



New rates of Indian Ocean carbonate production by encrusting coral reef calcifiers: Periodic expansions following disturbance influence reef-building and recovery



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ABSTRACT

Encrusting marine calcifying organisms, including coralline algae, bryozoans, calcareous worms, foraminifera and oysters, contribute to the geological development of reefs by precipitating calcium carbonate that binds detrital sediment and coral framework, and may produce new sediment after their death. However, it is difficult to quantify the relative importance of encrusting communities within contemporary reef carbonate production budgets because of a lack of regional datasets of either encrusting calcification or diversity, and the factors that control their settlement and growth. Here, we report rates of encrusting carbonate production for the Maldives in the Indian Ocean, determined by deploying artificial settlement substrates in shallow-water reef sites for 13 months. Eight taxonomic groups are identified with high average rates of net calcification (mean = $0.056 \pm 0.02 \text{ g cm}^{-2} \text{ yr}^{-1}$). Encrusting communities vary between exposed (upwards-facing) and cryptic (downwards-facing) reef habitats ($p < 0.05$), driving inter-habitat differences in carbonate production rates (median cryptic = $0.066 \text{ g cm}^{-2} \text{ yr}^{-1}$; median exposed = $0.042 \text{ g cm}^{-2} \text{ yr}^{-1}$). These changes are a function of differences in light availability, grazing pressure, and wave exposure reflecting reversing monsoon conditions. Non-geniculate coralline algae are the dominant encrusting group (~50% cover) and major contributors to net calcification. The rapid expansion of coralline algae on post-mortem coral frameworks following the 2016 mass bleaching event in the Maldives has important implications for short-term carbonate cycling and reef budgetary states (pre-bleaching encrusting production = $0.24 \text{ kg m}^{-2} \text{ yr}^{-1}$; post-bleaching = $0.40 \text{ kg m}^{-2} \text{ yr}^{-1}$). Our findings suggest that encrusting communities add meaningful quantities of carbonate to reefs, and that their increased expression following declines in coral health could offset negative budgets on reefs where bioerosion rates are low, and aid future reef recovery by facilitating coral settlement.

1. Introduction

The health of coral reefs is in global decline as a consequence of multiple stressors, including coral disease, increased storm activity, coral bleaching, pollution and eutrophication, and elevated sedimentation (Bruno and Selig, 2007; De'ath et al., 2012). Degraded reef states are typically associated with reduced coral cover, depleting the key framework-building taxon. This results in low habitat diversity and structural complexity (Alvarez-Filip et al., 2009), but also the removal of the major producers of calcium carbonate on reefs (Perry et al., 2013). Encrusting calcifiers, which include coralline algae, bryozoans, serpulid and vermetid worms, foraminifera and oysters, collectively referred to as “sclerobionts” (sensu Taylor and Wilson, 2003), perform an important function on reefs by precipitating calcium carbonate and

contributing to the reef structure. In areas of ecological disturbance, or within reef habitats unsuitable for coral growth (e.g., with high wave energy or long periods of sub-aerial exposure), rates of carbonate production by encrusting communities may exceed those of some coral species to become dominant drivers of reef calcification and/or sediment production (Adey, 1998; Yamano et al., 2000).

The capacity of encrusting taxa to rapidly colonize reef substrates and coral surfaces after disturbance (Kuffner et al., 2008; Mallela et al., 2017), particularly following periods of ecological stress or coral die-off (e.g., Perry and Morgan, 2017), means that they can contribute significant volumes of carbonate that will be preserved in the fossil record (Adey, 1998; Gischler et al., 2008; Hubbard, 2005; Martindale, 1992). The proportion of carbonate produced by encrusting taxa varies between reef zones, and also in response to changes in benthic community

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structure through time (Esteban, 1996). However, quantifying the relative contributions of encrusting species to gross calcification in contemporary reefs remains difficult. The few existing datasets have mostly examined atypical reefs, either in high-latitudes (e.g., Japan: Matsuda, 1989), or in areas in which large-scale changes to water quality and reef condition have already occurred (e.g., the Caribbean: Bak, 1976; Kuffner et al., 2013; Mallela, 2007). Thus, rates determined in these areas may not be directly applicable to more remote oceanic settings with different environmental conditions. Rates of calcification by encrusting species in relatively optimal reef settings (i.e., shallow-water equatorial reefs), and data on how these vary across individual platforms, are sparsely described but are critical parameters underlying models of reef growth potential and carbonate production budgets for such reefs.

Encrusting community compositions and calcification rates in contrasting reef habitats across a broad geographic range are needed because they underpin ecological processes at a very basic level. In order to generate estimates of encrusting calcification artificial settlement substrates have been deployed over periods of 12–36 months, (Bak, 1976; Hubbard et al., 1990; Kuffner et al., 2008; Mallela, 2013, 2007; Mallela et al., 2017; Matsuda, 1989). These studies have highlighted how changes in both the diversity of encrusting forms and the rates at which they calcify may change across environmental gradients. Environmental factors include wave forcing, light attenuation, substrate type and roughness, substrate orientation, and pressure from grazing, which interact to influence both organism settlement and survivorship. These are seen at a range of scales; between reefs exposed to different fluvial/terrestrial suspended sediment concentrations (Fabricius and De'ath, 2001; Mallela, 2007), or as a result of differences in the microtopography, colour, or material type of settlement surfaces (Mallela et al., 2017; Mason et al., 2011).

Here we have used artificial settlement substrates deployed over a 13 month period to determine encrusting community composition and net carbonate production for shallow-water reefs in the Maldives, Indian Ocean. Importantly, we examine the factors that may drive intra-reef variability in encrusting calcification; specifically, habitat type (from exposed- and cryptically-orientated substrates), and wave exposure (reef aspect). Our findings provide a novel regional data set for the Indian Ocean that suggests net calcification by encrusting organisms, especially calcareous algae, is rapid. However, rates of production may vary as a function of changing light intensity and grazing pressure on substrates, and to a lesser extent with variations in turbulence, reflecting reversals in seasonal monsoon wind/wave energy. These results inform predictions regarding future rates of reef growth and/or estimates of sediment production on reefs, and highlight the importance of habitat-specific regional data in gross reef-scale assessments. Lastly, we discuss the consequences of the recent mass coral bleaching in the Maldives, its bearing on the periodic expansion of encrusting growth, and the implications this may have for short-term reef carbonate production and coral recovery.

2. Regional setting

Vabbinfaru is a small (3.23 km²) carbonate platform in the south-central interior of North Malé Atoll, Maldives (Fig. 1). The platform rises from the atoll basin floor ~40 m deep to mean sea level (MSL) and is aligned east-to-west on its longest axis (~800 m), with the shortest axis (~500 m) north-to-south, reflecting prevailing monsoon wind and wave conditions. The platform experiences a diurnal microtidal regime (0.9 m tidal range), with small seasonal fluctuations in sea surface temperature (28.5–30 °C). Climate is driven mainly by seasonal reversals in the South Asian monsoon (Young, 1999). The November–March period brings calm weather from the north to north-east (0–45°; maximum wind velocity 6.6 m s⁻¹), whereas from April–November strong winds are from the west to south-west (230–305°; maximum velocity 14 m s⁻¹). Incident wave energy is predominately

from the west (during the SW monsoon) with a mean significant wave height (*H*_s) of 0.21 m, and a maximum wave height (*H*_{max}) of 0.99 m (Beetham and Kench, 2014).

The reef occupies a small area (22% of the platform surface) at the platform periphery (0.071 km²; -1 m MSL) but supports high coral cover (Feb 2010: 52 ± 7.6%) comprising mainly *Acropora* spp. (73 ± 9.5%) and *Porites* spp. (14 ± 9.2%) corals (Morgan and Kench, 2016a). Following the 2016 bleaching event in the Maldives, coral cover on the reef crest and shallow fore-reef slope (1–2 m depth) has declined ~76%, with *Acropora* worst affected (see Perry and Morgan, 2017). Dead coral framework (16 ± 5.2%) provides the substrate for calcareous encrusting growth, most commonly non-geniculate (non-articulated, unsegmented) coralline algae (*Lithothamnion* sp., *Peyssonnelia* sp., *Hydrolithon* sp.) that covers ~4% of reef surfaces (Feb. 2010). A shallow central lagoon (2.04 km²; -1.17 m MSL) comprises a mixed sand-rubble (branched *Acropora* sticks) surface that occupies most of the platform area. A small vegetated reef island (0.47 km²; +1.2 m MSL) sits atop of the leeward platform.

3. Materials and methods

3.1. Deployment and analysis of experimental substrates

Carbonate production rates and community composition of encrusting calcifiers were examined using artificial settlement substrates (Fig. 2). A total of 32 sets of unglazed identical ceramic tiles (10 × 10 cm) were deployed at eight sites on the outer platform of Vabbinfaru reef (4 sets per site, sites: V1–V8) at different platform aspects (Fig. 1). Tiles were pre-conditioned in running seawater for 48 h prior to deployment. At each site, tiles were fixed to metal stakes secured into the reef substrate ~10 cm above the reef surface (mean depth: 1 m below MSL), and were attached to create one upwards-facing (exposed) surface and one downwards-facing (cryptic) surface to mimic different reef habitats. Tiles were left for 13 months (Feb 2011 to March 2012) before collection (29 out of 32 were recovered). In the laboratory, they were washed with distilled water, and allowed to dry before both surfaces were photographed. The community composition of the sclerobionts were determined by digitizing 200 randomized points across the photographs in JMicroVision v1.2.7 software (excluding a 1 cm border around the tile perimeter to discount any edge effect), and identifying the encrusting taxa under each point to the lowest taxonomic level.

Carbonate production rates by encrusting species were calculated by measuring the amount of calcium carbonate (CaCO₃) deposited on substrates over the experimental period. Recovered tiles were treated with a 10% solution of sodium hypochlorite (NaClO) for 24 h to remove all organic tissue, leaving the carbonate deposited intact. After rinsing in distilled water, they were dried at 60 °C until a constant weight was reached. Each tile was weighed (*a*) and then placed in a dilute solution of hydrochloric acid (HCl: 10%) to dissolve all calcium carbonate. Following dissolution, tiles were rinsed, dried and reweighed (*b*). Carbonate production (g cm⁻² yr⁻¹) was calculated as the total mass (*g*) of net carbonate accretion (*a* - *b* = *c*), divided by the deployment duration (days), and standardized to a planar unit area (g cm⁻²) by dividing the pre- and post-dissolution weight difference (*c*) by the surface area of the tile (excluding the 1 cm border). The relative contributions of encrusting taxonomic groups to carbonate production were calculated by attributing the proportion of the area occupied by each taxon as part of the total weight deposited on tiles (following Mallela, 2013). Although this approach assumes uniform skeletal density and morphology of encrusting organisms, the nature of encrusting growth on tiles means that isolating individual taxonomic groups is not possible. Datasets were compared to those reported from a pilot study by Morgan and Kench (2013) for vertical PVC pipes at the same sites on Vabbinfaru reef.

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