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Peer Review File

Crustose coralline algal can contribute more than corals to coral reef carbonate production

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23rd Jan 23

Dear Dr Cornwall,

Your manuscript titled "Increasing importance of crustose coralline algae to coral reef carbonate production under ongoing climate change" has now been seen by our reviewers, whose comments appear below. In light of their advice I am delighted to say that we are happy, in principle, to publish a suitably revised version in Communications Earth & Environment under the open access CC BY license (Creative Commons Attribution v4.0 International License).

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Best regards,

Clare

Clare Davis, PhD
Senior Editor
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REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

The manuscript entitled “Increasing importance of crustose coralline algae to coral reef carbonate production under ongoing climate change” by Cornwall and co-authors is an original contribution to our understanding of CCA role in the framework of the ongoing climate crisis and future changes affecting coral reefs.
The authors were able to show that, under certain conditions, CCA may match or even exceed the contribution of corals to coral reef carbonate production. However, despite their major role as carbonate producer on a global scale, CCA are often inaccurately recorded in benthic surveys or even entirely missing from coral reef carbonate budgets. The authors provide also a case history from published data about the effect of reef dynamics over the coralline/coral carbonate production in French Polynesia. It is provided also a useful review of the different methods that may improve the inclusion of CCA in reef carbonate budget.
The paper is rather well written and provides a step forward in the global understanding of coralline algae importance. However, some minor points need to be improved. In particular,

there is some confusion about some scientific terms such as the growth form of corals and corallines, the meaning of the acronym CCA, the taxonomy of some of the mentioned coral species.
I recommend to review the correct use of these terms (see the annotated manuscript for details), including in the pictures, and avoid to use new terms that may be confounding. Also be consistent in the orthography and improve pictures where requested.

Reviewer #2 (Remarks to the Author):

In the current era of increasing CO2 emissions and the resulting climate change, major efforts are being made regarding the assessment of the impacts and future trajectories of coral reefs, one of the marine ecosystems that have suffered major losses in the last years. The increasing frequency and intensity of bleaching (and other disturbance) events have a major impact on coral reef carbonate production and hence structure, which is often accompanied by community shifts, from being dominated by corals to dominated by other calcifiers or non-calcifiers that affect the services these ecosystems provide. Thus, an accurate assessment of coral reef carbonate budgets is essential to monitor reef trajectories.
This study represents a much needed call for including so far overlooked, but important contributors to coral reef carbonate production – the crustose coralline algae (CCA). While it has long and widely been acknowledged that CCAs play key functions within reefs ("glue" that cements the reef, substrate for coral recruitment), their net carbonate production and hence, contribution when estimating coral reef carbonate budgets, is currently ignored.

The authors did a great job to make their point (a) by using the existing evidence regarding CCA carbonate production to demonstrate that it without doubt represents an essential, but so far missing part for accurately estimating reef carbonate budgets, (b) showing through modeling and with a case study that CCA contribution can become even more significant in disturbed reef environments, and (c) by giving a detailed guide of how this can be resolved, including a critical assessment of the methods.

My only major concern is that I am not fully on board with the title, as in my opinion it does not reflect the main question/outcome, but is based on quantitative evidence of a single case study and modelled trade-offs. From my point of view, and I am open to be convinced otherwise, the take-home message (i.e., main question) of this paper is that CCAs are important, but so-far mostly overlooked contributors to coral reef carbonate production that should be considered and included in future reef budgets. To support this claim, the authors present convincing quantitative and modelled evidence, including that CCAs can become increasingly important (i.e., increased cover and contribution to coral reef carbonate production) when coral cover declines, i.e. during disturbance events (not all of them related to climate change – COT outbreak). For me, the latter represents more of an argument supporting the need of considering the contribution of this group for more accurate coral reef carbonate budgets, instead of the main message, as indicated by the title.
Unquestionable, the evidence presented here, by modeling changes in coral vs. CCA cover

and contribution to reef carbonate production and using a case study from Moorea (French Polynesia), shows clearly the increased importance of CCAs in case of declining coral cover due to disturbance events (not all of them related to ongoing climate change in the case study). However, I would refrain from generalizing, as this is just one scenario for a reef trajectory after a disturbance and will occur only under certain conditions and in specific reef environments. There are many other studies that have shown different scenarios (e.g., shift to octocoral, sponge, turf algal dominance), with herbivore and grazer abundance being one of the drivers (e.g., O'Leary & McClanahan 2010).
If the authors agree with my comment, the title should be changed, though the MS itself would not need any re-writing, as it actually is organized and written as I commented above (i.e., using the modelling and the case study as a supporting arguments to demonstrate the importance of CCAs in reefs).

O'Leary, J. K., & McClanahan, T. R. (2010). Trophic cascades result in large-scale coralline algae loss through differential grazer effects. Ecology, 91(12), 3584-3597.

SPECIFIC COMMENTS (line numbers correspond to the Word version)
- Figure 1a: It is not clear where the numbers come from. Montaggioni & Braithwaite (2009) is given as reference, but as far as I can tell by looking through the book, there are no carbonate production rates given for all these groups. Please specify.

Montaggioni LF, Braithwaite CJR. (2009). Quaternary Coral Reef Systems: History, Development Processes and Controlling Factors. In: Developments in Marine Geology) (2009).

- line 97: "by individual organism calcification"
- Figure 2+5: I think it is a bit confusing and also unnecessary to include data of articulated coralline algae and Halimeda in these figures, as (i) non-experts on algae might not be aware of the distinction, i.e. that articulated coralline algae and Halimeda are not part of the CCA group, and (ii) it seems unnecessary, as these data are not included in the calculated mean carbonate production rates and effect sizes, shown in the figures. In any case, if the authors chose to keep these groups in the figures, please make it very clear for the readers that these are not CCAs (and maybe use a different color for Halimeda).
- Figure 2: To adhere to the FAIR principle for publications, I would suggest showing the studies you include here for the calculations, either as Supplementary Material or as online Data File.
- line 134: Shouldn´t it be 61 and 66 studies? See line 145.
- line 138: Add "and" before (b) and (c).
- line 141: "collected"
- line 156: Maybe better "66 records of calcification rate measurements".
- line 158+163+164: Maybe better "group-specific".
- line 249: Numbers for references.
- line 252: "Mo'orea reef carbonate budget"
- line 261: Just a suggestion, but this section might benefit by including a scheme summarizing and illustrating the methods of best-practice to assess CCA carbonate production/accretion.
- line 397: I assume that (c) represents the influence on biomass-normalized calcification

rates and (d) that for area-normalized calcification rates? I recommend clarification to avoid confusion.
- line 418: It is unclear which the other benefit was.
- line 468: "thus grazing may…"
- line 477: Maybe a good recommendation would be a multi-year deployment, with yearly measurements?
- line 480: "no measurements"
- line 481: "repeated structure from motion"? What do you mean here? Seems like a relatively new term that originated from the two papers cited below (Lange & Perry 2020, Rossi et al 2020). Maybe use the same term as in the papers ("Structure-from-Motion photogrammetry")? Also, I think it would be good to specify here for the non-expert that it is a combination of underwater imaging and 3D-modelling.
- line 490: "reef" used repeatedly. Better "contemporary accretion rates of reef flat environments".
- line 502: Better "Structure-from-Motion photogrammetry".
- line 504+505: These two studies are missing in the reference list. Also, a recently published study indicates that hyperspectral imaging might also be a good option, as it apparently can distinguish coralline algae quite well (Schürholz & Chennu 2022. Digitizing the coral reef: Machine learning of underwater spectral images enables dense taxonomic mapping of benthic habitats. Methods in Ecology and Evolution, doi.org/10.1111/2041-210X.14029).
- line 511: Maybe better "as previously used".
- line 517: Not sure if "constrain" is the correct term here, maybe better "assess" or "determine".
- line 518: Maybe better "of coral reefs, given the here outlined potential underestimates of CCA cover…".
- line 527-528: Yes and no. YES, if you only consider global warming and associated bleaching (or other disturbance) events, but NO if you consider the higher susceptibility of CCAs to OA, compared to corals (as stated and shown repeatedly in recent publications of some of the authors, Cornwall et al. 2019, 2021, 2022). Thus, in view of the currently increasing frequency and intensity of high-temperature events that cause massive coral bleaching, CCAs might maintain positive reef accretion rates by increasing their cover and by overgrowing dead corals, thereby also decreasing dissolution of the dead coral skeletons. However, considering their higher susceptibility to OA, reefs with higher CCA cover might experience higher dissolution rates.

Cornwall CE, Diaz-Pulido G, Comeau S. (2019). Impacts of Ocean Warming on Coralline Algal Calcification: Meta-Analysis, Knowledge Gaps, and Key Recommendations for Future Research. Frontiers in Marine Science 6, 186.
Cornwall, C. E., Comeau, S., Kornder, N. A., Perry, C. T., van Hooidonk, R., DeCarlo, T. M., ... & Lowe, R. J. (2021). Global declines in coral reef calcium carbonate production under ocean acidification and warming. Proceedings of the National Academy of Sciences, 118(21), e2015265118.
Cornwall, C. E., Comeau, S., Putnam, H., & Schoepf, V. (2022). Impacts of ocean warming and acidification on calcifying coral reef taxa: mechanisms responsible and adaptive capacity. Emerging Topics in Life Sciences, 6(1), 1-9.

Congratulations to this much needed work!

Best, Nadine

Reviewer #3 (Remarks to the Author):

The authors reevaluate the contribution of coralline algae to reef carbonate budgets. They argue that, in most cases, we have likely been severely underestimating their contributions to carbonate budgets, and that CCA will probably become an increasingly important component as corals experience losses due to climate change. Further, they provide recommendations about how to do a better job of characterizing CCA contributions going forward.

This is a great paper addressing a very timely and important knowledge gap. I could not agree more with the authors about the problem of severely underestimating the contribution of CCA to reef carbonate budgets when using many of the typical approaches. This is a problem that the field needs to acknowledge, understand, and correct.

I have only some minor comments for the authors:

Line 155-157, Totally agreed. I hope that this study will help to ameliorate this widespread misconception among the community.

Line 219-244, But using the traditional survey techniques here (and as are used in most studies), these estimates probably only provide a lower limit to the contribution of the CCA. An absolutely critical point which the authors make above, and which I think needs to be emphasized throughout the manuscript, is that a lot of CCA are growing in cryptic microhabitats across the reef and most traditional survey techniques are simply missing the majority of the CCA that is growing and calcifying on the reef. Again, I think this example is a useful place to emphasize that these are probably lower limits to the CCA contribution and more sophisticated techniques (fine-scale 3-D imaging) would probably at least help us to get closer to the true values.

Line 277-282, I would be explicit in recommending 3-D photogrammetry to capture these cryptic spaces. While more challenging than traditional methods, this is probably the best available method to improve census-based approaches and start accounting for the huge fraction of CCA (and other biota) which are almost completely missed in most surveys.

Again, this is a great paper which should absolutely be part of the literature.

Increasing importance of crustose coralline algae to coral reef carbonate production under ongoing climate change

Cornwall, C.E.[1,*], Carlot, J.[2], Branson, O.[3], Courtney, T.A.[4], Harvey, B.P.[5], Perry, C.T.[6], Andersson, A.J.[7], Diaz-Pulido, G.[8], Johnson, M.D.[9], Kennedy, E.[10], Krieger, E.C.[1,9], Mallela, J.[11], McCoy, S.J.[12], Nugues, M.M.[13], Quinter, E.[14], Ross, C.L.[15], Ryan, E.[16], Saderne, V.[9], Comeau, S.[2]

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Abstract:
Understanding the drivers of net coral reef calcium carbonate production is increasingly important as ocean warming, acidification, and other anthropogenic stressors threaten the maintenance of coral reef structures and the services these ecosystems provide. Despite intense research effort on coral reef calcium carbonate production, the inclusion of a key reef forming/accreting calcifying group, the crustose coralline algae (CCA), remains challenging both from a theoretical and practical standpoint. While corals are typically the primary reef builders of today, ongoing declines in coral cover due to a range of environmental perturbations will likely increase the relative importance of CCA and other non-scleractinian calcifying taxa to coral reef carbonate production. Here, we demonstrate that CCA are important carbonate producers that, under certain conditions, can match or even exceed the contribution of corals to coral reef carbonate production. Despite their importance, CCA are often inaccurately recorded in benthic surveys or even entirely missing from coral reef carbonate budgets. We outline several recommendations to improve the inclusion of CCA into such carbonate budgets under the ongoing climate crisis.

Introduction:

Coral reefs host an incredible array of diversity and are formed via the production and accretion of calcium carbonate ($CaCO_3$) by resident calcifying species. The existence of reefs requires the maintenance of calcium carbonate structures that depends upon the balance of processes that produce and remove calcium carbonate [1, 2]. These processes have been the subject of intense scientific effort to determine the carbonate ‘budgets’ of reefs [3, 4]. Calcium carbonate ($CaCO_3$) on coral reefs is predominantly produced by corals, which build three dimensional frameworks that allow for rapid accretion, with additional contributions to the framework from other calcifying organisms such as crustose coralline algae (CCA), and sedimentary contributions from the breakdown of corals, CCA, and from the skeletal remains of other calcifying taxa including *Halimeda* spp., foraminifera, and molluscs [5]. Calcium carbonate is removed from the reef framework via chemical dissolution, physical erosion, and bioerosion from parrotfishes, sea urchins, sponges, cyanobacteria, and many other taxa that live within the calcium carbonate structure of the reef [6, 7]. Determining these rates of net calcium carbonate production is also termed the “carbonate budget” when referring to estimates at a reef level. The magnitude of the contribution of each production and erosion process is driven by numerous environmental and biogeographic factors, and varies highly across spatiotemporal scales [3]. Understanding how these rates of net calcium carbonate production vary is important for predicting the provisioning of ecosystem services by coral reefs in the future under ongoing environmental change and sea level rise [8].

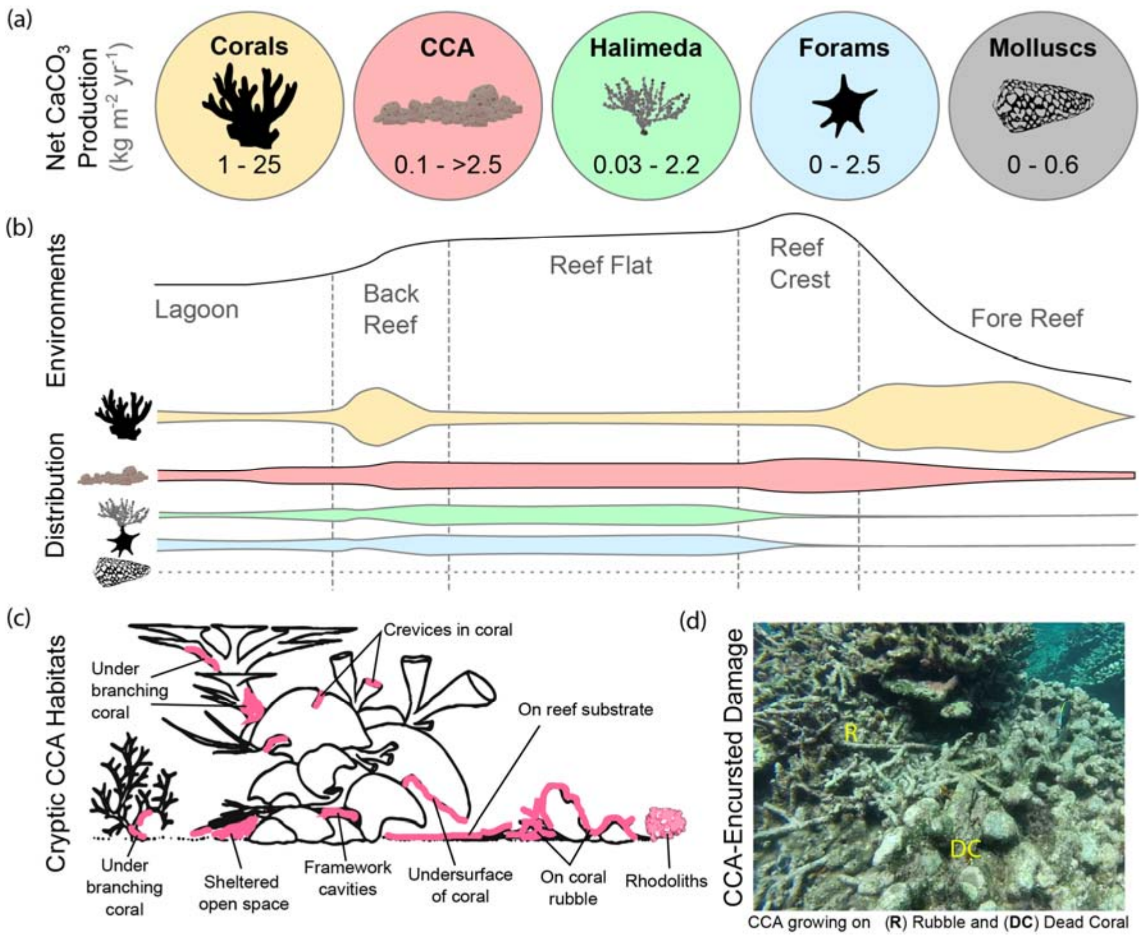

Figure 1: Coral Reef Carbonate Production and Crustose Coralline Algae (CCA). (a) The contribution of the main groups of reef calcifiers to carbonate budgets (corals, CCA, *Halimeda* spp., foraminifera (forams), and molluscs; [5]), along with (b) their approximate distribution across a range of reef environments based on observations by the authors of this study (molluscs are not straightforward because they can be mobile). (c) CCA may be found in numerous cryptic environments within reef habitats, schematic adapted from [9], and (d) commonly encrust dead coral and reef rubble after bleaching or storm damage.

Numerous calcifiers contribute to coral reef carbonate budgets (Fig. 1a), but the contribution of these groups is not equivalent for the maintenance of the reef structure [5]. Some calcifying taxa predominantly add to integral reef framework structures, whereas others produce particulate carbonate that contributes primarily to reef sediments [10, 11]. The two main contributors to the most commonly occurring framework structures are corals, which are typically the principal producers of calcium carbonate in coral reef ecosystems, and CCA, an often important but often overlooked framework carbonate producer [12]. However, determining how CCA contribute to coral reef net calcium carbonate production and structural stability will be increasingly important as the effects of climate change manifest to reduce coral cover [13]. In such a scenario, CCA-driven gross carbonate production will become increasingly important in coral reef net calcium carbonate production [14, 15, 16].

Rates of calcium carbonate production vary greatly across different sections of the same reef, between reefs, within regions, and between larger geographic regions [8, 17, 18, 19]. This is due to variation in the balance between gross calcium carbonate production and erosion that together comprises net carbonate production. Both gross calcium carbonate production and erosion are largely determined by the environmental controls on benthic community composition and on individual organism calcification and bioerosion (e.g., light, water motion, water quality, temperature, carbonate chemistry) [20, 21, 22, 23, 24, 25]. Spatial variation in these environmental conditions across coral reef ecosystems can lead to CCA-dominated habitats or even entire regions, such as algal reef flats, reef crests and algal ridges (Fig. 1b) [26, 27, 28]. Temporal shifts in environmental conditions or major disturbances to the coral community (e.g., bleaching or storm damage) can also allow previously coral-dominated reefs to become CCA-dominated [1, 14] (Fig. 1d). Variation in environmental conditions can give rise to entire reef structures dominated by CCA, for example in the Kimberley region of Australia (380 km^2) [29], smaller reefs in Taiwan [30], Atol das Rocas in Brazil [31], or the unique Cup reefs of Bermuda [32]. These CCA-dominated reefs maintain positive carbonate production despite very low coral cover, suggesting that CCA can contribute meaningfully to coral reef carbonate production. The existence of CCA reefs further implies that they represent an alternative stable state for reef systems, although the exact conditions that give rise to them, and the threshold and mechanisms at which transitions may occur are unknown. Collectively, these lines of evidence indicate that CCA carbonate production is potentially significant in the context of coral reef carbonate production, particularly following disturbances such as coral bleaching events, and in the context of a changing climate that may drive regime-shifts in reef systems (ocean acidification aside).

Here, we: i) present a meta-analysis of CCA and coral calcification rates to develop a conceptual model for CCA contribution to coral reef net carbonate production; ii) explore the temporal dynamics of coral vs. CCA net carbonate production through disturbance events using an example from Mo'orea; and iii) present several suggestions to improve the inclusion of CCA within existing and future estimates of net carbonate production. We focus specifically on the role of CCA in coral reef net carbonate production; and there are extensive resources available for understanding carbonate budgets in general [1, 3, 33]. We aim to offer suggestions for both generalists and specialists working within the coral reef sciences to improve our understanding of CCA contribution to carbonate budgets. We consider that there are large uncertainties in many present-day estimates of net carbonate production. Recording accurate net production of a vital group of calcifying taxa will be even more important under the ongoing climate crisis.

How important are CCA for reef budgets?

How much do CCA calcify?

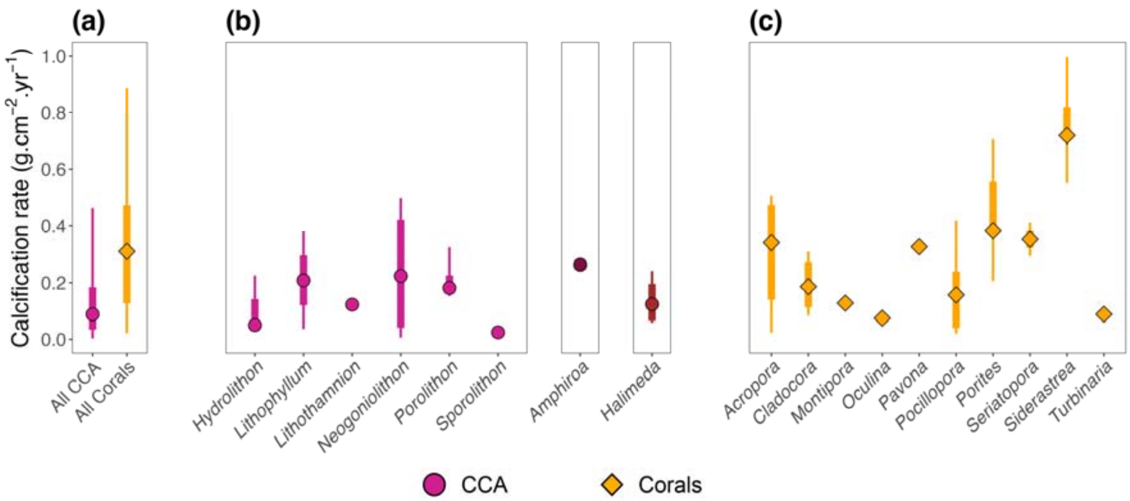

Figure 2: Crustose Coralline Algae (CCA) and coral calcification rates from laboratory measurements. Genus-specific, area-normalised calcification rates for a range of common CCA and coral species compiled from 55 and 66 studies, respectively. Note these are normalised to organism surface area, rather than reef horizontal area. Points show the median, thick error bars show the interquartile range, and thin error bars show the 99% quantile. Aggregate CCA and coral statistics in (a) are calculated from all underlying data for corals, and exclusively for non-articulated data for CCA. Smaller panels in (b) denote articulate taxa and *Halimeda* sp. (b) and (c) highlight the important variability across different coral and CCA genera.

To compare the rates of CCA and coral calcification we combine data from two different sources. We combined the data collated by Cornwall et al. [34] with additional studies identified using Web of Science with the search term “coralline algae” AND “calcification” OR “growth” OR “carbonate production”, which identified a total of 89 studies from 1979 to

2022. All studies representing calcification rate as a percentage change over time were discarded, resulting in a total of 61 studies. Each study was labelled with the climate zone (Tropical, Warm Temperate, Cool Temperate, and Polar) [35] and the method used to measure the calcification rate (Isotopes, Buoyant-Weight (BW) or Relative Growth Rate (RGR), Total Alkalinity Anomaly, X-Ray, CT-scan, and Staining). The dataset was then split into three subsets based on the type of calcification rate measurement, which were either standardised by biomass or by surface area. To compare each study, we converted calcification rates into the most common unit in each subset (e.g., μmol g^{-1} h^{-1}, mg cm^{-2} d^{-1}, and mm yr^{-1}).

To compare the calcification rates of CCA to corals we used data taken from Kornder et al. [36], which includes 288 estimates of coral calcification rates. Within this dataset, we selected only those rates measured by techniques overlapping with the CCA data highlighted above (i.e., buoyant weight and total alkalinity anomaly methods), resulting in 66 calcification rate measurements over ten coral genera. Comparison of rates for corals and CCA shows that organism-specific, surface area normalised calcification rates for corals and CCA are highly variable but span similar ranges (Fig. 2). This contrasts with the prevailing opinion in the coral reef community that CCA produce orders of magnitude less gross calcium carbonate than corals and therefore play a minor role in reef building (Fig. 1a). However, corals tend to grow more complex 3-dimensional structures than CCA, complicating the comparison between organism-specific calcification rates and reef accretion rates. To explore the implications of these organism-specific rates for reef carbonate budgets, we construct a conceptual model of the relative contributions of CCA and corals accounting for colony and reef-scale structural complexity.

Conceptual model of CCA contributions to coral reef carbonate production

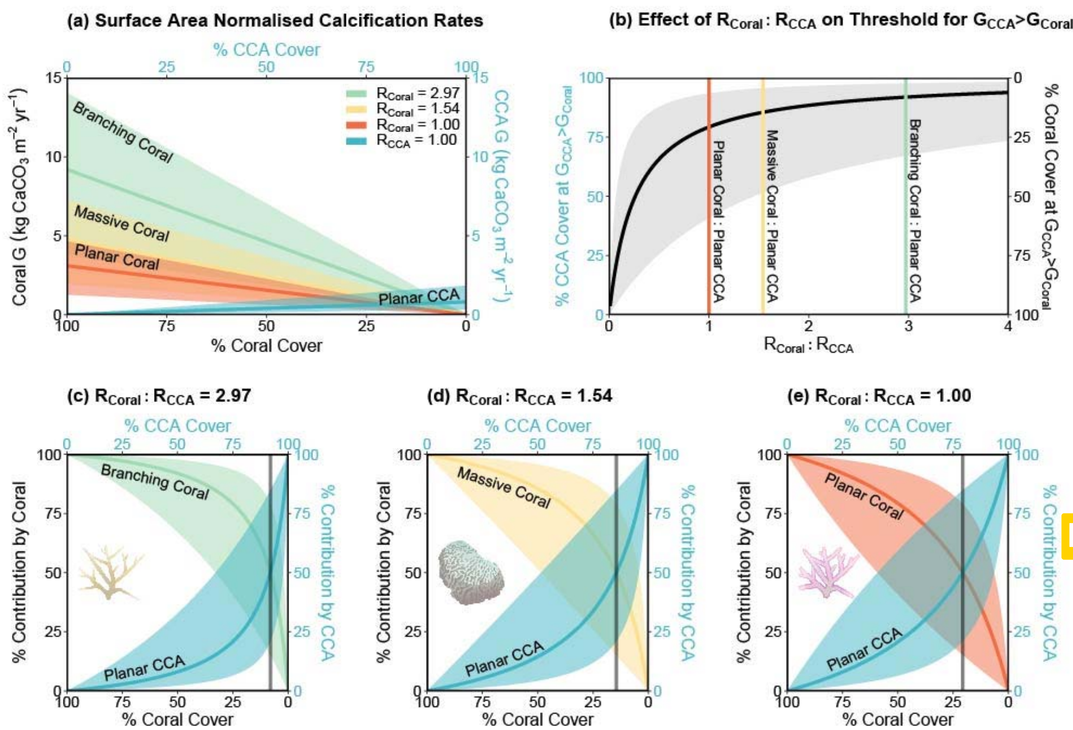

Figure 3: Simulated tradeoffs between CCA and coral carbonate production (G, kg $CaCO_3$ m^{-2} y^{-1}) for reefs dominated by scleractinian corals vs CCA (i.e., $\%_{Coral} + \%_{CCA} = 100\%$). (a) ~~Represents the~~ surface area normalised calcification rates (median ± interquartile range) from a literature search of CCA and coral calcification rates normalised to surface area of growing tissue scaled to reefs ranging from 100 % coral cover to 100% CCA cover. Given that corals typically build more complex~~, vertical $CaCO_3$~~ structures than CCA, the relative rugosity of corals will typically be greater than the rugosity of CCA (i.e., R_{Coral}:R_{CCA}>1). We therefore multiplied the area normalised coral calcification rates by a rugosity factor of R_{Coral}:R_{CCA}=2.97 (branching *Acropora prolifera* rugosity[37]) to represent branching corals (green), a factor of R_{Coral}:R_{CCA}=1.54 (*Porites astreoides* rugosity;[37]) to represent massive corals (yellow), and a factor of R_{Coral}:R_{CCA}=1.00 (*Undaria humilis* rugosity; [37]) to represent encrusting corals (red) compared to the planar surface area normalised calcification rates (R_{Coral}:R_{CCA}=1.00) for CCA (blue). (b) Simulates the % cover of CCA (median ± interquartile range, left axis) required to contribute more $CaCO_3$ than the remaining % cover of scleractinian corals (median ± interquartile range, right axis) for a range of structural complexities wherein R_{Coral}:R_{CCA} ranged from 0 to 4. Vertical lines represent scenarios for branching (R_{Coral}:R_{CCA}=2.97; green), massive (R_{Coral}:R_{CCA}=1.54; yellow), and encrusting corals (R_{Coral}:R_{CCA}=1.00; red). Note, however, that R_{Coral}:R_{CCA}=1.00 (red) represents any scenario where corals have the same rugosity as CCA, which could, for example, represent either encrusting corals and encrusting CCA (R_{coral}=R_{CCA}=1), branching corals overgrown by encrusting CCA (R_{coral}=R_{CCA}=2.97), or any scenario where R_{Coral} = R_{CCA}. Values of R_{Coral}:R_{CCA}<1 might represent situations where the rugosity of CCA exceeds the rugosity of coral, for example colonisation of structurally complex dead corals or coral rubble (Fig. 1). (c-e) Show the % contribution by CCA

and (c) branching corals growing over planar CCA (R_{Coral}:R_{CCA}=2.97), (d) massive corals growing over planar CCA (R_{Coral}:R_{CCA}=1.54), and (e) encrusting corals growing over planar CCA or any scenario where corals have the same rugosity as CCA (R_{Coral}:R_{CCA}=1.00) for a simulated benthic community ranging from 100% coral cover to 100% CCA cover. Vertical grey lines indicate the threshold where CCA carbonate production is equal to coral carbonate production. Coral icons are courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

The surface area normalised calcification rates (kg $CaCO_3$ m^{-2} yr^{-1}) for CCA and corals (median ± IQR) from our meta-analysis (Fig. 2) were used to create a conceptual model of the relative contribution of CCA and corals to overall carbonate production (G; kg $CaCO_3$ m^{-2} yr^{-1}). This is affected by their relative cover and ratios of coral rugosity (R_{coral}) to CCA rugosity (R_{CCA}) within a given reef (i.e., R_{coral} : R_{CCA}, see Fig. 3 caption for further details on the conceptual model). The morphology of a coral will influence its surface area and, consequently, carbonate production within a given planar reef area. More structurally complex branching corals have a greater colony surface area (R_{coral} = 2.97) compared to massive corals (R_{coral} = 1.54) or flat encrusting corals (R=1.00; [37] Fig. 3a). The threshold (% cover) at which the relative contribution of CCA exceeds the relative contribution of coral to the carbonate production ($G_{CCA} > G_{Coral}$) increases logarithmically with R_{coral} : R_{CCA} from 0 to 4 (Fig. 3b). We find that reefs comprised of branching corals and flat CCA (R_{coral} : R_{CCA} = 2.97) will require CCA cover to exceed 92% for $G_{CCA} > G_{Coral}$ (Fig. 3c), and with massive corals (R_{coral} : R_{CCA} = 1.54) this reduces to 85% (Fig. 3d). When the rugosity of CCA is equal to that of the corals (R_{coral} : R_{CCA} = 1), such as with encrusting corals/CCA or when CCA covers structurally complex dead coral skeleton following a disturbance event thereby inheriting the complex morphology, the CCA cover threshold is reduced to 80% (Fig. 3e). Therefore, as reef flattening progresses under ongoing environmental change [38], lower % CCA cover is required to exceed the relative contribution of coral to net reef carbonate production, albeit with CCA dominated reef sites likely producing less $CaCO_3$ than coral dominated reef sites (i.e., on the basis of lower surface area normalized calcification rates; Fig. 3a). Moreover, it is important to note that this conceptual model only accounts for shifts from coral to CCA dominated reef-states and that declining overall calcifier cover (e.g. shifts to turf, upright fleshy macroalgae, or bare substrate) would nonetheless lead to reduced carbonate production and more complicated net coral reef carbonate production scenarios than those explored here (see ternary diagram and discussion in Perry et al. [1]).

Case Study: Mo'orea (French Polynesia)

To compare our conceptual model to a real-world example, we use a case study of disturbance-driven coral community decline and subsequent recovery from Mo'orea, French Polynesia, which demonstrates the increasing contribution of CCA to coral reef carbonate production following a disturbance. We estimate shifts in CCA and coral carbonate production by combining the area-normalized CCA and coral calcification rates from this study (Fig. 2) with measurements of coral reef benthic community composition from Carpenter et al. [39] and structural complexity from Carlot et al. [40] assuming a planar reef with structurally complex corals such that $R_{CCA} = 1$ and $R_{coral} = R_{survey}$. Coral cover rapidly declined from ~35% in 2005 to 5% in 2011 due to a combination of crown-of-thorns starfish (COTS) outbreak from 2006-2010, a coral bleaching event in 2007, and Cyclone Oli in 2010 [41, 42, 43, 44, 45, 46] with a subsequent recovery of coral cover to 31 (± 15%) by 2016 (Fig. 4a). Over the same period, CCA cover increased from 10% in 2005 to 25% in 2010 and subsequently declined to 15% in 2015 (Fig. 4a). Coral carbonate production (% cover coral × coral calcification rate × structural complexity) declined sharply from 3.46 ± 0.58 kg m^{-2} y^{-1} in 2005 to 0.2 ± 0.15 kg m^{-2} y^{-1} in 2011 with a subsequent recovery to pre-disturbance levels by 2016 (Fig. 4b). In comparison, CCA carbonate production (% cover CCA × CCA calcification rate [mean of Fig 2.]) increased slightly from 0.12 ± 0.03 kg m^{-2} y^{-1} in 2005 to 0.29 ± 0.08 kg m^{-2} y^{-1} in 2010, returning to around 0.19 ± 0.07 kg m^{-2} y^{-1} by 2015 (Fig. 4b). As a result of these shifts in coral and CCA carbonate production, the relative contribution of CCA to the $CaCO_3$ budget (% CCA contribution = CCA carbonate production / (coral + CCA carbonate production) × 100) increased from 3.38 ± 0.91% in 2005 to 55 ± 26.5% in 2010 and subsequently declined to 6.32 ± 4.15% by 2016 (Fig. 4c). These results are consistent with the outputs of our conceptual model (Fig. 3) as well as previous studies highlighting the increasing contribution of CCA to coral reef carbonate production following coral bleaching disturbance events (Kayanne et al., 2005; Courtney et al., 2018; Courtney et al., 2020).

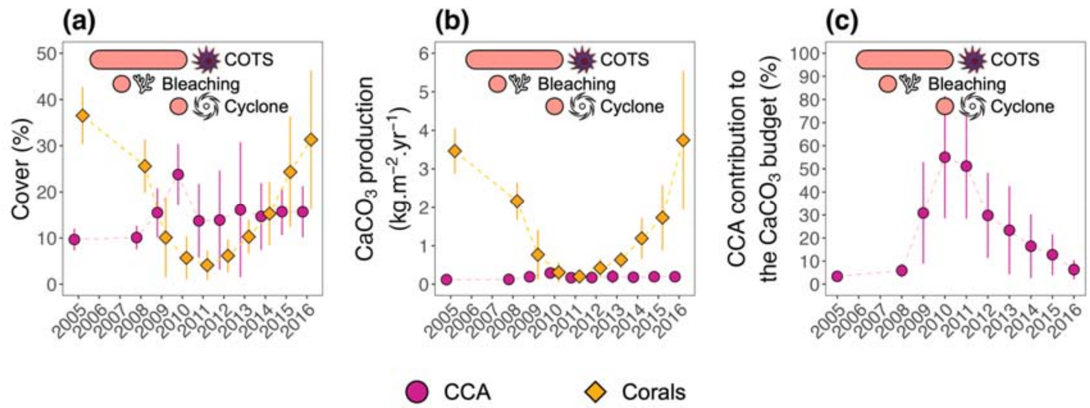

Figure 4: Case study of CCA contribution to Mo'orea carbonate budget. (a) Annual mean ± SD % cover of CCA (pink circles) and coral (orange) diamonds are reported for the fore reef of Mo'orea, French Polynesia [39] before, during, and after a series of disturbance events including a crown-of-thorns starfish outbreak from 2006-2010, a coral bleaching event in 2007, and Cyclone Oli in 2010 [25]. (b) The respective % cover from panel (a) were multiplied by CCA calcification rate for CCA and by coral calcification rate from Fig. 2 x reef-scale rugosity for corals [40] to determine mean ± SD community-level, area-normalized CCA and coral calcification rates. (c) The mean ± SD % contribution of CCA to the total $CaCO_3$ budget (i.e., total G = CCA G + coral G) are reported for each year.

How do we better include CCA in coral reef carbonate budget studies?

Census-based carbonate budgets assign gross calcium carbonate production and loss terms (erosion usually) to benthic and fish survey data to estimate the net calcium carbonate production or net loss of calcium carbonate (net erosion) [3]. Therefore, we must accurately determine both the total cover of CCA and their rugosity with benthic surveys and the net calcium carbonate production rates by measuring CCA net calcification and subsequent bioerosion. For each of these steps, we provide a brief overview of the methods with general recommendations to better include CCA in coral reef carbonate budgets derived from census-based methods.

Surveys for census-based carbonate budgets

The first step in creating a census-based carbonate budget is to survey the reef to determine the relative cover of each carbonate producing taxa and the rugosity of the reef. While non-coral benthic components can be difficult to accurately identify, it is nonetheless important to explicitly differentiate live CCA from bare rock, dead pavement, turf, or other non-calcareous macroalgae categories - each of which would limit the inclusion of CCA in carbonate budgets. Moreover, distinguishing between visually similar types of encrusting algae is also important since morphologically similar red encrusting Peyssonneliales (e.g., *Peyssonnelia* spp., *Ramicrusta* spp.) contain much lower proportions of calcium carbonate than CCA [28, 47] and therefore substantially lower contributions to carbonate budgets. CCA coverage may also be underreported in census-based surveys due to what the observer is able to physically ~~see~~ and measure [3, 48]. For example, cryptic habitats (i.e., crevices, holes, the undersides of coral colonies, underneath overhangings, and other hidden reef recesses *sensu* [49]; Fig. 1c) can account for 30–75% of total reef substrate [49, 50, 51, 52]. Visual surveys can provide some data on cryptic communities, and endoscopic reef surveys can provide even more insight to the communities that dwell inside reef frameworks [53]. From the limited data that exist, calcified algae comprise a significant proportion of many coral reef cryptic assemblages [50]. While individual calcification rates may be lower than, or on par with, or more than their exposed calcifying algal communities [54, 55, 56], cryptic calcifying algae undoubtedly play a role in reef carbonate budgets and need to be fully resolved and accounted for. Quantifying CCA coverage alone would allow first-order estimates of CCA contributions to carbonate budgets using average calcification rates (e.g., Fig. 2). However, CCA community structure and calcification rates can be highly variable between sites, making it more appropriate to determine site-specific calcification using the methods outlined below. Ideally, CCA should be identified at species or genus level in the field and in measurements of calcification rates in estimates of gross calcium carbonate production. This might be difficult in situ, but sampling in the field paired with molecular identification of sub samples and individuals used in estimates of calcification rates would improve estimates in the most accurate of carbonate budgets [57, 58]. This could be paired with environmental DNA to determine whether the coralline algal sub samples match those of the community at each reef.

Special adaptations also need to be made when surveying sites impacted by recent disturbance (e.g., storm damage, bleaching), which can alter the location, rugosity, and community composition of CCA as well as their carbonate production rates [59, 60]. For example, CCA tends to rapidly colonise dead corals following disturbance events (Fig. 1d), allowing them to inherit the 3-dimensional structure and thus the rugosity of the former reef for some time [61, 62]. This would potentially represent a situation where the rugosity of CCA could exceed the rugosity of surviving coral (Fig. 3b, where $R_{coral} : R_{CCA} < 1$). Subsequently, dead corals that are covered with CCA (Fig. 1d) should be recorded as CCA during any survey, rather than classifying them as coral rubble. While this often occurs, it should be noted that at other times turf rapidly colonises and the coral rubble can break into segments that are not colonised by CCA. Additionally, such turf assemblages could also contain CCA, which should be quantified in the most accurate carbonate budgets.

Measuring carbonate production

Measurements of individual CCA calcification rates are critical for understanding their contribution to the reef framework and carbonate budgets, and their role in binding together substrates on reef habitats [56, 63]. Selecting the ideal technique and timeframe for CCA calcification rate measurements largely depends on the research question, purpose of the study, and the morphology and physiology of the CCA at the site. Here, we group these methods into three general classes: 1) measurement of the calcification rates of individual coralline algae; 2) rates of the accretion of the mass of calcium carbonate onto artificial substrates; and 3) new 'framing techniques' that measure reef/organism vertical accretion rates.

Direct measurements of CCA calcification rates

Three main techniques exist to directly measure the net calcification rates of CCA: total alkalinity anomaly, buoyant weighing, and use of isotopes. A calcification rate measurement for use in carbonate budget calculations must be standardized by time and by mass or by surface area, and we therefore exclude vertical accretion measurements such as linear extension from our consideration here.

The total alkalinity anomaly technique has been widely used for estimating net calcification rates of reef organisms since total alkalinity changes by a factor of two for every mole of $CaCO_3$ precipitated or dissolved [64]. A known volume of CCA can be placed in sealed vessels with a known volume of seawater to determine the rate of calcification from the change in seawater total alkalinity over time. Calcification rates measured using the total alkalinity anomaly technique is typically integrated over short timeframes (e.g., hours) and are therefore best suited for quantifying short-term calcification rates in response to changes in environmental conditions. Ideally, incubations over a broad range of light, temperature, pH, nutrient, and/or flow conditions are important to encapsulate the range of conditions organisms are exposed to in the natural environment (although some parameters are more important than others) [23]. Moreover, light and dark incubations are required to approximate net diel calcification. Adequate water velocity should be simulated within any incubators, as the diffusive boundary layer limits movement of dissolved substance exchange around coralline algae [65]. It could lead to artefactual accumulation or depletion of gases and nutrients, due to the combined effect of photosynthesis, respiration, and calcification, within the diffusive boundary layer. This altered boundary layer chemistry would expose the organism to an unnatural chemical environment and alter calcification rates [66].

While the alkalinity anomaly method is effective, depending on the environment, the experimental duration, design, and subject, there are potential sources of error that can lead to over- or under-estimates of calcification rates that need to be considered. For example, the presence and titration of particulate $CaCO_3$ during alkalinity measurements can significantly bias the results, but can be avoided by filtering seawater samples prior to analysis. Furthermore, changes in dissolved organic acids or bases [67] and/or nutrient uptake or release [68] during incubations can in certain cases contribute significantly to the total change in alkalinity. Dissolved nutrients can be accounted for by the change in nutrient concentration during the incubation and contribution from organic alkalinity can be estimated by modified titration methods [67]. However, in most oligotrophic coral reef settings, contributions from organic alkalinity and/or inorganic nutrients to changes in total alkalinity are likely small compared to the contribution from calcification, but could become important in enclosure experiments or in areas of elevated dissolved organic material and/or nutrients.

The buoyant weight technique consists of attaching CCA to a substrate and quantifying the changes in buoyant weight over longer timescales of weeks to months to provide an integrated measure of day and night calcification [69, 70, 71, 72]. The buoyant weight technique reflects the net sum of primary net calcification (i.e., active and controlled construction of skeletal material), secondary infilling of the skeleton (i.e., non-active infilling after diagenesis or skeletal breakdown by internal eroders), and skeletal dissolution in addition to any erosion (physical, biological, and chemical) when conducted *in situ*.

Isotopes can be physically embedded into the calcium carbonate that is taken up during calcification, with the benefit of the ability to detect growth at much finer scales than stains and weighing techniques, which is useful in slow growing species or during very short growth experiments (i.e., hours). The use of stable isotopes of carbon and oxygen present fewer logistical hurdles than the use of radioisotopes and follow the same general concepts [73, 74, 75]. The most commonly employed stable isotope tracer is ^{13}C, which is added to seawater as a bicarbonate salt ($H^{13}CO_3^-$) and incubated with specimens for several hours with the incubation duration dependent on the concentration of added ^{13}C. Significant and consistent uptake have been noted within four hours at high tracer concentrations, with variable signals after one hour even at very high doses [76]. The mass of calcium carbonate deposited during the incubation period (i.e., calcification rates) is calculated using the known concentration of the stable isotope label following mass spectrometric carbonate analysis.

All these techniques must be accompanied by measurements of organism surface area to provide an area-normalised calcification rate for use in carbonate budget calculations [71, 77, 78]. Numerous techniques exist for estimating surface area, spanning a wide range of spatial resolution and precision. The most appropriate technique will depend on the object being measured and the required accuracy of the surface area measurement. Common techniques used for estimating calcifier surface area include, in approximate order of increasing accuracy sensu [79], foiling [80], photogrammetry [3, 81, 82] wax coating [83], and CT scanning [84].

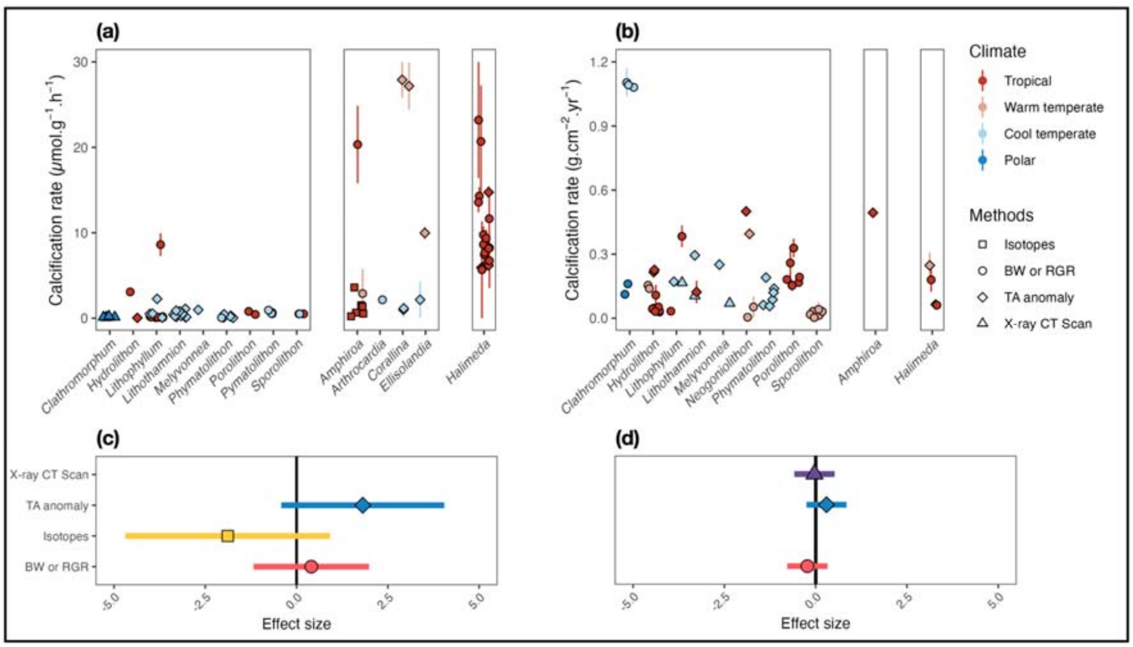

Figure 5: Comparison of methods to measure calcification rate in individual CCA. We apply a general linear mixed model (GLMM) to our meta-analysis data to examine the influence of measurement method on calcification rate measurements, while accounting for the influence of genus and climate zone (Calcification rate | Methods ~ Genus + Climate zone). (a–b) Calcification rates from all genera of CCA in our meta-analysis with measurement methods and climate zone shown. Smaller panels denote articulate taxa and *Halimeda* sp. (c) and (d) the influence of the measurement method on the reported calcification rate determined from the GLMM model.

Accretion substrates for net calcification measurements

Experimental accretion substrates, also known as settlement plates or tiles, are widely used as a non-destructive method to assess the recruitment and growth rates of calcareous reef building organisms including CCA and other encrusting organisms. The deployment of experimental accretion substrates quantifies net calcium carbonate production over a known surface area for a discrete period of time, typically months to years [85, 86]. A variety of accretion substrates, both artificial and natural, have been used to measure *in-situ* accretion and the development of CCA communities within different reef habitats. Experimental substrates range in size, shape, and material from dead coral to individually crafted ceramic tiles, glass slides, limestone plates, plastic cattle ear tags, and polyvinyl chloride (PVC) poles, flat tiles, and cards [4, 85, 87]. The substrate type, orientation, microhabitat, and the period of immersion on the reef can significantly impact rates of net carbonate production and CCA species diversity [86, 88]. Recruitment patterns and carbonate production also differ between experimental substrates with CCA communities having rapid initial growth rates until crusts mature [2, 86].

To quantify net production of calcium carbonate by CCA on accretion tiles, organisms such as sponges, non-calcareous algae, and other encrusting organisms (i.e., serpulids, gastropods, bryozoans) should be removed and accounted for in the budget if they calcify [56]. Another benefit of using accretion tiles to estimate CCA carbonate production is that naturally occurring processes of bioerosion (both internal and external) are co-occurring with CCA carbonate production. Accretion tiles therefore represent estimates of net CCA carbonate production and not gross carbonate production when paired with the percent cover of CCA. Also, advice around taxonomic identity should be followed for carbonate budgets to obtain greater details on contribution of different species to the local budgets. However, the duration of deployment and intrinsic material (i.e., ceramic, PVC, limestone) of the experimental accretion substrates will also influence the bioeroder community composition and their bioerosion rates [20, 24]. Bioerosion has already been implicitly accounted for in the measurements of net carbonate production by CCA, as opposed to gross calcification inferred from linear extension and skeletal density of corals [3], so particular attention should be made to ensure that bioerosion is not accounted for twice for CCA when following census-based carbonate budget methods.

Best practice accretion tile studies for CCA carbonate budget assessment should therefore ground truth results from artificial substrates with naturally occurring reef communities at experimental sites [89]. Substrates should mimic orientation, habitat, and substrate topography as closely as possible. For example, including both upright and downward facing surfaces allows for settlement by both cryptic and non-cryptic CCA [55] while the sandwiched tiles of Calcification Accretion Units (CAUs) [90] and complex interstices of Autonomous Reef Monitoring Structures (ARMS) simulate other cryptic spaces [91]. It is also recommended that CCA communities are measured to include seasonal differences, but it is unknown what the ideal duration is, and whether multiple deployments would therefore be needed. Normalisation of carbonate accretion to surface area and time is critical for facilitating meaningful comparisons through space and time and between different sized artificial substrates, individuals, and species.

Recruitment issues and density dependence

Thick encrusting coralline algae can be a dominant feature of shallow high energy tropical reef crest habitats [26, 92], potentially contributing substantially to reef development [63, 93, 94, 95]. CCA are too often treated as a single functional group [96], but they exhibit variable recruitment, survival, development, and growth rates which can complicate estimates of net community calcification derived from both recruitment tiles and quadrats. Importantly, links between recruitment and adult populations are not well established and density dependence is less well quantified than it is in coral. This increases the complexity for methodological approaches that rely on settlement tiles.

Recruitment patterns depend on supply (e.g., reproduction), which can be related to environmental conditions, where temperature, carbonate chemistry, light, hydrodynamics, and nutrients all could impact reproduction of resident adult CCA and also settlement of juveniles and their post-settlement growth rates [66, 97]. There can also be a seasonal element to reproduction [98]. This means timing and duration of settlement tile deployment might influence CCA cover and calcification estimates of experimental accretion substrates. Once established, post-settlement growth of juveniles on tiles can also vary temporally: following spore settlement and germination rapid cell division is followed by outward expansion of thalli but this tapers off, with calcification faster in the first 3 months compared to six [85] and cover peaking between 6 and 11 months [99]. Another consideration is that CCA colonisation can be successional with community shifts on tiles developing over weeks to months [100].

Finally, adult contributions to net carbonate production may have a density dependent element, with space and competition limiting population size and lateral growth [101], and contribution to carbonate budgets could thus be influenced by continual low-level surface grazing [102]. Examination of growth rates of adult fragments (2–4 cm in size) showed rapid outward extension of thalli followed by slower upward growth [97] that grazing may even stimulate productivity of crusts and promote community diversity [103], and which is further evidenced by wound healing mechanisms in coralline crusts [101, 104]. This means that three different issues could cause the calculation of lower carbonate production rates across tiles deployed for different time periods: 1) increasing bioerosion of older tiles; 2) density dependence in older tiles; or 3) the propensity of CCA to switch from rapid horizontal calcification to slower vertical calcification when older. For example, CCA carbonate production was ~5 times higher on substrates deployed for less than one year compared to greater than one year [3]. Future research should attempt to resolve these issues using multiple experimental approaches.

Other methods for quantifying CCA accretion

While they are not measurements of carbonate production, radiometrically-dated reef cores, coral reef accretion frames, and repeated structure from motion provide direct measurements of CCA accretion. Here we do not discuss linear extension since these measurements typical are not accompanied with estimates of density and surface area that could be used to calculate calcification rates. Reef cores are typically used to measure coral reef framework accretion rates over geological time frames (usually millennia) [105, 106, 107, 108]. Unlike coral cores which target linear extension and calcification rates of individual colonies [109], reef cores sample coral framework, the reef sediment matrix, coralline algae and other framework-contributing components relative to radiometric dates to quantify accretion per unit time.

Coral reef accretion frames can directly quantify contemporary reef accretion rates of reef flat environments [110]. This methodology also allows micro-scale interpretation of specific taxa accretion/erosion contributions to overall reef accretion, including direct quantification of areas of the reef flat surface that are dominated by coralline algae. This works by setting a frame with a series of moveable poles that is removed then redeployed over several time periods to determine the vertical accretion of the organisms, also accounting for erosion. Reported accretion rates from nodular CCA averaged 19.3 mm y^{-1} and areas dominated by flat CCA typically accreted at slower rates between 4–6 mm y^{-1} [110]. While this coral reef accretion frame is a useful tool to accurately measure vertical accretion *in situ*, deployment of the tool is time consuming and to date has been implemented in only one location in the Indian Ocean. These data will need to be corroborated with data from additional time periods (years) and locations to explore inter-annual and inter-site variability in coralline algal growth and reef accretion rates.

Repeated structure from motion photogrammetry has been used to measure individual coral linear extension rates (Lange and Perry 2020) and reef accretion rates (Rossi et al. 2020). To our knowledge, it has not been used to quantify coralline algal accretion rates. It also cannot detect skeletal infilling, and accretion rate measurements using this approach would ultimately need to account for the variation in the skeletal density of different reef calcifiers. This is an interesting avenue for future research given the non-destructive capacity to repeatedly sample reef substrates using this method. Additionally, future work could explore the use of microerosion meters, and laser scanning of tidally-exposed reef upper surfaces, as have been used on rock reefs to measure erosion with sub-mm scale precision [111, 112]. However, there are inherent limitations that would need to be tested and resolved, including those associated with reflectance of surface water.

Conclusions

We highlight that CCA carbonate production can be spatially and temporally high. Presently, it is difficult to constrain the global contribution of CCA to carbonate production of coral reefs owing to underestimates of CCA cover and area-normalized calcification rates. However, through conceptual models and the Mo'orea case study presented here, we have shown that CCA can account for significant proportions of coral reef carbonate production, especially following disturbances such as coral mass mortality events. Additional emphasis on CCA, and other non-scleractinian calcifiers, and the inclusion of the methods discussed above will be important for the coral reef community to improve estimates of coral reef carbonate production and the relative contribution of CCA to this important process. Intensifying frequency and intensity of coral bleaching events under the ongoing climate crisis will continue to drive further declines in coral cover suggesting that CCA are likely to emerge as increasingly important contributors to the construction and maintenance of coral reef carbonate structures in the Anthropocene.

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Code and data are available at https://github.com/JayCrlt/CCA_Methods

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VICTORIA UNIVERSITY OF WELLINGTON
Te Whare Wānanga o te Ūpoko o te Ika a Māui

Dr. Christopher E. Cornwall
Rutherford Discovery Fellow | Lecturer
School of Biological Sciences
Victoria University of Wellington

Dear Clare Davis,

27th February 2023

Senior Editor,

Communications Earth and Environment

On the 24th of January we received three reviewer reports and a decision to publish the manuscript in principle if we edited it to account for the comments of the reviewers and the editorial checklist.

We thank you and the three reviewers for your time and effort placed into appraising this manuscript, and we consider it will make a great addition to the literature that will be of interest to the readers at *Communications Earth and Environment.* We have taken these comments on board to improve the manuscript. Below we list our revisions we have undertaken, with reviewer comments in quotation marks and italics, followed by our revisions and responses to comments in plain text.

Sincerely,

Dr C. E. Cornwall and co-authors.

"EDITORIAL REQUESTS:

Please review our specific editorial comments and requests regarding your manuscript in the attached "Editorial Requests Table"."

We have revised the manuscript so that it adheres to all of the requirements detailed in the editorial requests table.

"REVIEWERS' COMMENTS:

Reviewer #1 (Remarks to the Author):

The manuscript entitled "Increasing importance of crustose coralline algae to coral reef carbonate production under ongoing climate change" by Cornwall and co-authors is an original contribution to our understanding of CCA role in the framework of the ongoing climate crisis and future changes affecting coral reefs.
The authors were able to show that, under certain conditions, CCA may match or even exceed the contribution of corals to coral reef carbonate production. However, despite their major role as carbonate producer on a global scale, CCA are often inaccurately recorded in benthic surveys or even entirely missing from coral reef carbonate budgets. The authors provide also a case history from published data about the effect of reef dynamics over the coralline/coral carbonate production in French Polynesia. It is provided also a useful review

of the different methods that may improve the inclusion of CCA in reef carbonate budget. The paper is rather well written and provides a step forward in the global understanding of coralline algae importance. However, some minor points need to be improved. In particular, there is some confusion about some scientific terms such as the growth form of corals and corallines, the meaning of the acronym CCA, the taxonomy of some of the mentioned coral species.
I recommend to review the correct use of these terms (see the annotated manuscript for details), including in the pictures, and avoid to use new terms that may be confounding. Also be consistent in the orthography and improve pictures where requested."

We thank the reviewer for their positive appraisal and further detail each of their comments below, along with our responses.

"Line 67: I suggest to have a look to the geological record and longterm record of coral vs coralline dominance in the Earth history. Future already occurred... Pomar et al 2017 Reef building and carbonate production modes in the west-central Tethys during the Cenozoic"

We now include reference to this paper and revise the introduction to state: ", similar to what occurred in past oceans when atmospheric CO_2 concentrations where elevated [1] and calcareous algae were more dominant".

"Articulated coralline algae NOT articulate taxa. These are by definition excluded from CCA."

Fig 2: Our apologies, this was an error brought about by changing the figures at the last moment in several places to also include articulate coralline algae and *Halimeda* spp. We now amend this error.

"Fig 3: planar coral is not existing in literature, as far as I know"

Flat corals exist, but we understand and how now amended to adjust the wording here.

"Fig 3: Why the cartoon here is branched if platy and encrusting corals are dealt with?"

We have amended figure 3 now to better represent a planar organism here.

"Line 166: I would try to shorten this long and complex caption by deleting the unnecessary repetition of concepts already in the maintext, and by using a more synthetic style."

We have now amended the figure legend to address this comment. Our original intent was that it could be quickly skimmed and read alongside the figure.

"Line 175: please check the validity of this name and update if needed. I think is Agaricia humilis"

Amended.

"Line 277: detect"

Now changed to "visibility detect", as eDNA surveys would detect coralline algae which would not give the meaning we intended.

"Line 281: Add citation for Caragnano et al 2009 published in Coral Reefs, an early contribution tackling this issue"

We have now added this citation.

"Line 315: Use these same titles for the corresponding sections below"

We now change this text to match the sub-headings used below.

Line 362: incorporated"

Amended.

"Fig 5: Amphiroa, Arthrocardia Corallina Ellisolandia are not CCA. They are articulated coralline algae that do not contribute to reef structure, rather, they are post-mortem sediment contributors. They are confounding. I suggest to remove them"

We agree that they are not the same as CCA, however, we wanted to give the reader an understanding of general calcareous algal carbonate production rates where possible. This could be important for future papers that attempt to deal with the sediment production side of the carbonate budgets.

"Line 389: taxa are not articulate nor crustose. Taxa have no growth form. Articulated coralline algae maybe?"

Apologies, we have now amended this.

"Line 495: why these references are explicit and not numbered?"

Thank you for picking up this formatting error, we have now changed them to numbers.

"Reviewer #2 (Remarks to the Author):

In the current era of increasing CO2 emissions and the resulting climate change, major efforts are being made regarding the assessment of the impacts and future trajectories of coral reefs, one of the marine ecosystems that have suffered major losses in the last years. The increasing frequency and intensity of bleaching (and other disturbance) events have a major impact on coral reef carbonate production and hence structure, which is often accompanied by community shifts, from being dominated by corals to dominated by other calcifiers or non-calcifiers that affect the services these ecosystems provide. Thus, an accurate assessment of coral reef carbonate budgets is essential to monitor reef trajectories. This study represents a much needed call for including so far overlooked, but important contributors to coral reef carbonate production – the crustose coralline algae (CCA). While it has long and widely been acknowledged that CCAs play key functions within reefs ("glue" that cements the reef, substrate for coral recruitment), their net carbonate production and hence, contribution when estimating coral reef carbonate budgets, is currently ignored.

The authors did a great job to make their point (a) by using the existing evidence regarding CCA carbonate production to demonstrate that it without doubt represents an essential, but so far missing part for accurately estimating reef carbonate budgets, (b) showing through modeling and with a case study that CCA contribution can become even more significant in disturbed reef environments, and (c) by giving a detailed guide of how this can be resolved, including a critical assessment of the methods."

We thank Dr Schubert for her positive comments about the strengths of this manuscript.

"My only major concern is that I am not fully on board with the title, as in my opinion it does not reflect the main question/outcome, but is based on quantitative evidence of a single case study and modelled trade-offs. From my point of view, and I am open to be convinced otherwise, the take-home message (i.e., main question) of this paper is that CCAs are important, but so-far mostly overlooked contributors to coral reef carbonate production that should be considered and included in future reef budgets. To support this claim, the authors present convincing quantitative and modelled evidence, including that CCAs can become increasingly important (i.e., increased cover and contribution to coral reef carbonate production) when coral cover declines, i.e. during disturbance events (not all of them related to climate change – COT outbreak). For me, the latter represents more of an argument supporting the need of considering the contribution of this group for more accurate coral reef

carbonate budgets, instead of the main message, as indicated by the title. Unquestionable, the evidence presented here, by modeling changes in coral vs. CCA cover and contribution to reef carbonate production and using a case study from Moorea (French Polynesia), shows clearly the increased importance of CCAs in case of declining coral cover due to disturbance events (not all of them related to ongoing climate change in the case study). However, I would refrain from generalizing, as this is just one scenario for a reef trajectory after a disturbance and will occur only under certain conditions and in specific reef environments. There are many other studies that have shown different scenarios (e.g., shift to octocoral, sponge, turf algal dominance), with herbivore and grazer abundance being one of the drivers (e.g., O'Leary & McClanahan 2010).
If the authors agree with my comment, the title should be changed, though the MS itself would not need any re-writing, as it actually is organized and written as I commented above (i.e., using the modelling and the case study as a supporting arguments to demonstrate the importance of CCAs in reefs).
O'Leary, J. K., & McClanahan, T. R. (2010). Trophic cascades result in large-scale coralline algae loss through differential grazer effects. Ecology, 91(12), 3584-3597."

We agree, and have now changed the title to the more appropriate "Importance of crustose coralline algae to coral reef carbonate production"

"SPECIFIC COMMENTS (line numbers correspond to the Word version)
- Figure 1a: It is not clear where the numbers come from. Montaggioni & Braithwaite (2009) is given as reference, but as far as I can tell by looking through the book, there are no carbonate production rates given for all these groups. Please specify.
Montaggioni LF, Braithwaite CJR. (2009). Quaternary Coral Reef Systems: History, Development Processes and Controlling Factors. In: Developments in Marine Geology) (2009)."
We now create this figure from scratch using our own drawings and take the values from Reference 10 in our paper (Kobluk).

"- line 97: "by individual organism calcification""

Added "rates here at the end of calcification".

"- Figure 2+5: I think it is a bit confusing and also unnecessary to include data of articulated coralline algae and Halimeda in these figures, as (i) non-experts on algae might not be aware of the distinction, i.e. that articulated coralline algae and Halimeda are not part of the CCA group, and (ii) it seems unnecessary, as these data are not included in the calculated mean carbonate production rates and effect sizes, shown in the figures. In any case, if the authors chose to keep these groups in the figures, please make it very clear for the readers that these are not CCAs (and maybe use a different color for Halimeda)."

We make it clearer now to non-experts that Halimeda and articulate corallines are different groups by using different font colours and point colours where possible.

"- Figure 2: To adhere to the FAIR principle for publications, I would suggest showing the studies you include here for the calculations, either as Supplementary Material or as online Data File."

Our apologies, we did not make this clear in our original submission. This is also uploaded with the code. See in text citation for where to obtain this. On the website, it is under CCA_Methods/Data/CCA_CC_SC.xlsx

"- line 134: Shouldn´t it be 61 and 66 studies? See line 145."

Amended.

"- line 138: Add "and" before (b) and (c)."

Amended.

"- line 141: "collected""

Amended.

"- line 156: Maybe better "66 records of calcification rate measurements"."
Amended.

"- line 158+163+164: Maybe better "group-specific"."

Amended.

"- line 249: Numbers for references."

Amended.

"- line 252: "Mo'orea reef carbonate budget""

Amended.

"- line 261: Just a suggestion, but this section might benefit by including a scheme summarizing and illustrating the methods of best-practice to assess CCA carbonate production/accretion."

We now create Figure 6 to display these different methods.

"- line 397: I assume that (c) represents the influence on biomass-normalized calcification rates and (d) that for area-normalized calcification rates? I recommend clarification to avoid confusion."

Correct. We now amended to state "(c) [biomass normalised rates] and (d) [surface area normalised rates] demonstrate the influence of the measurement method on the reported calcification rate determined from the GLMM model.".

"- line 418: It is unclear which the other benefit was."

Amended to state "one benefit".

"- line 468: "thus grazing may…""
Amended.

"- line 477: Maybe a good recommendation would be a multi-year deployment, with yearly measurements?"

Agreed. Now we state: "Future research should attempt to resolve these issues using multiple experimental approaches and using multi-year deployments with yearly measurements."

"- line 480: "no measurements""

Amended.

"- line 481: "reef" used repeatedly. Better "contemporary accretion rates of reef flat environments"."

Amended.

- line 473: "repeated structure from motion"? What do you mean here? Seems like a relatively new term that originated from the two papers cited below (Lange & Perry 2020, Rossi et al 2020). Maybe use the same term as in the papers ("Structure-from-Motion photogrammetry")? Also, I think it would be good to specify here for the non-expert that it is a combination of underwater imaging and 3D-modelling."

Amended.

"- line 502: Better "Structure-from-Motion photogrammetry"."

Amended, we now state “Structure-from-Motion photogrammetry, a combination of three-dimensional modelling and imaging, has been used to measure individual coral linear extension rates”.

“- line 504+505: These two studies are missing in the reference list. Also, a recently published study indicates that hyperspectral imaging might also be a good option, as it apparently can distinguish coralline algae quite well (Schürholz & Chennu 2022. Digitizing the coral reef: Machine learning of underwater spectral images enables dense taxonomic mapping of benthic habitats. Methods in Ecology and Evolution, doi.org/10.1111/2041-210X.14029).”

Apologies, we did not use the reference manger software correctly here, these references have now been added. We also now add the above cited reference, thank you for bringing his to our attention.

“- line 511: Maybe better “as previously used”.”

Amended.

“- line 517: Not sure if “constrain” is the correct term here, maybe better “assess” or “determine”.”

Amended to “assess”

“- line 518: Maybe better “of coral reefs, given the here outlined potential underestimates of CCA cover…”.”

Amended to “Presently, it is difficult to assess the global contribution of CCA to carbonate production of coral reefs, given the underestimates of CCA cover and area-normalized calcification rates outlined here.

“- line 527-528: Yes and no. YES, if you only consider global warming and associated bleaching (or other disturbance) events, but NO if you consider the higher susceptibility of CCAs to OA, compared to corals (as stated and shown repeatedly in recent publications of some of the authors, Cornwall et al. 2019, 2021, 2022). Thus, in view of the currently increasing frequency and intensity of high-temperature events that cause massive coral bleaching, CCAs might maintain positive reef accretion rates by increasing their cover and by overgrowing dead corals, thereby also decreasing dissolution of the dead coral skeletons. However, considering their higher susceptibility to OA, reefs with higher CCA cover might experience higher dissolution rates.

Cornwall CE, Diaz-Pulido G, Comeau S. (2019). Impacts of Ocean Warming on Coralline

Algal Calcification: Meta-Analysis, Knowledge Gaps, and Key Recommendations for Future Research. Frontiers in Marine Science 6, 186.
Cornwall, C. E., Comeau, S., Kornder, N. A., Perry, C. T., van Hooidonk, R., DeCarlo, T. M., ... & Lowe, R. J. (2021). Global declines in coral reef calcium carbonate production under ocean acidification and warming. Proceedings of the National Academy of Sciences, 118(21), e2015265118.
Cornwall, C. E., Comeau, S., Putnam, H., & Schoepf, V. (2022). Impacts of ocean warming and acidification on calcifying coral reef taxa: mechanisms responsible and adaptive capacity. Emerging Topics in Life Sciences, 6(1), 1-9."
Yes, we agree that CCA will be impacted by ocean acidification much more than corals, and that in the future we think they will be strongly impacted by ocean acidification compared to their present day rates of calcification if we compare on an organism level. However, given that corals will be so much more strongly impacted by thermal events than CCA will be impacted by ocean acidification, we consider this statement will still be true.

"Congratulations to this much needed work!
Best, Nadine"
We thank Dr Schubert for her time and positive appraisal of this manuscript.

"Reviewer #3 (Remarks to the Author):

The authors reevaluate the contribution of coralline algae to reef carbonate budgets. They argue that, in most cases, we have likely been severely underestimating their contributions to carbonate budgets, and that CCA will probably become an increasingly important component as corals experience losses due to climate change. Further, they provide recommendations about how to do a better job of characterizing CCA contributions going forward.

This is a great paper addressing a very timely and important knowledge gap. I could not agree more with the authors about the problem of severely underestimating the contribution of CCA to reef carbonate budgets when using many of the typical approaches. This is a problem that the field needs to acknowledge, understand, and correct.

I have only some minor comments for the authors:

Line 155-157, Totally agreed. I hope that this study will help to ameliorate this widespread misconception among the community."

We thank the reviewer for their positive assessment of the manuscript, comments from all three reviewers are very encouraging, thank you.

"Line 219-244, But using the traditional survey techniques here (and as are used in most studies), these estimates probably only provide a lower limit to the contribution of the CCA. An absolutely critical point which the authors make above, and which I think needs to be emphasized throughout the manuscript, is that a lot of CCA are growing in cryptic microhabitats across the reef and most traditional survey techniques are simply missing the majority of the CCA that is growing and calcifying on the reef. Again, I think this example is a useful place to emphasize that these are probably lower limits to the CCA contribution and more sophisticated techniques (fine-scale 3-D imaging) would probably at least help us to get closer to the true values."

We now add this caveat.

"Line 277-282, I would be explicit in recommending 3-D photogrammetry to capture these cryptic spaces. While more challenging than traditional methods, this is probably the best available method to improve census-based approaches and start accounting for the huge fraction of CCA (and other biota) which are almost completely missed in most surveys."

"Again, this is a great paper which should absolutely be part of the literature."

Thank you. We now recommend photogrammetry specifically in our conclusions.

References used in the response to reviewers' letter:

1. Pomar L, Baceta JI, Hallock P, Mateu-Vicens G, Basso D. Reef building and carbonate production modes in the west-central Tethys during the Cenozoic. *Marine and Petroleum Geology* **83**, 261-304 (2017).