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REPORT

Evaluating measurements of coral reef net ecosystem calcification rates

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Abstract Monitoring the rates and drivers of coral reef net ecosystem calcification (NEC) under anthropogenic environmental change is critical for predicting associated changes in reef structures and ecosystem services. However, NEC studies to date show weak agreement between studies and notably reveal no relationship between NEC and benthic calcifier cover. In this study, we tested for the sensitivity of calculated NEC to uncertainties in seawater depths and residence times (± 83% relative to 6 m and 6 h, respectively) using a coral reef total alkalinity (A_T) simulator (reefCA$_T$S) and found that these errors can interact to drive large asymmetric uncertainties ranging from − 91% to + 1000% in NEC. Furthermore, numerical simulations of hypothetical NEC for coral populations occupying reefs with increasing structural complexity (rugosity = 1–4) showed that the effects of reef-scale rugosity on NEC can be as important as benthic community composition. As a result, uncertainties in seawater depth, residence time, and/or reef structural complexity are enough to mask any potential real correlation between NEC and percent calcifier cover in the field. To improve comparability and validity of NEC studies, we recommend that future studies place a high degree of scrutiny on measurements of seawater hydrodynamics, report all NEC equation parameters ± uncertainties, and ideally include benthic community composition and structural complexity data to further explore the relationship between NEC and calcifier cover.

Keywords Coral reef · Net ecosystem calcification · Structural complexity · Rugosity · Ecosystem services · Climate change · Biogeochemistry · Ecosystem monitoring

Introduction

Coral reefs are currently undergoing rapid declines in coral cover globally (Gardner et al. 2003; Bruno and Selig 2007; Jackson et al. 2014), which can decrease coral reef growth and shoreline protection for coastal human populations around the world (Harris et al. 2018; Perry et al. 2018; Storlazzi et al. 2018). Monitoring coral reef growth (i.e., coral reef growth = calcification − $CaCO_3$ dissolution + $CaCO_3$ sediment import − $CaCO_3$ sediment export [Chave et al. 1972; Stearn et al. 1977; Kleypas et al. 2001]) is therefore necessary to predict potential changes in the maintenance of coral reef $CaCO_3$ structures and the resulting ecosystem services these structures provide (Kleypas et al. 2001; Edmunds et al. 2016; Courtney et al. 2018; Cyronak et al. 2018; Perry et al. 2018). However, accurate and precise measurements of modern coral reef growth have proved a challenging task.

Reef growth can be directly measured from reef sediment cores (Aronson and Precht 2001; Montaggioni 2005) or by long-term changes in bathymetric mapping (Yates et al. 2017). However, these methods lack the temporal resolution to track higher frequency changes in reef growth and metabolic performance associated with shifting benthic community compositions and oceanographic forcing,

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which are increasingly important given the current status of coral reef declines. Alternatively, census-based $CaCO_3$ budget methodology is one approach used to approximate annual net coral reef $CaCO_3$ production by assigning annual rates of $CaCO_3$ production and erosion to benthic survey data, but by definition generally omits the net import/export of $CaCO_3$ terms required to fully calculate reef growth (Chave et al. 1972; Stearn et al. 1977; Hubbard et al. 1990; Perry et al. 2012, 2018). These methods can be rapidly applied across a range of coral reef systems, but typically rely on literature-derived annual mean $CaCO_3$ production/erosion rates that are assumed to be constant across geographic and environmental conditions (Perry et al. 2012). As a result, these census-based budgets often fail to capture sub-annual variability in net reef $CaCO_3$ production (Courtney et al. 2016) and site-specific variability in rates of $CaCO_3$ production and erosion. Another approach to estimate net coral reef $CaCO_3$ production utilizes chemistry-based methods (i.e., net ecosystem calcification [NEC] = calcification–$CaCO_3$ dissolution) that address these shortcomings by measuring alkalinity anomalies ($\Delta A_T = A_{\mathrm{Tinitial}} - A_{\mathrm{Tfinal}}$ where A_{Tfinal} represents the seawater total alkalinity that has been modified by the coral reef from its initial value of A_{Tinitial}) as a proxy for net removal of Ca^{2+} and dissolved inorganic carbon (DIC) by NEC on time-scales of approximately hours to days (Broecker and Takahashi 1966).

While a broad range of NEC methods exists, they all rely on difficult to constrain measurements of seawater hydrodynamics that mediate the length of time and total amount of the seawater that has been in contact with and modified by the benthos to calculate NEC from alkalinity anomalies (Broecker and Takahashi 1966; Smith and Key 1975; Gattuso et al. 1996; Silverman et al. 2007; Venti et al. 2012; Zhang et al. 2012; Falter et al. 2013; Lowe and Falter 2015; Courtney et al. 2016). Historically, studies have utilized slack tides, temporal isolation during low tide, unidirectional flow regimes (Eularian or Lagrangian), enclosures, or calculated atoll seawater residence times to estimate NEC (Broecker and Takahashi 1966; Smith and Key 1975; Kinsey 1985; Gattuso et al. 1996). The advantages and disadvantages of these earlier methods have previously been discussed by Kinsey (1985), but see also more recent eddy covariance and benthic gradient flux methods (Long et al. 2015; Takeshita et al. 2016).

Typically, NEC is calculated from measurements of seawater alkalinity anomaly (ΔA_T), density (ρ), depth (z), and residence time (τ) as per the following equation (Smith and Key 1975; Langdon et al. 2010):

$$\mathrm{NEC} = \frac{\Delta A_T \rho z}{2\tau} \tag{1}$$

Of these parameters, seawater A_T can be precisely measured within ± 2 μmol kg^{-1} using established sampling and analytical methods (Dickson et al. 2007) and seawater density can be precisely measured or calculated from seawater temperature, salinity, and pressure via the seawater equation of state to within ± 0.002 kg m^{-3} (McDougall and Barker 2011; Roquet et al. 2015). LIDAR (Light Detection and Ranging)-produced digital elevation models (Yates et al. 2017) allow for precise measurements of reef-scale seawater depths (z) and advancements in current profiler technologies (DeCarlo et al. 2017), numerical models (Lowe et al. 2009), and chemistry-based seawater residence times (Venti et al. 2012; Muehllehner et al. 2016) have improved our ability to quantify coral reef hydrodynamics. However, precisely determining the z and τ of the hydrochemical footprint (i.e., spatial area and length of time over which the water has been modified by the benthos) associated with the measured ΔA_T remains a significant challenge owing to the spatiotemporally complex hydrodynamics of coral reef environments, which consequently can generate potentially large uncertainties in NEC calculated from z and τ via Eq. 1 (Venti et al. 2012; Zhang et al. 2012; Falter et al. 2013; Lowe and Falter 2015; Courtney et al. 2016). For example, Shamberger et al. (2011) and Courtney et al. (2018) used seawater flow rates and residence times, respectively, to calculate NEC using similar ΔA_T and hydrodynamic conditions at overlapping portions of the Kāne'ohe Bay reef flat, but the differences in characterizing this flow were the primary driver of diverging NEC rates by approximately an order of magnitude between the two studies (Courtney et al. 2018). Thus, we suggest that the uncertainties associated with constraining the z and τ of the hydrochemical footprint require further investigation to ensure greater consistency and comparability of NEC between studies.

Intuitively, increasing cover of calcifiers (e.g., the typical dominant reef calcifiers are scleractinian corals, red coralline algae, molluscs, *Halimeda* calcifying algae, and benthic foraminifera [Montaggioni and Braithwaite 2009]) should positively correlate with increasing NEC due to increasing $CaCO_3$ production rates. This relationship is inherent in census-based studies (but note that this is in part an artifact of the budget methodology [Perry et al. 2012]) and has been observed in a chemistry-based mesocosm study (Page et al. 2017), but field-based NEC rates show no relationship with calcifier cover (DeCarlo et al. 2017). This lack of an observed relationship between calcifier cover and NEC in the field could be due to mechanistic factors such as altered calcification rates under local environmental conditions (DeCarlo et al. 2017) or competitive interactions (Tanner 1995, 1997; McWilliam et al. 2018), the provisioning of additional surface area to calcifiers by three-dimensional reef-scale structural complexity (Hubbard et al. 1990; Pichon 1997; Szmant 1997, 2002; Perry et al. 2012), underreported calcifier cover owing to difficulties in surveying under canopies (Goatley and Bellwood 2011), relative proportion of faster and slower calcifiers (Chave et al. 1972; Pichon 1997; Szmant 2002; Perry et al. 2015), and/or the effects of $CaCO_3$ dissolution and chemical $CaCO_3$ bioerosion (Andersson and Gledhill 2013; Eyre et al. 2018). Alternatively, the previously described difficulties associated with constraining complex seawater hydrodynamics over coral reef environments and resulting NEC uncertainties can be large (Falter et al. 2013) and we hypothesize that these potentially large and underreported NEC uncertainties may be masking any potential real correlation between NEC and calcifier cover.

To test this hypothesis, we developed a coral reef total alkalinity simulator (reefCA$_T$S) to calculate expected ΔA_T for a given NEC under varying seawater depths and residence times and to perform a sensitivity analysis of how errors in seawater depth and residence time affect calculated NEC. We then further calculated a range of expected NEC for given coral cover, community composition, and reef structural complexity drawing from census-based and mesocosm/enclosure NEC studies to serve as a reference for evaluating future NEC studies.

Materials and methods

The coral reef total alkalinity simulator (reefCA$_T$S) is a simple box model consisting of a seawater reservoir overlying a coral reef community that measures the change in seawater A_T owing to NEC. The purpose of this study was not to fully simulate the dynamic physical and biogeochemical processes occurring over a reef flat (e.g., see Falter et al. [2013]), but instead to generate the simplest example of a calcifying benthic community chemically modifying the overlying seawater chemistry (Fig. 1) to (1) calculate ΔA_T for a range of seawater depths and residence times with calcification by two representative coral species and (2) isolate the sensitivity of NEC calculations to uncertainties associated with constraining seawater depth (z) and residence time (τ).

reefCA$_T$S model overview

Seawater hydrodynamics were simplified by assuming a steady state of seawater flux into (SW$_{in}$; kg h^{-1}) and out of (SW$_{out}$) the seawater reservoir (i.e., SW$_{in}$ = SW$_{out}$) with a fixed 1 km^2 planar area and constant parameterized depth that assumes no influence of tides and waves on the volume of seawater in this reservoir. Furthermore, seawater was assumed to only flow into the reef seawater reservoir from source water of constant A_T (A_{Tin}; µmol kg^{-1}) that was completely and instantaneously mixed and remained for a fixed residence time before flowing out of this reservoir (Fig. 1). Alkalinity flux owing to calcification [$F(A_{Tcalcification})$; µmol h^{-1}] was parameterized based on literature values (see subsequent section) and was the sole process changing A_T within the seawater reservoir. No other processes (e.g., no $CaCO_3$ dissolution, no heating/cooling, and no evaporation/precipitation) modified seawater properties. The mass balance of total alkalinity in the seawater reservoir was represented by the following differential equation:

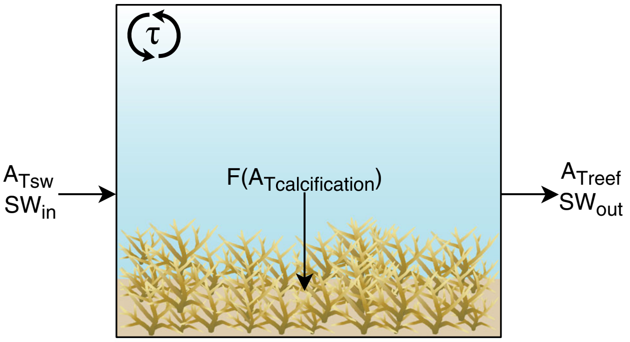

Fig. 1 reefCA$_T$S diagram shows the parameterized fluxes of seawater total alkalinity (A$_T$) into and out of the 1-km^2 planar area coral reef seawater reservoir with volume controlled by parameterizing reservoir depth (z). A_{Tsw} is the total alkalinity of the seawater flowing into the box (SW$_{in}$), which is instantaneously mixed for the duration of the seawater residence time (τ). A_{Treef} is the total alkalinity of the seawater flowing out of the reef box (SW$_{out}$), z is the depth which controls the volume of seawater in the reef box, and F(A$_{Tcalcification}$) is the total alkalinity flux out of the reef seawater owing to model parameterized calcification

$$\frac{dA_{Treef}}{dt} = \mathrm{SW_{in}} \times [A_{Tin}] - \mathrm{SW_{out}} \times [A_{Treef}] - F(A_{Tcalcification}), \tag{2}$$

and thus, at steady state:

$$0 = \mathrm{SW_{in}} \times [A_{Tin}] - \mathrm{SW_{out}} \times [A_{Treef}] - F(A_{Tcalcification}) \tag{3}$$

The seawater residence time (τ; h) was defined as the ratio of the total mass of seawater in the reservoir (M_{SWreef}; kg) over the seawater inflow or outflow, assuming a steady state:

$$\tau = \frac{M_{SWreef}}{\mathrm{SW_{in}}} = \frac{za\rho}{\mathrm{SW_{in}}} \tag{4}$$

where z is the depth of the reef seawater reservoir (m), a is the area of the reef (m^2), and ρ is the density of seawater (kg m^{-3}). Thus, the differential equation for the rate of change of reef seawater total alkalinity (dA_{Treef}/dt; µmol kg^{-1} h^{-1}) can be expressed as:

$$\frac{dA_{\mathrm{Treef}}}{dt} = \frac{A_{\mathrm{Tin}} - A_{\mathrm{Treef}}}{\tau} - \frac{F(A_{\mathrm{Tcalcification}})}{za\rho} \quad (5)$$

This equation (Eq. 5) was solved at 0.1-h time steps using the *ode45* ordinary differential equation solver in the statistical software *R* (R Core Team 2017) package *deSolve* (Soetaert et al. 2010). Each model simulation was run for 2500 h to ensure a steady state in the reef seawater reservoir before calculation of the alkalinity anomaly ($\Delta A_{\mathrm{T}} = A_{\mathrm{Tin}} - A_{\mathrm{Treef}}$) and NEC via Eq. 1.

Parameterized values

All reefCA$_{\mathrm{T}}$S runs were calculated using a 1 km × 1 km planar reef area with fixed calcification rates for a range of seawater depths (1–11 m at 1 m intervals) and residence times (1–11 h at 1 h intervals) to simulate a broad range of coral reef hydrodynamic states and resulting ΔA_{T}. Fixed calcification rates were used to avoid confounding the results of this analysis with diel variability in calcification rates. A rate of 33.8 mmol m^{-2} h^{-1} by 100% coral cover of *Acropora nasuta* (calcification = 29.6 kg $CaCO_3$ m^{-2} yr^{-1} sensu Morgan and Kench [2012]) was used because it represents an approximate upper rate for calcifying reef corals (Pratchett et al. 2015). While the subsequent sensitivity analyses were based on 100% cover *A. nasuta* calcification rates, additional simulations were conducted using a calcification rate of 15.7 mmol m^{-2} h^{-1} that represents calcification by 100% cover of the more slowly calcifying *Porites lobata* (calcification = 13.8 kg $CaCO_3$ m^{-2} yr^{-1} sensu Morgan and Kench [2012]) to serve as an additional reference for expected ΔA_{T}. For reference of the values used in this study, the 1–11 m seawater depths used in this study are within the range of mean (± standard deviation) depths for typical reef flats (1.3 ± 0.5 m) and channels (6.3 ± 9.8 m) from Falter et al. (2013). Similarly, the 1–11 h residence times in this study are within the range of 1.4–14.7 h it would take for seawater to transit and be biogeochemically modified by a typical reef flat assuming mean (± standard deviation) unidirectional, depth-averaged flow rates of 0.16 ± 0.06 m s^{-1} and reef flat widths of 3.7 ± 2.6 km from Falter et al. (2013). However, it is important to note that recirculation patterns, oscillating seawater flows, and reef morphologies are capable of generating longer and spatially variable seawater residence times than predicted from mean unidirectional flow rates across a reef flat, which consequently can drive greater and more spatially variable coral reef ΔA_{T} (Lowe et al. 2009; Venti et al. 2012; Zhang et al. 2012; Falter et al. 2013; Lowe and Falter 2015; Muehllehner et al. 2016). To address this potential for longer residence times and better represent lower coral cover systems, we included additional ΔA_{T} simulations with residence times ranging from 1 to 144 h, depths ranging from 1 to 11 m, and 10% coral cover calcification rates (i.e., 10% *A. nasuta* or 10% *P. lobata*) occupying a planar 1 km^2 reef area. Models were parameterized using mean surface ocean total alkalinity (A_{T} = 2310 μmol kg^{-1}) and average seawater density (ρ = 1023 kg m^{-3}) for the upper 50 m at station ALOHA from the Hawai'i Ocean Time-series for 1988–2017 (hahana.soest.hawaii.edu/hot/hot-dogs).

Sensitivity analysis

The model simulation for a seawater depth of 6 m and residence time of 6 h using the fixed 33.8 mmol m^{-2} h^{-1} calcification rate by 100% cover *A. nasuta* calcification resulted in a ΔA_{T} of 66 μmol kg^{-1}. This ΔA_{T} was then used to calculate NEC (Eq. 1) using the actual seawater depth and residence time and for a range of erroneous seawater depths (1–11 m) and residence times (1–11 h). While we do not know the actual range of typical errors in seawater depth and residence time across NEC studies, these simulated ranges were calculated as the percent error relative to the model parameterized reference value such that $z = 6 \pm 5$ m (± 83%) and $\tau = 6 \pm 5$ h (± 83%) to generalize these results to other NEC studies with varying mean seawater depths and residence times. Similarly, erroneously calculated NEC from the sensitivity analysis of this study was determined as the percent error relative to the actual parameterized reefCA$_{\mathrm{T}}$S NEC. The resulting errors in NEC were assessed with respect to (1) seawater depth, (2) residence time, or (3) both seawater depth and residence time.

Literature review

A literature review of NEC supplementing the work of DeCarlo et al. (2017) with more recent studies and separating studies conducted in mesocosms and enclosures from field-based studies was then performed to further test for linear scaling of NEC with calcifier cover (see supplementary NEC review datasheet). Linear models between NEC (previous studies were converted to mmol $CaCO_3$ m^{-2} h^{-1}) and percent calcifier cover were fitted using the function *lm* and assessed using ANOVA for the mesocosm/enclosure and field-based studies separately to test for linear correlations between NEC and calcifier cover.

Effects of reef structural complexity on NEC

Additional calculations were made to assess the effects of reef structural complexity and coral community composition on NEC. We used rugosity (R) = linear/planar distance along the reef surface with typical ranges of R = 1–4 (Graham and Nash 2013) to model the effects of structural complexity on NEC in this study. Single-species benthic communities of 0–100% *A. nasuta* and *P. lobata*, respectively, were simulated over reef-scale rugosities ranging from 1 to 4 to simulate potential upper bounds of NEC for reef sites of varying structural complexity occupied by a rapidly calcifying coral (*A. nasuta*) and a more slowly calcifying coral (*P. lobata*). These simulations allow us to explore the interactions between calcification rates and reef structural complexity (Pichon 1997; Szmant 1997, 2002; Perry et al. 2012; Graham and Nash 2013; Pratchett et al. 2015) to calculate expected NEC for hypothetical coral reef ecosystems.

Results

reefCA$_{\mathrm{T}}$S alkalinity anomalies

The reefCA$_{\mathrm{T}}$S runs for a range of seawater depths (1–11 m) and residence times (1–11 h) for the parameterized 33.8 mmol m^{-2} h^{-1} calcification rate (100% cover *A. nasuta* planar reef) generated ΔA_{T} ranging from 6 µmol kg^{-1} (1 h, 11 m simulation) to 726 µmol kg^{-1} (11 h, 1 m simulation) (Table 1). Simulations for the parameterized 15.7 mmol m^{-2} h^{-1} calification rate (100% cover *P. lobata* planar reef) yielded ΔA_{T} ranging from 3 µmol kg^{-1} (1 h, 11 m simulation) to 338 µmol kg^{-1} (11 h, 1 m simulation) (Table 1). The longer residence time simulations for the 10% *A. nasuta* and 10% *P. lobata* planar reefs with depths of 1 to 11 m and residence times of 1 to 144 h followed a similar pattern (Table 2). In essence, the ΔA_{T} is dependent on the ratio of calcification rate to seawater volume wherein shallower seawater depths have exponentially decreasing seawater volumes that are more intensely chemically modified by calcification and result in greater ΔA_{T} (Tables 1, 2). Longer seawater residence times allow for a greater contact time between the overlying seawater and underlying calcifiers, resulting in greater seawater ΔA_{T} (Tables 1, 2).

reefCA$_{\mathrm{T}}$S sensitivity analysis

The *A. nasuta* simulations evaluating the effect of erroneous depths show that errors of ± 83% in z relative to the actual parameterized depth of 6 m (i.e., 1–11 m) yielded erroneously calculated NEC increasing linearly from − 83% to + 83% (5.6–61.9 mmol m^{-2} h^{-1}) relative to the actual rate of 33.8 mmol m^{-2} h^{-1} (Fig. 2a). Conversely, *A. nasuta* simulations evaluating the effect of erroneous residence times show that errors of ± 83% in τ relative to the actual parameterized residence time of 6 h (i.e., 1–11 h) yielded erroneously calculated NEC exponentially decreasing from + 500% (202.6 mmol m^{-2} h^{-1}) to − 45% (18.4 mmol m^{-2} h^{-1}) relative to the actual rate of 33.8 mmol m^{-2} h^{-1} (Fig. 2b). Thus, underestimates of τ produced greater NEC errors (i.e., − 83% τ = + 500% NEC) than overestimates of τ (i.e., + 83% τ = − 45% NEC, Fig. 2b). Simulations in which both of these simulated errors in seawater depth (± 83%) and residence time (± 83%) were made concurrently resulted in a mean (± SE) NEC error of + 65 ± 18% owing to the nonlinear range of erroneously calculated NEC from − 91% to + 1000% (3.1–371.4 mmol m^{-2} h^{-1}) relative to the actual NEC of 33.8 mmol m^{-2} h^{-1} (Fig. 2). Equivalently, the percent error in NEC owing to any combination of errors in z and τ can further be generalized by solving the % error NEC equation for those terms:

Table 1 Seawater total alkalinity anomalies (ΔA_{T}; µmol kg^{-1}) expressed across the range of seawater depths (z = 1–11 m) and residence times (τ = 1–11 h) explored in this study. ΔA_{T} represents $A_{\mathrm{Tsw}} - A_{\mathrm{Treef}}$ after the reefCA$_{\mathrm{T}}$S runs for the respective seawater depth and residence times have reached steady state for fixed calcification rates of 100% cover by *Acropora nasuta* (33.8 mmol m^{-2} h^{-1}, bold) and *Porites lobata* (15.7 mmol m^{-2} h^{-1}, italics) occupying a 1 km^{2} planar reef flat. Coral calcification rates are sensu Morgan and Kench (2012)

	Residence time (h)										
	1	2	3	4	5	6	7	8	9	10	11
Depth (m)											
1	**66**	**132**	**198**	**264**	**330**	**396**	**462**	**528**	**594**	**660**	**726**
	31	*62*	*92*	*123*	*154*	*185*	*215*	*246*	*277*	*308*	*338*
2	**33**	**66**	**99**	**132**	**165**	**198**	**231**	**264**	**297**	**330**	**363**
	15	*31*	*46*	*62*	*77*	*92*	*108*	*123*	*138*	*154*	*169*
3	**22**	**44**	**66**	**88**	**110**	**132**	**154**	**176**	**198**	**220**	**242**
	10	*21*	*31*	*41*	*51*	*62*	*72*	*82*	*92*	*103*	*113*
4	**16**	**33**	**49**	**66**	**82**	**99**	**115**	**132**	**148**	**165**	**181**
	8	*15*	*23*	*31*	*38*	*46*	*54*	*62*	*69*	*77*	*85*
5	**13**	**26**	**40**	**53**	**66**	**79**	**92**	**106**	**119**	**132**	**145**
	6	*12*	*18*	*25*	*31*	*37*	*43*	*49*	*55*	*62*	*68*
6	**11**	**22**	**33**	**44**	**55**	**66**	**77**	**88**	**99**	**110**	**121**
	5	*10*	*15*	*21*	*26*	*31*	*36*	*41*	*46*	*51*	*56*
7	**9**	**19**	**28**	**38**	**47**	**57**	**66**	**75**	**85**	**94**	**104**
	4	*9*	*13*	*18*	*22*	*26*	*31*	*35*	*40*	*44*	*48*
8	**8**	**16**	**25**	**33**	**41**	**49**	**58**	**66**	**74**	**82**	**91**
	4	*8*	*12*	*15*	*19*	*23*	*27*	*31*	*35*	*38*	*42*
9	**7**	**15**	**22**	**29**	**37**	**44**	**51**	**59**	**66**	**73**	**81**
	3	*7*	*10*	*14*	*17*	*21*	*24*	*27*	*31*	*34*	*38*
10	**7**	**13**	**20**	**26**	**33**	**40**	**46**	**53**	**59**	**66**	**73**
	3	*6*	*9*	*12*	*15*	*18*	*22*	*25*	*28*	*31*	*34*
11	**6**	**12**	**18**	**24**	**30**	**36**	**42**	**48**	**54**	**60**	**66**
	3	*6*	*8*	*11*	*14*	*17*	*20*	*22*	*25*	*28*	*31*

Table 2 Seawater total alkalinity anomalies (ΔA_T; μmol kg^{-1}) expressed across the range of seawater depths (z = 1–11 m) and longer residence times (τ = 1–144 h). ΔA_T represents $A_{Tsw} - A_{Treef}$ after the reefCA$_T$S runs for the respective seawater depth and residence times have reached steady state for fixed calcification rates of 10% cover by *Acropora nasuta* (33.8 mmol m^{-2} h^{-1}, bold) and 10% cover by *Porites lobata* (15.7 mmol m^{-2} h^{-1}, italics) occupying a 1 km^2 planar reef flat. Coral calcification rates are sensu Morgan and Kench (2012)

	Residence time (h)							
	1	3	6	12	24	48	96	144
Depth (m)								
1	**7**	**20**	**40**	**79**	**158**	**317**	**633**	**950**
	3	*9*	*18*	*37*	*74*	*148*	*295*	*443*
2	**3**	**10**	**20**	**40**	**79**	**158**	**317**	**475**
	2	*5*	*9*	*18*	*37*	*74*	*148*	*221*
3	**2**	**7**	**13**	**26**	**53**	**106**	**211**	**317**
	1	*3*	*6*	*12*	*25*	*49*	*98*	*148*
4	**2**	**5**	**10**	**20**	**40**	**79**	**158**	**238**
	1	*2*	*5*	*9*	*18*	*37*	*74*	*111*
5	**1**	**4**	**8**	**16**	**32**	**63**	**127**	**190**
	1	*2*	*4*	*7*	*15*	*30*	*59*	*89*
6	**1**	**3**	**7**	**13**	**26**	**53**	**106**	**158**
	1	*2*	*3*	*6*	*12*	*25*	*49*	*74*
7	**1**	**3**	**6**	**11**	**23**	**45**	**90**	**136**
	0	*1*	*3*	*5*	*11*	*21*	*42*	*63*
8	**1**	**2**	**5**	**10**	**20**	**40**	**79**	**119**
	0	*1*	*2*	*5*	*9*	*18*	*37*	*55*
9	**1**	**2**	**4**	**9**	**18**	**35**	**70**	**106**
	0	*1*	*2*	*4*	*8*	*16*	*33*	*49*
10	**1**	**2**	**4**	**8**	**16**	**32**	**63**	**95**
	0	*1*	*2*	*4*	*7*	*15*	*30*	*44*
11	**1**	**2**	**4**	**7**	**14**	**29**	**58**	**86**
	0	*1*	*2*	*3*	*7*	*13*	*27*	*40*

$$\%_{\mathrm{err}}\mathrm{NEC} = \left(\frac{\tau z_{\mathrm{err}}}{z \tau_{\mathrm{err}}} - 1\right) \times 100 \qquad (6)$$

where z and τ are the actual seawater depth and residence time and z_{err} and τ_{err} are the erroneously measured seawater depth and residence time.

Scaling of NEC with calcifier cover

Linear models between NEC and percent calcifier cover from previous studies revealed a statistically significant linear correlation for studies conducted in mesocosms and enclosures (NEC ± SE [mmol m^{-2} h^{-1}] = 0.10 ± 0.02 × % calcifier cover + 0.03 ± 1.2; R^2 = 0.68, df = 13, F = 27.7, p = 0.0002; Fig. 3a), but not for field-based studies (R^2 = 0.054, df = 29, F = 1.7, p = 0.21; Fig. 3b). Hypothetical scaling of NEC for 0–100% cover of *A. nasuta* and *P. lobata* for planar reefs (R = 1) revealed that many literature-based NEC studies exceed expected *A. nasuta* calcification rates (Fig. 3b). However, increases in reef-scale structural complexity would increase the expected NEC for a 1 m^2 planar area with the highest structural complexity (R = 4) yielding maximum NEC of 135.0 mmol m^{-2} h^{-1} for 100% *A. nasuta* coral cover and 63.0 mmol m^{-2} h^{-1} for 100% *P. lobata* coral cover (Fig. 4). Structurally complex reefs at the reef scale (R = 3–4) occupied by 100% *P. lobata* yielded greater NEC (47.2 and 63.0 mmol m^{-2} h^{-1}, respectively) than planar reefs (R = 1) occupied by 100% *A. nasuta* (NEC = 33.8 mmol m^{-2} h^{-1}; Fig. 4).

Discussion

Coral reefs are structurally complex environments that complicate accurate calculations of seawater hydrodynamics and thereby challenge precise calculations of NEC (Lowe et al. 2009; Falter et al. 2013; Lowe and Falter 2015). However, reducing NEC uncertainty is critical for monitoring the rates and drivers of reef-scale calcification to understand current and future maintenance of coral reef CaCO$_3$ structures in a changing ocean (Kleypas et al. 2001; Silverman et al. 2009; Albright et al. 2015; Edmunds et al. 2016; Courtney et al. 2018; Cyronak et al. 2018; Perry et al. 2018). Here we have synthesized findings from in situ coral calcification rate data, CaCO$_3$ budget methodologies, and NEC from previous studies with a biogeochemical modeling approach to improve our understanding of ΔA_T, uncertainties in NEC, and the relationship between NEC and calcifier cover. In doing so, the reefCA$_T$S runs provide a range of ΔA_T for the given parameterized *Acropora nasuta* and *Porites lobata* calcification rates under varying seawater depths and residence times (Tables 1, 2). The true uncertainty of characterizing seawater depth, residence time, and calculated NEC remains a significant challenge and warrants additional investigations in the field. Nonetheless, the uncertainty analysis in this study generalizes to any combination of errors in z and τ via Eq. 6 and can therefore be used to calculate % NEC error with respect to z_{err} and τ_{err} for any study.

Assuming that there is an equal probability of either overestimating or underestimating seawater depth and residence time (i.e., normal distribution of errors in z and τ centered around the actual z and τ, respectively), the mean modeled + 65 ± 18% NEC error in these simulations initially suggests studies may therefore be more likely to overestimate NEC owing to the greater uncertainties in NEC associated with underestimating seawater residence time. Furthermore, residence times can vary across a given coral reef system from hours up to days (or longer),

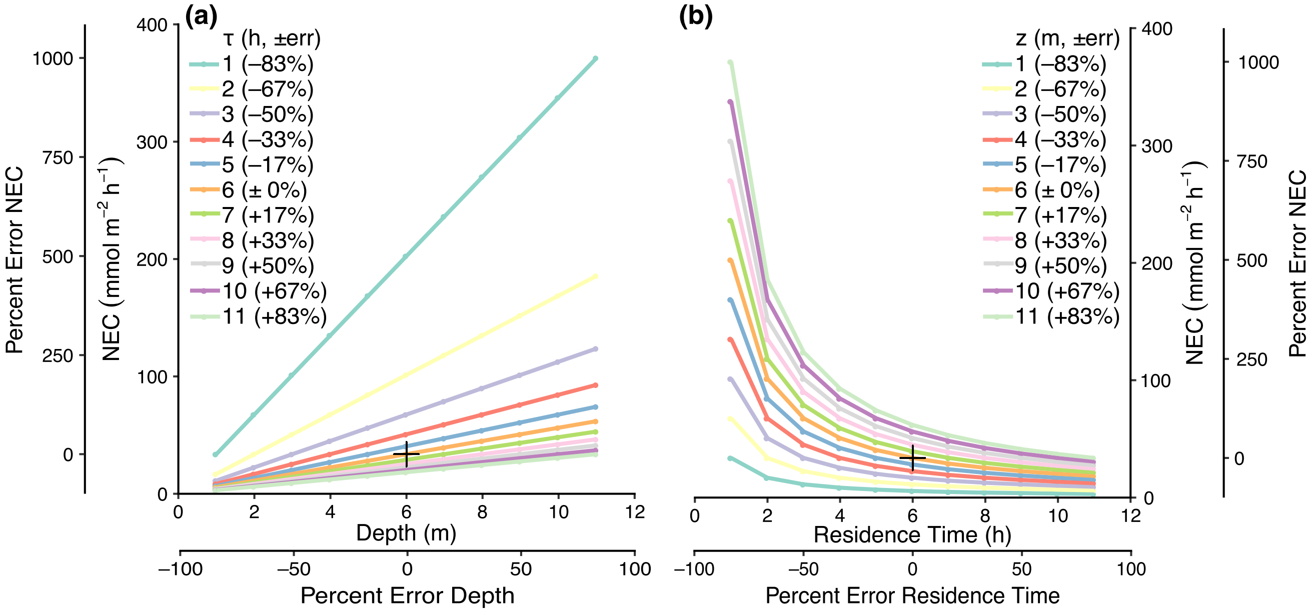

Fig. 2 Net ecosystem calcification (NEC) is erroneously calculated for a range of seawater depths (z = 1–11 m, ± 83% error) and residence times (τ = 1–11 h, ± 83% error) using the reefCA$_T$S generated alkalinity anomaly for calcification by 100% cover *Acropora nasuta* (*z* = 6 m, *τ* = 6 h). Each panel shows the erroneously calculated NEC values relative to the actual NEC rate (+) as a function of (a) depth for each residence time (colored lines) and (b) residence time for each depth (colored lines). Primary x-axes report erroneous (a) depth and (b) residence time, whereas primary y-axes show calculated NEC. Secondary axes report percent errors in depth, residence time, and calculated NEC

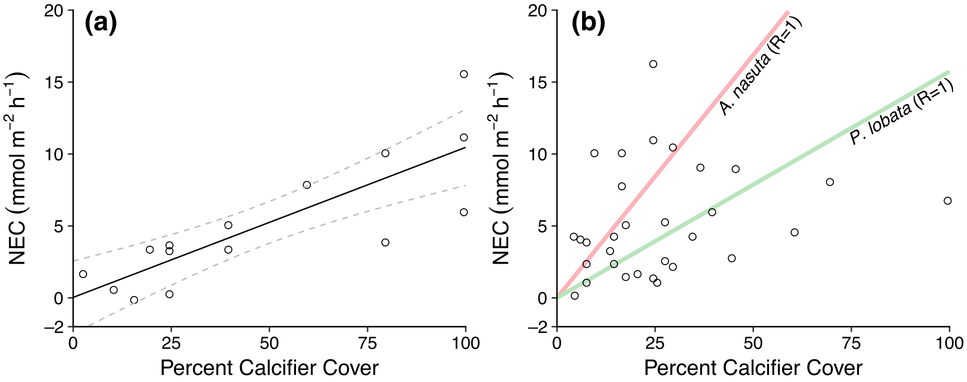

Fig. 3 Literature-derived values of net ecosystem calcification (NEC) as a function of percent calcifier cover (black circles) based on results from (a) mesocosm and enclosure experiments and (b) in situ measurements. (a) Significant positive linear correlation between NEC and percent calcifier cover in mesocosms and enclosures is denoted by the black line (± 95% confidence intervals in gray dashed lines). (b) The expected calcification rates for 0–50% cover of *A. nasuta* (pink line) and 0–100% *P. lobata* (green line) overlying a planar reef (rugosity, R = 1) are plotted relative to in situ NEC rates

suggesting the uncertainty in attributing ΔA_T measurements to residence times for calculation of NEC could be similarly large (Lowe et al. 2009; Venti et al. 2012; Zhang et al. 2012; Falter et al. 2013; Lowe and Falter 2015; Muehllehner et al. 2016). To provide a scalable example for how these potential differences in residence times could impact calculated NEC rates, an erroneous residence time of 6 h that in fact is 6 d results in a 2300% error in NEC (i.e., based on Eq. 6: $\%_{err}$NEC = [144 h/6 h − 1] × 100; Zhang et al. 2012; Courtney et al. 2018). Collectively, these findings suggest that residence time is likely the greatest source of error in NEC calculated from Eq. 1.

The capacity for the large modeled errors in NEC owing to errors in seawater depth and residence time in this study leads us to conclude that even relatively modest uncertainties less than the ± 83% in seawater depth and residence time have the potential to mask any real relationship between NEC and calcifier cover in the field. For example, the large errors in NEC (− 91% to + 1000%; 3.1–371.4 mmol m^{-2} h^{-1}) from the reefCA$_T$S sensitivity

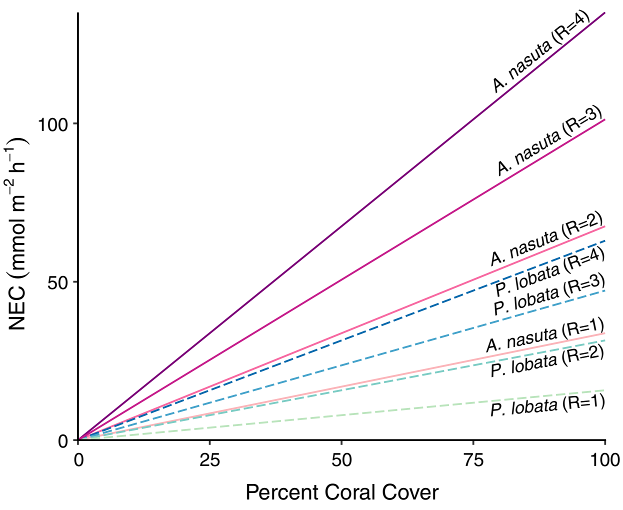

Fig. 4 Net ecosystem calcification (NEC) rates were simulated for 0–100% cover communities of *Acropora nasuta* (solid lines) and *Porites lobata* (dashed lines) corals occupying reefs with a range of structural complexities from planar (rugosity, R = 1) to highly structurally complex (R = 4) utilizing coral calcification rates from Morgan and Kench (2012)

analysis are approximately an order of magnitude greater than the 100% calcifier cover NEC of 10.5 ± 2.6 mmol m^{-2} h^{-1} (mean ± 95% confidence interval) extrapolated from the literature review of mesocosms and enclosures. Interestingly, this 100% calcifier cover NEC from mesocosm and enclosure studies agrees well with 100% coral/algae cover NEC of 10 kg $CaCO_3$ m^{-2} y^{-1} (11.4 mmol m^{-2} h^{-1}) hypothesized by Chave et al. (1972) and observed by Kinsey (1979, 1981), but is less than the maximum daytime NEC (44 mmol m^{-2} h^{-1}) recorded by DeCarlo et al. (2017) in Dongsha Atoll. Further research may therefore be necessary to explore a potential upper bound for coral reef NEC rates.

However, we further found that many in situ NEC studies from the literature exceeded our simulated planar reef 100% *Acropora* rates (Fig. 4) leading us to explore the influence of reef-scale structural complexity as an explanatory variable. For example, the finding that the more slowly calcifying *Porites lobata* occupying structurally complex reefs (R = 3–4) can generate higher NEC than an equivalent cover of *Acropora nasuta* occupying a planar substrate (Fig. 4) suggests that reef-scale structural complexity may be as important as benthic community composition for driving NEC. It is important to note that while reef structural complexity and benthic community composition are often linked, larger-scale reef rugosities are maintained even for degraded reefs (Richardson et al. 2017). This suggests that natural or artificial re-colonization of reef-scale structurally complex reefs by stress-tolerant corals may act to stabilize potentially declining NEC associated with declining coral cover and shifting coral communities (Gardner et al. 2003; Bruno and Selig 2007; Jackson et al. 2014; Perry et al. 2015; Hughes et al. 2018) and projected increases in $CaCO_3$ dissolution (Andersson and Gledhill 2013; Eyre et al. 2018) under global environmental change.

While it is not possible to directly assess the validity of NEC from previous studies with the results presented here, the insights gained in this study provide a framework for improving the validity and comparability of future NEC rates and their uncertainties. First and foremost, the model results of this study highlight the potential for extremely large errors in NEC primarily owing to uncertainties in constraining the seawater depth and residence time associated with the ΔA_T of the hydrochemical footprint. To improve comparability of NEC between sites and studies, we recommend that studies provide a detailed report of all parameters ± uncertainties of the NEC calculation (Eq. 1) and especially ΔA_T to improve our collective understanding of NEC and ΔA_T in coral reefs. Ideally future studies could leverage traditional NEC methods with any combination of established model-based approaches (Falter et al. 2013), dye/chemical tracers of seawater hydrodynamics (Falter et al. 2008; Venti et al. 2012; Muehllehner et al. 2016), eddy covariance/benthic gradient flux measurements (Long et al. 2015; Takeshita et al. 2016), and/or expectations of NEC for a given calcifier cover (Fig. 3a, Fig. 4). To further evaluate the potential correlation between NEC and calcifier cover, we suggest future studies report NEC along with preexisting or contemporaneous measurements of benthic community composition and reef structural complexity.

Monitoring coral reef calcification will prove to be a key aspect for understanding and predicting potential changes in coral reef structures and the ecosystem services they provide (Kleypas et al. 2001; Edmunds et al. 2016; Courtney et al. 2018; Cyronak et al. 2018). NEC calculations are a convenient tool for monitoring real-time coral reef calcification under changing environmental conditions and benthic communities, but here we have shown that a high level of scrutiny should be placed on measuring the seawater depth and residence time of the hydrochemical footprint due to their potentially large contributions to calculated NEC error. While the true uncertainty of NEC represents a difficult and ongoing challenge, incorporating secondary approaches and/or expectations from the simulations presented here can provide greater confidence in our ability to accurately monitor reef-scale calcification and further explore the relationship between NEC and calcifier cover in the field.

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Author contributions TAC and AJA conceived the study. TAC constructed the reefCA$_T$S model simulations and wrote the first draft of the manuscript with input from AJA.

Compliance with ethical standards

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

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