

A peer-reviewed version of this preprint was published in PeerJ on 6 February 2018.

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House JE, Brambilla V, Bidaut LM, Christie AP, Pizarro O, Madin JS, Dornelas M. 2018. Moving to 3D: relationships between coral planar area, surface area and volume. PeerJ 6:e4280
<https://doi.org/10.7717/peerj.4280>

1 **Moving to 3D: relationships between coral planar** 2 **area, surface area and volume**

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Abstract

Coral reefs are a valuable and vulnerable marine ecosystem. The structure of coral reefs influences their health and ability to fulfill ecosystem functions and services. However, monitoring reef corals largely relies on 1D or 2D estimates of coral cover and abundance that overlook change in ecologically significant aspects of the reefs because they do not incorporate vertical or volumetric information. This study explores the relationship between 2D and 3D metrics of coral size. We show that surface area and volume scale consistently with planar area, albeit with morphotype specific conversion parameters. We use a photogrammetric approach using open-source software to estimate the ability of photogrammetry to provide measurement estimates of corals in 3D. Technological developments have made photogrammetry a valid and practical technique for studying coral reefs. We anticipate that these techniques for moving coral research from 2D into 3D will facilitate answering ecological questions by incorporating the 3rd dimension into monitoring.

Introduction

Coral reefs are one of the most diverse and more highly threatened ecosystems on the planet. Monitoring how corals respond to the vast array of threats and disturbances that they face (Hoegh-Guldberg 1999; Hughes et al. 2003) is a crucial part of management and conservation. The challenge is understanding how best to quantify change in the corals themselves, and the wide range of ecosystem goods, functions and services which they provide (Moberg & Folke 1999). Here, we develop a methodology to allow incorporating 3D metrics into coral reef monitoring.

The proportion of live coral cover on a reef is one of the most widely used metrics of reef health (Leujak & Ormond 2007). It is used as a proxy for coral biomass and reef building ability, and virtually all of the techniques used to assess this involve linear or horizontal planar estimates (Hill & Wilkinson 2004; Leujak & Ormond 2007; Vroom 2010). However, it is increasingly clear that 2D estimates of coral cover alone are not always the best indicator of reef health (Balmford et al. 2003), and that a reef's 3D structure provides valuable information about reef health (Goatley & Bellwood 2011). 3D surface area and volume can provide more proximate metrics of coral abundance,

and thus allow capturing changes to the reef more accurately. In this work, we quantify the relationship between 2D metrics of coral cover and 3D metrics, and how this varies for different colony morphotypes. We also outline a technique for generating 3D models of corals and for measuring colony surface area and volume using photogrammetry based on open-source software. Our goal is to improve how we quantify change in coral reefs.

A variety of techniques are used for research and monitoring of coral reefs, most of which focus on 2D (planar) measurements of colony size or coral cover (Gardner et al. 2003; Sweatman et al. 2011; Bruno & Selig 2007). The ubiquity of 2D representations of coral reefs enables standardization between and within different monitoring programmes, allows them to be carried out on a range of spatial scales, and facilitates the fast collection of estimates of abundance and cover (Hill & Wilkinson 2004; Shuman & Ambrose 2003; Booth et al. 2008). Our study uses planar area as an example of this type of 2D metric. Throughout this paper, we use the term “planar total surface area”, abbreviated to “PL TSA”, to refer to the projected surface area of a single plane, bird’s-eye view of a coral specimen. Despite the widespread use of 2D methods, there is increasing recognition of the limitations of these approaches. For example, overlooking the vertical aspect of coral reefs results in an inability to fully assess their structural complexity and measure ecologically significant changes (Goatley & Bellwood 2011). Furthermore, there is growing evidence that the role of different morphotypes should be considered when assessing coral reef health and structure (Burns et al. 2015).

Coral morphotypes differ in their demographic rates and play different roles in the ecosystem. For example, morphotypes differ in their response to disturbance (Madin & Connolly 2006) and in their mortality schedule (Madin et al. 2014). Moreover, changes in the relative abundance of different morphotypes of corals may influence the provision of ecosystem services and biodiversity (Alvarez-Filip et al. 2011; Burns et al. 2015). Using 3D approaches to better understand the structure and function of different coral morphotypes, as well as their vulnerability to disturbance, is an important step towards elucidating the goods and services that reefs provide. This

study will contribute to this effort by exploring whether 3D metrics can be inferred from 2D estimates and colony morphotype.

Surface area and volume are two 3D metrics particularly relevant for estimating the ecosystem services and functions performed by corals. Specifically, these two variables are critical for corals' reef building capability, which modulates many coral reef ecosystem services (Moberg & Folke 1999). For example, the size and structure of coral reefs provide effective coastal defenses (Ferrario et al. 2014) and support reef fish assemblages (Graham et al. 2006). As such, metrics such as biomass, growth rate and production of carbonate, which are all related to volume (Cocito et al. 2003), should be considered. Other ecologically significant metrics, such as filtering capability and biomass of tissue, are related to colony surface area (Cocito et al. 2003). The importance of quantifying the reef in 3D also relates to the overall structure of the reef. The structural complexity of the reef influences the biodiversity of reef fish (Graham et al. 2006), and the loss of this complexity is a major consequence of disturbance that leads to the degradation of biogenic habitats (Airoidi et al. 2008).

There is increasing recognition of the need to develop better techniques for measuring coral colonies and reefs in 3D (Burns et al. 2015; Burns et al. 2015; Goatley & Bellwood 2011; Courtney et al. 2007). However, establishing these methods has traditionally proved to be problematic. In comparison to 2D techniques, methods that collect 3D data are costly, time consuming and difficult to carry out (Goatley & Bellwood 2011; Laforsch et al. 2008; Naumann et al. 2009), in addition to often being invasive or imprecise (Naumann et al. 2009).

Photogrammetry, the science of measuring objects by piecing multiple photographs of them together in order to create digital models, provides an efficient approach to estimating coral surface area and volume. It is not invasive, but had until recently proved to be prohibitively time-consuming, costly or inaccurate (Courtney et al. 2007; Kruszyński et al. 2007). However, there is increasing success with this method following recent technological developments (Burns et al. 2015). The main improvements are the advent of Structure-from-Motion (SfM) photogrammetric

techniques, which no longer require specification of known 3D locations prior to calculating camera positions (Westoby et al. 2012), and the ability to automatically match corresponding points across images. SfM approaches address many of the historical limits of photogrammetry, and are particularly useful for marine ecological research having been successfully applied underwater by divers (Burns et al. 2015; McCarthy & Benjamin 2014). An additional benefit of current SfM technology is the increasing availability of open-source software options for applying this technique (Falkingham 2012), even though this has not yet been employed for studying coral colonies.

This paper addresses two aspects of moving from measuring corals in 2D to 3D. First, we ask whether we can predict 3D metrics of coral abundance from 2D metrics. We hypothesize that coral morphotypes differ in their scaling relationships between 2D and 3D metrics. The second aim of our study is to measure corals in 3D directly. We determine whether photogrammetry provides accurate estimates of the surface area and volume of coral skeletons, and ask whether there are biases in this technique associated to different morphotypes.

In order to capture 2D and 3D data, we used three methods for measuring coral skeletons, as outlined in Figure 1. First, we measured PL TSA from birds-eye-view photographs of the colonies with a scale. Computed tomography (CT) scans and photogrammetry (PH) were used on the same specimens to produce information about 3D metrics, namely colony total surface area and volume (hereafter abbreviated to CT TSA, CT Vol, PH TSA and PH Vol respectively). In order to explore the most biologically useful information, the surface area of the colony that had been covered in corallites was also measured. This “live” surface area was produced from the results of all three methods; planar photography (PL LSA), photogrammetry (PH LSA) and CT scanning (CT LSA). Due to its high resolution, accuracy and inherent 3D nature, the data collected using CT scans was used as a baseline (Veal et al. 2010) with which to compare the other two methods. Using this suite of techniques enabled us to examine the relationship between 2D and 3D metrics, as well as address some of the difficulties with collecting 3D data.

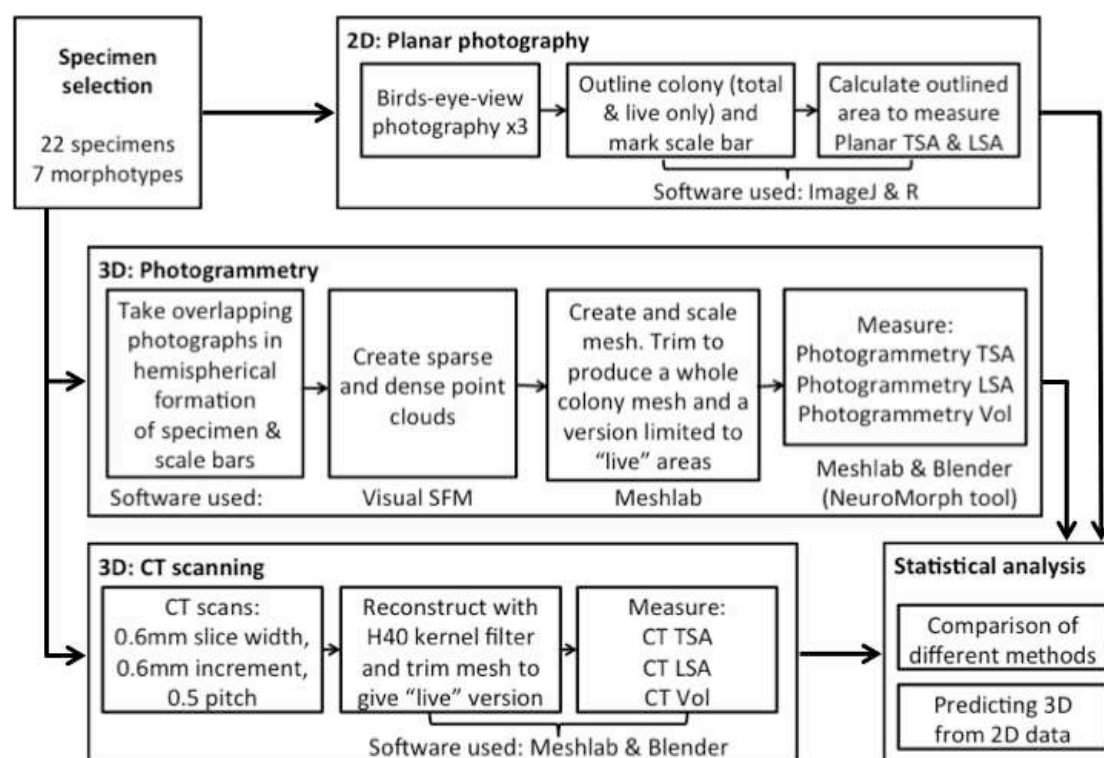


Figure 1: The complete process used to measure TSA, LSA and volume in 2D and 3D for each specimen, including the measurement techniques and software used.

We selected coral skeletons from the collection at the Bell Pettigrew Museum, University of St Andrews with replicate specimens across different morphotypes and sizes. Each specimen was identified to species, and their morphotype was classified as branching, encrusting or massive. The resulting selection of coral skeletons includes 22 specimens described in Table S2.

Photography and planar surface measurement

Coral specimens were photographed from above with a 10cm x 10cm chessboard-style calibration pattern using a digital camera (Nikon D40, 18-55mm lens) as seen in Figure 2a. The specimens were positioned in such a way as to replicate their natural orientation on the reef as much as possible. Each coral skeleton was photographed three times to quantify and minimize the effect of measurement error. The three sets of photographs were not taken consecutively, and the specimens were repositioned for each set so as to minimize bias resulting from a particular position or camera angle.

All of the photos were then processed using the image analysis software ImageJ (Rasband 2014). For each step the image was zoomed in as much as possible, whilst keeping the entire colony and scale completely in view. A graphics tablet (medium Intuos, Wacom) was used to draw the outline of the whole coral colony and the areas that consisted of corallites. These contours were saved as a series of XY coordinates. The corners of the calibration pattern were also marked and saved as coordinates, in order to convert the pixel measurements into length (cm). After the necessary information had been extracted from the images and converted into XY coordinates, R (R Core Team, 2013) was used to calculate PL TSA and PL LSA from the relevant outlines (in square centimetres), using methodology and code from Madin et al. (2014).

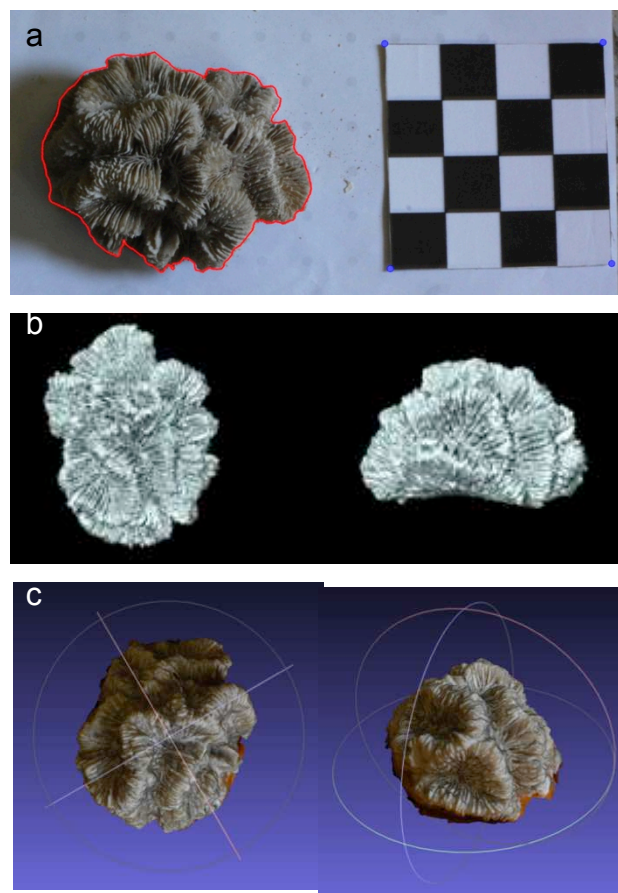
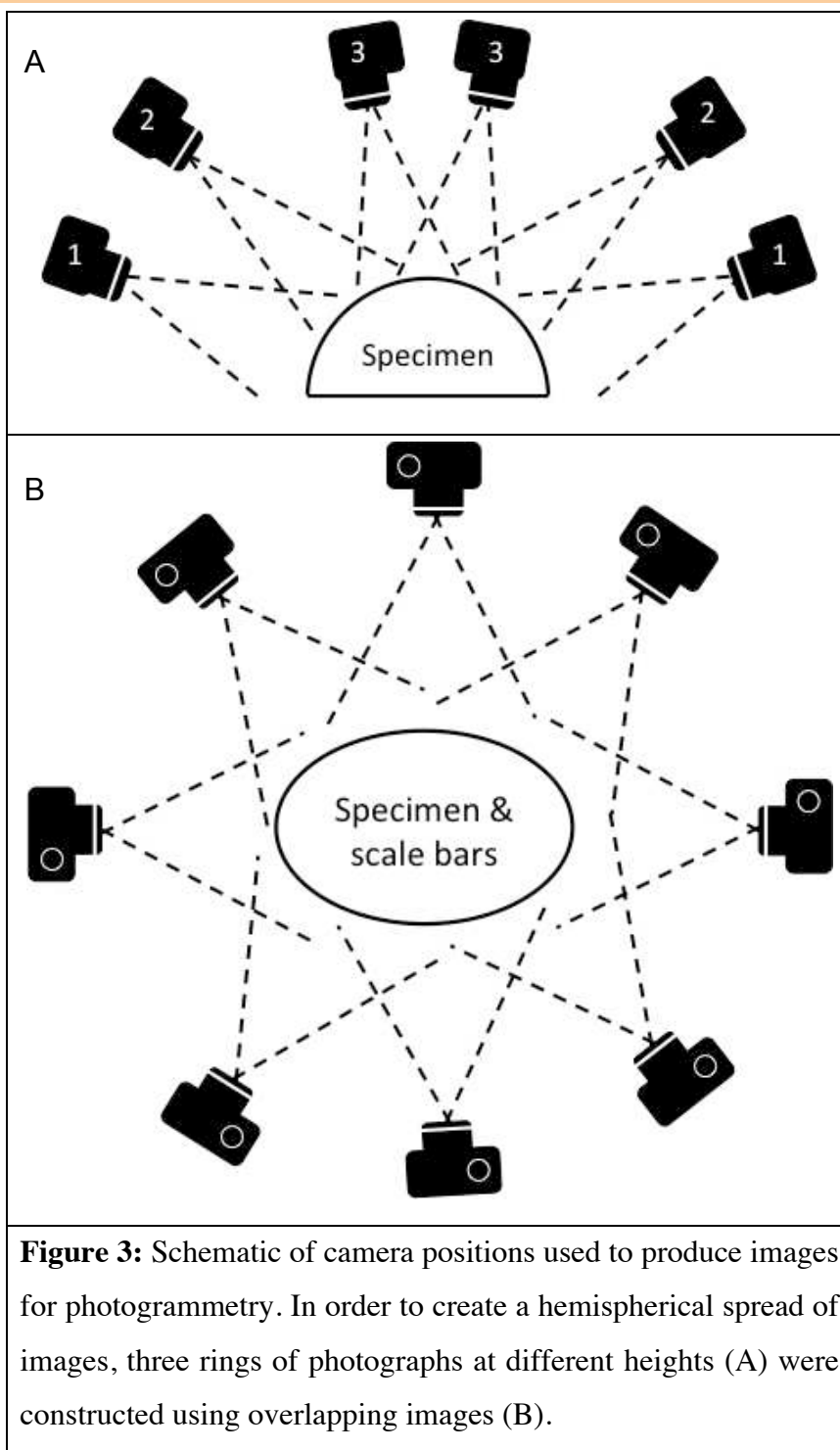


Figure 2: Example of a) planar photography of a coral colony having been outlined and scaled using ImageJ and R, b) the surface generated using CT scanning, and c) the equivalent surface generated using SfM photogrammetry.

Photogrammetry

Photographs were taken using the same digital camera and a static off-camera flash set-up as for the planar photography. The specimens were placed on a table with four 10cm scale bars positioned in a square on the surface around them. Photographs were taken with the camera positioned at various locations on a virtual hemispherical dome above the specimen, as illustrated in Figure 3. This created a hemisphere-like spread of images of the specimen from various viewpoints. Significant overlap between images is needed in order to automatically identify shared points that can then be reconstructed as 3D coordinates. The number of views varied from 39 to 164 based on the size and complexity of the specimen. Specimens with occluding structures require the highest number of photographs in order to produce the necessary coverage.



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206 The open-source software package Visual SFM (Wu, 2011; Wu et al 2011, Wu 2007)

207 was used to create a point mesh from the overlapping images by determining camera

208 positions and generating a sparse point cloud. This was then followed by dense

209 reconstruction using an additional package for Clustering views for Multi-View

Stereo (CMVS) and Patch-based Multi-View Stereo (PMVS v2) (Furukawa & Curless 2010; Furukawa & Ponce 2010).

The dense point cloud was then imported into MeshLab (Cignoni et al. 2008) and spurious points were removed. A surface layer was created from the point mesh using Poisson Surface Reconstruction. The scale bars were used to determine the coefficient needed to convert the mesh from pixels to absolute units, in this case millimetres. The model was then trimmed to remove the table and non-coral objects, as shown in Figure 2c. The volume and surface area for these meshes were calculated using Blender (www.blender.org) with the NeuroMorph plug-in (Jorstad et al, 2014), thus producing PH TSA and PH Vol. Since the specimens had sections of their surface that had not been the site of living corallites, Meshlab was used to remove these areas from the models. The PH LSAs were then calculated because this variable is more ecologically meaningful than the specimen's entire surface area. To reduce the influence of any measurement errors, three models were produced for each specimen using different sets of images.

Computed tomography and 3D surface measurement

The coral specimens were scanned in air using a medical CT scanner, Siemens Biograph mCT-128. The protocol was based upon that of Naumann et al (2009). The images were acquired at 0.6mm slice width, 0.6mm increments and 0.5 pitch. Xray tube voltage was 120kV with effective mAs of 341 (automatically varied) and a field of view that was adapted to the size of each specimen. Three back-projection reconstructions were then produced for each colony from the spiral mode acquisition dataset, with sharp, medium and smooth kernel filters (H30, H40 & H50). Of these, the H40 reconstruction was selected for subsequent calculations because it gave the best compromise between high spatial resolution and low image noise. Using the corresponding 3D reconstructions of the coral colonies (example shown in Figure 2b), measurements of CT TSA and CT Vol were generated in square and cubic millimeters, respectively. As with the meshes produced through photogrammetry, Meshlab was used to trim away areas without corallites, and the CT LSA was then measured in Blender through the NeuroMorph toolset. Examples of CT and PH models are included in Figures 2 and S1.

Statistical analysis

We used CT scan metrics of size as our benchmark (i.e. the response variables in our models), as these are recognised as the most accurate way of measuring corals in 3D (Veal et al. 2010). To address the first aim of testing whether 3D metrics can be inferred from 2D metrics of size, we fitted Ordinary Least Squares linear models predicting CT TSA, CT LSA, and CT Vol from PL TSA or PL LSA and morphotype. Models with and without morphotype were compared using the Akaike Information Criterion (AIC) to assess whether differences in scaling among morphotypes affect the compromise between goodness of fit and model complexity. In addition, Adjusted R^2 's were used to assess the predictive ability of the different models.

Our second aim was to assess the ability of photogrammetry to estimate 3D metrics of coral size. As per the previous aim, we fitted Ordinary Least Squares linear models predicting CT TSA, CT LSA, and CT Vol from PH TSA, PH LSA, or PH Vol and morphotype. We performed model selection as above to investigate morphotype associated bias in the estimates. Finally, we compared Adjusted R^2 's of these models with those of a model with slope 1 and intercept 0.

These models used single measurements for CT TSA and CT Vol, but mean values were used for each specimen's PL TSA/LSA, PH TSA/LSA and PH Vol. All variables were log transformed to improve symmetry in the distribution of the residuals and to linearize the relationship between area (mm^2) and volume (mm^3). Statistical analysis was carried out in R (R Core Team, 2013).

Results

PL TSA and PL LSA can be used to infer accurate estimates of CT TSA, CT LSA and CT Vol. As predicted, 3D surface area is higher than 2D area, however the former scales tightly with the latter (Figure 4 A, B). Also, 3D volume is lower than the volume of a cube with a similar area, but again the scaling relationship is remarkably tight (Figure 4 C). The proportion of variance explained by the best model for each of these variables range between 0.81 and 0.90 (Table 1). Model selection suggests that morphotypes differ in their scaling relationship only for CT LSA (Figure 4, B, Table 2). For both CT TSA and CT Vol the slope in the best model is constant across morphotypes, although for CT Vol morphotypes differ in their intercept (Figure 4, Table 2).

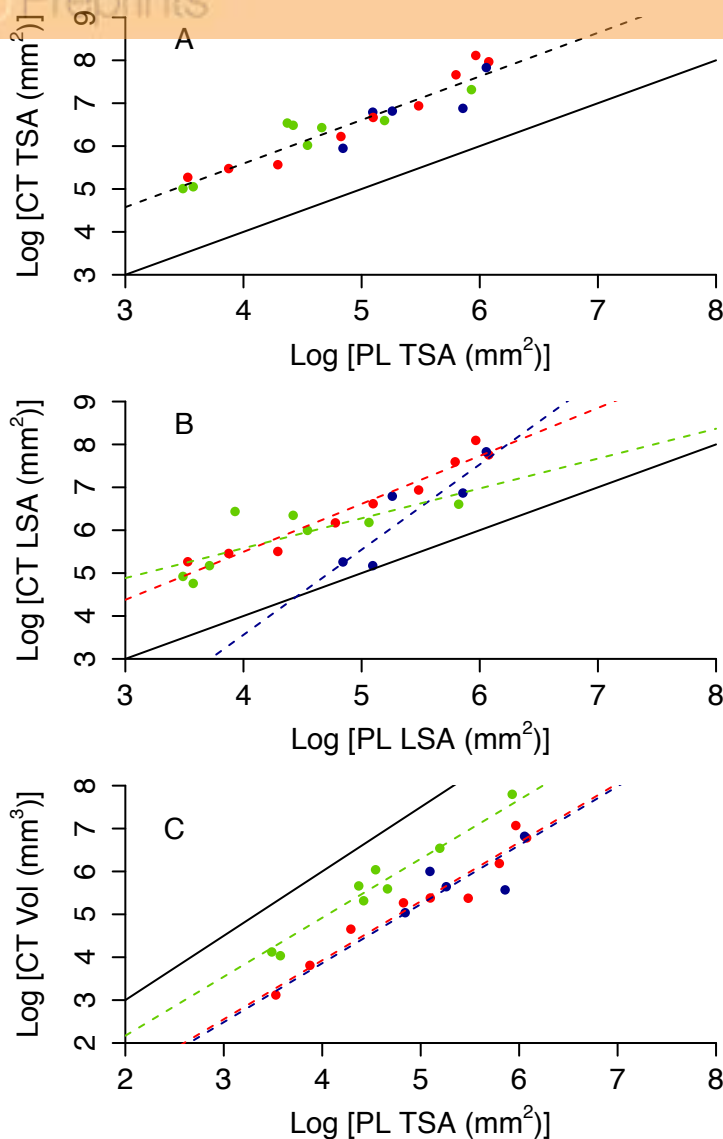


Figure 4. 3D metrics of size as a function of 2D metrics. Red circles represent branching colonies, blue encrusting and green massive. The solid lines represent a model where 3D metric is equal to the 2D metric (A,B) or the relationship predict for a cube (C). Dashed lines represent predictions for the best model, with different colours for different morphotypes as per the symbols when morphotypes differ in parameter estimates.

Table 1: Predictive accuracy of planar total or live surface area (PL TSA/LSA) when used alone and with morphotype to estimate CT TSA, CT LSA, CT Vol, respectively. Adjusted R^2 , p-value and Akaike's Information Criterion (AIC) are given to 2 significant figures.

| Response | Predictor(s) | Adjusted R^2 | p | AIC |
|----------|---------------------|----------------|------------------------|-------|
| CT TSA | PL TSA | 0.88 | 5.40×10^{-11} | 15.03 |
| | PL TSA + morphotype | 0.88 | 2.55×10^{-8} | 16.01 |
| | PL TSA * morphotype | 0.88 | 7.22×10^{-8} | 18.07 |
| CT LSA | PL LSA | 0.70 | 3.65×10^{-7} | 39.67 |
| | PL LSA + morphotype | 0.745 | 3.55×10^{-6} | 37.86 |
| | PL LSA * morphotype | 0.81 | 3.31×10^{-6} | 32.88 |
| CT Vol | PL TSA | 0.73 | 2.42×10^{-7} | 42.85 |
| | PL TSA + morphotype | 0.90 | 9.76×10^{-10} | 23.14 |
| | PL TSA * morphotype | 0.90 | 1.79×10^{-8} | 23.67 |

Table 2: Parameter estimates for best models to predict CT TSA, CT LSA and CT Vol from PL TSA or LSA to for coral colonies of a range of morphotypes. All variables in the regression models were log transformed hence a general predictive function is $C = e^{\alpha + \beta \ln(P)}$, where C is CT TSA, CT LSA or CT Vol and P is PL TSA, or PL LSA as per Figure 1.

| Response | morphotype | α (CI) | B (CI) |
|----------|------------|----------------------------|-------------------------|
| CT TSA | all | 1.528 (0.692 to 2.365) | 1.016 (0.849 to 1.184) |
| CT LSA | branching | 1.024 (-0.749 to 2.797) | 1.118 (0.768 to 1.468) |
| | encrusting | -4.387 (-10.597 to -0.225) | 1.987 (-0.093 to 1.830) |
| | massive | 2.796 (-0.812 to 4.355) | 0.696 (-0.975 to 0.132) |
| CT Vol | branching | -1.570 (-2.671 to -0.469) | 1.375 (1.160 to 1.589) |
| | encrusting | -1.638 (-0.501 to 0.364) | |
| | massive | -0.579 (0.610 to 1.373) | |

303
 304 Photogrammetry provides fairly accurate estimates of the surface area and volume of
 305 coral skeletons: R^2 of best fit models range between 0.70 and 0.97 (Table 3).
 306 However, paired t-tests showed that the techniques for measuring 3D information, CT
 307 scanning and photogrammetry, produced significantly different measurements from
 308 each other for specimen volume ($p=0.0186$), TSA ($p=0.00837$) and LSA ($p=0.00205$).
 309 Photogrammetry generally underestimated TSA and overestimated volume (Figure 5).
 310 Both photogrammetry and planar photography were less accurate at predicting CT
 311 LSA than CT TSA. Model selection does not reveal bias associated to morphotype for
 312 TSA and LSA, as the best model has constant scaling across morphotypes (Figure 5
 313 A, B, Table 3). In contrast, the best model for Vol does include different slopes and
 314 intercepts for different morphotypes, as for massive colonies PH Vol is virtually
 315 identical to CT Vol, but for both encrusting and branching colonies the PH Vol
 316 increasingly overestimates CT Vol as colony sizes increase (Figure 5 C).
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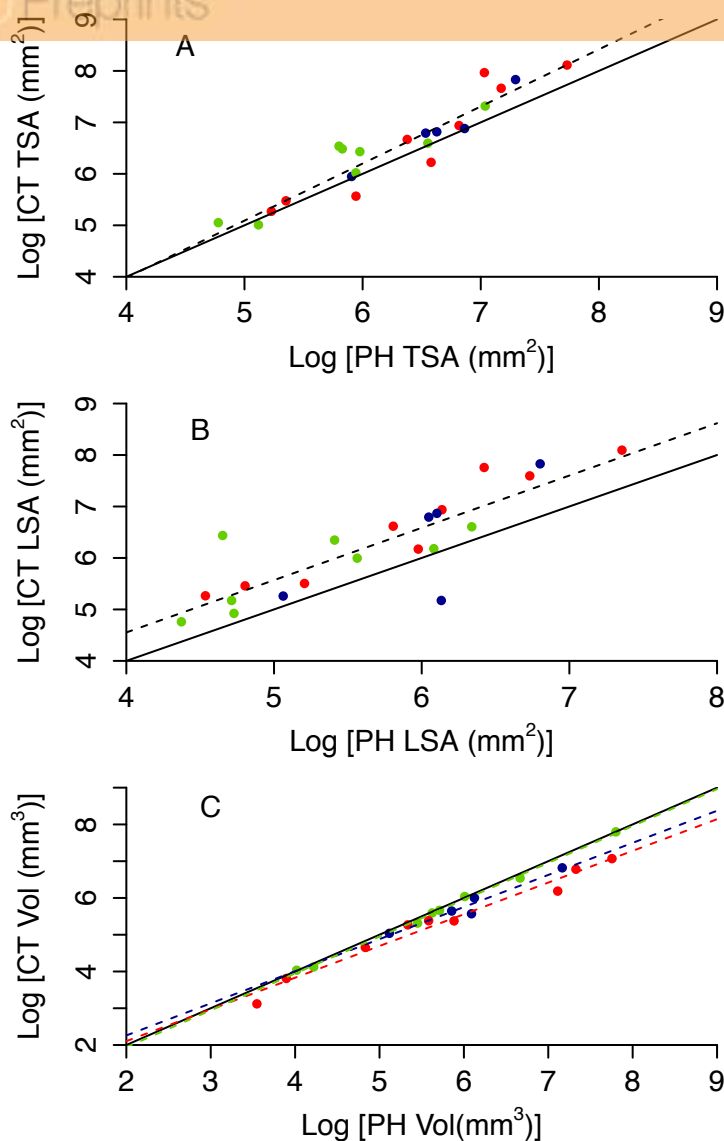


Figure 5. Relationship between CT and PH estimates of colony size. Red circles represent branching colonies, blue encrusting and green massive. The solid lines represent a model where the two metrics are identical. Dashed lines represent predictions for the best model, with different colours for different morphotypes as per the symbols when morphotypes differ in parameter estimates.

Table 3: Predictive accuracy of Photogrammetry total and live surface area, and volume (PH TSA, PH LSA, PH Vol, respectively) when used alone and with morphotype to estimate total and live surface area and volume according to CT scanning (CT TSA, CT LSA, CT Vol, respectively). Adjusted R^2 , p value and Akaike's Information Criterion (AIC) are given to 3 significant figures.

| Response | Predictor(s) | Adjusted R^2 | p | AIC |
|----------|---------------------|----------------|------------------------|--------|
| CT TSA | PH TSA | 0.876 | 9.75×10^{-11} | 16.319 |
| | PH TSA + morphotype | 0.875 | 5.92×10^{-9} | 18.074 |
| | PH TSA * morphotype | 0.868 | 1.84×10^{-7} | 20.686 |
| CT LSA | PH LSA | 0.702 | 3.64×10^{-7} | 39.601 |
| | PH LSA + morphotype | 0.692 | 3.55×10^{-6} | 41.983 |
| | PH LSA * morphotype | 0.690 | 3.31×10^{-6} | 43.560 |
| CT Vol | PH Vol | 0.955 | 1.02×10^{-6} | 3.271 |
| | PH Vol + morphotype | 0.973 | 2.52×10^{-10} | -6.432 |
| | PH Vol * morphotype | 0.976 | 6.45×10^{-9} | -7.847 |

Discussion

We have improved our understanding of the relationship between 2D and 3D metrics of coral colonies size and outlined an approach for converting between the two. Our results support the hypothesis that 3D metrics of size scale consistently with 2D metrics. Moreover, we demonstrated the potential for photogrammetry to predict CT TSA/LSA and CT Vol. Together, our results suggest that 2D data can be converted into more ecologically meaningful 3D metrics, such as colony surface area and volume, when combined with information about colony morphotypes. Measuring corals in 3D on a large scale is thus becoming feasible.

The measurements collected using photogrammetry were found to be significantly different from the results of the CT scans, but were nevertheless excellent predictors when combined with information about the morphotype of the colony. The differences observed are linked to the different resolutions of the two methods (much higher for CT scans, see appendix 2). Lower resolution 3D photogrammetry models cause both the underestimation in surface area and the overestimation in volume. Our study adds to growing evidence that the previously prohibitive aspects of photogrammetry are being overcome by technological improvements (Burns et al. 2015; Falkingham 2012). The possibility of applying this technique using open-source software opens it up to a wider audience. The application of photogrammetry to measuring reef topography (Burns et al. 2015) combined with our detailed modeling of individual coral colonies illustrates the wide range of potential applications this technique can have in monitoring and studying coral reefs and their ecology.

There are costs in time associated to quantifying cover in 3D rather than 2D. We found that photogrammetry was easier to carry out when dealing with less complicated morphotypes, which required less processing time and fewer photographs. Photogrammetry is particularly effective for colonies with simpler structures and few occlusions, and it has been suggested that it could be a valuable technique in areas with a high prevalence of hemispherical colonies, such as the Caribbean (Courtney et al. 2007). In contrast, calculating PL TSA/LSA took less time because it required fewer photographs and less image processing. Although more complicated morphotypes still required more processing than simple colony shapes,

the difference in time and effort was negligible compared to when using photogrammetry. The labour-intensive nature of measuring corals in 3D, despite recent technological developments, does suggest that the option of converting 2D measurements into 3D metrics may provide a useful alternative in cases where conducting monitoring in 3D is not feasible due to the time or costs involved, but 2D measurements alone are not sufficient. There is still scope for further improvements to photogrammetry, as well as other 3D techniques, through technological advances that will lead to their much broader application *in situ*. Future work could focus on optimizing the imaging stage to improve the quality of the reconstructions whilst streamlining the time and effort needed to collect images. For example, determining the best camera position, field of view, number of images and how these might change when applied *in situ* would provide valuable insight. Furthermore, other techniques for measuring in 3D, such as laser scanners or stereo cameras could be considered as they continue to improve alongside the methods used here.

In addition to the consideration of costs, there are data from the past for which we cannot measure surface area and volume in 3D. However, we may still be able to recover an estimate of this information retrospectively by converting historical 2D data into 3D metrics. We have produced empirical formulae that combine PL TSA/LSA and morphotype categories to predict colony TSA/LSA or volume. Importantly, the predictive power of these conversion models is similar to the estimates obtained through photogrammetry. Our results indicate the importance of recording the morphotype of a colony when conducting monitoring, as this trait determines the relationship between some of the 2D and 3D metrics. Increasing the number of specimens for each morphotype and widening the size spectra would further improve these formulae, and it would be valuable also to expand them to additional morphotypes in the future.

Morphotype categories are not always clear-cut and the variability within groups supports the need to move from discrete classifications of morphotypes towards individual level continuous traits that measure colony shape. Moreover, our work suggests that surface area and volume, as well as the ratios between these variables and PL TSA, are potential candidates as useful traits. This shift in focus would also

address the fact that corals can exhibit a high degree of morphological plasticity within species (Todd 2008), with colonies of the same species fulfilling different categories of morphotype. This level of plasticity suggests that when our equations are used in the future they should be applied based on the morphotype observed in the field, rather than one that is based on species identification. This is particularly true because species level identification of corals is difficult.

Improved understanding of the relationship between 2D and 3D parameters for different morphotypes should contribute towards our grasp of the ecological role of different coral morphotypes. We already know that morphotypes respond differently to disturbance (Madin & Connolly 2006) and play different ecological roles (Alvarez-Filip et al. 2011). It has also been suggested that examining the ratio of different coral morphotypes on reefs can give insight into reef health (Edinger & Risk 2000). However, many coral survey techniques entail intrinsic bias and require very large sample sizes to measure changes in the abundance of individual morphotypes (Leujak & Ormond 2007). Our approach can provide a transition between traditional methods and accurate 3D modeling, which will improve our understanding of the contribution of different morphotypes to the services and functions provided by coral reefs. In addition to applying our findings to future research, a significant benefit of using the equations developed herein is that they can be applied to archived images and historical data sets. This will enable data comparisons over as long a timescale as possible, minimising the “shifting baseline” effect (Knowlton & Jackson 2008).

Conclusions

In conclusion, coral colony surface area and volume can be predicted effectively from both PL TSA and morphotype. This development provides a stepping-stone by which we can shift to a more 3D orientated approach to measuring corals and may enable better understanding and exploitation of historical data. Furthermore, photogrammetry clearly contributes towards addressing the question of how best to measure corals because it is a widely accessible, non-invasive and cost effective method for making 3D measurements in-situ. This paper illustrates two specific areas for studying corals in ways that better capture changes amongst corals and the ecological processes

430 associated with them. We hope that these approaches will eventually enable more
431 accurate coral reef monitoring and conservation.

432

433 **Acknowledgements**

434 We thank the curator and staff at the Bell Pettigrew Museum for allowing us use of
435 museum specimens, and the Behaviour and Biodiversity group at University of St
436 Andrews for feedback.

437

438 **Funding**

439 We thank the School of Biology, University of St Andrews for support and funding.
440 MD is grateful for support from the Scottish Funding Council (MASTS -grant
441 reference HR09011).

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