NOTE

Linear extension, skeletal density, and calcification rates of the blue coral *Heliopora coerulea*

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Abstract The brooding reef-building octocoral *Heliopora* is widespread on Indo-West Pacific reefs and appears to be relatively resistant to thermal stress, which may enable it to persist locally while scleractinians diminish under Anthropocene conditions. However, basic physiological measurements of "blue corals" are lacking and prevent their inclusion in trait-based studies. We address this by quantifying rates (mean ± SE) of linear extension $(0.86 \pm 0.05$ cm yr$^{-1})$ and skeletal density $(2.01 \pm 0.06$ g cm$^{-3})$ to estimate calcification rates $(0.87 \pm 0.08$ g cm^{-2} yr$^{-1})$ for the small branching/columnar morphology of *Heliopora coerulea*. We postulate that *H. coerulea* may become an increasingly important reef-builder under ocean warming due to its relative resistance to thermal stress and high skeletal density that make colonies less vulnerable to storm damage under ocean acidification. Moreover, *Heliopora* corals are likely dispersal limited suggesting they may be an underappreciated genus for restoration of stress-tolerant reef-building capacity on degraded reefs.

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Introduction

Calcium carbonate production represents one of the core functions of coral reef ecosystems (Brandl et al. 2019) and can be approximated from estimates of benthic cover and taxa-specific calcification rates as part of census-based coral reef carbonate production budgets (Perry et al. 2012). While notable efforts have advanced estimates of carbonate production states through the aggregation of publicly accessible coral linear extension, skeletal density, and calcification rate data (e.g., Perry et al. 2012; Madin et al. 2016), basic physiology measurements of the reef-building octocoral genus *Heliopora* are largely absent from these databases. To the best of our knowledge, these are limited to rates of lateral overgrowth of 2.1 ± 0.9 cm yr^{-1} for *H. coerulea* over *Porites* spp. corals reported by Guzman et al. (2019) and a solitary *H. coerulea* calcification rate estimate of 0.48 g cm^{-2} yr^{-1} (by Planck et al. 1988 in Ryan et al. 2019) in the scientific literature.

Widely distributed across the Indo-Pacific, *Heliopora* corals are distinct in that they represent the only known genus of hermatypic octocorals (Zann and Bolton 1985). Often termed "blue corals" owing to the incorporation of iron salts into their skeletal aragonite, *Heliopora* are generally typified by their iconic blue skeletons (Hill 1960; Richards et al. 2018). *Heliopora coerulea* was considered the only extant species, but recent genetic evidence has suggested cryptic speciation within *H. coerulea* between small and flat branching morphologies (Yasuda et al. 2014) that have asynchronous reproductive timing (Villanueva

2016). *Heliopora hiberniana* was also recently described in north Western Australia (Richards et al. 2018). Interestingly, *Heliopora* appears to have higher optimal temperature ranges compared to many scleractinian corals as evidenced by apparent range retractions during periods of cooling (Zann and Bolton 1985), high degree of bleaching resistance and resilience during recent thermal stress events (Kayanne et al. 2002; Donner et al. 2010; Phongsuwan and Changsang 2012; Harii et al. 2014; Richards et al. 2018; Guzman et al. 2019; Ryan et al. 2019), apparent increasing competitive advantage in warmer waters (Atrigenio et al. 2020), and growth rates that increase with seawater temperatures up to at least 31 °C (Guzman et al. 2019). *H. coerulea* also contributed to the maintenance of positive coral reef carbonate production states following a coral bleaching event (Ryan et al. 2019), providing further evidence that *H. coerulea* may become increasingly important reef-builders under ongoing ocean warming.

Owing to the absence of basic physiology data for *Heliopora* corals, it remains unclear how the increasing relative abundance of *Heliopora* corals may impact coral reef geo-ecological functions under ongoing ocean warming and acidification. In this study, we quantify linear extension and skeletal density to estimate morphology-specific calcification rates to fill these gaps in the trait-based coral literature and speculate as to the role of *Heliopora coerulea* as an emerging reef-builder and potential restoration target in the Anthropocene.

Methods

Linear extension

Large and small *Heliopora coerulea* fragments ($n = 100$) of mean ($\pm$ SE) initial planar area of 22.3 ± 1.5 cm^2 ($n = 50$ large fragments) and 5.2 ± 0.2 cm^2 ($n = 50$ small fragments) were used to estimate linear extension rates from repeated measures of height through time. All
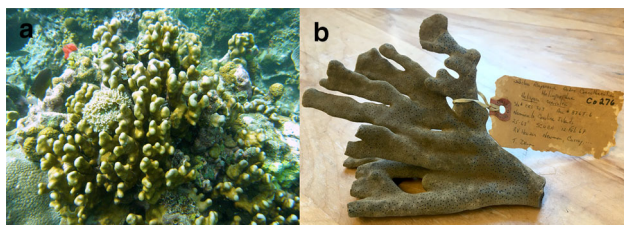
Fig. 1 a *Heliopora coerulea* from Bolinao, Philippines showing the typical light brown coloration of living colonies. Photograph by JR Guest. **b** *Heliopora coerulea* skeletal specimen from the Scripps Institution of Oceanography Benthic Invertebrate Collections (SIO-BIC Co276) showing the iconic blue skeletal coloration. Photograph by TA Courtney

fragments represented the small branching/columnar morphology sensu Yasuda et al. (2014) and Villanueva (2016) (Fig. 1a). Fragments were sourced from 25 independent colonies (four fragments per colony) and epoxied (Pioneer Epoxyclay Aqua^{TM}) onto replicate calcium carbonate substrates (locally aquacultured *Tridacna gigas* shells) mounted on plastic mesh frames between mid-December 2005 and mid-January 2006 in five replicate plots at 2.9–3.4 m depth within the lagoon north of Silaqui Island, Philippines (16°26′22.0″N 119°56′37.8″E). All linear extension data presented here were collected as part of a larger experiment to examine coral growth and survival rates (e.g., see Guest et al. (2011) for further details on study design and photographs of outplanted corals). Linear extension was determined from repeated caliper (precision = 0.1 mm) measurements of fragment height on six occasions in February, May, and October 2006, April and September 2007, and finally in May 2008. Over the $\sim$ 2.25 years of the study, none of the 100 fragments suffered mortality, but two were either broken or became unattached, so only prior growth was recorded. Linear extension (cm yr^{-1}) was estimated from the least squares regression line slope of height (cm) vs. time (yr) from each survey for each fragment to make use of the six repeated height measurements for each fragment and minimize effects of individual measurement error.

Skeletal density

In the absence of direct, contemporaneous skeletal density measurements on the outplanted *Heliopora coerulea* fragments, we used three specimens collected from the Federated States of Micronesia in 1967 and preserved in the Scripps Institution of Oceanography Benthic Invertebrate Collection (i.e., SIO-BIC Co151, Co276, Co277) (Fig. 1b) to quantify *H. coerulea* skeletal density and estimate calcification rates. Archimedes' principle was used to determine bulk skeletal densities (g cm^{-3}) from the mass of skeletal material (g) divided by the volume of water displaced (cm^3) (Jokiel et al. 1978; Morgan and Kench 2012). The mass of each skeletal fragment was determined via direct measurement of the dry skeleton. The volume of displaced water for each respective skeletal fragment (cm^3) was determined via the seawater equation of state (i.e., *R* package *seacarb*; Gattuso et al. 2020) using the mass (g), temperature (°C), and salinity (ppt) of the displaced water upon submergence of the skeleton in deionized water. We assumed that *H. coerulea* skeletal voids were small and poorly connected with minimal influence on bulk skeletal density measurements and therefore did not dip the specimens in paraffin wax prior to displacement in water (Bucher et al. 1998). Mass was determined via an Ohaus Scout SPX422 balance (precision = $\pm$ 0.01 g) that was

verified for accuracy with a calibration weight prior to measurements. A YSI Pro 2030 was used to measure temperature (precision = $\pm$ 0.3 °C) and salinity (precision = $\pm$ 0.1 ppt). Skeletal densities were compared to recent bulk skeletal densities of Indian Ocean scleractinians determined using analogous methods (Morgan and Kench 2012).

Calcification rates

The scaling of coral calcification rates represents a considerable ongoing challenge owing to the three-dimensional structural complexity of coral skeletons, so we used methods analogous to Morgan and Kench (2012) to directly compare our estimated calcification rates to those of that study. The small branching/columnar *H. coerulea* specimens in this study most closely approximated the *Pocillopora meandrina* submassive morphology from Morgan and Kench (2012), so we used the adjustment coefficient of 0.5 for that species to account for the open space in our estimates of *H. coerulea*. We therefore estimated mean ($\pm$ SE) *H. coerulea* calcification rates from the product of linear extension, skeletal density, and the 0.5 adjustment coefficient following Morgan and Kench (2012).

Results and discussion

Linear extension

Mean ($\pm$ SE) linear extension did not differ significantly between the large (0.88 $\pm$ 0.08 cm yr^{-1}) and small (0.83 $\pm$ 0.06 cm yr^{-1}) fragments (two-sample *t*-test, $p = 0.531$), so we calculated the mean ($\pm$ SE) linear extension rate for all *H. coerulea* fragments ($n = 100$). This rate (0.86 $\pm$ 0.05 cm yr^{-1}) was lower than the extension rates of 2.1 $\pm$ 0.9 cm yr^{-1} reported for *H. coerulea* laterally overgrowing massive *Porites* spp. by Guzman et al. (2019). It is unlikely that environmental and/or genotypic controls caused these differences in growth rates (Pratchett et al. 2015) as the data were collected from approximately the same study locations (Bolinao, Philippines). We posit that these differences were most likely due to measurements of linear extension of skeletal branches (this study) versus lateral extension of a thin veneer of encrusted skeletal material over massive *Porites* spp. (Guzman et al. 2019). Our mean ($\pm$ SE) extension rate of 0.86 $\pm$ 0.05 cm yr^{-1} for *H. coerulea* is less than the branching, corymbose, digitate, and massive scleractinians, similar to submassive scleractinians, and greater than mushroom and encrusting scleractinians observed by Morgan and Kench (2012) (Fig. 2).

Skeletal density

Mean ($\pm$ SE) skeletal densities for *Heliopora coerulea* of 2.01 $\pm$ 0.06 g cm^{-3} in this study were higher than any of the scleractinian skeletal densities observed by Morgan and Kench (2012) (Fig. 2). Ocean acidification (OA) threatens to reduce scleractinian coral skeletal density, which could lead to increased breakage of coral skeletal materials and decreased reef-building capacity (Hoegh-Guldberg et al. 2007). Whether distinct differences in the skeletal morphology of *H. coerulea* may confer some resilience to OA by these reef-building octocorals remains to be tested (Atrigenio et al. 2020). Regardless, the comparatively higher skeletal density of *H. coerulea* relative to its scleractinian morphological counterparts suggests that *H. coerulea* skeletons could be more resistant to such physical breakage under OA. However, we cannot rule out the possibilities that slight differences in methodologies (i.e., omission of paraffin wax dip in this study) or that *Heliopora* skeletal densities were indeed higher in 1967 and have since decreased under ongoing environmental change, so further research remains necessary to test any hypothesized resiliency of *Heliopora* corals and their skeletal components to environmental change.

Calcification rates

Mean ($\pm$ SE) estimated calcification rates for *Heliopora coerulea* were 0.87 $\pm$ 0.08 g cm^{-2} yr^{-1} for the small branching/columnar morphology investigated in this study (Fig. 2). This rate is greater than the solitary calcification rate estimate of 0.48 g cm^{-2} yr^{-1} for *H. coerulea* by Planck et al. (1988) in Ryan et al. (2019), which may in part be due to differences in methodologies and/or morphologies between the previous measurement and this study. Notably, *H. coerulea* calcification rates are less than those for branching, corymbose, digitate, and massive scleractinians, in general agreement with rates for submassive morphologies, and are greater than mushroom and encrusting scleractinian calcification rates by Morgan and Kench (2012) (Fig. 2). While variability in calcification rates through space and time (Pratchett et al. 2015) confound a more direct comparison of calcification rates between taxa, these estimates nonetheless suggest that offsetting slower linear extension and higher density skeletal material of *H. coerulea* generate carbonate production rates similar to other reef-building scleractinian taxa.
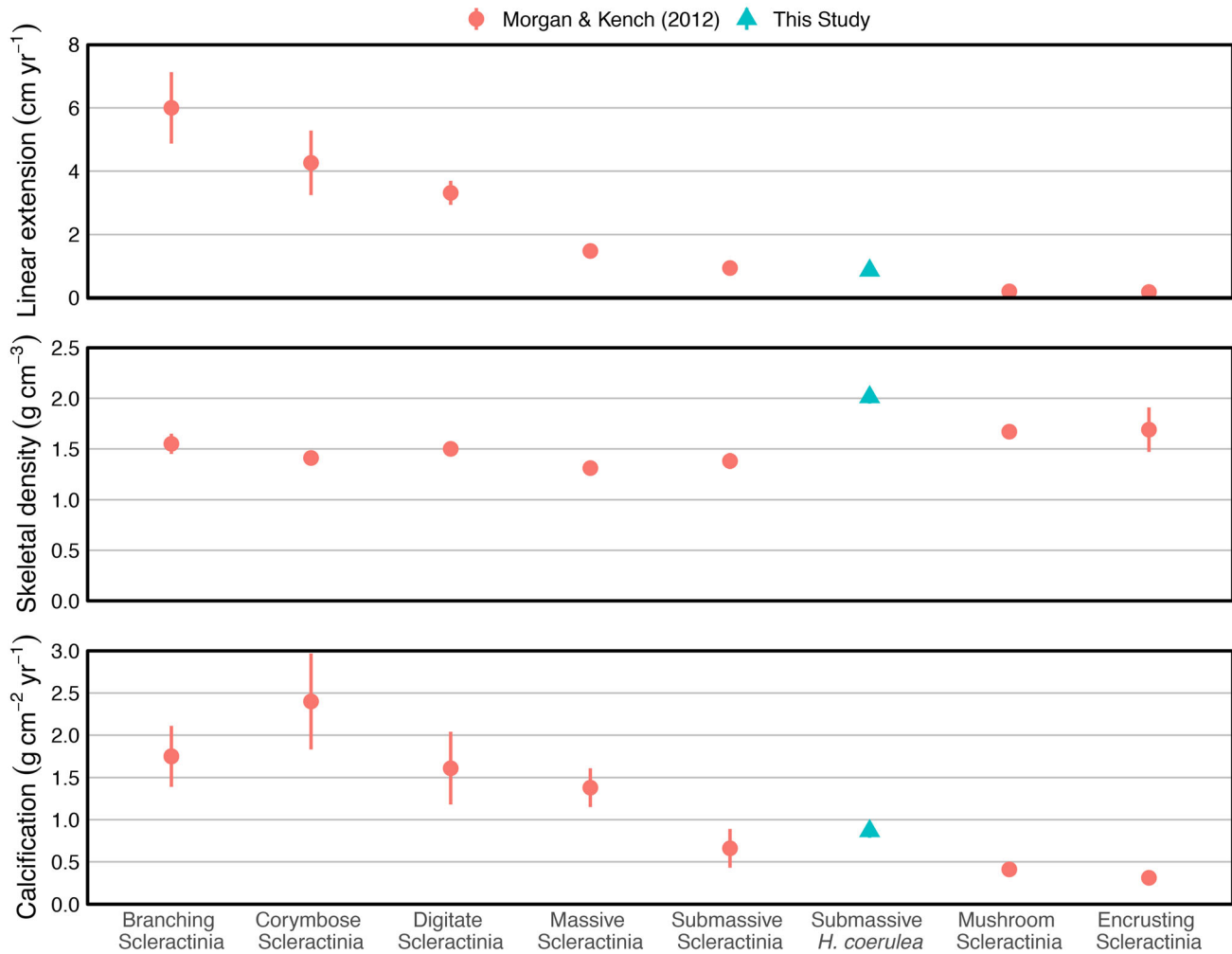
Fig. 2 Mean (± standard error) linear extension, skeletal density, and calcification rates for *Heliopora coerulea* from this study are plotted relative to Indian Ocean scleractinian corals from Morgan and Kench (2012)

Implications for reef building and restoration in the Anthropocene

Owing to their higher degree of resilience to thermal stress anomalies and apparent increasing ability to outcompete scleractinians under ocean warming, *Heliopora* corals may become increasingly abundant reef-builders (Kayanne et al. 2002; Donner et al. 2010; Phongsuwan and Changsang 2012; Harii et al. 2014; Richards et al. 2018; Guzman et al. 2019; Ryan et al. 2019; Atrigenio et al., 2020). Interestingly, *Heliopora* tends to form dense aggregations and may be dispersal limited owing to benthic planulae that settle near the parent colony (Zann and Bolton 1985; Harii et al. 2002). We posit that outplanting of stress-tolerant reef-building *Heliopora* corals to degraded reef systems within its current geographic range may enable restoration of structural complexity and calcium carbonate production to select reefs. However, such restoration strategies could

inhibit growth and/or recruitment by scleractinian corals (Atrigenio et al. 2017; Guzman et al. 2019; Atrigenio et al. 2020) and should therefore critically evaluate any potential resulting consequences as part of a broader decision-making framework (National Academies of Sciences 2019). We conclude that *Heliopora* corals warrant further research as potentially emerging reef-builders and target taxa for restoration and adaptation efforts in the Anthropocene.

authors, the corresponding author states that there is no conflict of interest.

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