



NOTE

3D photogrammetry improves measurement of growth and biodiversity patterns in branching corals

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Abstract Photogrammetry is an emerging tool that allows scientists to measure important habitat characteristics of coral reefs at multiple spatial scales. However, the ecological benefits of using photogrammetry to measure reef habitat have rarely been assessed through direct comparison to traditional methods, especially in settings where manual measurements are more feasible and affordable. Here, we applied multiple methods to measure coral colonies (*Pocillopora* spp.) and asked whether photogrammetric or manual observations better describe short-term colony growth and links between colony size and the biodiversity of coral-dwelling fishes and invertebrates. Using photogrammetry, we measured patterns in changes in coral volume that were otherwise obscured by high variation from manual measurements. Additionally, we found that photogrammetry-based estimates of colony skeletal volume best predicted the abundance and richness of animals living within the coral. This study highlights that photogrammetry can improve descriptions of coral colony size, growth, and associated biodiversity compared to manual measurements.

Keywords 3D modeling · Biodiversity · Branching coral · Microhabitat · Moorea · Reef ecology

Introduction

Successful integration of new technology into ecological research requires clear understanding of how it can improve predictions of biological processes. Photogrammetry is a tool that renders detailed models of landscapes and organisms from images, enabling sophisticated examination of habitat structure (Burns et al. 2015; Ferrari et al. 2021). However, photogrammetric applications can be more expensive than traditional data collection methods in terms of equipment, time, and training (Young et al. 2017; Couch et al. 2021; Urbina-Barreto et al. 2021). Despite such costs, photogrammetric measurements of basic habitat characteristics may be very similar to data collected using traditional surveys (Raoult et al. 2016; Million et al. 2021). Studies that explicitly measure the same ecological phenomena using photogrammetry and manual approaches are therefore needed to critically examine the benefits of this emerging technique.

Photogrammetry may provide an especially useful research tool in settings where interactions among animals and structurally complex habitats govern ecosystem function, such as coral reefs (Burns et al. 2015; Lavy et al. 2015). For example, photogrammetry has helped to measure connections between reef habitat and fish communities (Gonzalez-Rivero et al. 2017; Urbina-Barreto et al. 2020), assess patterns in coral growth (Ferrari et al. 2017; Conley and Hollander 2021), and generate novel descriptions of coral geometry (Reichert et al. 2017; Aston et al. 2022). Among studies that have included both manual and photogrammetric measurements, most have focused on the accuracy of

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photogrammetry, which has been robustly demonstrated (Courtney et al. 2007; Veal et al. 2010; Figueira et al. 2015; Lavy et al. 2015). However, few studies have quantified differences in analogous ecological measurements derived from photogrammetric and traditional measurements of reef habitat, likely because photogrammetry is often used to describe large-scale characteristics when no practical manual equivalent is available (Reichert et al. 2017; Aston et al. 2022).

Some direct comparisons of ecological interpretations derived from manual and photogrammetric approaches indicate that photogrammetry can provide more accurate estimates of coral growth (Kikuzawa et al. 2018; Conley and Hollander 2021) and stronger predictions of links between fish biodiversity and reef-scale habitat complexity (Gonzalez-Rivero et al. 2017). However, photogrammetric measurements do not always lead to different conclusions than comparable field-based estimates. For example, Million et al. (2021) measured nearly identical colony growth using photogrammetric and manual methodologies, while Agudo-Adriani et al. (2016) observed that simple, manually measurable colony features drove more variation in fish communities than complex, photogrammetry-derived habitat characteristics.

In this paper we explore whether photogrammetry improves measurements of growth and habitat provisioning of branching cauliflower corals (*Pocillopora* spp.) over traditional approaches. Specifically, we asked: (1) Do manual or photogrammetric methods better describe short-term, volumetric growth across a range of coral sizes, and (2) Does photogrammetry improve our ability to predict the abundance and biodiversity of coral-associated animal communities?

Methods

We collected data in Moorea, French Polynesia, as part of a study of feedbacks between *Pocillopora* spp. and coral-associated fishes and invertebrates (CAFI). Although CAFI diversity and abundance have been shown to increase with host colony size, these relationships were previously modeled using coarse geometric measurements (Caley et al. 2001). We hypothesized that photogrammetry would better quantify linkages between coral volume and CAFI community characteristics.

We initiated an experiment in August 2019 consisting of 60 *Pocillopora* colonies (5–50 cm diameter). Corals were removed from the reef and sorted into control ($n = 30$) and CAFI-removal treatments ($n = 30$), then deployed into an experimental array (see Supplement). Directly after deployment, we measured coral size using both manual and photogrammetric approaches (Fig. S1). For manual measurements, a single observer used a flexible tape to estimate

colony length (L , longest horizontal axis), width (W , longest perpendicular measurement to length), and height (H , perpendicular to L and W). We calculated manual coral volume as a hemi-ellipsoid:

$$V_{\text{ellipsoid}} = \frac{4}{3}\pi \frac{L}{2} \frac{W}{2} \frac{H}{2} \quad (1)$$

a measurement previously used to relate *Pocillopora* spp. volume to CAFI biodiversity (Caley et al. 2001; McKeon et al. 2012).

For photogrammetric measurements, we used Agisoft Metashape (v1.6.2; Agisoft LLC, St. Petersburg, Russia) to create 3D models of coral colonies, following the protocol outlined by Ferrari et al. (2017). Full details are outlined in the Supplement, and in our online protocol (<https://github.com/stier-lab/Stier-Coral-Morphometrics-2020>). Using our complete and isolated 3D models, we estimated skeletal volume (V_{skeleton}), as well as length, width and height of each colony in Metashape. From photogrammetric linear dimensions we calculated photogrammetric ellipsoid volume ($V_{\text{photo_ellipsoid}}$) to directly approximate manual volumetric measurements ($V_{\text{ellipsoid}}$). We also used Meshlab (v2020.06; Cignoni et al. 2008) to estimate convex hull volume (V_{hull}), the size of the smallest convex 3D object that can encase a coral colony. Convex hulls provided an additional semi-elliptical measurement of exterior coral volume, but one that is not based on geometric calculation from multiple observer-based component measurements. To assess coral growth, we remeasured colonies after 105 days in December 2019 using the same observers.

We excluded six corals (of 60) from all analyses which did not yield high-quality photogrammetric models, due largely to incomplete photo coverage and turbidity. We also excluded 21 colonies from growth measurements that by December had experienced partial mortality or attracted dense fish aggregations which obscured the coral in photographs. In total, we analyzed $n = 33$ colonies for coral growth (measured at both time points) and $n = 26$ colonies to link CAFI biodiversity and coral volume (using data from August).

Analysis

We estimated growth as the proportional change in volume, calculated as $(V_{i,\text{December}} - V_{i,\text{August}})/V_{i,\text{August}}$ where i represents measurement method (manual ellipsoid, photogrammetric ellipsoid, hull, or skeleton). We used correlation analysis to compare manual and photogrammetric estimates of colony size and growth. We compared mean growth estimates using a repeated-measures ANOVA with a Greenhouse–Geisser correction and a post hoc Tukey HSD test (Bathke et al. 2009). We measured whether August colony volume predicted growth by performing linear regression

on colony-wise growth and initial volume measurements. To measure the link between colony volume and CAFI biodiversity, we performed power-law regressions of CAFI abundance and richness against all four volumetric measurements (see Supplement). We compared goodness of fit among regressions of the same response variable using AIC and root mean square error (RMSE) values (Chai and Draxler 2014). We performed analyses using R v3.6.3 (R Core Team, 2022) at a significance threshold of $\alpha = 0.05$.

Results and discussion

Manual measurements of colony size and volume were strongly correlated to photogrammetric measurements (Table S1; Fig. S2). In contrast, manual growth estimates ($V_{\text{ellipsoid}}$) were not correlated with any of the three photogrammetric growth estimates, whereas all three photogrammetric estimates of growth were positively correlated with each other (Table S1). Average proportionate growth varied slightly among the four methods (ANOVA: $F_{3,126} = 4.9$, $p = 0.014$, Fig. 1), with the only pairwise difference being between photogrammetric ellipsoid growth and manual ellipsoid growth (Diff (95% CI) = 14.6% (2.2%, 27.1%), $t_{32} = 14.6$, $p = 0.014$). Changes in ellipsoid volume (both manual and photogrammetric) were over twice as variable ($SD_{\text{ellipsoid}} = 23.9\%$, $SD_{\text{photo_ellipsoid}} = 25.6\%$) as growth estimates derived from photogrammetric measurements of V_{skeleton} and V_{hull} ($SD_{\text{skeleton}} = 9.99\%$, $SD_{\text{hull}} = 12.7\%$). Over a third of manual growth measurements were negative (13/33), whereas only 4/33 photogrammetric ellipsoid measurements, 2/31 photogrammetric hull measurements and 0/33 photogrammetric skeletal measurements were negative. Finally, all photogrammetric growth measurements were positively correlated with initial coral volume, whereas manual ellipsoid growth was uncorrelated with initial volume (Fig. S3).

All volumetric measurements, including manual ellipsoid volume, suggested that CAFI abundance and richness increased with coral size (Fig. 2). However, photogrammetry-based measurements of V_{skeleton} provided better predictors of CAFI abundance and biodiversity than manual estimates ($\Delta\text{AIC}_{\text{abundance}} = -5.8$, $\Delta\text{AIC}_{\text{richness}} = -3.6$; RMSE reduced by ~10%; Table S2). In contrast, all other photogrammetric estimates performed similarly to each other and to manual ellipsoid volume (Table S2).

Our findings demonstrate that photogrammetry can yield useful descriptions of coral colony structure and growth, and quantify the value of its application over traditional measurement methods. The tight correlation of manual and photogrammetric measurements corroborates that both approaches provide consistent assessments of coral linear dimensions and exterior volume (Courtney et al. 2007; Veal et al. 2010; Lavy et al. 2015; Fig. S2).

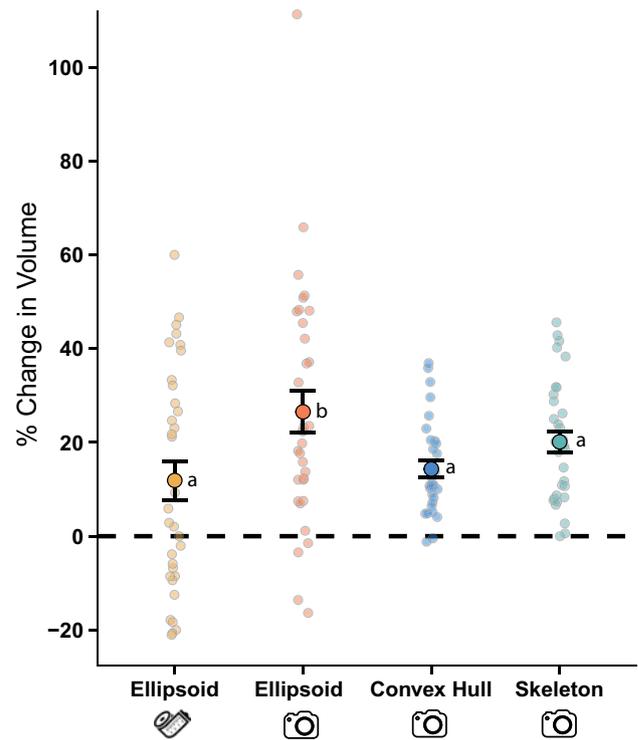


Fig. 1 Mean (\pm SE) proportional change in coral volume between August and December 2019 derived from manual measurements of ellipsoid volume (yellow) and photogrammetric measurements of ellipsoid (red), convex hull (blue), and skeletal volume (green). **a**, **b** indicate statistically significant differences based upon ANOVA followed by Tukey's HSD tests

However, photogrammetric measurements of skeleton and convex hull volume yielded the least variable and most biologically realistic (i.e., moderate and positive) estimates of growth over our three-month experimental period. Conversely, ellipsoid-based calculations (both manual and photogrammetric) provided more extreme and variable growth measurements, possibly due to error propagation when multiplying component linear measurements (Kikuzawa et al. 2018, see Supplementary material). In particular, our inclusion of large corals may have led to error in both manual and photogrammetric ellipsoid-based calculations due to increased departure from an elliptical shape (Conley and Hollander 2021; Million et al. 2021). Despite their high levels of variability, photogrammetric ellipsoid growth, unlike manual ellipsoid growth, was correlated to other photogrammetric growth measurements, possibly due to reduced error in component photogrammetric linear measurements compared to manual equivalents (Couch et al. 2021). In addition, all three photogrammetric volume measurements better described the expected allometry between growth and colony size (See Supplement, Fig. S3). Therefore, photogrammetric growth measurements were more broadly consistent and informative

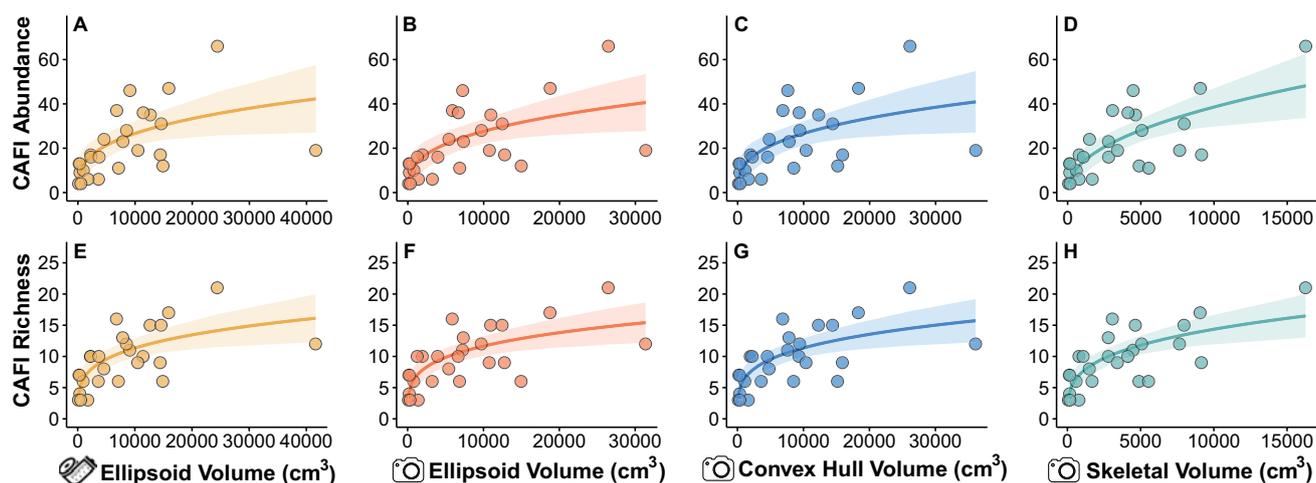


Fig. 2 Power-law regressions of CAFI abundance (A–D) and richness (E–G) against manual coral ellipsoid volume (A, D, yellow) and three photogrammetry-derived measurements: ellipsoid (B, E, red),

convex hull (C, F, blue), and skeletal volume (D, G, green). Shaded areas are 95% CIs of fitted regressions (Table S2)

than manual growth estimates, even at monthly timescales and across a wide range of colony sizes.

Additionally, photogrammetric skeletal volume most strongly predicted CAFI abundance and richness, outperforming manual ellipsoid volume and other photogrammetry-based measurements. The similarity in performance of photogrammetric ellipsoid volume, hull volume, and manual ellipsoid volume suggests that any methodological differences in accuracy did not yield improvements in modeled relationships with CAFI biodiversity. Instead, the advantage of photogrammetry was its ability to describe habitat in ways that are difficult using noninvasive manual techniques, in this case through estimates of skeletal volume. Although coral skeletal volume can also be measured by buoyant weighing or CT-scanning, these techniques are generally destructive and challenging to perform on large corals (Conley and Hollander 2021). Our photogrammetric measurements offer the first linkages of CAFI biodiversity to *Pocillopora* spp. skeletal volume, improving resolution of habitat-biodiversity relationships over our best available manual approximation of coral volume.

The application of photogrammetry to nondestructively measure 3D coral colonies in situ offers an exciting opportunity for researchers to study the ecology and structure of corals across a broad range of sizes. We conclude that photogrammetry may be especially valuable when 3D measurements are desirable but hard to obtain using field-based approaches, or where repeated measurements are required. By allowing noninvasive description of habitat characteristics, photogrammetry can generate tremendous value for studies of reef ecology and coral-animal interactions, even in settings where more affordable in situ measurements are available.

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Author contributions CO and AS designed the research; JC and AP collected field data; JG developed the photogrammetry protocol; JC and JG analyzed data; JC led manuscript writing. All authors contributed critically to drafts and gave final approval for publication. On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data availability Data, code, and detailed photogrammetry protocols are available at: <https://github.com/stier-lab/Stier-Coral-Morphometrics-2020>.

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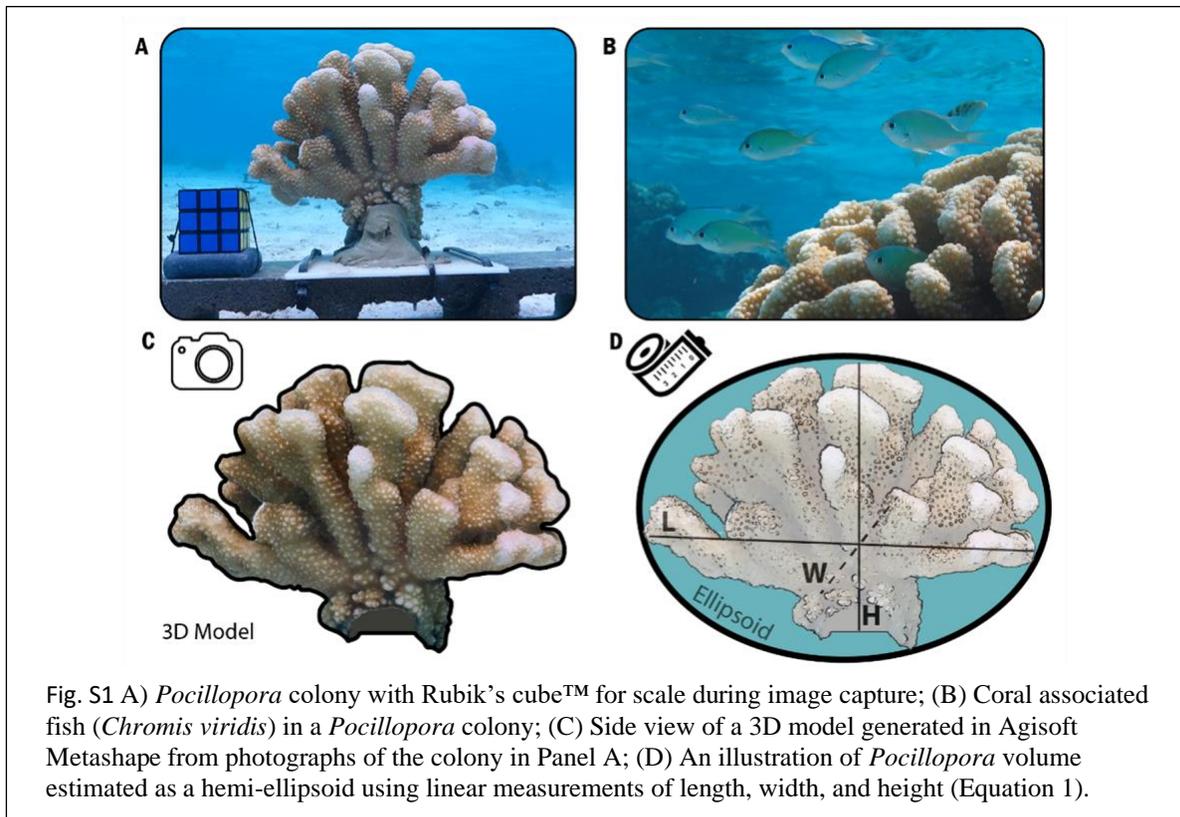
SUPPLEMENTAL INFORMATION

3D Photogrammetry improves measurement of growth and biodiversity patterns in branching corals

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Experiment set-up

Our study quantified the information gained through the application of 3D photogrammetry to measure the growth and habitat provisioning of *Pocillopora* spp. colonies over traditional, observer-based measurement approaches (Fig. S1). During collections, we enclosed corals in a polypropylene sack to retain coral-associated fishes and invertebrates (CAFI), symbiotic animals that can affect the growth, condition, and survival of host colonies (McKeon et al. 2012). We then chiseled colonies from the reef and transported them to a boat at the surface. We removed CAFI from half the colonies ($n = 30$) by immersing corals in an anesthetic solution (100 mg eugenol/L seawater), which we poured through a 1 mm mesh before collecting all visible animals (Stier and Leray 2014). This short-term exposure to relatively low concentrations of seawater (<10%) is not expected to cause long-term effects on coral growth or condition (Boyer et al. 2009). We preserved CAFI in 90% ethanol for identification within 72 hours. After CAFI removal, we attached corals to PVC plates using Z-spar epoxy and zip-tied



each module to a single cinder block. Corals with intact CAFI communities (controls, $n = 30$) remained enclosed in sacks until deployment. Manual estimates of coral volume were based on hemi-ellipsoid size, which we calculated using measurements of length, width, and height. Ellipsoid volumes have been shown to predict total linear extension in branching corals (Kiel et al. 2012), and were used in previous studies to relate coral volume to CAFI biodiversity (Abele & Patton, 1976; Caley et al., 2001).

Colony measurements

Photogrammetric measurements were based on 3D models created and calibrated following the protocol of Ferrari et al. (2017). First, we photographed corals from multiple angles alongside a 3D scale bar of known volume (Rubik's Cube™) attached to a dive weight. Specifically, we imaged the coral in two 360° circles from a perpendicular perspective (minimum 20 photographs/circle), then in eight arcs over the coral at 45° increments (minimum 15 photographs/arc). For photography we used one of two cameras: a Canon G16 with a Big Eye Mark-2 adapter or an Olympus TG-5 in wide-angle mode. On average, we captured 175 photos per coral (range: 112 – 268 photos).

After image capture, we edited photos in Adobe Lightroom (v10.1, Adobe Inc., San Jose, CA, USA) to achieve a consistent quality standard, mostly adjusting contrast, brightness, and white balance. We then imported images into Agisoft Metashape (v1.6.2; Agisoft LLC, St. Petersburg, Russia) and aligned them at “high” accuracy. After alignment, we created three 2D scale bars from markers placed on four corners of the digital Rubik's Cube, which we assigned a known length of 5.7 cm. We manually refined marker locations on at least three photos to minimize the difference among software-estimated scale bar lengths (average difference: 0.221 mm). Marker locations were refined until among scale-bar variation was reduced below 0.5mm (a threshold set by Ferrari et al. (2017)), refinement of an additional marker location from the most “novel” viewpoint did not improve reprojection error, and examinations of at least 10 randomly selected images consistently showed markers in the correct position. After optimizing alignment, we constructed a mesh from a dense point cloud at “high” accuracy, which we manually cropped to remove the background. Finally, we “closed holes” to create a watertight mesh, which was analyzed for length, height, width, and skeletal volume using built-in Metashape tools. Due to our strict adherence to the principles of this and similar protocols (see below), which have been robustly vetted and repeatedly applied, we assume our photogrammetric measurements to be highly accurate.

Our step-by-step workflow is available on GitHub (<https://github.com/stier-lab/Stier-Coral-Morphometrics-2020>). Since developing our analytic pipeline, other similar protocols have been presented, building a strong resource base for users with diverse applications and computing resources to adopt photogrammetry (Bayley and Mogg 2020; Lange and Perry 2020; Aston et al. 2022). In our protocol, we describe our approach for achieving visual consistency among batches of images using Adobe Lightroom and calculating convex hull volume using

Meshlab. We also provide Python scripts, created by collaborator Matthew Gottlieb (UCSB), that facilitate basic processing of batches of images into completed 3D models (<https://github.com/Mgla96/OceanRecoveryLabScripts>). These allow processing to proceed uninterrupted, saving valuable personnel hours that contribute to the costs of photogrammetry.

Correlations of manual and photogrammetric measurements

Photogrammetric and manual measurements of linear dimensions were strongly correlated, as were the geometrically-derived calculations of ellipsoid volume (Fig S2, Table S1). These tight correlations indicate that manual measurements of coral dimensions were generally consistent with photogrammetric equivalents. On average, manual estimates of coral length and width deviated less than 1 cm from photogrammetry-based measurements ($L_{\text{diff}} \pm \text{SD}$: 0.17 ± 1.8 cm; $W_{\text{diff}} \pm \text{SD}$: 0.99 ± 1.7 cm), while height estimates were more variable ($H_{\text{diff}} \pm \text{SD}$: 1.8 ± 2.5 cm). Still, some individual measurements diverged dramatically between the two approaches, with maximum absolute differences of 4.5 cm (length), 5.1 cm (width), and 9.4 cm (height). Our findings suggest that coral height may be more difficult to consistently characterize than length or width, and reduction of error in height measurements could most strongly improve geometric calculations of coral volume.

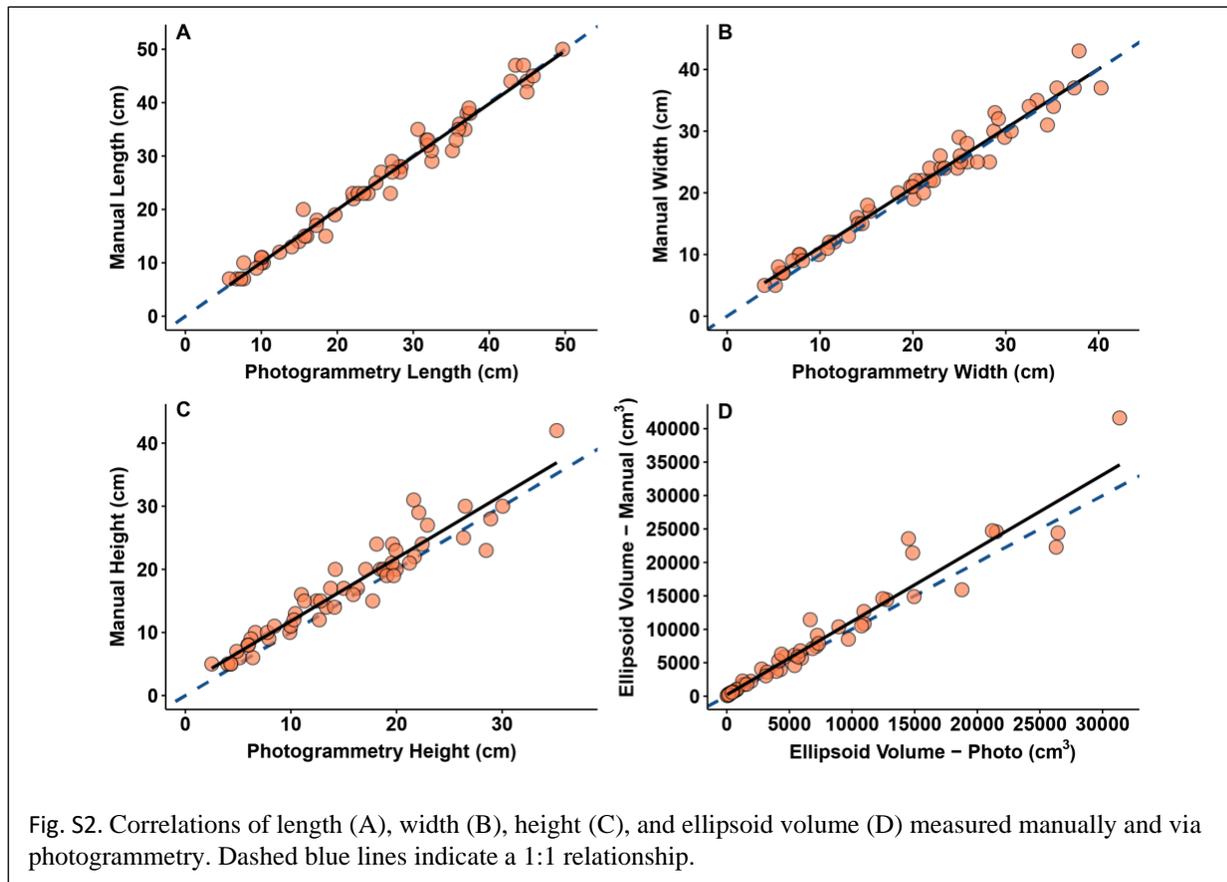


Fig. S2. Correlations of length (A), width (B), height (C), and ellipsoid volume (D) measured manually and via photogrammetry. Dashed blue lines indicate a 1:1 relationship.

CAFI Biodiversity

For analyses of linkages between coral morphology and CAFI abundance and diversity, we compared the fits of linear ($y = \beta_0 + \beta_1 x$) and power ($y = \beta_0 x^{\beta_1}$) functions to each measurement dataset, and compared models using Akaike's Information Criteria (AIC, Bozdogan, 1987). The power function provided a better fit for V_{hull} and $V_{\text{ellipsoid}}$ ($\Delta\text{AIC} > 4$), while linear and power function fits were indistinguishable for analyses using V_{skeleton} ($\Delta\text{AIC} < 2$). For consistency, we therefore report results using the power function (Table S2), which fit the overall dataset better than linear models. 95% confidence bands were calculated on regression parameters using Taylor expansions via the R package 'investr' (Greenwell & Kabban, 2014, Fig. 2).

<i>Size</i>					
Variable 1	Variable 2	df	<i>t</i>	<i>r</i>	<i>p</i>
<i>Length (Man)</i>	<i>Length (Photo)</i>	52	48.7	0.989	<0.001
<i>Width (Man)</i>	<i>Width (Photo)</i>	52	40.8	0.985	<0.001
<i>Height (Man)</i>	<i>Height (Photo)</i>	52	22.4	0.952	<0.001
<i>Ellipsoid (Man)</i>	<i>Ellipsoid (Photo)</i>	52	27.2	0.966	<0.001
<i>Ellipsoid (Man)</i>	<i>Hull (Photo)</i>	51	36.9	0.982	<0.001
<i>Ellipsoid (Man)</i>	<i>Skeleton (Photo)</i>	52	12.0	0.857	<0.001
<i>Ellipsoid (Photo)</i>	<i>Hull (Photo)</i>	51	44.0	0.987	<0.001
<i>Ellipsoid (Photo)</i>	<i>Skeleton (Photo)</i>	52	14.1	0.891	<0.001
<i>Hull (Photo)</i>	<i>Skeleton (Photo)</i>	51	15.5	0.908	<0.001
<i>Proportional Growth</i>					
Variable 1	Variable 2	df	<i>t</i>	<i>r</i>	<i>p</i>
<i>Ellipsoid (Man)</i>	<i>Ellipsoid (Photo)</i>	31	0.569	0.102	0.574
<i>Ellipsoid (Man)</i>	<i>Hull (Photo)</i>	29	0.905	0.166	0.373
<i>Ellipsoid (Man)</i>	<i>Skeleton (Photo)</i>	31	1.92	0.326	0.0642
<i>Ellipsoid (Photo)</i>	<i>Hull (Photo)</i>	29	5.56	0.718	<0.001
<i>Ellipsoid (Photo)</i>	<i>Skeleton (Photo)</i>	31	3.13	0.490	0.00382
<i>Hull (Photo)</i>	<i>Skeleton (Photo)</i>	29	4.32	0.626	<0.001

Table S1. Results of Pearson correlations of coral size and proportional growth measurements made using manual (man) and photogrammetric (photo) techniques. Estimates of *t* that differ significantly from 0 ($p < 0.05$) are in bold

<i>CAFI Abundance</i>									
Variable	Method	β_0	SE(β_0)	β_1	SE(β_1)	$t(\beta_1)$	$p(\beta_1)$	AIC	RMSE
<i>Ellipsoid</i>	Manual	1.36	1.31	0.323	0.104	3.11	0.005	207.55	11.67
<i>Ellipsoid</i>	Photo	1.25	1.21	0.336	0.104	3.23	0.004	206.52	11.44
<i>Convex Hull</i>	Photo	1.23	1.23	0.334	0.107	3.11	0.005	207.38	11.63
<i>Skeleton</i>	Photo	0.578	0.557	0.456	0.111	4.1	<0.001	201.76	10.44
<i>CAFI Richness</i>									
Variable	Method	β_0	SE(β_0)	β_1	SE(β_1)	$t(\beta_1)$	$p(\beta_1)$	AIC	RMSE
<i>Ellipsoid</i>	Manual	1.17	0.66	0.247	0.0614	4.01	<0.001	141.42	3.27
<i>Ellipsoid</i>	Photo	1.23	0.66	0.244	0.059	4.14	<0.001	140.38	3.21
<i>Convex Hull</i>	Photo	1.1	0.625	0.253	0.0618	4.1	<0.001	140.68	3.22
<i>Skeleton</i>	Photo	1.05	0.547	0.284	0.0615	4.61	<0.001	137.8	3.05

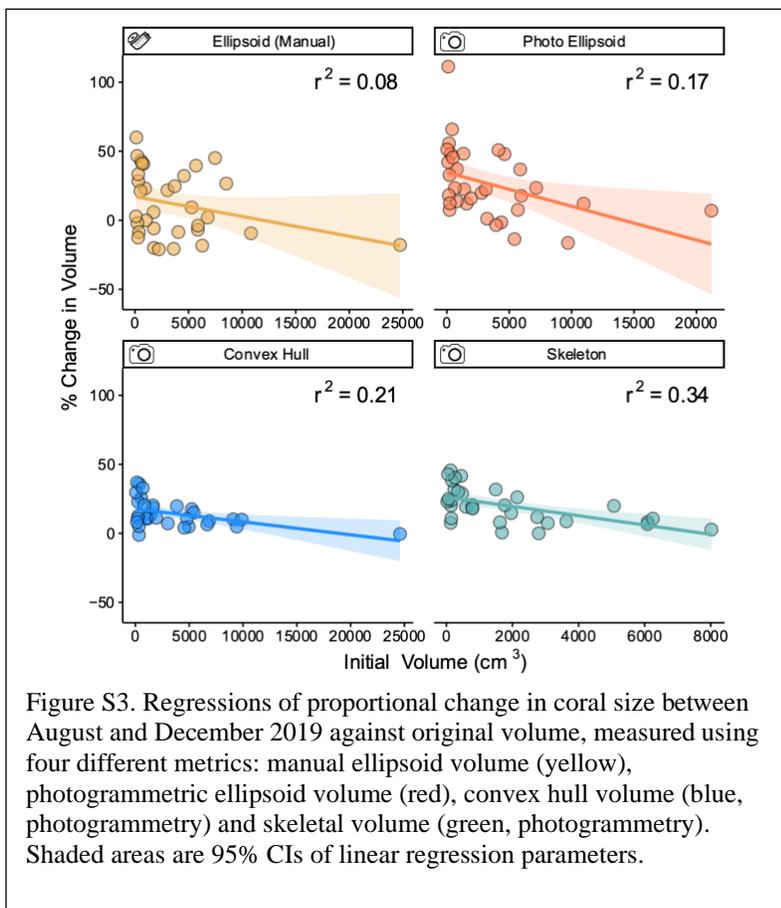
Table S2. Results from non-linear power law regressions ($y = \beta_0 x^{\beta_1}$) of CAFI abundance and species richness against coral volumetric measurements. Estimates of β that differ significantly from 0 ($p < 0.05$) are bolded, and in all cases were sublinear ($0 < \beta_1 < 1$). Akaike's Information Criteria (AIC) and root mean squared error (RMSE) values are provided as relative estimates of information provided by the regression or goodness of fit, respectively. AIC and RMSE values can only be compared among regressions with the same dependent variable (i.e., abundance or richness), the lowest of which (i.e., the better supported model) is in bold for each dependent variable.

Growth measurements

We suggest that the broad variability of ellipsoid-based growth measurements (both photogrammetric and manual) is at least partially attributable to error propagation, in which even slight errors in component linear measurements become compounded in the variance of the estimated volume. If the error in all three linear measurements is independent, then the CV of the volume would be slightly larger than $\sqrt{3}$ -times the CV for a single dimension. Growth estimates would be even more variable because they require two such size estimates, each derived from three measurements that are subject to error (6 measurements in total). Kikuzawa et al. (2018) described this challenge as the likely reason that manual measurements of volume were assessed in <20% of studies that have studied coral growth. We cannot assess or explicitly compare the accuracy of either measurement method due to a lack of a “control” object of known volume (outside of the Rubik's Cube™, which was used for photogrammetric calibration). However, manual observer error has been shown to be larger for manual measurements of coral diameter than photogrammetric observer error (Couch et al. 2021) and may more easily become

compounded into growth estimates than photogrammetric measurements that are derived from only two observations (rather than six, e.g., hull and skeletal growth). Therefore, we reasonably assume that at least some of the variation in ellipsoid-based growth estimates is driven by the heightened opportunity for the multiplication of small inaccuracies. This conclusion is supported by the result that convex hull volume outperformed photogrammetric ellipsoid volume (less variable, more positive, and more tightly related to August coral volume) as a growth metric despite their tight correlation and similar shapes, possibly because the convex hull is derived from a single measurement less prone to influence from observer or measurement error than ellipsoid volume.

Variation in growth measurements can obscure valuable inference regarding coral ecology. For instance, initial ellipsoid volume was a poor predictor of manual ellipsoid growth, whereas photogrammetry-based growth measurements were size-dependent (Fig. S3). Photogrammetric measurements could therefore be used to assess scaling relationships between *Pocillopora* volume and growth (Photo Ellipsoid: $F_{1,31} = 2.519$, $p = 0.017$; Hull: $F_{1,29} = 7.87$, $p = 0.008$; Skeleton: $F_{1,31} = 15.72$, $p < 0.001$) while manual ellipsoid measurements did not capture this important aspect of coral biology ($F_{1,31} = 2.76$, $p = 0.11$).



One important note regarding our methodology is that we sampled two branch tips (terminal ~2cm) from each coral prior to deployment (and prior to the initial measurements) in August 2019 for an unrelated study of coral physiology. These removed tips had completely regrown by our second site visit in December 2019. Although we don't expect that tip regrowth constituted the only skeletal growth over this 105-day period, especially in larger colonies, it is possible that our growth measurements differed from what we might have observed in wholly intact coral colonies. The magnitude and direction of the effect of branch removal on coral growth across such a broad size

range is difficult to predict. However, comparisons of growth measurements using different methods should not have been affected, because all measurements were made after removal of branch tips (August) and regrowth (December).

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