



RESEARCH ARTICLE

A quick, easy and non-invasive method to quantify coral growth rates using photogrammetry and 3D model comparisons

Ines D. Lange | Chris T. Perry

Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, UK

Correspondence

Ines D. Lange
Email: i.lange@exeter.ac.uk

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Abstract

1. Coral growth rates vary significantly with environmental conditions and are thus important indicators of coral health and reef carbonate production. Despite the importance of this metric, data are sparse for most coral genera and species globally, including for many key reef-building species. Traditional methods to obtain growth rates, such as coral coring or staining with Alizarin are destructive and only work for a limited number of species and morphological growth forms.
2. Emerging approaches, using underwater photogrammetry to create digital models of coral colonies, are providing novel and non-invasive ways to explore colony-scale growth patterns and to address existing knowledge gaps. We developed an easy-to-follow workflow to construct three-dimensional (3D) models from overlapping photographs and to measure linear, radial and vertical extension rates of branching, massive and encrusting corals after aligning colony models from subsequent years.
3. The method presented here was applied to measure extension rates for 46 colonies of nine coral species in the remote Chagos Archipelago, Indian Ocean. Proposed image acquisition and software settings produced 3D models of consistently high resolution and detail (precision ≤ 0.2 mm) and variability in growth measurements was small despite manual alignment, clipping and ruler placement ($SD \leq 0.9$ mm). Measured extension rates for the Chagos Archipelago are similar to published rates in the Indo-Pacific where comparable data are available, and provide the first published rates for several species. For encrusting corals, the results emphasize the importance of differentiating between radial and vertical growth.
4. Photogrammetry and 3D model comparisons provide a fast, easy, inexpensive and non-invasive method to quantify coral growth rates for a range of species and morphological growth forms. The simplicity of the presented workflow encourages its repeatability and permits non-specialists to learn photogrammetry with the goal of obtaining linear coral growth rates. Coral growth rates are essential metrics to quantify functional consequences of ongoing community changes on

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coral reefs and expanded datasets for key coral taxa will aid predictions of geographic variations in coral reef response to increasing global stressors.

KEYWORDS

3D model, Agisoft Metashape, Chagos Archipelago, CloudCompare, coral extension rates, coral growth rates, photogrammetry, structure-from-motion

1 | INTRODUCTION

Scleractinian corals are the main carbonate framework producers in coral reef ecosystems (Chave, Smith, & Roy, 1972), contributing to structural complexity of habitats (e.g. Graham & Nash, 2013) and providing food and shelter for many organisms (e.g. Brandl, Goatley, Bellwood, & Tornabene, 2018; Stella, Pratchett, Hutchings, & Jones, 2011). Critically, a combination of local stressors and climate change over the past decades has led to a global decline in coral cover (Gardner, Côté, Gill, Grant, & Watkinson, 2003; Wilkinson, 2008), reef complexity (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Graham et al., 2006), calcium carbonate budgets (Januchowski-Hartley, Graham, Wilson, Jennings, & Perry, 2017) and reef accretion potential (Perry et al., 2018). Many reef communities are shifting towards assemblages dominated by more stress-tolerant but slow-growing, non-framework-building taxa (e.g. de Bakker et al., 2016; Green, Edmunds, & Carpenter, 2008). The key metric to quantify the functional impacts of these changes is coral growth, representing an important life-history trait (Darling, Alvarez-Filip, Oliver, McClanahan, & Côté, 2012) and underpinning reef health indices such as the *ReefBudget* method (Perry et al., 2012) and the *Reef Functional Index* (González-Barrios & Alvarez-Filip, 2018).

Despite the importance of this metric, a recent analysis of available growth data reveals a severe paucity for most corals: over 74% of species in the Caribbean and 70% of genera in the Indo-Pacific are represented by <3 data points (Lange, Perry, & Alvarez-Filip, 2020). Even for the few relatively well-studied species, geographic or environmental variability is poorly constrained. The most common metrics of coral growth are linear and radial skeletal extension rates, measured as unidirectional change in branch length or colony radius respectively (Pratchett et al., 2015). Traditional methods for measuring these rates rely on either: (a) repeated direct measurements of tagged branches (Anderson, Pratchett, & Baird, 2012; Simpson, 1988), which is only feasible for branching species and raises concerns that the tagging process impedes coral growth (Oliver, 1984); (b) repeated measurements of colony height or diameter in situ or from photographs (Anderson, Heron, & Pratchett, 2015; Stimson, 1985), also known as morphometrics, which does not take into account patterns of colony growth, i.e. different axis of growth or local effects of damage (Pratchett et al., 2015); (c) coring and x-radiography (Cooper, O'Leary, & Lough, 2012; Knutson, Buddemeier, & Smith, 1972), which only supports data acquisition for ~7% of, mostly massive, coral species (Pratchett et al., 2015); or (d) staining with Alizarin (Barnes, 1972; Holcomb, Cohen, & McCorkle, 2013), which works

well for a range of growth forms but is time-consuming to perform, prone to poor stain uptake (Harriott, 1999), and after which corals must be sacrificed for measuring.

In contrast, emerging approaches using underwater photogrammetry to create digital models of coral colonies are providing novel and non-invasive ways to explore colony-scale growth patterns. Photogrammetry is the science of making measurements from photographs. It involves taking a series of overlapping pictures with a single camera from multiple perspectives around a given object. Structure-from-motion (SfM) software then detects and matches common features in multiple photographs to reconstruct a digital, true-scale, three-dimensional (3D) model (e.g. Luhmann, Robson, Kyle, & Boehm, 2014). Consequently, this method provides a permanent, measurable 3D record of an object and only requires a consumer-grade digital camera and basic training to ensure overlap of photos (McCarthy & Benjamin, 2014). Bythell, Pan, and Lee (2001) were among the first to use photogrammetry in reef studies, identifying the need to measure surface areas of corals and other organisms in situ and unrestricted by size limitations and thereby replace destructive methods such as foil wrapping or wax dipping. Since then, underwater photogrammetry has proven to be an accurate technique for measurements of surface area, volume and rugosity at the coral colony scale (e.g. Burns, Delparte, Gates, & Takabayashi, 2015b; Bythell et al., 2001; Cocito, Sgorbini, Peirano, & Valle, 2003; Courtney, Fisher, Raimondo, Oliver, & Davis, 2007; Figueira et al., 2015; Gutiérrez-Heredia, D'Helft, & Reynaud, 2015; Lavy et al., 2015). Besides assessing the accuracy and precision of photogrammetric measurements, some of these studies introduced field applications including quantitative assessment of partial tissue mortality (Bythell et al., 2001), quantification of carbonate standing stock and biomass (Cocito et al., 2003) and taxonomic identification (Gutiérrez-Heredia, Benzoni, Murphy, & Reynaud, 2016). With technical advancements in camera equipment, SfM software and computing power in the last years, the main focus of photogrammetric applications has shifted towards the reef scale, quantifying a range of structural complexity parameters and assessing the implications for ecosystem functions (Anelli et al., 2019; Bayley, Mogg, Koldewey, & Purvis, 2019; Bryson et al., 2017; Burns, Delparte, Gates, & Takabayashi, 2015a; Burns et al., 2016; Ferrari et al., 2016, 2018; Figueira et al., 2015; Friedman, Pizarro, Williams, & Johnson-Roberson, 2012; González-Rivero et al., 2014; Guo et al., 2016; Leon, Roelfsema, Saunders, & Phinn, 2015; Storlazzi, Dartnell, Hatcher, & Gibbs, 2016; Williams et al., 2012) or quantifying changes in reef height or volume over time (Bayley, 2019; Neyer, Nocerino, & Gruen, 2018; Rossi, Castagnetti, Capra, Brooks, & Mancini, 2019).

Interestingly, despite suggestions that 3D coral models can support the tracking of colony growth and morphological changes over time (Burns et al., 2015b; Lavy et al., 2015), only few studies to date have used photogrammetry to actually measure coral growth rates. First, Bennecke, Kwasnitschka, Metaxas, and Dullo (2016) quantified growth rates for deep-water octocorals by comparing the total length of 3D models along the main growth axis over time, and by measuring distances between cross-sectional outlines. Second, Ferrari et al. (2017) quantified surface area and volume changes of large tabular *Acropora* spp. colonies and calculated annual linear extension rates based on changes in the maximum radius of 3D models. Third, Bayley (2019) estimated extension rates of juvenile tabular *Acropora* spp. and *Porites* spp. colonies included in large modelled reef area sections by comparing the maximum radius or distance between point cloud surfaces respectively. Building on these studies, we propose that photogrammetry techniques offer a great opportunity to determine annual linear extension rates for a wide range of coral species and morphological growth forms.

We present an easy-to-follow workflow to construct 3D models of coral colonies from in situ photographs and to overlay models from subsequent years. Instead of comparing colony sizes of each model as suggested by traditional morphometric analyses, we directly quantify distances between colony surfaces. This method was developed in order to fill important gaps in available growth rate data for the central Indian Ocean region, which are also presented in this publication. The successful application of the presented workflow demonstrates the use of photogrammetry and 3D modelling as an alternative approach to destructive staining and coring methods.

2 | MATERIALS AND METHODS

2.1 | Image acquisition

Series of photographs were taken of individual coral colonies at two fore-reef sites (8–10 m depth) in the remote Chagos Marine Protected Area, central Indian Ocean. In May 2018, 59 coral colonies of the species *Acropora* spp. ($n = 12$), *Pocillopora meandrina* ($n = 7$), *Montipora* spp. ($n = 7$), *Isopora palifera* ($n = 7$), *Leptastrea aequalis* ($n = 5$ encrusting, $n = 3$ massive), *Favites stylifera* ($n = 5$), *Pavona varians* ($n = 5$), *Porites lobata* ($n = 5$) and *Astreopora myriophthalma* ($n = 3$) were marked with numbered cattle tags. Colonies were 10–60 cm in diameter and located on relatively exposed reef surface substrates to enable photography from all angles. Tags were attached to surrounding dead reef substrate with stainless steel nails or cable ties. The locations of colonies were mapped in relation to marked transects (GPS and subsurface buoys at start and end points) to allow rediscovery in the following year (Figure 1a). Depending on colony size and detail, sets of 30–70 photographs were taken from all angles around each colony following a pattern along arcs from top to bottom and moving around the colony in steps of ~40°, with an additional top-view circle of photographs from a slightly larger distance and at ~45° angle to the substrate (Figure 1b). We used a digital compact camera (Canon PowerShot G7 X Mark II, 20.1 Megapixel) in a

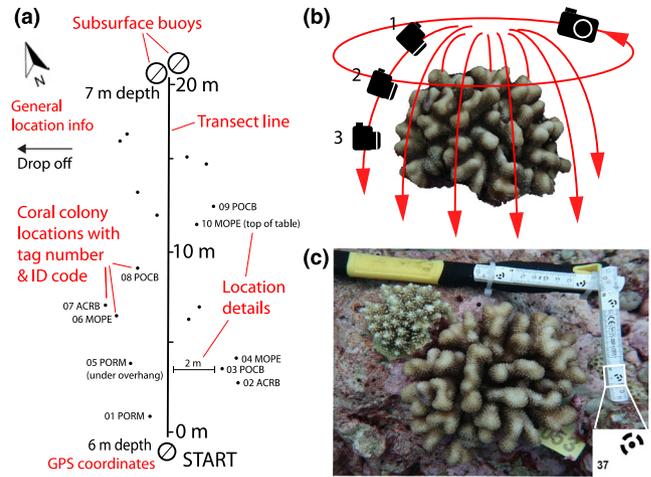


FIGURE 1 Image acquisition. (a) Example of map to rediscover tagged coral colonies along a transect tape which is deployed between marked start and end points at the beginning of each visit. (b) Suggested pattern for image acquisition around a coral colony, taking 3–5 photos along each arc from top to bottom and 8–12 photos along a larger top-view circle (c) Reference ruler (here attached to a hammer to avoid movement in swell) with 4 automated targets fixed in known distances to each other (here 7 cm). The inset shows an example target which can be printed from the software Metashape Professional (Agisoft LLC)

Canon underwater housing (flat lens port) with the settings: underwater mode, autofocus, no flash. The SfM software is capable of resolving the optical characteristics of the lens directly from the images, thus pre-calibration of the camera is not necessary (McCarthy & Benjamin, 2014). During image acquisition it is important: (a) to ensure a 70%–80% overlap between pictures; (b) to adhere to the same image orientation, preferably landscape and (c) to not use camera zoom. With two divers, one marking coral colonies and one taking pictures, we were able to photograph 10–15 colonies during a 70-min dive. A white folding ruler with black markings placed next to each colony served as a reference for scaling the resulting 3D models, and should not be moved during image acquisition. The reference does not have to be visible in every photograph but should be fairly close to the colony to be depicted well in the model construction. We recommend that automated targets are attached to the reference in known distance to each other (see Figure 1c). These standardized symbols can be detected by the SfM software and thereby speed up the scaling process. In March 2019, 300 days after the initial marking and imaging, sites were revisited, transect tapes deployed between marked start and end points, colonies located using the habitat maps and photographed in the same manner as described above. Difficulties that were encountered during image acquisition and following model reconstructions are listed in Table S1 together with respective counter measures to facilitate repeatability of this method.

2.2 | 3D model construction

Three-dimensional models of coral colonies were constructed using the Software Metashape Professional version 1.5.1 (former

PhotoScan, Agisoft LLC) on an off-the-shelf laptop (HP EliteBook 830 G5, Windows 10, 64-bit, Intel® Core™ i7-8650U @2.1 GHz CPU, 16 GB RAM, Intel® UHD Graphics 620 @1.2 GHz, 6.5 GB GPU). This relatively low-cost commercial SfM software was chosen as it has been used in many prior studies, is relatively easy to work with, yet offers many customization and quality control options, does not require pre-calibration of camera equipment and offers helpful resources in the form of a handbook and tutorials. The specifications of the computer used were sufficient to construct models within our targeted size class (10–60 cm diameter, 30–70 photos) within ~60 min, whereas much larger models and more photographs will require more computing power and/or time for model construction. The Metashape handbook indicates that 16 GB RAM allows processing of models with up to 300–400 photographs.

The workflow for 3D model constructions, including the description of functions, settings and an approximate time for each step, is described in Table 1 and demonstrated in a video tutorial at <https://youtu.be/FxMwujCJEI4>. In brief, all photos of a colony are added into a 'chunk' in the workspace and image quality is estimated by the software based on the sharpness level of each picture. It is recommended to disable images with values <0.3, and to check images with values <0.5 and disable if blurred. From the remaining pictures, Metashape's algorithm constructs a sparse point cloud by detecting and matching common features on multiple photographs and thereby determining the position for each camera. After this step we recommend that potential errors in the reconstruction are reduced by deleting points above/below certain levels of uncertainty and accuracy as described in the workflow. The result is a sparse cloud with less, but highly accurate points, which speeds up the next processing step. While moving through the error reduction steps, the projection error in each image should be monitored in the Reference pane, with the aim of reducing Error (pix) to 0.3–0.7 for most images while at the same time keeping the final number of points in the cloud at around 10,000–15,000. In our examples, error reduction reduced the number of points in sparse clouds from 30,000–70,000 to 7,000–20,000. From the optimized camera positions and the photographs Metashape then generates a dense point cloud, which can be scaled with the help of automatically detected or manually added markers before being exported for further analysis. A continuous and textured surface mesh can be constructed for demonstration purposes and to facilitate model scaling (examples in first column of Figure 2). However, we recommend the use of dense point clouds for all following analyses, as these represent the most accurate reconstruction of the actual colony surface, while the construction of meshes may introduce uncertainties by interpolating over missing data or smoothing out important details (Lague, Brodu, & Leroux, 2013).

If photosets of several colonies are loaded into the same workspace as separate 'chunks', the camera alignment and dense cloud construction can be processed for all these models consecutively with one click using batch processing. We used this feature to process the time- and computing power-intensive dense point cloud construction of up to 10 models overnight. Details for each model, including the

number and resolution of aligned images and the number of points in constructed dense point clouds, are listed in the raw data table accessible at <https://doi.org/10.24378/exe.2243>.

To estimate the precision of 3D model construction, six additional models for each of the three colonies (one of each growth form, colonies depicted in Figure 2) were built from the same set of photos after randomly removing 10% of pictures from each dataset (following Ferrari et al., 2017; Figueira et al., 2015). Resulting subset point clouds were aligned to the original point cloud of the respective colony in CloudCompare as described below, with precision calculated as the average distance between point clouds (in mm).

2.3 | Measurement of coral growth rates

Scaled dense point clouds of the same colony in 2018 and 2019 were imported into CloudCompare v2.10.2 (Zephyrus) for subsequent analysis as described in detail in Table 2 and demonstrated in a video tutorial at <https://youtu.be/BqA64SVwJjM>. In brief, clouds are aligned by picking at least three equivalent point pairs in the area surrounding the colony and, if necessary, further adjusting the alignment by tilting and slightly moving one of the clouds. Both clouds are segmented around the outlines of the most recent point cloud (i.e. larger colony) to remove the surrounding reef area. Next, the distances between the remaining point clouds are computed and displayed as a colour ramp. Extension rates are then measured depending on colony morphology (also see Figure 2):

- Branching, corymbose and digitate colonies grow primarily at branch tips and linear growth rates are therefore measured using the point–point distance tool to mark individual corresponding points in branch tips of both colonies ($n \geq 10$ for each colony to calculate average [avg.] \pm SD).
- Massive colonies grow in all directions at the same time, although this growth can be fairly asymmetrical. Radial extension rates are thus defined as the average distance between corresponding points in both point clouds, acquired from the histogram of absolute distances.
- Encrusting colonies primarily grow in the horizontal plane, but also grow vertically to form a thicker crust. To accommodate for both growth directions, radial growth is measured as the distance between colony borders using the point–point distance tool ($n \geq 10$ for each colony to calculate avg. \pm SD). Vertical growth is defined as the average distance between corresponding points in both point clouds, acquired from the distance distribution histogram.

Annual coral growth rates can be calculated by dividing the measured extension rates by the number of days between image acquisitions and multiplying by 365 days. Raw data on growth measurements in this study can be accessed at <https://doi.org/10.24378/exe.2243>.

TABLE 1 Workflow for three-dimensional model construction from overlapping photographs in Agisoft Metashape Professional 1.5.1. Time estimated for each step is based on a user accustomed to the program and method. Time necessary for processing steps (in green) depends on CPU, GPU and RAM of the used work station and values given here are based on using a HP EliteBook (2.1 GHz CPU, 16 GB RAM, 6.5 MB GPU). The last two steps (in blue) are optional, as the following analyses are done on point clouds. If several models are loaded into the same workspace as separate chunks, 'Alignment' and 'Dense Cloud' generation can be processed for all those models in one step ('Workflow' - 'Batch process' - 'Add Job' and choose settings)

Steps	Menu	Function	Action	Time (min)
Photo setup, Alignment				
1	Main Menu - Workflow	Add Photos	Navigate to directory with photos. Select and add all colony photos. Ensure consistent orientation and good quality of all photos (landscape)	2
2	Photo Panel - right click on any photo	Estimate Image Quality - All Cameras	Check values (☒ change view to details), disable cameras if <0.3, check cameras if <0.5 and remove if blurry	2
3	Main Menu - Workflow	Align Photos	Settings: high, generic preselection, 40,000, 4,000, do not apply masks	15-20
4	Reference Panel	Optimize Cameras ☒	☒ check all except k4, b1, b2, p3, p4 (default)	1
Total time				20-25
Error reduction				
5	Main Panel	☒ Resize Region	If area around colony is very large, decrease the size of the bounding box	
6	Main Menu - Model Gradual Selection	Reconstruction Uncertainty (Pixel matching Errors)	Set level 10-15 (if more than 30% of pts are selected, increase the level) Delete the points, Optimize cameras, ☒ check all except k4, b1, b2, p3, p4 If necessary repeat until level is closer to 10-15 (e.g. 1st step: 15, 2nd step: 12)	1
7	Main Menu - Model Gradual Selection	Projection Accuracy (Pixel matching Errors)	Set level 3-5 (if more than 30% of pts are selected, increase the level to 5-9) Delete the points, Optimize cameras, ☒ check all except k4, b1, b2, p3, p4 Repeat 1-2 times until level is closer to 3-5 (e.g. 1st step: 7, 2nd step: 4) Monitor in references, cameras: Projections goal > 100, Error (pix) goal = 0.3-0.7	1
8	Reference Panel	☒ Settings - Tighten Tie Point Accuracy	Change tie point accuracy from 1 to 0.1 Optimize cameras, ☒ check all Monitor SEUW in console which should get closer to 1	1
9	Main Menu - Model Gradual Selection	Reprojection Error (Pixel Residual Errors)	Set level 0.3-0.5 (if more than 10% of pts are selected, increase the level) Delete the points, Optimize cameras, ☒ check all Repeat 2-3x on same level until reaching it without having to delete points Monitor: Projections goal > 100, Error (pix) goal = 0.3-0.7, SEUW (console) = 1.0	2
Total time				5
Dense Point Cloud, Mesh, Texture				
10	Main Menu - Workflow	Build Dense Cloud	Settings: medium, aggressive, do not reuse depth maps, point colours	30-35
11	Main Menu - Tools References Panel	Markers - Detect markers	Circular 12 bit, tolerance 50. Or add markers manually (right click, add marker). Projections should be >3 for markers used for scaling Mark two markers, 'Create Scale Bar', add distance (in 'View Source' ☒ mode), ☒ update, check for errors (in 'View errors' ☒ mode)	3
12	Main Menu - File	Save as	Save project as.psx	1
13	Main Menu - File	Export - Export Points	Export dense point cloud as.ply	1
14	Main Menu - Workflow	Build Mesh (optional)	Settings: dense cloud, arbitrary, count medium, interpolation enabled	(20)
15	Main Menu - Workflow	Build Texture (optional)	Settings: generic, all cameras, mosaic	(10)
Total time (including mesh and texture)				35-40 (70)

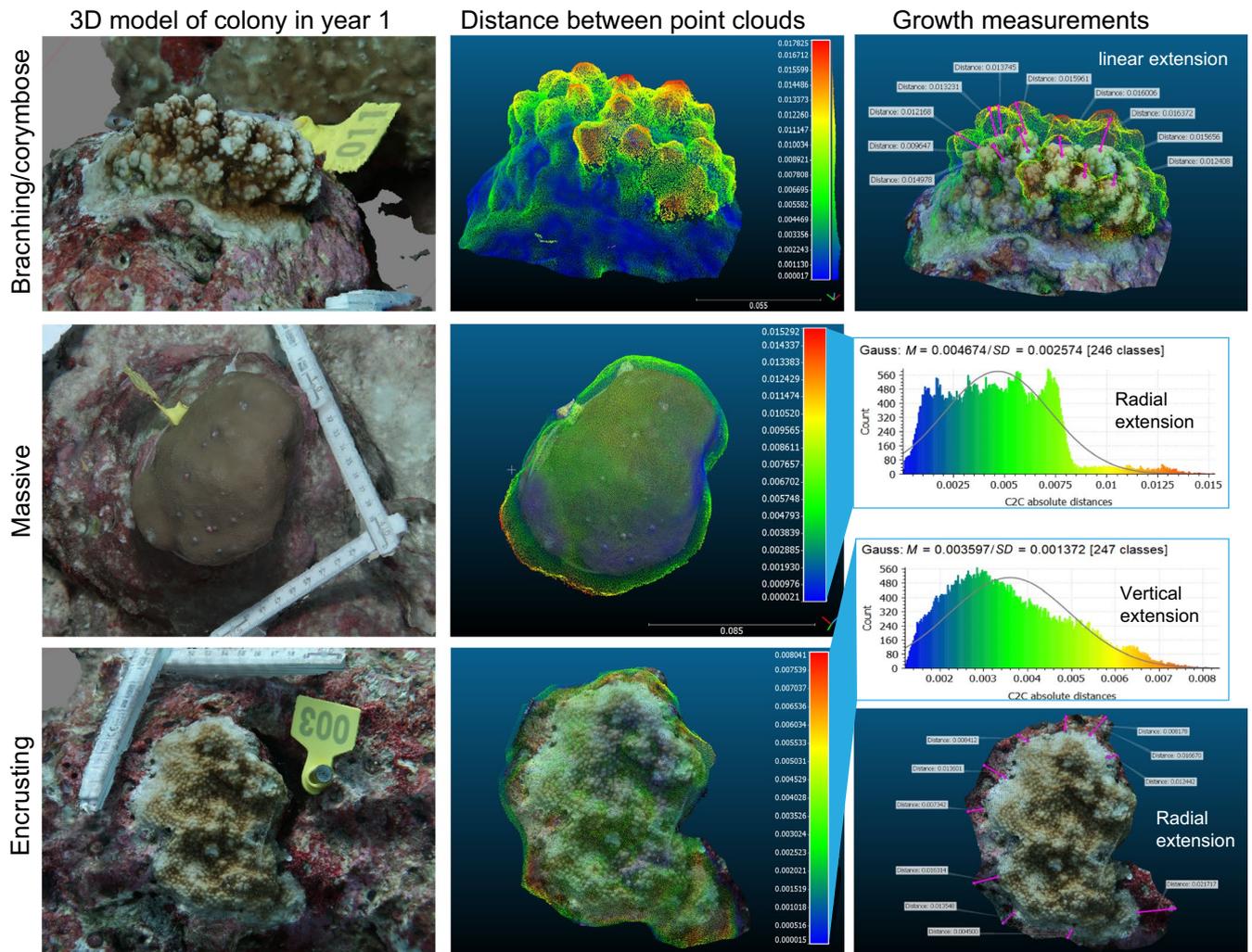


FIGURE 2 Measurement of coral growth rates. Column 1 shows textured 3D models of corymbose *Acropora* spp. (row 1), massive *Porites lobata* (row 2) and encrusting *Isopora palifera* colonies (row 3) in year 1. Column 2 shows point clouds of the same colonies in year 2, with colours indicating distances to year 1 clouds (in m). Column 3 shows either point-to-point measurements between branch tips or colony borders ($n = 10$) which are averaged to yield linear and radial extension rates for branching/corymbose and encrusting colonies, respectively; or the frequency distribution of distances between corresponding points in both point clouds ($n =$ number of points in year 2 cloud) with means and standard deviations (in m) representing radial and vertical extension rates for massive and encrusting colonies, respectively

To estimate the errors introduced by manual model alignment, clipping and point-point measurements, the process of alignment and measurements as described above was repeated six times for each of the three colonies (one of each growth form, colonies depicted in Figure 2). Resulting standard deviations were compared to within-colony variations in growth and the coefficient of variation (CV), which is defined as the ratio of the standard deviation to the mean, was calculated for comparison with similar studies.

3 | RESULTS

3.1 | Image acquisition

In March 2019, 46 out of the 59 originally tagged colonies (78%) were successfully located and re-photographed, while 13 colonies

(six of which were *Acropora* spp.) were either not found or buried under collapsed reef structure.

3.2 | 3D model construction

Three-dimensional model construction was successful for all colonies, with upper surfaces consistently pictured in good detail, while obscured lower parts of colonies or areas between branches sometimes resulted in small holes or sparse point density. Image resolution was unintentionally set lower in the second year, resulting in visibly lower point cloud densities in 2019 than in 2018 models (on average ~1,000,000 and 4,000,000 points/model respectively). However, small holes or lower point numbers in 2019 models did not affect growth measurements as all models were of high detail resolution and extension rates were measured at well-depicted surfaces and branch tips. Scaling of

TABLE 2 Workflow for three-dimensional model comparison and growth rate measurements in CloudCompare v2.10.2 (Zephyrus). Time estimated for each step is based on a user accustomed to the program and method and can be longer, especially if alignment of models is difficult

Steps	Menu	Function	Action	Time (min)
Align point clouds, measure growth rates				
1	Main Panel	Open	Navigate to directory with point clouds. Select and add point clouds (.ply) of the same colony of two subsequent years (=A older, B more recent cloud)	1
2	DB Tree Panel Main Panel	Align Point clouds	Highlight 1 cloud, translate/rotate, move cloud next to other cloud in similar orientation Highlight both clouds (ctrl + left click), align the two clouds by picking at least three equivalent point pairs (not located in one line or plane), align, ok If the fit is not perfect, adjust alignment by translate/rotate 1 cloud Highlight <u>both</u> clouds, segment around the outline of cloud B by polygonal selection, segment in/out, ok, switch off cloud. remaining	5
3	DB Tree Panel Main Panel	Compute cloud/ cloud distance	Highlight <u>both</u> clouds, compute cloud/cloud distance, choose cloud A as reference, compute, ok	1
4	DB Tree Panel Properties Panel	Scroll down	Highlight cloud B, display Scalar Field, Colour Scale-Visible to display scale, change scale if desired (Steps, Current, move sliders, ...)	2
5a	DB Tree Panel Main Panel	Branching colonies	Highlight <u>both</u> clouds (display Scalar Field or RGB for cloud B), use to measure point-point distances between branch tips, click after each pair to save labels = linear extension (n ≥ 10 → calculate avg. ± SD)	5-10
5b	DB Tree Panel Main Panel	Massive colonies	Highlight cloud B, display Scalar Field, Distribution: Gauss displays average distance (in all directions) = radial extension (avg. ± SD)	5-10
5c	DB Tree Panel Main Panel	Encrusting colonies	Highlight cloud A, use to measure point-point distances between colony border and segment border (which represents cloud B border), click after each pair to save labels = radial extension (n ≥ 10 → avg. ± SD) Highlight cloud B, display Scalar Field, Distribution: Gauss displays average distance (mostly along z-axis) = vertical extension (avg. ± SD)	5-10
6			Highlight <u>all</u> layers, save as cloud compare entities (.bin)	1
Total time				15-20

Abbreviations: avg., average; SD, standard deviation.
Choose step 5a, b or c (in blue) depending on growth form.

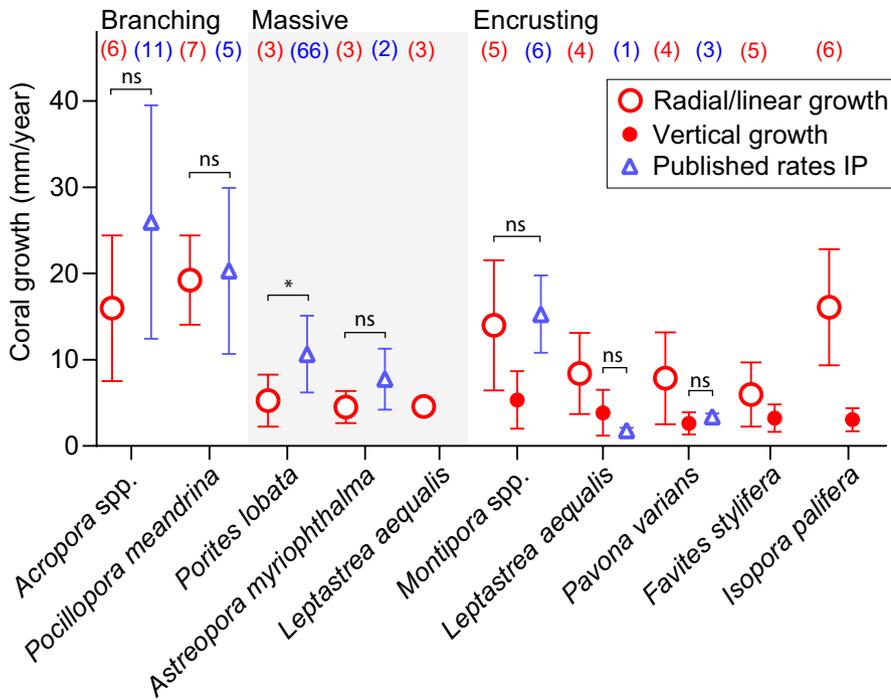


FIGURE 3 Annual growth rates for a range of coral species and morphological growth forms. Mean measured extension rates in the Chagos Archipelago (red circles; average [avg.] \pm SD) are compared to average published rates in the Indo-Pacific (IP) (blue triangles, studies referenced in Table S2). For encrusting colonies, extension was determined along two growth axis: radial (empty circles) and vertical (full circles). Differences between measured and published rates are non-significant (ns, unpaired t tests $p \geq 0.05$, details Table S2) for all species/genera except *Porites lobata* ($*t = 2.07$, $p = 0.042$). Number of colonies (Chagos, red) or studies (published rates, blue) are indicated in brackets above each average

models was fast and easy through automatic marker detection, displaying error distances of usually ≤ 0.1 mm and maximally 0.5 mm. In some instances, the reference scale was moved during image acquisition, resulting in a blurred or uncomplete reference scale. Nevertheless, scaling was possible for each of these models by manually placing markers along well-depicted parts of the reference scale or on the colony tags.

The precision of model construction was assessed by aligning six subset models to the original 3D model. The average (\pm SD) distance of subset models to the original model at any point of the cloud was 0.20 ± 0.01 mm for branching/corymbose, 0.18 ± 0.03 mm for massive and 0.14 ± 0.03 mm for encrusting colonies. Over 95% of the points in subset models were $< 0.58 \pm 0.04$ mm (branching/corymbose), 0.43 ± 0.09 mm (massive) or 0.29 ± 0.08 mm (encrusting) distant from the original model. Given that the growth rates we have measured are at least an order of magnitude larger than these errors, we consider the precision of the 3D models to be fully sufficient for measuring annual colony extension rates.

3.3 | Measurement of coral growth rates

Repeated ($n = 6$) alignment of colony models and measurements of growth rates resulted in standard deviations of < 1 mm for extension rates of all morphological growth forms (0.94 mm for branching/corymbose, 0.85 mm for massive and 0.50–0.66 mm for encrusting colonies). These standard deviations are two to seven times smaller than within-colony growth variations and represent 5%–7% (point–point distances, cm range) and 14%–15% (average point cloud distances, mm range) of the actual measured growth rates (i.e. CV). The low variations in measurements confirm that the proposed workflow is suitable to measure annual coral extension rates in the range of few mm to several cm.

3.4 | Coral growth rates

Figure 3 and Table S2 present annual coral growth rates measured at two fore-reef sites in the Chagos Archipelago using the described workflow. To our knowledge, these are the first growth rates published for this region except for *P. lobata* (Leupold, Pfeiffer, Garbe-Schönberg, & Sheppard, 2019). Measured growth rates for branching and massive corals are similar to published rates for the same species or genera in the Indo-Pacific (unpaired t tests $p \geq 0.05$, statistical details and compared studies in Table S2), except for *P. lobata* ($t_{2,67} = 2.07$, $p = 0.042$). For encrusting corals, the comparison to published rates emphasizes the importance of differentiating between radial and vertical growth. Growth rates for *Montipora* spp. in published studies were measured from changes in diameter or distance between external growth ridges (Edmondson, 1929; Jokiel & Tyler, 1992; Ma, 1958; Stimson, 1985) and therefore represent radial extension rates. Previously published rates for *Leptastrea purpurea* and *Pavona varians* were, in contrast, determined from Alizarin staining (Guzman & Cortes, 1989; Manzello, 2010; Morgan & Kench, 2012) and therefore represent vertical extension rates, reflected in the similarity to rates measured in this study (unpaired t tests $p \geq 0.05$, statistical details in Table S2).

4 | DISCUSSION

In this study, we demonstrate that photogrammetry techniques in combination with 3D manipulation software provide a quick, easy and non-invasive method to obtain coral colony growth rates for a variety of morphological growth forms using minimal equipment. Following the described workflow we measured annual skeletal extension rates for dominant coral genera in the remote

Chagos Archipelago, including for species without any prior data on growth.

4.1 | Image acquisition

The proposed approach was optimized for working in a remote field location with the goal of conducting rapid surveys of many coral colonies with minimal equipment. We showed that the quality of images taken with a modern compact camera allows detailed 3D model construction for a range of colony types, although it has been suggested that single lens reflex cameras are preferable for image analysis due to their large sensors which provide better light sensitivity (Burns et al., 2015a). Image acquisition can be compounded by difficulties inherited by underwater photography such as water movement, turbidity, light intensity changes and limited time due to diving restrictions (Bowens, 2008; Lavy et al., 2015). In this study, water clarity was excellent and working depths of 8–10 m created a relatively constant light environment. Considerable experience in diving and the use of weights on the reference bar solved problems associated with swell and wave movements. We recommend that users pay particular attention to obtaining high-quality, high-resolution photographs and that too many rather than too few are taken. If necessary, image contrast or lighting should be improved in photo processing software before uploading to the SfM software.

The process of feature matching within the SfM software is particularly sensitive to non-static scenes and anything that moves may increase the noise or prevent automatic feature matching (McCarthy & Benjamin, 2014). All images should therefore be carefully inspected and photographs with disrupting elements (fish, hands or diver in image) deleted before camera alignment. Study sites with a high cover of moving soft corals, sea fans or seaweed in close proximity to pictured coral colonies, as for instance often present in the Caribbean, may require additional steps of either removal or temporal immobilization of moving objects prior to image acquisition (bearing in mind the ecological impact) or masking all pictures before model construction (this involves considerable effort), which forces the program to ignore points beside the actual coral colony. This has not been necessary at our sites.

4.2 | 3D model construction

Model construction was achieved in high detail for each coral colony. Dense point clouds of branching corals sometimes displayed gaps between branches, as crevices can fail to be represented due to occlusions and poor illumination (Gutiérrez-Heredia et al., 2016; Lavy et al., 2015). However, as the measurements for linear growth estimates are taken at the well-depicted branch tips, this is not as relevant as it would be for surface or volume estimates, when poorly represented areas are automatically smoothed over during mesh generation.

Accuracy of 3D model construction (i.e. closeness to true colony dimensions) was not estimated in this study, as laser scanning of our

study objects, which usually serves as ground-truth, was not feasible. A comparable study on branching coral skeletons has shown that 77% of points in photogrammetric models were located within 0.3 mm and 90% within 1 mm of the ground-truth laser scan, with largest errors at branch bases (McKinnon, He, Upcroft, & Smith, 2011). These small errors suggest that model construction will not confound accurate detection of growth rates in the range of mm to cm, especially because these are measured at the upper colony surfaces where errors are smallest.

Precision of 3D model construction (i.e. reproducibility of the same result) obtained in this study was excellent for all growth forms, with errors similar to or lower than in comparable studies (Figueira et al., 2015: 1.7–5.8 mm for different morphological growth forms, Ferrari et al., 2017: 1.0 ± 1.2 mm for tabular colonies).

4.3 | Measurement of coral growth rates

Despite manual alignment, clipping and point–point distance marker placement, which are all prone to introduce variation, the standard deviations of repeated growth rate measurements in this study were very small. Calculated CV are similar to previously determined CVs for rugosity (1.1%–10.2%; Figueira et al., 2015), yet higher than those for surface area and volume (1.5% and 2%, respectively; Ferrari et al., 2017), as the latter typically have higher mean values than rugosity or extension rates. Given that the variation introduced by repeated alignment and measurements was smaller than within-colony variation in growth, we are confident that this method accurately detects extensions rates in the range of few mm to several cm. However, to ensure accurate detection of extension rates for very slow-growing coral colonies, we suggest to allow 2–3 years between image acquisitions if growth is likely to be <2–3 mm/year.

Except for the potential cloud alignment error, similar variation would occur from repeated measurements of stained and slabbed corals, where skeletal extension is measured from the top of the stain line to the colony periphery (e.g. Morgan & Kench, 2012). In general, our approach of measuring distances between the colony surfaces compares more directly to Alizarin staining than to morphometric approaches, which quantify differences in colony diameter, height or planar area over time (e.g. Anderson et al., 2015; Stimson, 1985). Taking similar linear measurements from 3D models would certainly be possible, but would fail to quantify growth along all axes of linear extension or to reveal effects of localized increased growth or injuries (Pratchett et al., 2015). Additionally, as the base of the colony or a branch is often difficult to define, comparison of heights or lengths over subsequent years could introduce a considerable error.

4.4 | Coral growth rates

The proposed method is applicable to a range of different coral species and growth forms and is unrestricted by colony size, although larger colonies require more pictures and processing time. The

method works very well for encrusting coral species, for which coring and x-radiography is not an appropriate method and which have therefore been underrepresented in previous studies (Pratchett et al., 2015). The location of colony clearly plays a role in image acquisition, with colonies hidden in crevices or the understorey of reef formations difficult to photograph. Restrictions are also apparent for coral genera with very fleshy polyps, vesicles or tentacles (e.g. *Lobophyllia*, *Symphyllia*, *Plerogyra*, *Euphyllia*) as the expansion of polyps can be different over the years prohibiting accurate distance measurements between skeletons.

A direct comparison to growth rates obtained using traditional invasive methods was not possible due to working in a strict nature reserve. However, based on the assumption that photogrammetry accurately represents coral colony dimensions (e.g. Figueira et al., 2015; Gutiérrez-Heredia et al., 2015; McKinnon et al., 2011), and due to the fact that growth directions that are measured are the same as in traditional methods (i.e. linear distance between branch tips or colony surfaces for branching/corymbose and massive/encrusting colonies, respectively), we argue that the photogrammetry method produces estimates comparable to Alizarin staining or coring. This is supported by the fact that measured extension rates in the Chagos Archipelago are similar to published growth rates from across the Indo-Pacific. Significantly lower rates for *P. lobata*, and slightly lower than average growth rates for *Acropora* spp. and *A. myriophthalma* at the study site possibly reflect relatively small colony size and prolonged physiological stress after the extensive recent bleaching event in 2015–2016 (Head et al., 2019; Sheppard et al., 2017). Supportively, almost identical average growth rates of 5.25 mm/year have been measured for *Porites* corals in the Chagos Archipelago during years of high water temperatures and localized coral bleaching (Leupold et al., 2019).

For encrusting coral species, the comparison with published rates emphasizes the importance of clearly distinguishing between radial and vertical growth, both of which are reported alongside each other as annual extension rate in review papers (Pratchett et al., 2015) and databases such as the Coral Trait Database (<https://coraltraits.org/>) (Madin et al., 2016) although their magnitudes may differ substantially. As an example, calcification calculations from benthic surveys (e.g. *ReefBudget* method) presently assume that published growth rates represent radial extension rates, and factor for an additional vertical extension of 10% of the radial extension. This results in underestimations of real annual calcification if published rates are in fact vertical extension rates. The approach proposed here provides a tool for addressing this gap.

4.5 | Impact and future outlook

Extension rates are an essential metric for the quantification of coral and reef calcification, and data for many species and genera are urgently needed for a range of locations and environmental conditions (Lange et al., 2020). Ongoing changes in environmental conditions due to climate change are expected to have generally negative

consequences on coral growth, a problem for potential reef growth further exacerbated by shifts in community structure towards relatively slow-growing species (Pratchett et al., 2015). Therefore, the development of non-invasive and low-cost methods to determine growth rates and other metrics for a range of coral species and growth forms is crucial (Bythell et al., 2001; Veal, Holmes, Nunez, Hoegh-Guldberg, & Osborn, 2010). Photogrammetry and 3D model construction provides a permanent record of the coral colony and enables repeatable measurements of rugosity, surface area and volume (e.g. Burns et al., 2015b; Bythell et al., 2001; Cocito et al., 2003; Courtney et al., 2007; Ferrari et al., 2017; Figueira et al., 2015; Lavy et al., 2015). Here we present a method that further enables measurements of annual extension rates and morphological changes by monitoring 3D models of coral colonies over time. The simplicity of the presented workflow supports its repeatability and permits non-specialists to learn photogrammetry with the goal of obtaining linear coral growth rates. In the future, similar workflows will hopefully allow additional growth metrics, such as volume and complexity changes over time, to be explored. All of these metrics are important for understanding the functional consequences of ongoing community changes in coral reefs and for determining how coral reefs will respond to exponentially increasing global stressors, such as climate change and ocean acidification (Goatley & Bellwood, 2011; Graham & Nash, 2013).

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AUTHORS' CONTRIBUTIONS

I.D.L. and C.T.P. conceived the ideas and collected the data; I.D.L. designed the methodology, analysed the data and led the writing of the manuscript; C.T.P. contributed critically to the draft and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Details on 3D models and raw data on growth measurements are available through the Open Research Exeter (ORE) repository at <https://doi.org/10.24378/exe.2243> (Lange & Perry, 2020). Video tutorials guiding through the workflows are available at the MethodsEcolEvol YouTube channel. Part 1: 3D model construction <https://youtu.be/FxMwujCJEI4>, Part 2: Growth measurements <https://youtu.be/BqA645VwJjM>.

ORCID

Ines D. Lange  <https://orcid.org/0000-0001-9888-2694>
Chris T. Perry  <https://orcid.org/0000-0001-9398-2418>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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