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Assessing the impact of acute disturbances on the structure and composition of a coral community using innovative 3D reconstruction techniques

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Abstract

Loss of live coral and declines in the structural complexity of reef habitats affects ecosystem-level processes such as energy flow, nutrient cycling, and community dynamics. Scleractinian corals are the primary contributor to the biological and physical three-dimensional (3D) structure of coral reef ecosystems. Disturbance events that induce coral mortality can alter the 3D structure of reefs habitats and lead to disruptions in trophic structure and organismal relationships that drive ecological processes. The coral reef ecosystem at Wai‘ōpae, southeast Hawai‘i Island, experienced several acute disturbance events in 2014, including a hurricane, tropical storms, and a severe coral bleaching event. This study utilized innovative 3D reconstruction techniques to create high-resolution models of the coral reef habitat and quantify structural metrics known to affect the biodiversity and abundance of associated reef organisms. A volumetric analysis was applied to the reconstructed 3D point clouds to determine the precise loss of habitat that occurred throughout the surveyed reef area. Conducting a temporal analysis using 3D reconstructions enabled us to test the hypothesis that volume and 3D architectural complexity of the coral community at Wai‘ōpae was significantly impacted by the acute disturbance events.

Introduction

Structural complexity supports high levels of diversity and abundance of organisms by creating an array of microhabitat types (Crowder and Cooper 1982, Goatley and Bellwood 2011, Graham and Nash 2013). Changes in habitat structural complexity affects ecosystem-level processes such as energy flow, nutrient cycling, and community dynamics (Risk 1972, Connell 1978, MacArthur 1984, Pratchett et al. 2014). The three-dimensional (3D) structure of an ecosystem is partly provided by underlying substrata, however, living organisms that serve as ecosystem engineers are key drivers of habitat complexity. In coral reef ecosystems, scleractinian corals are the predominant contributors to both biological and physical structural complexity. When disturbances, such as storms, runoff, and changes in rainfall and/or temperature alter the 3D structure of corals, it can disrupt trophic structure and lead to decoupling of organismal relationships that drive ecological processes in the coral reef ecosystem. As the frequency and intensity of disturbances affecting coral reefs are projected to increase (Hoegh-Guldberg et al. 2007, De'ath et al. 2012), it is crucial to develop methods capable of accurately quantifying changes in structural complexity in order to predict how ecological processes and assemblages of reef organisms will respond to habitat degradation.

Nearshore coral reef ecosystems of Hawai'i are an essential source of cultural importance, sustenance, coastal protection, and support an estimated total economic value of US \$9.7 billion (Cesar et al. 2002, Friedlander et al. 2005, Gregg et al. 2015). Due to isolation and high levels of endemism, the structure and function of coral reefs in Hawai'i are inherently susceptible to disturbance (Tissot et al. 2009). Coral reefs in Hawai'i and

other locations in the Pacific have remained relatively stable over the last several decades, while coral cover in the Caribbean has declined substantially due to bleaching, disease, and disturbance (Hughes 1994). The decline in coral cover throughout the Caribbean has resulted in dramatic shifts in community structure and declines in associated reef organisms (Harvell et al. 1999, Pratchett et al. 2014). The coral reefs of Hawai'i may become more vulnerable to future disturbances as seawater temperatures are projected to increase causing severe and frequent coral bleaching in the near future (Rodgers et al. 2015). Considering the importance of coral reef ecosystems in Hawai'i, it is critical to develop methods capable of assessing the impacts of disturbance on reef structure and function.

The Wai'ōpae coastline is located at the southeastern tip of Hawai'i Island and supports a high abundance and diversity of coral in a network of submerged pools formed by permeable basaltic substrate. Wai'ōpae receives a high frequency of natural and anthropogenic disturbances, both chronic and acute (Takabayashi et al. 2010, Burns et al. 2011). Long-term monitoring of the coral population at Wai'ōpae has shown minimal change in the prevalence and severity of diseases and conditions of reduced health, and no widespread mortality events (Takabayashi et al. 2010). Wai'ōpae experienced several acute disturbance events between August and October 2014, when three major tropical storm systems impacted Hawai'i Island. Hurricane Iselle made a direct landfall in Wai'ōpae and surrounding areas on August 7th, 2014, and Tropical Storm Julio followed within two days. On October 19th, Hurricane Ana passed south of the Wai'ōpae coastline. These storm events generated powerful waves, compromised wastewater treatment systems in coastal residences, and produced substantial runoff from rainfall. In addition

101 to these acute stressors, Wai‘ōpae experienced elevated sea surface temperatures
102 associated with the 2014-2015 El Niño that resulted in intense coral bleaching and
103 widespread mortality of both corals and mobile invertebrates. This study created 3D
104 reconstructions of a coral reef at Wai‘ōpae coral reef to decipher how these disturbance
105 events and subsequent coral mortality affected the structural complexity of this habitat.

106 Creating 3D reconstructions of underwater environments has primarily relied on
107 techniques that utilize complex equipment that can be financially prohibitive for small-
108 scale research studies. Structure-from-Motion (SfM) is a recently developed range
109 imaging technique that provides a relatively simple, efficient, and affordable alternative
110 for high-resolution 3D reconstruction from 2D image sequences (Westoby et al. 2012,
111 McCarthy and Benjamin 2014, Burns et al. 2015a). SfM was developed from the
112 underlying principles of stereoscopic photogrammetry, which is the process of creating
113 reliable 3D reconstructions of physical objects, environments, and terrain by processing
114 overlapping 2D image sequences. Unlike conventional photogrammetric methods, SfM
115 can determine the geometry of the photographed scene, camera positions, and orientation
116 without a priori specification (Snavely et al. 2008, Westoby et al. 2012). The SfM process
117 uses feature-matching algorithms to determine spatial coordinates for invariant
118 components detected in the images and produces a 3D point cloud representing the
119 photographed scene. The resulting 3D point cloud and mesh models can be exported in
120 various formats and integrated with geospatial software in order to quantify 3D
121 topographic characteristics of the reconstructed environment (Fonstad et al. 2013, Burns
122 et al. 2015a). The ability to automate the computation of scene geometry and requiring
123 only consumer-grade camera equipment, a computer, and affordable software makes SfM

substantially more practical and cost-effective than traditional photogrammetric methodologies (Remondino et al. 2012, McCarthy and Benjamin 2014). The accuracy of SfM techniques for high-resolution 3D topographic reconstruction and analysis has been validated by studies in both terrestrial and marine environments, and has proven to be a fast and affordable method to create highly accurate models (Harwin and Lucieer 2012, Delparte et al. 2014, Javernick et al. 2014, Burns et al. 2015a, Figueira et al. 2015, Lavy et al. 2015). SfM methodology has also proven to be highly accurate for analyzing spatial features of coral, and is capable of detecting statistically distinct 3D structural features associated with specific coral species and morphologies (Burns et al. 2015a,b).

Our study utilized SfM techniques to accurately quantify the impact of the acute disturbance events on the 3D structural complexity of the coral reef habitat at Wai‘ōpae. The field of coral reef ecology has historically been limited to using 2-dimensional (2D) planar survey techniques for assessing temporal changes in coral composition and structure. Although this conventional approach is simple to implement, it fails to capture or quantify the intricate structural complexity of corals that influences habitat facilitation and biodiversity. We present methods to create high-resolution 3D models of a coral reef habitat and quantify topographic metrics (curvature, slope, surface complexity, rugosity, volume) known to affect the biodiversity and abundance of associated reef organisms. Conducting a temporal analysis of the 3D reconstructions before and after the disturbance events enabled us to test the hypothesis that the 3D architectural complexity of the coral community at Wai‘ōpae was significantly impacted by disturbances.

Methods

Photographic survey of the coral community

Images were collected of a coral community at Wai‘ōpae (19°29’55” N 154°49’06” W), southeast Hawai‘i Island, using methods developed specifically for reconstructing coral reef habitats (Burns et al. 2015a). A transect tape was deployed on the substrate in a rectangular pattern to create a 25 x 10-m plot of the coral community within the largest submerged pool at Wai‘ōpae, which is located near the shoreline and exposed to terrestrial runoff (Takabayashi et al. 2010). This pool was surveyed because it was impacted by surge and runoff generated by the storm events, as well as the intense coral bleaching associated with the 2014 El Niño. Ground control points (GCPs) were placed at the corners and midpoints of the plot. The relative distances among the GCPs and depths were recorded to create x,y,z reference coordinates for each GCP. GPS coordinates were marked for the initial GCP, and the bearings between all GCPs were recorded to enable accurate georeferencing of the survey plot. A calibration grid and a scale marker were placed at the border of the survey plot to validate accuracy and precision of the resulting 3D reconstructions. Overlapping photographs were taken from planar and oblique angles while swimming 3-m above the substrate in a boustrophodonic pattern above the 25 x 10-m plot. All photos were taken with a Canon 5D Mark III digital SLR camera with a 24-70mm lens set at 24mm (Canon USA Inc., New York, USA) in an Ikelite housing with an 8-inch hemispheric dome port (Ikelite Underwater Systems, Indianapolis, USA). The 8-inch hemispheric dome port significantly reduces distortion due to refraction and improves the ability of the software to accurately calibrate and align the images (Bruno et al. 2011, McCarthy and Benjamin 2014). The 25 x 10-m coral reef plot was

photographed in July of 2014 before the occurrence of the acute disturbance events, and after the disturbance events in April of 2015.

3D reconstructions of the coral community

3D reconstructions of the 25 x 10-m coral reef plot were rendered using Agisoft modeling software (Agisoft LLC., St. Petersburg, Russia). PhotoScan was utilized due to the affordable cost of this software, practical user interface, capability to determine intrinsic and extrinsic camera parameters to perform calibration, local processing, and the multiple exportable 3D file formats that are compatible with geospatial software tools. For a critical overview of automated image orientation packages and investigation of potentialities and performances when dealing with large and complex datasets see Remondino et al. 2012.

Images were uploaded into the PhotoScan software and camera calibration was performed using Brown's distortion model, which resolves optical characteristics of the camera lens using information from the image metadata. PhotoScan aligned the images using algorithms that detect invariant features from the overlapping image sequences. The invariant features were then used to create geometrical projective matrices and determine the exact position and orientation of the camera for each sequential image (Verhoeven et al. 2012, Westoby et al. 2012). 3D geometry was constructed on the 2D image plane using the extrinsic parameters, which define the location and orientation of the camera reference frame with respect to a known world reference frame and in conjunction with the intrinsic parameters, which link the pixel coordinates of an image point with the corresponding coordinates in the camera reference frame (Stal et al. 2012). Iterative bundle adjustments were used to refine the 3D coordinates of the scene

geometry and minimize re-projection error in order to create a sparse 3D point cloud that accurately represented the structure of the photographed coral reef plot. Markers were digitally annotated onto each of the GCPs using the PhotoScan software, and the location of each marker was manually reviewed and corrected in all photos containing the GCPs. The known x,y,z values of the GCPs were manually entered into PhotoScan to optimize the alignment of the photos and to ensure the resulting models were spatially accurate. After the photo alignment was optimized, a dense point cloud was generated and used to construct a continuous mesh surface that was then triangulated and rendered with the sequential images to create textured 3D digital surface models representing the coral reef habitat.

Quantification of Spatial Properties

3D features of the reconstructed coral community at Wai‘ōpae were quantified using spatial analysis tools in ArcMap (ArcGIS 10.1, Environmental Systems Resource Institute, California, USA) to characterize the configuration, conformation, contour, form, and shape of the reconstructed coral reef (Burns et al. 2015a). Digital elevation models (DEM's), representing the habitat before and after the disturbance events, were exported from PhotoScan into ArcMap and layered with the orthophoto mosaics (Figure 1). The cell size of the DEM was set to 1.0-cm to detect intricate 3D characteristics of the coral reef habitat. Fifteen 4 x 4-m quadrats were digitally annotated onto the same locations of both DEMs using the editor function within ArcMap and 3D metrics were calculated within each quadrat using spatial analysis tools (Burns et al. 2015a). Surface-complexity was measured as a ratio of 3D/2D surface area. Slope was measured as the maximum rate of elevation change from each cell to its neighbors in a 3 x 3 cell window. Slope values

were calculated with the average maximum technique, thus small values reflected flat terrain and large values indicated steep terrain (Burrough and McDonell 1998). The following equation was used to quantify values of slope:

$$\text{percent slope} = \text{tangent}(\theta) * 100$$

A slope with an equal rise and run (45^0) has a percent slope value of 100; as the angle approaches horizontal the percent slope value approaches 0, and as the angle approaches vertical the percent slope value approaches infinity. Curvature was measured as the second derivative of slope across the DEM surface in order to identify areas of rapid change in slope or aspect. Curvature is computed with the following equation:

$$Z = Ax^2y^2 + Bx^2y + Cxy^2 + Dx^2 + Ey^2 + Fxy + Gx + Hy + I$$

This metric (Z) represents the rate of change in surface curvature and quantitatively represents convexities and concavities, thus identifying distinct physical features such as peaks, ridges, pass, planar regions, channels, and pits (Pittman et al. 2009, de Smith et al. 2015). Combined curvature, planform curvature and profile curvature were all quantified with the ArcMap 3D analyst tool. Large values of curvature are indicative of complex terrain. Combined curvature represents all directional changes in slope or aspect, while positive or negative values of planform and profile curvature represent either upwardly concave or convex surface in the perpendicular and parallel direction, respectively, of maximum slope (Burns et al. 2015a). Surface rugosity was quantified for the entire survey plot by measuring the ratio of contour distance to linear distance (Luckhurst and Luckhurst 1978, Friedlander and Parrish 1998). Virtual measurements of rugosity from stereo-image and SfM reconstructions are highly correlated to conventional chain-tape methods, provide very high-resolution data, and are robust and easily repeatable

(Friedman et al. 2012, Hu et al. 2012, Burns et al. 2015a, Leon et al. 2015). A mean rugosity value was derived from 9 permutations using the path distance tool in ArcMap, which allows for a measuring contour and linear distance between two points across the reconstructed coral habitat.

The orthophoto mosaics were uploaded into CoralNet software to compute percent coral cover and coral species diversity before and after the disturbance events (Beijbom et al 2012). 1,000 random points were annotated onto each orthophoto mosaic and classified manually. Coral species diversity was calculated using the Shannon-Wiener diversity index (H),

$$H = - \sum (p_i [\ln(p_i)])$$

where p_i is the proportion of individuals found in the i th species (n_i/N) for each transect.

3D Point Cloud Comparison

Alignment of the 2014 and 2015 coral point clouds was completed using a two-step process in CloudCompare (v. 2.6.1, 2015): (1) A rough alignment was performed using the point pairs picking tool to select four matching pairs of points in each cloud, followed by (2) a fine registration, using an Iterative Closest Point (ICP) algorithm (Besl and McKay 1992). The ICP algorithm was modified to allow for adjusted scaling of the source cloud to the reference cloud. To measure difference between the 2014 and 2015 point clouds, the Multiscale Model to Model Cloud Comparison (M3C2) algorithm was applied due to its superiority in measuring natural feature surface changes captured with terrestrial LiDAR or photogrammetry techniques, compared to other distance comparison

approaches (Lague et al. 2013). Areas of significant change were exported to geotiff format and brought into ArcMap for calculations of volumetric change.

Statistical Analyses

Statistical analyses were performed to compare the structural metrics derived from the 3D reconstructed coral reef plots before and after the disturbance events. Data were checked to ensure that the classical statistical assumptions of independence, heteroscedasticity and Gaussianity were not violated. Mean values of each 3D structural feature, coral cover, and coral diversity were compared using two sample t-tests in order to conduct a temporal comparison and determine if statistical differences ($\alpha = 0.05$) exist between the survey dates. All statistical tests were run using R version 3.2.2. The MC32 algorithm was used to determine areas of significant volumetric change, with a 95% Level of Detection (LOD), between the two dense 3D point clouds.

Results

Ground sampling distance (GSD) is the distance between two consecutive pixel centers, and is used as a standard measure of spatial resolution in remote sensing. Smaller GSD values correspond to greater spatial resolution and ability to detect intricate spatial features. In PhotoScan, the error (pix) is defined as the root mean square error for X, Y coordinates on an image for a GCP location averaged over all the images. The GSD (resolution/pixel) of the resulting 3D models were 0.0013- and 0.0007-m/pix with errors of 0.729- and 0.796-pix, thus the designated DEM cell size of 1.0-cm was well within the range of model accuracy. 100% of the images were matched for both 3D reconstructions.

There were statistically significant differences in mean values of the 3D structural metrics before and after the disturbance events (Figure 2). Slope, surface complexity, rugosity, planform and profile curvature were all significantly greater in 2014 compared to 2015 (two sample t-test, $t=2.25 - 5.61$, $p<0.05$). Coral cover was also significantly greater in 2014 compared to 2015 (two sample t-test, $t=6.12$, $p<0.01$). Mean values of both combined curvature and coral diversity decreased after the disturbance events, yet not to a statistically significant level (two sample t-test, $t=-0.22 - 1.53$, $p=0.827 - 1.53$).

For the alignment process, the 2014 point cloud was used as the fixed reference and the 2015 cloud was transformed to the best fit. The fine registration process with the ICP algorithm was iterative with registration error decreasing until a set threshold difference of $1e-8$ was reached between the last error iterations. The final root mean square (RMS) error was: 0.0119948 (computed on 2,000,000 points).

To compare change between the 2014 and 2015 point clouds, the M3C2 algorithm derived each distance measurement with a of 95% LOD (Lague et al. 2013). LOD corresponds to the minimum detectable change, taking in to account point cloud roughness and level of registration errors. Figure 3a highlights the significant change between the two point clouds. For the area of interest, there was a significant change over 36% of the coral reef habitat between the 2014 and 2015 dense 3D point clouds. Figure 3b shows the areas of the reef substrate where habitat volume both increased (blue) and decreased (red) over time. The volumetric comparison in ArcGIS quantified a net loss in habitat volume of 1.173 m^3 , and a net gain in habitat volume of 2.062 m^3 .

Discussion

306 This study applied 3D reconstruction techniques to evaluate how a series of acute
307 disturbances involving a hurricane, tropical storms, and coral bleaching altered the
308 structural complexity and composition of a coral reef habitat at Wai‘ōpae, southeast
309 Hawai‘i Island. 3D reconstructions were created for a 25 x 10-m plot in July of 2014, and
310 the same plot was surveyed again after the disturbance events in April 2015 to assess the
311 impacts. While a larger spatial and temporal context would improve our understanding of
312 how this coral reef system changes over a long-term, this study was able to document the
313 direct impact of these acute events. Due to the direct landfall of hurricane Iselle on the
314 entire southeast coastline of Hawai‘i Island, we were unable to utilize a control site
315 unaffected by the hurricane. Long-term monitoring has found minimal changes in coral
316 composition and mortality in the face of persistent chronic stressors (Takabayashi et al.
317 2010). Thus the large scale mortality documented in this study is likely caused by the
318 acute disturbance events that took place between the two observations in a short period of
319 time.

320 Specific structural features were analyzed in order to assess meaningful changes
321 in 3D structure that affect habitat facilitation and ecological processes. Values of surface
322 complexity, slope, curvature, and rugosity were compared before and after the
323 disturbance events, as these metrics are known to drive the distribution, abundance,
324 biomass, and diversity of vertebrate and invertebrate marine species as well as affect
325 hydrodynamics and irradiance (Friedlander and Parrish 1998, Jones and Syms 1998,
326 Kostylev et al. 2005, Guinan et al. 2009, Pittman et al. 2009, Pittman and Brown 2011).
327 Orthophoto mosaics representing the surveyed habitat were also analyzed with
328 conventional point count techniques to quantify changes in overall coral cover and coral

diversity in order to assess impacts to coral composition (Figures 1,2). It is worth noting the high resolution orthophoto mosaics can be used for standard 2D image analyses, thus this technique does not diminish the ability to quantify data that is comparable to studies utilizing conventional planar metrics. The reconstructed 3D point clouds were compared to determine if any loss occurred to the overall volume of live coral and reef substrate. It is important to assess changes in the volume and structure of live coral because coral loss can have sublethal effects on coral reef fishes (Booth 1995, Feary et al. 2009), and cause detrimental reductions in overall ecosystem productivity (Abdo et al. 2006, Anthony et al. 2009, Pratchett et al. 2014).

The resulting data showed all metrics of 3D habitat complexity, excluding overall curvature, decreased significantly after the disturbance events (Figure 2). The significant reductions in slope, surface complexity, rugosity, planform and profile curvature indicate a substantial loss of habitat complexity was caused by the acute disturbances. Coral cover also decreased significantly, indicating that live corals are responsible for architecturally complex habitat space at this site. Recent studies have found that 3D structural complexity can increase at reefs where coral bleaching and subsequent mortality has occurred (Ferrari et al. 2015). This finding was caused by the greater vulnerability of plating taxa compared to branching taxa, and the resulting shift in coral composition led to an overall increase in habitat complexity. Additional monitoring of the coral community at Wai'ōpae across a longer temporal scale, such as the 4-year timeframe used by Ferrari et al. 2015, may elucidate how 3D habitat complexity changes in association with recovery and shifts in coral community structure. The 3D point cloud comparison provided a novel method for detecting change in the volume of coral and reef

substrate, and the analysis showed a net loss in habitat volume of 1.173 m^3 with a net gain in habitat volume of 2.062 m^3 . The storm events displaced several basalt rock features on the coral reef and affected the net gain in reef structure as well as some of the net loss, which occurred when rocks were displaced from their location in July 2014 (Figure 1c,d and Figure 3). Despite the net gain in reef substrate from displaced basalt rock, 3D architectural complexity decreased significantly, thus illustrating the importance of live coral for providing complex habitat structure. Several coral skeletons remained intact as stable features, yet a large portion of coral skeletons eroded and left behind only bare substrate, which contributed to the overall net loss in substrate. The significant reduction in overall 3D habitat structural complexity and coral volume will likely affect ecological processes at Wai'ōpae.

The degradation of 3D habitat complexity has the potential to reduce the diversity and abundance of associated reef organisms because complex habitat provides more refuge space, decreases the encounter rate between competitors, and promotes niche specialization (Kostylev et al. 2005, Komyakova et al. 2013). High values of slope, planform and profile curvature are indicative of terrain features such as ridges, valleys and pits. The significant reduction in these topographic features occurred alongside reductions in coral cover and volume, suggesting the disturbance-induced mortality has led to an overall flattening of the habitat. Slope, surface complexity, and curvature can also act as proxies for benthic current velocities, which affects particle food supply for suspension feeding corals, gas exchange, calcification, and disease (Guinan et al. 2009, Burns et al. 2011). The observed reduction in 3D habitat structure may cause a negative feedback loop by reducing both benthic current velocities and the abundance of algal

375 grazers, which may ultimately inhibit the ability of corals to recover at this site. Isolated
376 coral ecosystems have exhibited recovery from severe disturbances (Gilmour et al. 2013),
377 and Hawaiian coral reefs often exhibit a steady increase in coral cover following acute
378 disturbance (Rodgers et al. 2015). However, sites with chronic recurring disturbances
379 show inhibited recovery of coral cover and drastic declines in coral habitat and reef fishes
380 (Rodgers et al. 2015), thus further long-term monitoring of this coral reef habitat is
381 necessary in order to examine the mechanics of coral recovery and possible phase shifts
382 associated with these disturbances.

383 Utilizing innovative SfM techniques to create 3D reconstructions of a coral
384 community at Wai‘ōpae vastly improved the capability to assess how disturbance affects
385 habitat characteristics that drive key ecological processes. The high-resolution orthophoto
386 mosaics and 3D models enabled precise quantification of changes occurring to coral
387 biomass and structural complexity, which is essential for understanding how coral reefs
388 respond to stressors and disturbance. The methodology presented here can be
389 incorporated into a range of ecological studies to improve our understanding of how the
390 projected increase in disturbances will alter ecological processes and services of
391 ecosystems.

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Figures captions

Figure 1. Orthophoto mosaics (10 x 25-m) representing the coral reef habitat at Wai‘ōpae (A) before (July 2014) and (B) after the multiple disturbance events (April 2015). The black boxes indicate areas (C,D) where basalt rocks were displaced by disturbance (white circles) and caused changes to 3D habitat structure.

Figure 2. Mean values ($\pm$ S.E.) of 3D structural metrics, coral cover, and coral diversity before (blue) and after (red) the disturbance events at Wai‘ōpae. α and β denote groupings identified by statistical significance ($p < 0.05$)

Figure 3. Comparison between 3D point clouds representing significant gain or loss of coral reef habitat at Wai‘ōpae after the disturbance events. The M3C2 algorithm reported (A) significant change over 36% of the reef structure, as shown in red. Measured change (B) depicts loss (red) and gain (blue) of reef substrate, and arrows indicate features contributing to the changes in 3D structure (a – displaced feature [basaltic rock], b – deposition [coral growth], c – removal [coral mortality and erosion of skeleton], d – stable feature [remaining coral skeleton]).

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