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Calcium Carbonate Production, Coral Cover and Diversity along a Distance Gradient from Stone Town: A Case Study from Zanzibar, Tanzania

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Photosymbiotic scleractinian corals are major bioengineers in tropical coastal waters, where they build structurally complex geological features and provide substrata for a manifold of macro and microhabitats. On a local scale, ecological competition and physical parameters—natural as well as human-derived, alter species richness, biodiversity, and morphological adaptation on tropical coral reefs. Here, we compared four coral reefs in the Zanzibar Archipelago at different distances from Stone Town and under different management regimes. To assess the ecological health of these reefs, calcium carbonate production, structural complexity, and α-diversity were determined. The unprotected reefs in the direct vicinity of Stone Town, which are exposed to fishing pressure, land-derived pollution, unregulated tourism, and careless anchoring, showed the lowest calcium carbonate production (8.47 ± 4.37 kg $CaCO_3$ m^{-2} yr^{-1}), coral cover ($52.4 \pm 13.9\%$), and diversity ($H' = 0.94 \pm 0.37$). Conversely, the furthest reef and marine protected area showed the highest net calcium carbonate production (16.90 ± 9.70 kg $CaCO_3$ m^{-2} yr^{-1}), coral cover ($67.4 \pm 8.7\%$), and diversity ($H' = 1.74 \pm 0.20$). In comparison to other bioregions and/or reefs of the Indian Ocean, estimates of calcium carbonate production and coral cover (>50%) were relatively high. Moreover, coral community structure differs significantly with distance from Stone Town, in that, the most homogenous reefs dominated by massive and submassive species (*Porites lobata* and *P. rus*) occurred the closest to Stone Town.

Keywords: coral reefs, structural complexity, bioerosion, zanzibar archipelago, marine biodiversity, marine protected area (MPA)

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INTRODUCTION

Globally, coastal communities depend on coral reefs as they provide vital ecosystem services such as coastal protection, food acquisition and economic activities such as tourism (Bellwood et al., 2004). However, increasing local anthropogenic (coastal development, pollution and overfishing) and global climate-related pressures greatly threaten coral reefs (McClanahan et al., 2007; Mumby and Steneck, 2008; Graham and Nash, 2013). Reefs affected by local pollution show high framework bioerosion (Edinger, 1998; Holmes et al., 2000) and low skeletal density (Highsmith, 1981), which will limit if not inhibit accumulation of $CaCO_3$ over time.

The loss of coral cover, reef structural complexity and the associated mechanics are a pressing topic, as coral reefs have declined by 50% in the last 30–50 years and it is estimated that 60% of the world's coral reef ecosystems will disappear over the next 30 years (Hoegh-Guldberg et al., 2007; Burke et al., 2011). The structural complexity of the reef is the foundation of coral reef ecosystems because the inorganic carbonate matrix supports most of the reef biomass (Grigg, 1994). A number of studies have examined the positive relationship between reef structural complexity to biodiversity, biomass and associated ecosystem services (Luckhurst and Luckhurst, 1978; Bellwood et al., 2004; Cinner et al., 2009). In contrast, few studies have examined the actual relationship between coral cover and structural complexity, which is inconsistent with coral cover being the most widespread indicator used in ecological studies for reef health assessment (Jokiel et al., 2015). Most coral reefs show an average live coral cover of no more than 30% (Vroom, 2011). For example, coral cover in the Caribbean has declined dramatically over the past 30 years, where reefs have declined from about 50 to 10% coral cover (Gardner, 2003). Coral cover in this region has been correlated with $CaCO_3$ production (Perry et al., 2012, 2015), where Caribbean reefs showed drastically negative trajectories and budgets were estimated to become negative below a threshold of approximately 10% live coral cover (Perry et al., 2013).

Tropical carbonate secreting benthic assemblages are major bioengineers and sediment producers (Graham and Nash, 2013). Collectively, reef calcifiers produce 7,250 t $CaCO_3$ km^{-2} yr^{-1}, with corals dominating carbonate production (73%) (Hart and Kench, 2007). Calcium carbonate ($CaCO_3$) produced within coral reefs accounts for more than 25% of the total $CaCO_3$ buried in marine sediments globally (Jones et al., 2015). Calcium carbonate sediments are highly important in tropical marine environments because they contribute to reef islands, sand banks and beaches (Kench and Mann, 2017). A number of physical parameters, such as wave exposure, currents and temperature, affect the development of coral reefs, its biodiversity (Roberts et al., 2002) and reef morphology (Mallela et al., 2004; Webb and Kench, 2010; Perry et al., 2013). For instance, platy coral morphologies are more successful on deep fore reef sites, due to their ability to harvest light (Todd, 2008), whereas more robust, boulder corals are generally found in the reef crest under moderate to high hydrodynamic regimes (Storlazzi et al., 2002).

Some hydrozoans, octocorals, sponges and hexacorals have the ability to modify their morphology according to the nutrient, sediment, light or energy regimes in which they occur (Kaandorp and de Kluijver, 1992; Lesser et al., 1994; Sebens et al., 1997; Kaandorp, 1999; Kim et al., 2004; Kaandorp et al., 2005; Kruszynski et al., 2007). It is because of their response to surrounding environmental constraints, that corals morphological strategies are used as bioindicators of water quality (Roberts et al., 2002; Hallock et al., 2004), ecosystem health (Veron et al., 2009), ecological value and conservation priority (Edinger and Risk, 2000). High-resolution standardized census-based datasets can provide further information on coral demography, the population dynamics affecting calcifiers' demography, abundance (Jones et al., 2015) and ecosystem functions (i.e., shelter for marine organisms, coastline protectection, nutrient fixation and cycling) (Perry et al., 2012; Ferrario et al., 2014; Jones et al., 2015). In addition, regional, high-resolution datasets are essential for the overall assessment of reef conditions in a changing ecosystem (Dubinsky and Stambler, 1996).

A range of local stressors have been reported from Zanzibar, from overfishing in Bawe Reef (Lokrantz et al., 2009), pollution in Chapwani and Prison reefs (Moynihan et al., 2012) to mechanical damage by destructive fishing methods such as dragnets (Muhando, 1998; Mohammed et al., 2001) or careless anchoring (Muhando, 1998; Mohammed et al., 2001). At the same time, Zanzibar has a rapid population growth rate (National Bureau of Statistics, 2012) closely linked to the increase in resource demand and tourist infrastructure (Lange and Jiddawi, 2009).

Here we examine coral reef intrinsic factors i.e., biodiversity and structural complexity in some reefs that have received relatively little study (Johnstone et al., 1998). The aim of our study is to assess coral reef condition and determine the effects of local human impacts on hard coral community structure along a distance gradient from Stone Town. To achieve this we aim to: (1) measure the benthic community composition and associated spatial variability, (2) examine the reef structural complexity; (3) determine the net calcium carbonate budget; and (4) use bio-indicators i.e., biodiversity indices, coral structural complexity, $CaCO_3$ production and bioerosion rates in coral reefs along an offshore gradient of increasing distance from Stone Town, in western Zanzibar.

MATERIALS AND METHODS

Study Sites

The Western Indian Ocean (WIO) region is known to support approximately 21.6% of the global tropical coral reef area (Burke et al., 2011). Of the total world coral reef coverage, 1.2% is found in Tanzania, along the East Coast of Africa (UNEP-WCMC 2011). The Zanzibar Archipelago, off continental Tanzania, consists of three major islands including Pemba in the North and Zanzibar (Unguja) and Mafia Islands to the South (**Figures 1A,B**). The Zanzibar channel acts as a physical barrier, isolating Zanzibar Archipelago from Tanzanian coastal waters (Muzuka et al., 2010) and terrigenous sediments coming from mainland river discharges (Shaghude et al., 2002). Within the region, the annual air temperature ranges between 27 and 35°C (Shaghude and Wannäs, 2000) with annual average rainfall of 1,600 mm on Zanzibar Island (Mgaya, 1997). Southwest-driven monsoonal rains and high currents occur between March to May, while low precipitation and northeastern currents are typical between November and March (Newell, 1957). ROMS models (Regional Oceanic Modeling Systems) show that the semidiurnal mesotidal regime, triggers strong tidal currents from the north and south entrance along the Zanzibar Channel, converging off of Stone Town (Lwiza and Bigendako, 1988; Mukaka, 2014).

Fringing reefs off Stone Town (**Figure 1C**), located in the western shoreline of Zanzibar Island, are exposed to sewage outfall waters that discharge into coastal waters. The main

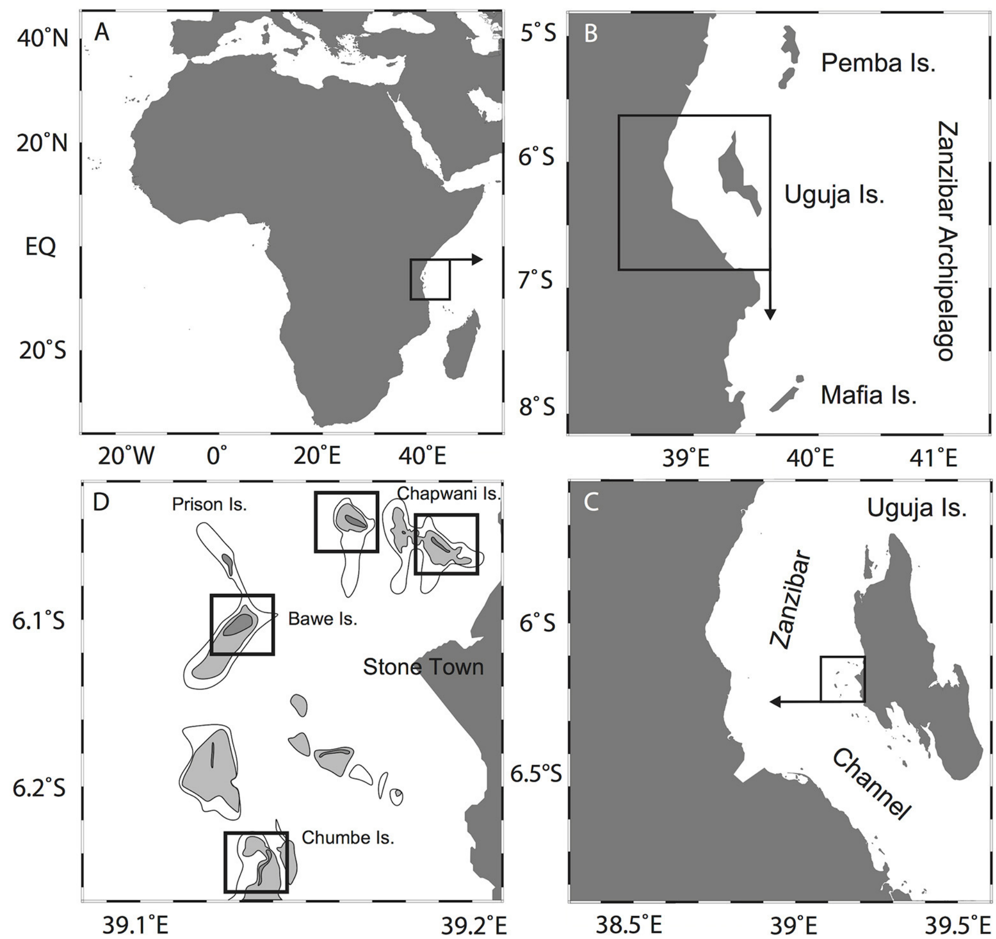

FIGURE 1 | Location of the study area showing **(A)** the African continent; **(B)** Zanzibar (Unguja) Island; **(C)** Zanzibar Archipelago, off of Stone Town; and **(D)** Zanzibar island chain and location of our study sites.

outfall, located adjacent to the Port of Stone Town, discharges an estimated 2.2×10^6 L d^{-1} of untreated sewage (Moynihan et al., 2012). Tidal currents distribute the flow of wastewater in a northward direction away from Stone Town toward three nearby reef sites that are important artisanal fishing grounds and tourist destinations (Johnstone et al., 1998; Mohammed and Mgaya, 2001; Mukaka, 2014).

Four of these fringing reefs north of Stone Town are the focus of the present study (**Figure 1D**). Chapwani Reef (6°7′35.89"S, 39°11′32.13″E), Prison Reef (6°7′7.57″S, 39°9′58.90″E), Bawe Reef (6°8′56.72″S, 39°7′57.04″E) and Chumbe Island Coral Park (CHICOP) (6°16′42.32″S, 39°10′40.29″E) are located at increasing distances from Stone Town (approx. 3, 5, 6, and 13 km, respectively). We measured the distance to the reef sites (to the reef slope) from the Institute of Marine Scienes, located adjacent to the Port of Stone Town. Bawe and Chapwani reefs possess well-developed fringing reefs along the island's north coast, whereas Prison Reef's main fringing reef faces the northwestern side of the Island. Prison and Bawe reefs are separated from Stone Town by a tidal channel (approx. 20–30 m deep) characterized by strong tidal currents (Mohammed and Mgaya, 2001). CHICOP has been an ecological sanctuary and marine protected area (MPA) since 1994. The high biodiversity and good condition of the reef in the early 90's was the motivation to privately preserve Chumbe coral reef (Nordlund et al., 2013). CHICOP is a strict no-take reef zone area, stretching along the western flank of the Island. Activities include sustainable eco-tourism and marine education among others, with a zero waste policy (Riedmiller, 1998).

Ecological Surveys

To determine the species composition and calcium carbonate production in our study sites, we applied the line intercept transect method (LIT) (English et al., 1997) and ReefBudget Method (Perry et al., 2012), respectively during a field excursion from August to October 2014. The (5 to 10 m) reef slope at each reef site was specifically chosen for being the most productive bioregion with the highest coral biodiversity and it was easily accessible from Stone Town. In addition, the reef slope is commonly studied and can be more easily compared to other reef studies (e.g., Januchowski-Hartley et al., 2017). By convention, six 10-m transects were randomly placed and independently recorded by SCUBA divers on the reef slope of each study site at shallow (5 ± 2 m) and deep (10 ± 2 m) areas, with the exception of Chapwani Reef, where transects were only recorded at 5 m, as the reef slope was bathymetrically constrained to approx. 7 m. The identification of corals was made to the genus and species level where possible, following taxonomic references (Veron, 2000, 2002; Huang et al., 2014) We also recorded the following benthic categories: coralline algae, sponge, corallimorph, others (e.g., seagrass, zoanthids, clams etc.), sub-category 1 (i.e., dead coral and rubble) and sub-category 2 (i.e., sand, mud and silt).

The relative percentage cover of each benthic category was calculated by the fraction it occupies (Xi) [cm] divided by the total transect (TL) [cm] multiplied by a factor of 100. In order to quantify the calcium carbonate production and reef structural complexity, we measured the substrata, benthic taxa and habitat, making use of a high-spatial resolution (1 cm) substrate analysis (English et al., 1997) and the ReefBudget Method (Perry et al., 2012) to the morphological level. Following the ReefBudget methodology, four morphological classes of coral were distinguished; branching, platy, massive and submasive. We applied density and calcification rates of each morphological group (Perry et al., 2012). We measured 5 (50 × 50 cm) quadrants per transect to measure boring sponge, urchin and crustose coralline algae (CCA) abundance and coverage. We used published data on boring sponge erosion rates (Scoffin et al., 1980; Perry et al., 2012) and the measured abundance to calculate the bioerosion at each location. The sea urchin bioerosion rates were calculated from the abundance data, where we measured 5 different size classes (0–20 mm, 21–40 mm, 41–60 mm, 61–80 mm, 81–100 mm) following Scoffin et al. (1980). To quantify parrotfish bioerosion rates we first measured parrotfish abundance. Secondly, we recorded 4 different size classes: 5–14 cm, 15–24 cm, 25–34 cm, 35–44 and over 45 cm. Third, we multiplied the parrotfish bite rate, the percentage of bites leaving scars and the volume of carbonate eroded per bite according to the fork size using published data (Bruggemann et al., 1994a,b, 1996; Perry et al., 2012). We assumed that the feeding behavior between Caribbean and Indian Ocean parrotfish were similar between the two regions. Thereafter, we calculated the net or total calcium carbonate production rates as a measure of gross calcium carbonate rates produced by carbonate secreting organisms, i.e., hard corals, CCA and calcifying macroalgae, minus bioerosion rates of parrotfish, sea urchin, boring sponge and micro-bioeroders.

The roughness, reef structural complexity or reef architecture, here defined as the three dimensionality property of the reef framework, was calculated as D1/D2 [m/m], where D1 is the contour measured of each substratum or feature and D2 the planar distance covered by the substratum (Hubbard et al., 1990; Harney and Fletcher, 2003; Mallela and Perry, 2006; Perry et al., 2012).

Data Analysis: Statistical Tests

To test the variance between multiple reef components (e.g., biodiversity indices, reef complexity, coral morphologies and carbonate production rates) to location, distance and depth, multiple two-way ANOVA was performed, considering all the variables. The Tukey's Honest Significant Difference (HSD) *post-hoc* tests were used to determine differences between the reefs. Multiple one-way ANOVA was used to test differences between mean coral cover values on shallow and deep zones at each location. To determine how representative the sampling method was and to validate the sampling strategy used in this study, we computed a rarefaction curve (S.2) of the abundance data using Kindt's exact method described in Oksanen (2015). The alpha diversity (biodiversity) of hard corals is given as the Shannon-Wiener Index natural log (Equation 1) and Margalef species richness (Equation 2).

$$H' = \sum_{i=1}^{S} -(Pi * LnPi) \qquad (1)$$

$$M = (S-1)/logN. \qquad (2)$$

Were Pi = proportional abundance of genera i, S = number of genus encountered, $\sum$ = sum from genus 1 to genus S, N = total counts.

All analyses were computed with R software (R Core Team, 2010). We used the following packages: Vegan (Oksanen, 2015), Companion to Applied Regression package (Fox and Weisberg, 2011), BiodiversityR (Kindt and Coe, 2005), tcltk (R Core Team, 2014), ggplot2 (Wickham, 2009) and Modern Applied Statistics with S (Venables and Ripley, 2002).

To describe the benthic beta diversity (distribution patterns of the biodiversity between sites) and to describe the community composition, we ran MDS (non-metric multidimensional scaling), ANOSIM (analysis of similarity) and SIMPER (similarity percentage) analyses on the hard coral relative abundance data (Clarke, 1993). Such analyses were computed with PRIMER-E software v.6 (Plymouth Routines In Multivariate Ecological Research).

RESULTS

Community Structure and Alpha Diversity

Our study sites showed high live coral cover (>50%). Mean live coral cover in shallow reef-slope areas (5 ± 2 m) was (Mean ± SD, $n = 6$) 52.5 ± 13.9%, 65.8 ± 10.6%, 72.7 ± 15.1% to 67.4 ± 8.8% for Chapwani, Prison, Bawe and Chumbe reefs, respectively. Deeper areas (10 ± 2 m) also show high live percentage cover; 74.5 ± 13.3, 71.5 ± 12.8, and 57.6 ± 17.9% for Prison, Bawe and Chumbe reefs, respectively. Overall, there were significant differences of live cover between depths at Prison Reef (one-way ANOVA, $F_{1-4} = 19.74$, $p = 0.011$) and Chumbe Reef (one-way ANOVA, $F_{1-4} = 10.31$, $p = 0.032$), but not at Bawe Reef ($p > 0.05$) second most abundant benthic category was dead coral and coral rubble (Sub-category 1, >12%), but at Chapwani and Prison Reef the second dominant benthic category in shallow reef-slope areas was Hexacorallia, order Corallimorpharia STEPHENSON, 1937. In total 33 hard coral taxa were observed when all transects were pooled (**Figure S1**). At Chapwani Reef 10 hard coral taxa were observed, whereas in Prison, Bawe and Chumbe reefs a total of 20, 21, and 27 taxa were observed, respectively following the most recent taxonomic revision (Huang et al., 2014). Biodiversity and richness increased southwards from Chapwani Reef to

Chumbe Reef (**Table 1**). In addition, deeper areas showed lower biodiversity than shallower areas, with the exception of Prison Reef (**Table 1**). Chumbe Reef has the highest Shannon-Wiener diversity (H' = 1.74 ± 0.20 and H' = 1.50 ± 0.25 at 5 and 10 m, respectively) and Margalef richness ($M = 2.35 \pm 0.35$ and $M = 2.01 \pm 0.40$ at 5 and 10 m, respectively). However, no significant difference in Shannon-Wiener diversity or Margalef richness indices were found between reefs and depths [two-way ANOVA, $F_{(3, 35)} = 2.324$, $p = 0.0918$].

Chapwani, Prison and Bawe reefs were dominated by *Porites rus* FORSKÅL, 1775, accounting for 50.7, 40.8, and 47.4% of the relative abundance, respectively (**Table S1**). *Galaxea* spp. OKEN, 1815 was the second most abundant taxon at Prison Reef and third most abundant taxon at Bawe Reef (S.1). The relatively high abundance of *Pocillopora* spp. at Bawe (6.4%) and Chapwani (6%) was similar between the two reefs. Branching coral *Acropora* spp. OKEN, 1815 was the most abundant coral taxa in Chumbe Reef, accounting for 31.6% of the total relative abundance. *Porites lobata*, *Acropora* spp. and *P. rus* along with *Seriatopora* sp. and *Fungia* spp. were found in the shallow reef areas, whereas *Galaxea* spp., *Pocillopora* spp. and *Porites cylindrica* were found generally in deeper reef areas (**Table S1**). No significant differences were found between shallow and deeper communities (55.77%).

At transect-scale we identified five distinct benthic goups (**Figure 2A**). The hard coral community composition in all locations has at least 20% percent overlap (Bray-Curtis dissimilarity matrix) (**Figure 2**). Groups 1 and 2 were characterized by *P. rus, Galaxea* spp. and *P. cylindrica* as dominant taxa. Group 3 was the cluster which included a diverse range of species (*Seriatopora* and *Pocillopora*) from all locations. This group shared the occurrence of a large range of coral genera, without a clear dominant taxon. Groups 4 and 5 were dominated by *Acropora* spp. and large *Millepora* spp. colonies. Overall, in Chumbe Reef, extensive *Acropora* spp. fields and distinctive coral species drove dissimilarities in benthic community composition between the reefs (**Figure 2**).

Morphological Strategies and Reef Structural Complexity

At all locations, platy corals were the least common morphotype (**Figure 3**). In Chapwani Reef this class was completely absent, whereas in Prison Reef small *Montipora* sp. and platy morphotypes of *P. rus* were recorded (**Figure 4**). Pooled data show that platy coral coverage in Prison Reef was relatively low (1.05%) compared to other reefs where platy corals had the most cover, for example in Bawe Reef (4.6%) and Chumbe Reef (5.2%). Massive and submassive corals were the most abundant morphotypes among the reefs (**Figure 3**), with the exception of Chumbe reef where we found high branching coral percentage cover (47.7%).

We found significant spatial differences in hard coral morphological strategies between reefs (**Figure 3**). Among all sites, we found high abundance and large colonies (>1 m diameter) of massive corals *Porites* spp. Strong spatial distribution differences were recorded for submassive and branching corals, $F_{3\text{-}38} = 16.04$, $p =$ 6.79e-07; $F_{3\text{-}38} = 7.197$, $p = 0.00061$, respectively (**Figures 3**, **4**).

TABLE 1 | Comparative table showing the mean and standard deviation and range in values for the Shannon-Wiener biodiversity index and Margalef richness.

Location	(Mean ± SD)			
	Shannon (ln)	Margalef	Range (H′)	Range (M)
Prison 5 m	1.16 ± 0.44	1.42 ± 0.72	0.63–1.76	0.69–2.73
Prison 10 m	1.39 ± 0.47	1.84 ± 0.86	0.98–2.16	1.11–3.24
Bawe 5 m	1.17 ± 0.33	1.55 ± 0.56	0.72–1.64	0.80–2.52
Bawe 10 m	1.07 ± 0.33	1.39 ± 0.45	0.82–1.38	0.86–1.89
Chumbe 5 m	1.74 ± 0.20	2.34 ± 0.49	1.47–2.04	1.55–2.95
Chumbe 10 m	2.01 ± 0.40	1.84 ± 0.86	1.51–2.58	1.13–2.27
Chapwani	1.46 ± 0.64	1.14 ± 0.46	0.43–2.65	0.43–1.89

Reef structural complexity or reef rugosity ranged from 1.18 to 1.51. Among all reefs, structural complexity was slightly higher at shallower rather than deeper areas of the reef slope. With the exception of Prison Reef, which presents higher reef complexity in deeper areas (1.47 ± 0.33 at 5 ± 2 m and 1.51 ± 0.24 at 10 ± 2 m). Prison Reef shows the highest reef structural complexity followed by Chumbe, Bawe, and Chapwani reefs (1.38 ± 0.12, 1.35 ± 0.48, and 1.22 ± 0.28, respectively at 5 m; **Table 2**). However, the reef complexity was not significantly different by location and by depth [$F_{(3, 35)} = 1.763$, $p = 0.172$].

Bioeroders

Corallivores were the major biogenic group (**Table 3**). A large variability of parrotfish bioerosion rates was recorded between and within reefs, which ranged from (0.44 ± 0.8 to 4.97 ± 8.00 kg $CaCO_3$ m^{-2} yr^{-1}). We surveyed parrotfish presence, sea urchin abundance and boring sponge (**Figure S2**) density. The relatively high sponge abundance and cover found at Bawe (2.52 ± 3.61%) and Prison (2.52 ± 3.02%) reefs contrasts with the relatively low sponge coverage found at Chumbe (1.30 ± 1.84%) (**Figure 5**) and Chapwani (1.05 ± 1.80%) reefs. There were no significant differences between calculated bioerosion rates of boring sponge in Prison and Bawe reef, which show similar bioerosion rates; 0.46 ± 0.19 and 0.46 ± 0.19 kg $CaCO_3$ m^{-2} yr^{-1}, respectively. However, Chapwani Reef presents very low coverage and thus erosion from boring sponge (0.02 ± 0.01 kg $CaCO_3$ m^{-2} yr^{-1}; **Figure 5**, **Table 3**). Conversely, Chapwani Reef showed very high sea urchin abundance and bioerosion rates (1.33 ± 0.18 kg $CaCO_3$ m^{-2} yr^{-1}), which were significantly different from sea urchin abundance and bioerosion rates in Prison ($p < 0.001$), Bawe ($p < 0.001$) and Chumbe reefs ($p < 0.001$) (**Figure 5**). Micro-bioerosion rates (<0.0001 kg m^{-2} yr^{-1}) are very low when compared to the rates calculated for macro-bioeroders on a reef-scale (**Figure 5**).

Calcium Carbonate Production

Along the western coast of Zanzibar the main carbonate producers are photosynthetic hermatypic corals. We calculated little carbonate production from crustose coralline algae (CCA)

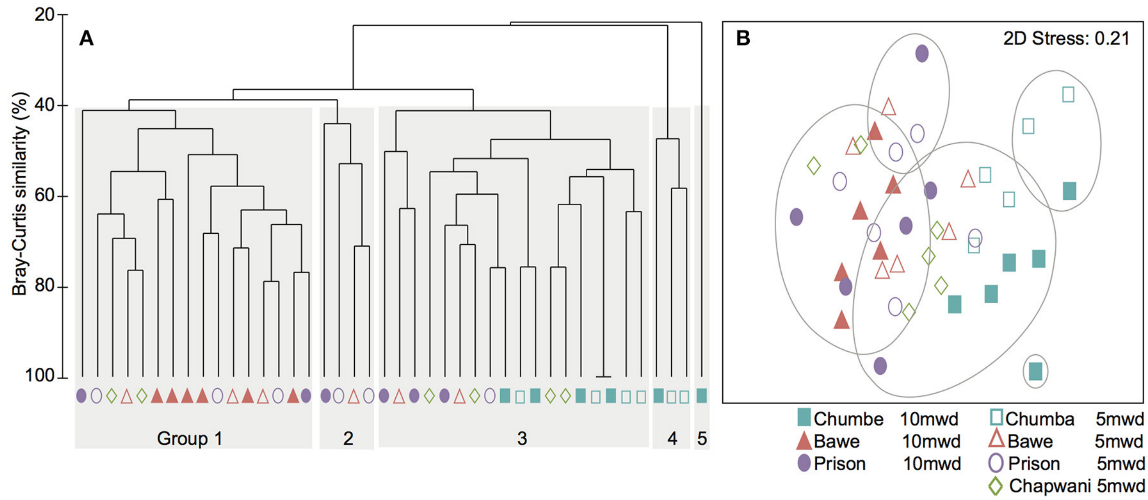

FIGURE 2 | (A) Cluster analysis showing the different groups according to the hard coral composition analysis. **(B)** The MDS ordination plot of the coral abundance data.

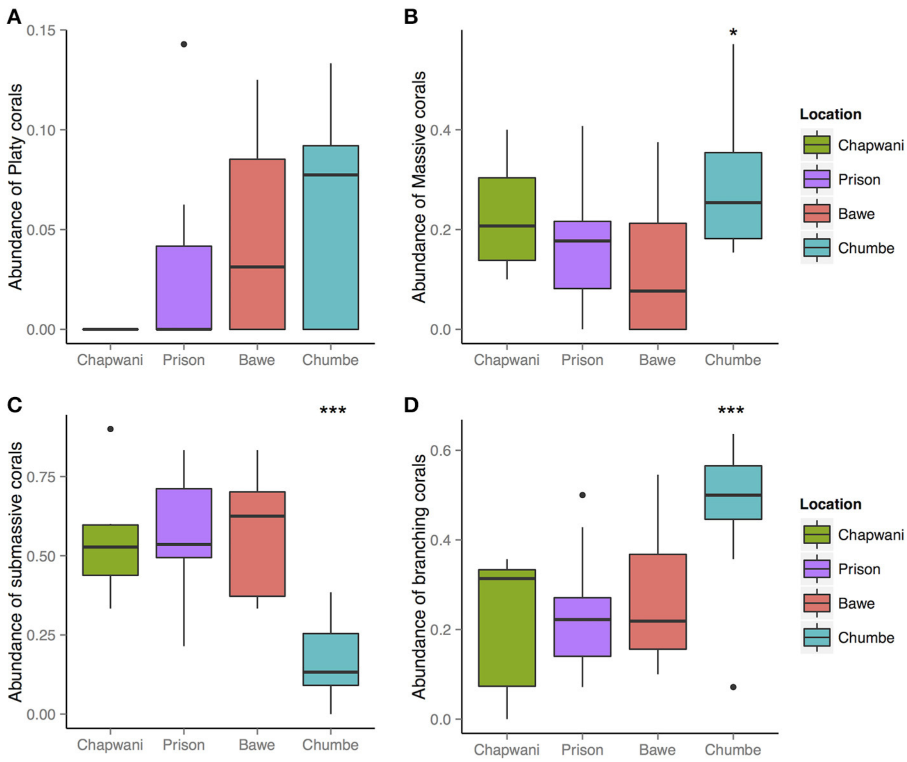

FIGURE 3 | Overview of the hard coral morphological categories: **(A)** platy; **(B)** massive; **(C)** submassive; and **(D)** branching corals. An analysis of variance showed significant differences between the massive, submassive, and branching coral morphologies $F_{3\text{-}38} = 4.257$, $p = 0.0109^{*}$; $F_{3\text{-}38} = 16.04$ 6.79e-07***; and $F_{3\text{-}38} = 7.197$, $p = 0.00061^{***}$, respectively. However, the distribution of platy corals do not show strong spatial differences $F_{3\text{-}38} = 2.444$, $p = 0.078$.

and almost no carbonate production from calcifying algae. The reef with the highest CCA percentage cover was Chumbe Reef (approx. 2%). Negligible occurrence was recorded on the other reefs (<0.05%).

Our study sites scored consistently high gross calcium carbonate production rates, 10.7 ± 4.09, 10.43 ± 2.37, 15.03 ± 7.76, and 18.95 ± 9.70 kg $CaCO_3$ m^{-2} yr^{-1}, at Chapwani, Prison, Bawe and Chumbe, respectively. The results showed that the

FIGURE 4 | Representative quadrants (0.5 × 0.5 m) taken on **(A)** Chapwani (*Porites rus*); **(B)** Prison (*Porites rus*); **(C)** Bawe (*Callyspongia* spp., *Pocillopora* spp., *Montipora* spp.) and **(D)** Chumbe (*Porites lobata, Acropora* spp., *Seriatopora* spp., *Montipora* spp., *Porites cylindrica*, and *Ctenactis* spp.) reef.

TABLE 2 | Comparative table showing the reef structural complexity or rugosity measured at the study sites.

Location	Complexity Mean ± SD	Depth (m)
Prison	1.47 ± 0.33	5
Prison	1.51 ± 0.24	10
Bawe	1.35 ± 0.48	5
Bawe	1.18 ± 0.13	10
Chumbe	1.38 ± 0.12	5
Chumbe	1.34 ± 0.23	10
Chapwani	1.22 ± 0.28	5

gross calcium carbonate production increased with distance from Stone Town (**Figure 6**) and was significantly different between reef sites [$F_{(3, 35)} = 3.459$, $p = 0.027$], but carbonate budgets were not significantly different when shallow and deep areas were compared [$F_{(1, 35)} = 0.066$, $p = 0.799$]. When we compared one to one gross calcium carbonate production rates, Chumbe Reef production differed significantly from the production recorded in Prison Reef and Chapwani Reef ($p = 0.004$ and $p = 0.020$, respectively). However, when we compared production rates found in Bawe Reef to those found in Chumbe or Prison reefs we did not see significant differences ($p = 0.161$ and $p = 0.114$, respectively).

Our study sites show high net calcium carbonate production rates (Gross production rates − bioerosion rates) ranging from 8.03 ± 4.37 to 16.90 ± 9.70 kg $CaCO_3$ m^{-2} yr^{-1}. The $CaCO_3$ production was positively correlated to biodiversity ($p = 0.010$) (**Figure 7**) and increases with increasing distance to Stone Town ($p = 0.003$) (**Figure 6**). Chapwani, Prison and Bawe reefs dominated by massive and submassive species show high net carbonate production rates 8.03 ± 4.37; 9.8 ± 2.4 and 14.11 ± 7.36 kg $CaCO_3$ m^{-2} yr^{-1}, respectively. However, the no-take zone of Chumbe Reef, dominated by branching ramose *Acropora* spp. shows the largest net calcium carbonate production (**Figure 8**).

DISCUSSION

Community Composition

Chronic stress has conspicuous consequences for coral reef community structure, recovery and resilience (Nyström and Folke, 2001) and can be exacerbated by compounding local pressures including nutrients, sedimentation, and temperature anomalies. Previous studies have suggested that nutrient levels primarily control coral community structure (Fabricius, 2005; Lapointe et al., 2011), however, nutrient variability is high and concentrations are low in western Zanzibar reefs (Narayan et al., in review). Regular boat traffic is a possible cause of sediment resuspension observed on the shallow reef areas (based on field observations) at Chapwani Reef. Additionally, recent temperature anomalies have seen massive die backs since the 1998 bleaching event throughout the Zanzibar Archipelago (Muhando and Lanshammar, 2008). The proximity to source pollution could have a significant influence on the current community structure and future resilience to local and global stresses.

The community composition of corals found on the reefs adjacent to Stone Town are depauperate and dominated by *P. rus*. This could be related to local stressors, i.e., land-based pollution and unregulated tourism (Moynihan et al., 2012). Chapwani Reef showed the lowest coral cover (52.4 ± 13.9%), biodiversity (H' = 1.2 ± 0.5) and calcium carbonate production (8.5 ± 4.4 kg $CaCO_3$ m^{-2} yr^{-1}). In addition, Chapwani Reef showed low CCA relative abundance (<0.05%), which is known to limit coral larvae settlement (Vermeij et al., 2011), reef calcification (Fabricius and De'ath, 2001), and overall coral reef recovery. Low CCA abundance has been reported at Chapwani and Prison

TABLE 3 | Key biogenic groups and microboring bioerosion rates.

Bioerosion rates [kgCaCO$_3$/m^2/yr]	Prison 5 m	Prison 10 m	Bawe 5 m	Bawe 10 m	Chumbe 5 m	Chumbe 10 m	Chapwani
Sp. Bioerosion	0.63 ± 0.81	0.46 ± 0.19	0.39 ± 0.23	0.45 ± 0.29	0.13 ± 0.05	0.47 ± 1.88	0.02 ± 0.01
Urchin Bioerosion	0.03 ± 0.04	0.03 ± 0.05	0.76 ± 0.61	0.14 ± 0.16	0.00	0.00	1.33 ± 0.18
Microbioeroders	0.04 ± 0.04	0.02 ± 0.03	0.04 ± 0.04	0.03 ± 0.02	0.05 ± 0.01	0.06 ± 0.02	0.10 ± 0.03
Parrot bioerosion	0.55 ± 1.75		4.97 ± 8.00		1.80 ± 3.04		0.44 ± 0.80

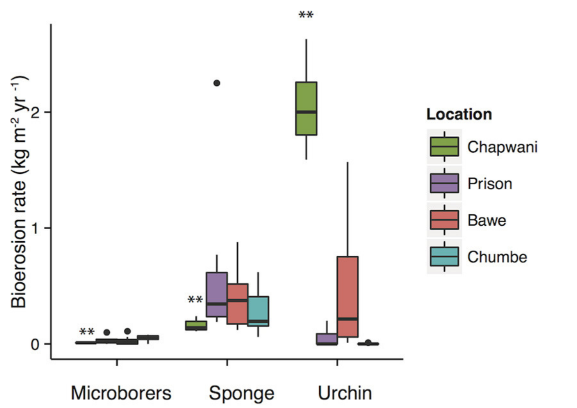

FIGURE 5 | Boxplots showing the bioerosion rates calculated for the different biogenic groups. The locations include Chapwani (green), Prison (purple), Bawe (red), and Chumbe (blue). **p-values < 0.05.

reefs (Szmant, 2002), which is consistent with our findings. CCA and stony coral demography are usually closely linked as those organisms require similar environmental conditions. Therefore the abundance and occurrence of CCA is commonly used as a bioindicator for water quality in coral reef studies (Vermeij et al., 2011). In addition, the impoverished benthic diversity on those reefs, indicate suboptimal (e.g., turbid or polluted waters) coral reef conditions (Szmant, 2002) and/or high sediment stress (Fabricius and De'ath, 2001).

In 1998 and 2005 Chumbe Reef was heavily affected by bleaching events (Muhando and Lanshammar, 2008). In 1998, 90% of the branching corals (mainly *P. cylindrica* and *Acropora* spp.) were affected and 50% of them were reported dead (Muhando, 1999; Mohammed et al., 2001; Muhando and Lanshammar, 2008). In 2005, shallow *Acropora* fields were also strongly impacted, consistent with reports that *Acropora* spp. are less resistant to bleaching (McClanahan et al., 2007). However, in a few years corals recovered their functionality and community structure at Chumbe Reef (McClanahan et al., 2007). In contrast limited recovery was generally found after the 1998 bleaching event on heavily exploited reefs globally which were subjected to fishing pressures and/or pollution (Wilkinson, 2008). Unfortunately, we cannot establish the recovery level at Chapwani, Prison and Bawe reefs after the 1999 and 2005 bleaching events as there is no information about reefs in the Zanzibar Archipelago other than Chumbe for this period of time.

The morphological plasticity of *P. rus* may favor the dominance of this particular coral species in Chapwani Reef, Prison Reef and to a certain extent at Bawe Reef (**Figures 3**, **4**). This coral species has been found in its submassive, branching, and platy forms in all three locations. We suspect that this coral species is highly resilient and therefore dominant in the reefs close to Stone Town. Presumably, corals adjust their skeletal shape to the main constraining environmental factors that control morphological specialization in corals, e.g., light intensity, water movement and sedimentation rates (Todd, 2008). Furthermore, our findings suggest that this mechanism drives beta diversity in our study sites as we found small scale (colony level) differences in the morphological strategies among sites (**Figure 3**). All study sites are protected from swells (Shaghude et al., 2002) and tides have an equal effect on all the study sites. Tidal-induced currents although energetic (5 to 20 cm s^{-1}), would not mechanically break corals, in contrast to wave-exposed coral reefs (Todd, 2008).

Chumbe Reef showed the highest biodiversity values (H' = 1.74 ± 0.20) whereas Chapwani and Prison reefs scored consistently low (H' = 0.94 ± 0.37) to medium (H' = 1.16 ± 0.44) biodiversity values when compared to other studies. We did not find a clear relationship between coral cover and structural complexity, which could be explained by the high coral cover measured when specific genera were dominant. For example on shallow *Acropora* spp. fields in Chumbe Reef or *P. rus* dominated fore reefs (at Prison and Chapwani reefs), the structural complexity remained low. However, we found that the roughness significantly increased with α-diversity. This was the case in Bawe Reef, where reef complexity was strongly correlated to biodiversity metrics ($p = 0.0005$).

We propose the use of biodiversity indices instead of live percentage coral cover or structural complexity (discussed above) as a discrete proxy for ecosystem health in the Western Indian Ocean. High coral cover favored by benthic ecological competition due to limited substrate availability has been reported from some locations with turbid waters. Similar results were found in nearshore reefs at the GBR, where hard coral cover was two times higher than mid- and outer-shelf reefs (Morgan et al., 2016). However, biodiversity indices gave us a finer overview; consistent with other studies reporting reduced biodiversity values close to highly populated cities in the coral triangle (Edinger et al., 1998).

Overall, the reefs studied showed moderate to excellent health; outstanding reef condition was estimated in Chumbe Reef and proved to be in agreement with other studies (McClanahan et al., 2007). $CaCO_3$ values (16.90 ± 9.70 kg $CaCO_3$ m^{-2} yr^{-1}), coral cover (67.37 ± 8.76%), reef structural complexity (1.36 ± 0.17) and medium-high biodiversity (H' = 1.74 ± 0.20 and H' = 1.50

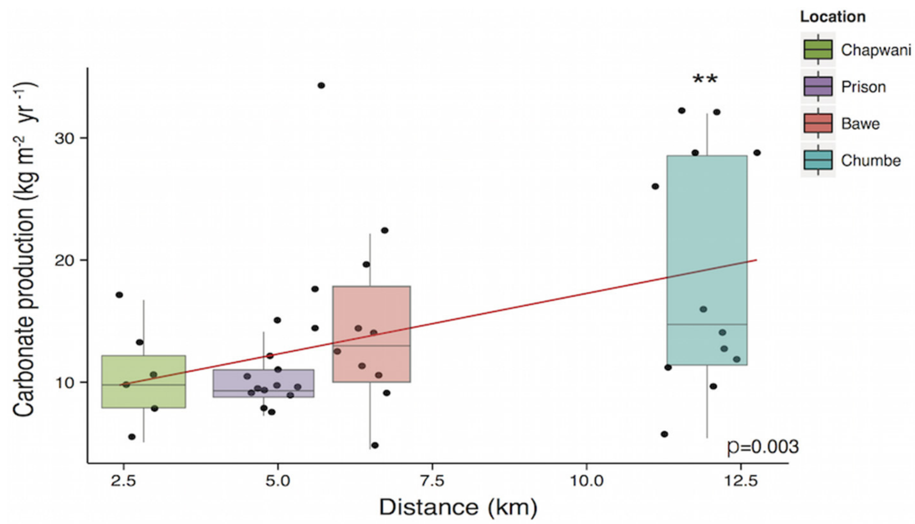

FIGURE 6 | Boxplot showing the gross calcium carbonate production per reef at 5 and 10 m. The linear regression model shows the correlation between the calcium carbonate production and distance to Stone Town. **p-values < 0.05.

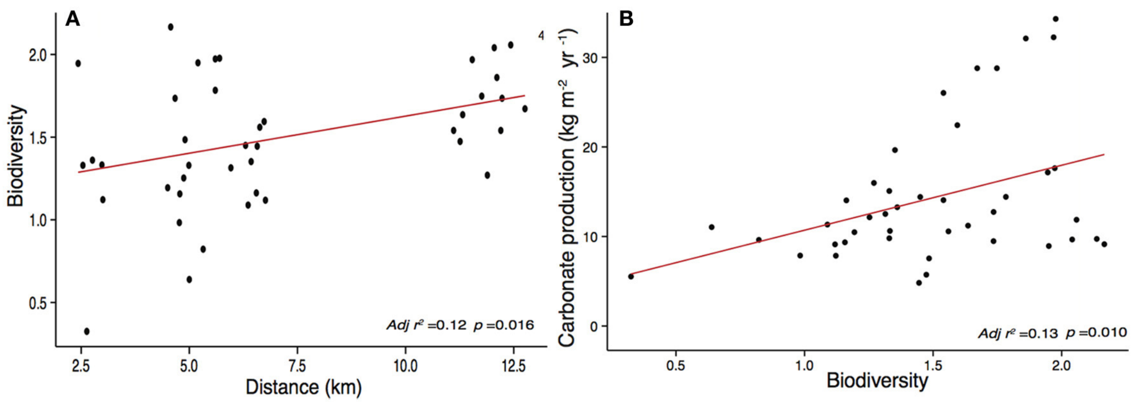

FIGURE 7 | Linear regression model showing the significant relationship ($p < 0.05$) between **(A)** biodiversity and distance to Stone Town and **(B)** calcium carbonate production and Shannon -Wiener biodiversity index.

± 0.24 at 5 and 10 m, respectively) and richness ($M = 2.3 \pm 0.41$) could be used as reference outer shelf coral reefs in the Western Indian Ocean. For example, Madang lagoon in Papua New Guinea is considered to have medium-high biodiversity (H' = 1.11), whereas Bunaken National Park, Indonesia has high biodiversity (H' = 1.65) (Fuad, 2010) and high coral cover (46%), and biodiversity values that are similar to CHICOP.

Calcium Carbonate Production and Reef Complexity

The model used to quantify calcium carbonate production gave us a good overview of the different biogenic groups crucial to produce, maintain and shape coral reef framework. We were able to quantify and assess the main community composition and compare them with global reefs by using keystone (i.e., sea urchin and parrotfish) species as ecological bio-indicators. Overall, we found a strong gradient that explained the calcium carbonate production in relation to distance to Stone Town (**Figure 7**). When compared to global carbonate budgets, Zanzibar's carbonate reefs are very productive (**Figure 8**; >8 kg $CaCO_3$ m^{-2} yr^{-1}). Among the reefs examined by this study, CHICOP (Chumbe Island Coral Park) marine protected area (MPA) stands out with high live percentage coral cover and a high calcium carbonate production rate (16.95 kg $CaCO_3$ m^{-2} yr^{-1}). Similar production rates have been reported within Caribbean MPAs. Bonaire, for instance, scored 16.68 kg $CaCO_3$ m^{-2} yr^{-1} (**Figure 8**).

Ecological interactions and ultimately bioerosion are key processes which shape reef geomorphology (Mallela et al., 2004). The classification and quantification of bioeroders has been discussed in the literature (Highsmith, 1981; Hutchings, 1986; Edinger et al., 2000; Holmes et al., 2000; Glynn and Manzello, 2015). We primarily measured parrotfish, urchins

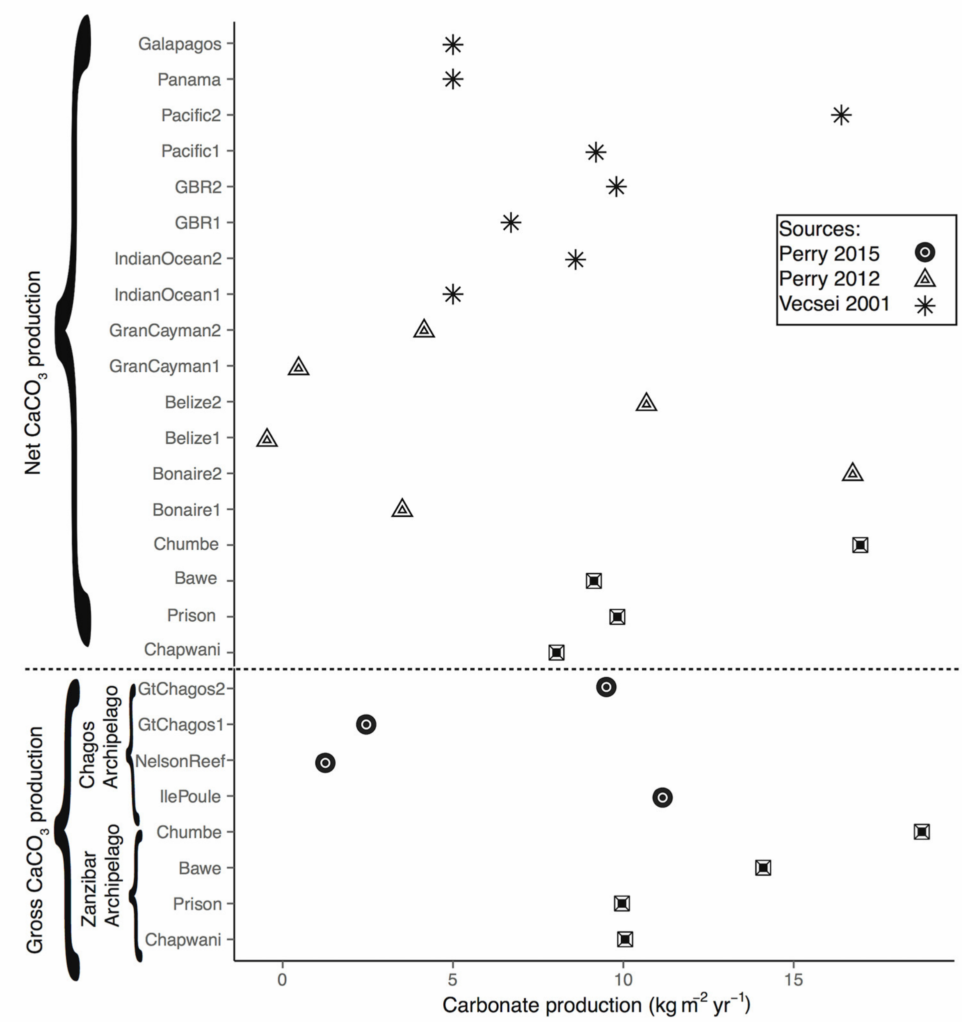

FIGURE 8 | Global comparison showing the $CaCO_3$ production at different locations. Filled dots present the gross calcium carbonate production in our study sites, squares show the gross calcium carbonate at Chagos Archipelago, as presented *sensu* (Perry et al., 2015), triangles shows the net calcium carbonate according to Perry et al. (2012) The numbering 1 and 2 indicate the minimum and maximum value. Asterisks represent the source Vecsei (2001). The numbering 1 and 2 indicate, either low or high ramose corals.

and boring sponges as they strongly affect reef community structure (**Figure S2**) and reef structural complexity (Mumby et al., 2006; Graham and Nash, 2013). We also estimated the effect of microborers, but when compared to sea urchins and corallivorous fishes, their effect was negligible. Prison Reef showed higher structural complexity than Bawe Reef, which suggests greater reef maturity (Graham and Nash, 2013). However, we observed that relatively high bioerosion and/or poorly cemented framework could lead to high structural complexity though the break-down and disintegration of the reef framework at Prison Reef (**Figure S3**). Therefore, crude measurements of structural complexity might lead to misleading ecosystem health interpretations since we associate high structural complexities to healthy and functional reefs (Graham and Nash, 2013).

In addition, Zanzibar's fringing reefs are spatially constrained to areas that were previously colonized by hard corals since hard surfaces are necessary for settlement of coral larvae (Wolanski et al., 2003; Fabricius, 2005). Thus, due to reduced recruitment, reef expansion in turbid settings takes place through the break-down and collapse of the fore-reef flank (Tudhope and Scoffin, 1994). Yet, initial disturbances causing coral mortality do not necessarily affect reef structure immediately (Graham et al., 2009). In the years that follow major coral mortality, the reef complexity will potentially deteriorate. For example, structural changes after the 1998 bleaching event happened in a time spam of 5–6 years (Graham et al., 2006, 2009).

MPA Relevance and Implication for Management

Zanzibar has shown rapid population growth rates (National Bureau of Statistics, 2012), an increase of tourist infrastructures (Jiddawi and Ohman, 2002) and coastal development in the past decade. Coastal development in particular affects water quality by increasing turbidity and the sediment load in the water column (Mumby et al., 2006) and has been well established to have a direct effect on coral community structure (Fabricius, 2005). Chapwani and Prison already show signs of pollution (Moynihan et al., 2012) and destructive fishing such as dragnets (Muhando, 1998; Mohammed and Mgaya, 2001) have been reported. Both natural and anthropogenic stressors including sedimentation stress, thermal stress, storm damage and overfishing, are constantly affecting reef health and community structure (Dubinsky and Stambler, 1996; Hatcher, 1997; Szmant, 2002).

Our results strongly demonstrate that α-diversity is negatively correlated with the proximity to Stone Town. In addition, the overall reef condition and the calcium carbonate production show a negative correlation with increasing distance from Stone Town. Differences in reef condition between sites suggest that previously described human pressures have an impact on Zanzibar's reefs. Furthermore, reef-scape degradation (loss of three-dimensional coral architecture, live coral cover and aesthetics) could have slow-to-reverse effects on Zanzibar's economy. Strategic conservation measures like boat moorings or wastewater treatment plants would improve prospects for resilience by the reduction of anchor damage and reduction of particulate suspended solids, which in turn would maximize coral reef ecosystem functioning.

When protected versus unprotected reefs were compared, the CHICOP conservation area was suggested in the literature to be effective in preventing impacts from local human pressures on the reefs (Johnstone et al., 1998; Lokrantz et al., 2009). The hard coral community structure on CHICOP was consistently different to the community found at unprotected reefs. First of all, the biodiversity in CHICOP was higher than in the other study sites. Also, the branching coral genera that have high conservation value according to Edinger and Risk (2000), occurred in CHICOP. Secondly, CHICOP showed very high calcium carbonate production values when compared globally. Lastly, the conservation area showed a high percentage coral cover and a complex reef architecture. Nevertheless, whether or not these differences in biodiversity, coral cover and reef condition were driven by natural-local environmental factors and/or the current conservation efforts remains unclear because the distance from Stown Town work as a confounding factor given that there is no studies on reef status previous to the establishment of the MPA at Chumbe Reef. A better understanding of coral reef trajectories in the Zanzibar Archipelago could help provide information on the effect and effectiveness of protected areas on reef functionality and overall reef condition.

Nonetheless, all indices of reef condition indicate that remediation and protection efforts are likely to succeed on Prison Reef and Bawe Reef. Prison Island is one of the key sites for the tourism industry in the vicinity of Stone Town. For this reason, the protection of the reef should receive the highest conservation priority. We propose the implementation of measures that avoid mechanical damage (e.g., careless anchoring, tourists walking on the reef flat). Moreover, conservation measures should account for the subsistence needs of local people. Bawe Reef is an important fishing ground for local communities, because its intertidal platform provides women and children an area to harvest small invertebrates (Fröcklin et al., 2014), whereas fishermen use fishing-nets close to the reef. In addition, the easy access and location close to the main trade market makes this location attractive for seasonal fishermen (Jiddawi and Ohman, 2002). Therefore, the conservation effort should be in concordance to local community needs. It should reinforce reef functioning by following a two-dimensional approach (ecological and social).

The healthy reef condition indicated by the ecological and structural traits examined in this study, reinforce the importance of functionality of the ecosystem and the capacity to cope with natural and human-induced disturbances. Reef associated human activities, such as fisheries and tourism, substantially affect reef condition, development and health (Souter and Lindén, 2000). The negative effect of these activities is excluded in CHICOP, where we see a resilient reef ecosystem due to the functional biodiversity and the calcium carbonate budget. Large branching *Acropora* fields and large massive coral colonies found in CHICOP are fundamental in resilient carbonate budgets (Januchowski-Hartley et al., 2017). However, other human induced-disturbances such as the potential effect of untreated wastewater remain unclear. Such factors are extremely relevant because MPAs are, in most cases, unable to protect coral reef ecosystems from poor water quality. A better understanding of the biogeochemical properties of the water column, such as the seasonal variability or is crucial in constraining the environmental factors that control benthic assemblages.

AUTHOR CONTRIBUTIONS

HW conceived the project; NH, GN, and CR collected the field data, performed the statistical analyses and drafted the figures. NH, GN, CR, and HW wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2017.00412/full#supplementary-material

Table S1 | Rank abundance raw data from the different taxon's encounter in our study sites.

Figure S1 | Sampling effort: illustration of the abundance-based functional rarefaction. The solid line represents the mean cumulative values and the gray area its associated confidence interval.

Figure S2 | Bioerosion by encrustation and excavation of an aggressive and unclassified boring sponge on a massive coral at Prison Reef.

Figure S3 | Collapse and fall of large coral colonies at Prison Reef.

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