Linking seasonal changes in benthic community structure to seawater chemistry

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Abstract. Ocean acidification (OA) resulting from rising atmospheric CO_2 represents a potential threat to marine calcifiers and the ecosystems they inhabit. Numerous studies suggest that decreases in net calcification could compromise coral reef ecosystems within the next few decades to century. The effects of OA, combined with physiological stress from rising temperatures, are global changes thought to cause shifts in community structure that accelerate degradation of coral reefs. The Atlantic OA test-bed (AOAT) in La Parguera, Puerto Rico provides a natural laboratory to autonomously monitor seawater chemistry *in situ* and understand the unique set of feedbacks and interactions between water column chemistry and benthic habitats. In 2011, seasonal benthic habitat characterizations were conducted at two reefs and one seagrass site at La Parguera to quantify the abundance of major benthic calcifiers and relate changes in benthic community structure to any observed changes in seawater carbonate chemistry. Both reef sites were dominated by fleshy macroalgae, and live coral cover ranged from 8 to 10% in all seasons. Observed seasonal patterns in seawater aragonite saturation state were largely decoupled from subtle changes in both soft coral and calcareous algae abundance. Further investigation of the relationship between algal abundance and overlying water column chemistry is ongoing to improve our understanding of potential feedbacks between reef ecosystems and reef water chemistry.

Key words: Ocean acidification, Coral reefs, Benthic community structure, Saturation state, Puerto Rico

Introduction

Ocean acidification (OA) resulting from rising atmospheric carbon dioxide (CO_2) represents a potential threat to calcifying ecosystems like coral reefs (Kleypas et al. 1999; Guinotte et al. 2003; Hughes et al. 2003; Feely et al. 2004; Sabine et al. 2004; Orr et al. 2005; Hoegh-Goldberg et al. 2007; Guinotte and Fabry 2008). OA combined with physiological stress from rising sea surface temperatures may cause shifts in community structure that accelerate degradation of coral reefs and potentially result in ecosystem collapse (e.g. Hoegh-Guldberg et al. 2007; Mumby et al. 2007; Silverman et al. 2009; Kleypas et al. 2011). There is spatiotemporal variability in OA (Guinotte et al. 2003; Gledhill et al. 2009) that can be exacerbated by taxa-specific calcification response (Ries et al. 2009; Hendriks et al. 2010) and habitat-driven changes in carbonate mineral saturation state (Silverman et al. 2007; Anthony et al. 2011; Kleypas et al. 2011). The level of benthic characterization required to evaluate interactions and feedbacks with local carbonate chemistry depends on the study objectives. Chamber measurements (e.g. Yates and Halley 2003), Lagrangian fluxes (e.g. Gattuso et al. 1996), and modeling efforts (e.g. Kleypas et al. 2011) may require a general characterization while the seasonal measurements (e.g. Kayanne et al. 2005; Bates et al. 2009) may benefit from more detailed information on potentially shifting community structure (algal abundance, coral bleaching, etc.).

Since 2008, the Atlantic OA test-bed (AOAT) has provided a natural laboratory in which program partners utilize sustained autonomous monitoring of near-reef carbonate chemistry, focused process studies, and modeling efforts to explicitly account for the effects of OA and determine its impact on coral reef ecosystems. A focal point of the 2011 field season at the AOAT was to obtain multiday measurements of net community metabolic processes and ambient carbonate chemistry in a variety of habitat types, and describe and quantify the benthic communities present in each habitat type. This provides both an understanding of the spatial variability relative to the sustained monitoring effort and the potential to scale up measurements across different habitat types for modeling efforts. This study presents quantitative descriptions of the biological communities at the AOAT in La Parguera, Puerto Rico, and describes the potential feedbacks between the benthic communities and the carbonate chemistry of the overlying water column.

Material and Methods

Physical Setting

Puerto Rico (18.25°N, 66.5°W) is a mountainous island in the northeastern Caribbean Sea. The southwestern shelf gradually slopes from 0 to 35 m depth over a distance of 8-10 km from the shoreline to the shelf break. The insular shelf has extensive mangrove forests, seagrass beds and coral reef communities (Ballantine et al. 2008), including coral reefs, hard grounds, and igneous or metamorphic rock reefs (García-Sais et al. 2003). The AOAT is situated in the La Parguera region of SW Puerto Rico, which has the best-developed reefs on the island with an average coral cover of 18% (Ballantine et al. 2008). Reefs in La Parguera typically have low cover of coralline algae but abundant turf algae, with macroalgal cover peaking in the summer (Pittman et al. 2010).

This study focused on three shallow (1.5 – 5 m depth) habitats (Fig. 1): the fore-reef at Cayo Enrique (CE), the back reef lagoon at San Cristobal (SC), and a seagrass bed west of Atravesado reef (AT). Surface currents in La Parguera typically flow eastward but can change with wind forcing (Ballantine et al. 2008). Similar patterns exist at Cayo Enrique and Atravesado, but the San Cristobal site is in the immediate lee of an island and water flow can be weak and northerly (W. McGillis, Columbia U. and B. Loose, Woods Hole Oceanographic Inst., pers. comm.). Habitats were surveyed during the local dry (10-13 January 2011), intermediate (30 April-2 May 2011), and wet (30-31 July 2011) seasons.

Figure 1: AOAT 2011 survey sites in La Parguera, Puerto Rico: CE = Cayo Enrique (fore reef, 2-5 m depth); SC = San Cristobal (back reef, 1.5-3.5 m); AT = Atravesado (seagrass bed, 2-3.5 m).

Field Surveys

The AOAT measures carbonate chemistry with a long-term fixed Moored Autonomous pCO$_2$ (MA$_P$CO$_2$) buoy on the fore-reef at Cayo Enrique for surface measurements (Gledhill et al. 2010), and repeated seasonal observations of net community productivity using a Coral Reef Oxygen Sensing System (CROSS; McGillis et al. 2011). The benthic survey methodology was selected to balance three objectives: 1) quantifying community components within a CROSS footprint, 2) to document any potential changes over the season, and 3) to facilitate scaling up of *in situ* chemistry measurements to other similar habitat types. Pittman et al. (2010) report the most spatially comprehensive benthic community data for La Parguera; those data were derived from visual estimates within replicate quadrats along 25-m transects. A transect-based method had limited utility here because the overall shape of a CROSS footprint depends on current speed and direction and can therefore change over time. Instead 10 m^2 grids were established immediately upstream and downstream of the CROSS at each reef site, surveying 20 randomly placed 1 m^2 quadrats with visual survey techniques analogous to those of Pittman et al. (2010). Briefly, quadrats were subdivided into 10 cm^2 units and cover estimated to the nearest 1% for most categories but unique scleractinian coral species were noted at 0.5% or 0.1%. The seagrass bed was visually homogenous for tens of meters in all directions, so only one 10 m^2 grid with 20 haphazardly placed quadrats was used. The same visual survey estimates were used in the seagrass bed to ensure comparability with the reef data. However, percent cover data are typically not reported in the seagrass literature, so shoot density was also counted in 10 randomly selected 10 x 10 cm cells within each quadrat. While CROSS data will be presented in a subsequent study; a broad community characterization and comparison with the MA$_P$CO$_2$ are given here. At all sites, five rugosity measurements (after Luckhurst and Luckhurst 1978) were made haphazardly along the transect tapes in each grid. There was no visually obvious change in reef topography during sampling, so rugosity measures were pooled at each site.

Carbonate Chemistry

The MA$_P$CO$_2$ provided autonomous measures of the partial pressure of CO$_2$ in seawater (pCO$_{2,sw}$), temperature (T) and salinity (S) every 3 hours. Empirical estimates of total alkalinity (A$_T$) were derived based on a function of T and S calibrated to discrete A$_T$ measurements made bi-weekly throughout the duration of the study (Gledhill et al. 2009). Collectively these empirical relationships exhibited an $r^2_{adj} = 0.77$, RMSD = 22 μmol kgsw^{-1}. Using these empirical estimates of A$_T$ paired with T, S, and pCO$_{2,sw}$ we solved for the carbonic acid system using the CO2SYS program (Lewis and Wallace 1998), applying the K$_1$ and K$_2$ dissociation constants of Hansson and Mehrbach refit by Dickson and Millero (1987) using the total pH scale.
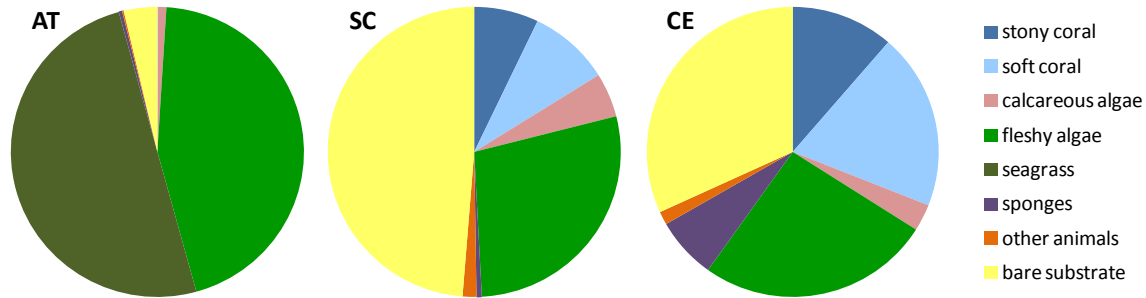
Figure 2: Percent benthic cover at instrument deployment sites at Atravesado (AT), San Cristobal (SC), and Cayo Enrique (CE).

Data Analysis
Benthic data were pooled within a site and community characteristics were compared using non-parametric multi-dimensional scaling (MDS). A one-way non-parametric pairwise analysis of similarities (ANOSIM) tested for differences in community composition, with post-hoc non-parametric similarity of percentages (SIMPER) to determine which taxa contributed to the similarity/dissimilarity. A more complete description of these statistical methods is given by Moyer et al. (2003). Rugosity and cover data were analyzed with analysis of variance or non-parametric equivalents if data were not normal after transformation.

Results

Site Differences in Benthic Communities
The seagrass bed at Atravesado had a substantially different community structure (Fig. 2; MDS plots not shown) than the two reef sites. Approximately half of the benthic cover was the seagrass *Thalassia testudinum*, while *Syringodium filiforme* was present but at lower abundance (0.8 shoots/.01 m^2 vs. 5.5 *Thalassia)*. Drift algae (mostly *Lobophora* sp.) comprised another 44% cover, while only 1% was calcifying green algae.

There was no significant difference in algal cover on the Cayo Enrique fore-reef and the San Cristobal lagoon; each site had ~25% cover. San Cristobal had virtually no sponges, with more bare substrate (primarily sandy bottom; Mann-Whitney U-test; Z = 4.11, p < 0.001), more calcifying algae (Mann-Whitney U-test; Z = 4.51, p < 0.001), fewer soft corals ($F_{1,238}$ = 40.48, p < 0.001), and lower scleractinian cover (Mann-Whitney U-test; Z = 3.88, p < 0.001) than Cayo Enrique. SIMPER analysis showed differences in scleractinian community composition; with differences driven by the presence of *Acropora cervicornis* at San Cristobal versus Cayo Enrique's *Siderastrea siderea*, *Porites astreoides*, and *Montastrea faveolata*. Cayo Enrique had significantly higher rugosity than San Cristobal (1.49 vs. 1.30;

Mann-Whitney U-test; Z = 2.35, p = 0.02). Topography at Cayo Enrique was primarily extant and relic massive corals, while San Cristobal had coral bommies and *A. cervicornis* over sand.

Temporal Differences in Benthos and Chemistry
Salinity (S) ranged from 34-36 ‰ with a maximum near April, and minimum in late fall. Temperature (T) exhibited an inverse relationship with S, ranging from 26-30°C during the study period, and T and S were positively correlated with aragonite saturation state (Ω_{Arg}; p < 0.05). While seasonal dynamics in Ω_{Arg} were dominated by the thermodynamic effects of T and S, diurnal changes in Ω_{Arg} anomalies were closely related to changes in light availability whereby Ω_{Arg} could be enhanced by as much as 4% during peak daylight hours. The largest Ω_{Arg} amplitude occurred in May, and the lowest in August (Fig. 3). Percent cover of benthic calcifiers increased over the year ($F_{2,237}$ = 8.13, p < 0.001), initially tracking the increase in Ω_{Arg} through April/May, but continuing to increase in July/August after Ω_{Arg} had begun to decrease (Fig. 3). January had fewer calcifiers than either April/May (Tukey HSD; p =0.025) or July/August (p < 0.001; Fig. 3). The pattern was consistent at both Cayo Enrique and San Cristobal, and was primarily driven by changes in octocoral cover (when octocorals are excluded, $F_{2,237}$ = 2.46, p = 0.088) and an increase in calcifying algae at San Cristobal ($F_{2,117}$ = 11.79, p < 0.001). There were no significant changes in non-calcifying algae (i.e. cyanobacteria, macroalgae, turf algae) at either reef. At the Atravesado seagrass bed, *Thalassia* shoot count decreased by the end of the summer ($F_{2,57}$ = 13.52, p < 0.001), while cover of drift algae increased (Kruskal-Wallis, H = 36.7, df = 2, p < 0.001).

Discussion
Bates et al. (2009) posed the coral reef ecosystem feedback hypothesis (CREF), which describes seasonal interactions between scleractinian corals/macroalgae and carbonate chemistry that enhances or suppresses calcification. On the high-
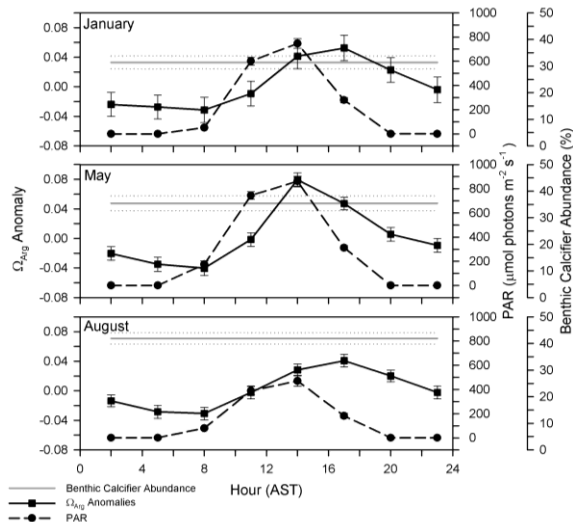
Figure 3. Monthly composite diurnal aragonite saturation state (Ω_{Arg}) anomalies (squares, solid lines) at Cayo Enrique compared to photosynthetically active radiation (PAR) values (circles, dashed lines). Abundance of benthic calcifiers (dominated by octocorals) is also shown.

latitude reefs of Bermuda, Ω_{Arg} is at a minimum during winter months, and steadily increases to an early summer maximum, closely tracked by calcification rates of reef biota (Bates et al. 2009). Much more muted seasonal dynamics in seawater carbonate chemistry were observed at Cayo Enrique relative to Bermuda (Fig. 3). While the total abundance of benthic calcifiers (dominated by octocorals) in Puerto Rico tracked the seasonal increase in Ω_{Arg} from January through April, benthic calcifiers continued to increase from May through August, becoming decoupled from decreasing Ω_{Arg} (Fig. 3). Thus, these data suggest other factors (e.g. temperature) may also exert control on benthic community structure, and do not show CREF as being an important factor driving benthic community structure in Puerto Rico. However, the monthly averaged diurnal data do show that there is an important diurnal control of carbonate mineral dynamic governed by net carbon productivity. Since changes in benthic calcifier abundance appear to have limited effect on the amplitude of this diurnal signal, we conclude that changes in carbonate chemistry at Cayo Enrique are primarily dominated by net organic carbon production, with net ecosystem calcification playing a lesser role (Fig. 3). These findings illustrate the importance of the total benthic community (i.e. octocorals and fleshy macroalgae), rather than just primary calcifiers (i.e. scleractinian corals and calcareous algae), on short-term carbon chemistry dynamics in reef ecosystems. In order to further investigate whether carbonate chemistry dynamics are driven by physical factors or geochemical feedback from reef biota, observing platforms (MA_PCO_2) data

and high-temporal and -spatial resolution CROSS measurements (e.g. McGillis et al. 2011) will be paired with high-spatial resolution benthic community data in subsequent studies.

Of the two reef sites, Cayo Enrique had higher coral cover and was more rugose, while San Cristobal had a greater abundance of fast-growing branching corals (i.e. *Acropora cervicornis*). Acroporids can deposit carbonate at a rate of an order of magnitude higher than other corals (Chave et al. 1972), and grow much faster than other Caribbean scleractinian species (Gladfelter et al. 1978). Therefore, the calcification potential, and hence the ability to modify reef water chemistry, at San Cristobal may actually be greater than that of Cayo Enrique. Previous gross primary productivity data at Cayo Enrique (122.1-173.4 mmol O_2 m^{-2} d^{-1}; McGillis et al. 2011) and San Cristobal (168.8 mmol O_2 m^{-2} d^{-1}; Rogers 1979) are comparable, though Rogers (1979) reported substantially higher coral cover (~60-70%) than was found at either of our study sites.

While the reef community at San Cristobal may have an increased ability to modify water chemistry, it may also represent a more ephemeral system. The San Cristobal *A. cervicornis* thickets suffered nearly 100% mortality during a 2005 bleaching event and are potentially subject to hurricane-induced mortality (Ballantine et al. 2008). Such disturbances may drive intra-annual variability in reef water chemistry within this system. Thus, long-term data sets of both seawater carbonate chemistry and benthic community structure data are necessary to understand the dynamic nature of reef systems that experience frequent natural disturbances.

A component of CREF is that net reef production is driven by the photosynthesis and respiration of coral/zooxanthellae and macroalgae (Bates et al. 2009). Macroalgae draw down CO_2 and elevate Ω_{Arg} (Anthony et al. 2011), improving the potential for coral calcification downstream. We observed relatively low macroalgal and turf algae cover at the Enrique and Cristobal sites—about half that reported in previous observations for nearby reefs (Kerr 2011). Given the low algal cover during this field season, seagrass beds like those at Atravesado may offer greater potential to draw down CO_2 in the La Parguera system. Seagrass beds in southwestern Puerto Rico had productivity of ~250-470 mmol O_2 m^{-2} d^{-1}, with little seasonal variability (Odum et al. 1959); those productivity rates were lower than what was reported for nearby reefs (though coral cover was likely much higher in the 1950s than today). Benthic maps of La Parguera (Kendall et al. 2001) do not show significant seagrass beds proximally upstream of the reef sites at Cayo Enrique or San Cristobal.

Acknowledgements

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