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Travis A. Courtney
University of California - San Diego


Andreas J. Andersson
University of California - San Diego

Nicholas R. Bates
Bermuda Institute of Ocean Sciences - United Kingdom

Andrew R. Collins
Bermuda Institute of Ocean Sciences - United Kingdom

Tyler Cyronak
University of California - San Diego, <tcyronak@nova.edu

See next page for additional authors

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Authors

Samantha J. de Putron

Bermuda Institute of Ocean Sciences - United Kingdom

Bradley D. Eyre

Southern Cross University - Lismore, Australia

Rebecca Garley

Bermuda Institute of Ocean Sciences - United Kingdom

Eric J. Hochberg

Bermuda Institute of Ocean Sciences - United Kingdom

Rodney Johnson

Bermuda Institute of Ocean Sciences - United Kingdom

Sylvia Musielewicz

University of Washington - Seattle; National Oceanic and Atmospheric Administration

Tim J. Noyes

Bermuda Institute of Ocean Sciences - United Kingdom

Christopher L. Sabine

National Oceanic and Atmospheric Administration

Adrienne J. Sutton

University of Washington - Seattle; National Oceanic and Atmospheric Administration

Jessy Tonicin

Universite Pierre-et-Marie-Curie - Paris, France

Aline Tribollet

Universite Pierre-et-Marie-Curie - Paris, France



Comparing Chemistry and Census-Based Estimates of Net Ecosystem Calcification on a Rim Reef in Bermuda

Travis A. Courtney^{1*}, Andreas J. Andersson¹, Nicholas R. Bates², Andrew Collins², Tyler Cyronak¹, Samantha J. de Putron², Bradley D. Eyre³, Rebecca Garley², Eric J. Hochberg², Rodney Johnson², Sylvia Musielewicz^{4,5}, Tim J. Noyes², Christopher L. Sabine⁵, Adrienne J. Sutton^{4,5}, Jessy Toncin⁶ and Aline Tribollet⁶

¹ Geosciences Research Division, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA, USA, ² Bermuda Institute of Ocean Sciences, St. George's, Bermuda, ³ Center for Coastal Biogeochemistry, School of Environment, Science, and Engineering, Southern Cross University, Lismore, NSW, Australia, ⁴ Joint Institute for the Study of the Atmosphere and Ocean, University of Washington, Seattle, WA, USA, ⁵ Pacific Marine Environmental Laboratory, National Oceanic and Atmospheric Administration, Seattle, WA, USA, ⁶ Institut de Recherche pour le Développement, Institut Pierre Simon Laplace - Laboratoire d'Océanographie et du Climat, Université Pierre-et-Marie-Curie, Paris, France

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USA

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*Correspondence:

Travis A. Courtney
traviscourtney@gmail.com

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Coral reef net ecosystem calcification (NEC) has decreased for many Caribbean reefs over recent decades primarily due to changes in benthic community composition. Chemistry-based approaches to calculate NEC utilize the drawdown of seawater total alkalinity (TA) combined with residence time to calculate an instantaneous measurement of NEC. Census-based approaches combine annual growth rates with benthic cover and reef structural complexity to estimate NEC occurring over annual timescales. Here, NEC was calculated for Hog Reef in Bermuda using both chemistry and census-based NEC techniques to compare the mass-balance generated by the two methods and identify the dominant biocalcifiers at Hog Reef. Our findings indicate close agreement between the annual 2011 census-based NEC $2.35 \pm 1.01 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$ and chemistry-based NEC $2.23 \pm 1.02 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$ at Hog Reef. An additional record of Hog Reef TA data calculated from an autonomous CO₂ mooring measuring pCO₂ and modeled pH_{total} every 3-h highlights the dynamic temporal variability in coral reef NEC. This ability for chemistry-based NEC techniques to capture higher frequency variability in coral reef NEC allows the mechanisms driving NEC variability to be explored and tested. Just four coral species, *Diploria labyrinthiformis*, *Pseudodiploria strigosa*, *Millepora alcicornis*, and *Orbicella franksi*, were identified by the census-based NEC as contributing to $94 \pm 19\%$ of the total calcium carbonate production at Hog Reef suggesting these species should be highlighted for conservation to preserve current calcium carbonate production rates at Hog Reef. As coral cover continues to decline globally, the agreement between these NEC estimates suggest that either method, but ideally both methods, may serve as a useful tool for coral reef managers and conservation scientists to monitor the maintenance of coral reef structure and ecosystem services.

Keywords: coral reef, net ecosystem calcification, budget, accretion, dissolution, calcium carbonate, biogeochemistry

INTRODUCTION

Coral reefs provide a great multitude of ecosystem goods and services to humanity including renewable food and material resources, shoreline protection, and nutrient cycling (e.g., Smith, 1978; Salvat, 1992; Spurgeon, 1992; Done et al., 1996; Moberg and Folke, 1999; de Groot et al., 2012). However, tropical reef coral cover is currently declining due to a combination of local and global pressures (i.e., overfishing, sedimentation, disease, warming, and acidification) with ~80% declines in coral cover observed across the Caribbean since the mid-1970s (Gardner et al., 2003). These declines in overall Caribbean coral cover are combined with an overall loss of reef structural complexity (Alvarez-Filip et al., 2009) and coral community shifts toward more slowly calcifying and less-structurally complex opportunistic coral species (Alvarez-Filip et al., 2013). Consequently, losses in coral cover, and changes in coral community composition have resulted in decreased net coral reef calcium carbonate (CaCO_3) production across the Caribbean (Perry et al., 2013, 2015). While hermatypic scleractinian corals are typically the dominant coral reef CaCO_3 producers (Vecsei, 2004), coral reef net ecosystem calcification (NEC) is the sum of gross calcification and gross CaCO_3 dissolution (Chave et al., 1972). Coral reef accretion and maintenance of geomorphic structure therefore depends on NEC as well as the net import, export, and erosion of CaCO_3 material (e.g., Scoffin, 1992; Milliman, 1993; Kleypas et al., 2001; Perry et al., 2008; Montaggioni and Braithwaite, 2009; Tribollet and Golubic, 2011; Perry et al., 2012).

The topic of spatial scale is of particular importance for the study of ecological phenomenon (Levin, 1992 and references therein) including coral reef calcification (e.g., Kinsey, 1985; Andréfouët and Payri, 2000; Vecsei, 2004; Edmunds et al., 2016). Measurements of coral reef calcification range from organismal to ecosystem and global scales (see discussion in Edmunds et al., 2016). By necessity, measuring CaCO_3 production at organism scales (e.g., Bak, 1976; Jokiel et al., 1978) fundamentally utilize different approaches than studies examining entire reef and global scales (e.g., Kinsey, 1979; Milliman, 1993; Kleypas, 1997; Vecsei, 2004). Coral reef CaCO_3 production at sub-reef to reef scales has historically been measured via census or accretion-based CaCO_3 budget approaches (e.g., Chave et al., 1972 and references therein; Stearn et al., 1977; Hubbard et al., 1990; Eakin, 1996; Harney and Fletcher, 2003; Perry et al., 2012, 2013) and chemistry-based alkalinity anomaly approaches (e.g., Broecker and Takahashi, 1966; Smith and Key, 1975; Smith and Kinsey, 1976; Gattuso et al., 1996; and summarized in Atkinson, 2011; Andersson and Gledhill, 2013).

Census-based budgets utilize bottom-up approaches to sum up the calcification by individual CaCO_3 producers whereas chemistry-based budgets provide a top-down integrated measurement of the entire reef NEC. Interestingly, CaCO_3 production on coral reefs in the Atlantic has historically been measured using census and accretion based approaches while chemistry-based approaches have been more widely used in the Pacific Ocean (Kinsey, 1981). Montaggioni and Braithwaite (2009) summarized the literature finding that

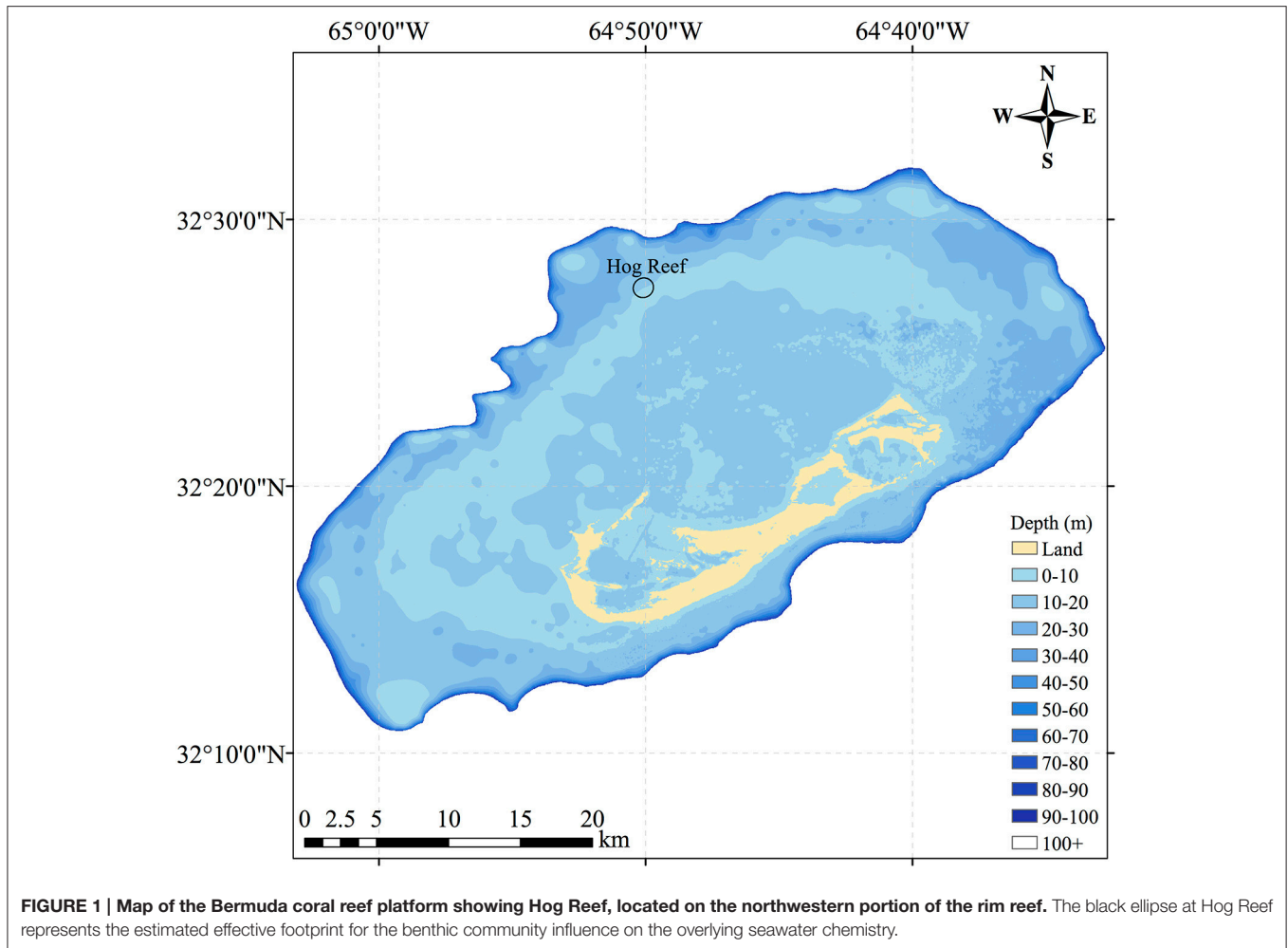
global coral reef calcification estimates range from 1 to 10 kg $\text{CaCO}_3 \bullet \text{m}^2 \bullet \text{y}^{-1}$ using census-based methods and from 0.5 to 10 kg $\text{CaCO}_3 \bullet \text{m}^2 \bullet \text{y}^{-1}$ based on alkalinity anomaly methods thereby concluding that the two methods are generally in close agreement. Measurements of census-based and chemistry-based CaCO_3 production at One Tree Island, Great Barrier Reef were scaled to the entire reef using remote sensing with a remarkably small 0.3% difference between the two methods (Hamylton et al., 2013). Thus, a robust comparison of these two methods at the same reef site allows the bottom-up census-based budget of NEC to be weighed against the top-down chemistry-based NEC, resulting in a more thorough understanding of the mechanisms of CaCO_3 production and maintenance of structure in coral reef environments.

In this study, NEC was calculated using census-based and chemistry-based budgets from September 2010 to September 2012 for Hog Reef ($32^\circ 27' 26.39''\text{N}$, $64^\circ 50' 5.10''\text{W}$), located on the northwestern rim reef of Bermuda between deeper oceanic waters and shallower sandy back-reef environments (Figure 1). The Bermuda platform is a reef system surrounded by deep oceanic waters located in the North Atlantic sub-tropical gyre and at the current latitudinal limit for tropical coral reef ecosystems (Kleypas et al., 1999; Andersson et al., 2014). The history of Bermuda NEC measurements (e.g., Bates, 2002; Bates et al., 2010) and characterization of Bermuda platform seawater residence times (Venti et al., 2012) further make Hog Reef an ideal location to conduct a chemistry-based NEC study. Briefly, calcifying organism growth rates, microborer CaCO_3 dissolution rates, and CaCO_3 sand dissolution rates were multiplied by their respective benthic area to produce a census-based NEC budget with seasonal variability at Hog Reef. NEC was calculated using chemistry-based alkalinity anomaly of reef seawater relative to offshore seawater via water samples taken monthly from Hog Reef. Seasonal and diel NEC variability was estimated by TA calculated from seawater measurements taken every 3 h by an autonomous $p\text{CO}_2$ mooring at Hog Reef. These estimates of coral reef NEC provide valuable insight into the net balance between calcification and CaCO_3 dissolution, thus serving as an important tool for monitoring the maintenance of coral reef structure and ecosystem services as coral reef function and health continue to change globally.

METHODS

Census Based Budget Formation Reef Surveys

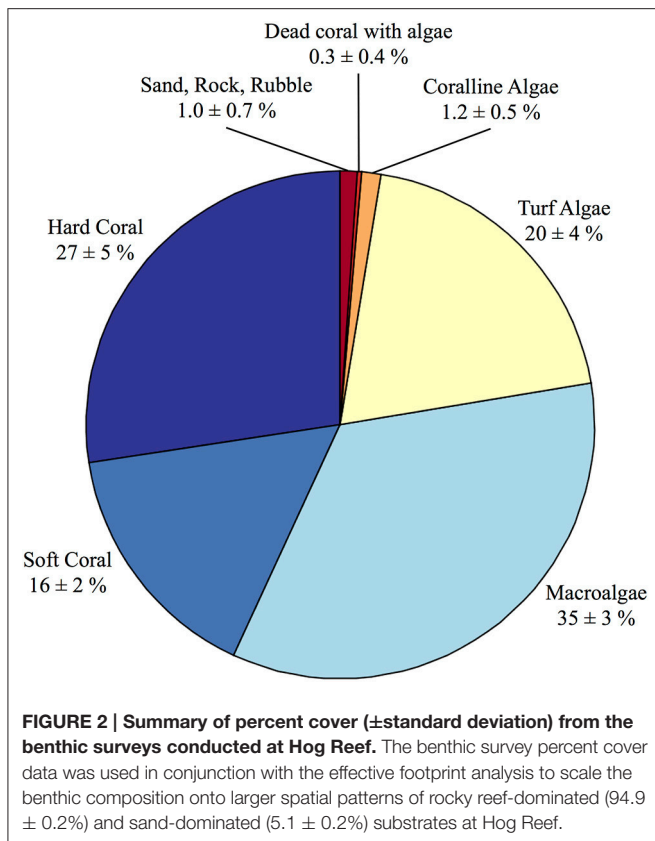
The census-based budgets were modeled after the standardized methods outlined in the *ReefBudget* project (Perry et al., 2012). Video transects were conducted in August 2010 at Hog Reef as part of an ecological monitoring project consisting of five permanent 30-m transects stationed at ca. 8 m depth at the reef site. For each transect, a video camera was pointed perpendicular to the benthos at a constant distance to film a 1-m wide band to the left side of each transect generating 5 • 30 m² transects. Each video transect was analyzed for percent cover by coral species, gorgonian, zoanthid, sponge, sessile invertebrates,



macroalgae, turf algae, calcifying algae, dead coral, unknown organisms, rock, rubble, and sand (Figure 2). Notably, mean percent cover (\pm standard deviation) of hard scleractinian corals at the survey site was $27 \pm 5\%$. Due to the structural complexity of the reef environment, reef rugosity (Spatial Scales I and II in Dahl, 1973) was calculated for each site to determine the total abundance of benthic organisms occupying a given planar area of the reef environment (Dahl, 1973). The Segmented Line and Measure tools in *ImageJ* were used to calculate reef rugosity from the ratio of reef profile distance and horizontal planar distance for each photograph ($n = 12$) resulting in a mean (\pm standard deviation) rugosity of 1.5 ± 0.2 . Hog Reef has a very complex three-dimensional structure consisting of many small caves and overhangs that is not currently measurable using traditional rugosity approaches (e.g., Dahl, 1973) and precludes some aspects of the benthos beneath underlying canopies from being surveyed in the planar video transects (Goatley and Bellwood, 2011). This additional structural complexity therefore underestimates this study's survey of benthic foraminifera, coralline algae, cryptic Porifera sponges, cryptic corals, and additional organisms or uncolonized substrate occurring in these unsampled microenvironments.

***In situ* Calcification Rates**

In situ calcification rates for *Diploria labyrinthiformis* and *Porites astreoides* corals and literature reported annual mean calcification rates aggregated in the ReefBudget data analysis sheets (Perry et al., 2012) for all other corals and calcifying algae were used in the formation of the census-based budget. Colonies of *D. labyrinthiformis* ($n = 17$) and *P. astreoides* ($n = 14$) were collected from Hog Reef and mounted on tiles at Hog Reef from September 2010 to September 2012 to calculate *in situ* calcification rates for the duration of the experiment. During the growth rate study, each coral was weighed every 2–3 months using the buoyant weight method (Jokiel et al., 1978) with a correction term for seawater density at the time of measurement and subtraction of the weight of the tile and Z-SPAR A-788 epoxy used to mount the coral to the tile. Mean initial coral weights (\pm standard deviation) were 358 ± 122 g for *D. labyrinthiformis* and 419 ± 124 g for *P. astreoides*. Mean calcification rates for each growth interval were calculated as the change in weight (mg) per day over each growth interval. Calcification rates were normalized to surface area using the foil method conducted at the end of the growth rate experiment (Marsh, 1970). Mean (\pm standard deviation) individual coral



colony surface areas in the growth rate experiment were $195 \pm 31 \text{ cm}^2$ for *D. labyrinthiformis* and $164 \pm 48 \text{ cm}^2$ for *P. astreoides*.

Seasonal Variability in Calcification

Temporal variability in *D. labyrinthiformis* and *P. astreoides* growth rates was determined by dividing growth rates at each weight interval by the mean growth rates over the approximately 2-year growth rate experiments to yield standardized growth rate values. These standardized growth rates through time were fit with a single-term Fourier model using the Curve Fitting Tool in MATLAB to model the seasonal variability in growth rates (±95% confidence intervals):

$$f(x) = 1.01 \pm 0.05 - (0.37 \pm 0.13)\cos[x(5.79 \pm 0.22)] - (0.29 \pm 0.15)\sin[x(5.79 \pm 0.22)] \quad (1)$$

where x is the date in decimal years centered at the year 2010 and $f(x)$ is the proportional, standardized seasonal variation of the mean annual growth rate. This seasonal variability relationship was used to scale the literature-derived annual mean coral and calcifying algal growth rates from the *ReefBudget* data analysis sheets (Perry et al., 2012) to approximate seasonal variability in the census-based data for comparison to the continuous chemistry-based budgets in this study.

Similarly, the *in situ* measured growth rates for *D. labyrinthiformis* and *P. astreoides* were fit with single-term Fourier models using the Curve Fitting Tool in MATLAB

to construct continuous estimations of calcification rates for the duration of the 2-year experiment. The equation for *D. labyrinthiformis* growth rates (± 95% confidence intervals) is:

$$f(x) = 3.12 \pm 0.17 - (0.86 \pm 0.56)\cos[x(5.83 \pm 0.30)] - (0.97 \pm 0.47)\sin[x(5.83 \pm 0.30)] \quad (2)$$

where x is the date in decimal years centered at the year 2010 and $f(x)$ is the seasonal variation of the *D. labyrinthiformis* annual growth rate ($\text{kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$). The equation for *P. astreoides* growth rates (± 95% confidence intervals) is:

$$f(x) = 2.53 \pm 0.19 - (1.32 \pm 0.39)\cos[x(5.71 \pm 0.30)] - (0.53 \pm 0.70)\sin[x(5.71 \pm 0.30)] \quad (3)$$

where x is the date in decimal years centered at the year 2010 and $f(x)$ is the seasonal variation of the *P. astreoides* annual growth rate ($\text{kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$). The Fourier fitted continuous growth rates for *D. labyrinthiformis* and *P. astreoides* were used to model the seasonal-variability of the census-based budget.

Summation of Net Calcification

Calcification rates of each calcifying species were multiplied by reef rugosity and percent cover of each species from the benthic surveys to determine species-level calcification at Hog Reef. These species-level calcification rates were summed to obtain the net calcification ($\text{kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$) by the benthic community at Hog Reef. Regrettably, calcification by benthic foraminifera, which could represent up to 50% of the sand composition at Hog Reef (unpublished data), was not included in the budget due to the lack of benthic survey data on these species. Despite large abundance in the sand, Bermuda reef benthic foraminifera CaCO_3 production was previously estimated to be $0.080 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$ (Langer et al., 1997), supporting earlier findings that the contributions by benthic foraminifera on coral reef NEC are an order of magnitude smaller than the CaCO_3 produced by non-Acroporid corals (Chave et al., 1972). Calcification by suborder holaxonia sea fans and sea rods ($16 \pm 2\%$ cover ± standard deviation of the benthic survey data; **Figure 2**) were also excluded from this analysis due to the high variability of calcified material within individuals (Esford and Lewis, 1990) and a lack of reliable linear extension rate measurements to pair with the percent cover survey data. Of the other dominant biocalcifying components of coral reef environments listed by Montaggioni and Braithwaite (2009), Mollusca were insufficiently surveyed to reliably estimate Mollusca calcification from the benthic survey data.

Net CaCO_3 Dissolution

Calcium carbonate dissolution at Hog Reef was measured as the sum of CaCO_3 dissolution by sediments, microborers, and sponges. Sediment CaCO_3 dissolution at Hog Reef was directly measured over a full diel cycle in summer 2015 (July) via the alkalinity anomaly measured in three independent benthic chambers following methods outlined in Cyronak et al. (2013b). Net sediment CaCO_3 dissolution (±standard deviation) for the

sand at Hog Reef was $-0.39 \pm 0.11 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{yr}^{-1}$. Given the lack of data for any temporal variability in sediment CaCO_3 dissolution at Hog Reef, this rate was assumed to be constant throughout the year and was multiplied by the percent sediment cover from the survey data at Hog Reef. No sponges were recorded in our transect data thereby precluding net CaCO_3 dissolution by sponges from the calculation of this budget. Mean (\pm standard deviation) microbore CaCO_3 dissolution rates of $-0.21 \pm 0.09 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{yr}^{-1}$ were determined from scanning electron microscopy of subsections from 3 experimental coral blocks cut from a single massive *Porites lobata* skeleton exposed at Hog Reef between September 2011 and September 2012 following methods outlined in Tribollet et al. (2009). These methods for estimating CaCO_3 dissolution differed from the *ReefBudget* calculations in that this study additionally included sediment dissolution, which is typically absent from census-based budgets (Eyre et al., 2014), while mechanical bioerosion by fish and urchins were omitted from this study. This distinction between mechanical and chemical bioerosion was made such that the census budgets would reflect only the chemical balance of calcification and CaCO_3 dissolution to allow for a better comparison between the census-based and chemistry-based budgets outlined in this study.

Effective Reef Footprint and Hydrology

To best compare the census-based and chemistry-based estimates of NEC, an effective reef footprint (i.e., the spatial extent of benthic community influence on water chemistry) was calculated to link the benthos to overlying water column carbonate chemistry. The mean water flow of the tidally driven currents at Hog Reef was integrated over a complete tidal cycle to estimate the spatial area of the benthos that a typical parcel of reefwater travels over a tidal cycle. This calculated area of reef therefore represents the estimated areal footprint over which the NEC carbonate chemistry signal has been integrated in the seawater. The estimated footprint was used with aerial imagery and digital elevation model data to calculate the percent hard reef vs. sandy substrate and an average water depth for calculations of the census based and chemistry based Hog Reef NEC.

A Nortek AS Aquadopp Profiler was mounted at approximately 12 m depth to measure current speeds in 0.5 m depth bins from surface to bottom at a frequency of 1.0 MHz from 18 July 2015 to 26 July 2015. In the absence of continuous current measurements during the ca. 2-year study, this later current profiler deployment was used to record many tidal cycles of the predominately tidally driven flow regime at Hog Reef with the caveat that typical current profiles may vary over longer time scales due to changing wind and storm activity. Calculations using potential changes in flow regime beyond the typically tidal influence have relatively small impacts on measured census-based and chemistry-based NEC due to the correspondingly small changes in percent hard reef substrate and depth of the effective reef footprint. To avoid the tidal influence on the occasional aerial exposure of the uppermost surface current bins, only bins from 0.4 to 10.9 m distance from the profiler were analyzed. Current speeds were converted into u and v components and averaged across depth bins from 0.4 to 10.9 m to yield the average water column

velocity for the duration of the deployment. An hourly low-pass Lanczos filter was used on the top-bottom averaged u and v components to filter out higher frequency turbulence from the current data. A principal components analysis was performed on the filtered top-bottom averaged u and v data following procedures outlined in Glover et al. (2011) to identify the primary (PC1) and orthogonal (PC2) principal components of seawater current. PC1 ($2.89 \text{ cm} \bullet \text{s}^{-1}$ at 335°) therefore represents the mean speed and direction of the dominant current flow and PC2 ($2.75 \text{ cm} \bullet \text{s}^{-1}$ at 245°) represents the mean speed of the flow 90° to PC1. These components of current velocity were scaled by a tidal period of 12.4167 h to yield a typical distance traveled by a parcel of water over a complete tidal cycle. The tidally scaled magnitudes and directions of these principal components (PC1: 1.29 km 335° ; PC2: 1.23 km 245°) were centered at the Hog Reef PMEL MAPCO₂ mooring to estimate an elliptical effective footprint (Figure 1) for the benthic community influence on seawater chemistry.

The coordinates for the effective footprint were imported into ArcMap[®] software and layered onto a Bermuda 1 arc-second sea level digital elevation model (Sutherland et al., 2014) and Bermuda marine aerial imagery (Bermuda Zoological Society, 1997). The ArcMap[®] Zonal Statistics as Table tool was used to calculate the mean (\pm standard deviation) depth from the digital elevation model for the elliptical Hog Reef footprint as $10.3 \pm 3.3 \text{ m}$. The elliptical footprint was used to crop and export the marine aerial imagery from ArcMap[®] software to ImageJ (Schneider et al., 2012) for analysis of percent cover by larger-scale reef and sand patches in the effective footprint. The image contrast was enhanced and converted to 8-bit grayscale before applying a black-and-white threshold with additional manual paintbrush tool interpretation of reef composition from the photograph such that areas of reef became black pixels and areas of sand became white pixels. The histogram of the ellipse was analyzed to determine the percent of black and percent of white pixels resulting in 94.9% hard reef and 5.1% sand composition. Because the reef survey data was collected over the dominantly reef section, the census-based budget data was scaled to represent 94.9% of the budget area and sand CaCO_3 dissolution rates were applied to the remaining 5.1% sand-covered portion of the effective reef footprint. Notably, this scaling of the transect data to the effective reef footprint resulted in a mean (\pm uncertainty) of $26 \pm 5\%$ hard coral cover for Hog Reef.

Chemistry Based Budget Formation Carbonate Chemistry Bottle Samples

Hog Reef seawater bottle samples were analyzed for total alkalinity (TA) to calculate the chemistry based NEC in this study. All water samples were collected approximately monthly using a 5-L Niskin bottle at 0.5–1.0 m depth according to best practices (Dickson et al., 2007). Samples were stored using 200 mL-Kimax glass sample bottles, fixed using 100 μL saturated solution of HgCl_2 , and subsequently analyzed for TA using a VINDTA 3S system and DIC using VINDTA 3C and AIRICA systems (Marianda Inc). The accuracy and precision of TA analyses were verified against certified reference material (CRM) provided by the laboratory of Prof. A. Dickson of Scripps Institution

of Oceanography. Analysis of replicate CRMs yielded a typical accuracy and precision of $\pm 2\text{--}4\ \mu\text{mol}\cdot\text{kg}^{-1}$ for both TA and DIC. Temperature (accuracy $\pm 0.15^\circ\text{C}$) and salinity (accuracy $\pm 1\%$) for all samples were measured using a YSI 556 *Handheld Multiparameter Instrument*. Additional seawater samples were collected for 66% of all bottle samples and analyzed for salinity using an *Autosal Salinometer* (accuracy $< \pm 0.002$). These salinometer salinity values were preferentially used over the YSI salinity measurements in the analysis for this project.

Offshore seawater bottle samples were collected approximately monthly at the Bermuda Atlantic Time-series Study (BATS; $31^\circ 50'\text{N}$, $64^\circ 10'\text{W}$) and analyzed for temperature, salinity, and TA. BATS is located $\sim 80\text{ km}$ southeast of Bermuda and represents typical surface seawater of the Sargasso Sea making BATS carbonate chemistry samples an ideal offshore reference for calculation of NEC in this study (Bates et al., 2001, 2010; Bates, 2002; Yeakel et al., 2015). BATS TA samples were collected in 200 mL-Kimax glass bottles, fixed with HgCl_2 , and sealed until analysis at Bermuda Institute of Ocean Sciences (Bates et al., 2012). TA was analyzed by a VINDTA 2S System (Marianda Inc) with typical replicate accuracy and precision of $< 0.2\%$ determined daily using CRMs. TA for the Hog Reef and BATS bottle samples were normalized to the mean salinity of $36.59\text{ g}\cdot\text{kg}^{-1}$ measured at Hog Reef. Because the BATS bottle samples were not collected at the same time as the Hog Reef samples, the BATS bottle samples were linearly interpolated to match the monthly Hog Reef seawater sampling dates for analysis of NEC in this study.

Hog Reef MAPCO₂ Mooring Carbonate Chemistry

Hog Reef seawater $p\text{CO}_2$ and modeled pH_{total} were used to calculate TA every 3 h to estimate variability in Hog Reef NEC at higher frequencies than the ca. monthly Hog Reef seawater bottle samples. Seawater $p\text{CO}_2$, atmospheric pressure, temperature, and salinity were measured every 3 h by the NOAA PMEL MAPCO₂ mooring stationed at Hog Reef ($32^\circ 27' 26.39''\text{N}$, $64^\circ 50' 5.10''\text{W}$). The MAPCO₂ mooring utilizes a Battelle Memorial Institute CO₂ system to measure CO₂ mole fraction and a Sea-Bird 16plus v2 plus to measure seawater temperature and salinity (Sutton et al., 2014). The Sea-Bird sensors failed after a few months during both deployments of the MAPCO₂ mooring in this study due to extensive biofouling. Mooring salinity records were thus completed using linearly interpolated salinity data from the monthly Hog Reef seawater samples. Daily averaged temperature from four HOBO loggers (mean standard deviation $\pm 0.11^\circ\text{C}$ between loggers) deployed at Hog Reef recording temperature every 8-min were used for the duration of this study. An average of the daily temperature values for the day before and the day after a brief, 4-day interval lacking temperature record in mid-July were used to fill that same 4-day interval to maintain a continuous temperature record during the study.

Hog Reef seawater TA and DIC bottle samples were used to calculate seawater pH_{total} and $p\text{CO}_2$ for each bottle sample. The high correlation between bottle sample pH_{total} and $p\text{CO}_2$ was used to predict seawater pH_{total} from MAPCO₂ mooring $p\text{CO}_2$. The combination of 3-h temporally resolved MAPCO₂ mooring $p\text{CO}_2$ and pH_{total} allowed Hog Reef TA to be calculated every 3 h

at Hog Reef. Hog Reef seawater TA and DIC bottle samples were used to calculate seawater carbonate chemistry using CO2SYS for MATLAB (van Heuven et al., 2011) using temperature and salinity measured at the time of sampling, the pH_{total} , K_1 and K_2 dissociation constants by Mehrbach et al. (1973) refit by Dickson and Millero (1987), $K_{\text{HSO}_4^-}$ by Dickson (1990), and total boron by Uppström (1974). Calculated pH_{total} was highly linearly correlated ($R^2 = 0.998$; $p < 0.0001$) with $\log(p\text{CO}_2)$ resulting in the following equation (\pm standard error):

$$\text{pH}_{\text{total}} = (-0.393 \pm 0.003) \times \log[p\text{CO}_2 (\mu\text{atm})] + (10.40 \pm 0.02) \quad (4)$$

The highly linear correlation between $\log(p\text{CO}_2)$ and pH_{total} over the range of values in this study allowed us to use the above equation to model pH_{total} as a function of the Hog Reef mooring $p\text{CO}_2$ data to create a 3-h temporal resolution pH_{total} record. The Hog Reef mooring $p\text{CO}_2$ and modeled pH_{total} data were used to calculate TA with CO2SYS for MATLAB (van Heuven et al., 2011) using the HOBO temperature and interpolated seawater bottle salinity data, and the same set of constants previously described. TA from this output was normalized to the mean salinity of 36.59 measured at Hog Reef to compare with the BATS bottle samples normalized to that same salinity. The BATS bottle samples (collected approximately monthly) were linearly interpolated to match the modeled TA data (calculated every 3-h) for analysis of higher frequency measurements of NEC in this study. We recognize using this modeled TA dataset yields some additional uncertainty relative to direct TA measurements; however, the higher frequency variability captured by this method provides valuable insight on the range of Hog Reef NEC over shorter timescales than would otherwise be possible from traditional bottle samples.

Seawater density for the MAPCO₂ mooring and bottle sample data were calculated using the TEOS-10 Gibbs Seawater (GSW) oceanographic toolbox (McDougall and Barker, 2011). For the bottle samples, seawater density was calculated using salinity of the bottles, temperature at the time of bottle sampling, and atmospheric pressure at the time of sampling (from the Bermuda Weather Service (2016) and MAPCO₂ mooring). For the MAPCO₂ mooring, seawater density was calculated from the MAPCO₂ and interpolated seawater bottle salinity data, HOBO logger temperature data, and MAPCO₂ pressure sensor data.

Net Ecosystem Calcification

NEC represents the effects of gross calcification and gross CaCO_3 dissolution integrated over a water column of given density (ρ), depth (z), and residence time (τ) as per the following equation (Smith and Key, 1975; Langdon et al., 2010):

$$\text{NEC} = \frac{\rho z (\text{TA}_{\text{offshore}} - \text{TA}_{\text{reef}})}{2\tau} \quad (5)$$

NEC was calculated for the discrete TA bottle samples and the MAPCO₂ mooring TA data relative to interpolated BATS offshore TA data, bottle and MAPCO₂ mooring seawater density data, depth of the effective footprint from ArcGIS, and a

mean residence time (\pm standard deviation) of 2.5 ± 0.4 days calculated at the nearby North Rock rim reef site using a multi-tracer approach (Venti et al., 2012). Trapezoidal numerical integration was used to calculate annual NEC for the bottle samples. Regrettably, a full annual cycle was not measured by the MAPCO₂ data (0.91 years) for the duration of this study (September 2010–September 2012). Trapezoidal numerical integration was thus applied to the mooring NEC data, bottle sample NEC data, and census-based NEC data over the longest MAPCO₂ mooring data record (0.91 year time period from February 2011 to January 2012) to allow for a direct comparison of the methods without temporal bias. The census-based NEC, seawater bottle chemistry-based NEC, and mooring chemistry-based NEC are hereafter referred to as the census NEC, bottle NEC, and mooring NEC throughout the remainder of this manuscript.

Propagation of Uncertainty

Uncertainty for the census, bottle, and mooring NEC budgets was estimated using standard procedures for propagation of uncertainties summarized by Ku (1966). Standard deviations for all measured and calculated data were used to propagate uncertainties with a few exceptions. Uncertainties in species-level growth rates from the literature were not included in this analysis. Uncertainty of measured TA ($\pm 4 \mu\text{mol}\cdot\text{kg}^{-1}$) was obtained from replicate measures of CRMs. An uncertainty of $\pm 21 \mu\text{mol}\cdot\text{kg}^{-1}$ was used for the uncertainty in MAPCO₂ mooring pH-*p*CO₂ predicted TA values. The mean difference between measured bottle TA and corresponding MAPCO₂ mooring pH-*p*CO₂ predicted TA at the time of water bottle sampling was $20.5 \mu\text{mol}\cdot\text{kg}^{-1}$, which is also consistent with an uncertainty of $\pm 21 \mu\text{mol}\cdot\text{kg}^{-1}$ estimated by Millero (2007) using ship-based *p*CO₂ and pH measurements. Subjective uncertainty for the Hog Reef footprint percent composition of reef and sand was estimated to be $\pm 2\%$ based on repeated *ImageJ* analysis of Hog Reef benthic composition.

RESULTS

Census Based Budget Formation

The mean census NEC (\pm uncertainty) for the entire length of the approximately 2-year *in situ* calcification study was $2.21 \pm 1.01 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Table 1; Figure 3). Calcification (\pm uncertainty) accounted for $2.53 \pm 0.99 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ and CaCO₃ dissolution (\pm uncertainty) was $-0.32 \pm 0.13 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Tables 1, 2; Figure 4). The percentage (\pm uncertainty) of total calcification for *D. labyrinthiformis* ($15 \pm 3\%$), *Pseudodiploria strigosa* ($29 \pm 10\%$), *Millepora alcicornis* ($26 \pm 12\%$), and *Orbicella franksi* ($24 \pm 9\%$) show they are the dominant CaCO₃ producers ($94 \pm 19\%$ for all four species) at Hog Reef (Table 1; Figure 4). Although measured rates of sand CaCO₃ dissolution were higher than microborer CaCO₃ dissolution rates per unit area, the smaller total area of sands resulted in areal CaCO₃ dissolution (\pm uncertainty) being dominated by microborers ($93 \pm 57\%$) with sand CaCO₃ dissolution ($7 \pm 4\%$) making up the remainder (Table 2; Figure 4). Integrated census NEC (\pm uncertainty) for 2011 was $2.35 \pm 1.01 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ and from 2011.2 to 2012.1 was $2.28 \pm 1.01 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Table 3).

Chemistry Based Budget Formation

The mean bottle NEC (\pm uncertainty) for the entire length of the approximately 2-year *in situ* calcification study was $2.85 \pm 1.02 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Table 3). The integrated bottle NEC for 2011 was $2.23 \pm 1.02 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ and from 2011.2 to 2012.1 was $2.46 \pm 1.02 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Table 3). Similarly, the mean mooring NEC (\pm uncertainty) was $3.73 \pm 1.34 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Table 3). There was insufficient data to calculate mooring NEC for 2011 using the MAPCO₂ data with the interval 2011.2–2012.1 representing the longest continuous record for the mooring NEC data. The integrated mooring NEC estimate for this interval was $4.09 \pm 1.34 \text{ kg CaCO}_3\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Table 3).

TABLE 1 | Summary table of calcification at Hog Reef.

Calcifying organism	Mean survey %-cover	Mean reef %-cover	ReefBudget calcification rates (kg CaCO ₃ ·m ⁻² ·y ⁻¹)	Mean study interval rates (kg CaCO ₃ ·m ⁻² ·y ⁻¹)	Mean reef calcification (kg CaCO ₃ ·m ⁻² ·y ⁻¹)	% of Total Hog Reef calcification
<i>Diploria labyrinthiformis</i>	9 ± 2	9 ± 1	4.64	3.00	0.38 ± 0.08	15 ± 3
<i>Pseudodiploria strigosa</i>	10 ± 3	9 ± 3	5.34	5.13	0.7 ± 0.2	30 ± 10
<i>Favia fragum</i>	0.04 ± 0.09	0.04 ± 0.09	9.76	9.38	0.01 ± 0.01	0.2 ± 0.5
<i>Madracis decactis</i>	0.04 ± 0.09	0.04 ± 0.09	33.46	32.16	0.02 ± 0.04	0.7 ± 1.6
<i>Millepora alcicornis</i>	1.8 ± 0.8	1.6 ± 0.7	28.10	27.01	0.7 ± 0.3	30 ± 10
<i>Montastraea cavemosa</i>	0.6 ± 0.6	0.6 ± 0.5	9.07	8.72	0.08 ± 0.07	3 ± 3
<i>Orbicella franksi</i>	5 ± 2	5 ± 2	9.06	8.71	0.6 ± 0.2	24 ± 9
<i>Porites astreoides</i>	1.1 ± 0.3	1.0 ± 0.3	6.32	2.36	0.04 ± 0.01	1.4 ± 0.5
Coralline algae	1.2 ± 0.5	1.2 ± 0.5	0.18	0.17	0.003 ± 0.001	0.12 ± 0.05

Percent cover (\pm standard deviation) from the benthic surveys and estimated reef footprint are reported alongside literature calcification rates aggregated by ReefBudget and the mean calcification rate over the entire study period after taking into account seasonal variability in calcification rates and using *in situ* calcification rate data for *D. labyrinthiformis* and *P. astreoides*. Mean calcification rates and percent of total calcification (\pm uncertainties) are reported for each species.

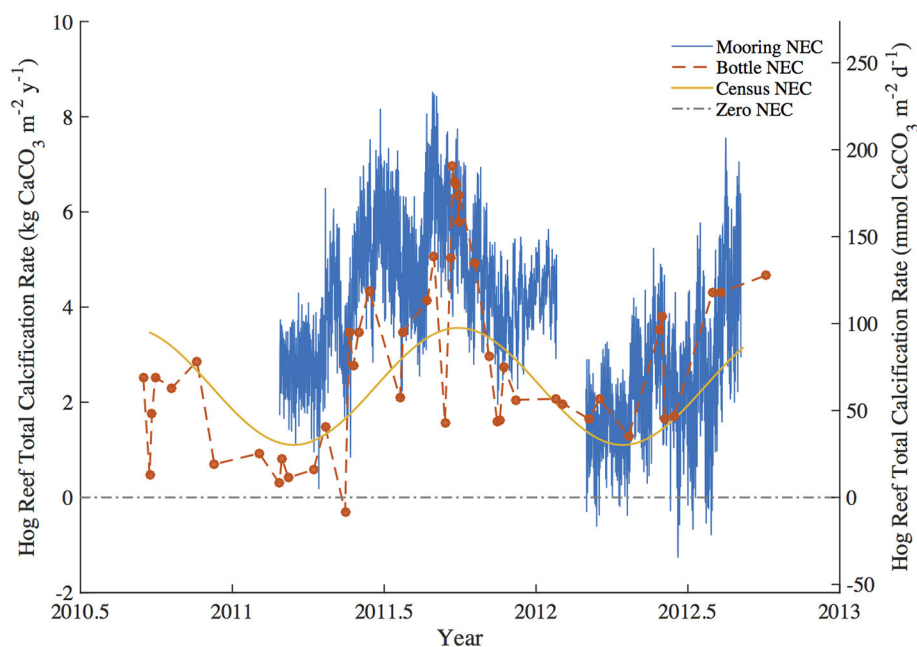


FIGURE 3 | Summary figure of Hog Reef Net Ecosystem Calcification (NEC) using the mooring NEC, bottle NEC, and census NEC approaches for the study period. The dashed zero-NEC line indicates the tipping point between net calcification (above the line) and net CaCO_3 dissolution (below the line).

TABLE 2 | Summary table of CaCO_3 dissolution at Hog Reef.

CaCO_3 dissolution type	Mean survey %-cover	Mean reef %-cover	Mean CaCO_3 dissolution rate ($\text{kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$)	Mean reef CaCO_3 dissolution ($\text{kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$)	% of Total Hog Reef CaCO_3 dissolution
Microborer	99.3 ± 0.4	95 ± 2	-0.21 ± 0.09	-0.3 ± 0.1	90 ± 60
Sand	0.7 ± 0.4	5 ± 2	-0.39 ± 0.11	-0.02 ± 0.01	7 ± 4

Percent cover from the benthic surveys (\pm standard deviation) and calculated from the estimated reef footprint (\pm uncertainty) are reported for substrate available to dissolution by microboring communities (dominated by pioneer chlorophytes such as *Phaeophila* sp. and *Ostreobium* sp.) and sand CaCO_3 dissolution. CaCO_3 dissolution rates (\pm standard deviation), mean CaCO_3 dissolution (\pm uncertainty), and percentage of total CaCO_3 dissolution (\pm uncertainty) are expressed for microborer and sand dissolution at Hog Reef.

DISCUSSION

Annual NEC for 2011 calculated by the census NEC ($2.35 \pm 1.01 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) and by the bottle NEC ($2.23 \pm 1.02 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) are in close agreement. Chemistry-based NEC estimates measure NEC via the TA anomaly technique thereby recording the integrated signal of calcification and CaCO_3 dissolution occurring within the reef ecosystem. These findings that the census-based budget are in close agreement with the bottle chemistry NEC suggest that the summation of the components of coral reef calcification and CaCO_3 dissolution are representative of the total balance between calcification and CaCO_3 dissolution occurring at Hog Reef.

Annual NEC calculated for 2011 for Hog Reef using census ($2.35 \pm 1.01 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) and bottle-based ($2.23 \pm 1.02 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) methods in addition to other census-based NEC studies from the Caribbean (Stearn et al., 1977; Mallela and Perry, 2007; Perry et al., 2013) generally fall within the $20\text{--}250 \text{ mmol CaCO}_3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ($0.73\text{--}9.13 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) range of average global coral reef flat NEC

(Atkinson, 2011; **Figure 5**). The relationship between percent hard coral cover and reef NEC in this study is in general agreement with trends observed in other census-based studies of Caribbean reefs (Stearn et al., 1977; Mallela and Perry, 2007; Perry et al., 2013; **Figure 5**). Notably, the annual Hog Reef census NEC and bottle NEC are in close agreement with the census NEC calculated for a Bonaire reef ($2.31 \pm 1.05 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$) with analogous hard coral cover (Hog Reef: $26 \pm 5\%$; Bonaire reef: $25.0 \pm 4.5\%$) and depth (Hog Reef: $10.3 \pm 3.3 \text{ m}$; Bonaire Reef: 10 m ; Perry et al., 2013; **Figure 5**). Collectively, these findings support earlier claims by Montaggioni and Braithwaite (2009) and measurements by Hamylton et al. (2013) that net coral reef calcification estimates using chemistry and census-based approaches are generally in close agreement.

To test for any temporal bias in the NEC rates calculated from daytime bottle sampling of NEC, the autonomous MAPCO₂ mooring recorded seawater $p\text{CO}_2$ every 3-h allowing for a higher temporal resolution of NEC to be measured. The mooring NEC values reveal the seasonal cycles and diel variability in NEC with generally higher NEC values of $4.10 \pm 1.34 \text{ kg CaCO}_3 \cdot \text{m}^{-2} \cdot \text{y}^{-1}$

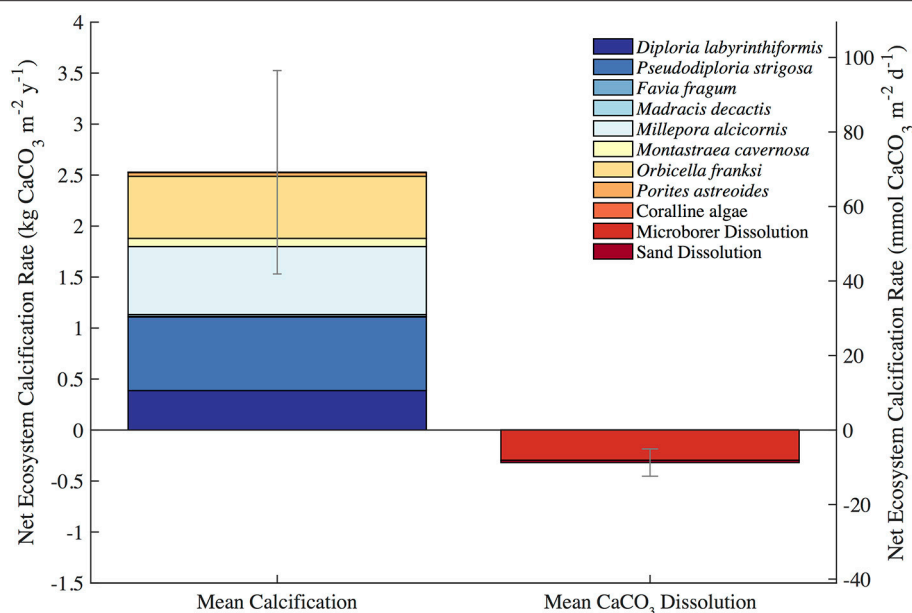


FIGURE 4 | Census-based summary of mean calcification and mean CaCO_3 dissolution. *D. labyrinthiformis*, *P. strigosa*, *M. alcicornis*, and *O. franksi* are the dominant biocalcifiers and microborer activity dominates CaCO_3 dissolution at Hog Reef.

TABLE 3 | NEC summary table for each method.

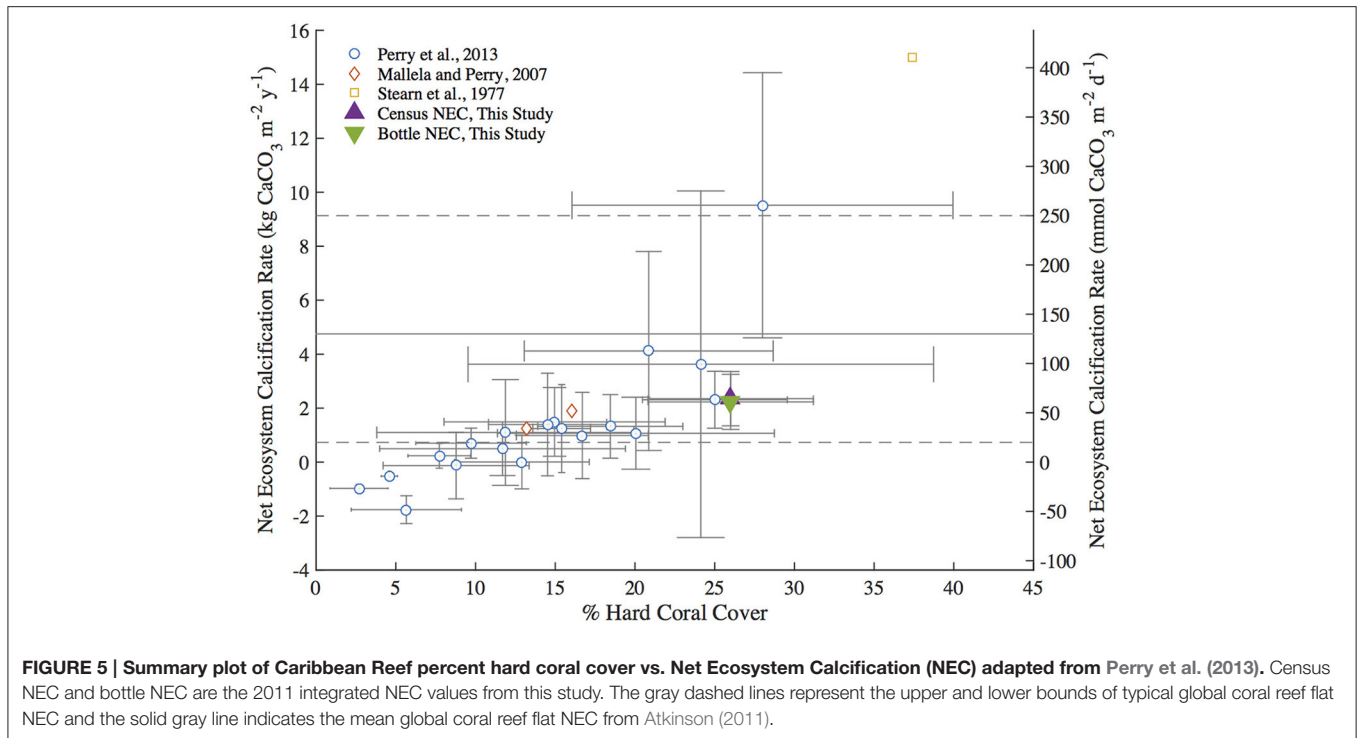
Method	Mean NEC (kg $\text{CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$)	NEC 2011 (kg $\text{CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$)	NEC 2011.2-2012.1 (kg $\text{CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$)
Census NEC	2.21 ± 1.01	2.35 ± 1.01	2.28 ± 1.01
Bottle NEC	2.85 ± 1.02	2.23 ± 1.02	2.46 ± 1.02
Mooring NEC	3.73 ± 1.34	Insufficient data	4.10 ± 1.34

NEC (\pm uncertainty) is calculated as the mean NEC over the entire study period, integrated annual NEC for 2011, and integrated annual NEC for the first mooring deployment.

compared to $2.35 \pm 1.01 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$ and $2.46 \pm 1.02 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$ for the census NEC and bottle NEC respectively during the same initial mooring deployment from 2011.2 to 2012.1 (Table 3; Figures 3, 6). These mooring NEC values may be higher due to additional uncertainty generated by modeling TA from MAPCO₂ mooring pH-pCO₂ and/or could relate to higher frequency variability in reef processes. The absolute mooring NEC values should therefore be treated with some caution, but the range nonetheless highlights the dynamic variability of Hog Reef NEC. Interestingly, agreement between the census and chemistry-based NEC methods varies over the 2-year period further highlighting the dynamic variability of coral reef environments (Figure 3). This may be in part due to unmeasured temporal variability in the rates of dissolution by microborers and sediments, species-level differences in seasonal calcification responses, higher frequency variability in calcification rates than the 2-month intervals measured by the *in situ* growth rate experiments, and or changes in seawater residence time resulting from changes in wind and currents. Mean annual CaCO_3 dissolution by microborers was used for the census NEC; however, recent work has shown that CaCO_3

dissolution of new substrates by microborers varies nonlinearly due to succession of microboring communities over time and a combination of biotic and abiotic factors (Vogel et al., 2000; Carreiro-Silva et al., 2005; Aline, 2008; Tribollet et al., 2009; Grange et al., 2015). Similarly, sediment CaCO_3 dissolution rates were measured once in the summer and thus do not account for any potential temporal variability in CaCO_3 dissolution rates. Further research should be conducted to quantify shorter temporal scale variability in growth rates of biocalcifiers, CaCO_3 dissolution rates, and changes in coral reef seawater residence time to better understand these changes and the factors driving variable NEC (Venti et al., 2012; Teneva et al., 2013).

The census NEC in this study was limited by the high structural complexity (i.e., caves and overhangs) of Hog Reef, lack of calcification by suborder holaxonia and phyla Mollusca, and potential differences in biocalcification rates in Bermuda relative to literature reported rates for the tropical Caribbean. The limitations imposed by “canopy effects” present in the planar video surveys of structurally complex Hog Reef (Goatley and Bellwood, 2011) lead to underestimates of calcification by benthic foraminifera, bryozoans, corals, and coralline algae as well as underestimates of CaCO_3 dissolution by cryptic bioeroders (Hutchings, 1986), uncolonized substrate, and sediments occurring in unsampled caves. A prior estimate of Bermuda coral reef benthic foraminifera CaCO_3 production ($0.080 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$; Langer et al., 1997) is significantly less than the census NEC ($2.35 \pm 1.01 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$) suggesting the absence of benthic foraminifera has a small influence on the Hog Reef NEC estimate. Additionally, the lack of published calcification rates for suborder holaxonia sea fans and sea rods and absence of phyla Mollusca and



Echinodermata in the benthic survey data further underestimate total calcification occurring at Hog Reef. Because Bermuda is located at the edge of the latitudinal limit for coral reefs, it remains unclear how the cooler waters may systematically reduce calcification rates of all biocalcifiers in Bermuda relative to literature reported rates for more tropical Caribbean reefs. Annual *in situ* calcification rates for 2011 in this study for *D. labyrinthiformis* ($3.02 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$) and *P. astreoides* ($2.70 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$) were 35 and 57% lower respectively than calcification rates aggregated by ReefBudget for Caribbean corals at 10 m-depth (Perry et al., 2012). Similarly reduced growth rates in Bermuda relative to elsewhere in the Caribbean were observed for *P. strigosa*, *D. labyrinthiformis*, *P. astreoides*, and *Scolymia cubensis* (Tomascik and Logan, 1990; Logan and Tomascik, 1991; Logan et al., 1994). These findings that calcification rates are potentially lower in Bermuda suggest that the Caribbean ReefBudget calcification rates (Perry et al., 2012) used for many of the calcifying species in this study overestimate Hog Reef NEC. While this study was unable to quantify the contributions by each of these components, the close agreement between the census NEC and the bottle NEC suggest the net effect of these uncertainties on NEC may cancel out or are small relative to the other components of the census-based budget.

The bottle and mooring NEC in this study were limited by the ability to measure residence time, reef depth, and TA of reef seawater relative to source seawater. Estimations of NEC via the alkalinity anomaly method are particularly sensitive to changes in residence time and flow rates of the seawater overlying the reef community (Venti et al., 2012; Zhang et al., 2012; Falter et al., 2013; Teneva et al., 2013). Controlled volume experiments and

numerical models further elucidate the necessity in measuring the height of the resulting mixed water column when calculating NEC (Zhang et al., 2012; Falter et al., 2013; Teneva et al., 2013). Prior work on residence times for nearby North Channel by Venti et al. (2012) and Bermuda platform bathymetry data from Sutherland et al. (2014) constrained these uncertainties in residence time and depth such that bottle and mooring NEC could be estimated for Hog Reef. To test for the contributions of uncertainty in residence time and seawater depth in this study, a sensitivity analysis was performed on the bottle NEC to test for a range of variability introduced within one standard deviation of mean residence times and depth of the effective reef footprint of Hog Reef (Figure 7). The source seawater TA for Bermuda rim reefs is well characterized by BATS making Hog Reef an ideal location to estimate chemistry-based NEC. Reef seawater TA for the bottle NEC estimates was directly measured ($\pm 4 \mu\text{mol} \bullet \text{kg}^{-1}$) while mooring NEC in this study requires reef seawater TA to be calculated from measured $p\text{CO}_2$ and modeled pH_{total} (estimated $\pm 21 \mu\text{mol} \bullet \text{kg}^{-1}$ from Millero, 2007). The resulting error between bottle NEC ($\pm 1.02 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$) and mooring NEC ($\pm 1.34 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$) reveals that the uncertainty introduced from predicting mooring TA is less than the combined uncertainties in seawater residence time and depth. This collectively shows that uncertainty in bottle and mooring NEC estimates are only as good as the ability to quantify the residence time and volume of the seawater overlying the benthic community.

The balance between coral reef calcification and CaCO_3 dissolution is of particular concern to the persistence of coral reef structure and other ecosystem services (Eyre et al., 2014). Coral community shifts and declining coral cover have already

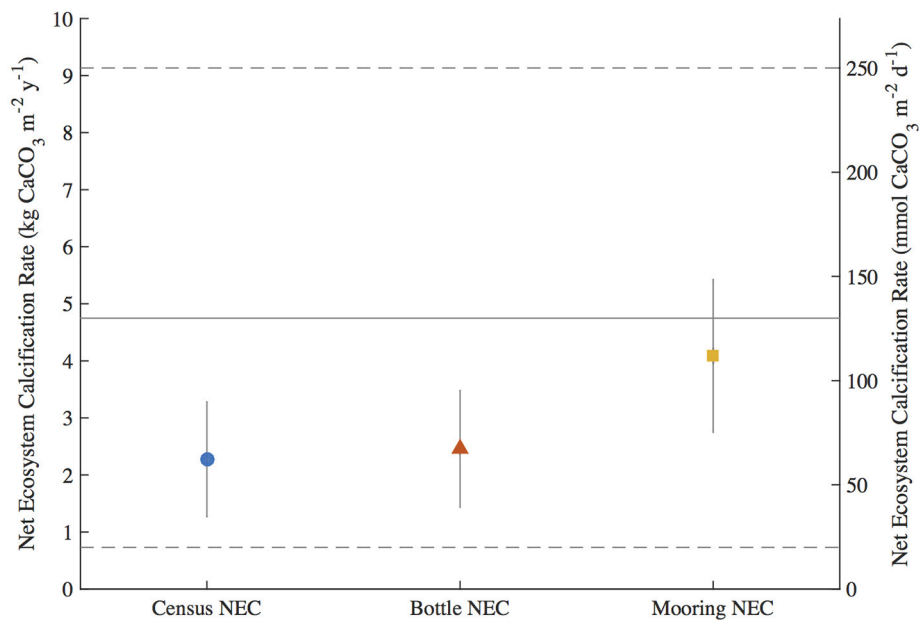


FIGURE 6 | Integrated Net Ecosystem Calcification (NEC) (\pm uncertainty) during the first mooring deployment from 2011.2 to 2012.1 for the census NEC, bottle NEC, and mooring NEC. The solid gray line and dashed gray lines represent the mean and range of NEC, respectively, for reef flats globally from Atkinson (2011).

decreased Caribbean reef NEC with a tipping point from positive to negative net CaCO₃ production occurring when hard coral cover falls below ca. 10% (Perry et al., 2013, 2015). In this study, census-based estimates of calcification greatly exceeded CaCO₃ dissolution at Hog Reef (**Figure 4**); however, chemistry based estimates reveal occasional measurements of net CaCO₃ dissolution occurring in spring and mid-summer (**Figure 3**). Despite larger-scale patterns of coral cover decline in the Caribbean over the most recent decades (Gardner et al., 2003), mean Bermuda rim reef hard coral cover has remained approximately constant over that time period (Dodge et al., 1982; CARICOMP, 2000; Linton and Fisher, 2004; MEP, 2007; Smith et al., 2013; Jackson et al., 2014). Because coral cover has remained approximately constant, any decadal-scale changes in calcification and CaCO₃ dissolution are therefore more likely to have changed due to changing rates and not changing benthic community composition. Notably, recent studies have shown that coral reef CaCO₃ dissolution is stimulated by changing climate and ocean chemistry (Andersson et al., 2009; Tribollet et al., 2009; Cyronak et al., 2013a; Reyes-Nivia et al., 2013) suggesting that even at constant coral cover, increased CaCO₃ dissolution could drive declines in net CaCO₃ production at Hog Reef. Further research should be conducted to see how these rates have changed in response to changing climate and ocean chemistry to better understand potential calcification-CaCO₃ dissolution tipping points for the rim reefs of Bermuda.

Continued global declines in coral cover and changing coral community composition highlight the importance for NEC measurements to be included in coral reef monitoring projects to assess the ability of a given coral reef to maintain positive

CaCO₃ production and therefore reef structure and function. Because NEC measures the capacity for *in situ* coral reef CaCO₃ production (Perry et al., 2012, 2013), it must be considered within the context of additional import, export, and erosion of CaCO₃ material if the monitoring goal is to directly measure net coral reef accretion (e.g., Scoffin, 1992; Milliman, 1993; Kleypas et al., 2001; Perry et al., 2008, 2012; Montaggioni and Braithwaite, 2009; Tribollet and Golubic, 2011). To date, much attention has been given to reef accretion processes highlighting the importance of additionally studying the dynamics of erosive processes, especially dissolution of CaCO₃ in sediment and by microborers, sponges, and other bioeroders. Although sediment dissolution was only a small component of the total dissolution in this study due to the small percentage surface area of sands, other reefs have a much larger percentage surface area of sands making sediment CaCO₃ dissolution a more important component of the CaCO₃ budget at those reefs (Cyronak et al., 2013a; Cyronak and Eyre, 2016). Nonetheless, census and chemistry-based NEC estimates represent relatively non-invasive means of measuring coral reef CaCO₃ production capacity. Census-based NEC and the relative CaCO₃ production contributions by the dominant biocalcifying species for Caribbean coral reefs can be estimated from benthic survey data using standardized methods and literature reported rates from the *ReefBudget* project (Perry et al., 2012). Notably, *D. labyrinthiformis*, *P. strigosa*, *M. alcornis*, and *O. franksi* contribute $94 \pm 19\%$ of the total calcification at Hog Reef (**Table 1**, **Figure 4**) suggesting conservation measures should focus on those four species to preserve positive CaCO₃ production at Hog Reef. Chemistry-based NEC estimates require well-constrained estimates of

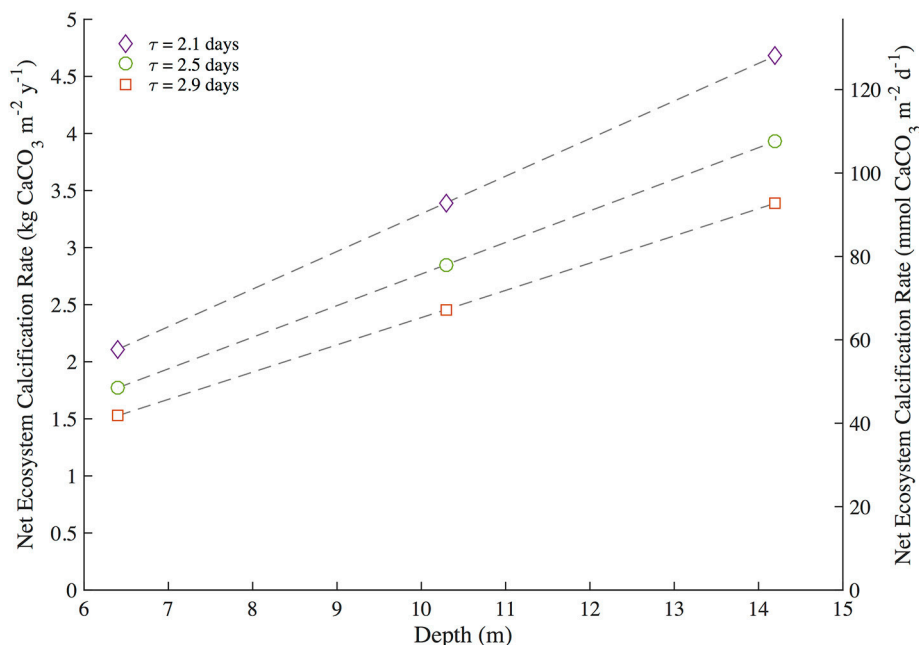


FIGURE 7 | Sensitivity analysis for bottle NEC at Hog Reef during the 2-year study period. Bottle Net Ecosystem Calcification (NEC) was calculated iteratively using mean depth \pm one standard deviation (10.3 ± 3.3 m) and mean residence time \pm one standard deviation (2.5 ± 0.4 days) to determine the sensitivity of NEC to the interacting uncertainty and variability of these measurements.

seawater residence time, bathymetry, source seawater TA, and reef seawater TA to capture the entire sum of calcification and CaCO_3 dissolution over shorter time scales (e.g., Langdon et al., 2010 and references therein). These shorter time scale NEC measurements allow the mechanisms (i.e., Smith and Buddemeier, 1992: temperature, light, carbonate chemistry, hydrodynamics, nutrients, salinity, and sea level) driving NEC to be further explored (Silverman et al., 2007; Shaw et al., 2012, 2015; Albright et al., 2015), thus providing a greater understanding of coral reef NEC and how coral reef CaCO_3 production may be affected by global change. The results of this study conducted at Hog Reef suggest that either method may be used with remarkable agreement over annual time scales (Hog Reef, 2011 census NEC $2.35 \pm 1.01 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$ vs. bottle NEC $2.23 \pm 1.02 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$) depending on the available resources and goals of the reef-monitoring agency. When used in conjunction, the census and chemistry-based NEC approaches corroborate estimates of NEC to provide species-level estimates of CaCO_3 production (census NEC; Table 1, Figure 4) while highlighting temporal variability (chemistry NEC; Figure 3) in coral reef CaCO_3 production.

CONCLUSIONS

The present study reveals that 2011 annual census NEC ($2.35 \pm 1.01 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$) and bottle NEC ($2.23 \pm 1.02 \text{ kg CaCO}_3 \bullet \text{m}^{-2} \bullet \text{y}^{-1}$) at Hog Reef are in close agreement. Census-based budgets allow for NEC to be subdivided into the

individual contributions by species or substrate on calcification and CaCO_3 dissolution over annual time scales and revealed that the vast majority of CaCO_3 production at Hog Reef ($94 \pm 19\%$) was by *D. labyrinthiformis*, *P. strigosa*, *M. alcornis*, and *O. franksi*. Alternatively, chemistry-based estimates capture the NEC of the entire reef at shorter temporal timescales allowing the high temporal variability of coral reef NEC to be analyzed relative to the potential drivers causing NEC to vary. Varying agreement between census-based and chemistry-based NEC was found during the ca. 2-year study interval further highlighting the dynamic nature of NEC and calling for further investigation of the mechanisms driving variability in biocalcification, dissolution, and seawater residence times at Hog Reef. These findings collectively suggest that either method, but ideally both methods, may be used to estimate coral reef NEC depending on the goals or available resources of the coral reef-monitoring project and that high temporal variability in coral reef environments must always be considered when studying biogeochemical processes such as calcification and CaCO_3 dissolution.

AUTHOR CONTRIBUTIONS

TAC and AJA designed the NEC study, analyzed the results, and wrote the manuscript. AJA, AC, TC, SdP, BE, RG, EH, RJ, SM, TN, CS, AJS, JT, and AT collected and provided data for various components of the NEC study. All authors commented on and approved the final draft of this manuscript.

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