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Incorporating benthic community changes into hydrochemical-based projections of coral reef calcium carbonate production under ocean acidification

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Abstract

The existence of coral reefs is dependent on the production and maintenance of calcium carbonate (CaCO3) framework that is produced through calcification. The net production of CaCO3 will likely decline in the future, from both declining net calcification rates (decreasing calcification and increasing dissolution) and shifts in benthic community composition from calcifying organisms to non-calcifying organisms. Here, we present a framework for hydrochemical studies that allows both declining net calcification rates and changes in benthic community composition to be incorporated into projections of coral reef CaCO3 production. The framework involves upscaling net calcification rates for each benthic community type using mapped proportional cover of the benthic communities. This upscaling process was applied to the reef flats at One Tree and Lady Elliot reefs (Great Barrier Reef) and Shiraho Reef (Okinawa), and compared to existing data. Future CaCO3 budgets were projected for Lady Elliot Reef, predicting a decline of 53 % from the present value by end-century (800 ppm CO2) without any changes to benthic community composition. A further 5.7 % decline in net CaCO3 production is expected for each 10 % decline in calcifier cover, and net dissolution is predicted by end-century if calcifier cover drops below 18 % of the present extent. These results show the combined negative effect of both declining net calcification rates and changing benthic community composition on reefs and the importance of considering both processes for determining future reef CaCO3 production.

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Incorporating benthic community changes into hydrochemical-based projections of coral reef calcium carbonate production under ocean acidification

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Abstract

The existence of coral reefs is dependent on the production and maintenance of calcium carbonate ($CaCO_3$) framework that is produced through biogenic calcification. The net production of $CaCO_3$ is likely to decline in the future, both due to declining net calcification rates (decreasing calcification and increasing dissolution rates) and shifts in benthic community composition from calcifying organisms (e.g. corals) to non-calcifying organisms (e.g. fleshy algae). Here we present a framework for hydrochemical studies that allows both declining net calcification rates and changes in benthic community composition to be incorporated into projections of coral reef $CaCO_3$ production. The framework involves upscaling net calcification rates for each benthic community type by using mapped proportional cover of the benthic communities. This upscaling process was applied to One Tree and Lady Elliot Reefs (Great Barrier Reef) and Shiraho Reef (Okinawa) and compared to existing data. Future $CaCO_3$ budgets were projected for Lady Elliot reef, predicting a decline to 47% of the present value by end-century (800 ppm CO_2) without any changes to benthic community composition. Under a 50% reduction in the benthic cover of calcifying organisms at Lady Elliot reef, $CaCO_3$ production was projected to decline to 18% of the present value. These results show the combined negative effect of both declining net calcification rates and changing benthic community composition on reefs and the importance of considering both processes for determining future reef $CaCO_3$ production.

Introduction

Coral reefs are comprised of a calcium carbonate ($CaCO_3$) framework that supports a high diversity of species and provide a wide range of essential ecosystem services and economic benefit to many countries (Moberg and Folke 1999). This $CaCO_3$ framework is produced biogenically through calcification by a diversity of marine organisms, primarily hermatypic corals and crustose coralline algae, and contributes significantly to the global $CaCO_3$ budget (Milliman 1993). Coral reef health is declining globally due to both local and global stressors (Hughes et al. 2003; Veron et al. 2009). Some stressors, such as ocean acidification, are predicted to directly reduce calcification rates in many calcifying organisms, leading to lower net community calcification of reefs (Kleypas and Yates 2009). The combination of local overfishing, water quality deterioration and global climate change is driving benthic community composition shifts toward less coral-dominated states, with an associated loss of the services they provide (Hoegh-Guldberg et al. 2007; Wilkinson and Global Coral Reef Monitoring Network 2008; De'ath et al. 2012).

Due to the functional importance of $CaCO_3$ production for coral reefs, it is important to know the current state of this process and how it might change in the future. Previous studies have used either census (e.g. Stearn et al. 1977) or hydrochemical approaches (e.g. Smith 1978) to calculate $CaCO_3$ production. The two methods use different approaches to the estimation of $CaCO_3$ production and have different advantages depending on the research question (Vecsei 2004). Census-based approaches quantify the amount of calcium carbonate produced by a single organism per unit area of reef surface covered to estimate potential production of a reef community (Chave Smith, and Roy 1972). $CaCO_3$ production is determined by assigning calcification rates ($gm/m^2/yr$-1) to each type of calcifier (e.g. observed or mapped benthic community type) and scaling up by multiplying the calcification rates (gm/m^2) by thearea of each benthic community type (Equation 1). In terms of geographical scope, scaling up can either apply to the local community (in which case, field based estimates of coverage are employed usually at the transect scale), or areas estimated from remotely sensed map products can be used to yield a measure of carbonate production for the entire reef.

The hydrochemical technique estimates net calcification (G_{net}, i.e. calcification minus dissolution) by measuring changes in seawater alkalinity, where each mole of $CaCO_3$ precipitated reduces seawater alkalinity concentration by two moles, with the reverse occurring for dissolution (Smith 1978). The hydrochemical technique integrates the net effect of calcification and dissolution from all biotic and abiotic components of the system, without need for the investigator to account for community composition, thus also including cryptic species and carbonate sediment. There are limitations to the locations where the hydrochemical method can be employed, with the majority of studies occurring on reef flat when mixing with oceanic waters is limited (Langdon et al. 2010). The hydrochemical method also measures G_{net} over short periods of time (e.g. hourly) and may be limited by the representativeness of when the measurements were taken.

A number of studies have related G_{net} of coral reefs, measured through hydrochemical techniques, to *in situ* variations in environmental parameters such as light, temperature, carbonate chemistry or nutrients (Silverman et al. 2007; Shamberger et al. 2011; Shaw et al. 2012). The relationships between carbonate chemistry and G_{net} have been used to predict future changes under ocean acidification. However, because these relationships were determined under constant community composition at specific locations, they only provide predictions of changes in calcium carbonate production, specific to that location and assuming a constant benthic community composition remain. Loss of coral cover is occurring globally resulting in altered community composition of reefs (Wilkinson and Global Coral Reef Monitoring Network 2008). These changes in community composition are predicted to continue into the future (Hoegh-Guldberg et al. 2007), making it important to incorporate these changes into future predictions of coral reef $CaCO_3$ production.

Here we present a framework for the incorporation of variable benthic community composition into hydrochemical estimates of present $CaCO_3$ production and future projections under an ocean acidification scenario. The hydrochemical method presented here has the advantage of incorporating processes, such as sediment dissolution, that are not readily incorporated into census techniques. We show for three Pacific reefs (Lady Elliot (Great Barrier Reef (GBR)), One Tree (GBR) and Shiraho (Japan)), how $CaCO_3$ production rates for each benthic community type can be scaled-up to determine community-scale $CaCO_3$ production across larger areas. Unlike census studies and previous larger scale upscaling studies, where calculated values cannot be compared with measured values, here we compare our scaled-up values with *in situ* community level measurements from each site at the same measurement and estimation scales. In this context “community level” refers to all benthic organisms and substrate (e.g. carbonate sediment) that form part of a mixed-community study area (e.g. a reef flat). We then demonstrate how this approach can be used to predict future levels of $CaCO_3$ production for future seawater chemistry and benthic composition scenarios.

Methods

Theory

Hatcher (1997) proposed three upscaling mechanisms for reef processes: additive, integrative or differential. Due to the absence of either known saturation effects with the geographical expansion of carbonate production across reef platforms, or non-linear interactions in calcification at smaller spatial scales (as may be expected with the alternative mechanisms), we assume here that net $CaCO_3$ production for different benthic communities is additive. This has previously been adopted for production and calcification of reefs at Moorea (Andréfouët and Payri 2001), Florida (Brock et al. 2006) and the Great Barrier Reef (Hamylton et al. 2013; Hamylton 2014). The total net $CaCO_3$ production can be calculated by the sum of the product of the net $CaCO_3$ production for an individual benthic type and the proportional area of each reef covered by that benthic community (Equation 1). This approach can be used to calculate present net $CaCO_3$ production as well as predict future values where benthic community composition and production rates are known or can be modelled (Fig. 1).

$$G_T = \sum_{i=1}^{N} G_i C_i \tag{1}$$

where G_T (mmol $CaCO_2$ m^{-2} d^{-1}) is the total net $CaCO_3$ production, G is the net $CaCO_3$ production for a particular benthic community type (i) (mmol $CaCO_2$ m^{-2} d^{-1}) and C is the proportional coverage of that community type (unitless).

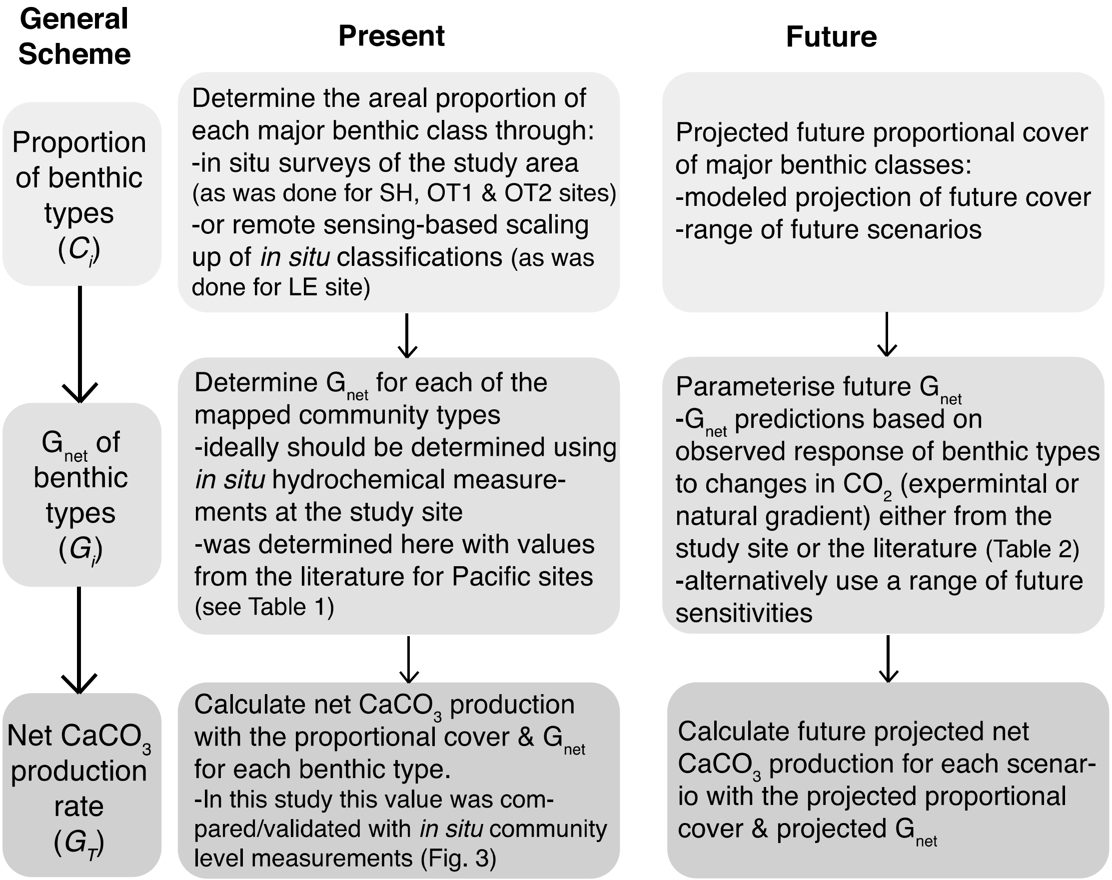

Fig. 1. Schematic diagram of the inputs for calculating present and future net $CaCO_3$ production rates under the proposed framework

The number of classes and the scale of the benthic community classifications can be determined for individual studies depending on the site-specific nature of the community, available data and the research question being addressed. The proportional coverage of each benthic type in a reef area can be determined through benthic surveys extrapolated across larger areas, or directly mapped from remote sensing imagery. For benthic surveys, the coverage could be classified to multiple scales, such as individual species or broad functional groups. The majority of mapping on coral reefs from airborne and satellites images has been at the coarser scales of functional groups or geomorphic zones. The final classification scale used may be dependent on the scale at which the $CaCO_3$ production rate data is available. For example, if benthic communities are mapped to the general growth form classes of coral (e.g. massive, branching) but G_{net} data is only available for a broad class of “live coral” then the benthic community classes will need to be generalised to match the descriptive resolution of the $CaCO_3$ production rate data.

$CaCO_3$ production rate data ideally should be collected *in situ* at the study site (Yates and Halley 2003; Brock et al. 2006). Alternatively, published values from other areas can be used under the assumption that they are representative of the study area and mapped features or classes. Where published values are adopted, these should ideally be extracted from the same reef province (e.g. IndoPacific vs. Indian Ocean vs. Caribbean) to control for macroscale environmental variation (Kleypas et al. 1999).

Upscaling case study in three Pacific reefs

We applied the approach described to three reefs in the Pacific for which suitable data were available. The chosen sites had benthic community composition data available, either through *in situ* surveys or remote sensing based mapping with *in situ* validation, as well as community-scale G_{net} measurements that could be used for validation of results. Study locations were Shiraho reef flat, Ishigaki Island, Japan (Kayanne et al. 1995; Suzuki et al. 1995), Lady Elliot reef flat, GBR (Shaw et al. 2012), and two sites at One Tree reef, GBR (Silverman et al. 2012; Shaw et al. 2015) (Fig. 2). We abbreviate the site names to SH and LE for Shiraho and Lady Elliot respectively, and designate the site used by Silverman *et al*. (2012) at One Tree as OT1 and the site studied by Shaw *et al*. (2015) as OT2.

Benthic community cover was based on transects surveyed during community metabolic studies at each site for One Tree and Shiraho (Suzuki et al. 1995; Silverman et al. 2012; Shaw et al. 2015) and from remote sensing image classification at LE (Hamylton 2014). The proportion of reef area covered by each benthic type is summarized in Table 1 for each of the sites.

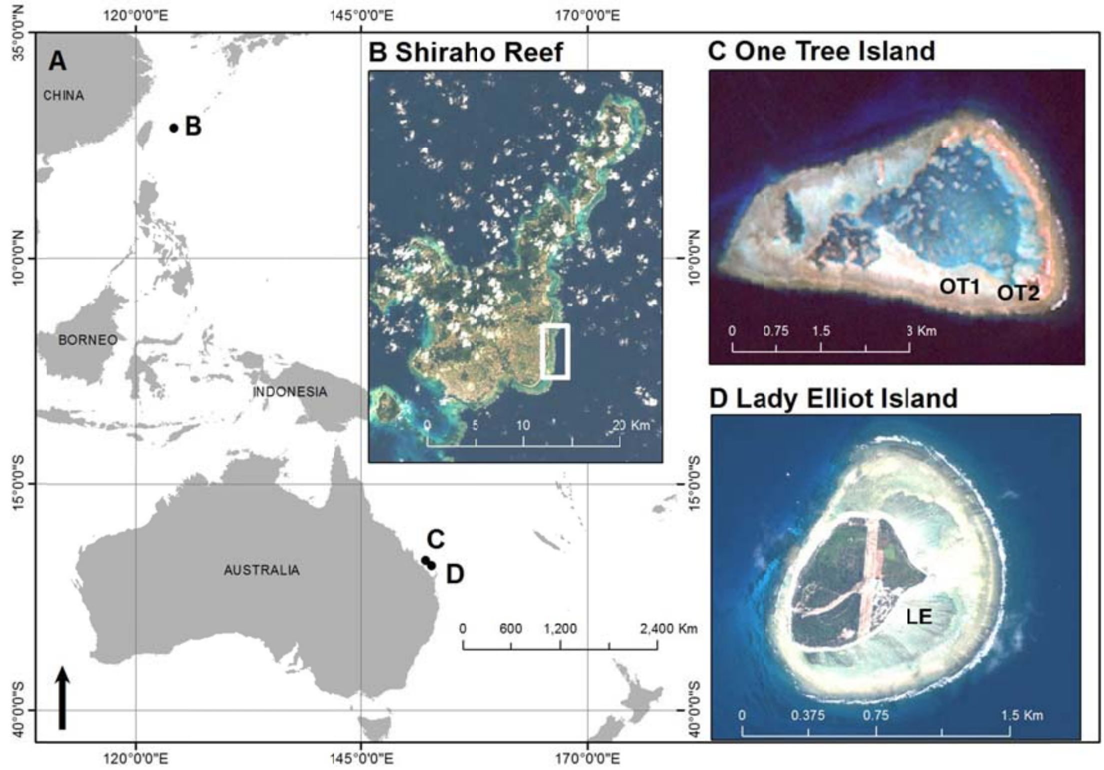

Fig. 2. Study sites. (A) Location of Ishigaki Island, One Tree Island and Lady Elliot Island in the Pacific. (B) The Shiraho Reef (SH) study site at Ishigaki Island. (C) The Lady Elliot site (LE). (D) The two sites at One Tree Reef (OT1 and OT2).

Table 1. Proportion of reef area (%) covered by each benthic type at each of the study sites as measured during community metabolic studies at SH (Suzuki et al. 1995), OT1 (Silverman et al. 2012) and OT2 (Shaw et al. 2015) and from remote sensing at LE (Hamylton 2014)

	SH	**OT1**	**LE**	**OT2**
Corals	19.0	13.7	11.8	25.2
Non-calcifying algae	18.6[a]	NA	NA	22.9
Coralline algae	0.2	1.3	42.0	7.3
Sand	62.2	10.3	39.2	18.5
Rubble/Dead coral	NA	65.5	NA	25.4
Halimeda	NA	NA	7.0	NA
Palythoa[b]	NA	5.2	NA	NA
Other	NA	4.0	NA	0.7

[a] Sum of turf and macroalgae

[b] Soft coral

The G_{net} parameterizations and source reference for each benthic community type are shown in Table 2. All rates were from *in situ* measurements using a hydrochemical approach except for *Halimeda*, which was taken from a review of existing *in situ* data of various methods for GBR locations (Rees et al. 2007), as a hydrochemical estimate was not available. The advantage of using *in situ* hydrochemical methods is that they are analogous to the methods used at the reef flat scale for comparison and that they are performed under natural, as opposed to laboratory, conditions. Cryptic species, such as some bioeroders and epiphytes, which contribute to the overall net community $CaCO_3$ budget, are also included when *in situ* hydrochemical methods are applied to individual benthic community types.

Table 2. G_{net} parameterizations for each benthic community type

Cover type	**Rate (mmol m^{-2} d^{-1})**	**Description**	**Reference**
Live coral	387.2[a]	Shiraho reef flat and Moorea	Nakamura & Nakamori (2009) Andréfouët and Payri (2001)
Non-calcifying algae	-11	Turf algae from Shiraho reef flat	Nakamura & Nakamori (2009)
Crustose coralline algae	63.3	Average of surface measurements. Lizard Is.	Chisholm (2000)
Sand	0.6	Diffusive conditions. Heron Is.	Cyronak *et al.* (2013)
Rubble/Dead coral	-10.7	Rubble. Molokai reef flat	Yates & Halley (2006)
Halimeda	60.2	GBR, from review of studies (not hydrochemical)	Rees *et al.* 2007
Palythoa	0	Unknown value	-
Other	0	Unknown value	-

[a] A value of 400 mmol m^{-2} d^{-1} was used for site SH as this is the value measured at that location. For sites LE, OT1 and OT2, the above average value from Shiraho and Moorea was used.

All data were taken from the Pacific to minimize regional differences in calcification rates. Rates were also taken from studies on shallow reef flat (shallower than 3m) benthic communities where possible to ensure consistency, both across the study sites and their associated geomorphic zones. The live coral data were taken from estimates of G_{net} for 100% coverage from studies in Moorea and Shiraho reef flat (Andréfouët and Payri 2001; Nakamura and Nakamori 2009). Non-calcifying algae were parameterized with data for turf algae from Shiraho reef flat (Nakamura and Nakamori 2009), as turf algae were the dominant non-calcifying algae mapped in the study sites and due to a lack of data on G_{net} for non-calcifying macroalgal communities. Sand was parameterized using data from Heron Island, GBR (Cyronak et al. 2013). The sand rate value was taken under diffusive conditions (c.f. advective conditions) to most closely match the slack water conditions of the overall G_{net} measurements for each reef flat site. Dead coral and rubble were combined into one category that was parameterized based on a rubble community on Molokai reef flat, central Pacific (Yates and Halley 2006). The crustose coralline algae (CCA) parameterization was from Chisholm (2000) based on the average rates of individual species measured at the surface (most comparable depth to CCA on our study sites). We had no data to parameterize *Palythoa* or "other" benthic classes, so assigned them a value of zero. This is likely to be of limited consequence for our study with *Palythoa* only recorded at OT1 (5.2%) and "other" recorded at OT1 (4%) and OT2 (<1%).

$CaCO_3$ production (mmol m^{-2} d^{-1}) was calculated for each study site using Equation 1 and the data from Tables 1 and 2. Each calculated value was compared to a measured value(s) for each study site. Both OT1 and OT2 have one measurement of daily $CaCO_3$ production, from Nov-Dec 2009 (Silverman et al. 2012) and Nov 2013 (Shaw et al. 2015), respectively. For LE, the data from Shaw *et al.* (2012) for summer, autumn and winter 2010 was integrated over a 24-hr day using a cubic fit for each period to calculate the net daily $CaCO_3$ production rates. The calculated value for SH was compared with data from both Suzuki *et al.* (1995) and Kayanne *et al.* (1995) who have each measured $CaCO_3$ production at SH during March/April/September 1990 and March 1993, respectively.

Incorporating changes in benthic community composition

We use the LE site to demonstrate how the framework presented here can incorporate changes in benthic community composition to future predictions of reef $CaCO_3$ production under changing net calcification rates. The LE site was chosen because there have been previous estimates of future $CaCO_3$ production in response to changing carbonate chemistry (Shaw et al. 2012). Initially, the map of the proportion of the reef flat covered by benthic community classes was used to compare with previous predictions from Shaw *et al.* (2012) that assumed no change in benthic community composition. Future G_{net} rates for each benthic community type were assigned based on values in the literature (Table 3). We estimated the change in $CaCO_3$ production from present-day Ω_{ar} of 3.6 (Shaw and McNeil 2014) to future Ω_{ar} of 2.1 (corresponding with ~800 ppm CO_2 levels). Although concurrent changes in sea surface temperature will also likely affect future calcification rates, our calculations are based on changes to calcification rates from changing carbonate chemistry alone, to be consistent with the predictions by Shaw *et al.* (2012). However, the framework presented here could be used to incorporate predicted changes in calcification rates from other compounding drivers.

We applied a decrease in the net calcification rate (G_{net}) of live coral of 15% per unit change of Ω_{ar} (Chan and Connolly 2013) from the present day rate (Table 2) over the 1.5 unit Ω_{ar} change from 3.6 to 2.1. There were no data on G_{net} for CCA at the target Ω_{ar} value of 2.1, so we interpolated between G_{net} values measured for control and two treatment CO_2 levels during a manipulation experiment of CCA from Heron Island (Anthony et al. 2008). The interpolation assumed a linear change in G_{net} from control to intermediate CO_2 and intermediate to high CO_2 treatments, which yielded a 92.5% decline in CCA G_{net} from present to the target Ω_{ar} of 2.1. Although change in G_{net} between treatment levels may not be linear, and short-term experiments have a number of limitations for predicting future long-term changes, the focus here is to demonstrate how to incorporate future community changes into $CaCO_3$ projections using available data.The future G_{net} for sand was taken to be the rate measured by Cyronak *et al*. (2013) under elevated (~800 ppm) CO_2 *in situ* at Heron Island, GBR (Table 3). For *Halimeda* we assigned a future rate of zero based on experimental data from Heron Island showing local *Halimeda* species no longer maintaining positive $CaCO_3$ production by Ω_{ar} of 2.1 (Sinutok et al. 2012).

These new rates (Table 3) were applied to the proportional area of benthic cover as described above in Equation 1. As we did not have future G_{net} rates for either rubble or non-calcifying algae, we assigned their current G_{net}, both of which were approximately -11 mmol m^{-2} d^{-1} (Table 2). This provides a conservative estimate of future declines in overall community G_{net}, as it is likely that higher dissolution levels will occur in the future (Silbiger and Donahue 2015).

Table 3. Net community calcification rate for each community type used under the future 800 ppm CO_2 scenario

Cover type	**Rate (mmol m^{-2} d^{-1})**	**Description**	**Reference**
Live coral	300	Applied a decline in G_{net} of 15% per unit Ω_{ar}	Chan & Connolly (2013)
Coralline algae	4.7	Interpolated from high-CO_2 treatments in experiment at Heron Is.	Anthony et al. (2008)
Sand	-3.6	Rate measured from *in situ* CO_2 addition experiment at Heron Is.	Cyronak et al. (2013)
Halimeda	0	Based on high-CO_2 experiments at Heron Is.	Sinutok et al. (2012)
Rubble/ algae	-11	Conservative estimate assuming present value due to insufficient data for future parameterization.	-

We applied changes in the future projected proportional area of each calcifying benthic community cover type to examine the effects of changing benthic community composition under the high CO_2 (800 ppm) scenario. Qualitative predictions suggest that coral reefs will become less spatially complex and have higher levels of algal cover (Hoegh-Guldberg et al. 2007). As we do not have quantitative predictions for expected declines in the area covered by each calcifying benthic community type, we applied a range of scenarios ranging from 0-100% of the present mapped coverage for each calcifier. For each scenario we reduced the cover of each of the calcifying benthic classes (live coral, CCA and *Halimeda*) equally. The area previously covered by calcifiers was then assigned to rubble/algae in line with the most common and significant phase shifts observed in coral reef communities in recent years (Done 1992). The proportional areal coverage of sand was kept constant. Although it is highly likely that the proportional areal coverage of the calcifying classes will not decline equally, we apply this simplification here to demonstrate how benthic community composition changes can be incorporated across a wide range of potential scenarios. Ideally future studies would have quantitative predictions of benthic community changes. Where these data are not available, this technique can be used to run multiple scenarios of benthic cover change and test the sensitivity of the overall $CaCO_3$ budget to losses in each benthic class.

Results

Upscaling case study in three Pacific reefs

The calculated G_{net} values, based on benthic community composition at each site, were lower than the measured value at each site except OT2 (Fig. 3). For OT1 and OT2 there was only one measured G_{net} value at each site, so it is not known how representative this one measured value is of other time periods and conditions. For OT1, the value that we calculated here is at the lower end of the standard error of the measured value calculated by Silverman *et al*. (2012) (Fig. 3). SH and LE had two and three measurements respectively at each site. Even with the small number of measurements, large differences can be seen at the same site. For LE, the calculated value was within the range of measured values, whereas for SH it was lower (Fig. 3).

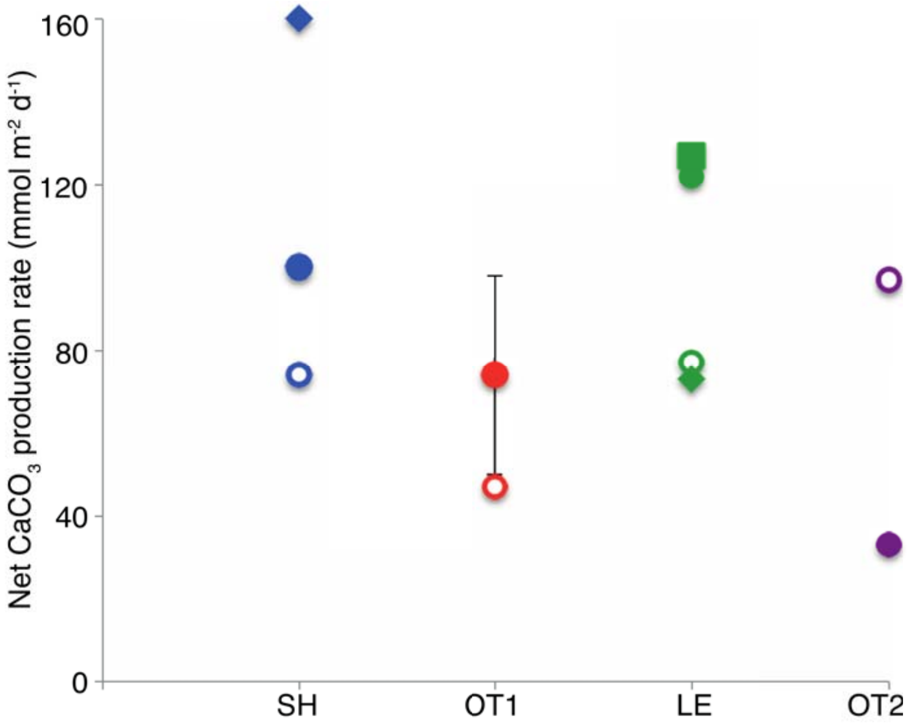

Fig. 3. Calculated (hollow symbols) and measured (solid symbols) net $CaCO_3$ production rates for Shiraho (SH), One Tree 1 (OT1), Lady Elliot (LE) and One Tree 2 (OT2) sites. Rates measured for SH by Suzuki *et al*. (1995) and Kayanne *et al*. (1995) are shown by diamond and circle symbols, respectively. LE summer, autumn and winter measured values are shown by diamond, circle and square symbols. The error bar on the OT1 measured value is the error estimate as provided by Silverman *et al*. (2012).

Future projections

When the areal proportion of benthic cover type was kept the same as present (Table 1), but G_{net} values for each community type were lowered, as expected for 800 ppm CO_2 (Table 3), the calculated $CaCO_3$ production rate for LE fell by 53%, from 77 mmol m^{-2} d^{-1} to 36 mmol m^{-2} d^{-1}. A previous study using an observed *in situ* relationship between G_{net} and Ω_{ar} at LE, predicted a greater rate of G_{net} decline of 51 mmol m^{-2} d^{-1} per unit of Ω_{ar} (Equation 5 of Shaw et al. 2012). However, the relationship by Shaw *et al*. (2012) is based on a higher present-day G_{net} value, such that the percent decline in G_{net} from that relationship is 53%, which is the same as the percent decline that we calculate here based on declines of individual community components. The different rates of decline in G_{net} with respect to Ω_{ar} may be due to uncertainties in each estimate and conform to the observation that predicted rates of G_{net} decline based on *in situ* community studies are greater than for individual species experiments (Pandolfi et al. 2011).

When we include a decline in areal proportion of calcifying benthic cover types, there is a further decline in predicted $CaCO_3$ production rate (Fig. 4). When 50% of the original calcifier cover was replaced with algae/rubble, projected $CaCO_3$ production at 800 ppm CO_2 declines from 47% percent of the original rate to 18% (Fig. 4). The projected future $CaCO_3$ production rate moves from being net positive to negative once calcifier cover drops to 18% of its original value (Fig. 4).

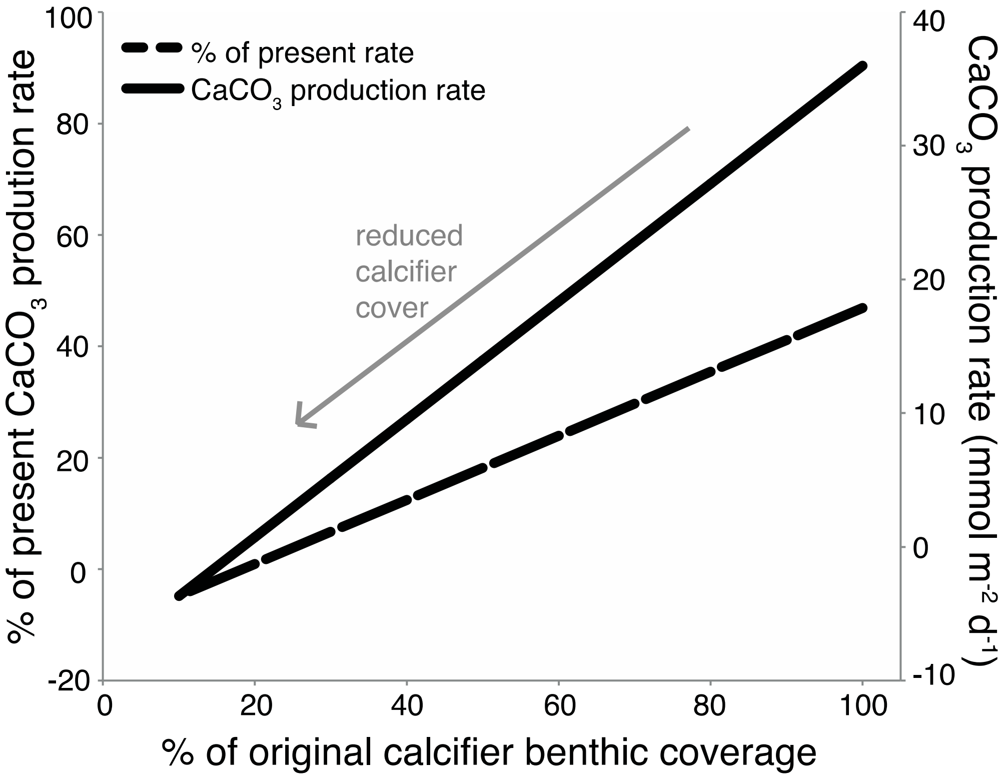

Fig. 4. Projected $CaCO_3$ production rates under 800 ppm CO_2 scenario ($\Omega_{ar} = 2.1$) and percentage change relative to current calculated levels for LE under different proportions of the current mapped calcifier coverage.

Discussion

Validation and comparison of $CaCO_3$ production estimates

Unlike previous scaled-up estimates of coral reef $CaCO_3$ production that have had no validation or relied on comparison only with other estimated values, we were able here to compare our upscaled $CaCO_3$ production rates with *in situ* measurements. Although the primary focus here was to demonstrate the scaling-up framework using available data from the literature, it was encouraging that the scaled-up value for LE was within the observed values and that other sites were all of the same order of magnitude (Fig. 3). There are however, a number of sources of uncertainty that could be addressed and improved from this analysis that would be expected to lead to higher accuracy results within the proposed framework, which are addressed below.

Uncertainties in the scaled-up production estimates are likely to occur due to error in both the rate parameterization for each community type and the estimate of areal proportion of benthic cover types. Rate parameterizations in this study were taken from the literature and were not site-specific. Ideally rates would be measured for each representative community type *in situ* at the study site as $CaCO_3$ production rates can vary in different locations due to environmental parameters, such as temperature, nutrients and carbonate chemistry (e.g Lough 2008; Manzello et al. 2008). Where *in situ* measurements cannot be made, rate parameterizations could potentially be improved by incorporating known geographic variations. For example, instead of having a uniform rate for coral calcification for all locations, it could be parameterized with respect to temperature, where latitudinal temperature gradients affect calcification rates (Lough 2008). Uncertainty also exists in the parameterization of calcification rates at the functional group scale used here, due to interspecific variability in calcification rates. For example, the CCA rate used was taken to be the average rate measured for three species, where the greatest rate measured for the three species was twice as high as the lowest (Chisholm 2000). The variability in calcification rate, combined with broad classifications that do not resolve species level, necessitate that there will be some uncertainty with the rate parameterization. However, this could be improved by performing *in situ* rate measurements with representative communities at the study site.

Errors in the scaled-up $CaCO_3$ production rates can also occur from limitations in mapping benthic communities. *In situ* classification methods are inherently subjective (e.g. is algae growing on dead coral classified as algae or dead coral?) and in the process of extrapolation, benthic cover types can be difficult to interpret on the basis of spectral information supplied from remote sensing instruments alone. While such approaches provide cost effective means of benthic community classification in reef environments (Mumby et al. 1999) over larger spatial scales (Goodman et al. 2013), an associated loss of resolution imposes a limit on capturing the fine scale details of calcifying communities. Furthermore, most standard *in situ* survey techniques and air and space borne remote sensing techniques generate 2-dimensional representations of benthic communities that are 3-dimensional (Goatley and Bellwood 2011). This leads to an underestimation of calcification processes occurring over rugose surface areas of community components, such as branching corals. Particularly in shallow reef flat environments, such as the study sites used here, the growth of certain corals is tidally constrained, with vertical surfaces that cannot be observed from above representing their active sites of lateral expansion, thus resulting in an underestimated coverage when only considered in two dimensions.

An underestimate of live coral cover from using 2-dimensional benthic survey techniques could have contributed to calculated values of $CaCO_3$ production that were lower compared with *in situ* measured values at three of the four study sites (Fig. 3). Due to the high rate of $CaCO_3$ production of live corals (Table 2), the total community $CaCO_3$ production rate is most sensitive to the proportion of live coral cover. For all sites, $CaCO_3$ production by live coral is the dominant contributor to overall net $CaCO_3$ production (Fig. 5). Therefore changes in live coral cover have a large potential to change total community production and errors in mapped coral cover can introduce potentially large uncertainty in the upscaled $CaCO_3$ production value.

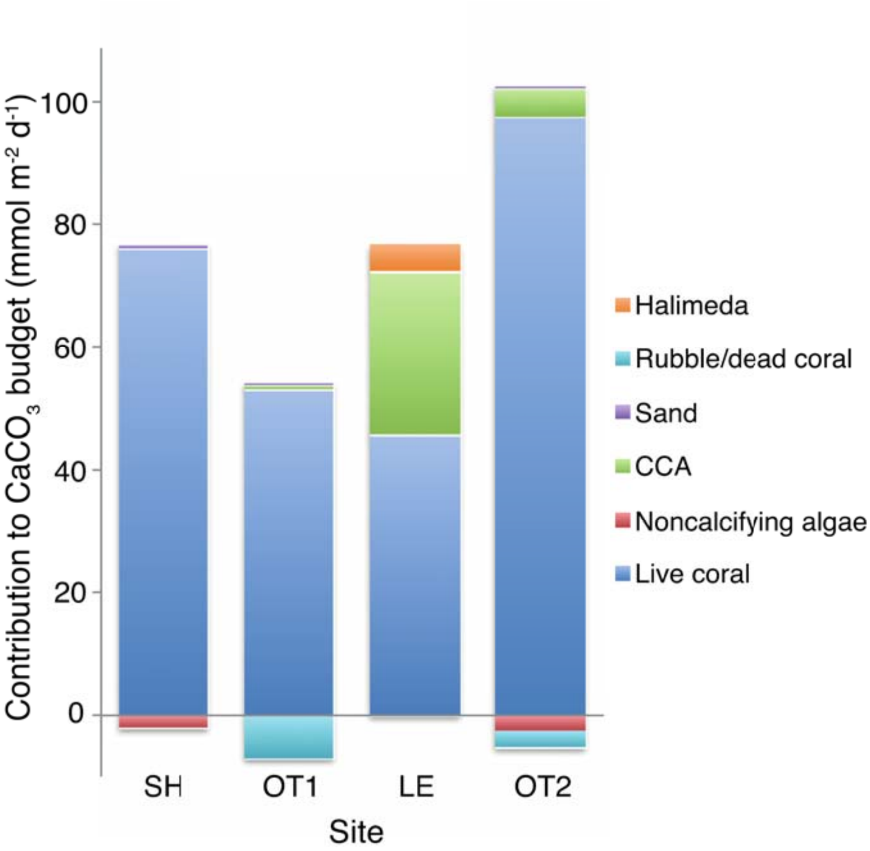

Fig. 5. Contribution of each benthic cover type to the overall $CaCO_3$ budget of each site

The three-dimensional structure of calcifying communities can be measured *in situ* at a number of spatial scales, including manual measurements of fine chain lengths draped over the census communities ??m, as in *ReefBudget* technique (Perry et al. 2012), use of *in situ* stereoscopic cameras to resolve fine-scale photogrammetric variation in the benthic community >?m (Friedman et al. 2012; Leon et al. 2015), the wider use of remote sensing techniques, such as sonar, single and multibeam echosounder (Goodman et al. 2013), or the estimation of bathymetry from multiple bands of optical satellite imagery (e.g. Stumpf et al. 2003). For the current application, an approach that defines a relationship between fine scale and broader techniques to categorize reef zones as high, medium and low levels of rugosity could provide a practical solution to the incorporation of structural complexity into estimates of calcification across reef platforms.

Differences between scaled-up values and *in situ* community measurements compared in this study could also be a result of the measured value adopted for comparison. Due to the labor intensity and number of samples required to integrate for one daily community G_{net} value (Langdon et al. 2010), often only a single daily G_{net} value is calculated. For the SH site, where G_{net} measurements have been taken by both Suzuki et al. (1995) and Kayanne et al. (1995) at different times, the value obtained by Suzuki et al. (1995) was 60% higher than the value from Kayanne et al. (1995) (Fig. 3). Similarly for LE, Shaw et al. (2012) measured G_{net} in autumn and winter that were 67% and 74% higher than the measured value from summer that year. This large temporal variability in community G_{net} may mean that even where upscaled values and measured values do not exactly agree, that the upscaled value may still be within the range of *in situ* values. This highlights the seasonal nature of calcification and indicates that, where possible, *in situ* measurements should be timed to coincide for meaningful comparison.

Incorporating benthic community changes into $CaCO_3$ production predictions

The benthic community composition of coral reefs is changing, with marked reductions in live coral cover observed in many reefs throughout the world (Gardner et al. 2003; Bruno and Selig 2007; De'ath et al. 2012). These changes are likely to continue into the future with further stress put on reefs from increasing sea surface temperatures and ocean acidity (Hoegh-Guldberg et al. 2007). Studies that have used *in situ* community scale measurements to predict the response of reefs to ocean acidification (Silverman et al. 2007; Shamberger et al. 2011; Shaw et al. 2012) have resulted in relationships of calcification and seawater carbonate chemistry assuming constant community composition. Here we provide an initial framework that overcomes this assumption by incorporating both changes in community composition and changes in calcification/dissolution rates to generate a more realistic prediction of future changes to coral reef $CaCO_3$ production.

Using our scaling-up approach we predict that community $CaCO_3$ production at LE would decline by 53% under constant community composition (Fig. 4), in agreement with predictions by Shaw et al. (2012) from *in situ* relationships. The rate of decline of $CaCO_3$ production increases with declining calcifier cover, such that a 50% decline in calcifier cover is predicted to result in an 82% decline in $CaCO_3$ production from present values (Fig. 4). Although end-century $CaCO_3$ production is still predicted to be positive under current levels of calcifier cover, we predict this to shift to negative if calcifier cover at LE drops to <18% of current levels. This prediction is based on a uniform decline in all calcifiers and would be higher if coral cover accounted for a greater proportion of decline than calcifying algae due to higher calcification rate parameterization of corals. Similarly, using census techniques, Perry et al. (2013) found a present-day threshold at which net $CaCO_3$ production shifts from positive to negative of 10% live coral cover.

Summary and future research directions

The framework proposed here utilizes hydrochemical-based measurements, which have the advantage of integrating both calcification and dissolution for carbonate budget calculations. While predictions of future coral reef G_{net} based on *in situ* hydrochemical relationships have previously been based on the unlikely assumption of constant community composition, the method proposed here incorporates both changing community composition and changes to calcification/dissolution rates of each community type. A recent review of coral reef carbonate models by Jones *et al*. (2015) has identified benthic community composition as a critically important factor that currently limits the predictive power of reef carbonate models. This framework allows multiple drivers of $CaCO_3$ production decline to be assessed together (lowered G_{net} from ocean acidification and changing benthic community composition from multiple stressors), where the assessment of multiple drivers of change and ecosystem-scale processes are presently major knowledge gaps for ocean acidification research (Riebesell and Gattuso 2015).

The proposed framework is also suited to upscaling using remote sensing imagery and its derived maps, allowing $CaCO_3$ budgets to be calculated for larger areas than previously used in hydrochemical studies, where the development of relationships between community metabolism and benthic communities for remote-sensing based upscaling has previously been identified as a future research requirement in the *Guide to Best Practices for Ocean Acidification Research* (Langdon et al. 2010). As incremental developments in remote sensing technology improve sensor spectral and spatial resolution, the level of detail and associated reliability with which calcifying communities can be mapped will improve the efficacy of the present framework. Although we have demonstrated application of the framework for calculation of $CaCO_3$ production, it could also be applied to calculation of organic carbon production based on net community production rates of benthic community types.

While it is promising that, by using calcification rate parameterizations from the literature, we can get reasonable agreement between upscaled and *in situ* measured $CaCO_3$ production rates, there are a number of areas of future research that could markedly increase our ability to predict and understand future changes in coral reef $CaCO_3$ production within the proposed framework:

1. Standardized, high quality benthic cover estimation techniques.
2. Incorporation of rugosity through use of 3-dimensional benthic cover mapping.
3. Development of quantitative predictions of future benthic community composition to improve estimates of future $CaCO_3$ production rates and to determine sensitivity to different future benthic cover scenarios.

Maintaining reef $CaCO_3$ framework is essential for the biodiversity and structural ecosystem services of coral reefs. The framework presented here is important because it helps us to understand how net $CaCO_3$ production is changing and will change in the future. Critically, it incorporates both benthic community composition transitions (Hoegh-Guldberg et al. 2007) and reductions in rates of net calcification (Andersson and Gledhill 2013) into future $CaCO_3$ production projections, and upscales current measurements to obtain $CaCO_3$ production budgets across entire reef systems. This represents a spatial scale at which meaningful statements can be made about the implications of these community changes for ecosystem services in reef environments. Together, the advances presented by this modeling framework facilitate a more deterministic and realistic understanding of the current and future states of calcification than has hitherto been possible.

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