Coral Reefs
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REPORT

Estimating rates of coral carbonate production from aerial and archive imagery by applying colony scale conversion metrics

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Abstract Recent interest in assessing coral reef functions has raised questions about how carbonate production rates have altered over the past few decades of ecological change. At the same time, there is growing interest in quantifying carbonate production on larger reef-scales. Resolving these issues is challenging because carbonate production estimates require three-dimensional survey data, which are typically collected in-situ over small spatial scales. In contrast, data that can be extracted from archive photograph or video imagery and high-resolution aerial imagery are generally planar. To address this disconnect, we collected data on the relationship between linear planar and *3D* contour lengths of 62 common Indo-Pacific hard coral genera-morphotypes to establish appropriate conversion metrics (i.e. coral class rugosity values, hereafter termed R_{coral}). These conversion values allow planar colony dimensions to be converted to estimates of 3D colony contour length, which can be employed within existing census budget methodologies like ReefBudget to estimate coral carbonate production (G, in kg $CaCO_3$ m^{-2} yr^{-1}). We tested this approach by comparing in-situ carbonate production data collected using the ReefBudget methodology against estimates derived from converted colony length data from video imagery. The data show a high level of consistency with an error of ~ 10%. We then demonstrate potential applications of the conversion metrics in two examples, the first using time-series (2006 to 2018) photo-quadrat imagery from Moorea, and the second using high-resolution drone imagery across different reef flat habitats from the Maldives. Whilst some degree of error must necessarily be accepted with such conversion techniques, the approach presented here offers exciting potential to calculate coral carbonate production: (1) from historical imagery to constrain past coral carbonate production rates; (2) from high quality aerial imagery for spatial up-scaling exercises; and (3) for use in rapid photograph or video-based assessments along reef systems where detailed surveys are not possible.

Keywords Coral · Coral morphology · Carbonate production · ReefBudget · Historical ecology

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Introduction

Recent increases in the magnitude, frequency and spatial footprint of ecological disturbances affecting coral reefs have led to a growing interest in the implications of these disturbances for reef ecosystem functioning (Hughes et al. 2018; Williams et al. 2019). In particular, there is a growing body of work assessing those geo-ecological processes that sustain reef frameworks through the addition and cycling of skeletal calcium carbonate (Perry and Alvarez-Filip 2019). In this context, reef carbonate budgets have been identified as an important indicator variable for the "health" and resilience of coral reefs and their responses to climate change (Mace et al. 2014; Brandl et al. 2019). Both census-based (e.g. ReefBudget; Perry et al. 2012) and hydrochemical (e.g. Courtney and Andersson 2019) methodologies have been developed to quantify reef

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carbonate budget states (G, in kg $CaCO_3$ m^{-2} yr^{-1}), and resultant datasets are providing us with a rapidly improving understanding of contemporary carbonate production regimes. This research has included multi-site assessments within countries (e.g. Muehllehner et al. 2016; de Bakker et al. 2019; Molina-Hernández et al. 2020) and across regions (Perry et al. 2015), and assessments of budget state response to recent environmental disturbances (e.g. bleaching: Perry and Morgan 2017; Manzello et al. 2018; Lange and Perry 2019) and across environmental gradients (e.g. Roik et al. 2018; Januchowski-Hartley et al. 2020). However, the relatively recent uptake of budget assessment methodologies, and a general paucity of budget data from prior to about 2010 (Lange et al. 2020), means that our understanding of how budget states have changed, even over the recent period of rapidly accelerating ecological degradation, is sparse. As a result, magnitudes and trajectories of contemporary and potential future coral carbonate production regime change are hard to place in a temporal context. On a spatial scale, there has been an increasing interest in upscaling habitat-specific budget rate data to reef-scale estimates of carbonate production regimes as a function of habitat size (Hamylton et al. 2013; Brown et al. 2021). To advance this area of study there is a need to better constrain habitat-specific production estimates as a function of coral colony abundance and size before upscaling, for which one can make use of increasingly high-resolution aerial imagery (e.g. Roelfsema et al. 2018; Hedley et al. 2018).

Historical and recent photo quadrat datasets (e.g. see the large global dataset of Rodriguez-Ramirez et al. 2020) and high-resolution drone acquired imagery (e.g. see Casella et al. 2017) can both capture data at sufficient (i.e. colony-level) resolution to support detailed measurements of coral cover. This imagery opens up the potential to address some of the historical budget state questions, and to support spatial up-scaling based on drone-derived reef habitat maps. However, to estimate coral carbonate production rates as accurately as possible, there is a requirement for data on the three-dimensional (3D) cover of corals along transects or across reef areas, not planar cover as standard reef survey methods or photograph imagery provide. This is because the most accurate census-based estimates of coral carbonate production rates require data at the colony level that can factor for differential colony growth morphologies (e.g. table/plating corals grow along edges, massive corals in all directions) and across colony variability in calcification rates (e.g. branch tips have higher extension rates than inter-branch areas) (Gladfelter 1984, 2007). Extracting 3D cover data from either historical imagery or from high-resolution aerial imagery requires an ability to convert planar data into 3D colony surface cover data using appropriate conversion factors at the lowest taxonomic level possible, and ideally at genera-morphotype level (i.e. *Acropora* branching, *Acropora* table, *Porites* massive, etc.). Such conversion factors would allow measured planar colony dimensions to be converted into a form that could be employed within existing budget methodologies like ReefBudget (Perry et al. 2012).

Colony-level rugosity metrics of this type have recently been collected for a range of Caribbean coral taxa (González-Barrios and Alvarez-Filip 2018) and utilised to convert historical coral cover data from the Atlantic and Gulf Rapid Reef Assessment (AGRRA) datasets to measures of colony surface cover and contour length, and coral carbonate production in the Mexican Caribbean region (Molina-Hernández et al. 2020). Applying the same approach across the ecologically diverse Indo-Pacific region is currently not possible due to the lack of colony-level rugosity metrics. To address this challenge, we collected data on the relationship between linear planar colony dimensions and contour lengths of 62 common Indo-Pacific hard coral genera-morphotypes (and three common soft corals) to establish appropriate conversion metrics (i.e. coral class specific rugosity values, hereafter termed R_{coral}). The accuracy of using the resultant Coral Colony Rugosity Index (CCRI) database to derive coral carbonate production rates from imagery was tested by comparing estimates from video-transects (planar measurements) to in-situ ReefBudget surveys (based on in-situ 3D contour length measurements). To further demonstrate potential applications of the approach, we used the conversion factors to estimate coral carbonate production rates from two types of imagery: first, from historical time-series photo quadrats from Moorea for the period 2006 to 2018; and second, from high-resolution drone-derived imagery from across different shallow reef habitats in the southern Maldives.

Study area and methods

Development of the CCRI database

To develop the Coral Colony Rugosity Index (CCRI) database, we first collected taxa-specific planar and contour length measurements for a wide range of common Indo-Pacific coral genera and morphotype classes. Measurements were made on individual coral colonies (n = 3172) spanning as wide a range of colony sizes as possible: (1) from a range of reef habitats at depths of 0–10 m around Lizard Island (14° 40′ S, 145° 2′ E) and Heron Island, Great Barrier Reef (23° 25′ S, 151° 55′ E); and (2) from the Natural History Museum's (London, UK) Indo-Pacific Dry Invertebrate collection. In each setting, coral colony rugosity was measured using the chain-tape technique (Risk 1972) by draping a 0.5 cm link length chain across four equidistant diameter profiles over each colony so as to follow the exact topography of each profile from base to base, including every feature forming the surface structure and, where possible, any overhanging portions of the corals. The respective planar lengths of each profile were also measured using a tape held horizontally just above each coral colony (Risk 1972). All corals were photographed, identified to the species or genus level (using Veron 2000), and assigned to a morphotype class (English et al. 1994).

To derive a metric for converting coral colony planar lengths into contour lengths, we analysed the relationship between the respective planar and contour length measurements of each colony in our dataset. Each of the four profiles measured for each colony were treated as individual data points to enable the corals full structural profile to be represented. Our working assumption was that the relationship would be linear (e.g. Richardson et al. 2017), which was confirmed by visual evaluation of plotted data and additionally tested by fitting generalized linear models (GLM) with linear, logarithmic and power functions to morphotype level data and comparing their fit using the Akaike Information Criterion (AIC). Models with linear regression lines provided the best fit for branching, table, massive, encrusting, columnar and plating taxa (Online Resource 1). Although the uncertainty of regressions increased slightly with increasing colony size for most morphotypes (due to increasing variability in morphology with colony size and fewer data points), the overall relationship between colony planar and contour length measurements was linear for most corals in our dataset with no significant deviations observed for smaller or larger corals. On this basis, we calculated a mean colony-level rugosity value (hereafter termed R_{coral}) for each coral genera-morphotype in our dataset by simply dividing contour by planar length, consistent with the approach used for Caribbean coral taxa (González-Barrios and Alvarez-Filip 2018). Mean rugosity was used to develop R_{coral} rather than the coefficients of regression lines, as in the latter approach few data points from larger colony sizes can disproportionally affect the coefficients. The taxa-specific R_{coral} values in the CCRI, currently comprising 62 coral genera-morphotype classes and 15 aggregated coral morphology classes (including soft coral) (see Fig. 1; Online Resource 2), enable an estimate of coral contour lengths to be calculated from measured planar data from imagery as:

$$\text{Coral colony contour length} = \text{Colony planar length} \times \text{Taxa-specific } R_{coral} \text{ value} \quad (1)$$

Testing the accuracy of the CCRI to estimate coral carbonate production rates

To assess the accuracy of using conversion metrics to estimate rates of coral carbonate production from coral planar measurements we compared carbonate production rate data derived from colony measurements in video imagery against rates based on in-situ coral colony measurements from along the same transects. Specifically, we used the CCRI database to calculate the contour lengths of living coral colonies along 26 video transects of 5 m length, recorded at 2–4 m depths along the southern reef edge of Kandahalagalaa Island (0° 13′ 25″ N, 73° 12′ 53″ E), southern Maldives. Each transect was defined by a tape running approximately parallel to the reef crest and videos were recorded using a CanonS101 camera by filming a planar view from directly above the tape. Immediately after recording we measured the contour lengths of each coral colony directly below the same transect tape. The only exception was for any open branching *Acropora* spp. colonies where we counted the number and measured the dimensions of branches intersecting the transect line: this is because any conversion of the linear extent of the entire colony would significantly over-estimate actual living tissue cover, and thus over-estimate carbonate production estimates. Video transects were subsequently analysed using Kinovea software (www.kinovea.org) with the visible tape used to calibrate the scale of each video frame, allowing us to measure the planar lengths of coral colonies directly underneath the axis of the transect lines while accounting for any slight change in diver height throughout the recording. The relevant R_{coral} conversion values were then applied to each colony to calculate contour lengths (Eq. 1). Both the in-situ measured contour length data and the contour lengths derived from planar lengths and CCRI conversion factors were input into the Indo-Pacific version of the ReefBudget coral carbonate production spreadsheets (available at https://geography.exeter.ac.uk/reefbudget/), enabling us to compare estimates of coral carbonate production (G in kg $CaCO_3$ m^{-2} yr^{-1}) for both data collection methods. To account for cumulative errors when calculating coral carbonate production from converted colony size, we added the standard errors (SE) of genus/morphotype-specific CCRI conversion factors and the SE estimated for coefficients of calcification equations for each coral colony in the ReefBudget spreadsheets using the root sum of the squares

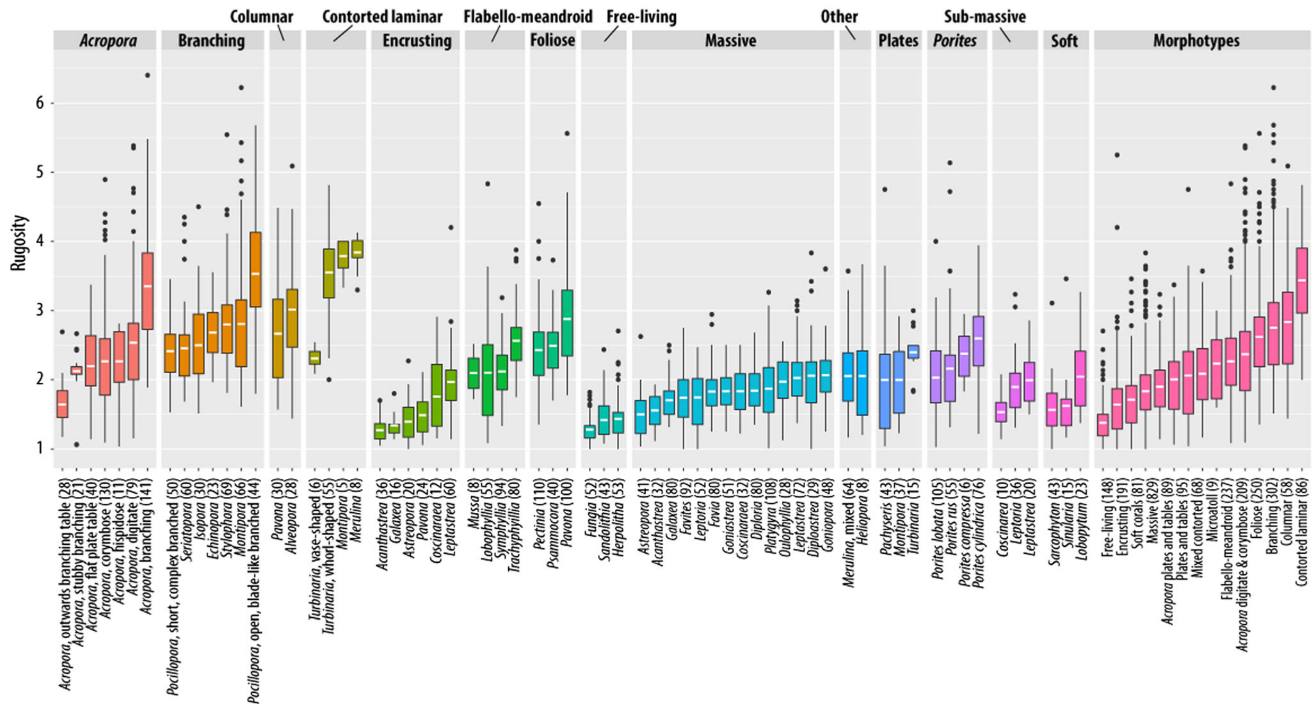

Fig. 1 Box (50% quartile) and whisker (95% quantile) plots representing mean coral colony rugosity (R_{coral}, white horizontal bars) of sampled coral genera-morphotypes (and aggregated morphology classes). Sample size is shown in brackets after the taxa class labels (see Online Resource 2)

error propagation method (Lindberg 2000). As the variability in R_{coral} conversion factors is very small compared to the variability in coral calcification rates, the consideration of R_{coral} SE resulted in negligible additions to transect-level uncertainties of carbonate production (< 1 g $CaCO_3$ m^{-2} yr^{-1}). Thus, while the potential error introduced by the conversion to 3D measurements should not be ignored, the much higher uncertainty in calcification estimates emphasizes the need for better constraining accurate and local colony growth and density values for dominant coral taxa (e.g. Lange et al. 2020).

Applying the CCRI database to calculate coral carbonate production from photo quadrat and drone-derived imagery.

On the basis of a strong agreement between rates of coral carbonate production calculated using the standard ReefBudget approach and those derived from the converted planar data (see "Results" section), we applied the CCRI database to estimate coral carbonate production rates from photo quadrat time-series data and from drone-derived reef imagery. For the photo quadrat analysis, we made use of the image collection for the Entre Deux Baies fore-reef site in Moorea (17° 28′ 56″ S, 149° 51′ 5″ W, French Polynesia) for the time period 2006–2018 accessible through the Service d'Observation (SO) CORAIL database. The site was impacted by a crown-of-thorns sea star (COTS) outbreak from 2006 to 2010, by bleaching in early 2007, and by Cyclone Oli in February 2010 (Adjeroud et al. 2018), thus allowing us to estimate changes in coral carbonate production following these disturbances. For every year (2006, 2008, 2010, 2012, 2014, 2016, 2018) we examined eight benthic photo quadrats (1 × 1 m), each from the exact same location. After pre-calibrating the size of each image using the reference grid of 1 × 1 m, we measured the planar length of every coral beneath the horizontal lines captured in each photograph using the '1D measuring' function in the image analysis software JMicrovision (https://jmicrovision.github.io/). Each coral was categorised to the highest taxonomic level possible, in almost all cases image quality being sufficient that corals could be identified to genus and morphotype level. Where corals could not be identified to genus level, due to only partial visibility or shading in the image, they were assigned a morphotype classification. We then converted each planar length measure for each colony to estimate its respective 3D contour length using the relevant R_{coral} conversion factor from the CCRI database. The only exceptions were open branching *Acropora* spp. colonies for which, to ensure consistency with the standard ReefBudget field method, we counted the numbers of branches intersecting the transect lines. Following the conversion of planar to contour length for each colony measured along every line in each quadrat, data were again input into the Indo-Pacific version of the ReefBudget carbonate production spreadsheet. In this case, the data from each quadrat (a total of 900 cm of linear distance measurements) represented a replicate transect and resultant estimates of coral carbonate production for each quadrat were extracted for analysis from the 'Results' tab. The approach thus replicates as closely as possible the collection of data that would be possible in a field location for use with the ReefBudget approach.

To test the potential for using the CCRI database with drone-derived imagery, we analysed high-resolution photographs collected just prior to the 2016 coral bleaching event from the southern side of Mahutigalaa reef (0° 17′ 18″ N, 73° 11′ 58″ E, southern Maldives). Image data were captured across the shallow reef flat habitat (0.5–1 m depth) using a DJI Phantom 3 Advanced drone (flying height max 45.5 m) and photographs were combined in Pix4Dmapper to generate a georeferenced orthomosaic image of the reef flat. The orthomosaic was then imported into *ArcMap* (v.10.6.1, ESRI) and three 10 × 10 m study areas were selected spanning inner-, mid- and outer-reef flat habitats. The selection of the different sites allowed us to not only examine the use of the conversion approach with drone imagery generally, but also to compare coral carbonate production rates across three different habitats with differing coral communities and coral cover. In each survey area, eight equidistantly spaced virtual horizontal transects (10 m length) were created over each habitat image at 1 m vertical intervals. Along each virtual transect we measured the planar lengths of each coral colony directly below the transect line and, as for the photo-quadrats, identified each coral to genera-morphotype level or morphology level before applying the appropriate R_{coral} conversion factor from the CCRI database. Image quality and resolution was sufficiently good under the very calm conditions on the day of imaging that not only could most corals be identified to genera-morphotype level (verified by in-water observations of the types of corals present in each survey area), but in addition the branches of open branching corals (*Acropora* spp.) intersecting the transect lines could be counted with confidence in most cases (see Online Resource 3). Resultant coral colony contour length data were again input into the ReefBudget spreadsheets allowing us to estimate mean coral carbonate production rates for each habitat.

Results

Accuracy of the CCRI

Analysis of the field-derived video transect data revealed a strong and significant relationship ($r^2 = 0.95$; linear regression: $F_{(1,\ 24)} = 445.2$, $p < 0.001$) between rates of coral carbonate production calculated from the planar lengths of coral colonies in the Maldives video transects and those measured via in-situ ReefBudget surveys (Fig. 2). However, the coral carbonate production rates calculated from planar colony lengths seem to slightly underestimate production compared to that derived from the in-situ coral measurements. In this dataset, the underestimation equates to a difference of 0.57 ± 0.10 G (mean ± SE), equivalent to 11.4 ± 2.2% of total estimated coral G.

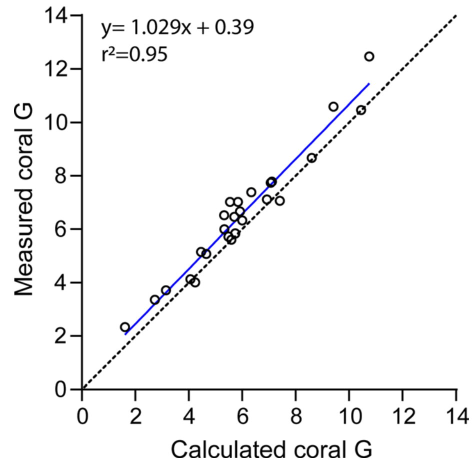

Fig. 2 Transect level coral carbonate production rates (G in kg $CaCO_3$ m^{-2} yr^{-1}) based on converted planar video data (x-axis) compared against rates based on in-situ contour measurements (y-axis) from shallow reef front sites around Kandahalagalaa, southern Maldives. The blue solid line represents the regression between calculated and measured values ($r^2 = 0.95$). The dashed line indicates the identity line ($y = x$) where values should fall if the two methods would yield identical results

Applications to time-series benthic photo quadrat imagery

Based on the above findings and accepting a margin of error of around ± 10% we used the R_{coral} conversion metrics in the CCRI database to estimate coral carbonate production rates from measurements of planar coral dimensions extracted from the Entre Deux Baies (Moorea) time-series benthic photo quadrat dataset for the period 2006 to 2018. This analysis revealed high mean (± SE) coral carbonate production rates at the start of the survey period (2006: 17.87 ± 1.62 G), with production dominated by branching *Pocillopora* spp. (11.33 ± 2.00 G) and, branching and digitate *Acropora* spp. (4.62 ± 0.47 G). Coral carbonate production estimates then collapse as a consequence of the COTS outbreak (and possibly additionally due to bleaching in early 2007), being estimated at 2.09 ± 0.96 G in 2008, and further declining to 0.07 ± 0.05 G by 2010 after Cyclone Oli (Fig. 3A). Small *Porites* spp. and other massive morphology taxa, and small

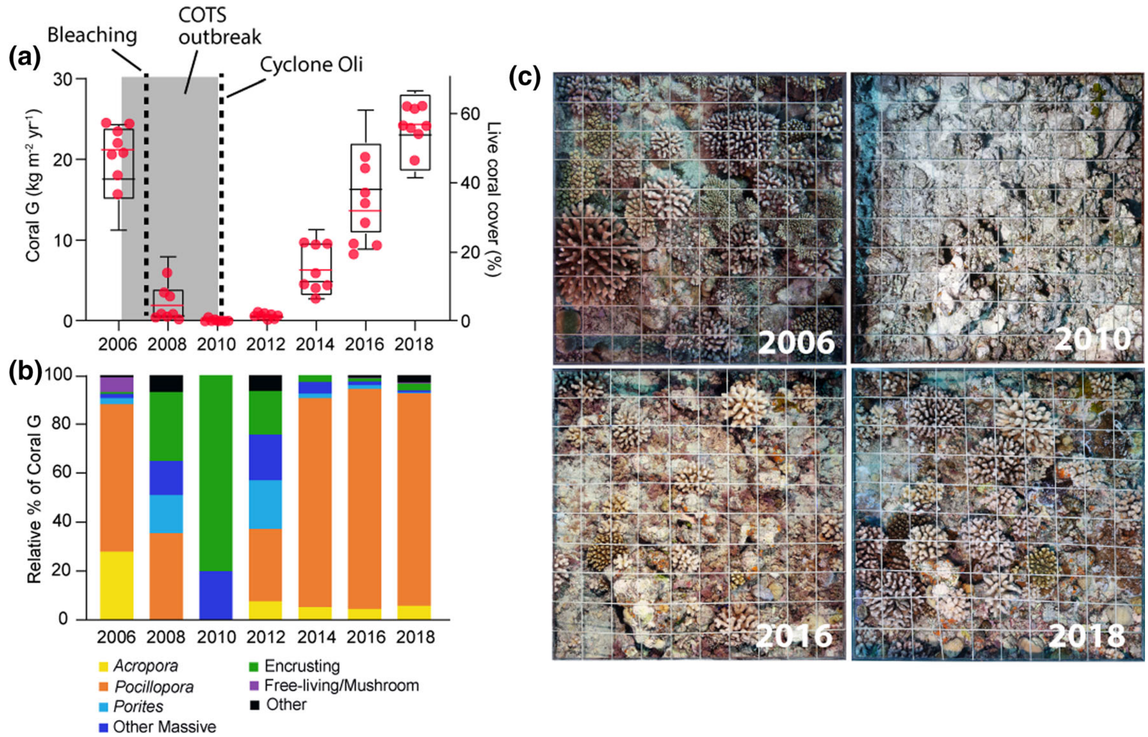

Fig. 3 **A** Box (median and 50% quartile) and whisker (95% quantile) plots showing changes in coral carbonate production rates (G in kg $CaCO_3$ m^{-2} yr^{-1}) at the Entre Deux Baies site in Moorea between 2006 and 2018. Red dots (and right hand axis) show per cent coral cover for each sample (n = 8 photo quadrats per time period), with red lines representing the mean for each year; **B** Changes in the relative contributions of coral genera to coral carbonate production over the 2006–2018 period; **C** Example photo quadrat images, each from the same location, in 2006, 2010, 2016 and 2018

encrusting corals made the highest contributions to the carbonate production in these years (Fig. 3B), when overall production rates and live coral cover were very low (< 1%). Our data then show that coral carbonate production remained low in 2012 (0.44 ± 0.08 G), but was followed by a period of rapid recovery over the following 6 yrs period (2014: 5.80 ± 1.13; 2016: 15.77 ± 2.07; 2018: 22.78 ± 1.38 G; Fig. 3A). These results are consistent with the rapid increase in live coral cover observed (reaching 56.8 ± 1.8% by 2018). It is interesting to note here that the coral recovery and associated rapid increase in coral carbonate production rates was dominated by the growth of branching *Pocillopora* spp. (Fig. 3C), and that branching and digitate *Acropora* spp., important producers of carbonate in 2006, had not yet returned in abundance at this site by 2018. The very high cover of *Pocillopora* spp., averaging > 23 colonies per m^{-2} in 2018 has resulted in coral production estimates in excess of those calculated just prior to the impacts of the COTS outbreak.

Applications to drone-derived imagery

In the second application of the approach, we explored the potential of the method to estimate coral carbonate production rates from high-resolution drone-derived reef imagery, based on images from three shallow reef subhabitats along the southern side of Mahutigalaa reef in the southern Maldives (Fig. 4A). The sub-habitats differed in mean per cent live coral cover; inner reef flat (60.0%), mid reef flat (95.4%), outer reef flat (89.1%), and in the relative cover of coral genera-morphotypes (Fig. 4B). Estimates of mean (± SE) coral carbonate production rates based on the conversion of planar colony measurements were 6.8 ± 1.5 G (inner reef-flat), 9.4 ± 0.9 G (mid reef-flat), and 18.0 ± 1.6 G (outer reef-flat) (Fig. 4C), with clear differences concerning the contributions of different coral genera-morphotype classes (Fig. 4D). The various growth forms of *Acropora* spp. drive most of the coral production in each zone, with highest relative contributions from table-like growth forms in the inner and mid reef-flat habitats, whilst corymbose/digitate forms dominate production in the outer reef-flat habitat. The large areas occupied by branching *Acropora* spp. in the inner and mid reef-flat habitats (Fig. 4A, B) interestingly do not equate to exceptionally high rates of coral carbonate production, because the open branching nature of these colonies leads to a large amount of open void space between actively growing branches. Production from massive *Porites* is generally low, but reaches 2.9 G (around 16% of production) in the outer reef flat zone.

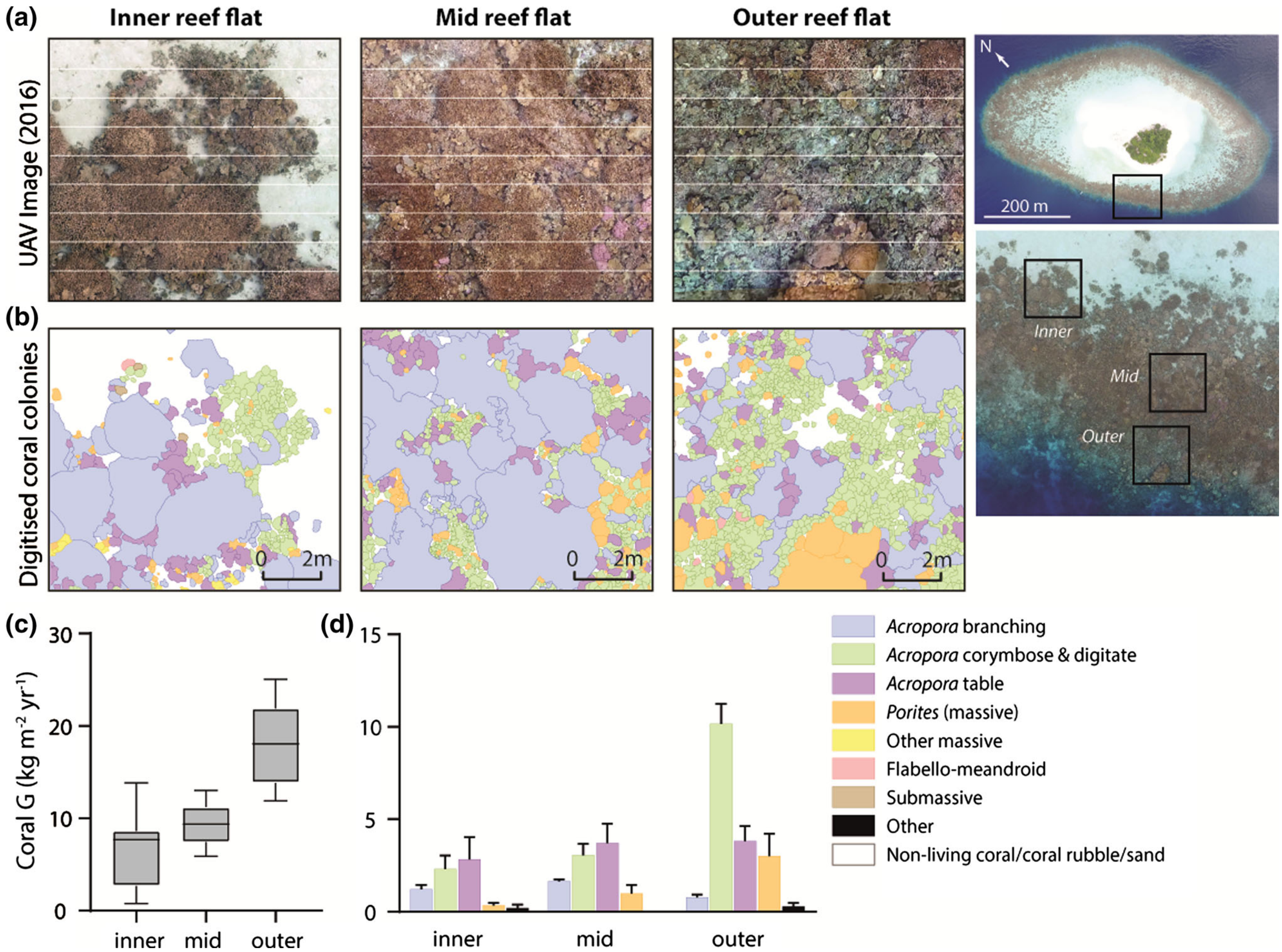

Fig. 4 **A** Close up images of reef flat habitats along the southern side of Mahutigalaa reef (see images top right). Images were taken in 2016 (pre-coral bleaching) and are overlaid by the position of each 10 m transect line along which planar coral colony size data were measured; **B** Digitised habitat maps showing the planar extent of different coral/substrate classes in each habitat; **C** Box (median and 50% quartile) and whisker (95% quantile) plots showing coral carbonate production rates (G in kg $CaCO_3$ m^{-2} yr^{-1}) in each habitat; **D** Bar plot showing mean (± SE) contributions to coral carbonate production by the major carbonate producing genera-morphology classes. Note that the categories 'other massive', 'flabello-meandroid' and 'submassive' delineated in the digitised images in **B** were combined into 'other' in **D**

Discussion

Recent work has clearly demonstrated the disproportionate and species-specific role of scleractinian corals in driving coral carbonate production rates on reefs (Perry et al. 2014, 2018), and how coral production rates and overall reef carbonate budgets vary with geographic location and disturbance history (Manzello et al. 2018; Perry et al. 2018; Roik et al. 2018; de Bakker et al. 2019; Pisapia et al. 2019). However, we lack much understanding of recent historical trends in budget states (i.e. over the past few decades of rapid ecological change and reef disturbance). Recent assessments based on changes in percentage coral cover suggest such changes can be significant at some sites (Courtney et al. 2020), but better constrained and more detailed insights into such trends are urgently needed to provide baselines for understanding contemporary carbonate production states—a key issue in the context of the shifting baseline concept (Knowlton and Jackson 2008). We have also only just started to explore the full potential of mapping reef carbonate production regimes as a function of community composition over larger spatial scales (see Brown et al. 2021). Opportunities for such reef-scale assessments are rapidly increasing with advances in high-resolution aerial imagery (e.g. Roelfsema et al. 2018; Hedley et al. 2018), through the application of airborne fluid lensing techniques to correct for light absorption and distortion in the water column (Chirayath and Earle 2016) and through growing implementation of digital photogrammetry to model reefscapes from underwater or drone imagery (e.g. Burns et al. 2015, Casella et al. 2017, Rossi et al. 2020).

Methodologies, such as the one presented here, open up the possibility to address these challenges by using photograph or video imagery datasets collected in-situ over the past few decades, or high-resolution aerial imagery collected by drones, if appropriate scale references are included. The quality of images (resolution, glare, and lighting) may obviously limit the accuracy of taxa identification and measurements in photographs, which has been discussed elsewhere (e.g. Hedley et al. 2016; Casella et al. 2017; Levy et al. 2018). Here we assess the advantages and challenges of converting planar data to 3D measurements for use in established survey methods. Specifically, our Coral Colony Rugosity Index (CCRI) database provides colony rugosity conversion metrics for a wide range of Indo-Pacific coral genera-morphotypes, augmenting similar data that has been compiled for the Caribbean (González-Barrios and Alvarez-Filip 2018). These rugosity metrics enable the conversion of planar measurements of coral colony size, such as image datasets can provide, to estimates of colony contour length, or 3D coral cover. Most importantly, the conversion then allows planar data to be used with existing census-based carbonate budget methodologies such as ReefBudget. Genera and morphotype-level conversion factors are essential for factoring for colony morphology, which strongly influences colony level carbonate production rates (González-Barrios and Alvarez-Filip 2018; Lange et al. 2020). Colony-level conversion also avoids the problems of using transect level rugosity values, such as in previous budget studies (Stearn et al. 1977; Harney and Fletcher 2003), and in the initial version of ReefBudget (Perry et al. 2012), which differentially over- or underestimates coral production rates depending on coral cover and reef community composition, as the large scale rugosity of a reef does not uniformly correlate to measures of coral colony rugosity and size (Vecsei 2004; Goatley and Bellwood 2011). As an example, analysis of a similar time series in Moorea using planar coral cover measurements show the same temporal pattern of reef-scale coral carbonate production, but resulted in $\sim 3\times$ lower estimates in 2006 when coral cover was high, yet $\sim 3\times$ higher estimates when coral cover was extremely low and composed mainly of massive corals (Courtney et al. 2020). This discrepancy emphasizes the importance of using 3D colony rugosity data to accurately estimate carbonate production.

As expected, the R_{coral} values governing the planar to contour colony relationships in the CCRI are highly variable between and within coral genera, with branching and contorted laminar corals having the largest values, and free-living, and massive and submassive corals the lowest (Fig. 1). Using taxa-specific average conversion factors with planar colony size data from video transects yielded very similar estimates of carbonate production rates to same transect in-field ReefBudget surveys and showed a strong correlation to each other. The slight underestimation ($\sim$ 0.5 G) using converted colony sizes is likely due to the fact that measured coral colonies were located at some distance below the transect tape which served as a size reference during image analysis, meaning measurements are slightly smaller than true colony sizes. This uncertainty should be reduced if image scales can be incorporated closer to the actual reef surface level. However, even the margin of $\sim$ 10% uncertainty is similar to that comparing census- and hydrochemical approaches to quantify reef carbonate budgets (Courtney et al. 2016). We thus suggest that this conversion approach can be considered as a viable option for estimating coral carbonate production rates from planar image datasets. The CCRI provides a standardised approach for converting planar, linear coral size data to 3D contour lengths at the colony scale, which can then be input into existing budget calculation systems such as ReefBudget to derive estimates of coral carbonate production from appropriate reef imagery.

Using the CCRI approach, our analysis of the time-series historical imagery from Moorea demonstrated clear temporal changes in coral carbonate production rates as a function of the impacts of the regional COTS outbreak in 2006 and a further loss of coral in early 2010 due to Cyclone Oli (Kayal et al. 2012; Lamy et al. 2016; Adjeroud et al. 2018). The analysis also highlighted the remarkably rapid recovery in coral production rates at these sites, reaching levels close to those in 2006 by 2016 and exceeding the 2006 value only 8 yrs after Cyclone Oli (by 2018). This rapid recovery is consistent with the high overall recovery rates that the reefs around Moorea have been reported to exhibit after disturbance (Adjeroud et al. 2018; Vercelloni et al. 2019; Carlot et al. 2020), and we note in our data the especially rapid recovery of *Pocillopora* spp. which contributes nearly 90% of coral carbonate production by 2018. In contrast, and whilst digitate and branching *Acropora* spp. also showed signs of recovery, their relative contribution to coral production rates as of 2018 was below that at the start of the time series.

The application of CCRI conversion metrics with linear colony size data collected from low-elevation drone imagery from sites in the Maldives also allowed us to show how such approaches can be used to compare coral production rate data across habitats within a shallow reef. The analysis highlighted clear differences across the three sub-habitat types examined, with estimated coral carbonate production rates ranging from 6.8 ± 1.5 G on the inner reef-flat to 18.0 ± 1.6 G on the outer reef-flat. Our accuracy test (Fig. 2) suggests we should have a good degree of confidence in the carbonate production data (< 10% error). We also note that the coral G rates calculated in this example are consistent with the general relationship that can be established between the percent live coral and coral G on reefs in the central Indian Ocean using in-situ ReefBudget surveys (Fig. 5). There is of course some expected variability around the mean trend depending on site-specific coral community composition, but these findings suggest that rates of coral carbonate production calculated from reef imagery correspond to those that derive from in-water surveys. Thus, our analysis provides an example of the potential of using drone imagery to estimate carbonate production rates at larger reef-scales.

There are, however, two important caveats to note in the context of using conversion metrics for the purposes we propose. The first is the obvious limitation of not being able to measure any corals growing below other corals or overhanging areas of reef framework. This constraint is a potential issue in the Maldives example because of the complex reef structure and presence of large table-like corals (see Fig. 4A, B). In structurally complex settings, we might thus assume the carbonate production rates we calculate represent a lower end estimate. The second issue relates to how confidently one can discern if the entire colony surface is covered in living coral tissue. Specifically, the conversion of planar to 3D contour length makes the necessary assumption that the whole colony has live tissue cover and is thus contributing to calcification. Even in coral communities with generally low coral tissue morality, this assumption may lead to a slight over-estimation of carbonate production as large colonies often experience partial tissue mortality in the lower sections, which is difficult to discern from planar imagery. In our study, partial mortality at the base of large *Porites* colonies has indeed been observed during in water observations in the Maldives but was not taken into account in the analysis of drone imagery. One might argue that in such cases some reduction in calculated contour lengths for certain taxa could be appropriate to better factor for partial mortality of coral colonies. Overall, whilst some degree of error must necessarily be accepted with any such conversion techniques, the approach presented here offers arguably the best option currently available for extracting coral carbonate production data from historical photo quadrat (or video transect) archives and from high resolution drone-derived imagery.

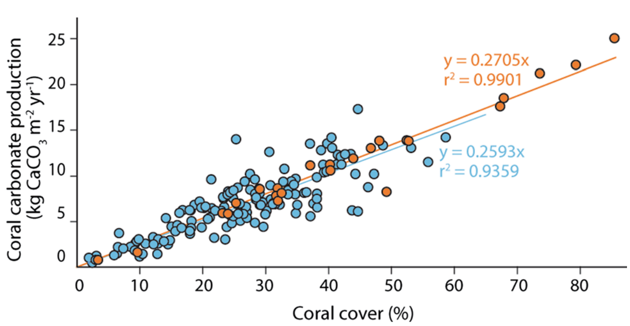

Fig. 5 Comparison of transect level % coral cover and coral carbonate production rate (kg $CaCO_3$ m^{-2} yr^{-1}) based on in-field measures using the ReefBudget methodology from sites in the Maldives and Chagos (blue dots; from Perry et al. 2018), and data calculated from drone imagery in the Maldives in this study (orange dots). Linear regression lines are forced through zero so that zero coral cover equates to zero coral carbonate production

Concluding thoughts

The application of the CCRI database to a range of reef imagery in this study demonstrates the potential of colony-scale conversion metrics to support quantification of past coral carbonate production states, and spatial up-scaling efforts for reef-scale production state mapping. The approach presented thus has clear value to improve ongoing, temporal assessments of changing carbonate production states in the Indo-Pacific and to contribute to our understanding of historical ecological changes on reefs and to constraining the shifting baseline effect (sensu Knowlton and Jackson 2008). The CCRI database represents a useful addition to existing similar datasets developed for the Caribbean (González-Barrios and Alvarez-Filip 2018) which have been used to underpin the application of a functional reef index scheme along the Mesoamerican Reef (González-Barrios et al. 2021), supported the extraction of carbonate production estimates from line-intercept surveys where individual colony sizes were known (Molina-Hernández et al. 2020), and, most recently, facilitated calculation of carbonate production from annotated images in CoralNet (Chan et al. 2021; Courtney et al. 2021). The approach we present could also be applied to photo- or video-based rapid ecological assessment efforts, enabling upscaling to reef-scale budget states even without aerial imagery. Collectively, temporal and spatial expansion of carbonate budget data will help to better understand the 'health' and resilience of coral reefs and their responses to climate change.

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Data availability 3. The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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