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Net Community Metabolism and Seawater Carbonate Chemistry Scale Non-intuitively with Coral Cover

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Coral cover and reef health have been declining globally as reefs face local and global stressors including higher temperature and ocean acidification (OA). Ocean warming and acidification will alter rates of benthic reef metabolism (i.e., primary production, respiration, calcification, and $CaCO_3$ dissolution), but our understanding of community and ecosystem level responses is limited in terms of functional, spatial, and temporal scales. Furthermore, dramatic changes in coral cover and benthic metabolism could alter seawater carbonate chemistry on coral reefs, locally alleviating or exacerbating OA. This study examines how benthic metabolic rates scale with changing coral cover (0–100%), and the subsequent influence of these coral communities on seawater carbonate chemistry based on mesocosm experiments in Bermuda and Hawaii. In Bermuda, no significant differences in benthic metabolism or seawater carbonate chemistry were observed for low (40%) and high (80%) coral cover due to large variability within treatments. In contrast, significant differences were detected between treatments in Hawaii with benthic metabolic rates increasing with increasing coral cover. Observed increases in daily net community calcification and nighttime net respiration scaled proportionally with coral cover. This was not true for daytime net community organic carbon production rates, which increased the most between 0 and 20% coral cover and then less so between 20 and 100%. Consequently, diel variability in seawater carbonate chemistry increased with increasing coral cover, but absolute values of pH, Ω_a, and pCO_2 were not significantly different during daytime. To place the results of the mesocosm experiments into a broader context, *in situ* seawater carbon dioxide (CO_2) at three reef sites in Bermuda and Hawaii were also evaluated; reefs with higher coral cover experienced a greater range of diel CO_2 levels, complementing the mesocosm results. The results from this study highlight the need to consider the natural complexity of reefs and additional biological and physical factors that influence seawater carbonate chemistry on larger spatial and longer temporal scales. Coordinated efforts combining various research approaches (e.g., experiments, field studies, and models) will be required to better understand how benthic metabolism integrates across functional, spatial, and temporal scales, and for making predictions on how coral reefs will respond to climate change.

Keywords: coral reef, metabolism, carbon chemistry, ocean acidification, coral cover

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INTRODUCTION

Coral reefs are one of the most diverse ecosystems in the world and provide numerous ecosystem goods and services including habitat provision, shoreline protection, nutrition, medicinal compounds, and monetary revenue from fisheries and tourism (Moberg and Folke, 1999; Costanza et al., 2014). The total economic valuation of the services provided by coral reefs has been estimated at several billions of U.S. dollars per year (de Groot et al., 2012; Costanza et al., 2014). In recent decades, the function of worldwide coral reefs has changed drastically owing to shifts in community structure with declines in coral cover and increases in turf and fleshy macroalgae (Wilkinson, 2008; Costanza et al., 2014; Chen et al., 2015; Bruno and Valdivia, 2016). In the Indo-Pacific region during 1980-1983, the majority of surveyed coral reefs had 20–50% coral cover with some reefs having up to 100% coral cover. In contrast, in 2003, the highest coral cover reported for this region was 70% with most reefs having less than 30% coral cover (Bruno and Selig, 2007). Similarly, reefs in the Caribbean have experienced massive declines in coral cover from an average of 50% in the mid-1970s to 10% now (Gardner et al., 2003).

The global trend of decreasing coral cover has been attributed to both local and global factors including disease outbreaks (Harvell et al., 1999), overfishing (Hughes et al., 2007), nutrient and sediment pollution (Koop et al., 2001; Szmant, 2002), storm damage, and climate change (Hoegh-Guldberg et al., 2007; Buddemeier et al., 2008; De'ath et al., 2012; Bruno and Valdivia, 2016). The major climate change concerns are prolonged periods of elevated seawater temperature, which can lead to mass coral bleaching events (Glynn, 1993; Brown, 1997; Hoegh-Guldberg, 1999; Baker et al., 2008; Rodgers et al., 2015), and ocean acidification (OA), i.e., a reduction in seawater pH and saturation state with respect to the calcium carbonate mineral aragonite (Ω_a) resulting from oceanic uptake of anthropogenic CO_2. It has been hypothesized that OA could cause reefs to shift from states of net accretion to states of net calcium carbonate ($CaCO_3$) dissolution and erosion (Kleypas and Yates, 2009; Silverman et al., 2009; Eyre et al., 2014; Enochs et al., 2016).

The potential response of corals and coral reef community metabolism (i.e., primary production, respiration, calcification, and $CaCO_3$ dissolution) to ocean warming and acidification has been studied extensively in laboratory and mesocosm experiments. Coral calcification rates are typically reduced when exposed to low seawater pH and Ω_a (Marubini et al., 2003; Ohde and Hossain, 2004; Anthony et al., 2008; Holcomb et al., 2010; Comeau et al., 2013; Horvath et al., 2016), which also has been observed for coral communities and rates of net community calcification (NCC = gross calcification – gross $CaCO_3$ dissolution) (e.g., Langdon et al., 2000; Leclerq et al., 2000; Andersson et al., 2009; Anthony et al., 2013). Similarly, relatively modest warming above summer maximum temperatures has been shown to affect coral skeletal growth and calcification negatively, although small increases in seawater temperature have been observed to increase coral calcification rates (Jokiel and Coles, 1990; Marshall and Clode, 2004; Bahr et al., 2016). In general, coral primary production and net community organic carbon production (NCP = primary production – autotrophic and heterotrophic respiration) decrease under elevated seawater temperatures (Coles and Jokiel, 1977; Brown, 1997) due to increasing rates of respiration, but the response of these processes to OA is less clear (Andersson et al., 2011). Langdon and Atkinson (2005) observed increased NCP for coral communities exposed to high pCO_2 and low pH seawater in flume experiments, but other experiments have reported a decrease or no effect on NCP under similar conditions (e.g., Anthony et al., 2013; Page et al., 2016). However, temperature and/or OA induced coral bleaching generally results in a reduction in NCP owing to decreased photosynthesis and increased respiration (Anthony et al., 2008; Crawley et al., 2010). Concurrent with the effects of warming and OA on coral reef metabolic processes, decreasing coral cover will also affect these processes. To date, this has received relatively little attention. As a result of decreasing coral cover, metabolic rates could change in non-intuitive ways because of changing resource availability, flow regime, boundary layer thickness, and intra- and inter specific competition (Lesser et al., 1994; Tanner, 1995; Ferrier-Pagès et al., 2003; Evensen and Edmunds, 2016).

Understanding how coral reef metabolism will change in response to decreasing coral cover and ocean warming and acidification is critical because it relates to a reef's ability to accrete $CaCO_3$ and its ability to locally alleviate or exacerbate OA (Anthony et al., 2011; Kleypas et al., 2011; Jury et al., 2013; Andersson et al., 2014; Page et al., 2016). Coral reef metabolism can have a significant influence on the local seawater carbonate chemistry (Bates, 2002; Bates et al., 2010; Hofmann et al., 2011; Andersson and Mackenzie, 2012; Shaw et al., 2012; Drupp et al., 2013), and diel and seasonal variations in coral reef CO_2 parameters (e.g., pCO_2, pH, and Ω_a) are much greater than in the open ocean. Many reefs may periodically already experience seawater pCO_2, pH, and Ω_a levels predicted to occur in the open ocean by the end of the century (Andersson and Mackenzie, 2012; Shaw et al., 2012; Drupp et al., 2013; Manzello et al., 2014; Albright et al., 2015) owing to strongly positive NCC, close to balanced trophic status, and negative NCP occurring at night. Positive NCC decreases dissolved inorganic carbon (DIC) and total alkalinity (TA) in a ratio of 1:2 resulting in a reduction of pH and Ω_a while negative NCP decrease pH and Ω_a owing to increased DIC. Furthermore, variations in metabolic rates and ratios of NCC to NCP between benthic functional groups (e.g., coral, turf and fleshy algae, coralline algae, sand, etc.) lead to different influences on seawater carbonate chemistry depending on community composition and structure (Anthony et al., 2013; Jokiel et al., 2014; Page et al., 2016), and these effects could either alleviate or enhance local seawater acidification or alkalinization. Based on mainly mesocosm and modeling experiments, changing community composition in favor of increasing coral cover has resulted in higher rates of NCC relative to NCP, causing a decrease in average seawater pH and Ω_a, while the opposite has been true for a decrease in coral cover in favor of macroalgae (Kleypas et al., 2011; Page et al., 2016).

The current understanding of the potential impacts of environmental perturbations to coral community metabolism and the effect of changing community structure on seawater

carbonate chemistry is limited with respect to the functional, spatial, and temporal scales of these impacts. To date, researchers have been constrained to extrapolating short term individual or community level responses observed in aquaria or mesocosm experiments to larger functional (e.g., ecosystems), spatial (e.g., regions or world), and/or temporal (e.g., years) scales. This approach often assumes that the whole response of coral reefs is equal to the sum of their individual components and frequently lacks consideration for the natural complexity of coral reefs, where organisms do not exist in isolation, but rather interact with other organisms and their physical environment (Mumby and van Woesik, 2014; Andersson et al., 2015; Edmunds et al., 2016). Being able to integrate effects of environmental perturbations on metabolic rates across functional scales, from organisms to reefs, however, is critical to better understand the fate of coral reefs in a future warmer and less alkaline ocean. Edmunds et al. (2016) proposed that existing ecological theories, namely metabolic theory of ecology (MTE; Brown et al., 2004), could provide the framework for this integration of metabolic rates. MTE states that allometric scaling between body size and metabolic rates governs ecological principles at higher functional scales (Brown et al., 2004). For example, net coral community calcification can be estimated as long as one knows (1) the functional relationship between coral colony size and calcification rate and (2) the abundance of different colony sizes within a reef (Edmunds et al., 2016). One of the first steps to develop a MTE for coral reefs is to better understand how colony sizes and coral densities relate to physiological rates in controlled, experimental settings, and then gradually evaluate these relationships for increasingly complex natural settings.

In this study, the main objectives were to examine the influence of different coral densities on rates of NCC and NCP (here referred to as "benthic metabolism") as well as their influence on the overlying seawater carbonate chemistry in two different locations, Bermuda and Hawaii. Through two sets of mesocosm experiments, we tested two hypotheses: (1) High coral cover has higher NCC and NCP rates compared to low coral cover, and rates scale proportionally to the percent coral cover, and (2) As a consequence of higher NCC and NCP rates, high coral cover results in greater diel variability of seawater pH, pCO_2, and Ω_a compared to low coral cover. As a complement to the mesocosm experiments, we also evaluated *in situ* seawater CO_2 measurements from three contrasting reef locations with different coral cover in Bermuda and Hawaii. It is not our intention to quantitatively link and connect the mesocosm results with these field observations, as this would require a range of additional data, but simply to provide a broader context in which to place the results of the mesocosm experiments. We also hope that these data will stimulate additional research aimed at quantitatively connecting experimental and field results which, combined, will strengthen our understanding of the links between coral communities, benthic metabolism, and seawater carbonate chemistry.

MATERIALS AND METHODS

Two mesocosm experiments were conducted to examine the relationships between coral cover, benthic metabolism, and diel seawater carbonate chemistry. An initial experiment was conducted at the Bermuda Institute of Ocean Sciences (BIOS) in 2012 to examine the effects of two treatments (40 and 80% coral cover) on daytime (06:00–00:00) seawater carbonate chemistry. This initial study was followed up by an experiment at the Hawaii Institute of Marine Biology (HIMB) in 2016 to include more coral cover treatments (20–100% coral cover) as well as a complete diel cycle (**Table 1**). These two sites (BIOS and HIMB) were primarily chosen because they contain outdoor, flow-through mesocosm facilities that experience natural fluctuations in environmental conditions representative of conditions experienced on a coral reef and allow control of flow rates. They also represent contrasting coral reef characteristics (e.g., different latitudes, high terrestrial vs. low terrestrial material inputs, and Atlantic vs. Pacific Oceans) and different dominant coral species.

Experiment 1: Bermuda 2012

Experimental Design

The experimental system at BIOS pumped filtered seawater from Ferry Reach, Bermuda into carboys which had gravity-fed flow into nine flow-through mesocosms with the dimensions 53 × 39 × 30.5 cm and flow rates (±1 std) averaging 1.67 ± 0.12 L min^{-1} (residence time, $\tau = 0.64 \pm 0.28$ h). Additionally, two fountain pumps circulated water within each mesocosm, ensuring that the seawater was well-mixed and corals were provided with extensive water flow. To prevent extreme temperature and light stress to the corals, shades were kept over the mesocosms throughout the experiment.

The coral communities in the mesocosms were made up of the scleractinian corals *Diploria labyrinthiformis*, *Porites astreoides*, and *Madracis aurentenra,* which are common to reefs in Bermuda (Bates et al., 2010; Courtney et al., 2016). Most of the corals had been previously collected from the Bermuda reef platform and acclimated to mesocosm conditions for over a year. However, to obtain higher coral cover in the mesocosms, additional *M. aurentenra* corals were collected from a shallow patch reef and acclimated for 1 week. Two coral cover treatments (40 and 80%) and controls (0% coral cover) were replicated in three mesocosms each ($n = 3$ per treatment). The 40% coral cover treatment contained five medium-sized colonies (<25 cm diameter) of *D. labyrinthiformis* and *P. astreoides* whereas 10 colonies total (five of each species) were used in the 80% coral cover treatment; *M. aurentenra* were filled in around these colonies to obtain the desired coral cover percentages.

Sampling Protocol

Seawater chemistry was monitored every 1–3 h from 06:00 to 00:00 (18 h total) on 29 August 2012 in order to encompass the full daylight period. Relative light intensity was measured using HOBO Pendant® temperature/light data loggers (Onset Computer Corporation) set to record light every 10 min. Seawater temperature (±0.15°C) and salinity (±1.0% of reading) were measured hourly using a YSI 556 multiprobe sensor, which was calibrated immediately prior to the experiment. Every 3 h, seawater samples were collected in 200 mL glass Kimax bottles for dissolved inorganic carbon (DIC) and total alkalinity (TA) analyses. These samples were immediately poisoned with a

TABLE 1 | Experimental design for mesocosm experiments in Bermuda and Hawaii.

Experiment	Day(s)	Hours sampled	Treatments (% Coral Cover)	Replication unit
Bermuda 2012	August 29	6:00–0:00	0, 40, 80	Mesocosm ($n = 3$)
Hawaii 2016	June 13–14, June 15–16	18:00–18:00	0, 20, 40, 60, 80, 100	Days ($n = 2$)

saturated solution of mercuric chloride to halt any biological activity in the samples.

Sample Analyses

Seawater samples were shipped to Scripps Institution of Oceanography (SIO) where they were analyzed for DIC and TA. DIC was measured using an Automated Infra-Red Inorganic Carbon Analyzer (AIRICA, Marianda Inc.) equipped with an infrared LI-COR 7000 CO_2/H_2O differential, non-dispersive infrared (NDIR) gas analyzer while TA was measured using an open-cell potentiometric acid-titration procedure outlined in Best Practices for Seawater CO_2 Measurements (Dickson et al., 2007). Precision for both instruments was typically within ± 3 μmol kg^{-1} while the accuracies, calculated as the average (± 1 std) offset from certified reference material (CRM) values, were 1.45 ± 2.62 ($n = 45$) and -0.85 ± 1.51 ($n = 24$) μmol kg^{-1} for DIC and TA, respectively.

Experiment 2: Hawaii 2016

Experimental Design

The mesocosm facility at HIMB (Smith et al., 1977; Andersson et al., 2009; Page et al., 2016) pumps water from Kaneohe Bay into a main header tank. This header tank flows into smaller header tanks that feed flow-through mesocosms with the dimensions $117 \times 117 \times 50$ cm. Water flows up into the mesocosm from the center of the bottom, causing seawater to be well-mixed and providing plenty of flow for corals. Flow rates for the mesocosms averaged 10.81 ± 0.14 L min^{-1} ($\tau = 0.74 \pm 0.01$ h) while water depth was $\sim$0.35 m. Mesocosms were kept exposed to full sunlight since the reef from which corals were collected was approximately the same depth as the mesocosms.

Two of the dominant coral species, *Montipora capitata* and *Porites compressa*, were collected from the patch reef along the north side of Coconut Island. These are among the five dominant coral species in the state of Hawaii (Rodgers et al., 2015). Five coral cover treatments in addition to a control (0% coral cover) were set up in the mesocosms: 20, 40, 60, 80, and 100%. These percentages were composed of approximately half *M. capitata* and half *P. compressa* (Supplementary Figure 1). These coral communities were acclimated to mesocosm conditions for 36 h before beginning sampling on the first day.

Sampling Protocol

Seawater chemistry was sampled every 1–3 h for two diel (24 h) cycles (18:00–18:00) during June of 2016, following a similar protocol described for Experiment 1. HOBO loggers recorded relative light levels every 5 min. Seawater temperature (± 0.2°C) and salinity ($\pm$ 1.0% of reading) were measured hourly using a handheld YSI Professional Plus multi-probe sensor which was calibrated to the certified salinity value (psu) for a CRM (Dickson Laboratory, SIO) immediately prior to each diel cycle. Every 3 h, seawater samples were collected in 250 mL glass Pyrex borosilicate bottles for DIC and TA analyses; these samples were immediately poisoned with a saturated solution of mercuric chloride.

Sample Analyses

Seawater samples were shipped to SIO where they were analyzed for DIC and TA using the same protocol as Experiment 1. Once again, the precision of the instruments was ± 3 μmol kg^{-1}. The instrument accuracies were -1.31 ± 2.98 ($n = 62$) and 0.33 ± 2.21 ($n = 23$) μmol kg^{-1} for DIC and TA, respectively.

Data Analysis and Calculations of Mesocosm Experiments

The HOBO loggers recorded relative light levels as lux. However, photosynthesis only utilizes specific wavelengths of light, and thus, photosynthetically available radiation (PAR) provides more insight into the light levels that can drive autotrophic carbon fixation. We converted lux to PAR by using the following equation: PAR (μmol photons m^{-2} s^{-1}) = LUX $\div$ 51.2 (Valiela, 1984; Smith et al., 2013).

Because the source water at each location passes through several ecosystems that modify carbon chemistry over diel cycles (Andersson and Mackenzie, 2012), variability in seawater carbonate chemistry of treatment mesocosms was due to changes both in the source water and modifications by the coral communities in the mesocosms. Additionally, plankton in the seawater may have modified seawater DIC and TA. To eliminate the influences of source water variability and plankton on seawater DIC and TA, and simply evaluate the influence of the benthic community in each mesocosm, the average control values were subtracted from treatment values. Thus, the resulting residual of DIC and TA of the treatment tanks represent modifications owing solely to the specific benthic community within each tank. Values of DIC and TA can be used to calculate NCC and NCP rates by modifying standard equations (Langdon et al., 2010) to:

$$\mathrm{NCC} = -\left[\frac{\mathrm{TA_{Treatment}} - \mathrm{TA_{Average\ Control}}}{\tau_{\mathrm{Treatment}}} \times \rho \times \mathrm{H} \times 0.5\right] \mathrm{mmol\ m^{-2}\ h^{-1}}$$

$$\mathrm{NCP} = -\left[\frac{\mathrm{DIC_{Treatment}} - \mathrm{DIC_{Average\ Control}}}{\tau_{\mathrm{Treatment}}} \times \rho \times \mathrm{H}\right] - \mathrm{NCC\ mmol\ m^{-2}\ h^{-1}}$$

where control values are averages for a specific sampling time, τ is the average residence time of seawater in the mesocosm (h), ρ is the seawater density (kg m^{-3}), and H is the height of the water column (m). The effect of gas exchange on the DIC in the treatment tanks is partly taken into account by subtracting the DIC from the control tanks, but fails to account for additional CO_2 flux as a result of biological modification of the seawater pCO_2. However, calculations of this flux (<0.2 mmol m^{-2} h^{-1}) show that it is small relative to the observed changes and residence time of the water.

Statistical analysis was performed using R v3.3.1 software (R Development Core Team, 2008) to test for differences in NCC and NCP rates between coral cover treatments. For Experiment 1, only rates occurring during daylight hours were used for this analysis; NCC and NCP rates were split into day and night for Experiment 2 since full diel cycles were measured. Data were first visually compared for no differences between replication units (mesocosm for Experiment 1 and day for Experiment 2). Since there were no differences between the replication units for either experiment, they were then combined for a one-way ANCOVA to determine statistically significant differences between coral cover treatments on NCC and NCP rates, controlling for time. When significance for treatment was detected, a *post-hoc* Tukey's HSD Test with a confidence level of 0.95 was used to examine which treatments were statistically different from one another.

In order to determine how NCC and NCP rates scaled to coral cover (Hypothesis 1), rates measured in Experiment 2 were scaled relative to the observed NCC and NCP rates for the 100% coral cover treatment on each day for each time point. For NCC, the following equation was used:

$$\text{Scaled NCC} = \frac{\text{NCC}_{\text{Treatment}}}{\text{NCC}_{\text{100\% Coral Cover}}} \times 100\%$$

Since NCP rates are in general positive during the day (primary production > respiration) and negative at night (respiration > primary production), day and night rates were evaluated separately. NCP rates measured at 18:00 were not used for this analysis since the rates at this time transitioned between net primary production and net respiration, and thus, caused misrepresentative scaling values. Therefore, daytime rates were scaled from 0 to 100% and nighttime rates from 0 to – 100%:

$$\text{Scaled NCP}_{\text{Day}} = \frac{\text{NCP}_{\text{Treatment}}}{\text{NCP}_{\text{100\% Coral Cover}}} \times 100\%$$

$$\text{Scaled NCP}_{\text{Night}} = \frac{\text{NCP}_{\text{Treatment}}}{\text{NCP}_{\text{100\% Coral Cover}}} \times -100\%$$

Using R v3.3.1 software (R Development Core Team, 2008), linear regression models (lm) were used to describe the relationships between coral cover and scaled rates.

Seawater pH, pCO_2, and Ω_a were calculated from measured temperature, salinity, DIC and TA using CO2SYS (Lewis and Wallace, 1998). K1 and K2 constants from Mehrbach et al. (1973), refitted by Dickson and Millero (1987) were selected for calculations on the total pH scale.

To further examine the relationships between coral cover, benthic metabolism, and seawater carbonate chemistry, a graphical analysis of TA and DIC vectors was performed (Deffeyes, 1965). Type II Linear Regressions were fit to TA and DIC data for each treatment from Experiment 2 using the lmodel2 package within R v3.3.1 software (R Development Core Team, 2008). The slopes provided by the major axis method, which assumes error in both the x and y axes, are reported and subsequently compared using an ANOVA after ensuring data meet assumptions for this statistical test. This analysis was not completed for Experiment 1 because the linear regressions were not significant ($p > 0.05$).

In situ Surface Seawater CO_2 Measurements in Bermuda and Hawaii

To put the mesocosm results into a broader context we evaluated the diel CO_2 variability and environmental conditions at three reef sites equipped with autonomous CO_2 sensors and contrasting coral cover for a period of 12 days coincident with the mesocosm experiments (**Figure 1**). In Bermuda, Crescent Reef is a patch reef located within a sandy bottom lagoon with water depth ranging from ∼2 to 7 m at the reef site. Coral cover is ∼15% (Jones, 2006). In contrast, Hog Reef is located on the rim reef with depth ranging from ∼6 to 11 m. The benthic community at Hog Reef is comprised of close to 30% hard (Scleractinian) corals with almost 70% of the community consisting of macroalgae, turf algae, and soft corals (Courtney et al., 2016). *D. labyrinthiformis* and *P. astreoides* constitute ∼10 and 1.5% of the benthic cover, respectively (Jones, 2006; Bates et al., 2010; Courtney et al., 2016). The seawater residence time on the rim reef is relatively short (1–4 days) while the lagoon experiences longer seawater residence times ranging from 5 to 12 days (Bates et al., 2010; Venti et al., 2012). In Hawaii, the monitoring site is a back reef environment located within Kaneohe Bay right at the shallow (∼2 m) transition zone between the barrier reef with ∼65% coral cover (Jokiel et al., 2015) and the inside deep (∼12 m) lagoon (**Figure 1**). The seawater residence time on the barrier reef of Kaneohe Bay, based on numerical simulations forced by historical wave, wind and tidal data is on the order of a day (Lowe et al., 2009), but can be much shorter depending on the wind strength and wave height conditions.

At each reef site, the mole fraction of CO_2 (xCO_2) in seawater and in air was measured every 3 h by NOAA PMEL $MAPCO_2$ systems (Sutton et al., 2014). The $MAPCO_2$ moorings utilize a Battelle Memorial Institute CO_2 system equipped with a LI-COR LI-820 infrared CO_2 gas analyzer and SHT71 relative humidity and temperature sensor (Sutton et al., 2014). The system calculates xCO_2 in air that has been equilibrated with seawater. The system is calibrated with a zero and a non-zero CO_2 reference gas provided by NOAA Earth System Research Laboratory (ESRL) and traceable to World Meteorological Organization (WMO) standards. The accuracy and precision of both air and seawater xCO_2 measurements are typically better than 2 μmol mol^{-1} (Sutton et al., 2014). At each of these sites, seawater temperature (°C) is also measured every 3 h by a Seabird 16plus V2 Seacat CTD. Tide and wind measurements were retrieved from nearby monitoring stations. Hourly mean lower low water (MLLW, m) data

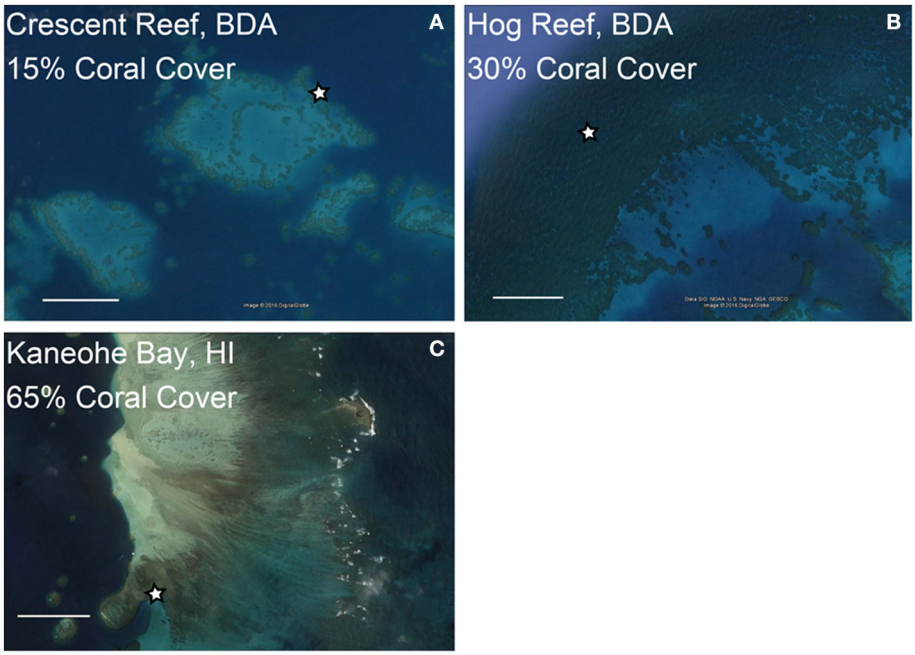

FIGURE 1 | Locations of coral reef buoys at reefs with contrasting coral cover in Bermuda (BDA, **A,B**) and Hawaii (HI, **C**). The stars indicate locations of coral reef CO_2 buoys and coral cover estimates are for the area surrounding these buoys. The scale bars represent 0.50 km in each image. Images were obtained from Google Earth.

were obtained for St. George's Island, Bermuda and Coconut Island (Mokuoloe), Kaneohe, Hawaii from NOAA/National Ocean Service (NOS) Center for Operational Oceanographic Products and Services (https://tidesandcurrents.noaa.gov). Wind data from Bermuda were taken from International Civil Aviation Organization (ICAO) standard observations at the LF Wade International Airport, Bermuda. The NOAA/NOS Data Buoy Center (www.ndbc.noaa.gov) provided hourly wind speed and direction for Coconut Island (Mokuoloe), Kaneohe, Hawaii.

RESULTS

All values are reported as the mean ±1 standard deviation, unless otherwise noted. The term "benthic metabolism" refers to the NCC and NCP rates for the communities containing different densities of coral within the mesocosms.

Experiment 1: Bermuda 2012

Environmental Conditions

The mesocosms experienced natural variations in seawater temperature, salinity, and light (**Figure 2**). From the beginning of the experiment, seawater temperature increased to a maximum of 30.37 ± 0.19°C at 15:00. Temperatures then decreased to 29.53 ± 0.07°C and remained fairly stable until the last sampling at midnight. Salinity fluctuated slightly around 36.67 psu for most of the experiment. There was a decline to 36.30 ± 0.15 psu at 21:00 due to a rain shower but salinity quickly recovered due to the short residence times of the mesocosms. Light started increasing slightly just before sunrise, which was at 6:52. Light levels reached a maximum (∼325 μmol photons m^{-2} s^{-1}) around 15:00 and then decreased to zero just prior to sunset (19:46).

Benthic Metabolism

NCC rates remained fairly stable throughout the experiment while NCP rates followed temperature and light closely, with the significantly highest rates occurring during the middle of the day (**Figure 3**). Coral communities maintained positive net calcification and organic carbon production throughout the day. Despite slightly higher rates for 80% coral cover throughout most of the day, there were no statistically significant differences in average daytime NCC or NCP between the two coral cover treatments (**Table 2**). The 40% coral cover treatment had an average daytime NCC rate of 3.37 ± 2.94 mmol m^{-2} h^{-1} while the 80% coral cover had a slightly higher average daytime NCC rate of 3.93 ± 2.55 mmol m^{-2} h^{-1}. NCP rates reached peak organic production at 15:00 when irradiance was highest and rates were ∼35% higher for high coral cover than for 40% coral cover (7.94 ± 3.82 vs. 5.93 ± 3.00 mmol m^{-2} h^{-1}).

Seawater Carbonate Chemistry

The net effect of NCC and NCP in the treatment mesocosms modified the seawater carbonate chemistry relative to the control, with positive NCC promoting acidification and positive NCP promoting alkalinization (**Figure 4**). Seawater pH and Ω_a increased throughout the morning until 15:00 after which they slightly decreased. In contrast, seawater pCO_2 started at maximum values and decreased until 15:00. At the start of the experiment, before sunrise, seawater pH was lowest for both coral cover treatments (7.85 ± 0.07 and 7.86 ± 0.02 for 40 and

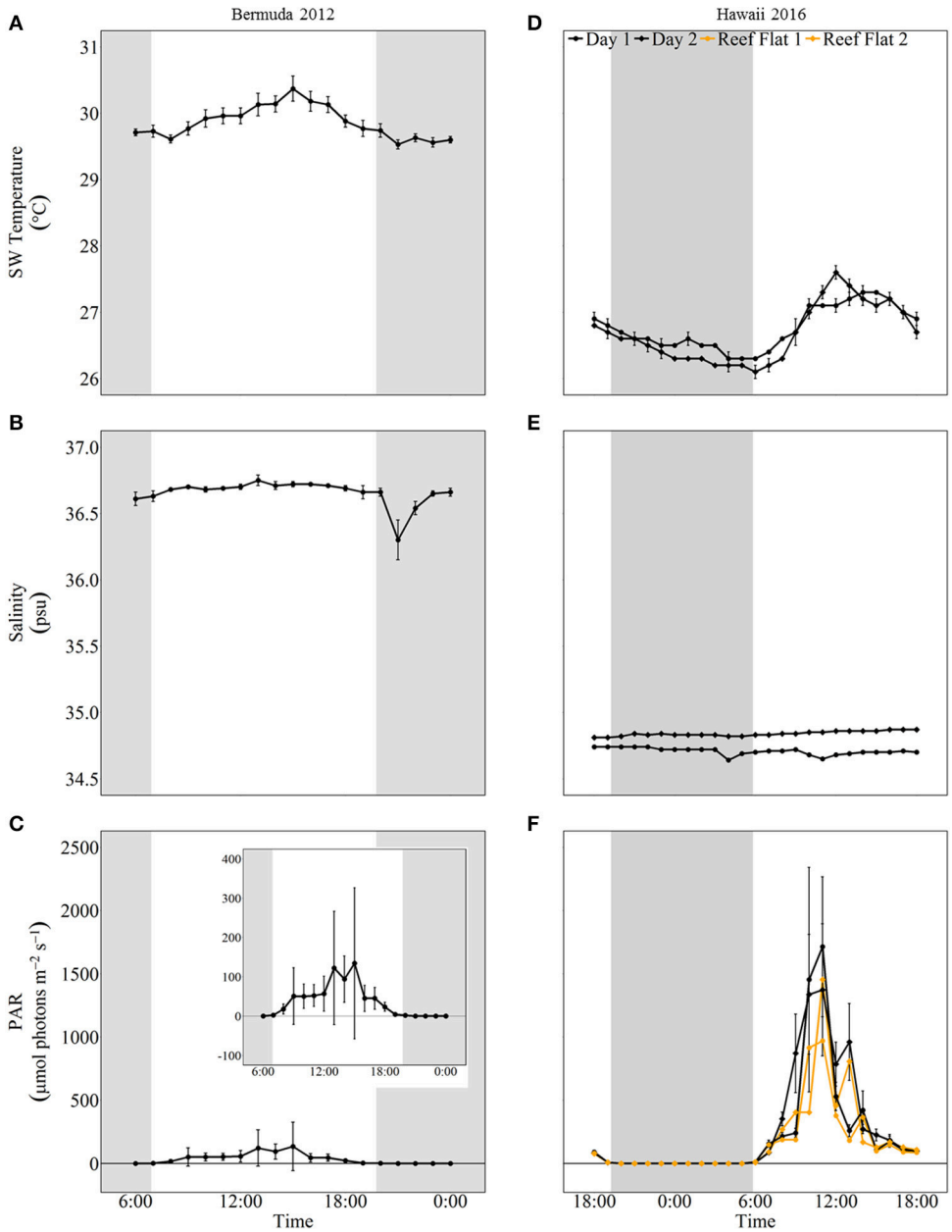

FIGURE 2 | Environmental conditions (mean ± 1 std) for mesocosm experiments in Bermuda 2012 (left panel, **A–C**) and Hawaii 2016 (right panel, **D–F**). The shaded areas show night as defined by sunset and sunrise times. In Hawaii, a light sensor was also placed on the reef flat where specimen were collected and these data are shown in orange.

80% coral cover, respectively) and lower than the control pH. Maximum pH for both treatments was 7.94 ± 0.01 which was 0.01 ± 0.01 higher than the control pH. Therefore, the pH range was 0.09 and 0.08 for 40 and 80% coral cover, respectively, which were twice the variability of seawater pH in the control (0.04). Seawater pCO_2 was highest in the morning and then decreased to 519.1 ± 10.3 μatm in 40% coral cover and 517.5 ± 11.4 μatm in 80% coral cover. The pCO_2 variability for 40 and 80% coral cover was 148.1 μatm and 122.9 μatm, respectively. Seawater Ω_a followed the same trend as seawater pH. The minimum values were 2.77 ± 0.40 for 40% coral cover and 2.83 ± 0.13 for 80% coral cover. The Ω_a rose to approximately maximum values of 3.33 for both coral cover treatments, which was 0.09 higher than the control (3.24 ± 0.04). The ranges of variability were 0.56 and 0.49 for 40 and 80% coral cover, respectively.

Experiment 2: Hawaii 2016

Environmental Conditions

Seawater temperature and light had strong diel variations while salinity remained stable throughout both days of sampling. The

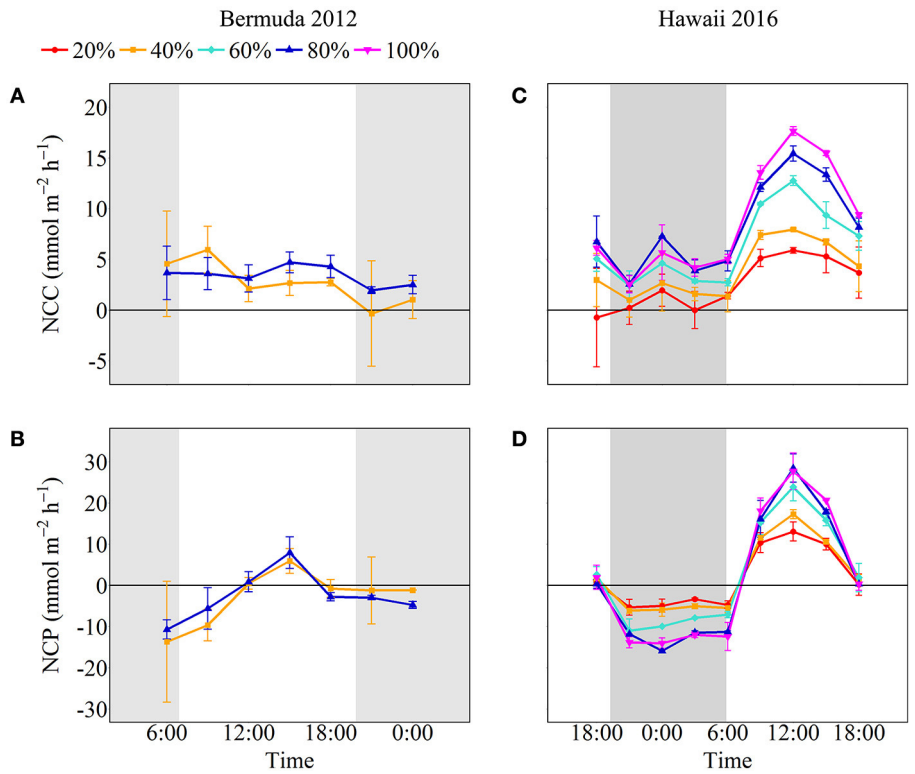

FIGURE 3 | NCC and NCP for Bermuda 2012 (left panels, **A,B**) and Hawaii 2016 (right panels, **C,D**) with colors and symbols representing coral cover treatments (red circle: 20%, orange square: 40%, aqua diamond: 60%, blue triangle: 80% and pink inverted triangle: 100%). The shaded areas show night as defined by sunset and sunrise times.

minimum and maximum seawater temperatures were similar for both days; the minimum temperature was around 26°C at night and then increased to ∼27.5°C during midday. On the first day of sampling, salinity averaged 34.71 ± 0.03 psu and was slightly higher on the second day, averaging 34.84 ± 0.03 psu. Light levels reached zero around 19:00 and started increasing when sunrise occurred just before 6:00. Maximum light levels (PAR) were ∼1,700 μmol photons m^{-2} s^{-1} during both days of sampling. These light levels were almost twice as high as measurements taken on the reef flat where corals were collected (**Figure 2**).

Benthic Metabolism

Both NCC and NCP followed similar diel trends to seawater temperature and irradiance; rates were low at night and then steadily increased to maximum rates during midday after which they decreased (**Figure 3**). Although all coral communities maintained net calcification most of the time, there were statistically significant differences between average night [ANCOVA, $F_{(4, 13)} = 5.048$, $p = 0.011$] and day [ANCOVA, $F_{(4, 35)} = 42.947$, $p < 0.001$] NCC rates (**Table 2**). The lowest rates of NCC were observed during night and the lowest coral cover had the lowest average NCC rate of 0.73 ± 1.6 mmol m^{-2} h^{-1}. This rate differed significantly from the highest nighttime NCC rates for 80% (4.0 ± 2.0 mmol m^{-2} h^{-1}) and 100% (4.1 ± 1.9 mmol m^{-2} h^{-1}) coral cover, which were not significantly different from one another. These differences between coral cover continued during the day as NCC rates followed the irradiance and temperature increase. The lowest coral cover (20%) had an average daytime NCC rate of 3.4 ± 3.0 mmol m^{-2} h^{-1} while the highest coral cover (100%) had an average daytime NCC rate of 11.2 ± 4.9 mmol m^{-2} h^{-1}.

All of the coral communities experienced net respiration at night and net organic production during the day. As observed for average NCC rates at night, there were also significant differences between treatment average NCP rates at night [ANCOVA, $F_{(4, 13)} = 53.43$, $p < 0.001$; **Table 2**]. The most negative average NCP rates were observed for 80% (−12.5 ± 1.9 mmol m^{-2} h^{-1}) and 100% (−13.3 ± 1.3 mmol m^{-2} h^{-1}) coral cover treatments. The 20 and 40% coral cover treatments had the least negative average night NCP rates at −4.5 ± 1.5 and −5.7 ± 0.97 mmol m^{-2} h^{-1}, respectively, and did not differ significantly from one another. The only significant interaction between coral cover treatment and time occurred for average daytime NCP rates [ANCOVA, $F_{(16, 35)} = 7.695$, $p < 0.001$] such that there were only differences between treatments at noon and 15:00 when maximum NCP rates were observed. At noon, 20% coral cover had the lowest positive NCP rate of 13.1 ± 2.3 mmol m^{-2} h^{-1} while the maximum NCP rate for the 100% coral cover treatment was approximately doubled at 27.7 ± 4.4 mmol m^{-2} h^{-1}.

Although there was quite a bit of variance in scaled NCC and NCP rates, linear regressions of scaled rates vs. coral cover

TABLE 2 | Statistical comparison of NCC and NCP rates for Bermuda 2012 and Hawaii 2016.

Experiment	Day/ night	Response	Factor	*df*	*F*-Statistic	*p*-value
Bermuda 2012	Day	NCC	Treatment	1	0.974	0.338
			Time	3	2.462	0.100
			Treatment*Time	3	3.114	0.056
		NCP	Treatment	1	2.715	0.120
			Time	3	15.72	<0.001*
			Treatment*Time	3	0.638	0.602
Hawaii 2016	Day	NCC	*Treatment*	4	42.95	<0.001*
			Time	4	50.30	<0.001*
			Treatment*Time	16	1.402	0.197
		NCP	*Treatment*	4	9.843	<0.001*
			Time	4	362.2	<0.001*
			*Treatment*Time*	16	7.695	<0.001*
	Night	NCC	*Treatment*	4	5.048	0.011*
			Time	2	5.891	0.015*
			Treatment*Time	8	0.302	0.952
		NCP	*Treatment*	4	53.43	<0.001*
			Time	2	6.425	0.012*
			Treatment*Time	8	1.021	0.467

For each analysis, an ANCOVA was used to compare the effect of coral cover on NCC and NCP rates while accounting for time. Results were considered significant when $p < 0.05$ and these significant results are italicized and indicated by asterisks.
**Indicates statistical significance.*

explained over 95% of this variance and thus were statistically significant for NCC ($R^2 = 0.98$, $p = 0.001$), NCP_{Day} ($R^2 = 0.96$, $p = 0.003$), and NCP_{Night} ($R^2 = 0.95$, $p = 0.003$). NCC rates scaled proportionally to coral cover with the linear regression having a slope of 0.99. (A linear regression with a slope of 1 would indicate increases in metabolic rates proportional to increases in coral cover.) The scaled NCC rates increased from 25 ± 33% to 89 ± 28% for 20% and 80% coral cover, respectively. NCP_{Night} also scaled relatively proportionally to coral cover with the linear regression having a slope of −0.90. The lowest coral cover (20%) had scaled NCP_{Night} rates of −35 ± 9% while 80% coral cover had scaled NCP_{Night} rates of −93 ± 12%. Unlike NCC and NCP_{Night}, scaled rates for NCP_{Day} did not scale proportionally to coral cover; the slope of the linear regression was only 0.66. The 20% coral cover treatment had scaled NCP_{Day} of 51 ± 6% and this scaled rate increased to 93 ± 9% for 80% coral cover (**Figure 5**). Comparison of rates of nighttime net respiration to daytime net production revealed that the balance between net respiration and net production shifts toward the former as coral cover increases (inset on **Figure 5**). Consequently, daily positive net community production remained relatively similar between treatments.

Seawater Carbonate Chemistry

Net calcification and net respiration at night resulted in low seawater pH and Ω_a and high pCO_2 while net organic carbon production during the day elevated seawater pH and Ω_a, and decreased pCO_2 (**Figure 4**). Interestingly, there were noticeable differences in seawater carbonate chemistry between different coral cover treatments at night but not during the day. Seawater pH for coral cover treatments was lower than control at night and had minimum pH ranging from 7.89 ± 0.00 (20% coral cover) to 7.84 ± 0.01 (80 and 100% coral cover). During the day, control pH reached a maximum of 7.96 ± 0.01 while the coral cover treatments had pH values 0.01–0.03 higher than the control. The diel variability of seawater pH was lowest for the control (0.04) and increased with increasing coral cover (0.08 for 20% coral cover to 0.14 for 100% coral cover). Maximum seawater pCO_2 occurred at the end of the night, just before sunrise. The control reached a maximum pCO_2 of 539.0 ± 3.5 μatm while coral cover treatment maxima ranged from 577.0 ± 4.2 (20% coral cover) to 662.0 ± 14.4 μatm (100% coral cover). Minimum seawater pCO_2 was observed at midday with coral cover treatments having lower pCO_2 relative to the control. As with seawater pH, these diel trends led to increasing variability of pCO_2 with increasing coral cover. Coral cover treatments had the lowest Ω_a during the night with minimum values of 2.48 ± 0.02 (20% coral cover) to 2.23 ± 0.04 (100% coral cover) and these were lower than the minimum value for the control (2.62 ± 0.01). During the day, coral cover treatments had slightly higher seawater Ω_a relative to control values. The diel variability of seawater Ω_a was lowest for the control (0.27) and increased with increasing coral cover (0.49–0.71 for 20 and 100% coral cover, respectively). Although the magnitude of changes observed in seawater TA and DIC differed between treatments (**Figure 6**), there were no differences between the slopes of TA:DIC ratios [ANOVA, $F_{(4, 5)} = 0.271$, $p = 0.885$; **Figure 7**]. These slopes ranged from 0.43 ± 0.10 for 40% coral cover to 0.54 ± 0.24 for 80% coral cover. This resulted in a pH range of 7.8–8.0 and pCO_2 range of 400–800 μatm for all coral densities.

In Situ Surface Seawater CO_2 Measurements in Bermuda and Hawaii

In general, *in situ* observations showed that reefs with higher coral cover experienced greater diel variability in seawater CO_2 than reefs with lower coral cover (**Figure 8**). Crescent Reef, which had the lowest coral cover, experienced a mean xCO_2 of 483.6 μmol mol^{-1} and a range of 455.2–521.8 μmol mol^{-1}. Hog Reef had slightly higher mean xCO_2 (501.5 μmol mol^{-1}) and range (444.9–574.8 μmol mol^{-1}) compared to Crescent Reef. The larger range of CO_2 at Hog Reef can be attributed to nighttime maxima always being greater than Crescent Reef whereas daytime minima were similar to or slightly lower than Crescent Reef. However, both reefs always had higher xCO_2 than the atmosphere, which averaged 385 μmol mol^{-1}. The reef in Kaneohe Bay experienced a much greater range of xCO_2 compared to the reefs in Bermuda with both nighttime maxima and daytime minima higher and lower, respectively. The minimum value during the study period was 306.0 μmol mol^{-1} while the maximum was 691.0 μmol mol^{-1} with a mean of 473.5 μmol mol^{-1}. The average seawater temperature in Bermuda was 29.3°C with a 1.5°C range while Hawaii was slightly

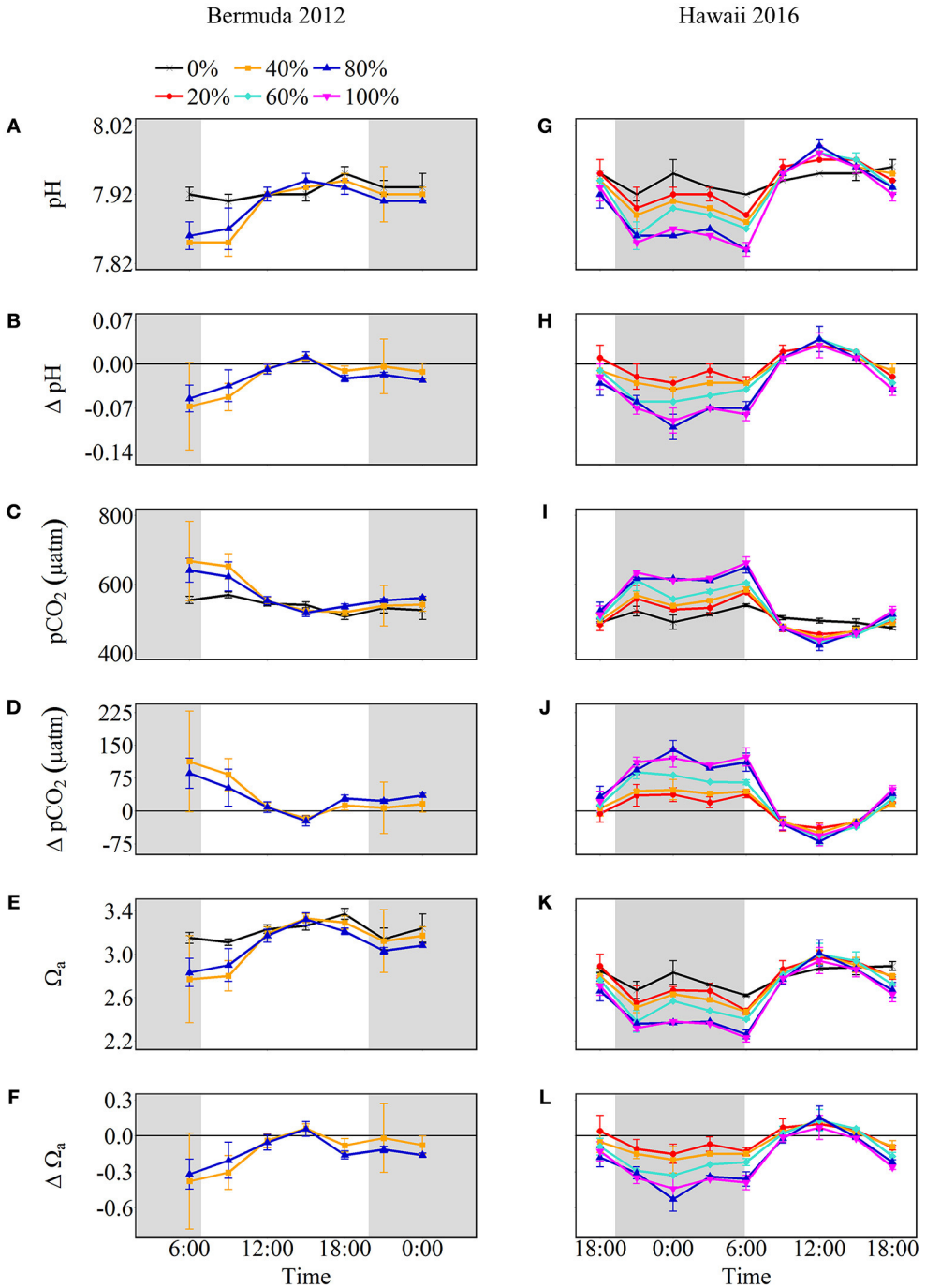

FIGURE 4 | Seawater carbonate chemistry shown as absolute values (pH, pCO_2, and Ω_a) and the difference from control (0%) values (Δ pH, Δ pCO_2, and Δ Ω_a) for Bermuda 2012 (left panel, **A–F**) and Hawaii 2016 (right panel, **G–L**). The shaded areas show night as defined by sunset and sunrise times while the colors and symbols represent coral cover treatments (black cross: 0%, red circle: 20%, orange square: 40%, aqua diamond: 60%, blue triangle: 80% and pink inverted triangle: 100%).

cooler (mean = 26.4°C) and experienced a larger range of 4°C. Both regions had semidiurnal tides with a tidal range less than or equal to 1 m. Wind speed and direction were variable in Bermuda while east to northeasterly trade winds dominated in Hawaii during the time frames examined (**Figure 8**).

DISCUSSION

This study was designed to test hypotheses relevant for the scaling of NCC and NCP rates and their influence on seawater carbonate chemistry for different coral densities. Higher coral density

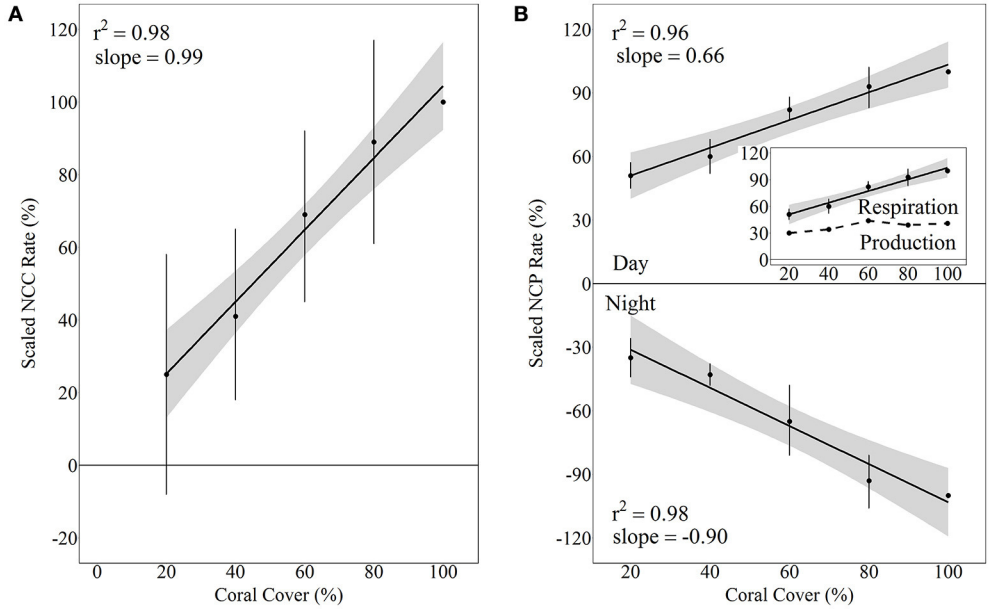

FIGURE 5 | Scaled NCC **(A)** and NCP **(B)** rates vs. coral cover treatments for Hawaii 2016 with linear regressions and shaded 95% confidence intervals during day and night. Separate linear regressions were performed for NCP day and night to show scaled rates for NCP_{Night} (net respiration, **B**, bottom panel) and NCP_{Day} (net organic carbon production, (**B**, top panel). The inset shows the daytime NCP rates as well as the difference between day and night NCP rates (dashed line), which essentially is a relative estimate of the integrated daily net production rate relative to daytime NCP in the 100% coral cover treatment.

sometimes, but not always led to higher NCC and NCP rates that scaled with increases in coral cover. In Bermuda, the higher coral density treatment (80%) did not have statistically significantly higher average daytime NCC or NCP rates (H1) compared to the low coral density (40%) treatment. Consequently, no significantly different influences on seawater carbonate chemistry were observed between low and high coral cover for this experiment (H2). In contrast, higher coral cover did lead to statistically higher average NCC and NCP rates in Hawaii (H1). Furthermore, these increases were roughly linearly proportional to the increases in coral cover for NCC and NCP_{Night}. That is, a doubling in coral cover doubled the rate of NCC and the rate of nighttime net respiration (-NCP) (H1). NCP_{Day} also increased with increasing coral cover, but was not directly proportional to the percent increase in cover. Notably, the observed increases in metabolic rates led to increases in diel variability of seawater pH, pCO_2, and Ω_a (H2). Likewise, field measurements of seawater xCO_2 in Bermuda and Hawaii showed greater diel ranges for reef areas with higher coral cover. We discuss these results further in the subsequent sections.

Coral Density and Benthic Metabolic Rates

The first experiment conducted in Bermuda during 2012 showed no significant difference between daytime NCC and NCP rates between two coral cover treatments. In addition, NCC rates remained relatively low and did not follow a clear diurnal cycle (average of 2.68 and 3.40 mmol m^{-2} h^{-1} for 40 and 80% coral cover, respectively), while NCP rates tracked light and temperature closely with the highest rates occurring in the late afternoon. These results were unexpected as we had anticipated high coral cover to have significantly higher metabolic rates than low coral cover (Kleypas et al., 2011). We had also expected NCC rates to track variations in light intensity and NCP due to light and/or production enhanced calcification (e.g., Vandermeulen et al., 1972; Gattuso et al., 1999; Albright et al., 2015; Cohen et al., 2016). However, the observed variability in NCC and NCP rates between treatments was high, masking any potential systematic differences (**Figure 3**). It is likely this variability was partly related to insufficient control and characterization of flow rates, and therefore residence time within the mesocosms, which has a large influence on calculations of NCC and NCP. Furthermore, shading cloth intended to moderate temperatures in the mesocosms resulted in low light intensities that only reached a maximum of 325 μmol photons m^{-2} h^{-1}. This may have resulted in metabolic rates that were insufficient to distinguish differences between the two treatments. In addition, limited light conditions may also explain the low and temporally flat NCC rates despite a distinct temporal trend in NCP, since photosynthesis and light enhanced calcification could respond differently to different wavelengths and intensity of light (Cohen et al., 2016). However, additional studies would be required to evaluate whether this could have been the case. Compared to the Hawaii experiments conducted under higher light conditions (max ∼1,700 μmol photons m^{-2} h^{-1}), NCP rates for the Bermuda experiment were much lower although the qualitative trend and difference between treatments were similar to the Hawaii experiments (**Figure 2**). Regardless of the shortcomings of this experiment, the results represent metabolic rates of two coral density treatments and their influence on seawater carbonate chemistry under the reported conditions, which could

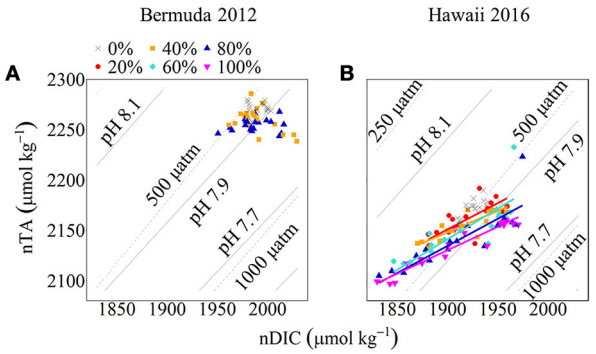

FIGURE 6 | nTA:nDIC plots with pH and pCO_2 isolines for Bermuda 2012 **(A)** and Hawaii 2016 **(B)**. Seawater pH and pCO_2 was calculated using nDIC, nTA, and average temperature and salinity for each site. The colored symbols show coral cover treatments (black cross: 0%, red circle: 20%, orange square: 40%, aqua diamond: 60%, blue triangle: 80% and pink inverted triangle: 100%) for both experiments. The colored lines show Type II Linear Regressions for each coral community.

naturally be experienced *in situ* on cloudy days or at deeper depths. The results also provide important information to be considered in the interpretation of other studies as well as in the design of future experiments.

Because of the somewhat inconclusive results achieved in Bermuda, the follow-up study in Hawaii was designed using the mesocosm facility at HIMB, which experiences full exposure to sunlight and has a proven ability to control seawater flow rates (Andersson et al., 2009; Page et al., 2016). Using more different coral cover treatments and full diel cycles also allowed a more incisive investigation into the effects of coral densities on benthic metabolism and seawater carbonate chemistry. In contrast to the Bermuda experiments, these experiments showed statistically significant increasing rates of NCC and NCP as a function of increasing coral cover. In addition, both NCC and NCP followed the light cycle with lower rates at night and higher rates during the day as expected based on previous mesocosm experiments at HIMB (Jokiel et al., 2014; Page et al., 2016). Coral communities typically maintained net calcification (positive NCC) throughout the experiments with a few instances of net $CaCO_3$ dissolution for the lower coral cover communities (20 and 40%) during the night. Interestingly, rates of NCC and NCP_{night} scaled directly to coral cover while NCP_{day} did not (**Figure 5**). Because rates of respiration are linked to body size and metabolic demand, the proportional link between coral cover and NCP_{night} seems reasonable. The same might be true for NCC assuming that this rate is directly linked to the energetic expenditure of the colonies within a community. However, this relationship between body size and metabolic demand for NCC would imply that communities with low coral cover require more energy to calcify or can store more energy for other processes than high coral cover since NCP_{day} rates were proportionally higher for low coral cover compared to high coral cover communities. For example, the 20% coral cover treatment had NCP_{day} rates on average approximately half of the rates for the 100% coral cover treatment, but maintained NCC rates at ∼20% of the rates observed in the 100% treatment. One possibility is that higher coral cover may have depleted the availability of resources (e.g, inorganic macro-nutrients) necessary for primary production, thus leading to proportionally lower NCP in these treatments. Mesocosms with higher coral cover also contained more complex topography, which could result in shading of some coral colonies and/or different boundary layer thicknesses (Shashar et al., 1996; Hearn et al., 2001), which could affect rates of primary production (Dennison and Barnes, 1988). Furthermore, intra- and inter-specific interactions in high coral density could reduce rates of physiological processes as organisms cope with stress and/or divert energy resources toward defense mechanisms against competitors (Rinkevich and Loya, 1985; Tanner, 1997). Regardless of the various factors that may have influenced the metabolic rates, it is unclear why NCC scaled proportionally with coral cover while NCP_{day} did not. Time may also be a factor with potential lag in responses that are not detected over the diel timescale of the current experiments. Experiments of longer duration could potentially reveal different relationships and scaling of metabolic rates in response to variations in environmental parameters. Our initial results indicate that additional studies are warranted to better understand how different environmental and physical properties interact and influence benthic metabolic rates.

Coral Density and Seawater Carbonate Chemistry

In general, positive NCC and negative NCP at night led to seawater acidification while positive NCP exceeding NCC during the day promoted alkalinization for most treatments (**Figure 4**). Intuitively, one might anticipate that higher coral cover and higher rates of NCC and NCP would lead to significantly different seawater pH, pCO_2, and Ω_a as well as different diel amplitude and variability, but this was not always the case. Naturally, for the Bermuda experiments, no differences in seawater pH, pCO_2, and Ω_a were observed between coral densities because NCC and NCP rates were not significantly different. However, even for the Hawaii experiments, no significant differences were observed in these parameters between coral density treatments during the day despite significantly different NCC and NCP rates. In contrast, seawater pH and Ω_a were progressively lower and pCO_2 higher with increasing coral cover at night, which resulted from increased net respiration and positive NCC as a function of higher coral cover. As a result of the differential influence by communities with different coral densities on seawater chemistry at night, the daily average pH and Ω_a, and the diel variability of these parameters decreased and increased slightly, respectively, with increasing coral cover.

Deffeyes diagrams (Deffeyes, 1965) provide a useful tool to understand the observed trends in carbonate chemistry and illuminate differences in diel variability of seawater pH, pCO_2, and Ω_a between coral cover treatments. These diagrams graphically depict seawater carbonate chemistry parameters (i.e., pH, Ω_a, and pCO_2) as a function of variations in TA and DIC owing to modification by biogeochemical processes such as NCC and NCP (Watanabe et al., 2006; Andersson and Gledhill, 2013).

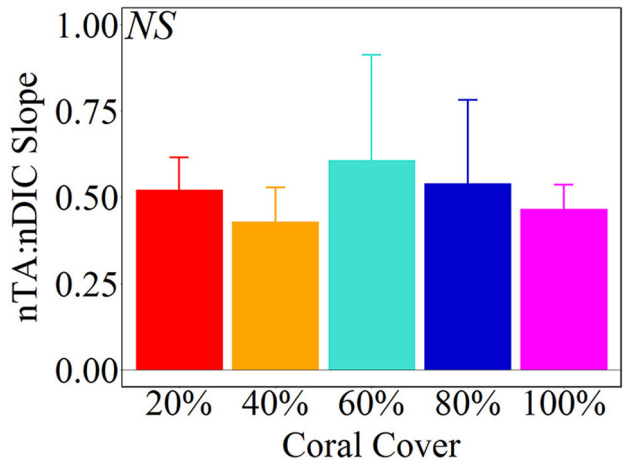

FIGURE 7 | Average (± 1 std) nTA:nDIC slopes from Type II Linear Regressions of the Hawaii mesocosm data. There were no statistical significant differences between coral cover treatments [ANOVA, $F_{(4, 5)} = 0.271$, $p = 0.885$].

Depending on the slope of the TA-DIC relationship, one can infer the relative importance of organic to inorganic carbon cycling (i.e., NCP vs. NCC) with slopes less than ∼1 indicating higher dominance by organic carbon cycling. In this study, the overall slopes of the vectors were always less than 1 for the duration of the experiments. Some of the observed variability in TA-DIC slopes could be accounted for by changes in the source water, but in general this was small compared to the changes due to metabolic processes within the mesocosms (**Figure 6**). Although TA-DIC slopes were similar across treatments, there was consistently lower TA with increasing coral cover owing to higher NCC rates, which combined with more negative NCP rates during night, led to differences in the daily mean and the range of variability of seawater pH, pCO_2, and Ω_a between treatments. At night, positive NCC and negative NCP acted additively in modifying seawater carbonate chemistry parameters while during the day, positive NCC and positive NCP counteracted the influence on these parameters (Page et al., 2016). Consequently, both the absolute NCC and NCP rates and the relative balance between these processes, which combined modify the seawater TA and DIC balance, are important to consider in evaluating the influence of biogeochemical processes on seawater pH, pCO_2, and Ω_a (Andersson and Gledhill, 2013).

Similar to the mesocosm results, natural coral reefs with higher coral cover experienced greater diel ranges of seawater CO_2 concentrations relative to reefs with lower coral cover. In Bermuda, observations of seawater CO_2 from Crescent and Hog Reefs qualitatively agreed with the mesocosm results with large differences at night, but similar conditions during the day between the two reef sites. At this time, it is not our intention to fully assess the *in situ* variability and quantitatively compare it to the mesocosm results, as additional data are required (see for example, Kayanne et al., 2005); however, initial assessments show that the range of *in situ* CO_2 and temperatures are comparable to values measured in the mesocosm experiments. Compared to the mesocosms, additional biological and physical factors influence seawater carbonate chemistry on natural coral reefs. Even though coral cover is the only biological metric reported here, additional functional groups (e.g., calcifying algae, fleshy macroalgae, and sand) differed between each reef site, but were not included in the mesocosms. The magnitude of the influence by benthic metabolism on seawater carbonate chemistry is likely to depend on benthic community composition. Previous mesocosm and flume studies have shown differential modification of seawater pCO_2, pH, and Ω_a(Anthony et al., 2011, 2013; Page et al., 2016) between fleshy algae, crustose coralline algae, coral, and sand communities due to differences in benthic metabolic rates. Although benthic metabolism typically has a large influence on the magnitude of CO_2 changes on a reef, physical drivers such as water depth, residence time, tidal flow, wind speed, and wave forcing strongly influence this variability as well (Suzuki and Kawahata, 2003; Drupp et al., 2013; Falter et al., 2013). Furthermore, air-sea gas exchange (Bates et al., 2001; Fagan and Mackenzie, 2007) and terrestrial influences (Kawahata et al., 2000; Suzuki and Kawahata, 2003; Drupp et al., 2011; Massaro et al., 2012; Cyronak et al., 2013) must also be considered as they may differ greatly between Bermuda and Hawaii (particularly terrestrial inputs). The Kaneohe Bay reef system is more strongly dominated by organic carbon cycling than inorganic carbon cycling (Massaro et al., 2012) while the opposite is true for the Bermuda reefs (Andersson et al., 2014). Consequently, additional studies would be required to tease apart the exact drivers of seawater CO_2 variability on these reefs and to determine the *in situ* relative importance of coral cover and other benthic components to this variability.

Integrating Effects across Scales to Predict Coral Reef Response to Environmental Changes

The results from this study highlight the need to develop a more comprehensive understanding of how metabolic processes and the subsequent effects on seawater carbonate chemistry integrate across functional, spatial, and temporal scales. Community scale mesocosm experiments provide an intermediate step between experiments with individual coral colonies and natural reef communities, and provide valuable insight into drivers of benthic community metabolism (e.g., coral cover, community composition, flow rates, and resource availability) (Anthony et al., 2013; Page et al., 2016). However, the question remains: how do these results translate to an entire reef system across different temporal and spatial scales? In this study, altering coral cover alone in mesocosms did not always change the influence on the magnitude of the variability of diel seawater pCO_2, pH, and Ω_a, but natural reefs with variable coral cover exhibited significantly different diel variability in seawater CO_2. It is clear from the current results that additional processes need to be considered to account for the *in situ* observations, which may include water depth, water flow, and the major functional groups' relative composition and metabolism. Nonetheless, the process of comparing results from controlled laboratory experiments with *in situ* observations is a necessary first step of developing a more sophisticated model that is able to account for the observed variability in the natural

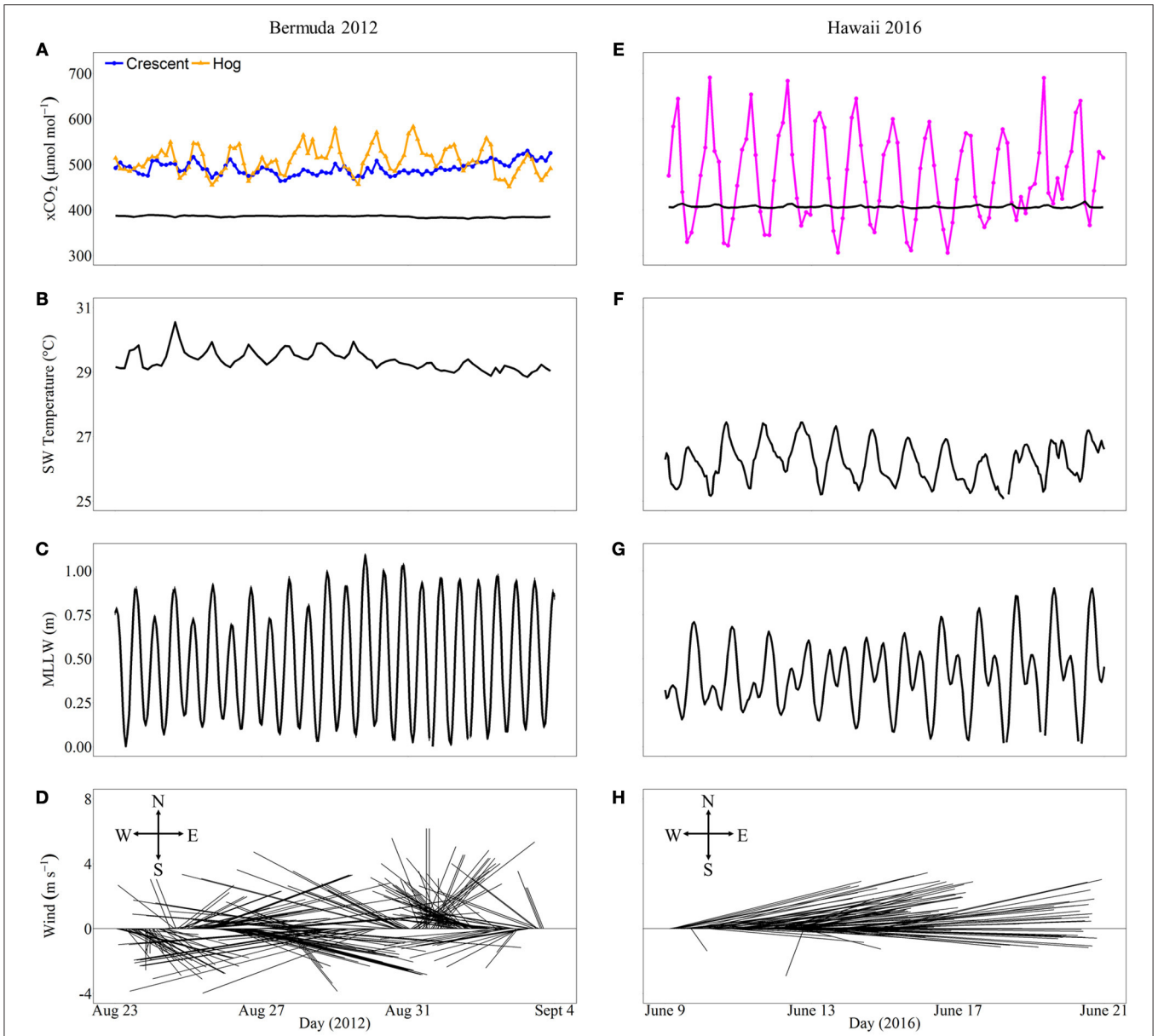

FIGURE 8 | *In situ* xCO_2(µmol mol^{-1}) and environmental conditions including seawater temperature, tidal range, and wind speed and direction that may influence xCO_2 variability for different reefs in Bermuda (left panel, **A–D**) and Hawaii (right panel, **E–H**) over 12 consecutive days overlapping the mesocosm experimental periods during 2012 and 2016, respectively. The xCO_2 for both the atmosphere (black lines) and seawater (colored lines) are shown **(A,E)**. Crescent Reef (orange circles) has the lowest coral cover while the reef in Hawaii (Kaneohe Bay barrier reef; magenta circles) has the highest coral cover.

environment. Combined with refinement and application of existing ecological theory, this approach provides an initial foundation to integrate metabolic rates across functional, spatial and temporal scales (Andersson et al., 2015; Edmunds et al., 2016; Shaw et al., 2016). Being able to integrate metabolic rates across scales will be critical to predict how coral reefs as a whole will respond to environmental perturbations, such as climate change and OA. The magnitude of OA will, at the local scale, partly depend on benthic metabolism and how it modifies seawater carbonate chemistry (Anthony et al., 2011, 2013; Kleypas et al., 2011; Jokiel et al., 2014; Page et al., 2016). Therefore, research priorities should first aim to understand the relationships between community composition, benthic metabolism and seawater carbonate chemistry, then how physical forcing/processes alter the "apparent" response of the seawater to the specific community metabolism and, finally, how these relationships are modified by climate change and OA. The pathway to accurately being able to scale results between different functional, spatial, and temporal levels will require a range of research approaches integrating laboratory experiments with

field observations and numerical modeling, but these efforts will be essential to advance our understanding regarding the future impacts of climate change and OA on these important systems (Andersson et al., 2015). One of the main challenges is related to the fact that different processes and drivers of net reef metabolism operate on different temporal and spatial scales, and perhaps this can only fully be accounted for by a well-defined numerical model integrating physical, ecological and biogeochemical processes.

AUTHOR CONTRIBUTIONS

HP and AA designed the study, analyzed the results, and wrote the initial draft of the manuscript. HP, TC, and AC conducted the experiments. ED contributed data. All authors contributed to writing of the revised manuscript.

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SUPPLEMENTARY MATERIAL

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