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RESEARCH ARTICLE

Impacts of "Reef Star" coral restoration on multiple metrics of habitat complexity

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Coral reefs face threats from climate change and local pressures that lead to reductions in their physical structure, impacting biodiversity by limiting habitat availability. Despite many efforts to actively restore damaged reefs, few projects provide thorough evaluations of their success. This study measured the success of the "Reef Star" method at the Mars Coral Reef Restoration Project in Indonesia in reestablishing the physical structure of reef habitats that were destroyed by blast fishing. We used photogrammetry surveys to measure the physical habitat structure of 17 large sites (1000 m^2 each), calculating three complementary measures of small- and large-scale habitat complexity across degraded, restored, and naturally healthy coral reefs. We demonstrate that the restoration efforts have successfully restored small-scale habitat complexity, as described by surface complexity metrics (3.22 $\pm$ 0.27 on restored reefs; 2.85 $\pm$ 0.26 on healthy reefs) and fractal dimension (2.27 $\pm$ 0.02 on restored reefs; 2.24 $\pm$ 0.02 on healthy reefs). This demonstrates the capacity for restored reefs to recover important ecosystem functions that are lost in degradation. However, while restoration has delivered some increases in large-scale habitat complexity compared to degraded reefs, restored reefs still exhibit lower values of maximum vertical relief than healthy reefs, due to a lack of large physical structures. This lack of available large-scale habitat might impact fish populations, meaning that restored reefs with limited large-scale complexity may only support a restricted range of ecosystem functions. Effective reef restoration strategies must use a mixture of different methods that target the recovery of structural complexity at multiple scales.

Key words: coral reefs, habitat complexity, Reef Star, restoration, small- and large-scale

Implications for Practice

- "Reef Star" coral restoration is effective at restoring small-scale habitat complexity, but not replacing vertical relief associated with large reef structures.
- Restoring corals using only a single method leads to only partial recovery of reef habitat complexity.
- Using a variety of restoration techniques, including artificial structures and different coral species that grow at varying scales, will help create a more balanced reef structure that closely mimics natural reef complexity.
- Restoration projects should focus not just on restoring physical structures but also on ensuring these structures support diverse biological communities and ecosystem functions.
- Coral restoration projects aiming to restore high fish abundance and diversity should consider using methods that support both small-scale and large-scale habitat complexity.

Introduction

Tropical coral reefs are among the most biologically diverse and valuable ecosystems on Earth. Coral reef ecosystems provide provisioning, regulating, cultural, and supporting services such as small-scale artisanal and commercial fishing, coastal protection, sand production, recreation, tourism, food, and medicines (Kennedy et al. 2013; Woodhead et al. 2019). Many of these services depend on the healthy functioning of living

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corals and the complex calcium carbonate structures that they produce. For example, reef growth can provide a natural breakwater for coastal protection, while complex three-dimensional habitat supports fish diversity and fisheries (Graham & Nash 2012; Kennedy et al. 2013).

Measurements of habitat complexity, also referred to as structural complexity, are essential metrics of reef health and strong predictors of several important ecological processes, including a reef's capacity to provide habitat, support biodiversity, influence fish community structure, and enhance ecosystem resilience (Graham & Nash 2012; Agudo-Adriani et al. 2019; Urbina-Barreto et al. 2021). The three-dimensional structure of a reef, characterized by gaps and crevices, increases protective space availability, fostering reef fish settlement (Santoso et al. 2022). By contrast, a decrease in complexity negatively impacts reef fish abundance and contributes to fish community decline (Garpe et al. 2006; Urbina-Barreto et al. 2021). Numerous tools are available for measuring the structural complexity of coral reef habitats. Historically, the "chain-and-tape" method was often used to compare the ratio of the linear distance of a chain placed on the reef's surface to its stretched-out length (Ferrari et al. 2016). More recently, more advanced techniques have been developed to estimate habitat structural complexity at different scales, made possible by advances in digital photogrammetry (Ferrari et al. 2016). This method presents a non-invasive tool for gathering the data needed to quantify the physical characteristics of coral reef habitats in three dimensions and contrast small-scale and large-scale complexity among sites (Ferrari et al. 2021; Urbina-Barreto et al. 2022).

Unfortunately, global and local pressures are causing declines in habitat-forming hard corals (Cheal et al. 2017; Eddy et al. 2021; Stuart-Smith et al. 2021). Global climate change and local stressors such as destructive fishing practices and poor water quality cause loss of both coral cover and reef structural complexity (Riegl et al. 2009; Spalding & Brown 2015). The degradation of structural complexity can be a direct result of physical disturbances such as cyclones or blast fishing, or due to slower bioerosion of dead coral substrates following coral mortality (Wilson et al. 2006). These processes are causing declines in reef structure across large spatial scales. For example, in the Caribbean, the structural complexity of reefs declined by 80% from 1977 to 2008, attributed to coral loss and shifts in communities toward reefs dominated by stress-resistant coral species, which are often less architecturally complex (Alvarez-Filip et al. 2011*a*, 2011*b*; González-Barrios et al. 2021).

Pantropical coral reef degradation has reached a point where local conservation strategies and natural recovery processes alone may not be effective in conserving and restoring the biodiversity and long-term integrity of coral reefs (Hein et al. 2017; Anthony et al. 2020; Ceccarelli et al. 2020). In response, active restoration efforts are burgeoning aimed at repairing damaged coral reefs (Boström-Einarsson et al. 2020; Razak et al. 2022). Various reef restoration techniques attempt to increase coral cover and the associated structural complexity of degraded coral reefs (Rinkevich 2014; Hein et al. 2017). This can be particularly effective in response to small-scale patchy disturbances such as historic blast fishing, where mobile rubble beds can preclude natural recovery (Fox et al. 2003). However, evaluation of the success of reef restoration in reestablishing structural complexity and at what scales this is achieved is lacking in the literature.

This study provides a first assessment of the recovery of reef structural complexity at one of the world's largest coral restoration projects. Structural complexity was compared among naturally healthy reefs, degraded reefs, and restored reefs as different habitat types at a large-scale coral restoration project in the Spermonde Archipelago, Indonesia. We use three metrics of both small-scale and large-scale structural complexity that were quantified using extensive photogrammetry three-dimensional reconstructions (50 × 20 m at each site) (for more details, see Section 2).

Methods

Study Sites

Data collection was performed in September 2022 at the Mars Coral Reef Restoration Project (www.buildingcoral.com), located at Bontosua Island, Spermonde Archipelago, South Sulawesi, Indonesia (4°56.9′S, 119°18.1′ E; Fig. 1). Several reefs around this island had been severely damaged due to the construction of a boat channel 30–40 years ago, blast fishing around 30 years ago, and extensive coral mining for house construction and a breakwater 20 years ago (Williams et al. 2019). There was limited natural recovery due to an abundance of loose dead coral rubble preventing the settlement of new coral recruits (Fox et al. 2003; Goreau & Hilbertz 2005; Ceccarelli et al. 2020). In response, the Mars Coral Reef Restoration Project was established to restore damaged reefs at this location using modular metal frames called "Reef Stars" to stabilize degraded rubble fields. Coral fragments were attached to the frames to enable coral growth and increase live coral cover. After deployment, regular maintenance was performed on all restored reefs; maintenance was carried out as often as required based on environmental conditions and algal growth rates throughout the first 3 months (Smith et al. 2021). Coral restoration has been carried out around Bontosua Island since 2017, with the total area of restored reef now 3.1 ha. As such, the reef around the island encompasses natural healthy reefs, degraded low coral cover reefs, and restored reefs. Seventeen study sites were selected to represent three different habitat conditions: healthy reefs, degraded reefs, and restored reefs (>3 years old). This included five healthy sites, six degraded sites, and six restored sites. Originally, the experimental design planned for six healthy sites; however, due to time constraints during fieldwork, we were only able to collect adequate data at five of these sites. Each site covered a minimum area of 50 × 20 m; situated on the edge of the reef flat next to the crest; in a water depth of 3–7 m; with a minimum of 20 m between adjacent sites (Fig. 1).

Image Acquisition

At each of the 17 sites, the reef substrate was three-dimensionally modeled using a consistent photogrammetry protocol. At each site, we outlined a rectangular area of 50 × 20 m using measuring tapes and added a further three measuring tapes

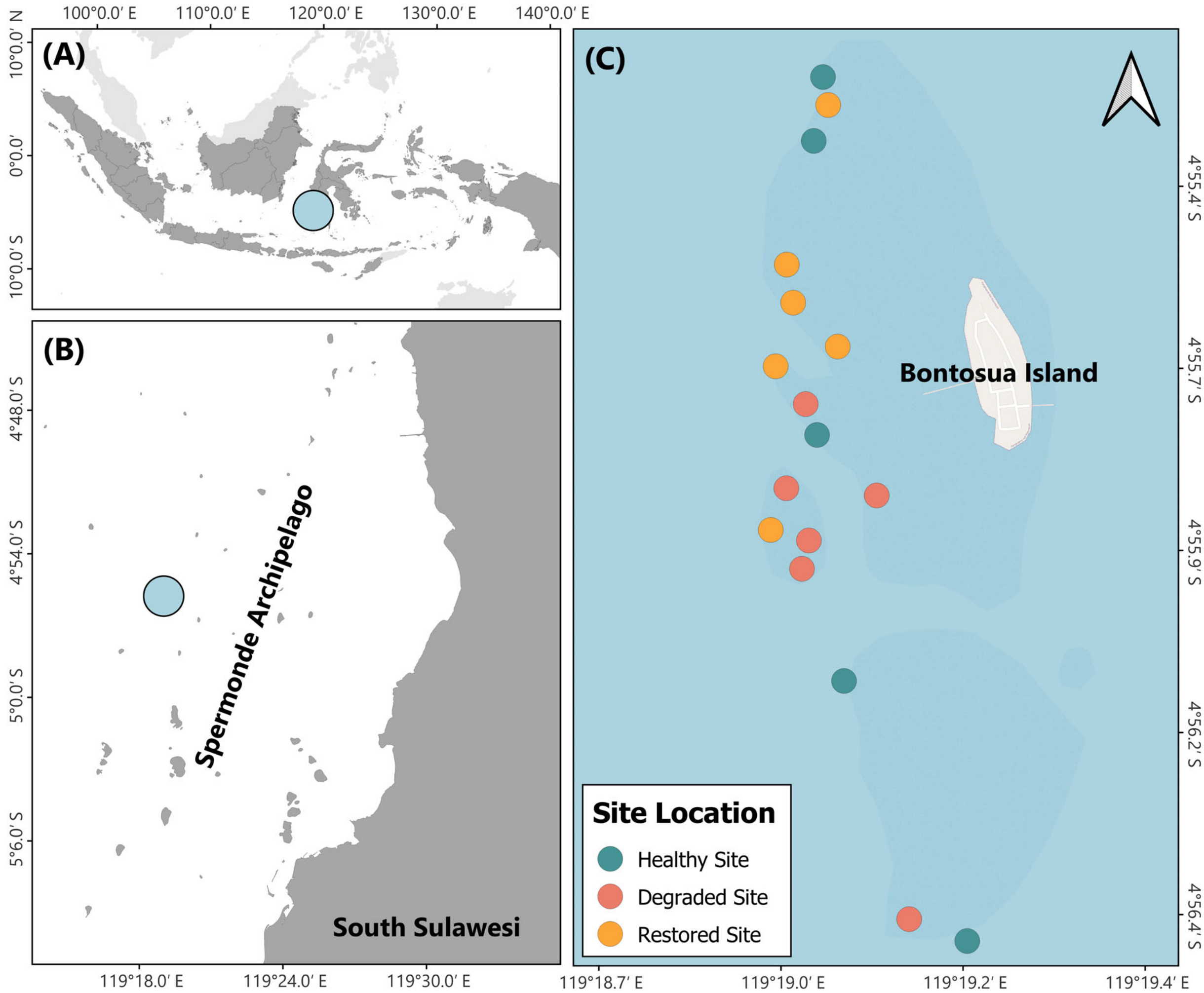

Figure 1. Location of Pulau Bontosua within (A) Indonesia and (B) the Spermonde Archipelago. (C) Map of the study sites (healthy, degraded, and restored) around Bontosua Island.

running the length of the area (50 m) at each 5 m point along its width (20 m) (Fig. 2). To capture images for use in photogrammetry, a SCUBA diver (R.T.V.) swam over the entire rectangular area at a consistent depth of 2 m above the substrate, following a "swimming lane" pattern that was modified from Bayley and Mogg method (Bayley & Mogg 2020) (indicated by the red line in Fig. 2). The diver held a bar with two GoPro Hero 10 cameras, mounted 60 cm apart on a horizontal bar and facing down toward the substrate at a perpendicular angle (Bayley & Mogg 2020; Carlot et al. 2020). We time-synced the cameras and used photo time-lapse mode (0.5-second interval) for automatic photo capture with the wide-angle setting at 5.3 K resolution. This process resulted in approximately 10,000 high-resolution images taken per site, with images overlapping and covering the whole 50 × 20 m area.

Generation of Three-Dimensional Models

Overlapping images were processed using Agisoft Metashape Professional version 2.0 (Agisoft LLC., 2023) to build three-dimensional models through a structure-from-motion (SfM) algorithm (Bayley et al. 2019; Fukunaga et al. 2019). The generation of three-dimensional models in Agisoft Metashape was configured according to settings outlined in Table S1. Subsequently, Digital Elevation Models (DEMs) were exported as GeoTIFF data files at a 1-mm resolution, complete with local coordinates for further processing (Fukunaga et al. 2019, 2020; Lazarus & Belmaker 2021). This process was executed by Tritonia Scientific (https://tritonia.scot/), using an AMD Ryzen Threadripper 3960X 24-Core Processor with 128 GB RAM and two NVIDIA GeForce RTX 3090 graphics cards. For a video visualization of an example of one of the three-dimensional models, see Video S1.

Quantifying Habitat Complexity

Structural complexity can be measured using different metrics at various scales (Lazarus & Belmaker 2021; Helder et al. 2022). We chose surface complexity and fractal dimension as small-scale metrics that measure complexity at centimeter scale, such as between the branches of corals (Dustan et al. 2013; Lazarus &

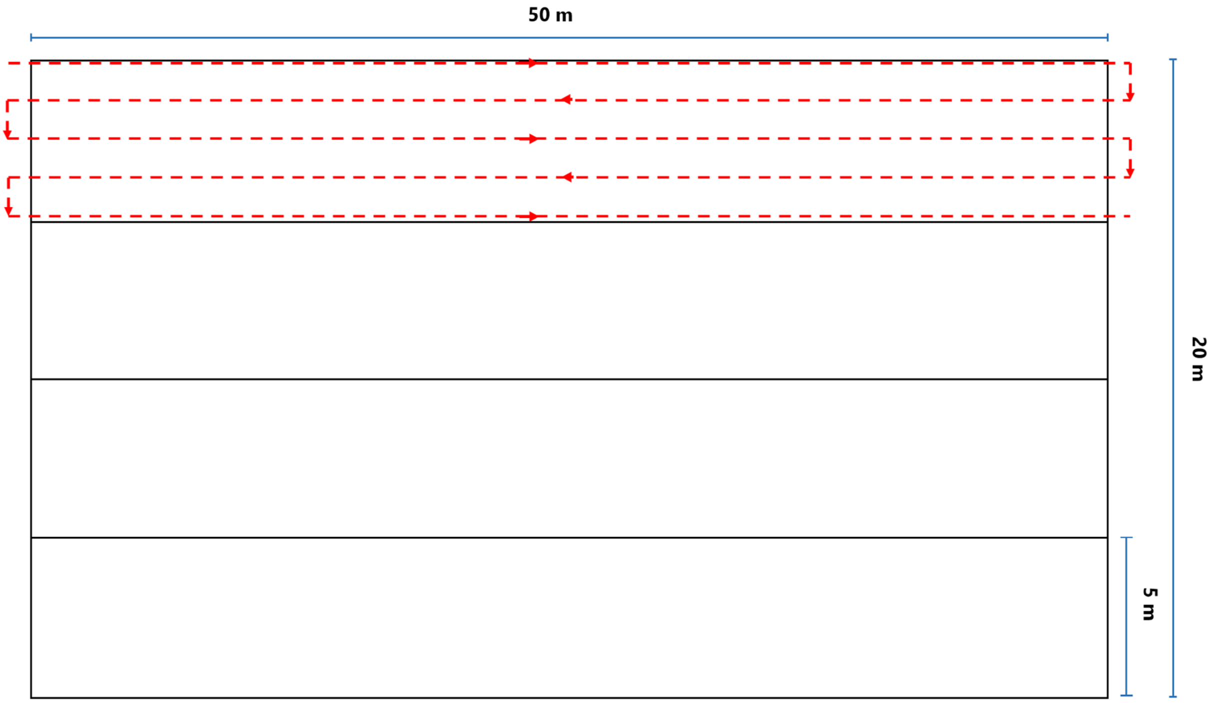

Figure 2. Research area illustration. Each black line represents a tape measure and the red dashed line indicates the path of the diver carrying cameras. This pattern was repeated across the entire area (in the diagram, it is only shown in one quarter of area).

Belmaker 2021; Helder et al. 2022). Conversely, vertical relief is a large-scale metric that measures complexity at meter scale, such as around bommies (individual massive coral structures) and drop-offs (González-Rivero et al. 2017; Lazarus & Belmaker 2021; Helder et al. 2022).

We used an R script modified from Fukunaga et al. (2019) to quantify the three structural complexity metrics from each DEM of the 50 × 20 m area. The area was divided into forty 5 × 5 m files to facilitate processing, with the resolution of DEMs changing from 1 mm to 1 cm. Furthermore, the script used the "*raster*" package's aggregate function to aggregate the DEMs by mean values to resolutions of either 64 or 128 cm, creating a clipping layer to remove any edge distortion artifacts (Fukunaga et al. 2019).

Surface Complexity. Surface complexity, often referred to as surface or three-dimensional rugosity, is determined by calculating the ratio of the three-dimensional surface area along reef contours to the two-dimensional planar area (Fig. 3A), with higher values indicating a more heterogeneous or complex structure (Young et al. 2017; Fukunaga et al. 2019; Helder et al. 2022). This measurement is analogous to the traditional "chain-and-tape" rugosity measure and is dependent on the grid cell size of DEM pixels and the total area measured. The three-dimensional surface complexity area was calculated using the surfaceArea function in the sp package at 1 cm resolution (Fukunaga et al. 2019).

Fractal Dimension. Fractal dimension quantifies morphology details from colony size to microarchitecture. A higher value within the 2–3 range for fractal dimension signifies greater complexity (Martin-Garin et al. 2007; Young et al. 2017). Fractal dimension serves as a measure of object irregularity, capturing information across various spatial scales (Fig. 3B). It is determined by altering the resolution of a DEM, quantifying the three-dimensional surface areas at each resolution, and assessing their changes by calculating the average elevation range at different observation scales (Young et al. 2017; Fukunaga et al. 2020; Fukunaga & Burns 2020). Calculating fractal dimension required changing the resolution of the DEMs using the aggregate function. For this study, we calculated the fractal dimension by changing the DEM resolutions from 1 cm to 2, 4, 8, 16, 32, and 64 cm. The selection of a 64 cm aggregation was based on preliminary investigations by Fukunaga et al. (2019), who examined the decrease in three-dimensional surface areas with increasing aggregation factors (i.e. decreasing resolutions).

Vertical Relief. Vertical relief, which indicates the total range of depth variation within a DEM (Fig. 3C), serves as an indicator of large-scale depth (z) changes in the profile. It is calculated by subtracting the lowest z value from the highest z value within the DEM window (Lazarus & Belmaker 2021; Helder et al. 2022). In this study, we obtained this metric by calculating the difference between the maximum and minimum depth values from the data processed using the R script. This metric reflects the variation introduced by significant topographic features, such as ridge or "patch" type reefs within the landscape (Helder et al. 2022). In addition to analyzing the raw vertical relief values, we also calculated the "max value vertical relief," which

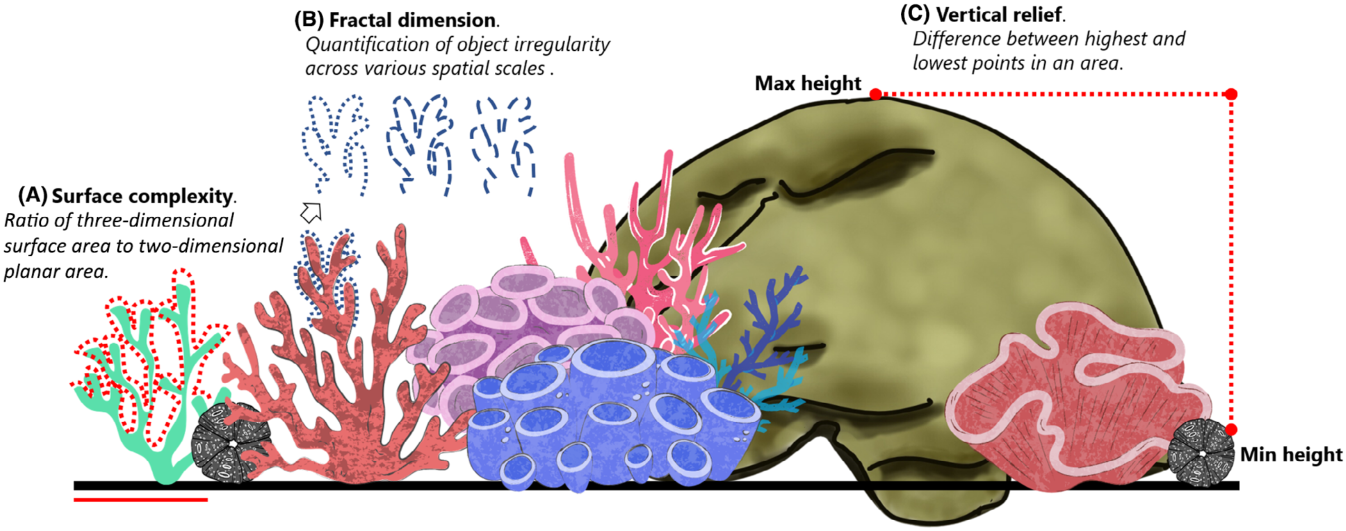

Figure 3. Schematic illustration for describing structural complexity metrics. (A) Surface complexity, (B) fractal dimension, and (C) vertical relief.

identifies the four highest values of vertical relief for individual 5 × 5 m areas within each 50 × 20 m site. This metric represents the areas within each site with the steepest drop-offs or overhangs. Finally, we also calculated the range of values of vertical relief for individual 5 × 5 m areas within each 50 × 20 m site. This metric represents the difference between the largest and smallest vertical relief values within each site.

Quantifying Benthic Cover

To quantify benthic cover at each site, data were collected as part of the standard monitoring procedures by Mars Sustainable Solution (MSS) (Smith et al. 2021). High-resolution photographs were taken every meter along two permanently located transects located within each research site, parallel to the 50-m block boundaries. The photographs were taken alternatively on the upper and lower sides of the transect, each representing an independent quadrat with an area of 0.25 m^2. The images were analyzed using CoralNet (Chen et al. 2021), with 20-point counts per quadrat. The relative abundance of different coral morphologies (abiotic, branching and digitate, massive and submassive, other biotic, plating and encrusting, and tabular) in each quadrat was determined. The analysis involved 2000 point counts across 100 quadrats per site (Smith et al. 2021).

Statistical Analysis

Statistical models were used to compare each of the habitat complexity metrics (surface complexity, fractal dimension, vertical relief, max vertical relief, and range vertical relief) across the 17 healthy, degraded, and restored habitat types. Different statistical models were employed based on the distribution of the data. If the data were normally distributed, linear models (LM) were used or linear mixed models (LMM) if random effects were involved. However, when data exhibited positive skew and non-normal distributions, gamma-distributed generalized linear mixed models (GLMM) were used to account for this. Evaluations of model fit were carried out using visual inspections of residual plots produced with the DHARMa package (https://CRAN.R-project.org/package=DHARMa). In all models, habitat type (healthy, degraded, or restored) was included as a fixed effect, and site ID was included as a categorical random effect. The overall effect of habitat type on the dependent variable was tested using Analysis of variances (ANOVA) comparisons to null models that were identical except for the omission of the fixed term. If this comparison was statistically significant ($p < 0.05$), post hoc Tukey's honestly significant difference (HSD) testing was conducted to provide between-habitat comparisons. Models were constructed in R using the packages "*lme4*" (Bates et al. 2015), "*multcomp*" (Hothorn et al. 2008), and "*emmeans*" (Lenth et al. 2018).

Regarding benthic composition, each benthic category was analyzed individually across the 17 healthy, degraded, and restored sites. For normally distributed data, an LMM was applied, and ANOVA comparisons were conducted to evaluate the overall effect of habitat type. Post hoc Tukey's HSD testing followed for significant comparisons ($p < 0.05$). In instances where the data violated the normality assumption required for parametric tests, the Kruskal–Wallis test was used, followed by pairwise Wilcoxon tests for between-habitat comparisons. As with habitat complexity models, habitat type and site ID were incorporated as fixed and categorical random effects, respectively, in all mixed-effects models.

Results

Small-scale structural complexity, which measures complexity at the centimeter scale, as indicated by surface complexity and fractal dimension, was significantly affected by habitat type (Fig. 4; surface complexity GLMM: $\chi^2 = 40.16$, degrees of freedom $(df) = 3$, $p < 0.01$; fractal dimension GLMM: $\chi^2 = 67.83$, $df = 3$, $p < 0.01$). Both metrics exhibited significantly higher values in healthy and restored habitats than in

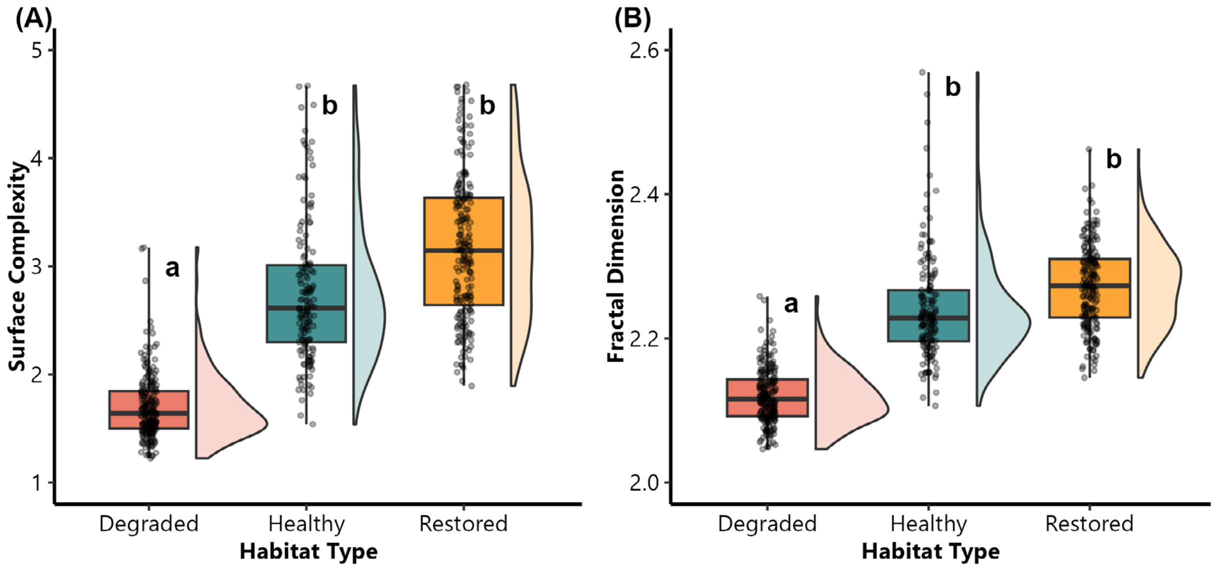

Figure 4. Metrics of small-scale structural complexity in different habitats. (A) Surface complexity and (B) fractal dimension for degraded, healthy, and restored habitat. Each point represents one 5 × 5 m area; boxplots represent the median (center line), interquartile range (boxes), and full range (whiskers) of the data, and adjacent kernels represent the distribution of the data points. Different letters represent significant differences in Tukey's honestly significant difference (HSD) post hoc testing, following a significant effect of habitat type in Gamma-distributed generalized linear mixed-effects models. The significance threshold in all cases was 0.05; for full models and post hoc comparisons, see Table S2.

degraded habitats (Fig. 4). Across both metrics, restored habitats exhibited marginally higher values than healthy habitats, but these differences were not statistically significant (Fig. 4; detailed model and post hoc comparisons in Table S2).

Vertical relief, indicating large-scale structural complexity, was also significantly affected by habitat type (GLMM: $\chi^2 = 19.96$, $df = 3$, $p < 0.01$; Fig. 5A). Both healthy and restored habitats exhibited significantly higher vertical relief than degraded habitats, with marginally higher average values in healthy habitats than restored habitats, albeit without a significant difference between these two habitat types (Fig. 5A; detailed model and post hoc comparisons in Table S3).

When considering max value vertical relief (the top four values of vertical relief from each 50 × 20 m site, representing areas with the most extreme drop-offs or overhangs), healthy sites exhibited significantly higher values than restored sites, which in turn exhibited significantly higher values than degraded sites (Fig. 5B; LMM: $\chi^2 = 66.50$, $df = 3$, $p < 0.01$; detailed model and post hoc comparisons test in Table S3). When considering range value vertical relief (the range of values of vertical relief within each 50 × 20 m site, representing the difference between the largest and smallest vertical relief values in each area), restored reefs again exhibited intermediate values between healthy and degraded reefs. Healthy habitats displayed significantly higher ranges of vertical relief than degraded habitats, with no significant difference between healthy and restored habitats, or between restored and degraded habitats (Fig. 5C; LM: $\chi^2 = 101.2$, $df = 3$, $p < 0.01$; detailed model and post hoc comparisons test in Table S3).

Each category of benthic composition was significantly affected by habitat type (Fig. 6; detailed model and post hoc comparisons in Table S4). The degraded habitats exhibited a significantly higher percentage of abiotic coverage (86%), which was two and a half times greater than that observed in restored (33%) and healthy habitats (32%) (LMM: $\chi^2 = 57.02$, $df = 3$, $p < 0.01$). Restored habitats displayed substantial recovery in benthic coral composition, particularly with a higher percentage of branching and digitate corals (46%) compared to degraded habitats (5%), even surpassing healthy habitats (34%) (LMM: $\chi^2 = 44.01$, $df = 3$, $p < 0.01$). Healthy habitats demonstrated the highest percentage of other benthic compositions, including massive and submassive corals (20%) and plating and encrusting coral morphologies (6%)—percentages twice as high as those in restored areas and five times higher than those in degraded areas. There were no significant differences between healthy and restored habitats, or between restored and degraded habitats, for these morphologies (massive and submassive LMM: $\chi^2 = 24.63$, $df = 3$, $p < 0.01$; plating and encrusting LMM: $\chi^2 = 20.72$, $df = 3$, $p < 0.01$). Additionally, there were no significant differences in other biotic and tabular coral morphologies between healthy and restored habitats (other biotic Kruskal–Wallis test: $\chi^2 = 72.32$, $df = 2$, $p < 0.01$; tabular Kruskal–Wallis test: $\chi^2 = 35.43$, $df = 2$, $p < 0.01$).

Discussion

General Findings

This study demonstrates that the Reef Star method can effectively restore reef habitat complexity after 3 years of deployment and maintenance, although the impact is varied between

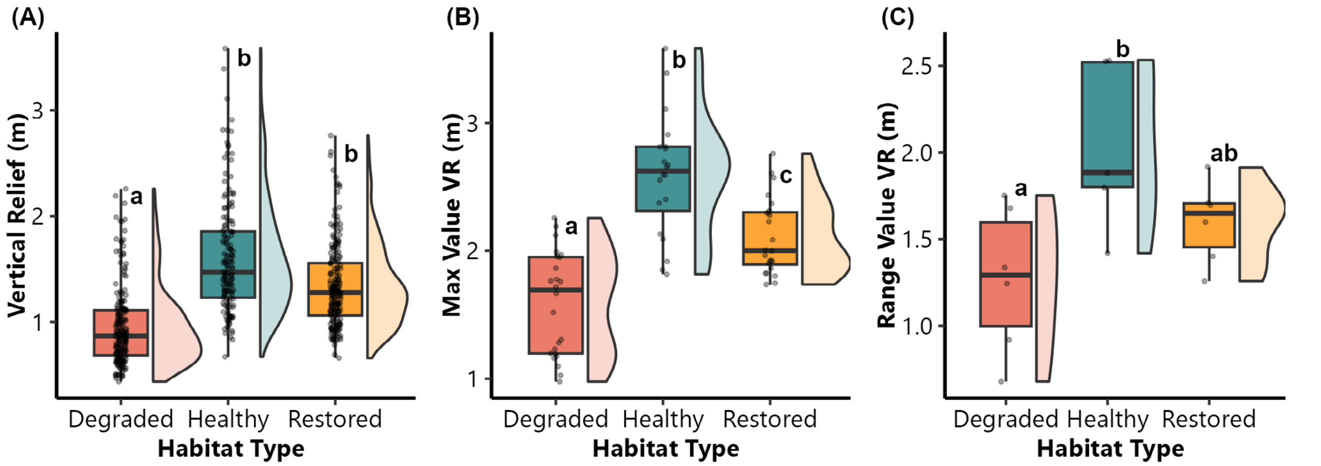

Figure 5. Metrics of large-scale structural complexity in different habitats. (A) Vertical relief (difference between maximum and minimum height) for 5 × 5 m^2 areas of degraded, healthy, and restored habitats. (B) The four highest values of vertical relief (in 5 × 5 m areas) from each 50 × 20 m site, representing areas within each site with particularly large drop-offs or overhangs. (C) The range of values of vertical relief (in 5 × 5 m areas) from each 50 × 20 m site, representing the difference between the largest and smallest vertical relief values within each site. In (A) and (B), each point represents a 5 × 5 m area, but (B) only includes the four highest vertical relief values for each site. In (C), each point represents the range of vertical relief values across all 5 × 5 m areas within each site. In all panels, boxplots represent the median (center line), interquartile range (boxes), and full range (whiskers) of the data; and adjacent kernels represent the distribution of the data points. Different letters represent significant differences in Tukey's honestly significant difference (HSD) post hoc testing, following a significant effect of habitat type in Gamma-distributed generalized mixed-effects models (A), linear mixed-effects models (B), or linear models (C). The significance threshold in all cases was 0.05; for full models and post hoc comparisons, see Table S3.

small and large-scale measures of complexity. Small-scale habitat complexity, described through surface complexity and fractal dimension metrics, was high on restored habitats and comparable to healthy natural habitats. This is likely due to the restored habitat's high percentage of branching corals, which contributes significantly to small-scale metrics of complexity. This is supported by previous findings that coral cover, and in particular the presence of branching corals, are often positively correlated with small-scale complexity (Graham & Nash 2012; Helder et al. 2022). Conversely, large-scale habitat complexity, measured through vertical relief metrics, exhibited a different pattern. While restoration has delivered some increases in large-scale habitat complexity compared to degraded reefs, restored reefs still exhibit lower values of maximum vertical relief than healthy reefs. Values of maximum vertical relief are likely to be driven by the presence of large coral bommies, which have a substantial range between their maximum and minimum heights. The restored sites generally had fewer of these large bommies and a lower overall percentage cover of massive and submassive corals than healthy habitats. Degraded habitats, characterized by almost flat areas and minimal structures, exhibited the lowest values for both small-scale and large-scale metrics. As such, restoration using this "Reef Star" method is effective at restoring small-scale habitat complexity but does not replace the highest values of vertical relief provided by large coral bommies.

Small-Scale Complexity

Restored areas exhibit a notable recovery of small-scale complexity, as characterized by two metrics (surface complexity and fractal dimension) that consider changes in depths between measurements a few centimeters apart (Lazarus & Belmaker 2021). Complexity at these microhabitat scales is primarily driven by small living corals, typically dominated by branching coral morphologies (Dustan et al. 2013; Lazarus & Belmaker 2021; Helder et al. 2022). The intricacies of branching morphology exhibit a significant positive correlation with small-scale metrics of complexity, especially when evaluating metrics at a 1 cm resolution (Fukunaga et al. 2020; Pascoe et al. 2021; Helder et al. 2022).

Small-scale complexity is particularly important in providing habitat for small-bodied fishes, such as settlement-stage recruits and juveniles (Agudo-Adriani et al. 2019; Lazarus & Belmaker 2021; Helder et al. 2022). Fish tend to align themselves with structures that are proportional to their body size (Nash et al. 2013*a*), with smaller fish requiring more intricate microhabitats to meet their needs (Graham & Nash 2012; Rogers et al. 2014). These early life history stage fish are essential for the success of restoration projects, as they play crucial roles in reef trophodynamics. They help in cycling trophic energy provided by microscopic prey to larger consumers, making them a highly productive group on coral reefs (Brandl et al. 2018, 2019). In addition, damselfish-derived nutrients can enhance coral thermal tolerance, influencing coral bleaching susceptibility, resilience, and recovery in warming oceans (Chase et al. 2018; Shantz et al. 2023). Small-scale complexity also increases the survival rate of small-bodied fish and juveniles from predators, leading to greater productivity and diverse community size structures. This, in turn, could enhance reef fish biomass over time at restoration sites (Rogers et al. 2014; Patranella et al. 2017). However, habitat that is suitable for small-bodied

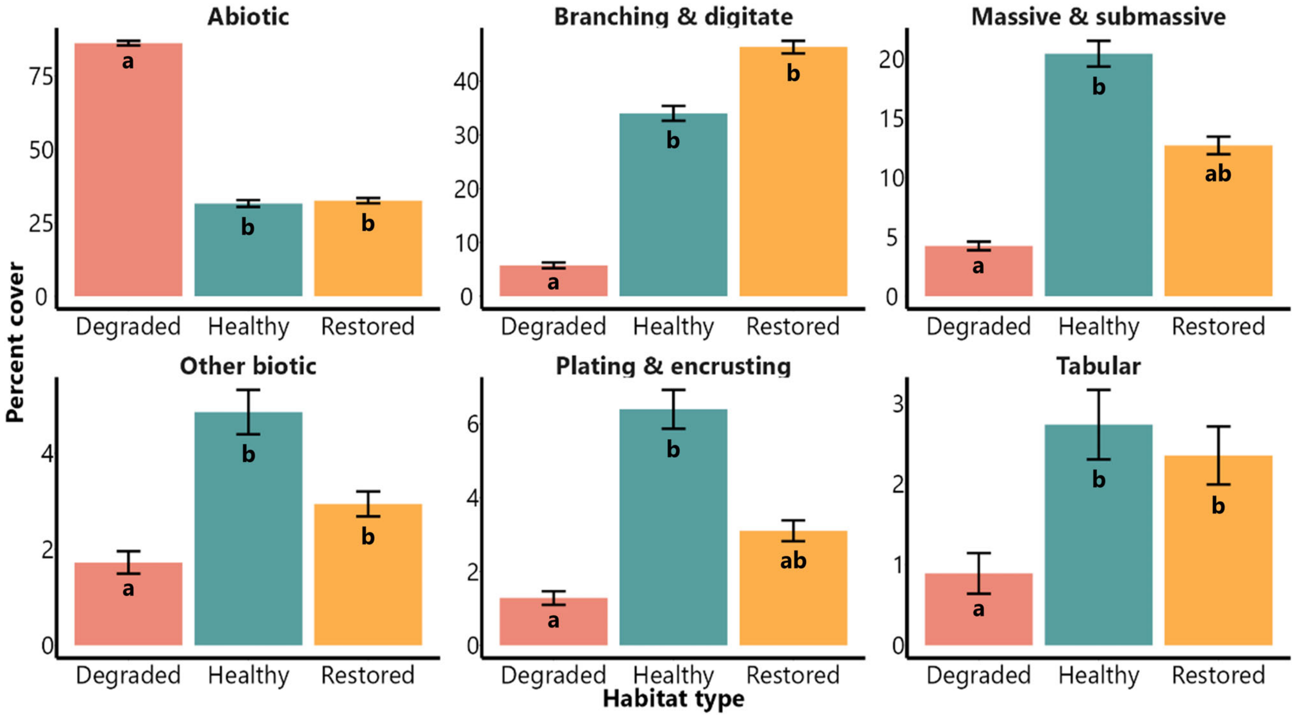

Figure 6. Characterization of habitat types. Bar graphs showing the mean percentage cover of different coral morphologies in each habitat. Error bars represent SD. Different letters represent significant differences in Tukey's honestly significant difference (HSD) post hoc testing, following a significant effect of habitat type in linear mixed-effects models. The significance threshold in all cases was 0.05; for full models and post hoc comparisons, see Table S4.

fish may lack the attributes that larger fish require (Rilov et al. 2007; Nash et al. 2013*b*).

Large-Scale Complexity

Larger scales of reef complexity are often dependent on older geologic features, including the underlying carbonate structural matrix (González-Rivero et al. 2017). We measured this complexity by using vertical relief metrics to identify significant variations in depth within a specific area (Lazarus & Belmaker 2021). We found that not all large-scale structural complexity metrics were supported on restored reef habitats. While restored reefs have shown some improvement in large-scale complexity when compared to degraded reefs, the lack of large bommies means that their maximum vertical relief is lower than that of healthy reefs. Large structures such as ridges and coral bommies (Lazarus & Belmaker 2021; Helder et al. 2022) are difficult to replicate in restored reefs due to the slow-growing nature of these structures. A recent study observed that massive corals such as *Favites abdita* display slow radial growth rates (approximately 5 mm/year), leading to outplanted corals achieving average diameters of approximately 6.6 cm after 6 years. This growth rate is notably slower (5–19 times) than that of *Acropora millepora* colonies also outplanted in the same location using similar methods, which exhibited radial growth estimates ranging from approximately 28 to 57 mm/year (Guest et al. 2023). This explains why the scale of complexity at such levels is lacking.

The presence of large physical structures can have a significant impact in determining the abundance and diversity of fish populations, particularly for larger-bodied individuals and species, with knock-on effects for fish recruitment and predator–prey dynamics (Rogers et al. 2014; Helder et al. 2022). When the relief or height of obstacles in the environment increases, it attracts more predators, such as large-bodied carnivores, resulting in heightened predation risk for certain grazers (Rilov et al. 2007; Rogers et al. 2014). To avoid these risks, some prey species may avoid habitats with high-relief obstacles, while others engage in schooling behavior, allowing them to navigate through preferred habitats regardless of exposure levels (Ferrari et al. 2018; Helder et al. 2022). Some large-bodied fishes can be important species influencing reef ecosystem dynamics, meaning their recovery and responses around restoration structures are important indicators of restoration success (Hein et al. 2020; Seraphim et al. 2020).

Consideration for Management

Differences in the composition of benthic communities lead to variations in the structural complexity of reef habitats. This, in turn, affects the populations and diversity of other reef organisms, defining ecosystem functions and services provided by the reef (Rogers et al. 2014; Darling et al. 2017; Richardson et al. 2017). Reef ecosystems offer substantial coastal defense, providing significant annual flood protection savings for people and property, especially during frequent storms. Lower structural complexity due to reef degradation increases the risk to coastal protection (Beck et al. 2018). Additionally, this complexity can also determine social interactions—influencing the presence of mates, competitors, or predators (González-Rivero et al. 2017; Lazarus & Belmaker 2021). Reefs with high levels of small-scale complexity tend to foster the abundance, biomass, and diversity of smaller gregarious species. On the other hand, large-scale complexity (relief) strongly relates to the presence of solitary, cryptic, nocturnal carnivores (Graham & Nash 2012; Ferrari et al. 2018; Helder et al. 2022). This reveals that this complex interaction between habitat complexity and organism behavior is an essential consideration when restoring degraded reefs to improve their ecological functioning.

This study focuses exclusively on the "Reef Star" restoration method (Smith et al. 2021). Methods similar to this—using modular metal frames to stabilize substrate and provide a platform for coral growth—are among the most commonly deployed methods for coral restoration worldwide (Boström-Einarsson et al. 2020; Razak et al. 2022). The global popularity of this method is probably due to its relative ease of deployment (small modular structures are relatively easy to manufacture and deploy, compared to larger structures), and its proven success in promoting rapid growth of some coral morphologies (Lamont et al. 2022). However, despite successes in reestablishing some aspects of reef functioning, this study demonstrates that such methods do not fully replicate all reef attributes; in this case, reefs restored using Reef Stars exhibited high levels of small-scale complexity, but only showed partial recovery of large-scale complexity when compared with nearby healthy habitat. To address complexity at multiple spatial scales, restoration practitioners should explore the possibility for a more diverse range of restoration methods to be used in tandem. For example, recent study demonstrate methods for restoring sexually mature massive coral populations within a decade (Guest et al. 2023), and micro-fragmentation facilitates the production and outplanting of massive and encrusting corals that fuse together to form larger colonies when attached to reef substrate (Page & Vaughan 2014; Forsman et al. 2015; Boström-Einarsson et al. 2020). A comprehensive approach involving multiple restoration methods holds promise for achieving varied complexity at different scales. While a mixed method may take longer, considering substantially longer recovery times for larger coral structures, it offers a varied return on investment and may yield higher long-term restoration returns (Guest et al. 2023). This approach, though time-consuming, emphasizes the need for a species mix in reef restoration, ensuring resilience against stressors.

In addition to considerations about structural complexity, practitioners are also likely to consider vulnerability to disturbance in their restoration strategies. Coral susceptibility to disturbance varies by species, with delicate morphologies becoming more vulnerable as they grow. Habitats dominated by fast-growing, branching morphologies are likely to be more vulnerable to environmental change, while those dominated by slow-growing, massive morphologies are more resistant (Richardson et al. 2017). When restoring coral, strategic decisions about species selection and deployment are crucial determinants of morphological vulnerability and resistance to disturbances, which play a crucial role in achieving long-term restoration outcomes (Hein et al. 2017; Bayraktarov et al. 2019). Coral communities with high diversity and richness can enhance resistance to disturbances (Boström-Einarsson et al. 2020; Pascoe et al. 2021). The presence of other species can enhance performance at the colony level and provide buffering effects at the community level, contributing to the maintenance of community structure and function during periods of disturbance such as storms, thermal bleaching, and also crown-of-thorns starfish (Dizon & Yap 2005; Cabaitan et al. 2015; Richardson et al. 2017). Furthermore, coral reef restoration projects must account for broader ecosystem contexts, including connections between adjacent marine habitats and human populations, as well as ecological connections across land and seascapes, to effectively support reef resilience and climate adaptation (Shaver et al. 2022). These considerations underscore the need for sustainable habitat management and effective conservation practices that support multiple habitat types and climate-resilient species assemblages.

In conclusion, this research highlights a notable example of how well-managed coral restoration efforts have successfully restored small-scale habitat complexity over a relatively large spatial area of restoration project. However, while there has been some improvement at larger scales of habitat complexity, this approach has not yet fully matched the large-scale habitat complexity of nearby healthy reefs. This emphasizes the need to carefully consider strategies to design future coral restoration projects that enhance both small and large structural attributes. While restoration using small, fast-growing fragments yields rapid results and is likely to be effective at replacing structure at the microhabitat level, it is unlikely to achieve success at larger scales of complexity. This nuanced understanding is essential for informed decision-making and effective management strategies in the realm of coral reef restoration. Restored reefs with limited structural complexity across different scales may only support a limited set of associated diversity and the ecosystem functions and services they provide. Therefore, restoration strategies should consider using a mix of complementary methods to reestablish structural complexity at multiple different scales, to ensure that restored reefs deliver as diverse a suite of ecological functions and services as possible.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Settings used to generate three-dimensional models in Agisoft Metashape Professional (v.2.0).

Table S2. Outputs from generalized linear mixed-effects models (using a Gamma distribution and a log link function) that investigate the impact of habitat type on small-scale structural complexity metrics.

Table S3. Outputs from generalized linear mixed-effects models using gamma (link = “log”), linear mixed-effects models, and linear models that investigate the impact of habitat type on large-scale structural complexity metrics.

Table S4. Outputs from linear mixed-effects models investigating the impact of habitat type on benthic morphologies.

Video S1. Video visualization of an example of one of the three-dimensional models from restoration site.

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