Coral Reefs
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NOTE

The contribution of corals to reef structural complexity in Kāneʻohe Bay

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Abstract The structural complexity of coral reefs provides important ecosystem functions, such as wave attenuation for coastal protection, surfaces for coral growth, and habitat for other organisms. Corals build much of this structure, but an understanding of how colonies of different species and sizes contribute to complexity is lacking. We quantified three interdependent descriptors of complexity—rugosity, fractal dimension, and height range—for reef patches as well as the corals growing upon them in Kāneʻohe Bay (Oʻahu, Hawaiʻi). Despite similar levels of reef-scale complexity throughout the bay, we found marked differences in how species contribute to this complexity. Variation in complexity among species was closely tied to colony morphology, but not to colony size. Together, our results show that no one species is sufficient to generate the full spectrum of habitat complexities we see on coral reefs, which has direct implications for reef recovery and restoration.

Keywords Habitat complexity · Coral reefs · Scleractinian corals · Photogrammetry · Structure from motion

Introduction

The structural complexity of coral reefs is vital for these ecosystems to thrive. Reef structures provide protection and nurseries for marine life (Darling et al. 2017; Graham and Nash 2013), dissipate wave energy and protect shorelines (Elliff and Silva 2017; Rao et al. 2015), and more complex reef structures attenuate wave energy faster (Monismith 2007). Structural complexity is essential for hydrodynamic processes that transport heat and nutrients and entrain larvae (Monismith 2007; Hearn et al. 2001; Hata et al. 2017). Reef complexity is important to many ecological patterns and processes, such as the maintenance of biodiversity (Torres-Pulliza et al. 2020), habitat zonation (Done 1982), and recovery following disturbances (Burns et al. 2016). While the importance of structural complexity has been recognized for decades (Alvarez-Filip et al. 2011; Graham and Nash 2013), little is known about how individual corals of different species, morphologies, and sizes contribute to reef complexity in an objective, quantitative manner. This knowledge gap exists because of past difficulties in measuring the three-dimensional (3D) complexity of large reef patches and the lack of standardized complexity metrics (Kovalenko et al. 2012).

In the last decade, photogrammetry has emerged as a way for marine scientists to capture the 3-dimensionality of benthic habitats (Friedman et al. 2012). When applied to coral reefs, photogrammetry can accurately capture a wide range of both two-dimensional (2D) and 3D data (House et al. 2018). Photogrammetric products such as point clouds, digital elevation models (DEMs), and orthomosaic imagery can be used to measure coral reef structural complexity (Anelli et al. 2019; Friedman et al. 2012; Figueira et al. 2015; Burns et al. 2015; Leon et al. 2015), coral growth (Ferrari et al. 2017), coral community composition

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(Burns et al. 2015; Torres-Pulliza et al. 2020), and structural changes in a reef environment (Burns et al. 2016; Fallati et al. 2020). Photogrammetric products can be spatially registered for repeat surveys that can measure ecological and structural changes to the reef (Edwards et al. 2017).

In this study, we measured the structural complexity of coral reefs and the individual colonies living upon them using three interdependent elements of complexity of reef surface descriptors with strong ecological linkages (Torres-Pulliza et al. 2020). Rugosity captures surface area per unit planar area and fractal dimension captures how much a surface fills volume. Both descriptors are dimensionless and additive, meaning that the estimate for a reef patch is the mean of those of its constituent parts (Williamson and Lawton 1991). The third descriptor, height range, captures the upper limit of vertical extent and applies across all constituent parts (Torres-Pulliza et al. 2020). Our study aimed to understand how individual coral colonies of various species contribute to each of these surface descriptors and therefore the overall 3D structure of reefs.

Methods

The study was conducted in six shallow-water (0.5–2 m depth) sites distributed haphazardly in Kāneʻohe Bay, Oʻahu, in September 2019 (Fig. 1, inset). We collected 2500–4500 overlapping images at each site with a Canon EOS Rebel SL3 DSLR camera using the spiral survey method described in Pizarro et al. (2017). To provide scale and orientation for each model, three scale markers were placed within each spiral area and their depths, distances, and angles among each other were measured. The images were then used to construct 3D models and orthomosaic images using Agisoft Metashape photogrammetric software (Fig. 1) following the workflow of Roach et al. (2021). The 3D meshes were inspected visually for outlying points and clipped as a planar circle with a 6 m radius from the center, which captured approximately 113 m^2 of reef area. Average mesh segment size for each site ranged from 20 to 30 mm^2, and so we used 25 mm^2 as the mesh resolution.

The orthomosaic images were used to visually locate and identify colonies of six coral species found in Kāneʻohe Bay (Bahr et al. 2015): *Montipora capitata* and *Porites compressa* that are abundant in the bay; *Pocillopora acuta* that is less abundant and difficult to tell apart from *Pocillopora damicornis* (these species were therefore grouped and labeled as *Pocillopora acuta* because their contributions to 3D structure are likely to be similar); and *Montipora patula*, *Pocillopora meandrina*, *Porites duerdeni,* and *Porites lichen*, which are all rare. Given difficulties capturing the 3D shape of colonies growing into one another, we haphazardly selected a maximum of 10 colonies of each species at a site that were isolated from other colonies. While carefully consulting the orthomosaic images, colonies were outlined in Metashape on the 3D mesh at the interface of the colony base and reef substrate (Fig. 1). The colonies were left in the same orientation as they were in the larger 3D mesh and saved as separate mesh files. A total of 142 isolated coral colonies were outlined and extracted from the 3D reef models. Only one colony of *P. lichen* was found and, therefore, was not included in analyses. We pooled species data from the six sites.

For the six sites, height range (HR) and surface area (SA) of 3D meshes were measured in Agisoft Metashape and planar area (PA) was calculated as a circle with a radius of 6 m (i.e., 113.1 m^2). Site-level HR was calculated as the difference between the highest and lowest point in the mesh. Site-level rugosity (R) was calculated by dividing SA by PA. Site-level fractal dimension (FD) was calculated from the HR and R estimates according to the plane equation in Torres-Pulliza et al. (2020; Eq. 1) with an extent of 12 m and grain size of 0.005 m (i.e., the square root of the mesh resolution 25 mm^2). For each extracted colony mesh, HR was measured as the distance between the lowest and highest point, and R was calculated by dividing SA by PA. It was not known whether the Torres-Pulliza et al. (2020) equation would provide accurate colony-level estimates of FD, given the geometric theory was developed for rectangular plots, and so FD was calculated both with the equation and also using the cube-counting method outlined in Zawada et al. (2019). Extents for equation FD calculations were the square root of PA for a colony, and grain was the same as for the site (i.e., 0.005 m).

We used ANOVA and Tukey's HSD tests to differentiate among species' contributions to site-level complexity. For each species, we also examined the relationships between colony size (as planar area) and each surface descriptor plus colony surface area. We used a linear regression to test whether the slopes of these relationships were significantly different from zero (i.e., size independent). R, HR, SA, and PA data were all log10-transformed prior to analyses. We viewed the areas occupied by species on the surface descriptor plane defined by FD and R using

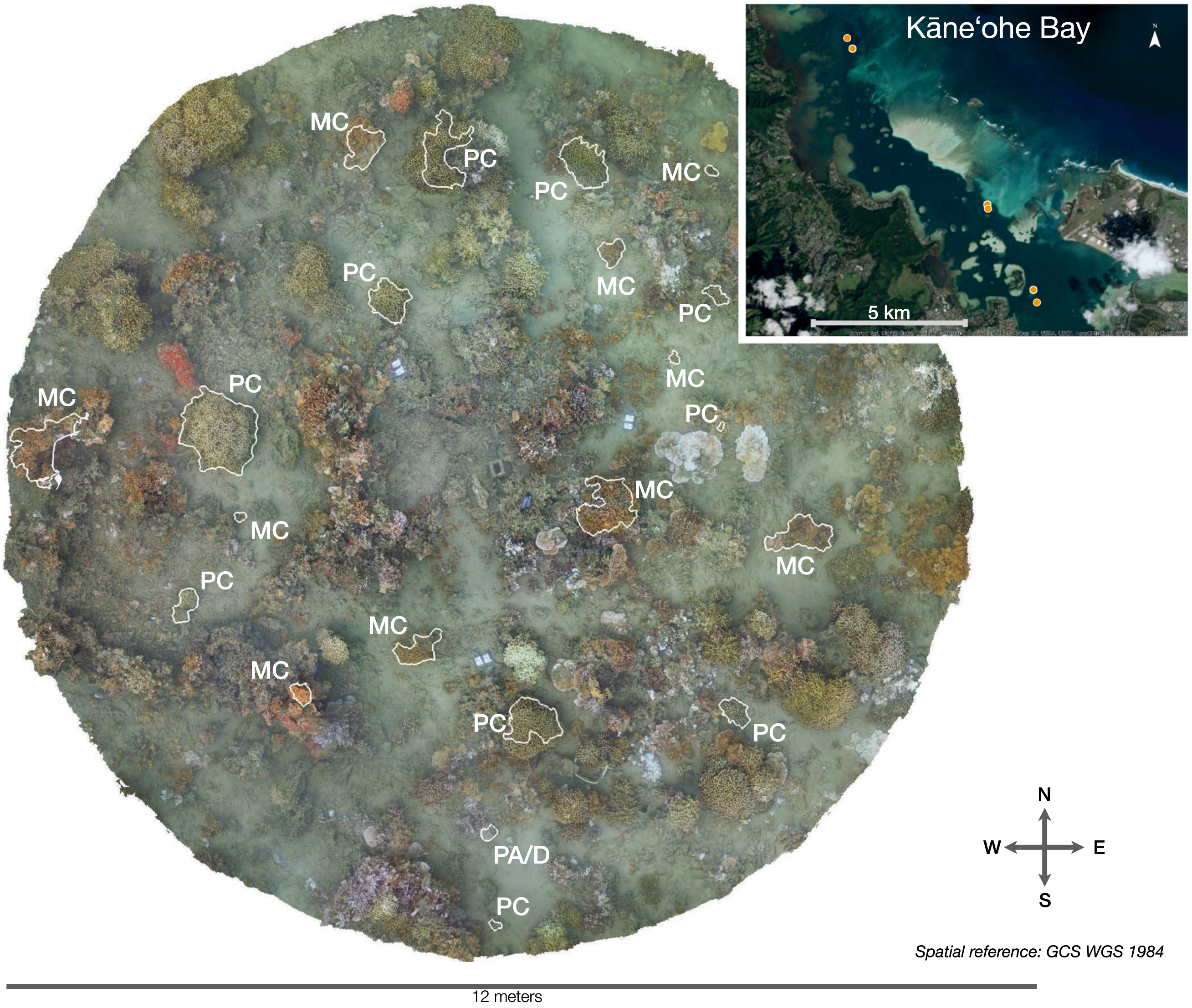
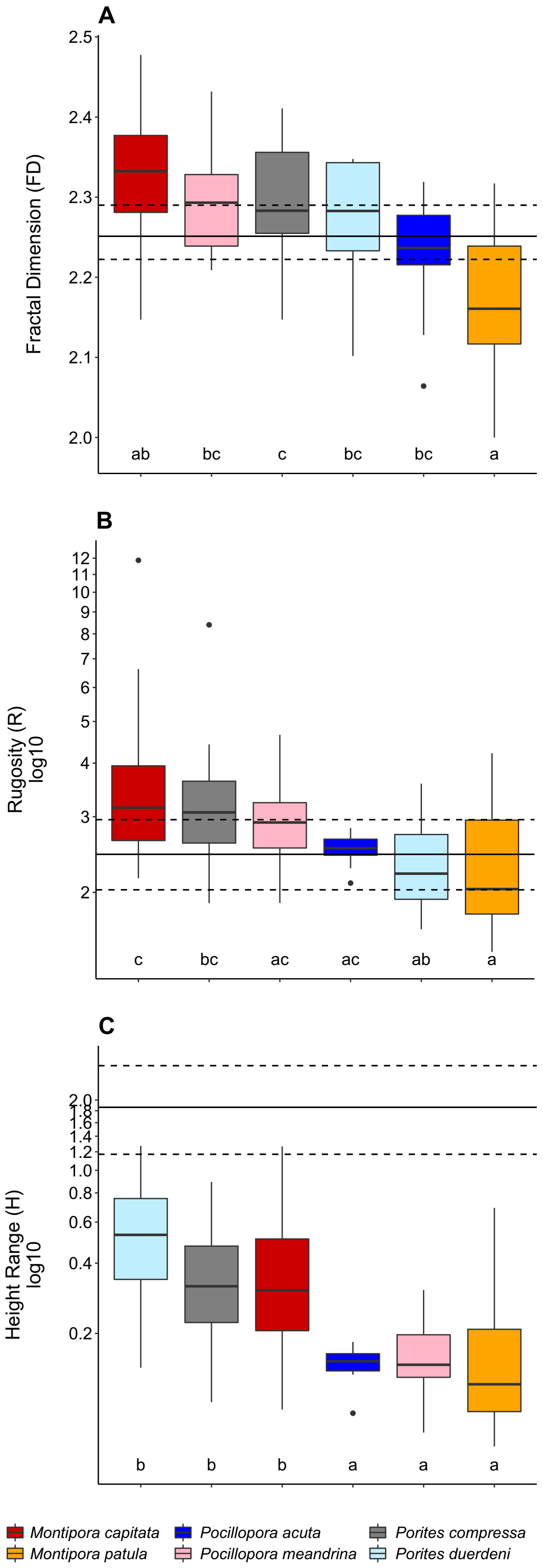


Fig. 1 Top-down view of a 3D mesh model for one of the six sites, illustrating outlined coral colonies. The diameter of the model is 12 m. MC is *Montipora capitata*, PC is *Porites compressa*, and PA/D is *Pocillopora damicornis/acuta*. Map inset shows the six sites in Kāne'ohe Bay

convex hulls. We used Pearson's correlation to examine the association between FD from cube counting and the Torres-Pulliza et al. (2020) equation in the supporting material; however, FD from cube counting was presented in all the main analyses. All statistical analyses were run using R statistical software (R Core Team 2020). All data and analyses, including code for creating figures, are available at https://github.com/jmadinlab/coral_contribution_to_complexity.

Results and discussion

Across the reef sites, structural complexity was remarkably similar (Fig. 2, horizontal lines, and Fig. 3, black points), suggesting that the shallow reefs in Kāne'ohe Bay differ little in their structural complexity at the scale the reefs were imaged (113 m^2 areas). However, the complexity of coral colonies living upon these areas varied substantially (Figs. 2 and 3). This variation was expected, given that



◀**Fig. 2** Boxplots of surface descriptors for colonies of each species ranked from highest to lowest median: (**A**) fractal dimension (cube counting), (**B**) rugosity, and (**C**) height range. Horizontal lines in each panel represent the median and range of surface descriptors at the six reef sites. Horizontal lines across panels represent the reef sites' mean (solid) and range (dashed). Shared letters below each coral species represent group similarity to other species based on Tukey HSD

larger-scale complexity is an average (or limit, in the case of height range) of the sub-parts from which it is composed. For instance, fractal dimension (FD) for sites, which can potentially range from 2 to 3, ranged only 0.08 units (approx. 2.3 to 2.38), whereas FD of coral colonies spanned almost half a dimension—from almost perfectly flat (2.0) to more space filling (2.48). Similarly, rugosity, which can potentially range from 1 to infinity, ranged from 2.03 to 2.95 units across the sites, whereas coral rugosity ranged an order of magnitude (1.45 to 11.87). Together these results demonstrate that the structural complexity of reef sites kilometers apart, with different species assemblages and size distributions, converged at relatively small areas of study reef. This result suggests that comparisons in structural complexity across regions and through time would benefit from focusing on the scale of the constituent parts that build that complexity, alongside assessments of structure for larger reef areas. Together, these approaches would result in a more holistic understanding of reef structure at different scales (Burns et al. 2015; Urbina-Barreto et al. 2021).

Colonies of different species contributed differently to reef-level structural complexity (Fig. 2, Table S1), which was largely attributable to their growth morphologies. Corymbose colonies of *Pocillopora meandrina* and *P. acuta* and digitate (i.e., encrusting with short branching uprights) colonies of *Montipora capitata* and *Porites compressa* contributed the highest levels of FD (Fig. 2A). These species were not statistically distinguished, and their median FD was all greater than the reef-scale FD. That is, these species acted to increase reef-scale FD. Meanwhile, the purely encrusting *M. patula* colonies acted to decrease reef-scale FD (Fig. 2A). Colonies of *M. capitata* had the highest median rugosity, and *M. patula* had the lowest (Fig. 2B); however, *M. patula* showed the broadest range of rugosities, presumably because this encrusting species reflects the reef surfaces it grows over. *Porites duerdeni* had intermediate levels of rugosity and the greatest height ranges, due to this species' massive (i.e., hemispherical) growth form. Three species formed low height range colonies (*M. patula* and the two *Pocilloporids*), and the other three species formed the highest vertical ranges (Fig. 2C). *Montipora capitata* exhibited the broadest range of all three descriptors, due to this species high levels of

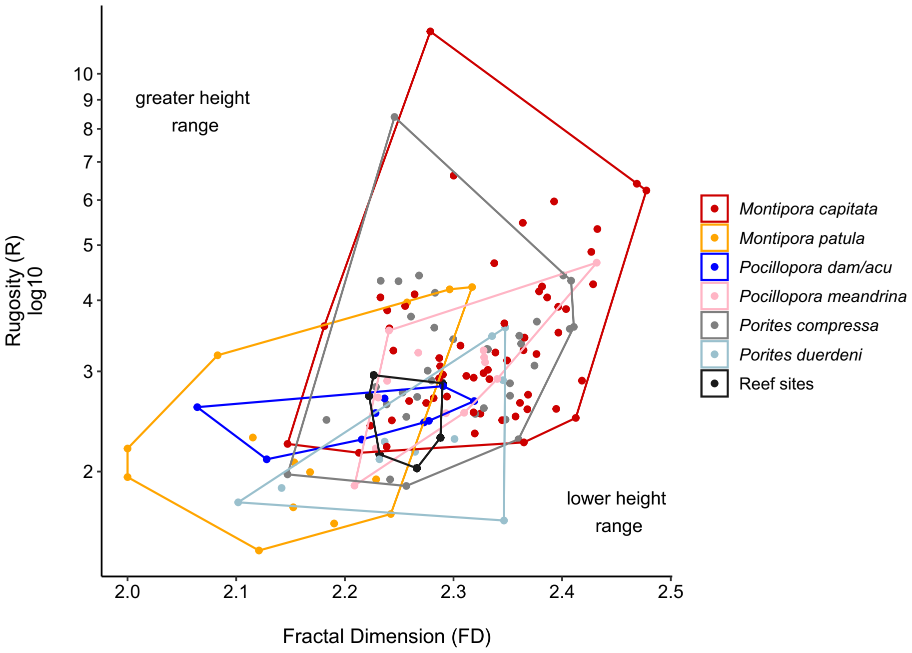


Fig. 3 The distribution of colonies over the geometric space framed by fractal dimension (cube counting) and rugosity. Convex hulls (colored lines encapsulating each species) help illustrate the position and extent of species in this space. Black points and lines are the reef sites. Given the geometric constraint among surface descriptors, an indication of where height range is higher and lower is given

plasticity (Bahr et al. 2015). Together, these results demonstrate how colonies of different growth forms contribute to structural complexity at larger scales.

Species occupy certain regions of the surface descriptor space with lots of overlap (Fig. 3). However, this variation was constrained by HR, because coral colonies tended to occupy only a limited spread of height ranges (10–50 cm high, Fig. 2C). Figure 3 shows the importance of the two abundant species, *Montipora capitata* and *Porites compressa*, for increasing structural complexity. Variation in complexity among species was likely driven either by levels of morphological plasticity, such as what is expected when growing in different flow and light levels (Burns et al. 2015; Urbina-Barreto et al. 2021), or by colony size. However, we did not find strong relationships between planar area and FD and R (Fig. 4A, B, Table S2). FD tended to increase with colony size, but only with marginal significance for two species (*P. compressa* and *M. patula*); that is, these species tended to fill significantly more 3D volume as they became larger. Despite a slight tendency for rugosity to decrease with size across all species (Fig. 4), there were no significant relationships (Table S2B). These results suggest that all our study species tend to grow isometrically; that is, surface area and planar area increase at the same rate as colonies grow (Zawada et al. 2019). All species increased significantly in HR with size, which is uncontroversial (Table S1C). Lastly, all species' surface areas scaled approximately linearly with size (Fig. S2D), which was expected following the isometric association of rugosity with size.

While Torres-Pulliza et al. (2020) show that FD can be calculated accurately from HR and R in square reef patches, their equation has not been tested for irregular colonies. We found that there was a significant association between colony FDs calculated using the equation and by cube counting (Fig. S1A); however, a Pearson's correlation coefficient of 0.54 suggested a mismatch. Part of this mismatch was related to the inconsistent orientations of colonies extracted from larger site-level meshes (which were not altered; see "Methods"). Colonies growing on slopes had inflated height ranges relative to their rugosities, which in turn resulted in lower FDs than expected. Another part of this mismatch was related to the planar shapes of colonies, where more irregular shapes led to equation FDs higher than expected, which was caused by lower-than-expected planar areas that inflated rugosities. Such mismatches led to different species rankings for FD between approaches (equation vs. cube counting; Fig. S1B). These results suggest that either (1) the more complicated cube-counting approach should be used for discrete coral colonies, or (2) that colonies should be extracted from meshes in a standardized manner (e.g., extracted as planar rectangles that encapsulate colonies).

This study has provided one of the first quantitative investigations of how coral colonies of multiple species and sizes contribute to the larger-scale 3D structural complexity of coral reefs. Identifying which species contribute more or less toward reef complexity as they grow will help with efforts to monitor and restore complexity, and subsequently biodiversity, resiliency, and overall function of coral reef ecosystems (Graham and Nash 2013).

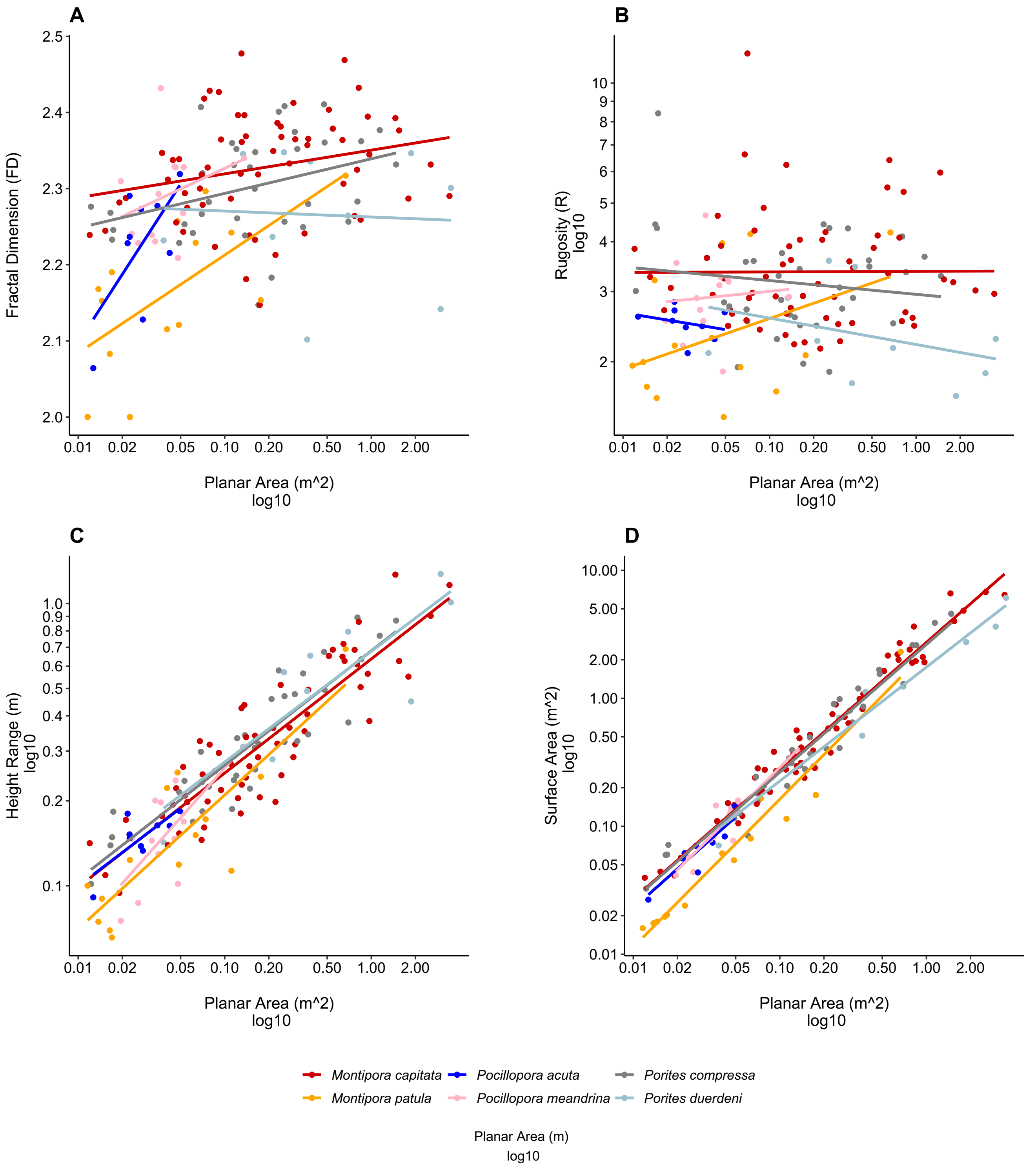


Fig. 4 Scatter plots of surface descriptors (**A–C**) as a function of planar area, as well as surface area (**D**) as a function of planar area, for each species. Lines in each panel represent a linear regression model for each species. Slope estimates are presented in Table S2

Further research can help identify key species in reef areas that need primary attention for conservation and restoration work.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-021-02190-y.

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Data and code availability https://github.com/jmadinlab/coral_contribution_to_complexity

Declarations

Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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