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REPORT

Coral surface area quantification–evaluation of established techniques by comparison with computer tomography

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Abstract The surface area of scleractinian corals represents an important reference parameter required for various aspects of coral reef science. However, with advancements in detection accuracy and novel approaches for coral surface area quantification, evaluation of established techniques in comparison with state-of-the-art technology gains importance to coral researchers. This study presents an evaluation of methodological accuracy for established techniques in comparison to a novel approach composed of computer tomography (CT) and 3-dimensional surface reconstruction. The skeleton surface area of reef corals from six genera representing the most common morphological growth forms was acquired by CT and subsequently measured by computer-aided 3-dimensional surface reconstruction. Surface area estimates for the same corals were also obtained by application of four established techniques: Simple and Advanced Geometry, Wax Coating and Planar Projection Photography. Comparison of the resulting area values revealed significant differences between the majority (82%) of established techniques and the CT reference. Genus-specific analysis assigned the highest accuracy to geometric approximations (Simple or Advanced Geometry) for the majority of assessed coral genera (maximum accuracy: 104%; Simple Geometry with *Montipora* sp.). The commonly used and invasive Wax Coating technique reached intermediate accuracy (47–74%) for the majority of genera, but performed outstanding in the measurement of branching *Acropora* spp. corals (maximum accuracy: 101%), while the Planar Projection Photography delivered genera-wide low accuracy (12–36%). Comparison of area values derived from established techniques and CT additionally yielded approximation factors (AFs) applicable as factors in the mathematical improvement of surface area estimates by established techniques in relation to CT reference accuracy.

Keywords Coral · Surface area · Methods · Evaluation · Computer tomography

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Introduction

Scleractinian corals exhibit an array of different growth forms and intricate skeletal structures. In coral reef studies, the surface area of corals serves as an important reference parameter, for example, regarding the standardisation of metabolic processes such as photosynthesis, respiration and the release of coral-derived organic material to the environment (Wild et al. 2005). Measurement of the actual coral tissue surface area remains a difficult approach. The challenge to develop feasible methodologies, adequately determining the surface area of the complex and species-specific skeletal structures of corals, has led to the publication of various methodological approaches over the past decades.

Geometric measurement techniques are probably the earliest approach used to assess the surface area of marine organisms (Odum et al. 1958). Geometric forms or shapes (e.g., cylinders, spheres, circles) that best resemble the complex structure and topography of the investigated organism are selected and basic dimensional parameters of the organism are measured; the surface area is calculated by the respective geometric formula. This approach offers important advantages as it can be rapidly carried out and is non-invasive; this has led to the frequent application of geometric approaches in ecological and physiological coral reef science (Szmant-Froelich 1985; Roberts and Ormond 1987; Babcock 1991; Bak and Meesters 1998) as well as in coral monitoring studies (Fisher et al. 2007).

Several coating techniques, involving the dipping of corals in liquids and the subsequent correlation of the amount of coating to the assessed surface area, have been described to date. These include coating of coral fragments with latex (Meyer and Schultz 1985), paraffin wax (Stimson and Kinzie 1991), or vaseline (Odum and Odum 1955) and the use of the dye Methylene Blue in a method designed for finely branched coral species (Hoegh-Guldberg 1988). In addition, coating with aluminium foil of known weight per unit area (Marsh 1970) has found application in several field studies (Fagoonee et al. 1999; Vollmer and Edmunds 2000; Wegley et al. 2004). Of these techniques, coating with paraffin wax appears most frequently in the literature (e.g., Glynn and D'Croz 1990; Chancerelle 2000; Vytopil and Willis 2001; Wild et al. 2005). All coating techniques require prior tissue removal or lead to mechanical damage of the tissue, and therefore unsuitable for experimental studies where continuous investigations on living corals are necessary.

The projected planar area of coral colonies has been used in numerous studies to estimate surface areas in combination with geometric assumptions (Falkowski and Dubinsky 1981; Muscatine et al. 1989) or by plain calculation of the covered benthic area (Jokiel and Morrissey 1986). In attempts to compare the projected planar area of corals with geometric approximations of substratum topography and coral morphology, surface indices (SI) were developed to find suitable means for the 3-D approximation of benthic reef coverage (Dahl 1973; Alcala and Vogt 1996) and coral colony surface area (Pichon 1978). Photography of the planar projection of corals, as a method to assess surface area (Kanwisher and Wainwright 1967), has found application in coral reef science on different scales of observation. Visual underwater surveys for benthic coverage make use of photographs taken from above the reef substratum to quantify and monitor reef community structures (Bohnsack 1979; Mergner and Schuhmacher 1979; Hughes and Jackson 1985). For studies on individual coral colonies, specific methods for surface area determination were developed, involving computer-aided digitisation of photographs (Benzion et al. 1991; Rahav et al. 1991; Tanner 1995). The shortcoming of the planar photographic approach is the 2-dimensional (2-D) projection of a 3-dimensional (3-D) form, which significantly underestimates the actual surface area. In order to reduce this limitation, photogrammetric methods have been described using object photographs from various perspectives, which are then combined by computer-aided design (CAD) to form a 3-D object surface reconstruction (Done 1981; Bythell et al. 2001; Cocito et al. 2003; Courtney et al. 2007; Jones et al. 2008). As the most recent advancement of methods applying optical surface detection and computer-aided object reconstruction, 3-D laser scanner systems have successfully been used for coral surface area quantification (Courtney et al. 2007; Holmes 2008).

Another computer-aided 3-D technique, computer tomography (CT), has found some application in coral reef sciences after its introduction (Hounsfield 1973). CT provides high-resolution X-ray images, which have shown to be particularly useful in studies focussing on coral growth (Bosscher 1993; Bessat et al. 1997; Goffredo et al. 2004) and have additionally found broad applications in geosciences (Ketcham and Carlson 2001). In recent years, computer-aided methods using CT-derived data were applied to virtually reconstruct coral morphological structures (Kruszynski et al. 2006) and to simulate coral growth patterns (Kaandorp et al. 2005). With the help of software packages, 3-D surface reconstructions of coral colonies can be generated using CT-derived data from which the virtual surface area is subsequently calculated, thereby providing high accuracy area measurement of the actual skeleton surface area (Laforsch et al. 2008). This procedure can be applied to bare skeletons as well as on living coral specimens. A limitation of CT measurements of corals is the restriction to measurements of the skeleton topography only, while coral tissue components remain undetected.

This study aimed to evaluate the accuracy of surface area estimates derived from the four established techniques in coral reef science (Simple and Advanced Geometry, Wax Coating and Planar Projection Photography) in direct comparison to a high accuracy CT-based methodology, used as reference. Analysis of method accuracy was extended to generate approximation factors (AFS) applicable in the mathematical improvement of surface area estimates by established techniques in relation to CT reference accuracy.

Material and methods

A total of 72 coral skeletons from six genera and four growth forms (warm water corals: *Acropora* spp., *Fungia* spp., *Galaxea fascicularis*, *Montipora* sp., and *Pocillopora damicornis;* cold water coral: *Lophelia pertusa*) were used in this comparative investigation of surface area quantification (see Fig. 1, panels a–f). The skeleton surface area of each of these coral colonies was determined by the use of established techniques comprising geometric approximations, Wax Coating and Planar Projection Photography. In addition, skeleton surface area measurements for all coral colonies were carried out by conventional medical CT and subsequent 3-D surface reconstruction, in order to allow for a direct comparison with the results derived from established techniques. Coral skeletons were obtained from collections of aquarists. For each genus, 11–13 colonies ranging from 1–17-cm maximum diameter were selected to account for differences between size classes. The bases of the colonies were ground to achieve an exact reference plane for all the mentioned techniques and then glued onto ceramic tiles (4 × 4 cm). The skeleton surface area was quantified by the following procedures. An example for the genus *Acropora* (*Acropora* specimen # 10) illustrating the application of the different techniques is displayed in Fig. 2.

Geometric approximations

Geometric measurements of coral colonies were divided into two approach categories, Simple Geometry and

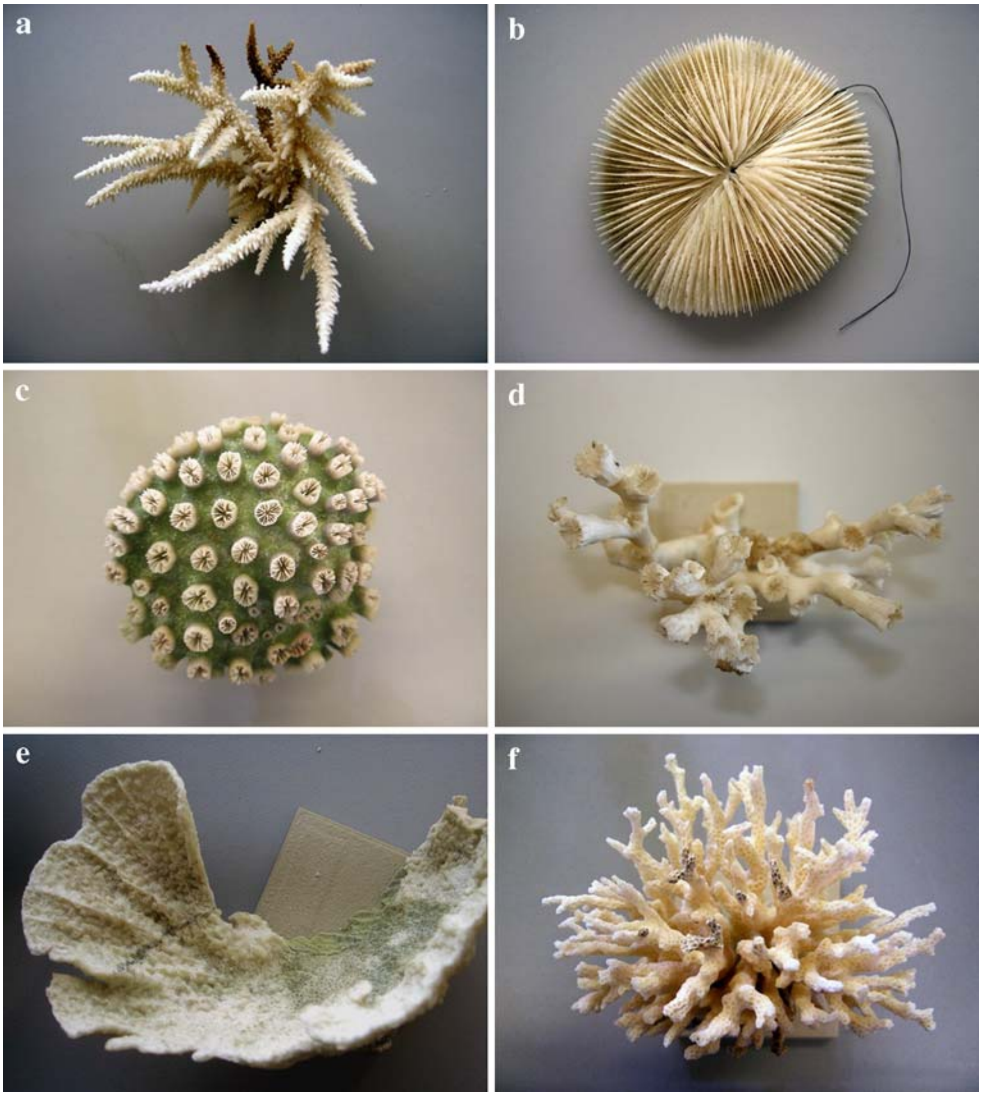

Fig. 1 Top view of specimens assessed in coral surface area measurements. Panels **a**, *Acropora* spp.; **b**, *Fungia* spp. with attached thread used for Wax Coating; **c**, *Galaxea fascicularis*; **d**, *Lophelia pertusa*; **e**, *Montipora* sp. and **f**, *Pocillopora damicornis*

Advanced Geometry, defined as follows: Simple Geometry assesses the whole structure of a coral colony at once and assigns a geometric body that shows the closest morphological similarity (e.g., cylinder, hemisphere or disc). Only few basic dimensional parameters (e.g., radius, height) need to be recorded once (Fig. 2, panel a). Advanced Geometry divides the coral colony into several sections and assigns an approximate geometric form or shape to each. Single measurements of dimensional parameters for each section are therefore necessary (Fig. 2, panel a). Measurements were carried out using conventional callipers (accuracy: ± 0.05 mm) and a flexible tape measure (accuracy: ± 1 mm). For both the approaches, measured parameters of all the geometric forms and shapes were put into the respective surface area equations (Table 1) to calculate the approximate area. Simple and Advanced Geometry were applied to all the coral genera, with the exception of *Fungia* spp. and *G. fascicularis,* for which only Simple Geometry was used.

Simple geometry

Branching growth form

Acropora spp. ($n = 12$), *L. pertusa* ($n = 13$) and *P. damicornis* colonies ($n = 12$) (small single branches and branched colonies) were interpreted as cylinders. The total height and the maximum and minimum horizontal diameters of the whole colony were measured in order to calculate the average horizontal diameter and radius. Height and average radius were used to determine the cylinder shell surface to which the cylinder cover, calculated as a circle using the average radius, was added.

Massive growth form

Colonies of the massive coral *G. fascicularis* ($n = 12$) were interpreted as hemispheres. Maximum and minimum horizontal diameters of each colony were measured, and the average radius was calculated. The height of the colony was assessed from the reference plane to the highest tip. Thereafter, colony surface area was calculated by the use of the surface area formula for hemispheres.

Foliose growth form

Colonies of a foliose species of *Montipora* ($n = 12$) were measured as rectangular plates. Side lengths and the overall perimeter were recorded with a flexible tape measure, taking into account curving skeleton characteristics. Average height (thickness) of the plate was measured with callipers at four points. The area of a rectangle was calculated by the side lengths and the result was doubled to represent both sides of the plate. The side of the corals was calculated as a rectangle from the perimeter and the plate thickness, and subsequently added.

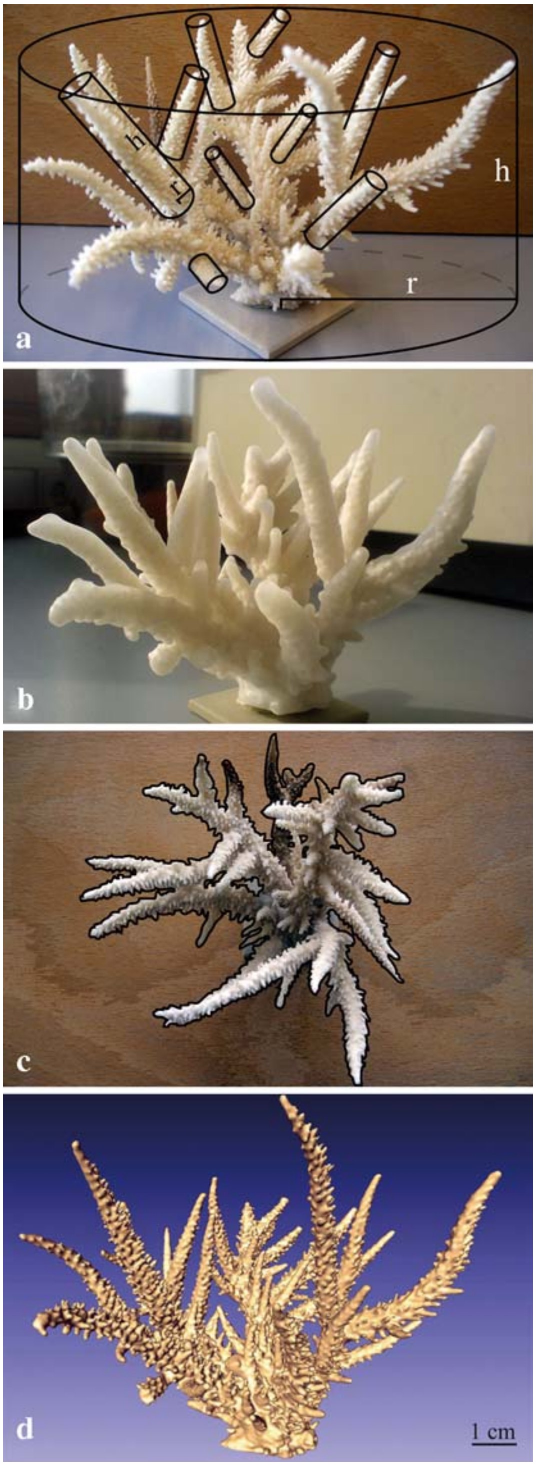

Fig. 2 Techniques for coral surface area quantification applied in this study. (Panels **a**–**d**, *Acropora* coral specimen #10); Panel **a**, Simple Geometry and Advanced Geometry; **b**, Wax Coating; **c**, Planar Projection Photography; **d**, 3-D surface reconstruction of computer tomography-derived data

Table 1 Area equations for geometric shapes and forms used in geometric approximation calculations (Simple and Advanced Geometry)

Geometry	Area equation
Cylinder shell surface	$A = 2\,\pi\,h\,r$
Hemisphere	$A = 2\,\pi\,r^2$
Circle	$A = \pi\,r^2$
Rectangle	$A = x\,y$ [a]
Right angle triangle	$A = \frac{1}{2}\,(m\,n)$ [b]

A = Area, π = pi, h = height, r = radius; [a] Where x and y are side lengths of a rectangle; [b] Where m and n are side lengths of a triangle

Disc-like growth form

A *Fungia* polyp resembles a disc, which is composed of two circular sides and a rectangular side. The maximum and minimum horizontal diameters of each polyp ($n = 11$) were measured, from which the average radius was calculated. Oral and aboral disc surface areas were then calculated as circles. The average height (thickness) of the disc was measured with callipers at four points. After the polyp perimeter was assessed with a flexible tape measure, the side could be calculated as a rectangle and was finally added to gain the total area of the disc.

Advanced geometry

Branching growth form

The surface area of the entirety of branches of *Acropora* spp., *L. pertusa* and *P. damicornis* colonies was calculated as cylinder shell surfaces, which showed closer approximation to CT reference in comparison to cone surfaces. For complexly branched colonies of *P. damicornis*, the total number of branches was counted and more than 10% of all the branches were measured; these surface areas were then extrapolated to the total number of branches. The radius and height of branches longer than 1 cm were assessed by measuring the branch diameter at the base of each branch and the height from branch base to tip. The cylinder cover area was only calculated and added for the main branch of each colony. Calculated surface areas from all branches were added to gain the total colony surface area estimate.

Foliose growth form

Montipora colonies were divided into several 2-D shapes (i.e., rectangles, right angle triangles, semi-circles and quarters of circles) and the respective parameters (side lengths and radii) were measured by flexible tape measure or callipers (where suitable). The surface areas of all shapes were calculated and doubled before the rectangular area (side of the coral) calculated by the perimeter and plate thickness, was added.

Wax coating

Surface estimates were determined by a paraffin wax coating technique modified from Stimson and Kinzie (1991) and Vytopil and Willis (2001). Paraffin wax (Merck, paraffin powder, melting point: 55–57°C) was melted at 58°C in a 5-l glass beaker inside a water bath. Coral colonies were dipped into the melted paraffin wax for 2 s and carefully shaken to remove drops. Through this procedure, the surface was sealed and equal adhesion could be ensured while preserving approximate skeleton topography. The initial weight of the wax coated colonies was measured after 5 min; they were then re-dipped for 5 s and weighed again 5 min later in order to determine the mass increment caused by the second wax coating (Fig. 2, panel b). Geometric bodies of different known surface areas (four metal cubes and four wooden spheres, 5.9–77.5 cm^2) were treated accordingly for calibration purposes. The use of different calibration body materials resulted in negligible differences concerning surface adhesion during the initial coating step. The regression relationship between mass increment and surface area of the calibration bodies ($y = 0.0008x–0.0909$, $r^2 = 0.9974$) was used to determine the surface area of all assessed coral colonies.

Planar projection photography

The planar projection of coral fragments was photographed using a digital camera (Casio® QV-R40; resolution: 4.0 megapixels) at a vertical position relative to the natural growth orientation of the colonies. Callipers were held in-plane with top extensions of the fragments for image scaling. Processing of photographs was carried out using image analysis software (*ImageJ*, V. 1.37 m, National Institutes of Health, USA). The *Straight line* tool and *Set scale* function were applied to transform the depicted callipers scale into pixel dimension. The perimeter of each fragment was then digitally encircled using the *Polygon* tool at 50% zoom (Fig. 2, panel c). The enclosed area was subsequently calculated (in square millimetres) using the integrated *Measure* function. Measurements at different zoom levels (50, 75 and 100%) of the three selected colonies representing the largest, smallest, and average size classes from three growth forms, resulted in an error of 0.3 ± 0.3%. The methodological error determined by repeated digitising of one fragment was 0.4%, which results in a negligible total error of <1%.

Computer tomography and 3-D surface reconstruction

Tomographic records of corals and calibration bodies (3 polyvinyl chloride cubes; accuracy: 0.01 mm; fixed onto ceramic tiles) were produced in air by conventional medical CT, using a Siemens Somatom Sensation 64® tomograph. CT tube voltage of 120 kV (Eff mAs 341) and a 310-mm field of view were applied. The integrated Somaris software (Syngo CT 2006A, Siemens, Germany) was used for data acquisition. Resulting stacks of image slices (DICOM image format; slice dimensions: 512 × 512 pixels; voxel size: 0.605 × 0.605 × 0.6 mm) were further processed in a computer-aided surface reconstruction procedure using the software *Amira*® (V. 4.1.1; Mercury Computer Systems SAS, France). Image stacks of the calibration bodies were loaded to *Amira*® and regular 3-D isosurfaces (object surface rendering within a 3-D scalar field with regular Cartesian coordinates) were created by application of the integrated *Isosurface* tool. The *Isosurface* tool combined all image slice data of an object and generated a polygonal surface model composed of triangles using a specific threshold value (Hounsfield Unit corresponding to X-ray attenuation values) defining the distinct boundary between object surface and the surrounding air. Different threshold values (75, 0, −100, −150, −200, −300, −400, −500 and −600) were tried for isosurface generation of all calibration bodies to determine the closest fit to the actual known surface area, followed by the creation of a new *Surface,* including a 3-D *Surface View* (option: vertex normal) within the *Surface Editor* tool. The *Surface Editor* tool was used to remove the ceramic tiles and remaining artefacts not belonging to the calibration bodies originating from background noise. Thereafter, a new *Surface* was computed to measure the surface area through the application of the *Surface Area* tool. Surface area values and threshold parameters in isosurface creation of calibration bodies showed a strong polynomial correlation ($r^2 = 0.9998$), which allowed for the calculation of a closest-fit threshold value (−354). This threshold value was used in the subsequent isosurface computation of all measured coral colonies.

Data acquisition and processing for coral colonies were carried out as described above using the closest-fit threshold value (−354) derived from calibration bodies for isosurface generation. The *Surface Editor* tool was applied to extract the reconstructed coral surface precisely along the reference plane lining the base of each colony. Critical visual inspections of generated 3-D coral models in comparison to the actual coral colonies were performed to ensure optimal settings for image processing (Kruszynski et al. 2006, 2007) and thus, realistic results of surface area measurements (Fig. 2, panel d).

Data analysis

Percentage accuracy of established techniques

Compiled surface area estimates derived from the four different established techniques were compared to CT-derived reference values for all coral specimens to calculate the percentage accuracy using the equation:

$$\%\ \text{of CT} = \text{Area value of established technique} / \text{Area value of CT} \times 100$$

From these results, the genus-specific average percentage accuracy was computed for all the established techniques. Differences found for surface area values between established techniques and CT reference were analysed by Wilcoxon signed ranks tests (2-tailed).

Approximation factors

Surface area values for all coral specimens derived from established techniques were subsequently compared to the respective CT reference values to generate AF (AF = ratio of CT-derived area to area from established techniques). Genus-specific average AFs were subsequently calculated from ratios of all the assessed specimens. The term AF was chosen in this study to prevent confusion with Dahl's (1973) term SI (surface index).

Results

Comparative analyses of area estimates by established techniques to CT reference showed significant surface area over- and underestimations for the majority (82%) of established techniques analysed and coral genera assessed (Table 2). An example of the different surface area values obtained by the use of different techniques for *Acropora* specimen # 10 is given in Table 3. The highest accuracy to CT reference values including all coral genera was found for geometric approximations; except for *Acropora* spp., for which Wax Coating nearly replicated area values obtained by CT (Table 2). Simple Geometry performed most accurately with branching *P. damicornis* and foliose *Montipora* sp. corals, while Advanced Geometry showed the highest accuracy in assessing branching *Acropora* spp.. In the case of *G. fascicularis*, Simple Geometry accuracy was identical to Wax Coating (55%). Similar accuracy resulting from under- and overestimation of CT reference was also found for Advanced Geometry and Wax Coating assessing *P. damicornis* (Table 2). Except for *Acropora* spp., Wax Coating reached intermediate accuracy, ranging from 47 to 74%. Planar Projection Photography displayed

Table 2 Accuracy of established techniques in comparison to CT reference

Growth form	Branching						Massive		Foliose		Disc	
Coral	*Acropora* spp.		*L. pertusa*		*P. damicornis*		*G. fascicularis*		*Montipora* sp.		*Fungia* spp.	
SG	258	$n = 12$**	168	$n = 13$**	116	$n = 12$ n.d.	55	$n = 8$*	104	$n = 12$ n.d.	78	$n = 11$**
AG	108	$n = 12$ n.d.	141	$n = 13$*	127	$n = 12$**	–		76	$n = 12$**	–	
WA	101	$n = 11$ n.d.	57	$n = 13$**	74	$n = 12$**	55	$n = 8$*	70	$n = 12$**	47	$n = 11$**
PP	19	$n = 12$**	21	$n = 13$**	21	$n = 12$**	36	$n = 8$*	12	$n = 12$**	27	$n = 11$**

Values are given as percentage accuracy of CT. Significant differences in surface area values found for the respective established techniques are indicated by asterisks: * $p < 0.05$; ** $p < 0.005$; n.d. indicates comparisons where no significant difference was found. Abbreviations: SG = Simple Geometry; AG = Advanced Geometry; WA = Wax Coating; PP = Planar Projection Photography; CT = Computer Tomography and 3-D surface reconstruction

Table 3 Surface area values for *Acropora* specimen #10 obtained by different techniques

Acropora coral #10	Method				
	SG	AG	WA	PP	CT
Surface area (cm^2)	537	333	327	41	361

Abbreviations: SG = Simple Geometry; AG = Advanced Geometry; WA = Wax Coating; PP = Planar Projection Photography; CT = Computer Tomography and 3-D surface reconstruction

low accuracy in the measurement of all genera (12–36%). The branching cold water coral *L. pertusa* was most accurately assessed by Advanced Geometry (141%), closely followed by Wax Coating (57%); while Simple Geometry delivered the highest accuracy to CT reference for *Fungia* spp. (78%). AFs computed by comparison of established techniques and CT area values reflected the results obtained for percentage accuracy of established techniques, indicated by established techniques of high accuracy showing AF values equal to, or closely approaching, 1 (Table 4).

Discussion

The majority of comparisons between established techniques and CT reference reveal significantly different results when quantifying the surface area of identical coral colonies. This demonstrates a need for standardisation, as many past studies have used and present studies use different approaches for coral surface area quantification to standardise equivalent parameters (Meyer and Schultz 1985; Tanner 1995; Goffredo et al. 2004). CT in combination with 3-D reconstruction offers accurate surface area quantification (Laforsch et al. 2008) and can therefore serve as a reference for standardisation.

The genera-wide identified high accuracy of geometric approximations indicates the appropriateness of these non-invasive and practical techniques for coral surface area quantification. Simple Geometry results for the finely branched *P. damicornis* and the foliose *Montipora* sp. show no significant differences to CT reference values. Furthermore, application of Advanced Geometry increases accuracy of Simple Geometry (by 27–150%) for 50% (branching corals: *Acropora* spp. and *L. pertusa*) of all coral genera assessed by both geometric approaches. Wax Coating demonstrates higher accuracy (101%) in the assessment of *Acropora* spp. compared with Advanced Geometry (108%), which may be explained by the sealing of the intricate skeleton topography of *Acropora* spp. colonies (e.g., protruding corallites) by the first coating step of Wax Coating and by CT scanning at a resolution of 0.6 mm, potentially resulting in the generation and subsequent measurement of similar surface topographies. For the

Table 4 Approximation factors (AF) for conversion of surface area values derived by established techniques in relation to CT accuracy

Growth form	Branching			Massive	Foliose	Disc
Coral	*Acropora* spp.	*L. pertusa*	*P. damicornis*	*G. fascicularis*	*Montipora* sp.	*Fungia* spp.
SG	0.44 ± 0.05	0.62 ± 0.03	0.94 ± 0.08	1.86 ± 0.09	1.00 ± 0.06	1.74 ± 0.32
AG	0.95 ± 0.04	0.75 ± 0.05	0.83 ± 0.05	–	1.37 ± 0.09	–
WA	1.00 ± 0.03	1.79 ± 0.07	1.36 ± 0.04	1.86 ± 0.10	1.44 ± 0.03	2.32 ± 0.27
PP	9.04 ± 1.28	5.41 ± 0.64	6.11 ± 1.12	2.82 ± 0.16	11.58 ± 1.99	4.59 ± 0.85

Values are given as average AF calculated from all specimens of the respective genus ($n = 8$–13) ± standard error. Abbreviations: SG = Simple Geometry; AG = Advanced Geometry; WA = Wax Coating; PP = Planar Projection Photography; CT = Computer Tomography and 3-D surface reconstruction majority of corals, application of Wax Coating delivers accuracy comparable to geometric approximations (e.g., Simple Geometry and Wax Coating with *G. fascicularis*), thus qualifying Wax Coating as a passable substitute for geometry. However, Simple Geometry and Advanced Geometry provide in addition to accuracy, low cost and ubiquitous applicability, the deciding advantages of non-invasive application with living coral specimens, which are not feasible by Wax Coating. Low accuracy found for Planar Projection Photography (12–36%) emphasises its apparent 2-D limitation. For all measured coral colonies, surface area values obtained by Planar Projection Photography underestimate CT reference by a factor ranging between 2.6 and 27.2. Overall, the lowest accuracy (12%) derived by Planar Projection Photography for the foliose coral *Montipora* sp. may result from the natural growth orientation (diagonal upright) of the corals during recording of photographs. Accuracy delivered by Planar Projection Photography for surface area estimates of rather horizontal coral growth forms (e.g., plate forms) that were not assessed by this study, may, however, stay within an acceptable range.

Improved accuracy of surface area values derived from established techniques can be achieved by mathematical approximation in relation to CT accuracy using AF values, presented here. Consequently, data from various studies can be transformed by application of AF to improved surface area estimates and facilitate standardised comparison. As this study represents the first comparison between a variety of established techniques and the contemporarily the most accurate CT-based method, AF values for Planar Projection Photography represent the only category comparable to existing literature data (i.e., SI). SI ratios developed by previous studies (Dahl 1973; Alcala and Vogt 1996) are lacking an accurate reference. Holmes (2008) presented SI ratios of surface area estimates from 3-D laser scanning and planar projection data using laser scanning accuracy as reference. As the resolution of laser scanning still differs considerably from the reference of the present study (laser: 2.5 mm; CT: 0.6 mm) only rough comparisons are feasible. Nonetheless, SI values presented by Holmes (2008) for *Open branching* and *Complex branching* (6.16 and 6.43, respectively) are in the same range as AF values found here for the branching *P. damicornis* (6.11). AF values computed for the massive *G. fascicularis* are lower (2.82) than the SI for massive corals shown by Holmes (2008) (3.20), which may be explained by the difference in resolution of reference methods. Owing to the distinct skeleton topography (i.e., large protruding corallites; see Fig. 1, panel c), causing a substantial increase in surface area, AF values calculated for the massive *G. fascicularis* by this study should only find application in the work with this species, as species specific growth characteristics alter AF values considerably, thus becoming unsuitable for massive coral species lacking similar skeleton topography (e.g., *Porites* spp.). For surface area quantification of massive corals exhibiting rather smooth surface topography, Courtney et al. (2007) have presented log-linear models applicable for in situ as well as for laboratory studies.

Accuracy of established techniques and specific AF values, presented in this study, are derived from comparison, and thus dependent on the accuracy of the reference technique (i.e., CT). As CT is limited to detection of the coral carbonate skeleton only, accurate CT measurements of the intricate skeleton topography may cause under- or overestimation of the actual tissue surface area composed by the polyps and the coenosarc. Therefore, further studies are necessary to find possible solutions for this limitation, e.g., by application of different tomographic imaging techniques (Frahm et al. 1986), supporting the possibility for detection and discrimination of organic and inorganic coral components. In addition, solely combination of the latter with measurements of living corals under natural conditions (i.e., submerged in seawater, extended polyps and tentacles), will finally provide high accuracy quantification of coral tissue surface area.

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