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Geological age and environments shape reef habitat structure

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Conflict of Interest
The authors declare that they have no conflict of interest.

Biosketch
The author team consists of marine ecologists with expertise in coral reef ecology. Authors share a common interest in reef system patterns, with special interest in habitat complexity to expand our understanding of coral reef ecosystems.

Title: Geological age and environments shape reef habitat structure
Running Title: Factors shaping reef habitat structure

Abstract

Aim: Habitat complexity plays an important role in the structure and function of ecosystems worldwide. On coral reefs, habitat complexity influences ecosystem services such as harvestable fish biomass and attenuation of wave energy. Here we test how three descriptors of surface complexity—rugosity, fractal dimension, and height range—trend with the geological age of reefs (0.2-5.1 million years old), depth (1-25 m), wave exposure (1-306 kW/m), coral cover (0-80%), and three habitat types (aggregated reef, rock and boulder, and pavement).

Location: We surveyed across 234 sites and 4 degrees of latitude in the eight main Hawaiian Islands.

Time Period: April 2019 – July 2019.

Major taxa studied: Reef building corals.

Methods: We estimate three surface descriptors (rugosity, fractal dimension, and height range) using structure-from-motion photogrammetry. We evaluate hypothesized relationships between these descriptors and geological reef age, depth, wave exposure, coral cover, and reef habitat type using generalized linear models that account for survey design.

Results: The rugosity of reef habitats decreased with geological reef age; fractal dimension (and coral cover) decreased with wave exposure; and height range decreased with depth. Variations in these patterns were explained by the different habitat types and the way they are formed over time. Nonetheless, the three surface descriptors were geometrically constrained across all habitat types, and so habitats occupied distinctly different regions of habitat complexity space.

Main conclusions: This study showed how broad environmental characteristics influence the structural complexity of habitats, and therefore geodiversity, which is an important first step towards understanding the communities supported by these habitats and their ecosystem services.

Keywords: Coral reef, Structure-from-Motion, habitat complexity, structural complexity, environmental drivers

Introduction

Habitat structure, defined as the physical three-dimensional (3D) surface of an environment, is fundamental to ecology. The complexity of habitat structure is studied in both

terrestrial and aquatic environments, and ranges from relatively simple and flat surfaces like grasslands and sandflats to architecturally complex surfaces like coral reefs and rainforests. While metrics of habitat complexity are often system-specific, the importance of structural complexity in mediating species distributions and abundances has been observed across ecosystems (Heck & Whetstone, 1977; Russell, 1977; Spies, 1998). Complex habitat structure can influence ecological processes such as predation and competition by providing more refuges and increased food resources (Huffaker, 1958; Almany, 2004; Juliano, 2009). Habitat complexity is subsumed by geodiversity, which describes how abiotic components and ecological processes that shape biodiversity (Lawler et al., 2015). Given the importance of habitat complexity for biodiversity and ecosystem functioning, it has become a growing theme in studies about the conservation and revitalization of ecosystems (Yanovski & Abelson, 2019).

Coral reefs are a prime example of the importance of habitat complexity in relation to ecosystem functions and services. Reefs with higher levels of structural complexity tend to be more diverse (Risk, 1972; Luckhurst & Luckhurst, 1978; Roberts & Ormond, 1987; Grigg, 1994; Kostylev et al., 2005), sustain a higher harvestable fish biomass (Graham, 2014), and attenuate more wave energy for coastal protection (Monismith, 2007). Ecological functions, such as the capacity to build calcium carbonate structure (Alvarez-Filip et al., 2013) and conduct productive nutrient cycling (Szmant, 1997), are influenced by reef habitat complexity. Reef building corals are capable of growing into large and structurally diverse morphologies. These calcium carbonate formations are the primary contributors of reef habitat complexity, which in turn improves the recruitment of their larvae and other reef associated species (Fabricius et al., 2014; Hata et al., 2017). In addition, structurally complex reefs tend to recovery faster following disturbances, such as prolonged, abnormally high sea surface temperatures (Graham et al., 2015) and storms (Graham & Nash, 2013).

Habitat complexity on coral reefs can be influenced by a range of biotic or abiotic factors. While reef building corals are the primary physical ecosystem engineer (Hatcher, 1997), the overall structural complexity and configuration of reef systems can be influenced by geological processes, such as physical erosion and subsidence (Fletcher et al., 2008). The geological age of a reef captures the accumulation of many interrelated processes, such that older reefs tend to exhibit distinct structural features such as spur and groove formations that are produced after long-term exposure to hydrological forcing (Duce et al., 2020). Geomorphological structure influences the distribution and composition of living coral communities, like the reef building corals, which in turn modifies structural complexity. Additionally, wave exposure, or wave energy, shapes coral community composition and physical topographic structure (Grigg, 1998). Wave energy can also directly and indirectly affect rates of erosion, sedimentation, and temperature fluctuation (Andrews & Gentien, 1982), and therefore the mortality of corals and their addition to structure (Rasser & Riegl, 2002). Finally, the depth of a reef will also influence susceptibility to erosion processes and the distribution of coral taxa, which in turn influences structural complexity (Huston, 1985). Though these factors influencing structural complexity on coral reefs are fairly well understood, the interplay among biotic and abiotic processes confounds the ability of scientists to quantify primary drivers of habitat complexity across a range of habitat types. Furthermore, confidence in these relationships is largely distorted by spatial scale (Bellwood et al., 2019), as studies commonly focus on a single resolution (Yanovski et al., 2017). Heterogeneity and arrangement of structures at centimeter scales (e.g., individual coral colony) are not the same patterns detected at kilometer scales (e.g., coastlines). Still, within a single resolution, various types of structural elements constitute habitat complexity, though may

not respond to biotic and abiotic factors in similar fashion. Integrative approaches, such as a combination of habitat structure metrics, are needed to more realistically approximate habitat structural complexity and the implications on reef ecosystems.

A habitat's surface structure can be described by three distinct metrics of structural complexity that constrain one another: rugosity, height range, and fractal dimension (Torres-Pulliza et al., 2020). Rugosity, the ratio between surface area and planar area, is most commonly used as an estimate of habitat complexity. It describes the spatial heterogeneity of a system and links between rugosity and marine communities have been studied extensively (Risk, 1972; McCormick, 1994; Idajdi & Edmunds, 2006; Fisher et al., 2007; Graham & Nash, 2012; Burns et al., 2015). For a given scale, rugosity alone cannot accurately differentiate coarse and fine structural features (Zawada & Brock, 2009). For instance, a reef composed of large mounding colonies may share the same value of rugosity as one dominated by a veneer of intricate branching morphologies. Fractal dimension describes space filling irrespective of area, and has been used to capture finer-scale components of structure, such as coral morphology (Basillais, 1997; Fukunaga et al., 2019). In virtually all ecosystems, niche availability is a precursor to species diversity and coexistence (Huston, 1979), and many studies have supported the influence of fractal dimension on species richness through its characterization of microhabitats (Palmer, 1992; Kostylev, 2005). Rugosity and fractal dimension can be linked when considering height range, the vertical extent by which structural complexity is bounded within. Height range is associated with fish biomass (Harborne et al., 2012), where taller coral colonies provide refuge for fish, and refuge availability tends to scale with colony height (Harborne et al., 2011). These three metrics are unique in that they describe distinct elements of habitat complexity. As such, with recent technological advancements, accurate estimates of different geometries of structure can be made, even within a single resolution.

Structure-from-Motion (SfM) photogrammetry has greatly improved our ability to study complex attributes of underwater environments (Burns et al., 2015). SfM is a photogrammetric process capable of producing high-resolution (<1mm) 3D reconstructions from underwater imagery. These reconstructions can be used to produce a digital elevation model (DEM), a 2.5D image that holds depth information within raster cells. DEMs can be used to estimate numerous metrics of habitat structural complexity. Analyzing DEMs provides a more robust and accurate approach to examine habitat complexity than traditional 2D measures, and link them with ecologically important questions (Magel et al., 2019, Helder et al., 2022). Large scale assessments of structural complexity on coral reefs across islands have been conducted using remote sensing methods such as acoustic imaging, light detection and ranging (LiDAR), and airborne imaging spectroscopy at a relatively high resolution (1m) (Asner et al., 2021; Lyons et al., 2020). However, in-water imagery collected in close proximity to the substrate is necessary to produce 3D habitat reconstructions at a resolution (< or equal to 1cm) capable of describing intricate features of 3D habitat complexity. A large-scale assessment of habitat complexity at such a high resolution is currently lacking. Furthermore, most studies solely focus on rugosity as a single unit of habitat complexity (Brock et al., 2004; Brock et al., 2006; Purkis et al., 2008; Wedding et al., 2008). However, biological communities are influenced by multiple aspects of habitat complexity, such as fractal dimension (Torres-Pulliza et al., 2020). Disentangling the contributions of biotic and abiotic factors on habitat complexity requires studying multiple metrics across large spatial scales and at a high resolution.

The main Hawaiian Islands present an ideal system to identify drivers of structural complexity along gradients in depth, geological age, wave exposure, coral cover, and habitat

type. In this study, we (1) estimated three metrics of 3D habitat structural complexity (rugosity, fractal dimension, and height range) from 300 digital elevation models (DEMs) at sub centimeter resolutions (2mm) across the eight main Hawaiian Islands, and (2) tested relationships among these metrics with depth, wave exposure, geological reef age, and percent coral cover, and explored how these relationships vary among three reef broad habitat types (aggregate reef, pavement, rock and boulder). To our knowledge, this is the first large-scale (e.g., hundreds of sites across > 500km) application of in-water SfM photogrammetry that quantifies how biotic and abiotic factors influence sub-colony to reef-scale structural complexity across an island chain.

Methods

1. Image Collection

Surveys were conducted between April and July 2019 in the eight main Hawaiian Islands as part of the NOAA Coral Reef Conservation Program's National Coral Reef Monitoring Program (NCRMP) (Figure 1). The study sites captured a broad gradient of reef habitat types, coral cover levels, wave exposure and geological reef age. Three-hundred sites were selected using a stratified random sampling design, where sites were randomly selected within hard bottom forereef habitats stratified into three depth strata (shallow: 0-6m, mid: > 6-18m, and deep: > 18-30m). Sample size within each stratum was proportional to the amount of hardbottom area and the variance of coral density in previous years (Swanson et al., 2011), such that more sites were sampled in strata with higher variance and more hardbottom.

At each survey site, a 30m transect line was deployed along the isobath and two to four scale bars (0.25 or 0.5m in length), which served as ground control points (GCPs), were placed at both ends of the transect, approximately 0.5m away from the transect line. Depths of each GCP were recorded to the nearest foot. JPEG images were collected using a Canon EOS Rebel SL2 digital camera enclosed in an Ikelite underwater housing with a 15.24cm dome port (6 inch), with the standard lens set to a focal length of 18mm and an aperture of F10. Camera settings were chosen to produce the highest quality images across a variety of diving conditions (e.g., overcast, sunny, clear, murky). Prior to image collection, the camera was white balanced at depth using an 18% grey card. A diver swam 1m above the transect collecting imagery continuously from 0m to 20m, swimming back and forth with a 0.5m spacing between passes, ensuring 60% side overlap and 80% forward overlap between photos. A total of six passes were completed, resulting in an area of reef measuring roughly 4 x 20 m following image processing (below); in depths greater than 18m, the survey area was restricted to 4 x 12m as a result of diver air limitations. At each site, latitude and longitude were recorded using a commercial grade GPS, and habitat type was recorded as one of the following: aggregate reef (94 sites), aggregate patch reef(s) (6 sites), pavement (62 sites), pavement with patch reef (2 sites), pavement with sand channels (6 sites), rock and boulder (78 sites), reef rubble (3 sites), spur and groove (3 sites), sand with coral and rock (9 sites). These habitat types were later reduced to three distinct types to exclude low-sampled habitat types. Images were assessed and those with unwanted objects (e.g., fins) or that were overexposed were removed.

To assess coral cover, a Canon G9x digital camera and housing mounted on a 1m pole was white balanced at depth using an 18% grey card. Images were collected every meter for a total of 30 images/site. On average, each photo had a footprint of $1m^2$, covering a total planar area of approximately $30m^2$ for each site. Benthic cover data were extracted from the images using the web-based software CoralNet (Beijbom et al., 2015). Benthic composition was

determined to the nearest functional group level, described as either hard coral, crustose coralline algae, turf algae, Halimeda sp., encrusting macroalgae, macroalgae, sessile invertebrate, soft coral, or sediment. For each image, the organism or type of substrate was identified beneath each of ten randomly overlaid points and points were pooled across all imagery to generate site-level percent of hard coral cover and other key functional groups (300 points/site). Twenty-three (23) sites did not have photos and subsequent benthic cover estimates, and were therefore removed from the analyses. On average across all sites, 69% was classified as turf algae, 12% as hard coral, 9% as encrusting macroalgae, 5% as sediment, 3% as crustose coralline algae, 2% of macroalgae, and less than 0.1% was sessile invertebrates and soft coral.

2. Model Generation

Three-dimensional model construction was performed using the software Agisoft Metashape Professional v.1.6.1 (Agisoft LLC., St. Petersburg, Russia). Details regarding system requirements, software settings, and model construction parameters were followed according to Suka et al. (2019). Briefly, images were aligned using high accuracy parameters with a 40,000 key point limit and 0 tie point limit. After, a medium quality, dense 3D point cloud with mild depth filtering was built and known GCP coordinates with x, y, and z values were used to create a geometrically accurate local reference system and scale the model. The dense point cloud was updated to reflect the local reference system. Two digital elevation models (DEMs) were generated for each survey site, one with default interpolation methods and one with interpolation methods disabled. Settings to build the DEMs were as follows: projection type geographic with local coordinates, dense cloud as source data and 0.002m resolution. Default interpolation was desired to acquire a DEM with no holes and was the product used for structural complexity metrics extraction. But, any area captured in at least one camera will be interpolated and can result in distorted model borders. To avoid these areas where limited data was interpolated, a non-interpolated DEM was extracted for use of the accurate reconstruction boundary. No analysis was performed on the non-interpolated DEM, but was used as a guide to trim the interpolated DEM. Ground sampling distances of the models ranged from 0.00014 to 0.00034 meter/pixel, with errors of 0.5 to 2.5 pixels, therefore a resolution of 0.002 meters was within the range of model accuracy.

3. Extraction of Habitat Metrics

Structural complexity metrics were extracted and analyzed using the statistical software R v3.6.1 (R Core Team, 2022). Digital elevation models (DEMs) were chosen over 3D mesh models for this analysis to avoid uncertainties and biases associated with overhanging surfaces (Fukunaga & Burns, 2020). Capturing overhangs can be specifically challenging when considering variability in environmental conditions (e.g., sun angle) and diver methods (e.g., angle which overhanging areas were captured). Though DEMs have the potential to underestimate surface rugosity and fractal dimension (Torres-Pulliza et al., 2020), the infrequency of overhanging surfaces in our study sites make this a negligible concern. Interpolated DEMs were clipped by the extent of the non-interpolated model to avoid inaccurate edges. Specifically, the non-interpolated DEM was aggregated with an aggregation factor of 100 using a mean function to smooth the edges, and converted to a polygon. The resulting polygon was used to crop the interpolated DEM, thereby removing the distorted edges. Each belt was subsampled to more easily sample across belts that varied slightly in model straightness and width. Five 2 x 2m boxes were placed on each belt transect by randomly pulling coordinates

from a normal distribution and only boxes that were fully within the bounding area were used (i.e., containing no NA values). Random boxes were continuously placed until five were achieved. Plots that were too thin for the 2 x 2m boxes were excluded (14 sites). We wanted to quantify structural complexity at the local box scale; that is, without the larger-scale influence of bathymetry (e.g., reef slope). Therefore, we corrected the tilt of boxes by fitting a linear regression model with z as a function of x and y, and replacing z with model residuals.

Scripts modified from Torres-Pulliza et al. (2020) were used to calculate three structural complexity metrics: rugosity, height range, fractal dimension (variation method). The three metrics were extracted from each 2 x 2m box; surface complexity and height range were calculated at a resolution of 1cm, while fractal dimension was calculated over a range of 1cm to 2m (thus over 2 orders of magnitude). Height range (H), fractal dimension (D), and rugosity (R) were transformed according to the geometric theory described by Torres-Pulliza et al. (2020), and shown in Equations 1-5:

$$H + D = R, \tag{1}$$

$$\square = \square\square\square 10\left(\frac{\square h}{\sqrt{2}\square 0}\right), \tag{2}$$

$$\square = \square\square\square 10\left(\frac{\square}{\square 0}\right)(\square - 3), \tag{3}$$

$$\square = \frac{1}{2}\square\square\square 10(\square^2 - 1), \tag{4}$$

$$\square\square\square 10\left(\frac{\square h}{\sqrt{2}\square 0}\right) + \square\square\square 10\left(\frac{\square}{\square 0}\right)(\square - 3) = \frac{1}{2}\square\square\square 10(\square^2 - 1), \tag{5}$$

where Δh is surface height range at the broadest scale, L (2m), d is the mean height range of the surface at different scales, detailed as the variation method (Zhou & Lam, 2005), r is surface complexity and $L0$ is the finest scale (1cm). Height range was estimated by taking the difference between maximum and minimum depth within the plot. Surface complexity, r, was calculated using the *surfacearea* function divided by planar area (4m^2). All analysis used these derivations of rugosity, height range, and fractal dimension.

4. *Predictor Variables*

To explore relationships between habitat complexity and the surrounding environment, five variables were chosen and hypothesized to have substantial influences that operate across different spatial scales: depth, geological reef age, wave exposure, percent coral cover, and habitat type. Site depth was estimated using a dive computer. A geological reef age raster was approximated using a series of literature sources that summarize substrate age based on the oldest reliable age of theoleiitic basalt estimates (K-Ar age) (Clague & Dalrymple, 1987; Moore & Clague, 1992). A raster illustrating average annual maximum wave power anomaly was chosen to represent exposure levels (Wedding et al., 2018). Specific exposure values were extracted from the raster using latitude and longitude coordinates of each site. Island age and wave exposure rasters had a resolution of 500 m. Percent hard coral cover at each site was acquired using methods described above. Habitat type was included given the distinct differences in development and construction of each habitat: aggregate reef, pavement, and rock and boulder (See Figure 2a-c for habitat examples). These categories represent the three dominant habitat types in the main Hawaiian Islands and had a large enough sample size to include in the models.

5. *Statistical Analyses*

Selection of the three habitat types (aggregate reef, pavement, and rock and boulder) were confirmed by Tukey's Honest Significant Differences test by comparing differences in mean level rugosity, fractal dimension, and height range between habitats. The remaining habitat types were dropped, resulting in a total of 234 sites that were included in the final analysis (Table S1). Correlation among independent variables were evaluated to ensure no multicollinearity (Figure S1).

To assess the assumption that rugosity, height range, and fractal dimension are geometrically constrained by a plane, we constructed a plane from the collection of points using a least squares solution approach, such that the summed squared residuals perpendicular to the main axis (i.e., z-axis) is minimized. This method was sufficient for this study since the points were close to the plane and not near perpendicular to the z = 0 plane. We estimated the centroid of the points and calculated the covariance matrix relative to it. We performed linear regression along the main axis to determine the plane of best fit. An r^2 was estimated by comparing fractal dimension data to fractal dimension calculated from the plane equation.

Principal components analysis (PCA) was used to visualize the relationships between structural complexity and the environment. PCA was carried out using the *prcomp* function in the R package 'stats', with calculations based on singular value decomposition. All variables were centered and scaled so that they contributed equally to the analysis. The first three principal components were retained following Kaiser criterion, such that they had eigenvalues greater than one. For each principal component, variables were deemed important based on whether their loadings exceeded the null contribution value of ±14.30 (1 divided by 7 variables * 100). Multivariate normal distribution ellipses were added, corresponding to the three habitat types.

Due to the complex sampling design across depth strata and unbalanced nature of this design, each site was weighted using the inverse proportional survey weights to generate unbiased estimates when using site-level data (Lumley, 2011). Survey weights were calculated as the total possible sites in a given stratum over the number of sites surveyed in that given stratum. The *svydesign* function in the R package 'survey' (Lumley, 2011) was used to incorporate the inverse proportional weights and define the nested structure as follows: Island, sub-island sector, depth bin and site using the 'strata' argument of the *svydesign* function. Generalized linear models were conducted for rugosity, fractal dimension, and height range, separately, using the *svyglm* function with gaussian response variables. Fixed effects included the five predictor variables and habitat type as an interaction term with all other predictors to assess the influences of different habitat forms and their potential underlying mechanisms. Marginal effects plots were used to visualize the relationship between structure and the predictor variables; the *svyglm* model for each structural metric was used to generate predicted values of a given structural metric across the observed range of each variable, setting all other predictors to their observed means within a given habitat. A second series of generalized linear models were conducted to assess the influence of the environmental predictors (habitat type, depth, geological reef age, and wave exposure) on coral cover alone using the *svyglm* function with gaussian response variables.

Results

The three structural complexity metrics formed a plane when framed together, upon which 97% of the variation in fractal dimension was captured by the plane (Figure 2d). The mean values for each habitat type revealed unique arrangements in 3D space (Figure 2e-g). Generally, aggregate reef had greater fractal dimension, intermediate height range, and

intermediate rugosity. Pavement habitats were characterized by marginally lower values of fractal dimension, but much lower values of rugosity and height range. Lastly, rock and boulder habitats possessed the lowest fractal dimension, and considerably greater height ranges.

The principal component analysis further illustrated these patterns, where 60% of the observed variation was captured by the first two principal components (PC) (Figure 3; Table S2). Habitat type had visible overlap in distributions. However, the structure of pavement was largely associated with geological age. The habitat structure of rock and boulder habitats mostly corresponded with height range and wave exposure. Lastly, structural complexity of aggregate reef was heavily influenced by rugosity, coral cover, and fractal dimension. Though depth was present as a factor in all habitat types, the PCA suggested minor effects in driving overall habitat patterns. The PCA also revealed an inverse relationship between coral cover and exposure.

Rugosity increased significantly with coral cover (t = 32.34, p < 0.05) but decreased with geological reef age (t = -24.08, p < 0.05; Figure S2a-d). Significant patterns between rugosity and depth emerged when including the effect of habitat, with a positive relationship in aggregate reefs (t = 9.23, p < 0.05) and a negative one in pavement habitats (t = -7.27, p < 0.05; Figure 4a; Table S3). The negative relationship between rugosity and geological reef age was largely driven by aggregate reefs (t = -14.24, p < 0.05; Figure 4b). Positive correlations between rugosity and exposure deviated in aggregate reefs, where rugosity trended negatively with exposure (t = -6.54, p < 0.05; Figure 4c).

Fractal dimension increased significantly with depth (t = 5.48, p < 0.05), geological reef age (t = 11.78, p < 0.05), and coral cover (t = 15.95, p < 0.05), but decreased with exposure (t = -8.54, p < 0.05; Figure S2e-h). However, when including habitat type, the pattern between fractal dimension and geological reef age dissipated in all three habitat categories (Figure 4f; Table S4). In pavement habitats, fractal dimension increased with exposure (t = 2.33, p < 0.05) and decreased with coral cover (t = -1.08, p < 0.05; Figure 4g-h). Likewise, fractal dimension and coral cover had a negative relationship in rock and boulder habitats (t = -3.27, p < 0.05; Figure 4h).

Height range had a significant but weak negative relationship with depth (t = -4.35, p < 0.05), decreased with geological reef age (t = -21.76, p < 0.05) and increased with exposure (t = 6.35, p < 0.05) and coral cover (t = 11.11, p < 0.05; Figure S3i-l). Depth had insignificant and weak influence on height range in all habitats when separated (Figure 4i; Table S5).

The interaction between depth and exposure was negligible for all metrics of structure in aggregate reef habitats (Figure S3a,d,g). In pavement habitats, rugosity and height range were highest at shallow habitats with lower wave exposure and deeper habitats with higher wave exposure, while fractal dimension was greatest at shallower habitats with higher wave exposure and deeper habitats with lower wave exposure (Figure S3b,e,h). However, in rock and boulder habitats, rugosity and height range were highest at shallow sites with high wave exposure, and fractal dimension was greatest at deeper sites with lower wave exposure (Figure S3c,f,i).

The models had an adjusted r^2 of 0.57, 0.43, and 0.59 for rugosity, fractal dimension, and height range, respectively. Habitat type appeared to be a significant predictor for all metrics of structural complexity with the highest effects on height range and fractal dimension (Figure S4).

Modeling coral cover by habitat type, depth, geological reef age, and wave exposure revealed an adjusted r^2 of 0.45. Coral cover was primarily influenced by habitat type and secondary drivers varied between habitats, such that coral cover was secondly driven by an interaction between depth and exposure in aggregate reefs and pavement and by geological reef age in rock and boulder (Figure S5).

Discussion

Over 50% of variation in the three metrics of habitat complexity was explained by coral cover, geological reef age, and environmental variables. The patterns that emerged between rugosity, height range, and fractal dimension and the environment are likely related to well-known reef processes. Higher coral cover reefs tend to exhibit greater values of structural complexity, notably rugosity (McClanahan & Shafir, 1990; Bergman et al., 2000; Mangi & Roberts, 2007). Though studied to a lesser extent, fractal dimension has also been found to increase with coral cover, specifically in community compositions similar to those found in the main Hawaiian Islands (i.e., no tabulate colony morphologies) (Burns et al., 2019). As expected, fractal dimension was greatest in aggregate reefs where coral cover is highest. However, coral skeletons can retain their complex morphologies for some time after dying (Martin-Garin et al., 2007; Reichert et al., 2017), and so an increase in fractal dimension does not necessarily indicate higher coral cover.

Habitat type and geological age explained a large amount of the variation due to the different ways these habitats form. Pavement reefs tended to be structurally simple compared to aggregate and rock and boulder reefs, with less coral cover. These habitats were more common in geologically older reefs and are explicitly described as contiguous areas of exposed basalt with cracks and crevices, suggesting the nature by which we characterize a habitat as pavement is inevitably accounting for geology and geomorphology. Mid-aged islands (Maui, Molokai, Oahu, and Kauai), where pavement is not as common, have areas of well-developed fringing reef where structure of the reef is developed by accretion of calcifying organism skeletons rather than taking the form of the underlying basalt. In contrast, the distinct rock and boulder habitat is characterized by large basalt boulders derived from lava flows, which explains the larger height ranges relative to other habitats. The exact origin of these habitats remains unclear and theories around their creation range from chaotic, random deposition to intricate formation (Goff et al., 2006). Nonetheless, these reefs tended to be associated with locations facing higher wave exposure (Hobson, 1974), and like pavement habitats, rock and boulder reefs tend to have low levels of coral cover with lower morphological complexity. Height range and rugosity increased with coral cover and exposure in these habitats, despite coral cover decreasing with exposure, exhibiting the importance of accounting for the underlying architecture. Our study supports the importance of including habitat type as a descriptor to decipher proper mediators of reef structural complexity (Alvarez-Filip et al., 2011). Future studies could also integrate data capturing coral morphotypes, rather than taxonomy or simple measures of live cover, as this may help to differentiate how specific morphologies (e.g., mounding, branching, plating) contribute to 3D habitat complexity.

Our study supports the concept that rugosity, height range, and fractal dimension are geometrically constrained (Torres-Pulliza et al., 2020). Accordingly, rugosity describes the surface area of a particular region and height range defines the bounding box, by which fractal dimension illustrates how the surface area twists and turns to fit within the bounding box. Torres-Pulliza et al. (2020) looked only at aggregate reef, and our results show the same relationship for reefs spanning a greater range of complexities and habitat types. These findings suggest that very complex surface habitats in any system can be captured with three ecologically-relevant structural complexity variables.

Worldwide, coral cover is declining at a rapid rate due to a combination of local and global stressors (Pandolfi et al., 2003). Decreases in coral cover are often associated with erosion

of the reef framework, or reef flattening, through a series of physical pressures and chemical imbalances (Alvarez-Filip et al., 2009). We found that all metrics of structural complexity decreased as coral cover declined, consistent with the idea of reef flattening. With many severe ecological consequences of reef flattening, such as reconfiguration of algae consumed by herbivores (Tebbett et al., 2019) and reduction of calcium carbonate deposition rates due to changes in coral assemblage (Alvarez-Filip et al., 2013), more work needs to investigate how structural complexity can be built into restoration programs. Though habitat complexity has become a priority for restoration, continued anthropogenic stress and rapid loss of coral reef habitats suggests additional methods are needed (Yanovski & Abelson, 2019). Therefore, restoring structural complexity in tandem with conserving structurally complex hotspots could mediate the effects of anthropogenic stress and climate change. For example, while general increases in habitat complexity are favorable for healthy systems, reefs with intermediate rugosity, high fractal dimension, and low height range have peaked biodiversity metrics (Torres-Pulliza et al., 2020).

Our study can be compared with studies measuring habitat complexity and coral cover along the same island chain using aerial surveys. Both our study and Asner et al. (2021) found that water depth was a dominant driver of fine-scale rugosity. However, Asner et al. (2020) suggested wave exposure and water depth to be important drivers of coral cover; whereas, we found that coral cover declined with wave exposure and was variable with depth (i.e., depth had a positive influence on rugosity in aggregate reef and a negative influence in pavement). Difference among the studies may occur because the Asner et al. (2020) study was limited to shallower depths and our study was limited in geographic extent. Nonetheless, aerial imaging data has many benefits, including the enormous scales over which it can be collected. However, cross-scale studies that validate broader scale inferences using high resolution in-water mapping are needed to fully understand how patterns can be scaled up (Donovan et al., 2022).

Ecosystem conservation and management should aim to match the scale of abiotic and biotic processes operating in the system they wish to protect (Bellwood et al., 2019). Our work contributes to our understanding of habitat structure in relation to biodiversity and geodiversity that could be used to guide current and future conservation efforts. For example, there is a well-known relationship between habitat structure and fish biomass (Grigg, 1994), because abundance and diversity of reef associated organisms tend to increase when niche space is maximized and habitat heterogeneity exists (Gámez & Harris, 2022). Therefore, our work provides a mechanistic understanding of where fish biomass might be greatest and could be used to assess the spatial distribution of essential fish habitats in Hawai'i (Friedlander, 2001). Furthermore, our model can be used to estimate habitat structures based on several, commonly recorded environmental and geological factors, allowing for spatial interpolation of both habitat structure, and by extension other ecologically interesting components, like fish biomass, coral species richness, and wave energy attenuation, especially in shallower areas. With this knowledge, restoration and preservation efforts can be directed toward areas of favorable structural complexity (i.e., values that enhance biodiversity), where there would be direct influence on the designation of management priority regions. Future work should continue to uncover the scales of complexity that are important to communities that occupy them.

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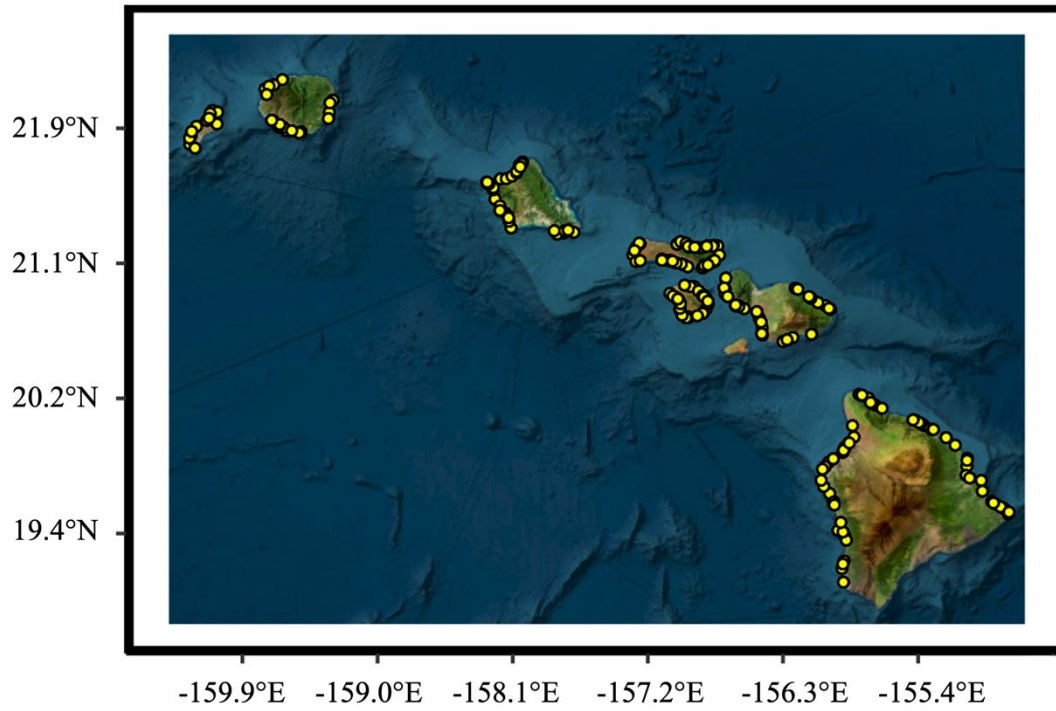
Data Availability Statement
The datasets presented in this study can be found in online repositories. The name of the repository and accession number can be found at:
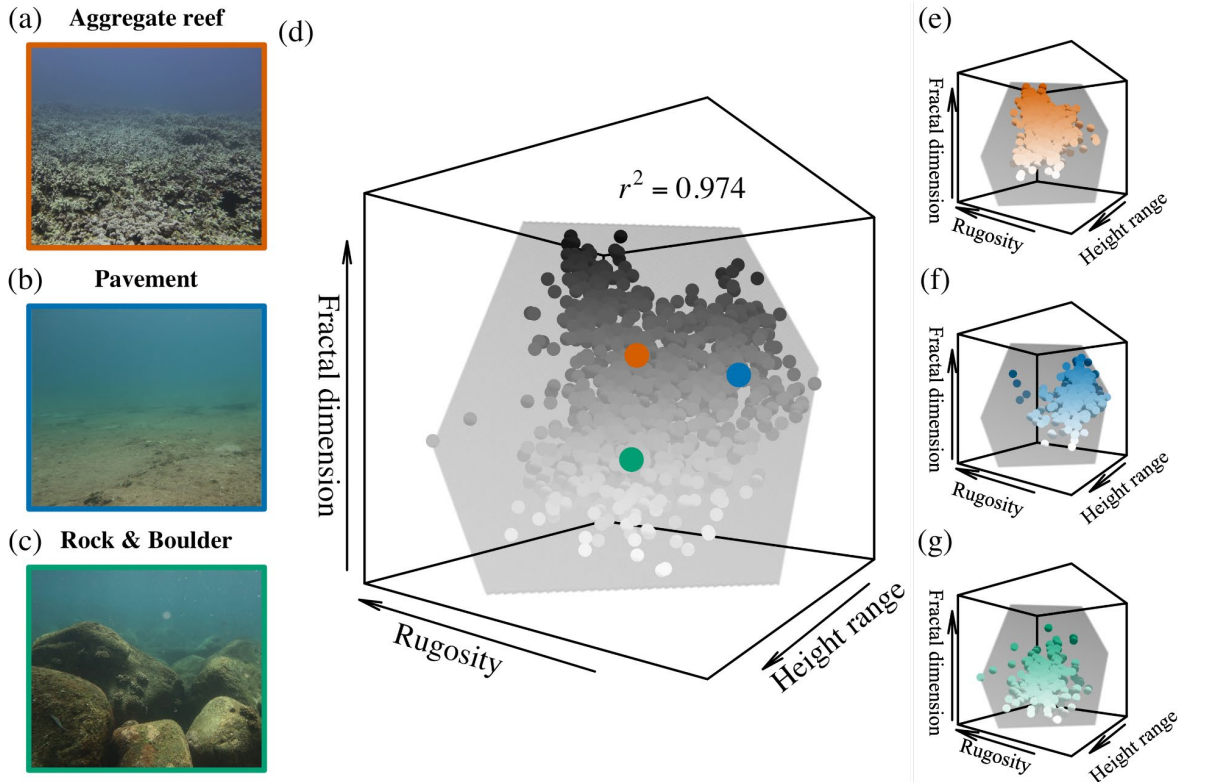https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.nodc:0268310.
All code to reproduce the analysis and figures will be available on github upon acceptance.
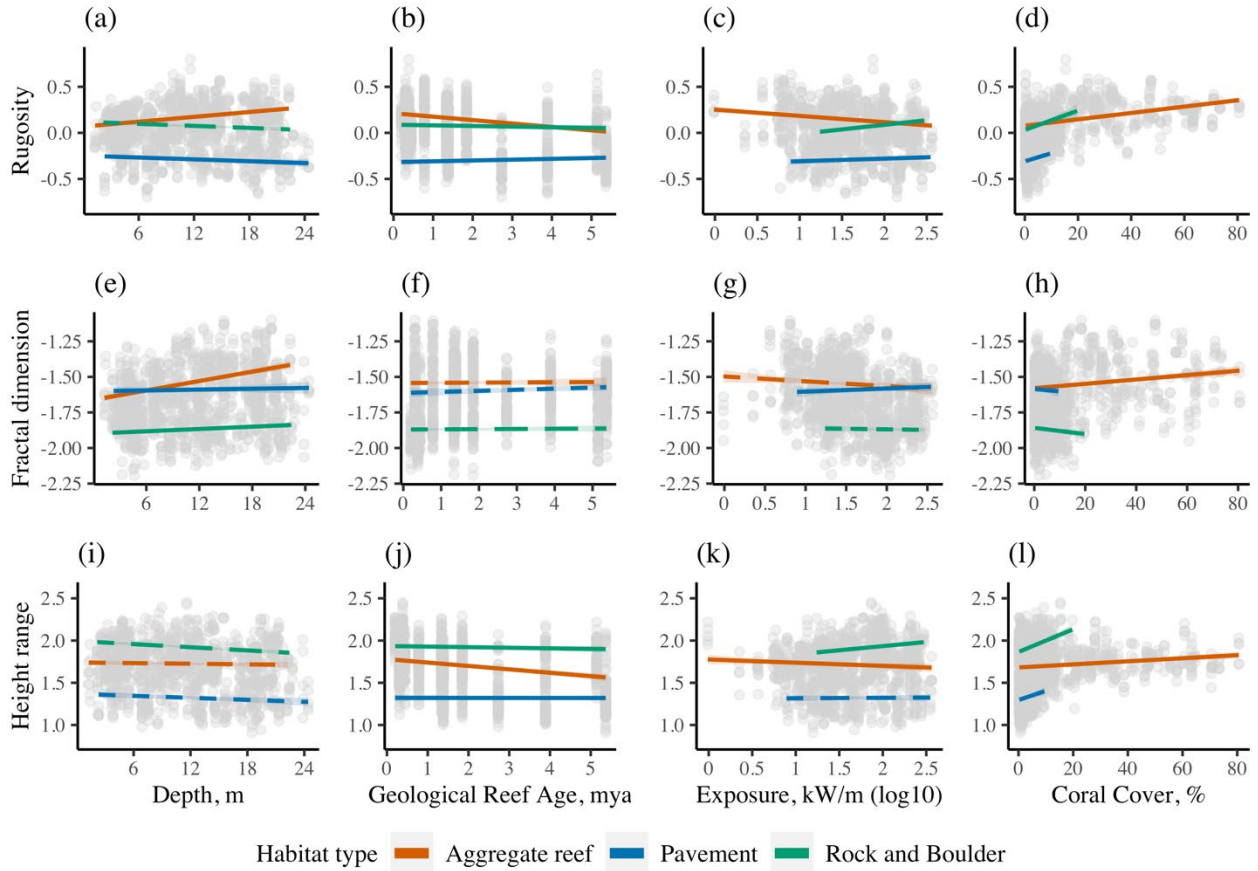
Figures

Figure 1. Locations of 234 Structure-from-Motion survey sites across the Main Hawaiian Islands, indicated by yellow points.

Figure 2. The geometric constraint among the three structural complexity metrics. The three main coral reef habitat types (a-c) in the Main Hawaiian Islands. The three complexity metrics form a plane (d) that captures 97% of variation in fractal dimension. Arithmetic mean for each habitat is colored respectively. (e-f) show the plane for the three habitat types. Orange, blue, and green are used consistently to denote aggregate reef, pavement and rock and boulder, respectively. Data points are replicate samples from the 234 sites, which are shaded by fractal dimension; more intense being higher values. Plane of best fit is colored in grey.
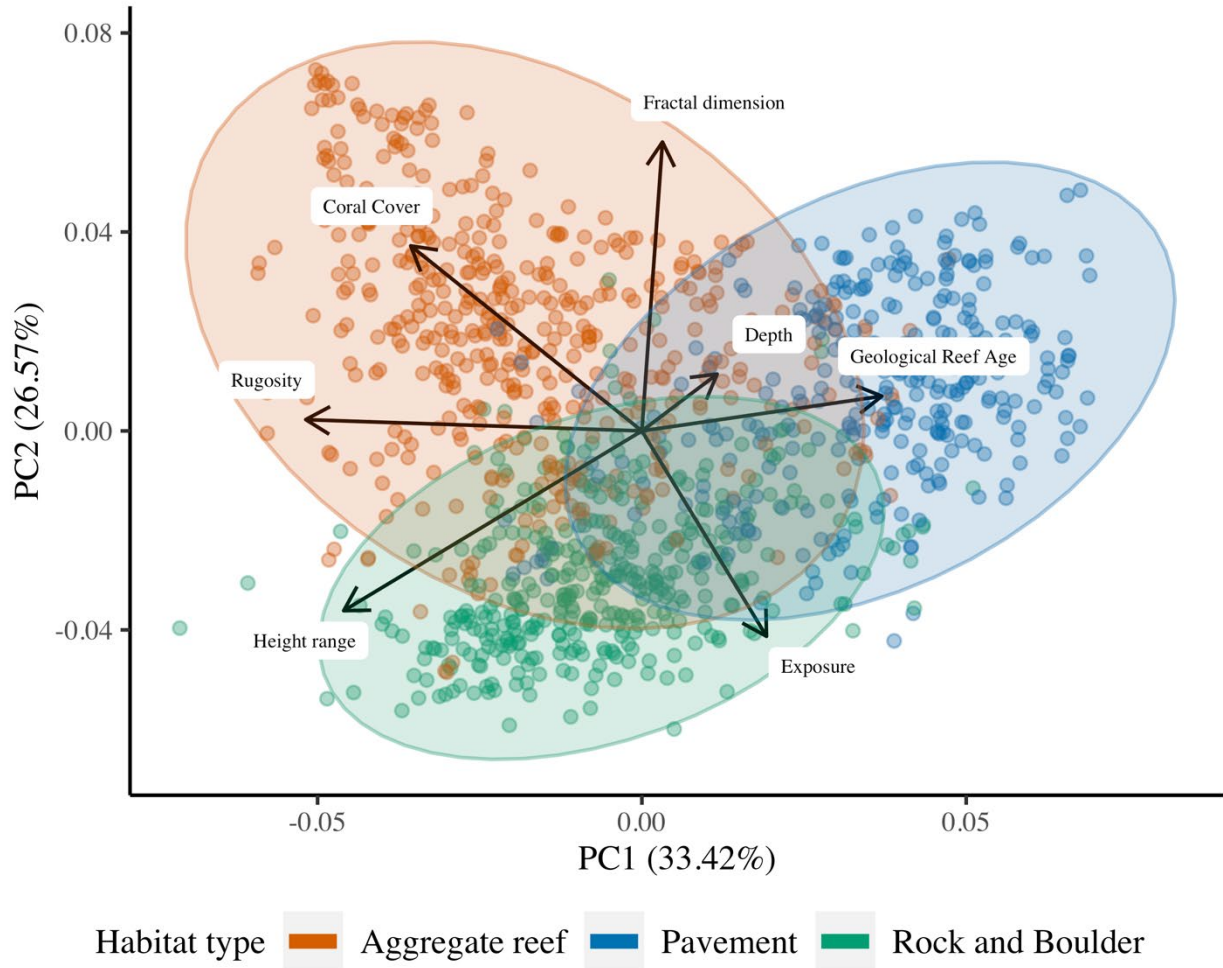
Figure 3. The 1170 replicate DEMs from the 234 sites plotted on the 1st and 2nd principal components (PC). Points are colored by habitat type with multivariate normal distribution ellipses. Arrows indicate the loading and direction of each variable.

Figure 4. Relationships between different metrics of structural complexity and geological and environmental variables in the main Hawaiian Islands. Colors represent habitat type: aggregate reef is orange, pavement is blue, and rock and boulder is green. Data points are replicate samples from the 234 sites. Solid lines represent marginal effects where 95 % confidence intervals did not overlap 0, and dashed lines indicate the 95% confidence intervals overlapped with 0. Shaded areas indicate 95% confidence intervals around prediction.