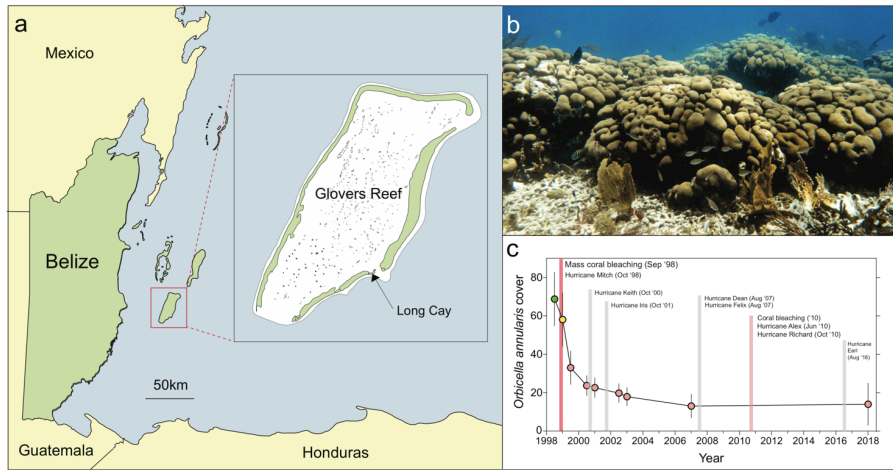
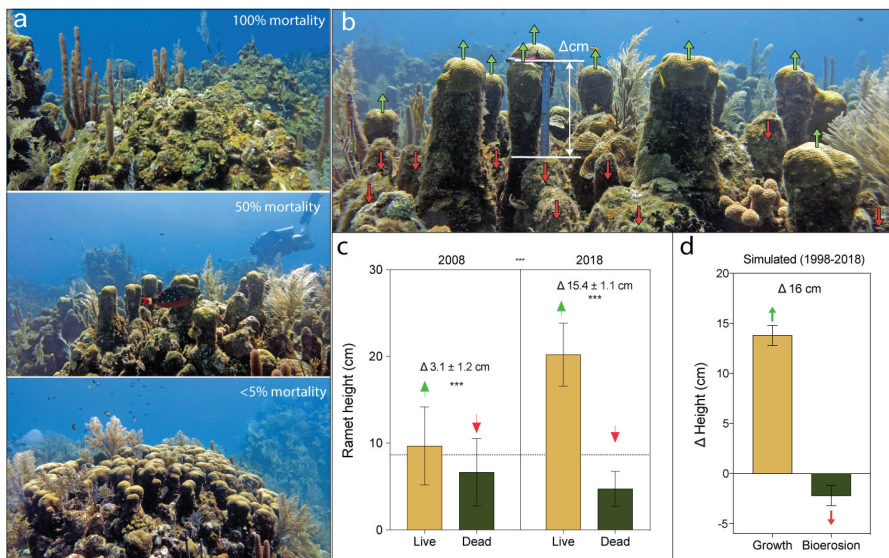
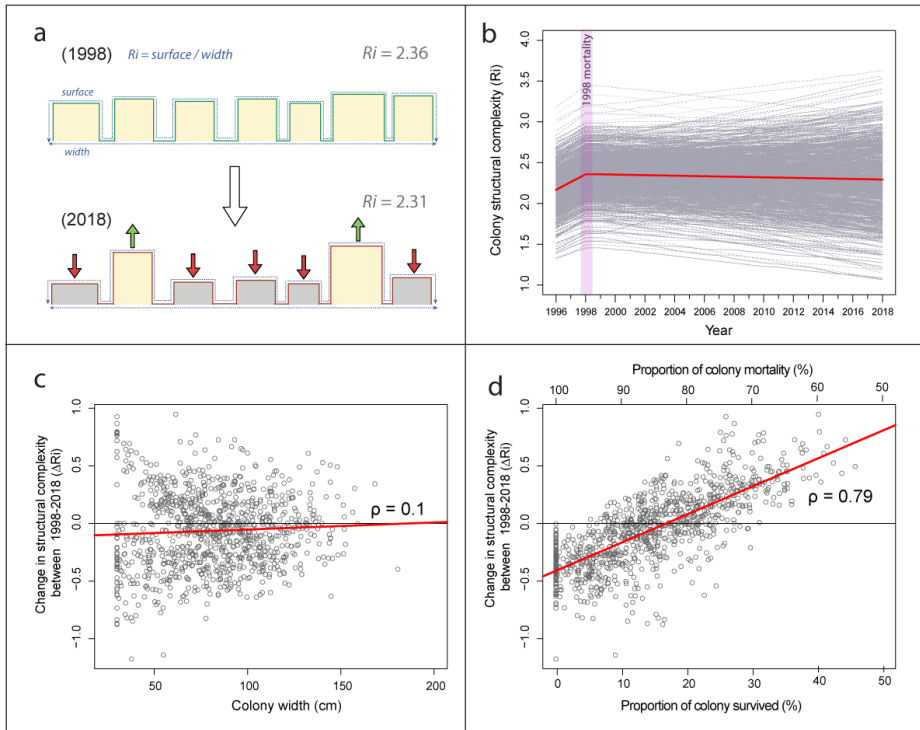


Figure 1 a) Map of Belize and study site (inset) at Long Cay, Glovers Reef, b) Living *Orbicella annularis* colonies forming a structurally complex framework on a Caribbean reef, c) time series of *O. annularis* cover at Glovers Reef and major disturbance events between 1998 and 2018

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430 **Figure 2** a) *Orbicella annularis* colonies from Long Cay in 2018 indicating high survival following the mass bleaching event (<5% mortality), complete (100%) mortality followed by algal overgrowth by *Lobophora variegata*, and partial mortality (~50%) resulting in characteristic “serrated” pattern and gaps, b) *O. annularis* framework at Long Cay in 2007 showing growth of surviving ramets (green arrows) protruding above the eroding dead ramets (red arrows) and difference in height between live and dead ramets (scale ruler = 15cm), c) height of “live” and “dead” ramet pairings in 2007 and 2018, showing a significant difference in height within years and a significant difference in average height of live ramets within years (*** = $p < 0.001$),
 435 d) simulated growth and bioerosion between 1998 and 2018 of based upon a linear erosion rate of $0.11 \pm 0.03 \text{ cm yr}^{-1}$ and growth rate of $0.69 \pm 0.1 \text{ cm yr}^{-1}$ (Roff et al., 2015).



440 **Figure 3** a) Cross-sectional structural model of *Orbicella annularis* indicating the method of estimating structural complexity ($R = \text{surface perimeter} / \text{width}$), and changes in R in 1998 (100% live prior to mortality) and 2018 following mortality, b) results of 1000 model simulations of changes in structural complexity between 1997 and 2018 (grey lines) and average values across simulations (red line), c) change in structural complexity between 1998-2018 (ΔR) of 1000 simulated colonies against colony size and d) proportion of colony survival / mortality.

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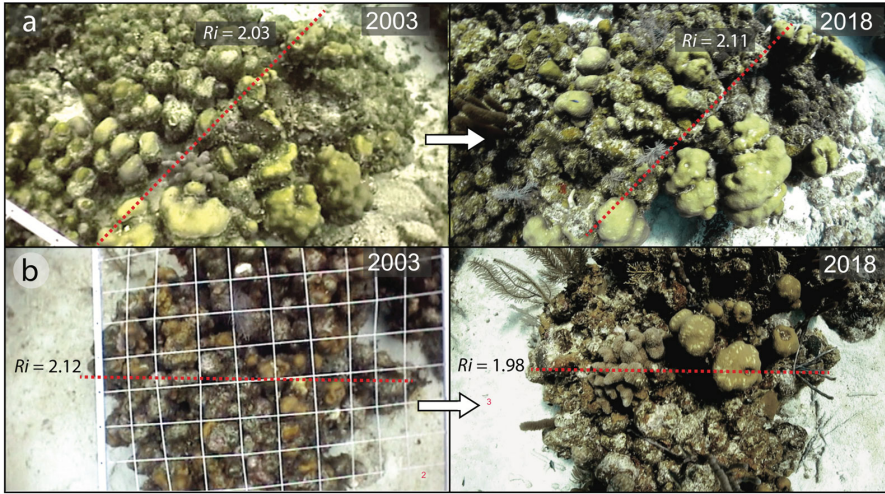


Figure 4 a-b) paired photographs of *Orbicella annularis* colonies from 2003 (5 years post-disturbance) and 2018 (20 years post-disturbance) and structural complexity (R) derived from model simulations showing growth (vertical extension) of surviving ramets above the colony and erosion of dead ramets in 2018.

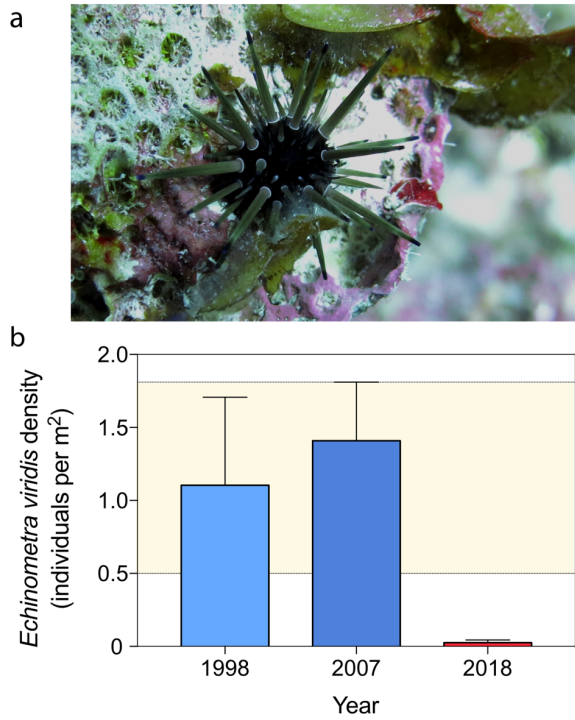


Figure 5 a) individual of *Echinometra viridis* among *Orbicella annularis* ramets at Long Cay in 2018 maintaining a cropped algal-free territory, b) density of *E. viridis* in 1998, 2007 and 2018 surveys (error band represents the maximum upper and lower standard deviation of the 1998 and 2008 surveys).