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Quantifying the shelter capacity of coral reefs using photogrammetric 3D modeling: From colonies to reefscapes

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ABSTRACT

Structural complexity plays a key role in the functioning of coral reef ecosystems. Reef-building corals are major contributors to this complexity, providing shelter and food for numerous invertebrates and fish species. Both structural complexity and shelter capacity of reefscapes are determined by several components such as spurs and grooves, slope, caves and holes, vegetation and coral colonies. Quantifying the shelter capacity from coral colonies to reefscapes is a fundamental step to estimating ecosystem potential to support biodiversity. Here, we applied underwater photogrammetry to quantify shelter volumes provided by individual coral colonies. Overall, 120 3D models of coral colonies from branching, massive, columnar and tabular growth forms were studied. Three reefscapes were also 3D modeled. The study encompasses three Indo-Pacific Islands: Reunion, Europa and New Caledonia. At the colony level, measurements of diameter, planar area, surface and shelter volume were computed. At the reefscape, the diameter and planar area of each colony were extracted from orthomosaics and then used to estimate shelter capacity. Linear models had high accuracy for predicting shelter volume (a 3D metric) from 2D metrics: the diameter= 83.1%, R^2= 0.95; the planar area= 87.5%, R^2= 0.95 and the colony surface= 87.3%, R^2= 0.96. The surface complexity and the shelter volume of the colonies allowed inferring the size of shelters provided by coral growth forms. Quantitative descriptors (i.e. relative percentage of shelter by growth form, the abundance of coral colonies, "Shannon-Shelter Index") revealed reefscape-scale shelter differences.

Our major finding is that planar area and diameter of coral colonies are satisfactory proxies for estimating shelter volume. These new proxies allow 2D metrics to quantify 3D shelter provision, which can support scientists and managers in conservation actions since such metrics are widely used in monitoring programs. Future investigations on the relationships between shelter provision and reef biodiversity will improve the understanding of these complex ecosystems.

1. Introduction

Structural complexity of ecosystems is a well-studied field in ecology. This important feature is mainly determined by abiotic characteristics (i.e. mineral composition, topography), biotic structures resulting from the activity of engineer organisms, and ecosystem age (Margalef, 1963; Loya, 1972; Jones et al., 1994; Richardsonet al., 2017a). The central role of structural complexity in ecosystem functioning and its influence on associated biodiversity and successional processes has been shown in terrestrial (Tews et al., 2004), freshwater (Kalacska et al.,

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2018) and marine ecosystems (Graham and Nash, 2013). In consequence studies increasingly recommended to prioritizing structurally complex habitats for conservation purposes (e.g. Rees et al., 2018; Fukunaga et al., 2019). Tropical reefs are among the most ecologically and structurally diverse ecosystems on the planet (Yanovski and Abelson, 2019). Representing only 0.1% of the oceans' surface, they host >25% of marine biodiversity. Yet, they are critically threatened by human impacts, natural catastrophes and climate change (Bozec et al., 2015; Cornwall, 2019).

As ecosystem engineers, scleractinian corals are the principal contributors to the structural complexity of tropical reefs. The spatial arrangement, morphology and abundance of living coral colonies largely shape the topographic complexity (Zawadaet al., 2010) and shelter capacity of reefscapes (Richardsonet al., 2017b), providing refuges from physical stress, competition and predation to a multitude of reef organisms (e.g. fishes, invertebrates) (Hixon and Beets, 1993). In addition, hydrodynamics and temperature condition the presence and abundance of coral growth forms, as well as the morphology of individual coral colonies, and may thus influence the availability of refuges (Monismith, 2007; Lenihan et al., 2015; Pu, 2016). Shelter availability in coral reefs is also determined by the structures of dead coral colonies, the caverns or interstices in the reef matrix, and at larger scales, by the spurs and grooves, fissures, walls and reef slopes (Friedlander and Parrish, 1998). Vegetative components, such as erect macroalgae can also contribute to shelter capacity and provide key habitats for diverse communities of epifauna, juvenile and adult fishes (Fulton et al., 2019; Pu et al., 2019). Overall, structural complexity enhances the diversity and biomass of fish assemblages (Darling et al., 2017; Wedding et al., 2019), and provides ecosystem services such as fish productivity (Rogers et al., 2014) and coastal protection (Harris et al., 2018). While quantitative assessments of structural complexity have become an important topic in reef research over the last two decades (e.g. Bythell et al., 2001; Knudby and LeDrew, 2007), technical limitations have hindered progress in this field. New tools are now available thanks to novel technologies and advances in computing power (Burns et al., 2015a; Burnset al., 2015b), but whereas these new technologies should increasingly complement coral reefs surveys (Obura et al., 2019), management applications are still lacking.

Photogrammetry is a non-invasive and efficient technique that uses images to create 3D models (Westoby et al., 2012). The high accuracy of 3D reconstructions provides a fine, cross-scale quantification of several embedded metrics from the coral colony to the entire reefscape (i.e. surfaces, volumes and fractal dimensions*)* (Figueira et al., 2015; Burns et al., 2016). These measures are especially valuable for temporal monitoring (Fukunaga et al., 2019) and analyses of reef functional ecology. For instance, the assessment of 3D metrics improves the prediction of the structure of fish assemblages and can contribute to explain associated biodiversity (Price et al., 2019; Wedding et al., 2019). Moreover, using 2D metrics from images to estimate 3D metrics allows incorporation of three-dimensional aspects into reef monitoring (House et al., 2018).

Coral morphology, more commonly known as 'growth form', is one of the most important life history traits of scleractinian corals (Darling et al., 2012) and an strong predictor of coral ecosystem functions (Denis et al., 2017). For instance, Kerry and Bellwood (2012), Kerry and Bellwood (2015) highlighted the importance of particular corals (i.e. tabular growth forms) as keystone structures that disproportionally influence the abundance of large benthic fishes and thus whole ecosystem functioning, confirming the results of previous studies (Tews et al., 2004; Alvarez-Filip et al., 2011). Wilson et al. (2008) observed that pomacentrid fishes used different growth forms (i.e. tabular or branching) depending on their life stage. The relation between individual colony features and the functional characteristics at the reefscape scale was investigated for the first time by González-Barrios and Álvarez-Filip (2018). These authors proposed a quantitative coefficient (Reef Functional Index, RFI) that combines coral cover, structural complexity and calcification rate to evaluate the functional contribution of reef-building and structural complexity for Caribbean coral communities. However, this approach did not include a quantitative estimation of shelter volume provided by the different colony growth forms. The role of the diversity of shelter volumes provided by specific growth forms in structuring associated biodiversity and ecosystem functioning at the reefscape scale is yet to be fully understood and, above all, quantified. This could considerably enhance the evaluation of the potential of a reefscape to support biodiverse and productive assemblages (e.g. fishes, invertebrates, etc.) and facilitates the assessment of ecosystem services like coastal protection and resource provision (Graham, 2014; Harris et al., 2018).

Our study proposes a novel method to quantify the shelter volume provided by living colonies of scleractinian corals from the individual colony to reefscape scales. Here, we used underwater photogrammetry to create 3D models of 120 coral colonies of varying growth forms and sizes. We quantified their shelter volume and surface complexity through 3D analyses and inferred the size of the shelters provided by each growth form. We then fitted predictive linear models of shelter volume (a 3D metric) based on either colony diameter, planar area and colony surface (2D metrics) for each major growth form of reef-building corals, enabling the use of 2D measures to estimate volumes. Finally, we applied these predictors at the scale of reefscapes (i.e. hundreds of m^2) to provide large-scale estimates of shelter volumes, overall and by coral growth form. We also evaluated the abundance and the size of coral colonies by growth form at the reefscape scale to further illustrate the wide range of possibilities offered by this new tool. In addition, we developed an R code to automate this process and make it easily usable by end users.

2. Material and methods

2.1. Study sites

The study was conducted at three islands of the French oversea territories of the Indian and Pacific Oceans from March 2018 to April 2019, encompassing outer reef slopes and shallow reef flats to obtain a wide representation of coral growth forms and sizes. The reefscape study sites were chosen such as to maximize contrast in structural complexity and conservation status. Two sites are located in the western Indian Ocean, Reunion and Europa islands, and one in the Southwest Pacific Ocean, New Caledonia (Fig. 1).

2.2. Coral colony-level workflow

2.2.1. Image acquisition

In situ sampling was designed to obtain the largest range of growth forms and sizes of reef-building coral colonies. In this study, we considered only living corals with a diameter ≥10 cm. This limitation rests upon two principal reasons: 1) only colonies with diameter ≥10 cm display a clear and defined growth form, and 2) technical limitations of image acquisition of small colonies in the field. Colonies were categorized as: branching, columnar, massive and tabular as proposed by Veron (2000). Foliaceous/laminar growth forms were analysed but not considered in this study due to insufficient sample sizes (see Supplementary Material Fig. S1). Also, helmet-shaped growth forms were excluded since only two colonies were found at our study sites. Encrusting growth forms were not included for two reasons: 1) the 3D model analyses are not suitable, and 2) it was assumed that they have no internal shelter volume (colony shape matches the underlying substrate).

Colonies were sampled haphazardly during one-hour dives on outer reef slopes and during two hours of snorkeling on reef flats. The observer was equipped with a Sony Alpha 7II camera and a Sony FE16-35 mm F4 lens in a Nauticam NA-A7II housing and 180 mm glass dome port. Images were taken from multiple angles, both zenith (i.e. pointing

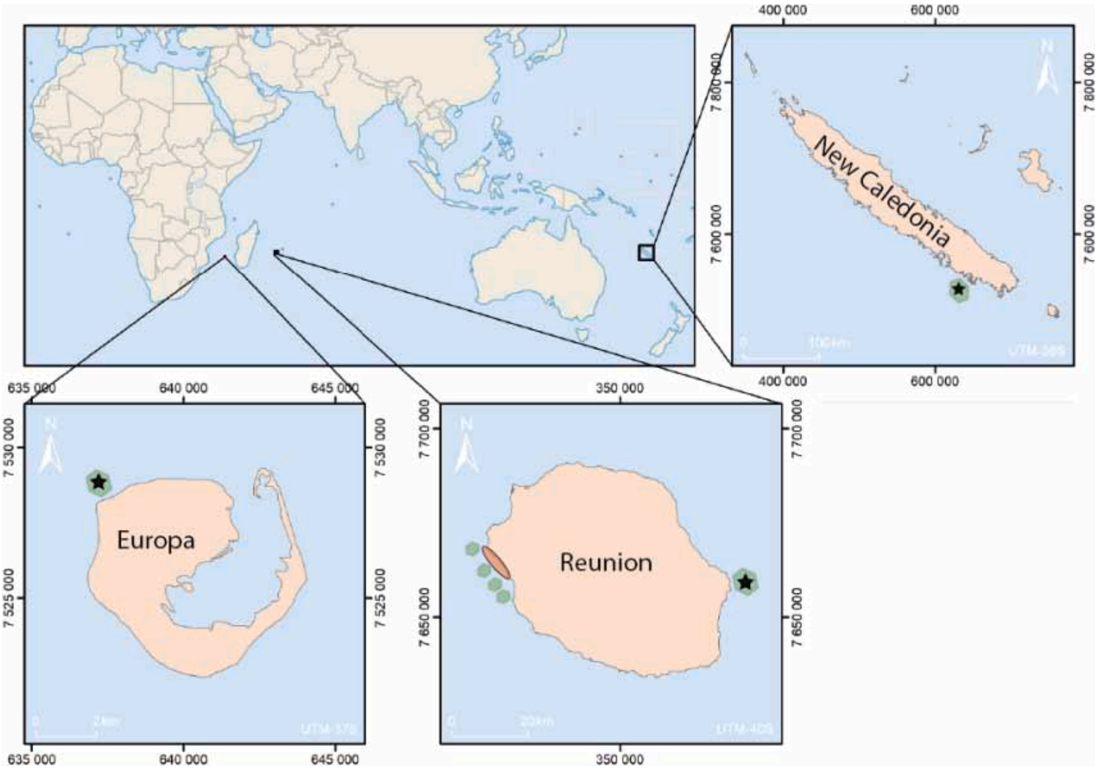


Fig. 1. Map of study sites. Stars indicate reefscape study sites. Coral colony sampling sites are marked with a green hexagon for outer reef slopes and with an orange ellipse for reef flats.

downwards) and oblique, and from two to four circles at different heights around the colony. This underwater photogrammetry protocol was conceived to ensure appropriate overlap of photographic images for 3D reconstructions (>70%). A scale bar was placed close to each colony and captured in the images for scaling the 3D model. The number of captured images depended on colony size and complexity (50–250 per colony). In total, 120 colonies were 3D-modelled for further analyses.

2.2.2. *Coral colonies 3D reconstruction*

For each colony, a 3D model was reconstructed using the photogrammetry software Agisoft Metashape Professional (version 1.5.0 build 7618) following five steps: (i) estimating image quality as function of the sharpness, exposure, focus, resolution and field depth of the images; (ii) aligning the cameras and generating a sparse point cloud calculated by the software (Fig. 2A); (iii) scaling the sparse cloud using the scale bar; (iv) building a dense point cloud, with depth information for each camera and densification algorithms (Fig. 2B); (v) building a 3D mesh, the points of dense cloud are connected to create triangles and define a shape (a polyhedral object). Mesh texture was processed, although this step it is not compulsory to perform the measures and 3D analyses (Fig. 2C). All models were oriented by the planar projection using the orthographic view (Fig. 2D), then isolated ("cleaning" coral colony model from other elements of reconstruction like reef foundation) and "closed" with Agisoft Metashape editing tools (mesh tool: *Close Holes)* (Fig. 2D, E). Finally, all models were exported for quantitative analysis and shelter volume computation.

2.2.3. *Measurement of 2D and 3D metrics*

For each colony 3D model, the planar area (i.e. 2D projected area) was calculated with the geographic information system (GIS) software Global Mapper (version 19.0), using spatial analysis tools from an orthographic projection of the 3D models (Fig. 3A, B). Then, the maximum diameter (henceforth called diameter) was computed using the open source GIS software QGIS (version 3.4.6 Madeira) applying the *minimum enclosing circles* tool (Fig. 3C). These parameters were calculated to obtain commons metrics at the colony and reefscape scale. Also, quantitative measures of the colony's external surface (Fig. 2F represented by a light blue line) and volume (V_c in Fig. 2F) were computed from the colony 3D models using the open source system for processing and editing 3D models, MeshLab (version 2016.12).

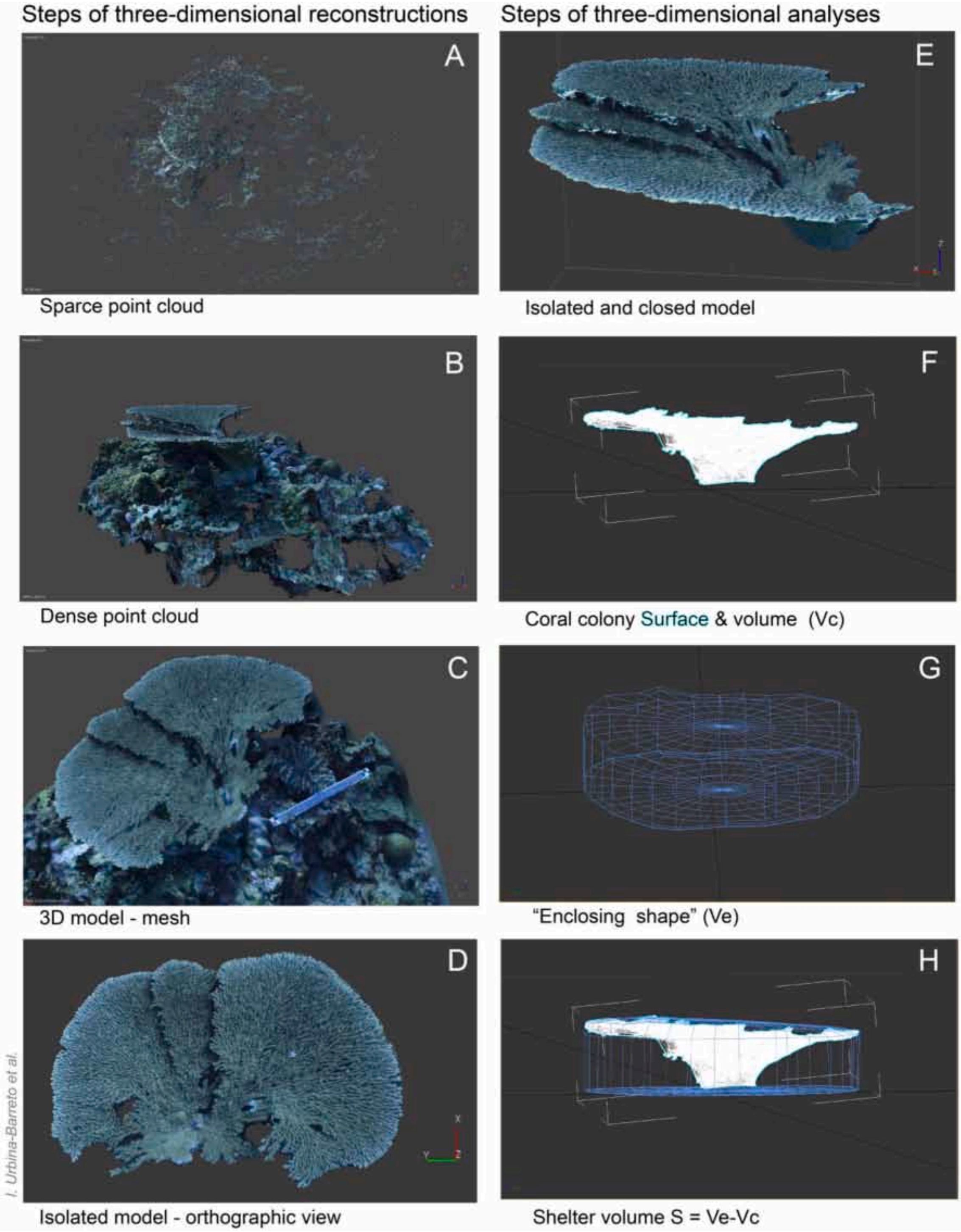
2.2.4. *Three-dimensional analyses: Shelter volume assessment and description*

Three-dimensional analysis for shelter volume estimation (in dm^3) was performed using the 3D computer graphic program Autodesk-3ds Max2020. For each coral colony model, the process followed four steps: (i) creating a geode composed of 960 faces enveloping the colony (ii) shrinking the geode to the shape of the coral colony with the basis defined by the planar projection bounds (Fig. 2H), thus obtaining an *"enclosing shape"* (Fig. 2G); (iii) computing the *"enclosing shape"* volume (V_e) using MeshLab software; (iv) calculating the shelter volume (S) as the difference between the "*enclosing shape*" volume and the colony volume (V_c). The shelter volume ($S = V_e - V_c$) represents the empty space within the enclosing shape and the coral colony volume (Fig. 2H).

Differences in the shelter provision by colonies across the four growth forms were described calculating: (i) the shelter size factor, as the ratio of the shelter volume to the surface of the colony; (ii) the surface complexity, as the ratio of the surface to the planar area of the colony. Both descriptors allow inferring the level of fragmentation/splitting of the shelter volume and the size of available spaces offered by the colony structure. Analyses of variance (ANOVA) and Tukey HSD post-hoc test were performed to test the differences across the four growth forms.

2.2.5. *Construction of shelter predictive models*

First, a Local Polynomial Regression (LOESS) smooth regression was fitted to view relationships between shelter volume and the three metrics previously computed (i.e. diameter, planar area, colony surface)



Sparce point cloud

Isolated and closed model

Dense point cloud

Coral colony Surface & volume (Vc)

3D model - mesh

“Enclosing shape” (Ve)

Isolated model - orthographic view

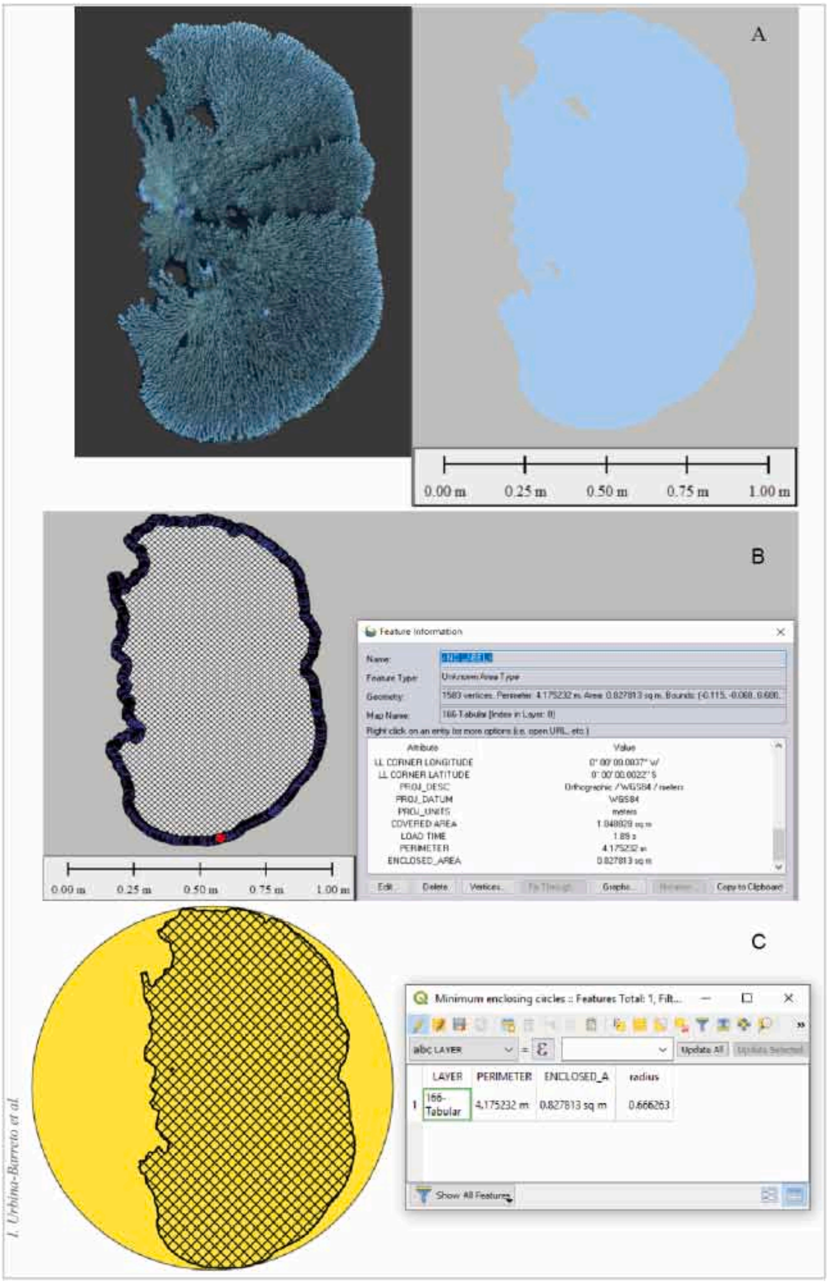
Shelter volume S = Ve-Vc

Fig. 2. Steps of 3D reconstruction in Agisoft Metashape (left column: A, B, C, D) and 3D analysis in Autodesk-3ds Max (right column: E, F, G, H) for a tabular coral colony model (Figs. S2, S3, S4 for branching, columnar and massive colonies).

without assumptions about the distribution or linearity of the data. Then, all data were log transformed and three log–log linear models of shelter volume (S, in dm^3) from 2D (diameter and planar area) and 3D (colony surface) metrics were estimated, taking into account the effects of site and growth form using the *‘lm’* function in R; adjusted-R^2 was calculated for each model. After log–log transformations, relationships between shelter volume and diameter, planar area and colony surface were viewed by study site (Fig. S5). Analyses of covariance (ANCOVAs) and Tukey HSD post-hoc test evaluated the possible influence of site and growth form on the predictions.

Third, predictor intervals (the uncertainty for a single specific outcome) and confidence intervals, both at 95%, were computed by bootstrap method. In addition, leave-one-out cross validations (LOOCV) were performed to test the fitness of the predictive models.

Data exploration and analyses were conducted with R sofware (R Core Team, 2019). To perform linear models, *‘car’* (Fox and Weisberg, 2019) and *‘multicomp*’ (Hothorn et al., 2008) packages were used. Figures were produced using *‘ggplot2*’ (Wickman, 2016) and *‘ggpubr’* (Kassambara, 2019) packages.



Feature Information

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Feature Type: Unknown Area Type

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Map Name: 166-Tabular [Index in Layer: 0]

Right click on an entry for more options (i.e. open URL, etc.)

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LL CORNER LATITUDE	0° 00' 00.0022" S
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PROJ_DATUM	WGS84
PROJ_UNITS	meters
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LOAD TIME	1.89 s
PERIMETER	4.175232 m
ENCLOSED_AREA	0.827813 sq m

Minimum enclosing circles :: Features Total: 1, Filt...

	LAYER	PERIMETER	ENCLOSED_A	radius
1	166-Tabular	4.175232 m	0.827813 sq m	0.666263

Fig. 3. Process to compute 2D metrics of coral colonies: orthographic view/projection (A), computation of planar area (B) and diameter (C).

2.3. Reefscape-level workflow

2.3.1. Image acquisition

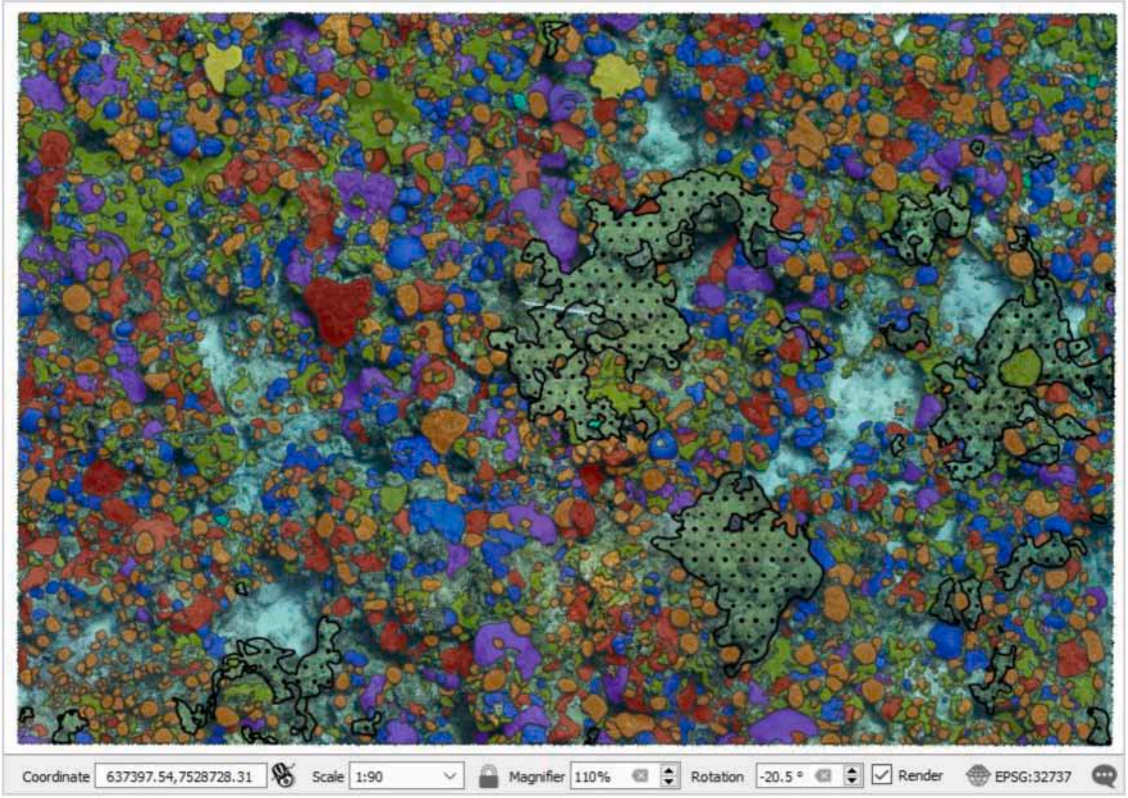
Images of the three reefscapes were collected by scuba divers and using the same photographic equipment used for coral colonies; the underwater photogrammetry protocol was conceived to cover an area of 150 m^2 (15 × 10 m patch) at ~15 m depth, following the method described in Elise et al. (2019). Images were taken along several parallel lines 3 m above, and oriented perpendicular to, the seafloor. Additional oblique images were taken for high-complexity reef components. In order to scale and georeference 3D models, three scale-bars and eight Ground Control Points (GCPs, metal pieces with checkered pattern) were placed across the study area. Geographical coordinates (x, y) and depth (z) were recorded with a GPS at the sea surface and depth gauge from dive computer on the bottom, respectively. The number of captured images ranged from 750 to 1200 per site.

2.3.2. Reefscape 3D reconstructions

For each reefscape, a 3D model was reconstructed following the steps described in 2.2.2 with two additional steps: georeferencing and the generation of the orthomosaics (geometrically rectified photographic projection covering 150 m^2) for the future quantitative assessments.

2.3.3. Measurement of 2D metrics

On the orthomosaics, each coral colony was manually delineated as a polygon in QGIS and classified by growth form (Fig. 4). Some growth forms were not included in our dataset (i.e. foliaceous, helmet-shaped, encrusting forms) and were excluded from further analyses. The surface of each polygon was calculated with the QGIS command: *area ($geometry)* in the field calculator tool. The maximum diameter was obtained for each polygon using the procedure presented for the coral colonies.



Coordinate 637397.54,7528728.31 Scale 1:90 Magnifier 110% Rotation -20.5 ° ☑ Render EPSG:32737

Fig. 4. Spatial analysis of Europa reefscape orthomosaic (150 m^2). Colors of polygons represent growth forms of coral colonies: branching (orange), columnar (cyan), encrusting (red), helmet-shaped (purple), massive (blue), tabular (yellow). Other categories like soft corals, algae, *Milleporidae* were also delineated but not considered in this study.

2.3.4. Application of shelter predictive models and calculation of descriptors at the reefscape scale

Planar area and diameter of each polygon delineated on the reefscape orthomosaics were then used to feed the predictive model and compute the corresponding shelter volume of each coral colony; a function in R code was developed to automatize this calculation (see in data availability). The overall shelter capacity (i.e. volume of shelter calculated for the entire reefscape) was obtained by summing the shelter volume estimate for all polygons; this analysis was also performed automatically using a code created in R programming language (R Core Team, 2019). In addition, we investigated the distribution of shelter volumes by growth form in a reefscape by adapting the Shannon index to shelter provider colonies as follows:

$$\text{Shannon shelter index},\ SSI = -\sum p_i log(p_i)$$

where pi = relative shelter volume of a given growth form.

To assess the importance of colony size in providing shelter volume, colonies were grouped into three size classes: small (diameter $\leq$ 30 cm), medium (30 < diameter < 60 cm) and large (diameter $\geq$ 60 cm) and their abundance calculated. Using abundances and shelter volumes, we estimated the mean colony shelter volume by growth form and the relative percentage of shelter volume by colony growth form and size for each reefscape.

3. Results

3.1. Shelter quantification and predictive models

Our training database comprised 3D models of 120 colonies: 52 branching, 26 massive, 25 tabular and 17 columnar. Taxonomically, the four growth forms were *Acropora* spp. and *Pocillopora* spp. for branching colonies, mainly *Favia stelligera* for columnar colonies, *Porites* spp. for massive colonies and *Acropora hyacinthus* for tabular colonies (Table S1). While all growth forms were present at the three sites, most of the largest tabular colonies were found only in New Caledonia. We here present shelter predictive models based on diameter and planar area (Fig. 5-right) and corresponding equations (Table 1); the predictive model based on colony surface is available in Supplementary materials (Table S2).

The LOESS smooth regressions of shelter volume versus each of the three metrics showed linear relationships until approximately 60 cm in diameter, 2,500 cm^2 in planar area (Fig. 5-left) and 5000 cm^2 in colony surface (Fig. S6, Table S2) for tabular, columnar and branching growth forms. Beyond these thresholds the relationships became exponential. For massive corals, relationships were almost linear throughout the size range (Fig. 5-left). ANCOVA and Tukey tests showed that there was no site effect (Tables S3–S5).

Shelter volumes were strongly correlated with the diameter (R^2= 0.95), planar area (R^2= 0.95) and surface (R^2= 0.96) of coral colonies (model summaries Tables S6–S8). The accuracy of the volume predictions (LOOCV- test) was high for the planar area model (87.3%) and the surface model (87,3%) and somewhat lower for the diameter model (83.1%).

For all growth forms, the predicted shelter volume is scaled to colony diameter to the power of approximately 3, to colony planar area and colony surface to the power of 1.5 (Table 1, Table S2). Only massive corals differed significantly from other growth forms for both metrics (colony diameter and planar area): M-T, M-C; M-B (all p < 0.001, Tukey HSD-tests).

While predictions of shelter volumes were generally accurate for all growth forms and metrics throughout the three study sites, this was not the case for the largest tabular colonies in New Caledonia (Fig. S7). The mean ground sample distance GSD (resolution/pixel) of 3D models was

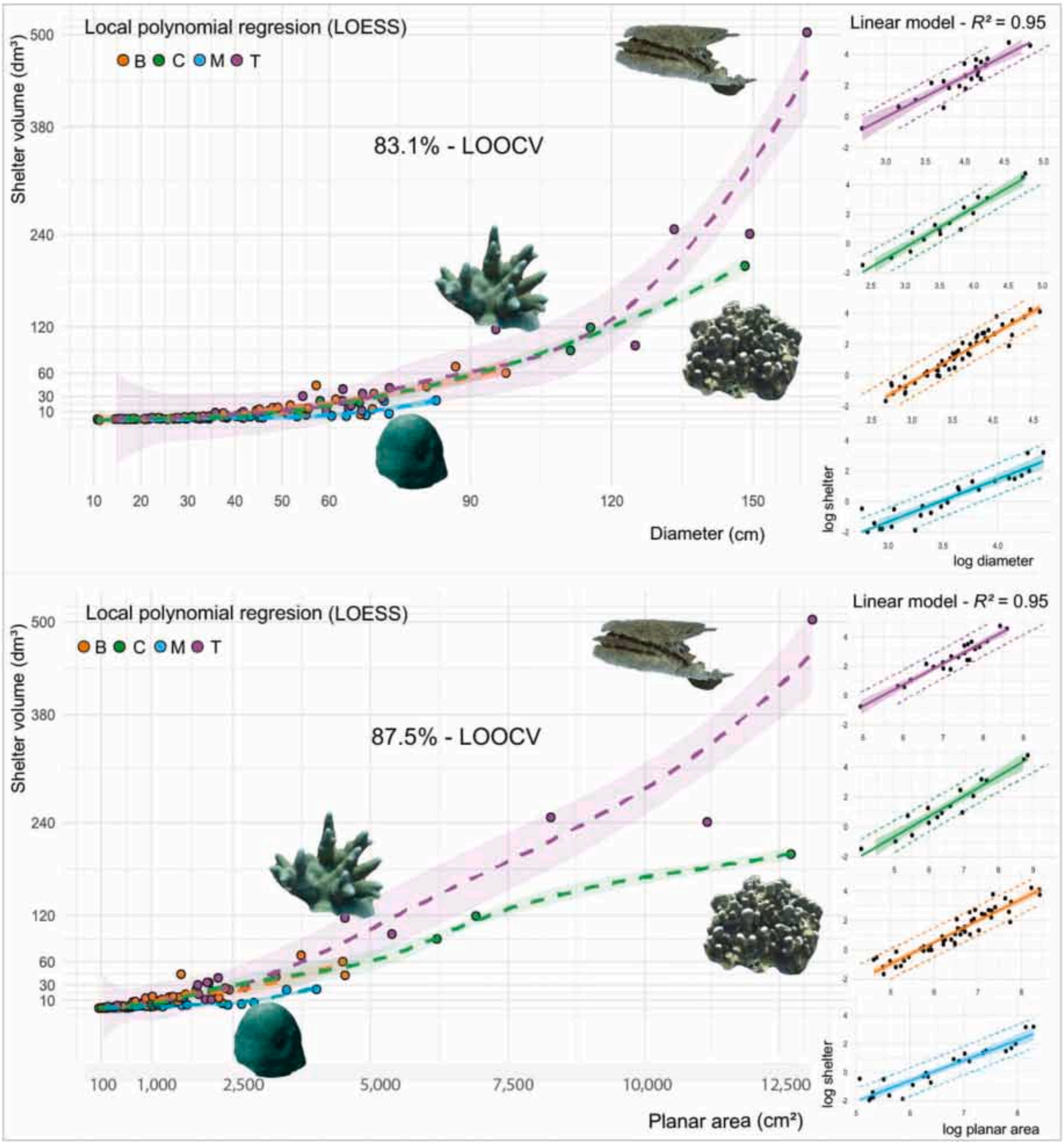


Fig. 5. Shelter volume (dm^3) as a function of diameter (top) and planar area (bottom) for each growth form: B: Branching (orange); C: Columnar (green); M: Massive (blue); T: Tabular (purple) using local polynomial regression. Confidence intervals (95%) are represented by light colored bands. The right column shows log–log linear models with colors indicating growth forms. The confidence intervals (95%) are represented by light colored bands and prediction intervals (95%) are represented by dashed lines.

Table 1

Shelter volume (S) for different coral growth forms predicted from colony diameter and planar area. Equations of the log–log linear models ($\log(y) = b + a \log(x)$) are shown. Different letter codes denote significant differences.

Growth form	Colony diameter (D)	Colony planar area (PA)
Tabular	$\log(S) = -8.66 + 2.83 \log(D) a$	$\log(S) = -8.32 + 1.50 \log(PA) a$
Columnar	$\log(S) = -8.50 + 2.74 \log(D) a$	$\log(S) = -7.37 + 1.34 \log(PA) a$
Branching	$\log(S) = -9.41 + 3.00 \log(D) a$	$\log(S) = -8.31 + 1.47 \log(PA) a$
Massive	$\log(S) = -10.20 + 2.91 \log(D) b$	$\log(S) = -9.69 + 1.49 \log(PA) b$

0.1 cm $pixel^{-1}$. Surface complexity was significantly greater for branching and columnar colonies than for massive and tabular colonies (ANOVA, F= 14.1, $p < 0.001$; Fig. 6 top). Shelter size factor was significantly higher for tabular colonies compared to branching, columnar and massive colonies (ANOVA, F= 16.6, $p < 0.001$; Fig. 6 bottom).

3.2. Estimation of shelter volumes in reefscapes (150 m^2)

As planar area was the most accurate predictor of shelter volume, overall shelter capacity at the scale of reefscapes was calculated based on this metric. Total shelter volume in 150 m^2 of reefscape provided by the coral colonies of four growth forms was highest in New Caledonia reef (1810 dm^3), intermediate at Europa (1045 dm^3) and lowest at Reunion (728 dm^3). Reunion presented higher shelter volumes by columnar and tabular forms compared to Europa, while shelter volume provided by large tabular colonies was higher at New Caledonia compared to the other sites. Accuracy of shelter volume predictions varied according to growth form and reefscape and was highest for

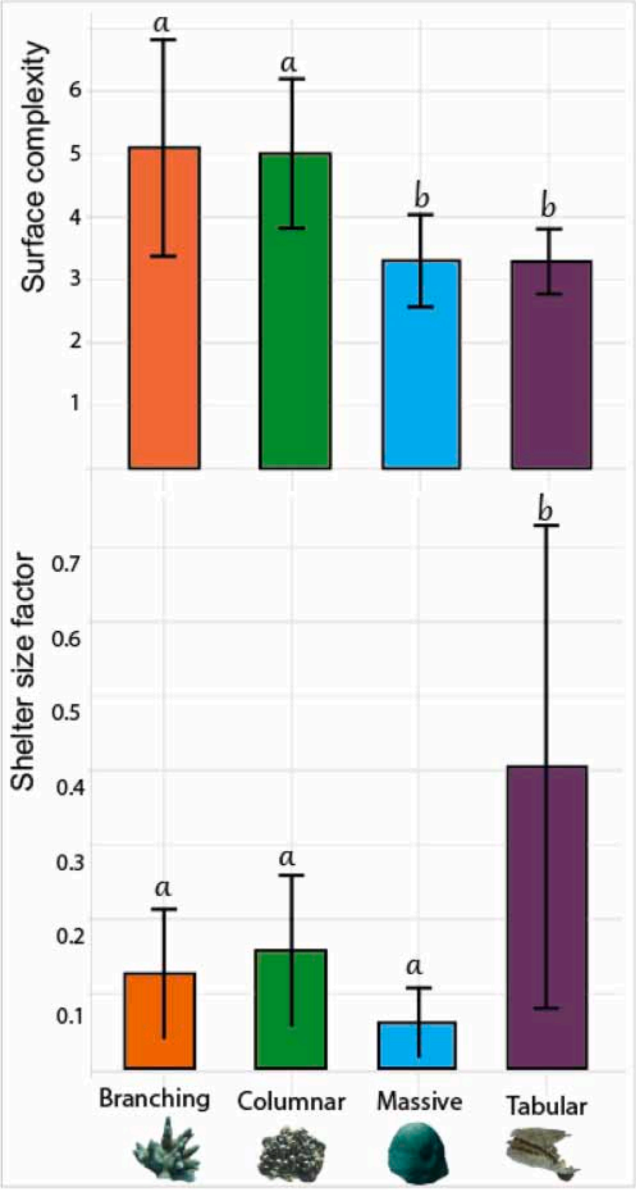


Fig. 6. Mean (±SD) of surface complexity (top) and shelter size factor (bottom). Different letter codes denote significant differences (ANOVA, $p < 0.001$).

Reunion and lowest for New Caledonia (Fig. 7).

The distribution of shelter provided by corals in reefscapes was represented using the treemapping method (Fig. 8). Abundance of shelter providing colonies (branching, columnar, massive and tabular growth forms) was 918 in New Caledonia, 1169 in Europa and 989 in Reunion. Tabular colonies were not abundant but they provided a significant volume of shelter. In contrast, massive colonies were widely represented but their contribution in shelter volume was lower than for other growth forms. The branching form was the principal shelter provider but also the most abundant growth form across the three reefscapes. Finally, the columnar growth form, despite providing high shelter volume, was poorly represented in the three reefscapes studied.

Tabular forms provided the highest mean shelter volume by colony followed by columnar, branching and massive forms (Table 2). It is important to note that this average is directly related to the relative abundance and size distribution of colonies (Table 3). Hence, New Caledonia exposes also the largest structures across all growth forms. New Caledonia's reefscape had the most balanced distribution of shelter providing colonies, i.e. the highest SSI, while SSI was higher at Reunion than at Europa (Table 2).

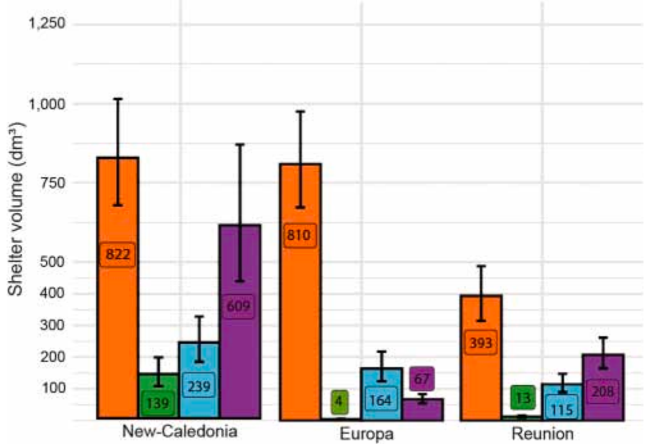


Fig. 7. Predictions for mean shelter volumes (bars) for each reefscape from planar area of colonies by growth forms: branching (orange), columnar (green), massive (blue) and tabular (purple) with lower and upper prediction intervals (black line). Prediction values are indicated for each bar.

4. Discussion

We built predictive models of shelter volume provided by reef building corals from 2D metrics for four major growth forms. Training data for these metrics were obtained entirely from 3D models, reconstructed by photogrammetry of *in situ* coral colonies growing on fore reef slopes and shallow reef flats. The main outcome of this study was the ability to predict shelter volume, a 3D metric, from proxies like colony diameter, planar area or surface, which are 2D metrics. The accuracy of predictions was highest for planar area (87.5%), followed by surface (87.2%) and colony diameter (83.1%). These proxies will make shelter volume estimation largely accessible and will be useful for managers and stakeholders in setting measurable targets for reef conservation adapted to local conditions.

Over the last decade, several quantitative studies investigated the ecosystem roles of corals' morphological traits (e.g. Ferrari et al., 2016; Madin et al., 2016; House et al., 2018; Zawada et al., 2019a). Such traits largely shape the structural complexity of reef habitats and determine the availability of niches, food, shelter and even hydrodynamic conditions (i.e. current velocity, shear, turbulence) (Monismith, 2007; Price et al., 2019), which in turn affect the associated biodiversity and functional process of reef ecosystems. Thus, shelter provision is an important facet of coral reef ecology, and has often been estimated by counting holes and measuring overhangs to better understand the relationships with reef fish assemblages (Friedlander and Parrish, 1998; Ménard et al., 2012). While few studies have attempted to quantify the shelter capacity of coral colonies, likely due to technical and technological limitations, Zawada et al. (2019a), Zawada et al. (2019b) did provide such quantitative measures using similar metrics (convex hull volume) to study the morphology of coral skeletons.

Our predictive models showed differences in shelter provision across the four growth forms. For a given size, tabular colonies provided highest shelter volumes, followed by columnar, branching and massive growth forms in decreasing order. Growth form also determines the size and form of provided spaces, with highest values of colony surface complexity corresponding to lowest values of the shelter size factor and thus smaller-sized shelters. Massive colonies were an exception in having low values of surface complexity combined with small-sized shelters. Indeed, massive colonies of our data set present protuberances and small grooves contributing to their shelter volume. It should be noted here that massive colonies that have a space at their basis were classified as 'helmet-shaped' forms and were not included in our data set. Thus, two

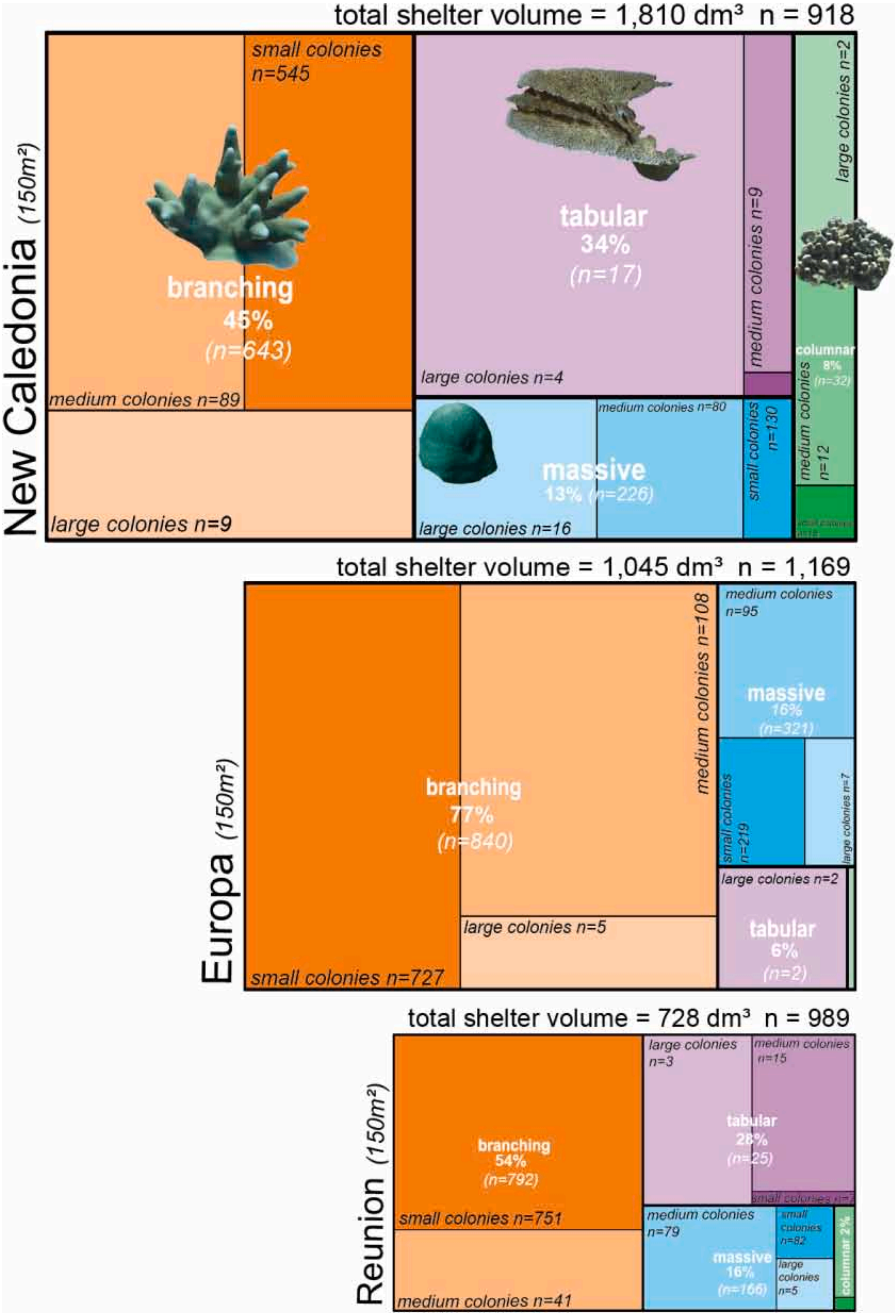


Fig. 8. Treemap presentation of the overall shelter volume provided by corals and its distribution by colony growth form and size for each reefscape. Colors denote different growth forms: branching (orange scale), columnar (green scale), massive (blue scale) and tabular (purple scale). Rectangle size represents shelter volume provided by each colony size class: small colonies (diameter ≤ 30 cm) in dark tone, medium (30 < diameter < 60 cm) and large colonies (diameter ≥ 60 cm) in light tone.

Table 2
Mean shelter volume per coral colony by growth forms and Shannon-shelter index at each reefscape, V_{Sh} = mean shelter volume (dm^3), n_{total} = total abundance of colonies by reefscape.

	Mean shelter volume by coral colony (V_{Sh}/n_{total})				Shannon-shelter index (SSI)
	Branching	Columnar	Massive	Tabular	
New Caledonia	822/643 = 1.27	139/32 = 4.35	239/226 = 1.05	609/17 = 35.85	0.51
Europa	810/840 = 0.96	2.72/4 = 0.68	164/321 = 0.51	67/2 = 33.56	0.29
Reunion	0.49	2.09	0.69	8.30	0.45

Table 3
Frequency of colony size classes by growth form and reefscape, S = small (diameter ≤ 30 cm), M = medium (30 < diameter < 60 cm) and L = large (diameter ≥ 60 cm).

	Branching			Columnar			Massive			Tabular		
	S	M	L	S	M	L	S	M	L	S	M	L
New Caledonia	545	89	9	18	12	2	130	80	16	4	9	4
Europa	727	108	5	6	–	–	219	95	7	–	–	2
Reunion	751	41	–	3	3	–	82	166	5	7	15	3

growth forms may have an identical shelter capacity but not necessarily the same spatial shelter distribution or shelter quality. For instance, branching corals will provide a greatly fragmented volume, which will favor small organisms, whereas a tabular coral of similar shelter volume will provide protection for larger organisms. Knowing that fish size (Kulbicki et al., 2015) is an important determinant of other life-history traits such as diet or home range, the relative proportions of the various forms of corals will influence the structure of fish assemblages and their associated ecological processes (Jones and Syms, 1998; Kerry and Bellwood, 2012, 2015; Pereira and Munday, 2016; Darling et al., 2017). Hence, knowing the structure of shelter capacity of reefs may expand our understanding of ecosystem functioning.

The differences in shelter capacity among reefscapes were directly related to the coral growth forms present, their abundance and size distributions at the study sites. Indeed, combinations of sizes and growth forms of colonies have been used as morpho-functional groups to better describe the architecture of coral reefs and their associated biodiversity and services (Alvarez-Filip et al., 2013; González-Barrios and Álvarez-Filip, 2018). For the three reefscapes studied, branching and tabular colonies were the major shelter providers, these coral morphologies have been particularly studied and reported as possible keystone reef structures in relation to the habitat or refuge for reef fishes (Noonan et al., 2012; Kerry and Bellwood, 2015). Reunion reef has the lowest shelter capacity. Its young age together with strong natural pressures (e.g. episodic austral and cyclonic swells) (Cordier et al., 2012) and higher human impacts (island population ~850,000) could explain the lower abundance and smaller size of the coral colonies found there. In contrast, New Caledonian reef offers the highest shelter capacity, mean shelter volume by colony and the most balanced combination of shelter providers (i.e., highest SSI). Among the three study sites, this reef is probably the most developed and least degraded (Marine Protected Area) and closest to the center of tropical marine biodiversity, the Indo-Australian archipelago. These factors may explain the diversity abundance of various growth forms and the presence of large colonies. The environmental setting at Europa is comparable to that at New Caledonia (Bonneton et al., 2007) but some growth forms that were excluded from our analysis (i.e. helmet-shaped, foliaceous/laminar) were well represented in this reefscape. As a consequence, we have likely underestimated its shelter capacity provided by the coral colonies as well as its Shannon-shelter index. Also, the Europa reefscape presents a steeper slope at New Caledonia or Reunion, which may affect the representation of structures on the orthomosaics. Indeed, sites presenting high structural complexity and/or steeply sloping sites are more impacted by the orthographic projection than flatter sites (unpublished results). In fact, the structures present on reef slopes or steep areas are underrepresented when projected. Consequently, the planar areas of colonies and the shelter estimations were probably underestimated, particularly at Europa. Despite our knowledge of this possible bias, we were unable to investigate it. This points to two of our study's limitations, which needs to be considered in case of further correlation analyses with associated biodiversity. In addition, in order to improve predictions, morphologies of coral colonies growing under extreme hydrodynamic conditions (very high or very low tidal or wave-induced currents) and temperatures (extremely high or low temperatures) should be included in the database. Indeed, these two factors influence coral growth (Lenihan et al., 2015; Pu, 2016) and may thus influence the shelter provided by coral colonies. In the present study, however, we observed that relationships between diameter (or planar area or surface) and shelter were consistent regardless of study site (Fig. S5). Overall, the training database could be enriched with new measurements, encompassing other coral growth forms, to improve the robustness of the predictive models.

Relationships between shelter volume and the colony diameter, planar area or surface correspond to the allometric growth of reef building corals: for all growth forms (branching, columnar, massive and tabular), the shelter volume is scaled to diameter to the power of 3 and to planar area to the power of ~1.5. These allometric scaling rules indicate that shelter provision by the principal growth forms of reef building corals follow the same principles of biological design of multicellular organisms (West et al., 2002). Our results are consistent with the findings of Dornelas et al. (2017), demonstrating that reef building corals have allometric rather than isometric growth rates. As in the present study, Dornelas and colleagues used the planar area to quantify coral growth (a 3D feature of colonies like shelter volume) and worked with morphologic groups rather than species that would allow more precise differentiation among groups. Now, shelter capacity of branching, columnar, massive and tabular colonies can be included and used in combination with size and growth rates to improve the predictions of habitat changes (Burns et al., 2019).

5. Conclusions and perspectives for coral reef conservation

Taken together, our findings contribute to the quantification of structural complexity and the shelter availability of reef ecosystems. Using a morpho-functional approach, we focus on reef building coral colonies as one of the major components providing habitat on reefs (for macrofauna/organisms >1 cm). Yet, the orientation of coral colonies used to calculate shelter volumes were based on their orthographic projections, while growth orientations are more variable depending on environmental characteristics (i.e. the habitat complexity, slope, light field), thus inducing possible bias in our estimates of shelter capacities. This point was noted on tabular growth form at New Caledonia which have shown lower accuracy of shelter predictions. This may be due to some uncontrolled and/or unquantified morphological features such as the number of plates in the colony structure, but also the height of the colony table with respect to the sea floor and the tilt compared to the zenith. This aspect should be further investigated to improve the accuracy of predictive models of shelters capacities. Also, the inclusion of other components contributing to the shelter availability of reefs, like grooves and spurs, holes and overhangs, dead coral structures, the internal cavities of the reef and vegetative component should improve the estimation of the overall shelter capacity of reefscapes. Nevertheless, our results advanced the description and quantification of the structural complexity considered to be a fundamental feature of habitats and reef-communities (Graham and Nash, 2013; Richardsonet al., 2017a; Agudo-Adriani et al., 2019).

The major conclusion of the study is that planar area and diameter of coral colonies are satisfactory proxies for estimating shelter volume. Since planar area is an accessible and commonly used metric in coral reef monitoring and diameter can be inferred from commonly surveys methods such as Line Intercept Method (e.g. Zawadaet al., 2019a, 2019b), shelter volume estimators have important potential applications for conservation purposes. Indeed, shelter volume quantification is feasible, especially with automated computation with a simple function in R code and could be used to estimate the shelter capacity of reefscapes in spatial and temporal surveys. Further analyses are needed to evaluate the 2D-3D relationships for other coral growth forms. Additionally, it is still necessary to enhance the data training (more colonies models and more diverse hydrodynamic and thermal conditions) to tune these predictors at other localities covering a wider geographical and environmental range, aiming to provide universal and accurate formulas which would make estimations of shelter provision by corals easier on large spatial and temporal scales. Shelter provision data will be an important complement to existing monitoring programs, helping in the forecast of recovery and resilience of reef ecosystems, and providing critical data for reef management.

6. Authors' contributions

IUB, RP, MA conceived the ideas; IUB, RP, VM, LP, MA, ED designed methodology; IUB, VM, LF, JPQ and RG collected the data; IUB, RP, VM and LF performed 3D models; IUB, FC, RP, SE performed data handling and analysed the data; IUB, MK, SE, HB, LP and MA led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

2D and 3D colonies metrics and R code to shelter estimations from diameter, planar area and surface will be available in https://zenodo.org.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.107151.

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