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REPORT

Growth rates of *Porites astreoides* and *Orbicella franksi* in mesophotic habitats surrounding St. Thomas, US Virgin Islands

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Abstract Mesophotic coral ecosystems (MCEs) are deep (> 30 m), light-dependent communities that are abundant in many parts of the global ocean. MCEs are potentially connected to shallow reefs via larval exchange and may act as refuges for reef organisms. However, MCE community level recovery after disturbance, and thus, community resilience, are poorly understood components of their capacity as refuges. To assess the potential for disturbance and growth to drive community structure on MCEs with differential biophysical conditions and coral communities, we collected colonies of *Orbicella franksi* and *Porites astreoides* and used computerized tomography to quantify calcification. The divergence of coral growth rates in MCEs with different environmental conditions may be species specific; habitat-forming *O. franksi* have slow and consistent growth rates of ~ 0.2 cm yr^{-1} below 30 m, regardless of mesophotic habitat, compared to ~ 1.0 cm yr^{-1} in shallow-water habitats. Slow skeletal growth rates in MCEs suggest that rates of recovery from disturbance will likely also be slow. Localized buffering of MCEs from the stressors affecting shallow reefs is therefore crucial to the long-term capacity of these sites to serve as refugia, given that skeletal extension and recovery from disturbance in MCEs will be significantly slower than on shallow reefs.

Keywords Mesophotic coral ecosystems · Sclerochronology · Refugia · Shelf edge reefs · *Orbicella* spp.

Introduction

Mesophotic coral ecosystems (MCEs) are deep (> 30 m), light-dependent communities that may be abundant throughout tropical and subtropical waters. These communities are strongly affected by reduced light relative to surface waters (Kahng et al. 2010) and a cooler thermal regime (Bak et al. 2005), which may have strong controls on community structure. MCEs are potentially removed from many anthropogenic stressors affecting nearshore and shallow reefs (< 30 m; Bak et al. 2005; Smith et al. 2008) and may be connected to shallow reefs via larval recruitment (Holstein et al. 2015). This has led to the hypothesis that these reefs serve as refugia for coral species against

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thermal stress and storm swell (Goldberg 1983; Glynn 1996; Riegl and Piller 2003). However, there is evidence to suggest that MCEs are not immune to wave action or storm disturbance (Bongaerts et al. 2013; White et al. 2013; Smith et al. 2016b) or thermal stress (Smith et al. 2016a). In addition, the potential for refugia and severity of disturbance may not apply equally to all species (Bongaerts et al. 2010; Pyle et al. 2016), which raises important questions on the vulnerability of MCEs versus their shallow-water counterparts. An important component of MCE vulnerability may be reduced skeletal growth rates at depth as this indicates that recovery after perturbation will be slower than on shallow reefs. The resilience of MCEs after perturbation is not well understood, and it may be imperative that these systems be isolated from the stressors degrading coral reefs to persist as refugia given that their recovery, and thus, resilience may be reduced.

The growth of individual organisms is a key variable driving the community structure and population demographics of ecosystems (Vandermeer 1981; Weiner and Thomas 1986; Forrester 1990). Growth of corals allows them to compete for and occupy space, ultimately leading to the creation of architecturally complex reef structures (Goreau 1963; Pratchett et al. 2008). The three-dimensional structure of reefs is the primary factor leading to the biodiversity and biomass of associated organisms (Graham and Nash 2013; Darling et al. 2017). The rate of recovery from disturbance that causes coral mortality is partially controlled by rates of coral growth. This is especially pertinent in an era of global reef degradation, as many reefs display very low rates of recruitment given the dwindling populations of large, reproductively active corals (Hughes and Tanner 2000; Bellwood et al. 2004; Pandolfi et al. 2011; De'ath et al. 2012; Clark et al. 2017). Thus, much of the recovery of present-day reefs is dependent on the growth of remnant tissues after mortality events.

There have been numerous studies on coral growth spanning more than 100 yrs, but these have been primarily from shallow-water environments (< 10 m depth) and growth in mesophotic environments is poorly understood (see most recent review by Pratchett et al. 2015). MCEs south of St. Thomas (STT), US Virgin Islands, are dominated by the genus *Orbicella* with coral cover reaching as high as 49% in some areas (Smith et al. 2010). In contrast, MCEs north of STT have limited coral cover, less than 5%, at the same depths as the southern habitats (Groves 2016). MCEs north and south of STT occur at similar depths, but MCEs to the north are exposed to long-period Atlantic swell, from which southern MCEs are buffered to some degree by the island of St. Thomas and the Puerto Rican shelf. Photosynthetically active radiation (PAR) decreases with increasing depth, but the relationship of PAR with depth may not be consistent at different locations (e.g., north and south of St. Thomas) if water movement and turbidity are not also consistent (Lesser et al. 2010; Costa et al. 2015. We posited that lower coral cover on the northern shelf may be related to lower growth rates caused by increased disturbance and stress (e.g., higher wave action and metabolic limitations such as reduced photosynthesis due to reduced light, or limitations on heterotrophic food availability). We tested the null hypothesis that there is no difference in growth rates between divergent mesophotic habitats using two common Caribbean coral species. We also compared potential signatures of bleaching from the skeletal records to explore historical disturbance in these habitats.

Materials and methods

Small (< 40 cm diameter) colonies or partial colonies (also < 40 cm diameter) of *Orbicella franksi* (formerly in the genus *Montastraea*; Budd et al. 2012) and *Porites astreoides* were extracted using a chisel and a mallet from a depth range of 6–47 m (Fig. 1). A total of 20 *O. franksi* and 30 *P. astreoides* samples were used in this study. By comparison, previous studies that have examined growth rates below 30 m depth have used comparatively smaller sample sizes (Hubbard and Scaturo 1985, $n = 3$; Huston 1985, $n \leq 5$ per species). An exception is Dustan (1975) who used 42 coral fragments. Samples of each species were haphazardly collected from a depth range of 27–47 m on the north shelf of STT (*O. franksi*, $n = 6$; *P. astreoides*, $n = 14$), at stratified random sampling sites during benthic surveys of a larger study (15 sites). On the south shelf of the island, *O. franksi* samples were collected from two locations (at 12 and 30 m depths) for use in a coral reproduction study and skeletons were used in this study to minimize impact on the species (30 m, n = 11; 12 m, n = 3). Mesophotic colonies of *P. astreoides* were collected from five sites over a depth range of 30–47 m ($n = 13$) and from three shallow sites at 6, 12 and 18 m depths ($n = 1$ at each shallow site). North shelf mesophotic sampling sites had a mean depth of 38.7 ± 6.3 m (SD) and mean coral cover of 2.4 ± 3.2%, while southern mesophotic sites had a mean depth of 33.5 ± 4.1 m and a mean coral cover of 23.5 ± 13.6%.

Colonies were cut into 2-cm-thick cross sections using a tile saw and scanned using a Siemens Somatom volume zoom computerized tomography (CT) scanner at 0.1-mm resolution (Fig. 2). The images from the CT scanner allow for more accurate identification of the growth axis than conventional X-ray techniques because the scanned image can be rotated in three-dimensional space (Cantin et al. 2010). Image stacks from the CT scanner were imported into the Amira software (FEI Visualization Sciences

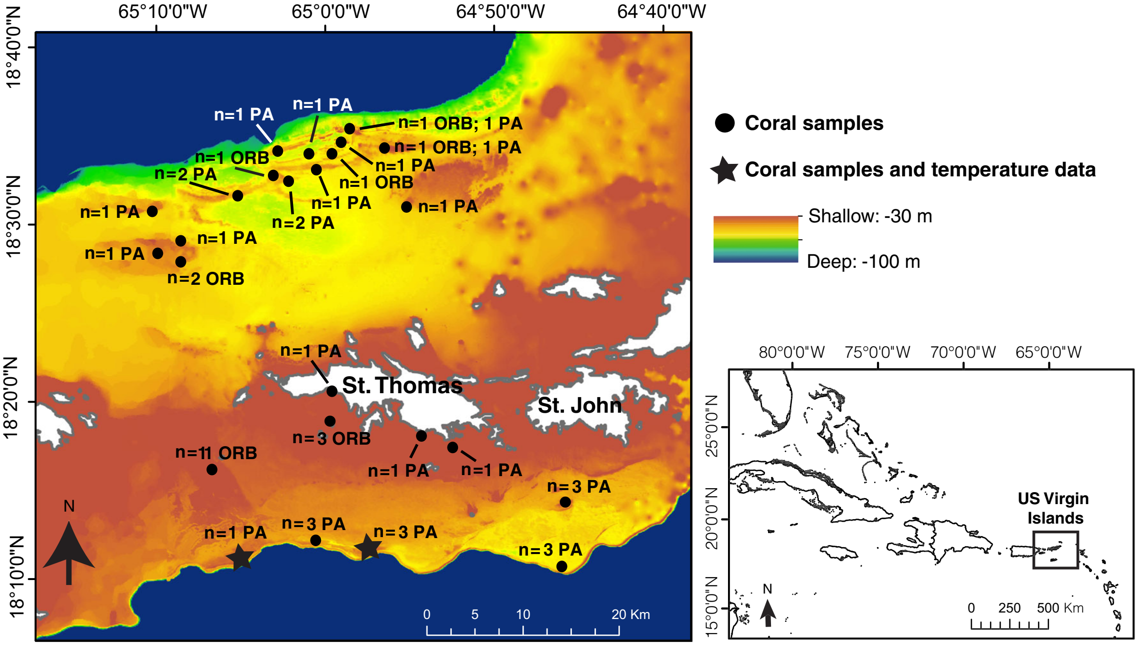


Fig. 1 Map of the Puerto Rican shelf with circles indicating location of coral sample collections and number of *Orbicella franksi* (ORB) and *Porites astreoides* (PA) colonies collected at each site. Starred sites indicate where long-term (since 2005) temperature data have been recorded. Blue areas of bathymetry are greater than 100 m depth

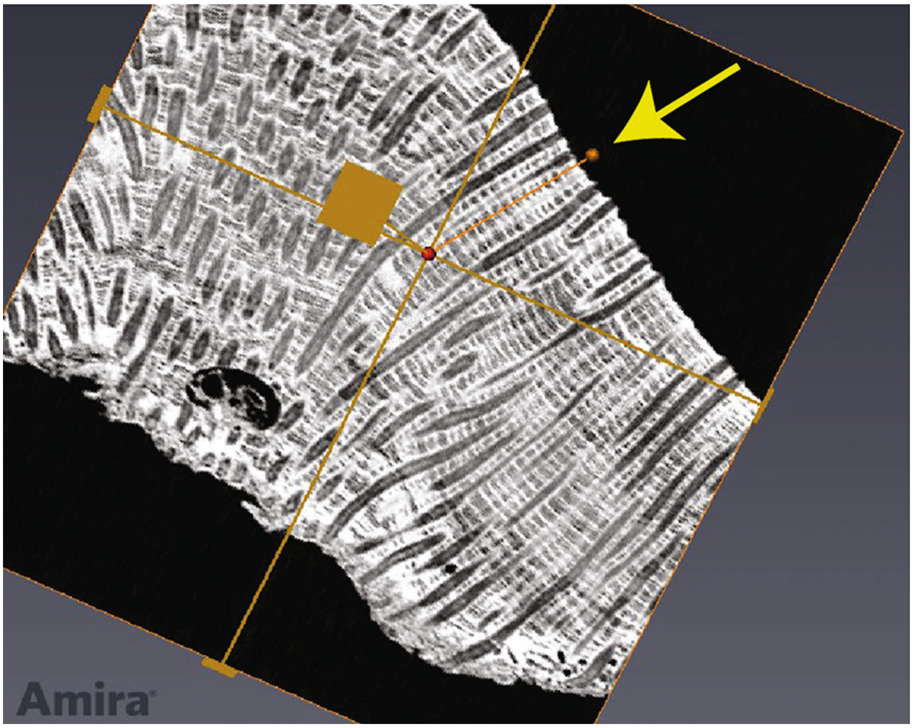


Fig. 2 Two-dimensional ortho-slice of an *Orbicella franksi* skeleton from 30 m depth created using ortho-slice in Amira software. Yellow arrow indicates the measured growth/density transect within the colony (orange line), gold lines indicate the two-dimensional axis within the image used to position the transect, and gold boxes indicate control points for rotating the image within Amira software

Group, Massachusetts, USA) in which growth axes were identified and density measurements were made along the longest axis (Fig. 2). Colonies with fewer than five visible growth bands were rejected ($n = 10$) as they were either too dense, too bioeroded, or too platy (flat) to accurately detect density banding. Grayscale values were converted to density (g cm^{-3}) by linear regression of coral standards of known density. Density/growth axis data were imported into Coral X-radiograph Densitometry System (Coral*XDS*) (Helmle et al. 2002) software where annual density bands (cm yr^{-1}) were delineated using the peak-to-peak (high-density band to high-density band) method. Linear extension and mean yearly density were calculated and used to calculate annual calcification rates (g cm^{-2} yr^{-1}).

A nested mixed linear model (MLM) was applied to mesophotic samples only to test the effects of depth (30–47 m) and region (side of island) within mesophotic habitats. For both species, adding an interaction term between region and depth did not significantly improve model fit for linear extension, density and calcification (χ^2, $p > 0.05$), so it was not used in the statistical model. A subset of colonies with ≥ 10 yrs of visible banding (six *P. astreoides* and three *O. franksi* from south of STT and two *O. franksi* from north of STT) were visually compared to long-term temperature data from the Virgin Islands Territorial Coral Reef Monitoring Program (TCRMP, 2005–2014; Smith et al. 2014). As part of the monitoring program, benthic thermistors (Hobo Water Temperature Pro v2, Onset Computer Corp, Bourne, MA, USA) have been deployed at 33 monitoring sites on a yearly basis since 2005. Coral colonies were collected from two monitoring sites, at 30 and 40 m depth, and the temperature data from these sites were used for the comparison. All statistical analyses used packages vegan (Oksanen et al. 2015) and Lmer4 (Bates et al. 2014) in R version 3.1.2. (R Core Team 2014).

Table 1 Mixed linear model results of the effect of region (side of island) and depth on linear extension, density and calcification between northern and southern mesophotic ecosystems

Species/interaction	*n*	AIC	*t*	*p*
Orbicella franksi				
Linear extension				
Region (north, south)	7.11	−452.7	−0.402	0.688
Depth			−1.767	0.080
Depth (all sites)	21	−483.5	−0.605	**< 0.001**
Density				
Region	7.11	−85.3	0.734	0.463
Depth			1.102	0.308
Depth (all sites)	21	−95.2	2.115	**0.034**
Calcification				
Region	7.11	−168.3	0.749	0.904
Depth			−0.717	0.473
Depth (all sites)	21	−184.9	−4.591	**< 0.001**
Porites astreoides				
Linear extension				
Region	14.13	−593.8	3.960	**< 0.001**
Depth			0.931	0.352
Density				
Region	14.13	−270.2	1.943	0.052
Depth			−0.497	0.620
Calcification				
Region	14.13	−337.2	4.799	**< 0.001**
Depth			0.781	0.434

For *Orbicella franksi*, there was no effect of region, so effect of depth was also tested for all samples. Significant effects ($p < 0.04$) in bold

Results

Growth rates in MCEs

MCE habitat of origin had species-specific effects that did not explain differential coral reef development. Within MCE depths, the linear extension, density and calcification rates of *O. franksi* showed no relationship with side of island (region, henceforth) or depth, indicating that growth rates of the dominant upper-MCE reef-building coral, *O. franksi,* are similar between MCE habitats with differing levels of coral reef development. This implies that growth rates alone do not explain these differences (e.g., coral cover; Table 1). Mean linear extension for the north shelf was 0.18 ± 0.008 cm yr^{-1} (SE) compared to 0.19 ± 0.007 cm yr^{-1} for the south. Mean density in the north was 2.23 ± 0.0823 g cm^{-3} compared to 2.17 ± 0.048 g cm^{-3}, while mean calcification was 0.40 ± 0.019 g cm^{-2} yr^{-1} compared to 0.42 ± 0.014 g cm^{-2} yr^{-1}. Because there was no effect of region on growth, density or calcification within MCE depths, we were able to apply the MLM to all samples (deep and shallow), to test the effect of depth on growth. Skeletal characteristics of *O. franksi* showed significant relationships with depth from shallow to deep. Density was higher and linear extension, and calcification rates were lower and of similar value among colonies at 30 m or deeper in MCEs. Specifically, linear extension for *O. franksi* decreased significantly (MLM, $p < 0.001$) between 12 and 47 m depth and ranged from 0.41 to 0.12 cm yr^{-1} (Table 1). Density increased significantly (MLM, $p = 0.034$) from 1.63 to 2.60 g cm^{-3}, while calcification decreased significantly (MLM, $p < 0.001$) from 0.76 to 0.28 g cm^{-2} yr^{-1} (Fig. 3a–c).

The relationship between growth, depth and region was more complex for *P. astreoides*. Within mesophotic samples, there was a significant effect of region on linear extension (MLM, $p < 0.001$) and calcification (MLM, $p < 0.001$) but no effect of depth. All growth variables were lower in the north, with a mean linear extension of 0.21 ± 0.005 cm yr^{-1} compared to 0.27 ± 0.007 cm yr^{-1} in the south, and mean calcification of 0.30 ± 0.008 g cm^{-2} yr^{-1} compared to 0.43 ± 0.012 g cm^{-2} yr^{-1} (Fig. 3d–f). Because there was an effect of region for this species, we were not able to test the effect of depth on all samples. When the model was applied to southern samples only, there was no effect of depth on linear extension, density or calcification from a depth range of

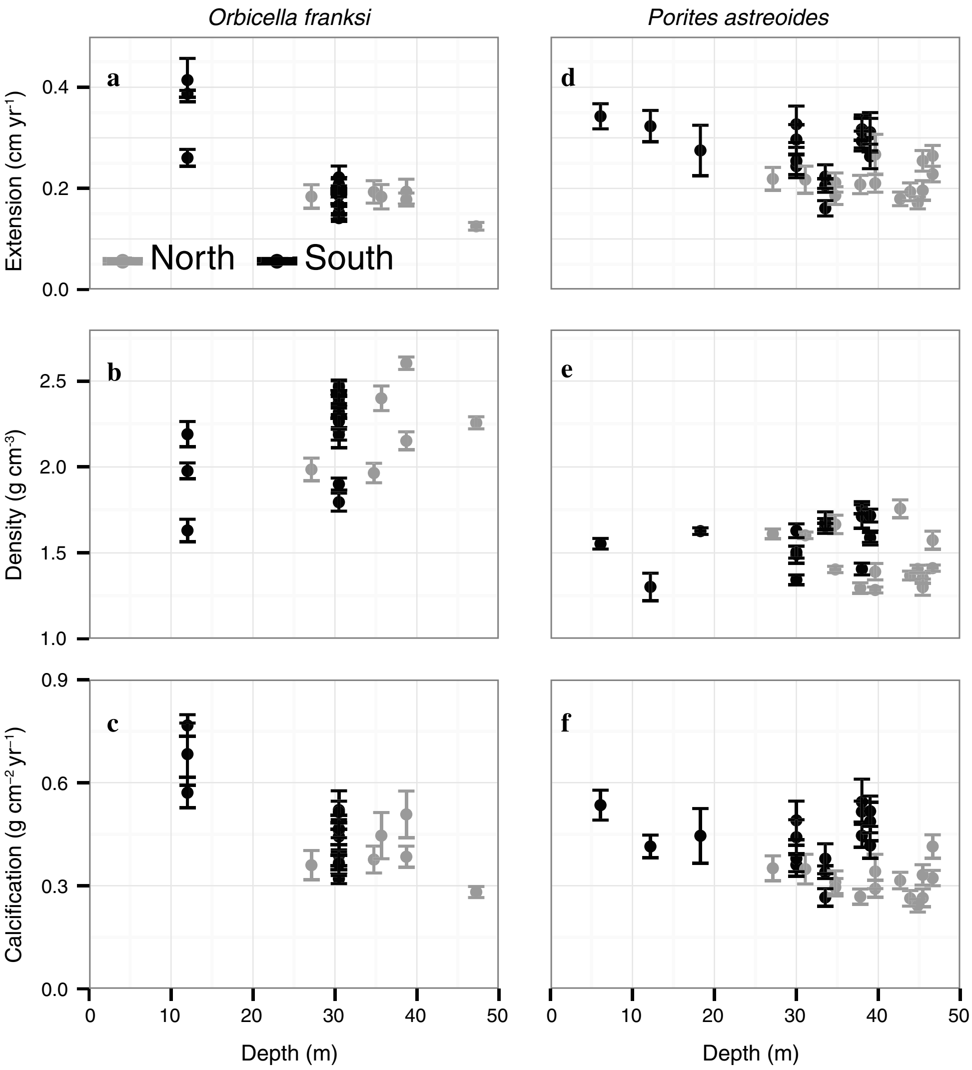


Fig. 3 Mean (± SE) linear extension (cm year^{-1}), mean density (g cm^{-3}) and mean calcification (g cm^{-2} year^{-1}) of *Orbicella franksi* (**a**, **b**; $n = 20$) and *Porites astreoides* (**d–f**; $n = 30$) as a function of depth, from two reef regions (north and south)

6–47 m. Linear extension ranged from 0.34 to 0.16 cm yr^{-1}, and calcification ranged from 0.54 to 0.26 g cm^{-2} yr^{-1}. While they both decreased with depth, this change was not significant. Density ranged from 1.28 to 1.75 g cm^{-3} and did not increase or decrease with depth.

Thermal stress response in growth of MCE corals

Trajectories in growth variables varied among colonies between 2001 and 2015. We found that three of the five *O. franksi* colonies examined for growth histories showed a decrease in linear extension and calcification in response to the 2005 bleaching event, and four of the five showed an increase in density (Fig. 4a–f). One colony from the northern shelf did not follow this trend in growth; all growth variables increased in this colony. In 2006, the year immediately following the bleaching event, growth rates of *O. franksi* decreased or stayed the same but increased again in subsequent years. In 2012, only one southern colony responded with a decrease in linear extension and calcification and increase in density, while the remaining two colonies surprisingly showed an increase in growth and calcification and a decrease in density. In the north, there was no detectable negative response in growth variables to the 2012 thermal stress event. Overall, the magnitude of change in the growth variables was not consistent by year or by colony.

For *P. astreoides*, growth responses to thermal stress were minimal (Fig. 5a–c). At the 30-m site, all growth variables decreased in 2005, while at the 40-m site, we observed an increase in linear extension and calcification and decrease in density, but all changes were small (< 0.1 for all growth variables) compared to the previous year. In 2012, we observed a decrease in linear extension and calcification and increase in density at the 30-m site, while the 40-m site showed a slight increase in all growth variables. However, the changes in growth variables between 2011

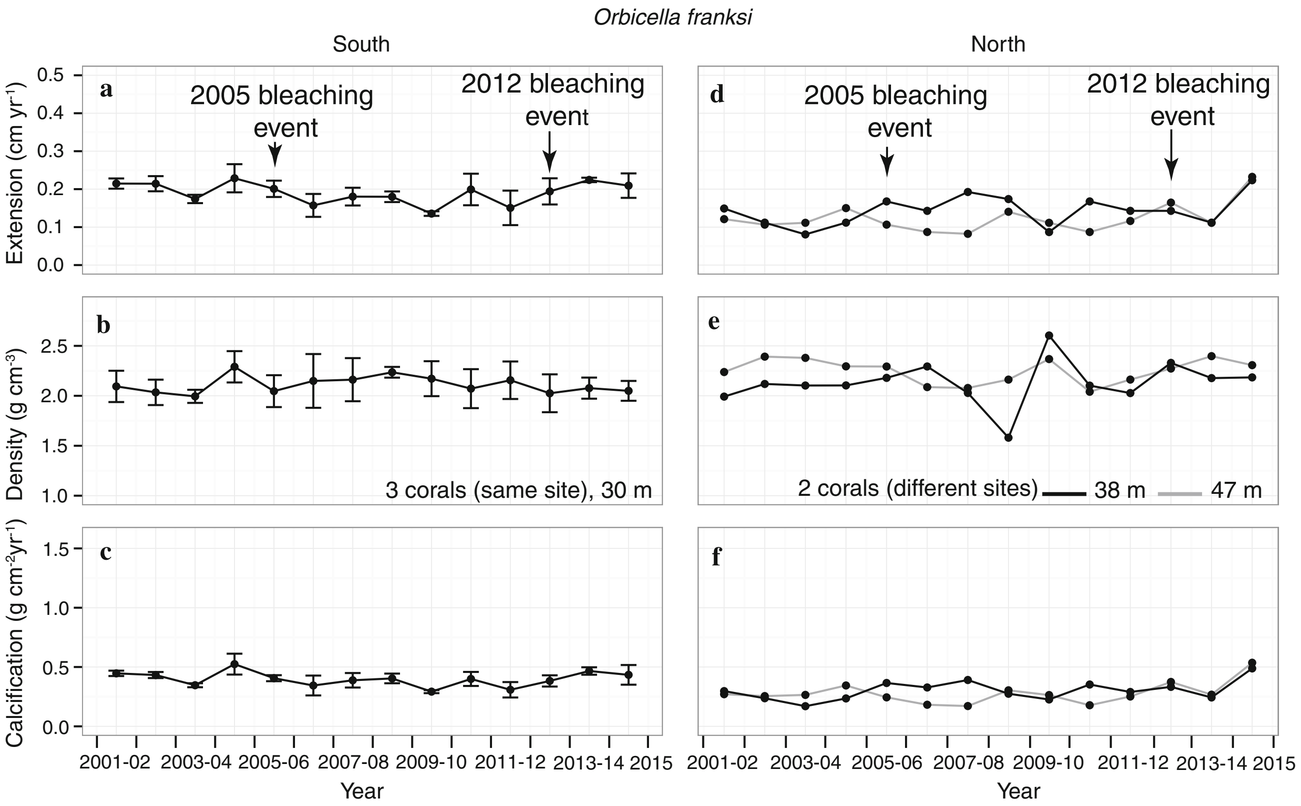


Fig. 4 Left: mean (± SE) annual linear extension (**a**), density (**b**) and calcification rates (**c**) of *Orbicella franksi* from 2004 to 2015 at one mesophotic site south of St. Thomas ($n = 3$). Right: mean (± SE) annual linear extension (**d**), density (**e**) and calcification rates (**f**) of *Orbicella franksi* from 2004 to 2015 at two mesophotic sites north of St. Thomas ($n = 1$ per site)

and 2012 were even smaller than 2004–2005, less than 0.05 for all growth variables.

Discussion

Mesophotic linear extension and density

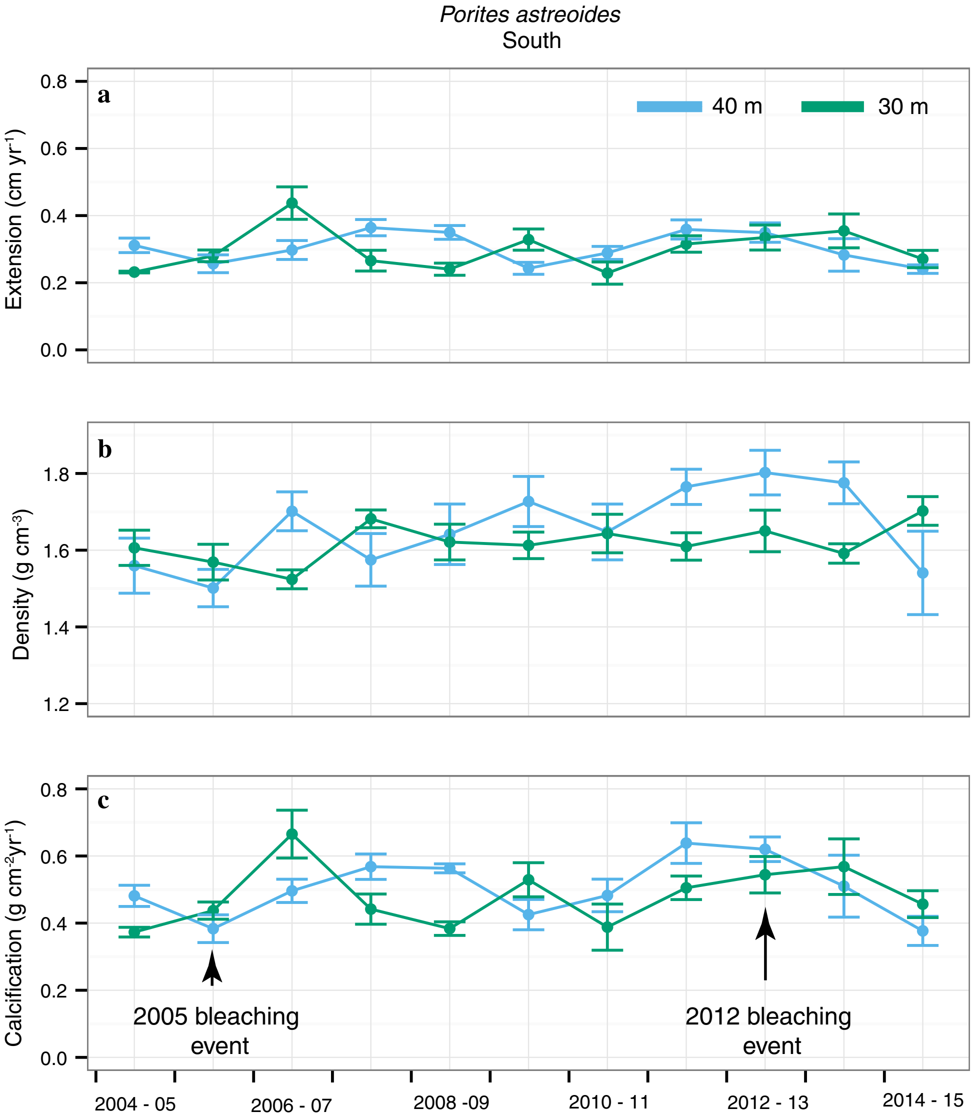
Orbicella franksi extension rates at 30–47 m depth in this study are consistent with findings of declining linear extension with depth in previous studies (Baker and Weber 1975; Dustan 1975; Huston 1985; Bosscher and Meesters 1992). Weinstein et al. (2016) found much slower linear extension at the colony edges of *O. franksi* from US Virgin Islands mesophotic reefs. Density values found in this study were also consistent with previous studies on mesophotic *Orbicella* spp. (Dustan 1975; Weinstein et al. 2016).

Rates of linear extension of *P. astreoides* also agree with growth rates found in previous studies (Hubbard and Scaturo 1985; Huston 1985; Chornesky and Peters 1987). While our shallow-water sample from 6 m is consistent with the density and calcification rates found in Manzello et al. (2015a), little information exists on the density and calcification rates of *P. astreoides* in depths below 30 m. Growth of *P. astreoides* did not show a clear relationship with depth, similar to the findings of Carricart-Ganivet et al. (2007) who found no significant change in linear extension, density and calcification in Pacific *Porites* spp. from 0 to 20 m depths. This may indicate that depth (light) may not be the primary driver of growth in this species or that it is able to adapt to changing light regimes across its depth range.

Multiple studies conducted in the Pacific have identified latitude (temperature) and distance from shore (exposure, i.e., wave action or tidal currents) as the strongest drivers of growth of *Porites* spp. Linear extension has a significant, inverse relationship with density and exposure (Lough and Barnes 1992, 2000; Scoffin et al. 1992) and significant, positive relationship with temperature (between ~ 25 and 27 °C; Lough and Barnes 2000). Density in *Porites* spp. showed no relationship with temperature but a significant, positive relationship with exposure (Risk and Sammarco 1991; Lough and Barnes 2000).

In this study, all three growth variables were lower on the north side of STT in *P. astreoides*. Groves (2016) found little variation in temperature between the north and south MCEs in 2015–2016. Alternatively, these environments

Fig. 5 Mean (± SE) annual linear extension (**a**), density (**b**) and calcification rates (**c**) of *Porites astreoides* from 2004 to 2015 at two mesophotic sites south of St. Thomas ($n = 3$ each site)



may experience differential temperature stress, which warrants future study. Swell events that affect the US Virgin Islands from the north can increase orbital velocities or wave-driven water movement at depth. For example, in 2008 maximum wave heights of 4.3 m caused benthic disturbance in the form of turbulence at 39.5 m depths (Bright et al. 2016) indicating that these swell events can impact mesophotic depths. The reduced linear extension and reduced calcification in *P. astreoides* collected from the north shelf in this study may be due to increased exposure to storm swell, as Groves (2016) found that orbital velocities in the north were greater than the south at comparable depths because of a high-magnitude northern surface swell. While the increased wave action on the north shelf may account for the decrease in extension, there was no significant inverse relationship between linear extension and density (linear regression, $R^2 = 0.005$, $p = 0.619$), which may help explain why all growth variables of *P. astreoides* were depressed in the north.

Below 20 m depths, growth rates of *Orbicella* spp. are slow ($\sim$ 0.2 cm yr^{-1}); light reduction with depth is likely the strongest influence (Chalker 1981). As light attenuates, corals undergo both morphological and physiological adaptations, such as plating growth forms and shifts in zooxanthellae communities to increase photosynthetic productivity (Todd 2008; Cooper et al. 2011). Lesser et al. (2010) found a steady decline in photosynthesis/respiration (P/R) ratios from 3 to 91 m depth, which suggests a decreased dependence on autotrophy but could also suggest a metabolic cost if energy requirements cannot be met through heterotrophy. Brandtneris et al. (2016) found that mesophotic corals were unable to maintain consistent caloric content (energy available for growth, reproduction and maintenance) of tissues throughout the year, with decreased levels occurring during spawning events. This also suggests that heterotrophic energy subsidy may not sufficiently protect mesophotic corals from energy stress; however, the degree to which heterotrophy may affect mesophotic coral growth rates is still unclear.

Orbicella franksi did not exhibit any north–south differences; thus, this species may be more resistant to wave action or chronic wave action is not sufficiently strong to differentially affect growth. The higher skeletal density in *O. franksi* may be a factor in this tolerance to increased exposure. Increased wave action also has the potential to increase turbidity through resuspended sediment, but the degree to which this might affect the already low growth rates is unclear and may warrant further study. Colonies of *O. franksi* at MCE depths may be growing near to their lowest growth potential, as determined by their light, calcification and metabolic limitations. Thus, although stress or disturbance may affect mortality in these corals, it may not affect growth in ecologically significant or even detectable fashion. The response to different habitats may be at the level of the population, with fewer colonies able to survive and contribute to coral cover, but those that do survive have similar growth rates.

Influences of thermal stress on MCE coral growth

Bleaching events in the south shelf STT MCE were documented during 2005 and 2012, with shallow bleaching in 2005 and 2010 (Fig. 6; Smith et al. 2016a). Empirically calculated degree heating weeks (DHW; NOAA 2006) were about 8 DHW for a reef at 38 m depth in 2005 and about 4 DHW for the same reef in 2012. While bleaching extent (degree to which a colony is affected) was higher in 2005, bleaching prevalence (proportion of colonies affected) was higher in 2012. In addition, the 2005 bleaching was followed by an outbreak of white plague disease in 2006, which in concert caused a 24.5% reduction in coral cover at mesophotic depths, while no remarkable change in coral cover occurred after 2012 (Smith et al. 2010. While it appears that thermal bleaching can cause a decrease in growth rates for the year in which it occurs, growth rates can recover, particularly if temperatures remain within optimal ranges in subsequent years (Jokiel and Coles 1977; Manzello et al. 2015b). As ocean temperatures increase globally, an overall decline in coral growth rates in shallow water is possible (Manzello 2010; Lough and Cantin 2014), but the degree to which this will affect the already low growth rates of mesophotic corals is still unclear.

Similar to our findings, Manzello et al. (2015a) also found an increase in extension and calcification in colonies of *P. astreoides* in the Florida Keys during the 2005 bleaching event and consistent growth during a local bleaching event in 2011. *Porites astreoides* is known to be a heat-tolerant species (Miller et al. 2011; Smith et al. 2013); the maintenance of growth rates during bleaching events may be an additional trait (weedy life-history strategy, relatively high fecundity across its depth range and brooded larvae that settle in high densities) that is contributing to the increasing abundance of this species (Bak and Engel 1979; Green et al. 2008; Knowlton and Jackson 2009; Holstein et al. 2016).

Growth rates can be used to estimate rates of recovery from disturbance and predict future trajectories for habitats under varying management scenarios (Gittings et al. 1988; Viehman et al. 2009). Slow skeletal growth rates in MCEs suggest that rates of recovery from disturbance will also likely be slow. Localized buffering of MCEs from the stressors impacting shallow reefs is therefore crucial to the long-term capacity of these sites to serve as refugia, given that recovery of coral cover via regrowth of remnant tissues in MCEs will be significantly slower than in shallow reefs.

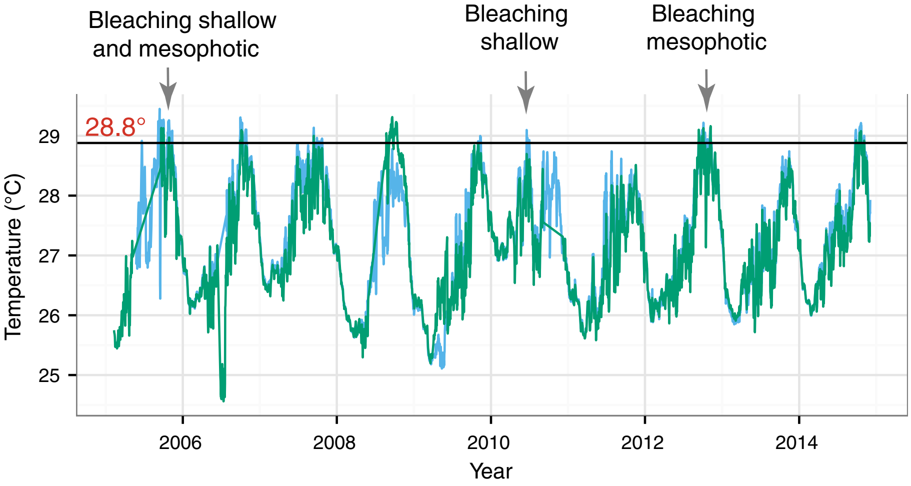


Fig. 6 Long-term mesophotic reef temperature data from 2005 to 2017. Three colonies of *Porites astreoides* were collected from each site at 30 m (green) and 40 m (blue) depths. Solid line indicates bleaching threshold calculated for the 40-m site (Smith et al. 2016a)

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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