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1 **Moving to 3D: relationships between coral planar**

2 **area, surface area and volume**

3

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16 **Abstract**

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

30

31

32 **Introduction**

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

40

41 The proportion of live coral cover on a reef is one of the most widely used metrics of
42 reef health (Leujak & Ormond 2007). It is used as a proxy for coral biomass and reef
43 building ability, and virtually all of the techniques used to assess this involve linear or
44 horizontal planar estimates (Hill & Wilkinson 2004; Leujak & Ormond 2007; Vroom
45 2010). However, it is increasingly clear that 2D estimates of coral cover alone are not
46 always the best indicator of reef health (Balmford et al. 2003), and that a reef's 3D
47 structure provides valuable information about reef health (Goatley & Bellwood 2011).
48 3D surface area and volume can provide more proximate metrics of coral abundance,

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

55

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

72

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

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

83

84 Surface area and volume are two 3D metrics particularly relevant for estimating the
85 ecosystem services and functions performed by corals. Specifically, these two
86 variables are critical for corals' reef building capability, which modulates many coral
87 reef ecosystem services (Moberg & Folke 1999). For example, the size and structure
88 of coral reefs provide effective coastal defenses (Ferrario et al. 2014) and support reef
89 fish assemblages (Graham et al. 2006). As such, metrics such as biomass, growth rate
90 and production of carbonate, which are all related to volume (Cocito et al. 2003),
91 should be considered. Other ecologically significant metrics, such as filtering
92 capability and biomass of tissue, are related to colony surface area (Cocito et al.
93 2003). The importance of quantifying the reef in 3D also relates to the overall
94 structure of the reef. The structural complexity of the reef influences the biodiversity
95 of reef fish (Graham et al. 2006), and the loss of this complexity is a major
96 consequence of disturbance that leads to the degradation of biogenic habitats (Airoldi
97 et al. 2008).

98

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

106

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

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

123

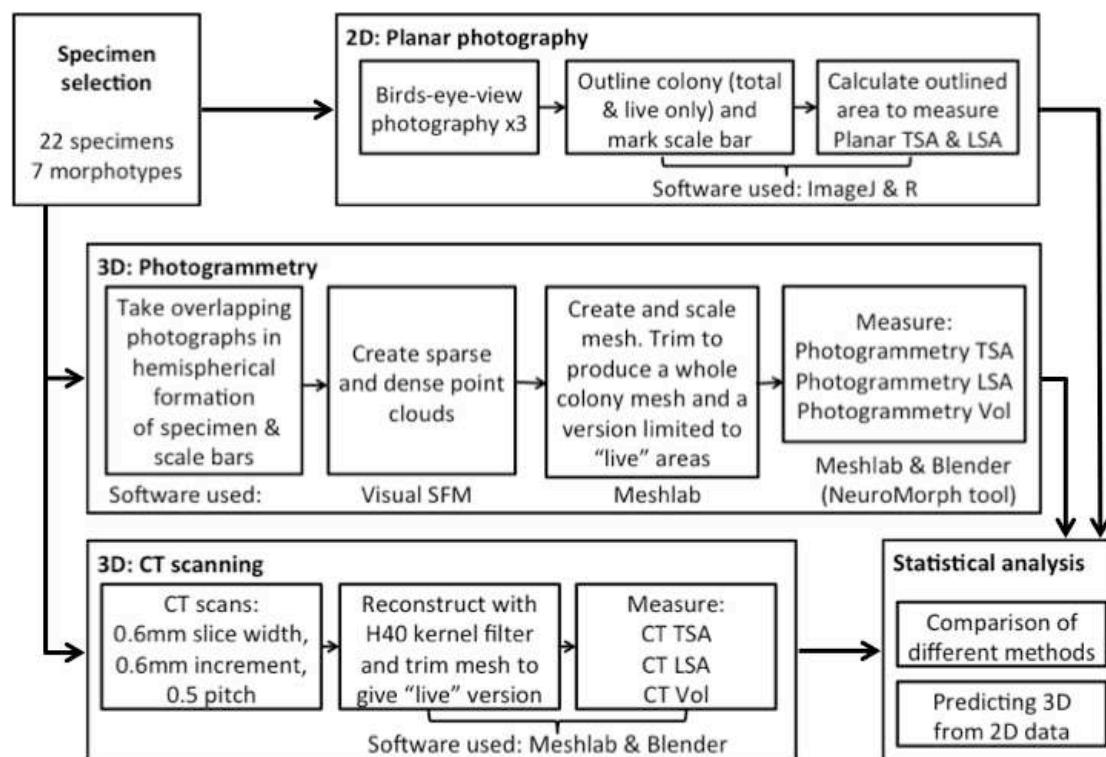
124 This paper addresses two aspects of moving from measuring corals in 2D to 3D. First,
125 we ask whether we can predict 3D metrics of coral abundance from 2D metrics. We
126 hypothesize that coral morphotypes differ in their scaling relationships between 2D
127 and 3D metrics. The second aim of our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

131

133 In order to capture 2D and 3D data, we used three methods for measuring coral
134 skeletons, as outlined in Figure 1. First, we measured PL TSA from birds-eye-view
135 photographs of the colonies with a scale. Computed tomography (CT) scans and
136 photogrammetry (PH) were used on the same specimens to produce information about
137 3D metrics, namely colony total surface area and volume (hereafter abbreviated to CT
138 TSA, CT Vol, PH TSA and PH Vol respectively). In order to explore the most
139 biologically useful information, the surface area of the colony that had been covered
140 in corallites was also measured. This “live” surface area was produced from the
141 results of all three methods; planar photography (PL LSA), photogrammetry (PH
142 LSA) and CT scanning (CT LSA). Due to its high resolution, accuracy and inherent
143 3D nature, the data collected using CT scans was used as a baseline (Veal et al. 2010)
144 with which to compare the other two methods. Using this suite of techniques enabled
145 us to examine the relationship between 2D and 3D metrics, as well as address some of
146 the difficulties with collecting 3D data.

147

148



149

150 **Figure 1:** The complete process used to measure TSA, LSA and volume in 2D and
151 3D for each specimen, including the measurement techniques and software used.

152

153

155 We selected coral skeletons from the collection at the Bell Pettigrew Museum,
156 University of St Andrews with replicate specimens across different morphotypes and
157 sizes. Each specimen was identified to species, and their morphotype was classified as
158 branching, encrusting or massive. The resulting selection of coral skeletons includes
159 22 specimens described in Table S2.

160

161 *Photography and planar surface measurement*

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

169

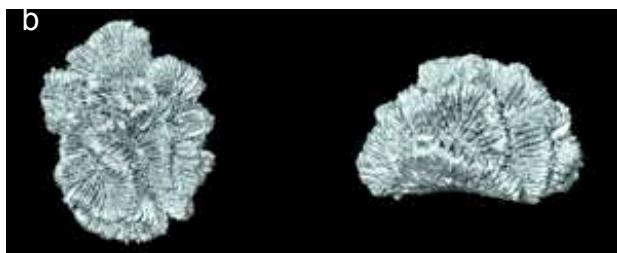
170 All of the photos were then processed using the image analysis software ImageJ
171 (Rasband 2014). For each step the image was zoomed in as much as possible, whilst
172 keeping the entire colony and scale completely in view. A graphics tablet (medium
173 Intuos, Wacom) was used to draw the outline of the whole coral colony and the areas
174 that consisted of corallites. These contours were saved as a series of XY coordinates.
175 The corners of the calibration pattern were also marked and saved as coordinates, in
176 order to convert the pixel measurements into length (cm). After the necessary
177 information had been extracted from the images and converted into XY coordinates,
178 R (R Core Team, 2013) was used to calculate PL TSA and PL LSA from the relevant
179 outlines (in square centimetres), using methodology and code from Madin et al.
180 (2014).

181

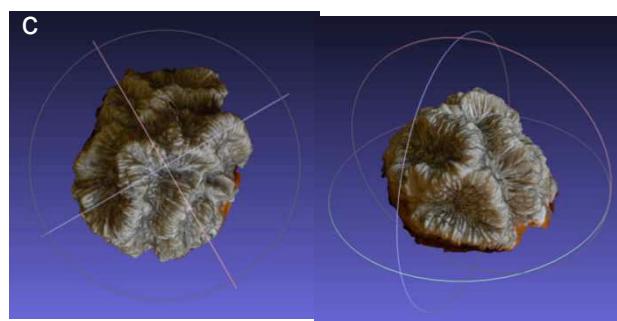
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184



185



186

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

190

191

192 *Photogrammetry*

193 Photographs were taken using the same digital camera and a static off-camera flash
194 set-up as for the planar photography. The specimens were placed on a table with four
195 10cm scale bars positioned in a square on the surface around them. Photographs were
196 taken with the camera positioned at various locations on a virtual hemispherical dome
197 above the specimen, as illustrated in Figure 3. This created a hemisphere-like spread
198 of images of the specimen from various viewpoints. Significant overlap between
199 images is needed in order to automatically identify shared points that can then be
200 reconstructed as 3D coordinates. The number of views varied from 39 to 164 based on
201 the size and complexity of the specimen. Specimens with occluding structures require
202 the highest number of photographs in order to produce the necessary coverage.

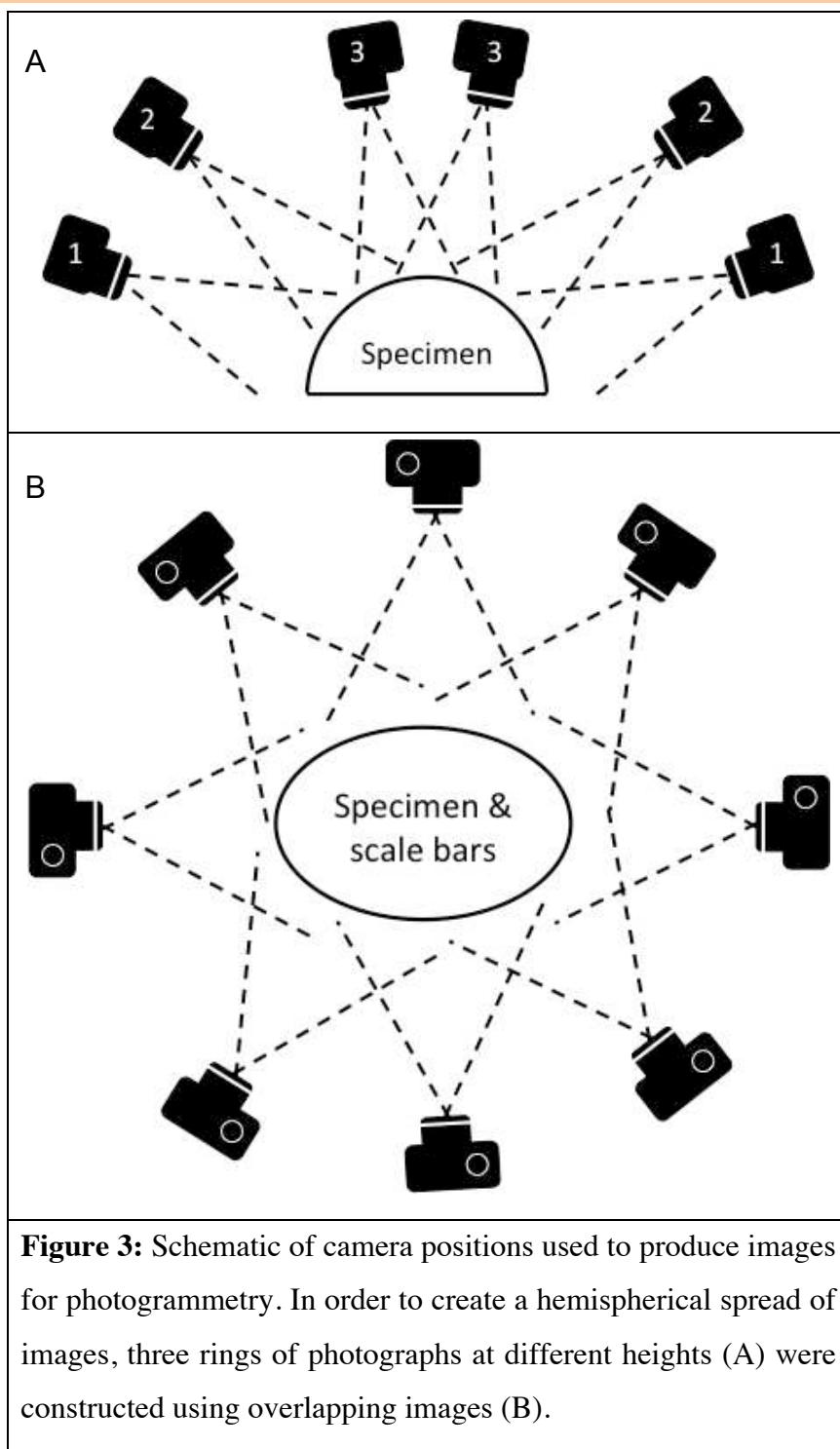


Figure 3: Schematic of camera positions used to produce images for photogrammetry. In order to create a hemispherical spread of images, three rings of photographs at different heights (A) were constructed using overlapping images (B).

204

205

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

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

212

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

226

227 *Computed tomography and 3D surface measurement*

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

243

244 *Statistical analysis*

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

254

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

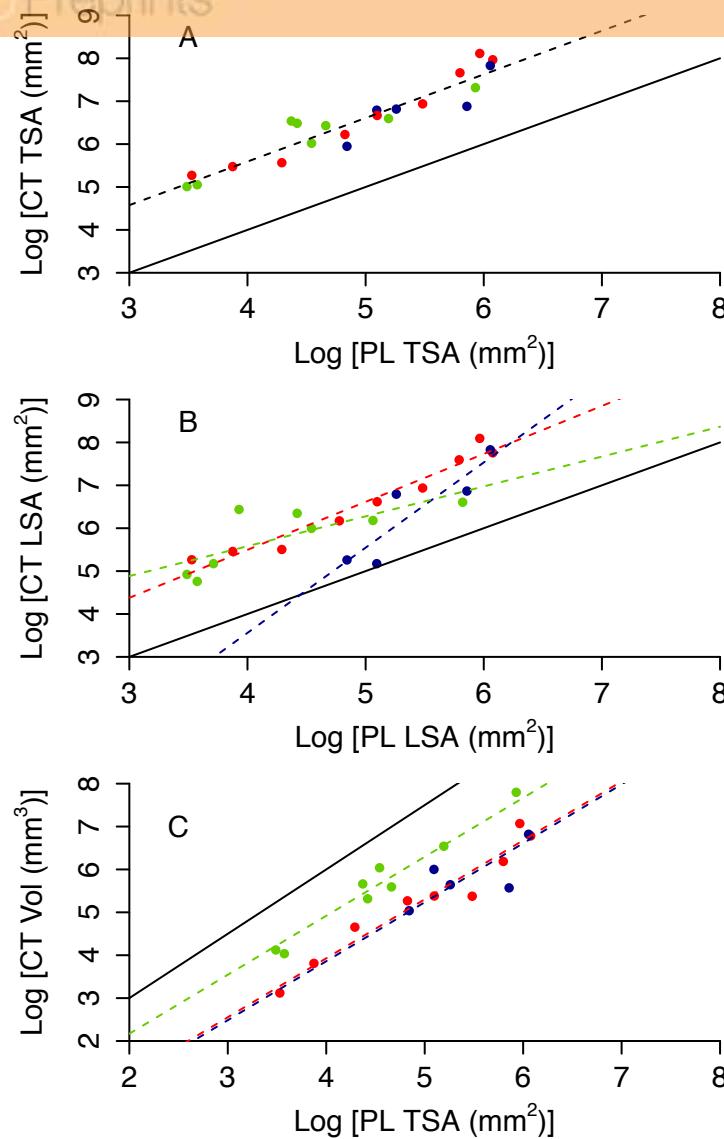
261

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

267

268 **Results**

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



279

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

286

288 **Table 1:** Predictive accuracy of planar total or live surface area (PL TSA/LSA) when
289 used alone and with morphotype to estimate CT TSA, CT LSA, CT Vol, respectively.
290 Adjusted R², p-value and Akaike's Information Criterion (AIC) are given to 2
291 significant figures.

Response	Predictor(s)	Adjusted R ²	p	AIC
CT TSA	PL TSA	0.88	5.40x10 ⁻¹¹	15.03
	PL TSA + morphotype	0.88	2.55x10 ⁻⁸	16.01
	PL TSA * morphotype	0.88	7.22x10 ⁻⁸	18.07
CT LSA	PL LSA	0.70	3.65x10 ⁻⁷	39.67
	PL LSA + morphotype	0.745	3.55x10 ⁻⁶	37.86
	PL LSA * morphotype	0.81	3.31x10 ⁻⁶	32.88
CT Vol	PL TSA	0.73	2.42x10 ⁻⁷	42.85
	PL TSA + morphotype	0.90	9.76x10 ⁻¹⁰	23.14
	PL TSA * morphotype	0.90	1.79x10 ⁻⁸	23.67

292

293

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

300

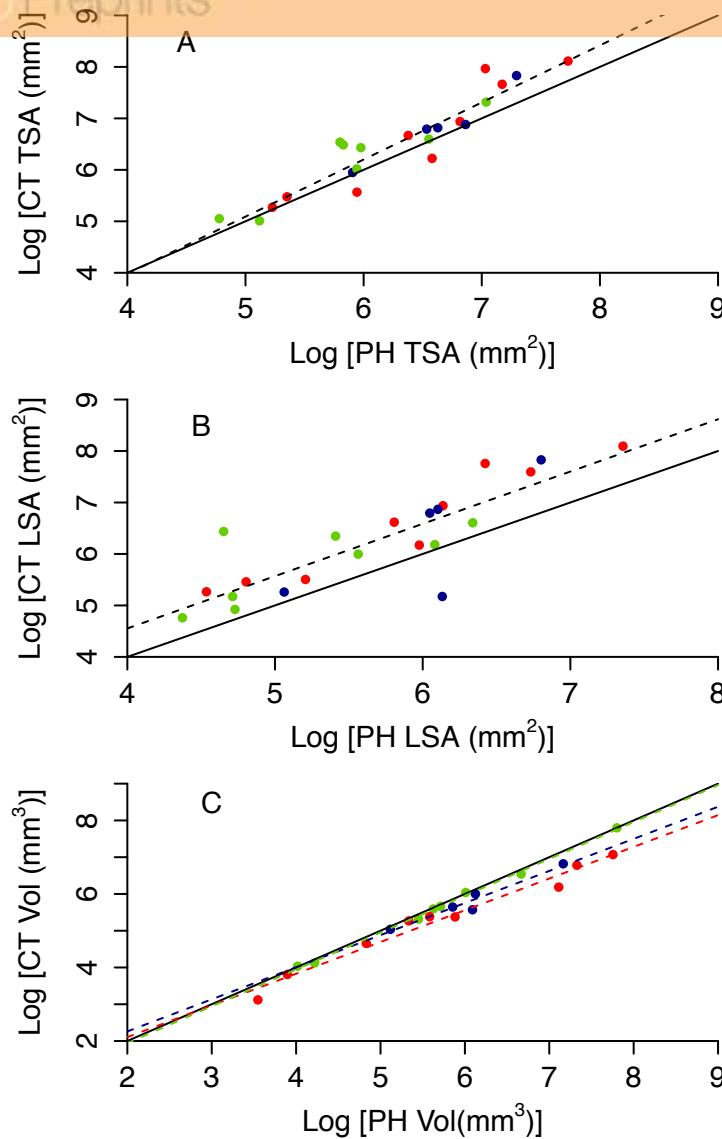
Response	morphotype	α (CI)	β (CI)
CT TSA	all	1.528 (0.692 to 2.365)	1.016 (0.849 to 1.184)
CT LSA	branching	1.024 (-0.749 to 2.797)	1.118 (0.768 to 1.468)
	encrusting	-4.387 (-10.597 to -0.225)	1.987 (-0.093 to 1.830)
	massive	2.796 (-0.812 to 4.355)	0.696 (-0.975 to 0.132)
CT Vol	branching	-1.570 (-2.671 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)	

301

302

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).

317



318

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

324

326 **Table 3:** Predictive accuracy of Photogrammetry total and live surface area, and
327 volume (PH TSA, PH LSA, PH Vol, respectively) when used alone and with
328 morphotype to estimate total and live surface area and volume according to CT
329 scanning (CT TSA, CT LSA, CT Vol, respectively). Adjusted R², p value and
330 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	9.75x10 ⁻¹¹	16.319
	PH TSA + morphotype	0.875	5.92x10 ⁻⁹	18.074
	PH TSA * morphotype	0.868	1.84x10 ⁻⁷	20.686
CT LSA	PH LSA	0.702	3.64x10 ⁻⁷	39.601
	PH LSA + morphotype	0.692	3.55x10 ⁻⁶	41.983
	PH LSA * morphotype	0.690	3.31x10 ⁻⁶	43.560
CT Vol	PH Vol	0.955	1.02x10 ⁻⁶	3.271
	PH Vol + morphotype	0.973	2.52x10 ⁻¹⁰	-6.432
	PH Vol * morphotype	0.976	6.45x10 ⁻⁹	-7.847

331

332 **Discussion**

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

341

342 The measurements collected using photogrammetry were found to be significantly
343 different from the results of the CT scans, but were nevertheless excellent predictors
344 when combined with information about the morphotype of the colony. The
345 differences observed are linked to the different resolutions of the two methods (much
346 higher for CT scans, see appendix 2). Lower resolution 3D photogrammetry models
347 cause both the underestimation in surface area and the overestimation in volume. Our
348 study adds to growing evidence that the previously prohibitive aspects of
349 photogrammetry are being overcome by technological improvements (Burns et al.
350 2015; Falkingham 2012). The possibility of applying this technique using open-source
351 software opens it up to a wider audience. The application of photogrammetry to
352 measuring reef topography (Burns et al. 2015) combined with our detailed modeling
353 of individual coral colonies illustrates the wide range of potential applications this
354 technique can have in monitoring and studying coral reefs and their ecology.

355

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

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

379

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

392

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

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

404

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

420

421 **Conclusions**

422 In conclusion, coral colony surface area and volume can be predicted effectively from
423 both PL TSA and morphotype. This development provides a stepping-stone by which
424 we can shift to a more 3D orientated approach to measuring corals and may enable
425 better understanding and exploitation of historical data. Furthermore, photogrammetry
426 clearly contributes towards addressing the question of how best to measure corals
427 because it is a widely accessible, non-invasive and cost effective method for making
428 3D measurements in-situ. This paper illustrates two specific areas for studying corals
429 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

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