

Using three-dimensional surface area to compare the growth of two Pocilloporid coral species

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Received: 31 December 2007 / Accepted: 11 August 2008 / Published online: 26 August 2008
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Abstract Many facets of coral research require coral colony surface area estimates. This study developed a relationship between the two-dimensional (2D) projected area and the three-dimensional (3D) whole colony surface area for two commonly studied Indo-Pacific coral species: *Pocillopora damicornis* and *Stylophora pistillata*. The surface index function was used to measure the growth of colonies in situ around Heron reef on the southern Great Barrier Reef. The results show that while growth between the two species was not significantly different when measured in two dimensions, the 3D area showed significantly different growth rates with *S. pistillata* growing at almost double the rate of *P. damicornis*. The study demonstrates that it is possible to make reliable estimates of the 3D surface area of entire colonies of these complex branching coral species, using the plan view of the coral and a pre-determined surface index function. In addition, this study shows that the 3D surface area provides a more useful measure of colony growth than the traditional methods of either 2D area or longest dimension.

Introduction

Many elements of coral biology such as biomass, symbiotic dinoflagellate density, chlorophyll concentration and respiration rates are standardized to surface area (Edmunds

and Gates 2002). Historically, estimates of the surface area of complex coral colonies have been problematic and usually involve the destruction of the colony. Initially, the two-dimensional (2D) projected area of a coral species was used as an estimate of the surface area for the calculation of physiological variables (Odum and Odum 1955; Kanwisher and Wainwright 1967). Here, depending on the variable of interest, either the projected area was used directly or it was scaled up by some factor, as an example, when it used for bacterial estimates (Odum and Odum 1955).

There have been several methods proposed for the determination of the three-dimensional surface area of coral colonies. Dahl (1973) and Alcalá and Vogt (1997) used geometric shapes with an easily calculated surface area to reconstruct coral reef objects and introduced the concept of a surface index (SI)—the ratio of the vertically projected area to the 3D surface area. Marsh (1970) estimated the 3D surface area either by the weight difference of an object before and after being wrapped in aluminium foil or from direct measurement of the unwrapped aluminium foil. Modern revisions replaced the aluminium foil with latex (Meyer and Schultz 1985), dye (Hoegh-Guldberg 1988) or paraffin wax (Stimson and Kinzie 1991), the latter being one of the most common methods currently used in coral biology. These methods provide a good estimate of the 3D surface area, but are practical only at small scales, and cannot be applied to colonies in situ. While they may be sufficient for some studies, there is a need for a method which allows non-destructive in situ measurements of whole colony surface areas. Methods such as photogrammetry (Bythell et al. 2001) and 3D reconstruction using video (Cocito et al. 2003) represent potentially useful tools for non-destructive measurement of surface area, but currently require significant amounts of

Communicated by P. Kraufvelin.

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digital image analysis to extract the required data. This can be a time consuming and therefore costly process.

This study revisited Dahl's (1973) SI concept of a relationship between the planar and 3D surface area of corals. Chancerelle (2000) examined this concept and found a linear relationship for five coral species of different growth morphologies [*Synaraea rus* (Forskål, 1775), *Porites lobata* (Dana, 1846), *P. verrucosa* (Ellis and Solander, 1786), *Fungia scutaria* (Lamarck, 1801) and *Acropora hyacinthus* (Dana, 1846)]. The current study investigated whether there is a linear relationship between the 2D projected area and actual 3D area of the two commonly studied complex branching Pocilloporid corals, *Pocillopora damicornis* (Linnaeus, 1758) and *Stylophora pistillata* (Esper, 1797).

Colony size and its frequency distribution have been used as a predictor of coral reef status (Bak and Meesters 1999; Mesters et al. 2001) and is a life history trait that helps understand coral population dynamics (Hughes and Jackson 1985; Hughes and Connell 1987). Most of these studies have used 2D projected areas as a proxy for colony size. Colony growth has also been studied in coral populations with changes in maximum diameter or 2D area as measurements of growth (Loya 1976a). This approach is valid if the relationship between the 2D and 3D areas is the same or very similar between the different species studied. If this is not the case, differences in life histories between different species can be missed by the lack of sensitivity inherent when using 2D area as a proxy for colony size.

Applying the SI technique to in situ colonies allowed for a comparison between the traditional approach of using the 2D projected area and the estimated 3D surface area. In addition, the aim of this study was to define the colony size and compare the growth of colonies of the two commonly studied Pocilloporid corals *P. damicornis* and *S. pistillata*.

Materials and methods

Study location

The study area was the reef surrounding Heron Island in the Southern Great Barrier Reef. To capture the environmental variability within the reef, four locations were selected with two on the southern and two on the northern side of the reef (Fig. 1). The locations were randomly chosen, ensuring at least a 2 km separation between the sites (if one randomly chosen spot was less than 2 km from a previous one, the randomization process was repeated until a minimum 2 km distance between sites was achieved). Within each location the upper reef slope (3–5 m) was examined in April 2006 and again in April 2007. Each site contained eight permanent photo transects

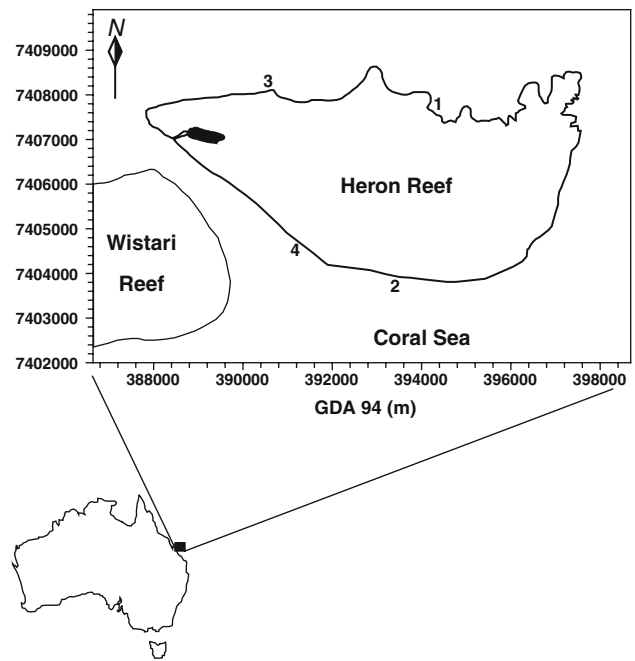


Fig. 1 Location of the four study sites

(15 m × 1 m) along a continuous line totaling a belt of 1 m by 120 m [the 8 transects were considered as a single 1 m × 120 m transect and the replicates per site were the actual coral colonies (n shown in Table 3)]. To standardize the focal distance (80 cm from the sea floor), a 1 × 1 m frame was attached to a 7 mega pixel digital camera with a 14 mm wide angle lens. The software PT Lens, (ePaper-Press) was used to correct for the distortion produced by the wide angle lens. Within each of the 120 photos, each colony of the two species studied were counted and measured ($n = 12–98$ depending on the species and site, Table 3). To obtain the 2D area of each colony, the colony perimeter was digitized and the software CPCE (Kohler and Gill 2006) was used to determine the outlined area. Colony growth (%) was calculated by determining the percentage of change in colony size from one time point to the next one for each colony.

Determination of actual 3D surface area

Coral skeletons ($n \geq 15$) from each species (*P. damicornis* and *S. pistillata*) were obtained from collections at the Queensland Museum and The University of Queensland. The skeletons were originally sourced from a wide geographic and depth range. No discrimination was given to collection location or depth in selecting skeletons for analysis. The 3D surface areas of colonies were calculated using a modified version of the Stimson and Kinzie (1991) paraffin wax method. Skeletons at room temperature were weighed and dipped into a paraffin wax bath (Paraplast®

Tissue Embedding Medium, Tyco Healthcare Group) maintained at 65°C for 2 s. When removed from the bath they were rotated around to optimize evenness of the coating. The initial coating seals the skeleton, reducing the influence of corallite rugosity and filling any cavities resulting from infaunal burrowers. Skeletons were reweighed at room temperature (25°C) before being dipped for a second time in the paraffin wax, and a final weight measurement being taken.

Calibration objects all of known surface area but of varying levels of complexity and surface texture (wood, plastic, coral, plastacene), were measured using the paraffin wax procedure. The objects ranged from simple geometric shapes (pyramids, cylinders, and cubes) to complex shapes comprising of multiple cylinders of differing diameter (to simulate a branching coral, $n = 14$). Using calibration objects of varying texture provided a check that surface roughness did not influence the conversion to area function (as would be identified by a poor correlation). The relationship between the weight of the second wax layer and the actual surface area of the objects was then used to calculate the 3D surface area of the coral skeletons. The calibration procedure was repeated four times to ensure repeatability, removing all wax between each analysis.

The accuracy of the wax method was assessed by comparing the calculated surface area of both calibration objects and coral skeletons ($n = 13$) with surface areas estimated using a laser scanner (Polhemus FastscanTM). Objects were scanned and processed to a final resolution of 2.5 mm.

Determination of 2D projected surface area

The projected area of coral skeletons was estimated using digital photography. The skeletons were oriented upright and photographed from above against a grid of 1 cm squares. Perspective error was minimized through maximizing the distance between the camera and the subject while utilizing the optical zoom of the camera to maintain a high resolution image. Each photograph was calibrated using the grid with standard digitizing software (Didger 2.0, Golden Software Inc) and the perimeter of the colony was drawn and recorded digitally as a polygon. Only the perimeter-based polygon was used in the analysis and no compensation was made for areas within the polygon that may not have contained coral material (i.e. gaps between coral branches internal to the perimeter of the colony). Digitizing of projected areas was all performed at the same resolution regardless of skeleton size, maintaining a consistent level of accuracy across all skeleton sizes and only sections of skeleton that would have contained live tissue at the time of collection were included. This allows the developed SI relationships to be applied to live tissue areas

excluding errors introduced by the influence of the abiotic basal zones of colonies.

Data analysis

All data were analyzed using Poptools v2.6.7 (Hood 2005), Statistica v7.0 and SigmaPlot 2001 v7.101. Regression analysis was used to determine relationships for the wax calibration and the projected 3D surface area for each coral species. The analyses were not forced through the origin. Although the curve must theoretically pass through zero, it cannot be assumed that the corals maintain the same morphology (i.e. ratio of the 3D to projected areas) at very small scales as larger, more developed colonies. Forcing the regression may therefore lead to erroneous results. Residuals were analyzed to assess for any departure from linearity or the impact of any outliers on the final analysis.

A general linear model was used to test for differences between the growth rate of the two species based on the method used to calculate the size (2D or 3D area), where method was stated as a repeated factor with two levels, site as a random factor with four levels and species as a fixed factor with two levels. When differences were found, a Least Significant Distances (LSD) multiple comparison test was used to determine which means were different.

A general linear mixed model with separate slopes mode was used to test whether there are differences between the colony growth, species and site as a function of original colony size. Where colony growth calculated using 3D area was the dependent variable, species was a fixed variable with two levels, site was a random variable with four levels and colony size at time zero was a continuous predictor (covariate). This analysis considers the effect of the continuous predictor (colony size at time zero) separately for each combination of levels of the two variables and provides an integrated statistic for the covariate. If the covariate effect is significant, the lineal relationship between the covariate and the different combinations of levels of the other variables can be explored obtaining linear coefficients for each relationship. A linear model was chosen after testing the Maximum likelihood with several combinations of distributions and non-linear link functions (generalized non-linear mixed model) and finding that none of them presented a better fit than the linear model.

Results

Surface index development

Regression analysis of the weight of the second wax coating to the 3D surface area showed a strong correlation between the calibration objects and the weight of the

second layer of paraffin wax deposited ($R^2 > 0.99$, $F_{1,12} = 1744.96$, $P < 0.001$). The existence of a very strong correlation coefficient indicates that the initial surface properties of the objects being coated do not play any significant role in calculating the 3D surface area of a dipped object from the weight of the second coating of paraffin. The average thickness [calculated from the density of the wax at room temperature ($SG = 0.8$)] of the initial layer of wax was 2 ± 0.5 mm (mean \pm SE) while the second layer had an average thickness of 0.3 ± 0.01 mm. The regression analysis was used to obtain the following calibration relationship:

$$\text{Surface area (cm}^2\text{)} = 34.3 (\text{cm}^2 \text{g}^{-1}) \times \text{weight (g)}.$$

Repeating the calibration procedure resulted in a standard error of the regression term of less than 10% ($n = 4$).

Correlation analysis between surface areas determined using laser scanning and the wax technique resulted in a very strong relationship ($F_{1,11} = 1759.9$, $R^2 > 0.99$, $P < 0.001$). The high level of correlation between the two techniques gives confidence in the surface areas estimated using the paraffin wax methodology.

Analysis of the photo data produced a SI relationship for both species. A significant linear relationship was established between the 2D projected and the 3D surface area (*P. damicornis*: $R^2 = 0.94$; $F_{1,13} = 196.5$, $P < 0.001$; *S. pistillata*: $R^2 = 0.94$; $F_{1,15} = 250.8$, $P < 0.001$) (Fig. 2). Of the two species *P. damicornis* showed the highest ratio of the 3D to projected surface area (9.05). In both cases, residuals analysis indicated no significant departure from linearity or undue influence of outliers on the regression results (Wald–Wolfowitz Runs test, $P > 0.5$ for both species).

Coral growth analysis

No significant differences between the growth rates of the two species were detected when using the 2D projected area to estimate colony size. However, *S. pistillata* grew almost twice as quickly as *P. damicornis* when using 3D surface area to estimate colony size (Fig. 3; Table 1).

The initial size of the colonies at time zero influenced the growth of colonies in the different sites (Table 2). Small colonies of *S. pistillata* grew quicker than bigger colonies in all four sites, while size was not significant for *P. damicornis* in any site (Table 3).

Discussion and conclusions

The results in this study support the findings of Chancerelle (2000) and suggest that the same technique may be applied to a wide range of coral species of various growth forms.

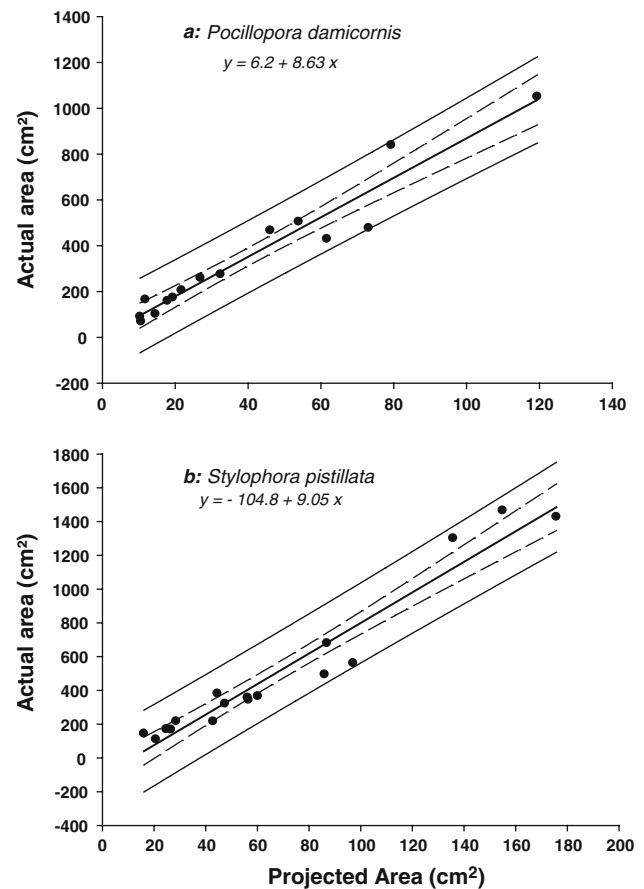


Fig. 2 Regression analysis of projected versus 3D surface area for **a**: *Pocillopora damicornis* and **b**: *Stylophora pistillata*. 95% confidence (dashed) and prediction (solid) lines are shown

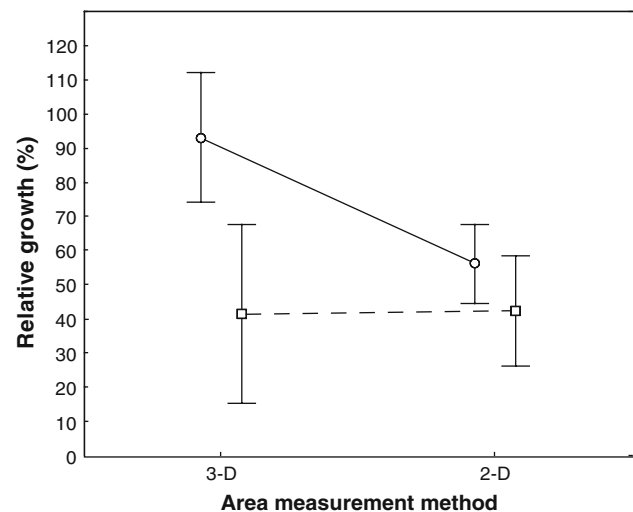


Fig. 3 Comparison of colony growth as determined using the 2D projected area and estimated 3D surface area of *P. damicornis* (open square) and *S. pistillata* (open circle). Error bars represent 95% confidence intervals

Table 1 General linear model results

	SS	DF	MS	F	P	LSD test
Intercept	159.796	1	159.797	79.871	<0.001	
Site	10.514	3	3.505	0.6331	0.642	
Species	12.716	1	12.716	48.72	0.006	
Site × species	16.609	3	5.536	2.767	0.042	
Error	656.226	328	2.001			
Method	3.843	1	3.844	14.289	0.032	
Method × site	0.808	3	0.269	1.031	0.490	
Method × species	4.199	1	4.199	16.088	0.028	3D <i>S. pistillata</i> > than all other
Method × site × species	0.782	3	0.261	1.439	0.231	
Error	59.440	328	0.181			

Differences in growth rate per species per site based on the method used in the calculation (3D *S. pistillata* = growth rate of *S. pistillata* based on 3-D area)

Table 2 General linear mix model with separate slope mode results for the effect of initial colony size (3D size) in colony growth (colony size in time zero is a covariate in the model)

	SS	DF	MS	F	P
Intercept	110.261	1	110.261	78.166	<0.001
Site × species × “3D size”	67.767	8	8.471	6.005	<0.001
Site	3.406	3	1.135	0.537	0.688
Species	7.362	1	7.362	3.764	0.120
Site × species	6.343	3	2.114	1.499	0.215
Error	451.393	320	1.411		

This method represents a simple, rapid and non-destructive technique to assess 3D coral surface areas in situ. It should be noted that the calculated SIs for *P. damicornis*, and *S. pistillata* are less than those calculated by Chancerelle (2000) for less complex growth forms. This may be due to differences in the techniques used to measure the 3D area of the skeletons. In order to obtain surface areas Chancerelle (2000) first varnished the skeletons followed by applying a single wax coat. Sealing skeletons with wax

rather than varnish results in a removable coating, but potentially reduces the rugosity of corallite structures to a greater degree. Chancerelle (2000) stated that a varnish thickness of between 0.1 and 0.5 mm was achieved (cf. 2 mm for the initial wax layer in this study). Chancerelle (2000) also used a much hotter paraffin bath (20°C above melting cf. 65°C in this study) which would result in a thinner final wax layer. If the effect of corallite rugosity is minimized, then it is the ratio of vertical to horizontal spread of colonies that most influences the SI relationship (Dahl 1973). Using two layers of wax (from a 65°C bath) results in an average wax thickness >2 mm. Therefore, any corallite structures <2–3 mm in diameter are likely to be eliminated from the analysis.

For the species examined in this study, the relationship between the 2D and 3D surface areas was linear and provides a robust basis for within species comparisons in situ, having been developed from colonies from a wide geographic and depth range. The existence of SI functions for these commonly studied species, as well as for those species examined by Chancerelle (2000), represents a potentially powerful research tool for coral reef biologists. It suggests that the same linear relationship may exist for a

Table 3 Relationship between colony size (covariate) and colony growth in the GLMM per species per site

Species	n	Site	Tolerance	Variance	R ²	B	t	P
<i>S. pistillata</i>	37	1	0.588	1.700	0.412	−0.276	−4.239	<0.001
<i>P. damicornis</i>	12	1	0.547	1.828	0.453	−0.093	−1.383	0.168
<i>S. pistillata</i>	98	2	0.600	1.666	0.400	−0.150	−2.331	0.020
<i>P. damicornis</i>	55	2	0.338	2.956	0.662	−0.098	−1.142	0.255
<i>S. pistillata</i>	45	3	0.676	1.479	0.324	−0.156	−2.569	0.011
<i>P. damicornis</i>	21	3	0.313	3.197	0.687	−0.132	−1.480	0.140
<i>S. pistillata</i>	42	4	0.740	1.351	0.260	−0.198	−3.416	0.001
<i>P. damicornis</i>	73	4	0.353	2.833	0.647	−0.083	−0.983	0.326

wide range of coral species. It is important to reiterate that the relationships developed in this study are unlikely to be valid for very small colonies. In order for this technique to be applied to small colonies a linear relationship must be confirmed at that size range. In addition, when developing SIs for a given species, it is important to take into consideration within species morphological differences. Variable growth forms can occur within a species due to environmental effects such as light levels and water flow regimes (Jokiel 1978; Muko et al. 2000; Kaandorp et al. 2005). A SI function would have to be calculated for each growth form if the species of interest shows significant morphological plasticity.

A similar approach to the SI concept was recently reported by Courtney et al. (2007) whereby the 3D surface area of a colony could be calculated by applying three linear measurements of a colony in the field to a pre-determined log-linear function. However, while this approach is also non-intrusive when applied to corals in the field, the accuracy was greatly reduced when applying the technique to branching colonies. In addition, unlike the SI methodology where surface area estimates can be made from a photograph, each colony must be manually measured, making the individual colony measurements more field intensive.

One important implementation of the SI relationship is in defining the size of in situ coral colonies. Typically, researchers will use the projected area of colonies to compare and contrast size distributions. For example, Hughes and Connell (1987) used projected area to define colony size distributions and growth of *Acropora*, *Pocillopora* and *Porites* colonies at Heron Island. The results of the current study, however, demonstrate that when comparing distributions, even within a single family, using the projected area alone can be misleading. The use of the SI to estimate the 3D surface area results in a much more rigorous measure of colony size and the non-intrusive nature of the technique (once a SI has been developed) makes it ideal for examining time dependent variables such as coral growth.

Comparing growth rates observed in this study with previous studies is complex due to the large variability in the growth rates of coral species resulting from differing environmental influences. Hughes and Connell (1987) studied the growth of *P. damicornis* on Heron Island reef flat reporting an average annual growth of 65% in one site of the reef flat, using only the 2D area to calculate the growth. Our results suggest an average growth of 40% for the four sites. Site 3 in the current study is adjacent to the Hughes and Connell (1987) site. The average growth at site 3 was 50% for both 3D and 2D calculations. Loya (1976b) documented an average of 110% for *S. pistillata* at a depth of between 3 and 4 m in Eilat (Red Sea) for colonies up to

10 cm across using maximum diameter as a measure of colony size. Loya (1976b) also showed that small colonies exhibited a higher growth rate in comparison to larger colonies. Although the average growth rate in the Loya (1976b) study was higher than the current one (55% in 2D), the Loya (1976b) data are biased to smaller colonies, potentially inflating the average growth rate. Given the potential for environmental factors to influence the growth rates across studies, the results of the current study still compare well with those found by the previous investigators.

The difference in coral growth rates observed in the current study demonstrates how significant patterns can be missed when using the 2D area to calculate growth. The main reason for this result is the fact that *P. damicornis* colonies become more complex at a smaller size than *S. pistillata*. This is illustrated by the negative intercept term in the regression equation compared with the small positive intercept for *P. damicornis*. This result is also supported by the fact that colony size was only significant for *S. pistillata*. Although it could appear surprising that the 3D method shows a growth rate of almost twice the 2D method for *S. pistillata*, this result is also supported by the fact that the average size of *S. pistillata* was larger than the size of *P. damicornis* in two of the four sites (data not shown).

The growth rate observed for these two species was not significantly different between the sites, showing that the potential environmental variability around the upper reef slope of Heron reef appears not to affect the average colony growth rate of these two species. Nevertheless, the small colonies of *S. pistillata* grew almost twice as quickly in site 1 in comparison to site 3 and were the ones with the strongest negative correlation between the initial size and the growth of the colony of all four sites (Table 3). Site 1 is located to the north of the Island and is the most wave sheltered of the four sites investigated (Fig. 1). These calmer conditions could facilitate the growth of the small colonies by reducing the physical erosion produced by the wave action (Loya 1976b).

The difference in life history strategies between these two species could be of particular interest in the context of an increasingly unstable environment where disturbances are becoming more frequent due to human pressure and climate change. The ability of *S. pistillata* to increase its biomass quickly in early life stages could confer this population a higher resistance to size dependent disturbances in comparison to the *P. damicornis* population.

The existence of a linear relationship between the 2D projected area and the 3D area for specific coral species as demonstrated by Chancerelle (2000) together with the current study, validates the use of the 2D projected area as a proxy for colony size for single species studies. However, as demonstrated above, when making comparisons across

species the 3D surface area provides an improved measure of colony size.

This study has demonstrated that rapid, non-destructive, in situ measurements can be made to assess whole colony 3D surface area using a scale photograph of the plan view of the coral and a pre-determined SI relationship. This information may prove to be a useful aid in the experimental design of future coral research. It allows for the extrapolation of physiological parameters determined at the sub-colony scale, providing researchers with the opportunity to better understand the dynamics of corals at the colony scale. The implementation of the SI function has demonstrated that the use of the 3D surface area provides a more reliable measure of coral colony growth than the traditional method of the projected 2D surface area for studies involving multiple coral species.

Acknowledgments The authors would like to thank Selina Ward and Ove Hoegh-Guldberg from The University of Queensland and Merrick Ekins from the Queensland Museum for access to coral skeletons and to the three anonymous reviewers for comments on the draft manuscript. All experiments undertaken within this study comply with the current laws of Australia, the country in which they were performed.

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