# High incidence of partial colony mortality constrains realized growth for three coral species in southeast Florida

**Nicholas P. Jones[1],***, **Morgan S. Pratchett[1,2], Rosanna J. Milligan[1], David S. Gilliam[1]**

[1]**Nova Southeastern University, Halmos College of Arts and Sciences, 8000 N Ocean Drive, Dania Beach, Florida 33004, USA**
[2]**College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia**

ABSTRACT: Coral colony growth rates are a key demographic trait which can reveal fundamental changes in population health and resilience. With changing environmental conditions, assessing spatial, temporal and taxonomic variation in net coral growth is fundamental to understanding the changing structure of coral assemblages, particularly in high-latitude reefs which may provide refugia against climate change impacts. The high-latitude Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) recently experienced mass coral mortality from heat stress and disease, and most remaining coral colonies are small. It is unclear whether the preponderance of small colonies is due to slow growth rates, high partial colony mortality or high colony turnover. To assess this, the net growth rates of 3 abundant species were quantified interannually between 2000 and 2020. Of 136 tracked colonies, 33% died and a further 61% had partial mortality. Small *Montastraea cavernosa* and *Porites astreoides* colonies generally grew faster than large colonies and had less partial mortality, but *Siderastrea siderea* consistently had high partial mortality. *M. cavernosa* and *S. siderea* net growth rates generally declined following excess heat stress or disease outbreaks, which caused partial and whole colony mortality, but growth rates in all species were negligible even during inter-disturbance periods. Maximum annual growth rates of each species aligned with those found in the Caribbean, but mean growth rates were low and confidence intervals included zero (linear extension, mean ± SD: *M. cavernosa* = 0.03 ± 0.6 cm yr$^{-1}$; *P. astreoides* = 0.2 ± 0.6 cm yr$^{-1}$; *S. siderea* = 0.1 ± 0.3 cm yr$^{-1}$). As a result, coral growth and colony size is significantly constrained, preventing reef growth. Without profound changes in the environmental conditions, recovery capacity will continue to be severely limited.

KEY WORDS: *Montastraea cavernosa* · *Porites astreoides* · *Siderastrea siderea* · Net growth · Linear extension · Long-term monitoring · Disturbance · Inter-disturbance

*—————— Resale or republication not permitted without written consent of the publisher ——————*

## 1. INTRODUCTION

Growth rates of individual coral colonies are a key demographic trait which can reveal fundamental changes in population health and resilience, the ability to absorb a disturbance and recover (Pratchett et al. 2015), and will affect the future abundance, size structure and viability of coral populations. For colonial coral species, growth mostly occurs by addition of coral polyps (Madin et al. 2020), although it is also

possible that some polyps die or are lost, effectively reducing colony size. When the incidence or extent of this partial mortality exceeds the rate of coral growth, then colonies will get smaller over time, reducing their reproductive and recovery potential (Pisapia et al. 2020).

Net growth of coral colonies (accounting for both growth and partial mortality) may vary spatially, temporally and taxonomically (Kuffner et al. 2013, Manzello et al. 2015, Madin et al. 2020), depending on

environmental conditions and disturbance regimes. Importantly, acute disturbances and chronic anthropogenic and natural pressures not only increase rates of partial mortality, but may also constrain rates of coral growth (Ortiz et al. 2018). For some coral species, growth can be suppressed immediately after acute heat stress (Cantin & Lough 2014, Gold & Palumbi 2018, but see Crabbe 2009), irrespective of whether corals bleach (Carilli et al. 2010, Neal et al. 2017). Elevated turbidity and inorganic nutrients can also suppress growth (Dodge et al. 1974, Dodge & Vaisnys 1977, Crabbe & Carlin 2007) and increase the prevalence or extent of partial mortality (Vega Thurber et al. 2014, Jones 2022). Elevated turbidity may exacerbate (Anthony & Connolly 2004) or mediate (Cacciapaglia & van Woesik 2016, Rippe et al. 2018) the effects of heat stress, thereby differentially affecting net growth rate (Helmle et al. 2011, Cooper et al. 2012), while elevated heterotrophic feeding rates of some species on turbid, inshore reefs can enhance lipid reserves and stimulate the recovery of colonies with partial mortality (Manzello et al. 2015). On high-latitude reefs, coral colonies are further subject to temperature and irradiance constraints, which may limit growth or increase partial mortality (Grigg 1981, Logan & Tomascik 1991, Anderson et al. 2015). Under climate change, however, high-latitude reefs have been posited as potential refugia for corals (Beger et al. 2014), but population viability hinges on the growth and survival of individual colonies, particularly recruits. With climate change altering environmental conditions and disturbance regimes on coral reefs (Nyström et al. 2000, Mellin et al. 2019, Pratchett et al. 2020), identifying spatial, temporal and taxonomic variation in net coral growth is fundamental in understanding the changing structure and dynamics of coral populations and communities.

The predominant method used in long-term studies to account for both growth and partial mortality is to measure changes in the planar area of individual coral colonies (e.g. Crabbe 2009, Pratchett et al. 2015, Gold & Palumbi 2018, Madin et al. 2020). Proportional changes in planar area generally decline with increasing colony size, partly due to increasing prevalence and extent of partial mortality in larger colonies (Tanner 1995, Dornelas et al. 2017, Madin et al. 2020, Fong & Todd 2021). While long-term studies have found that most colonies have net growth, particularly in small size classes (Dornelas et al. 2017, Brito-Millán et al. 2019), high rates of colony fission or shrinkage may occur following acute disturbances or environmental stress (Riegl & Purkis 2015, Riegl et al. 2017). Hughes & Tanner (2000) found two-thirds of surviving

*Orbicella annularis* shrank in a 6 yr period (1987–1993) in Jamaica, and Edmunds et al. (2004) found 25% of juvenile corals shrank or did not grow over 1 yr in the Florida Keys, USA. These findings show that apparent stability in colony density or coral cover may belie fundamental changes in demography that undermine population viability and resilience. Measuring planar growth may therefore capture intrinsic differences and the impact of extrinsic factors which cause partial mortality, such as acute disturbances and chronic pressures (Neal et al. 2017, Gold & Palumbi 2018, Rippe et al. 2018, Madin et al. 2020).

In the high-latitude Southeast Florida Coral Reef Ecosystem Conservation Area (ECA), heat stress and stony coral tissue loss disease caused mass coral mortality from 2014 to 2017 (Walton et al. 2018, Jones et al. 2022), with the natural recovery capacity largely dependent on the most abundant remaining coral species. Moderate increases in coral cover were seen on some ECA reefs from 2007 to 2014, prior to these major disturbances (Jones et al. 2022), but in most locations, coral colonies were and remain small. It is unclear whether this results from slow growth rates, high partial mortality or high turnover. To assess this, we tracked coral colonies of the 3 most abundant species (*Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea*) between 2000 and 2020. We quantified interannual net growth rates, which incorporate increases (i.e. growth) and decreases (i.e. partial mortality) in colony size, partial mortality prevalence by species, colony size and colony age, and recorded incidences of whole colony mortality of individual coral colonies. Using these data, we asked (1) How do net growth rate, partial and whole colony mortality prevalence vary by species, colony size and colony age? (2) Are spatial and temporal factors influencing net growth rates and whole colony mortality? To further understand the preponderance of small colonies, we compared the maximum (potential) and mean (realized) net growth rates of colonies which recruited during the study, to assess whether they are reaching their potential size.

## 2. MATERIALS AND METHODS

Variation in net coral growth and in partial and whole colony mortality was examined from 2000 to 2020 by annually tracking 136 coral colonies of 3 species (*Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea*) in fixed quadrats at 19 sites across 3 reef habitats (inshore, mid-reef and offshore) in southeast Florida (26.3114 to 26.0042° N;

Table S1 in the Supplement at www.int-res.com/ articles/suppl/m721p059_suppl.pdf). Each individual colony was tracked for 5 to 21 yr, with colonies added or removed as they recruited or died. All colonies were photographed in the same orientation every year. No surveys were conducted in 2009 due to funding constraints. A 5 yr minimum continuous time period was selected to avoid assessing colonies that appeared visibly healthy but had underlying conditions leading to immediate mortality and restricting growth; moreover, this timespan was hypothesized to sufficiently capture interannual variation and trends in growth of each colony. Surveys were typically conducted from October to December in each sample year. Habitats varied with depth and distance offshore. The inner reef habitat, 275–780 m offshore at a depth range of 4–10 m, comprises the nearshore ridge complex and linear inner reef. The middle reef habitat is 770–2000 m offshore at 11–16 m depth. The outer reef habitat is 1500–3000 m offshore at 16– 18 m depth. Sites were also assigned to 1 of 3 subregions, separated by latitude/by ports and inlets as per Jones et al. (2020). The Deerfield sub-region, furthest north, is between Boca and Hillsboro inlets (~9 km); the Broward/Fort Lauderdale sub-region is between Hillsboro Inlet and Port Everglades (~18 km); and the Hollywood/Miami sub-region is furthest south, between Port Everglades and the Broward/ Miami-Dade County line (~13 km).

## 2.1. Study species

The 3 study coral species were expected to have different growth and mortality rates, influenced by their life-history traits. *M. cavernosa* is a massive, gonochoric broadcast spawning coral, which dominates cover in the study area. Despite being considered relatively stress tolerant (Darling et al. 2012), recent bleaching and disease events have resulted in significant declines in *M. cavernosa* density and cover in the ECA (Walton et al. 2018, Jones et al. 2020). *P. astreoides* is a brooding, encrusting species, which has increased in cover and density on the ECA in recent years (Jones et al. 2020) and has previously been classified as resilient to disturbances and weedy (Darling et al. 2012). *S. siderea* is a massive, gonochoric broadcast spawning species, is considered stress tolerant (Darling et al. 2012), was not heavily impacted by recent disease and has a high recruitment rate in Florida (Hayes et al. 2022). Each species grows primarily in the horizontal plane in southeast Florida (Goldberg 1973, Lirman 2000).

## 2.2. Coral health and growth rate

Replicate colonies of *M. cavernosa* (n = 53), *P. astreoides* (n = 46) and *S. siderea* (n = 37) were surveyed over successive years in the ECA. Photographic images of each colony were taken annually using a digital camera in an Ikelite housing mounted at a fixed distance onto a 0.75 m$^2$ quadrat parallel to the colony surface. A scale bar of known width was attached to the edge of the quadrat, which was aligned with the uppermost surface of the colony when photographed. Incidences of partial or whole colony mortality were recorded *in situ*. It was not possible to distinguish whether all injuries occurred in the last year; therefore, incidences of interannual decline in colony size were calculated from net growth measurements using images. The interannual change in colony size was not calculated in a year that a colony died. Images were qualitatively inspected for skew, distortion or obstruction of the colony boundary, and images with inferred high parallax error or that did not capture the colony boundary were removed. Fifteen colonies were omitted from quantitative growth analysis due to high parallax error.

To calculate coral growth rate, the living tissue planar area of the remaining 121 colonies was measured annually from photographic images (*M. cavernosa*: n = 42, *P. astreoides*: n = 42, *S. siderea*: n = 37). Planar live tissue area was measured using Image J software (Schneider et al. 2012). Images were calibrated using the scale bar, and the outline of the colony was carefully traced to calculate the total area of living tissue at each timepoint (cm$^2$). From this, the arithmetic mean radius (AMR, cm), colony diameter (cm) and net growth rate of each colony were calculated (Eq. 1). Net growth rate was calculated as both the relative change in live tissue area (% yr$^{-1}$), which accounts for variation in colony size, and linear extension as the change in AMR (cm yr$^{-1}$). The colony diameter at each timepoint was calculated from the AMR:

$$\text{AMR} = \frac{\sqrt{t0}}{\pi} \qquad (1.1)$$

$$\text{Growth Rate} = \frac{([t+n]-t0)/n}{t0} \times 100 \qquad (1.2)$$

$$\text{Linear Extension} = \frac{([AMR + n] - AMR0)}{n} \qquad (1.3)$$

The AMR was calculated from the live tissue area (Eq. 1.1). Net growth rate was calculated as relative growth rate in percent per year (Eq. 1.2) and linear extension in cm per year (Eq. 1.3), where $t0$ is the live tissue area in year $X$, $t + n$ is the live tissue area at the

next timepoint, AMR0 is the AMR in year $X$, AMR + $n$ is the AMR at the next timepoint, and $n$ is the time between monitoring periods.

Potential vs. realized growth of juvenile colonies (<5 cm diameter and recruiting during the study period) was assessed by comparing the potential increase in AMR with the realized increase in AMR, where the potential increase in AMR is calculated as the mean of the maximum interannual change in AMR measured per colony and assumes isometric growth over time. The realized increase in AMR is the measured increase in AMR over time of juvenile colonies. Realized growth of juvenile colonies was specifically quantified to elucidate the long-term growth potential of recruits entering the system naturally or introduced as small colonies through restoration.

## 2.3. Statistical analysis

Statistical analysis was conducted in R (R Core Team 2022). Linear mixed effects models (LMMs) were used to assess variation in annual relative growth rate (% $yr^{-1}$; n = 1317) and change in AMR (cm $yr^{-1}$; n = 1317) using the 'lme' function in the 'nlme' package (Pinheiro et al. 2017). LMMs were used as growth rates and were normally distributed. Relative growth rate was assessed in relation to all factors: Species, Minimum Colony Age, Colony Diameter, Survey Year, Habitat and Sub-region. Change in AMR was assessed in relation to Species, Colony Diameter and Survey Year, to assess whether the preponderance of small colonies was linked to variation in partial mortality with colony size and to identify temporal factors that may be causing colony shrinkage. Species (3 levels), Survey Year (19 levels), Habitat (3 levels) and Sub-region (3 levels) were considered as categorical, fixed effects (Table S2). Minimum Colony Age (recorded as the number of years the coral was surveyed, not the exact age of the colony) and Colony Diameter (cm; calculated from projected area and considered at any given year as the diameter of live tissue in the previous year) were included as continuous, fixed effects. Repeated measurements of the same colony were accounted for by incorporating Colony ID as a random intercept in all models. A constant plus power variance structure was added to the relative growth rate model using the 'varConstPower' function (Pinheiro & Bates 2000), which incorporated heterogeneity in the variance of both Colony Diameter and Species (Eq. 2) following the protocol in Zuur et al. (2009):

$$\text{Var}(\varepsilon_{ij}) = \sigma^2 \times (\delta1 + |\text{Species}_{ij}| \text{Diameter}_{ij} | \delta2)^2 \quad (2)$$

Residual variance ($\varepsilon$) is proportional to the constant $\delta1$ plus the power of the variance covariates Species and Colony Diameter.

For relative growth rate, the full model consisted of all fixed effects, the interaction between Species and each fixed effect and the random effect Colony ID (Eq. 3). Interactions between other fixed effects were not assessed, as many model combinations failed due to lack of convergence, and the data suggested the main interactions were interspecific. For change in AMR, the full model consisted of the fixed factors Species, Colony Diameter and Survey Year, their interactions and the random effect Colony ID (Eq. 3):

$$\text{Growth Rate}_{ij} \sim \text{Gaussian}(\mu_{ij}) \quad (3.1)$$

$$\varepsilon_{ij} \sim N(0, \sigma^2) \quad (3.2)$$

Relative Growth Rate$_{ij}$ = Species$_{ij}$ +
Sub-region$_{ij}$ + Habitat$_{ij}$ + Survey Year$_{ij}$ +
Minimum Colony Age$_{ij}$ + Colony Diameter$_{ij}$ +
Species$_{ij}$ × Sub-region$_{ij}$ + Species$_{ij}$ × Habitat$_{ij}$ + (3.3)
Species$_{ij}$ × Survey Year$_{ij}$ + Species$_{ij}$ ×
Minimum Colony Age$_{ij}$ + Species$_{ij}$ ×
Colony Diameter$_{ij}$ + Colony ID$_i$ + $\varepsilon_{ij}$

Linear Extension $_{ij}$ =
Species$_{ij}$ × Colony Diameter$_{ij}$ × (3.4)
Survey Year$_{ij}$ + Colony ID$_i$ + $\varepsilon_{ij}$

$$\text{Colony ID} \sim N(0, \sigma^2) \quad (3.5)$$

Growth rate (both relative growth rate and linear extension) was modeled with a Gaussian distribution (Eq. 3.1), assuming residuals ($\varepsilon$) are normally distributed with mean 0 and variance $\sigma^2$ (Eq. 3.2). LMMs examined variation in relative growth rate, where growth rate $ij$ refers to the $j^{th}$ observation at Colony ID $i$ (Eq. 3.3). LMMs also examined the variation in linear extension, expressed as change in AMR (Eq. 3.4). Random intercept Colony ID is assumed to be normally distributed with mean 0 and variance $\sigma^2$ (Eq. 3.5).

Term selection to find the fitted minimum adequate model (MAM) was conducted via backwards selection from the full model, using Akaike's information criterion (AIC) scoring of multiple candidate models fitted by maximum likelihood. In the event of equivalent models (i.e. within an AIC score of 2; Burnham & Anderson 2004), the simplest model was selected. The MAM was validated by plotting standardized

residuals against fitted values and standardized residuals against each fixed effect. The MAM was run by restricted maximum likelihood to give estimates of the coefficients and allow for model interpretation.

Post hoc pairwise assessment of retained fixed effects in the MAM was conducted using the package 'emmeans' and the Tukey method, where differences in the response variable were analyzed between levels of a fixed effect (e.g. Species) or interaction (e.g. Species × Minimum Colony Age) based on model predictions (Lenth 2019). Emmeans linear contrasts were used to assess significant variation in levels of a fixed effect against the mean value. For interactions between categorical and continuous fixed effects (covariates), the 'emtrends' function was used to assess covariate trends between levels of the categorical, fixed effect.

# 3. RESULTS

## 3.1. Colony health

Of the 136 coral colonies monitored between 2000 and 2020, 33% died and a further 61% experienced partial colony mortality (n = 45 and n = 83, respectively; Fig. 1). Only 5 *Montastraea cavernosa* and 3 *Siderastrea siderea* colonies exhibited no partial mortality. All *Porites astreoides* had whole and/or partial colony mortality. Of the 45 colonies that died, 37 died between fall 2013 and 2016: 17 *M. cavernosa* colonies died from 2014 to 2015 and 7 from 2015 to 2016; 7 *P. astreoides* colonies died from 2015 to 2016; and 4 *S. siderea* colonies died between 2013 and 2015. Of the 91 colonies still alive in 2020, 12% had declined in size: 2 *M. cavernosa* on the inner reef, 2 *P. astreoides* on the inner reef, 1 *P. astreoides* on the middle reef and 3 *S. siderea* on each of the middle and outer reefs. Only 58% of the 45 colonies surveyed in 2000 survived until 2020: 50% of *M. cavernosa* colonies (12 of 24), 45% of *P. astreoides* colonies (5 of 11), but 90% of *S. siderea* colonies (9 of 10).

Coral growth rate was quantitively assessed on 121 colonies. For all 3 species, the average net growth rate was negligible and not significantly different from zero (Table 1, Fig. 2). Of these colonies, 86 were still alive in 2020, and 76 had a net increase in size (AMR) from their first to last survey point: 21 of 23 *M. cavernosa*, 29 of 31 *P. astreoides* and 26 of 32 *S. siderea*. The mean (±SE) increase in AMR (i.e. linear extension) in the 76 colonies with net growth was 0.13 ± 0.02 cm yr$^{-1}$ for *M. cavernosa*, 0.2 ± 0.02 cm yr$^{-1}$ for *P. astreoides* and 0.12 ± 0.01 cm yr$^{-1}$ for *S. siderea*.

## 3.2. Coral growth rate

Relative growth rate (assessed as proportional change in planar live tissue area, % yr$^{-1}$) varied among species, by colony diameter, minimum colony age, habitat and survey year (LMM; Table S3). Model coefficients indicated that the interaction between species and colony diameter had the biggest effect size on coral growth rate (Table S4). *M. cavernosa* growth rate varied little with colony diameter (estimate = −0.23, 95% CI: −0.52, 0.06), but some small colonies grew quickly (Fig. 2). *S. siderea* and *P. astreoides* growth rates declined with colony diameter (estimate = −3.04, 95% CI: −4.33, −1.76; estimate = −1.78, 95% CI: −2.63, −0.93; Fig. 2). *M. cavernosa*
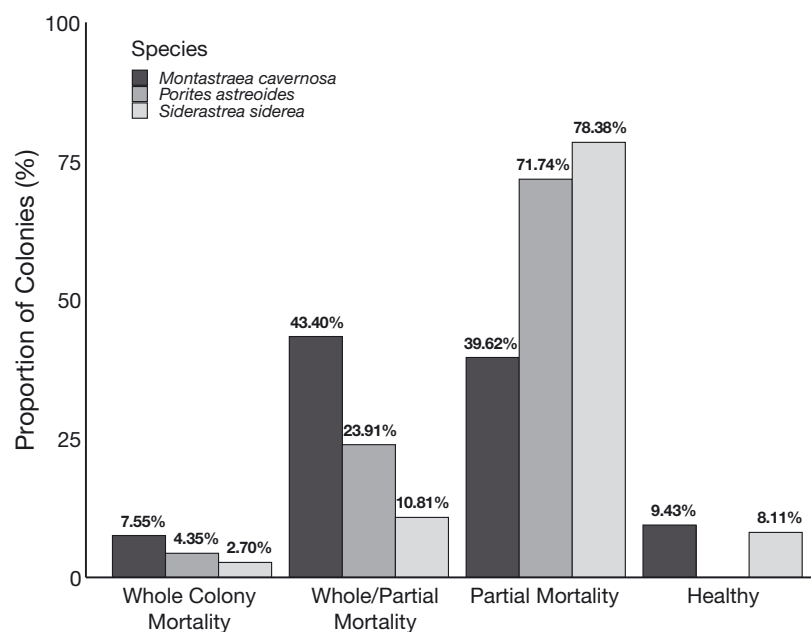


Fig. 1. Coral colony health (recorded as partial or whole colony mortality) from 2000 to 2020. Whole colony mortality = colony died but had no prior instances of partial colony mortality. Whole/Partial mortality = colony had partial mortality in at least one year and subsequently died. Partial mortality = colony had partial mortality in at least one year but was alive at the end of the study. Healthy = colony had no partial or whole colony mortality. The percentage reflects the proportion of colonies in each category

Table 1. Annual growth rates for the 3 coral species (mean ± SD). Relative growth rate: mean percentage change in planar area per year; AMR: arithmetic mean radius of colonies at their initial survey timepoint; max. change in AMR: species mean of the maximum change in AMR per colony

| Species | Relative growth rate (% yr$^{-1}$) | Planar change in area (cm$^2$ yr$^{-1}$) | AMR (cm) | Change in AMR (cm yr$^{-1}$) | Max. change in AMR (cm yr$^{-1}$) |
|---|---|---|---|---|---|
| *Montastraea cavernosa* | 8.42 ± 28.8 | −1.11 ± 43.2 | 5.1 ± 5.1 | 0.03 ± 0.6 | 0.48 ± 0.26 |
| *Porites astreoides* | 18.6 ± 39.1 | 4.18 ± 17.5 | 2.2 ± 1.3 | 0.17 ± 0.6 | 0.75 ± 0.36 |
| *Siderastrea siderea* | 20.1 ± 42.3 | 2.04 ± 7.3 | 1.6 ± 1.2 | 0.12 ± 0.3 | 0.51 ± 0.18 |

and *P. astreoides* growth rate declined with minimum colony age (estimate = −1.24, 95% CI: −1.98, −0.49; estimate = −1.25, 95% CI: −2.25, −0.24; Fig. S1). *S. siderea* had relatively consistent growth rate with minimum colony age, but this was around zero (estimate = 0.31, 95% CI: −0.63, 1.24).

Spatial variations in growth rate were less pronounced; the minimum adequate model suggested a mild effect of habitat on growth rate, but no significant effect of sub-region. *M. cavernosa* and *P. astreoides* growth rates did not significantly vary by habitat, but *M. cavernosa* growth rates were marginally lower on the inner reef than the mean growth rate for all colonies (emmeans linear contrasts, estimate = −4.1 ± 2.09% yr$^{-1}$ [SE], $t$ = −2.0, p = 0.07),

largely due to increased partial mortality prevalence and extent on larger colonies on the inner reef. *S. siderea* growth rate was significantly higher on the inner reef than the outer reef (estimate = 18.05 ± 5.5% yr$^{-1}$, $t$ = 3.3, p = 0.04).

Linear extension (assessed as change in AMR, cm yr$^{-1}$) varied by species, colony diameter and survey year, with a significant 3-way interaction (LMM; Fig. S2). During most years, linear extension declined with colony diameter in all 3 species (estimate: *M. cavernosa* = −0.008 ± 0.003 [SE]; *P. astreoides* = −0.17 ± 0.01; *S. siderea* = −0.12 ± 0.02; Fig. S3). Juvenile *M. cavernosa* and *P. astreoides* colonies (<5 cm diameter) generally had less partial mortality than larger colonies, but partial mortality in *S. siderea* was
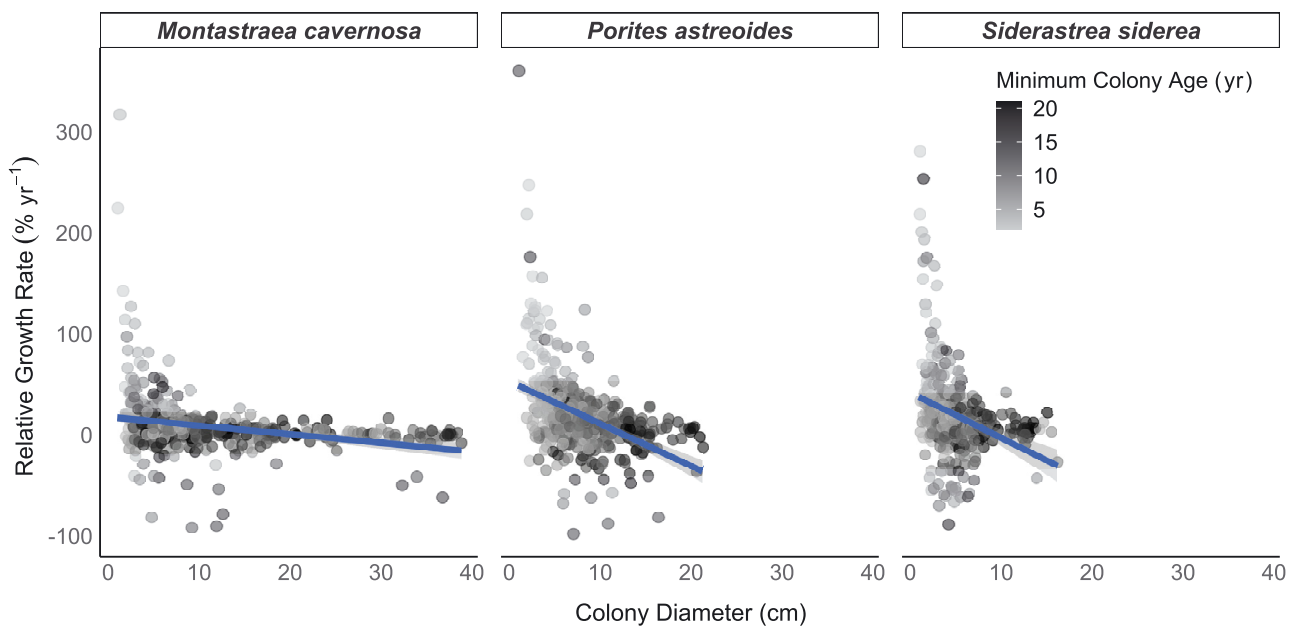


Fig. 2. Relative growth rate (proportional change in colony area) vs. colony size (colony live tissue diameter). Blue regression line represents trend in mean relative growth rate (linear mixed effects model [LMM] for relative growth rate vs. colony diameter: *Montastraea cavernosa*: estimate = −0.23% yr$^{-1}$, $t$ = −1.5, p = 0.1; *Porites astreoides*: estimate = −1.78% yr$^{-1}$, $t$ = −4.1, p < 0.0001, *Siderastrea siderea*: estimate = −3.04% yr$^{-1}$, $t$ = −4.63, p < 0.0001); shaded area represents 95% confidence interval. Points represent the relative growth rate of each coral colony during each timepoint (LMM for relative growth rate vs. minimum colony age: *Montastraea cavernosa*: estimate = −1.24% yr$^{-1}$, $t$ = −3.6, p = 0.001; *Porites astreoides*: estimate = −1.24% yr$^{-1}$, $t$ = −2.4, p = 0.02, *Siderastrea siderea*: estimate = 0.31% yr$^{-1}$, $t$ = 0.64, p = 0.5)

more consistent with colony size (Table 2). Older, larger colonies of all 3 species experienced interannual declines in AMR more frequently than smaller conspecifics (Table 3), and all large colonies decreased in size during at least 1 interannual period ($t0$ to $t + n$; Table 2).

### 3.3. Interannual growth pattern

Growth rate and linear extension fluctuated greatly between years (Fig. 3). For *M. cavernosa*, the annual growth rate (±SE) ranged from $0.42 \pm 3.5\%$ yr$^{-1}$ in 2017–2018 to $16.6 \pm 32.5\%$ yr$^{-1}$ in 2018–2019. For *P. astreoides*, annual growth rate was lowest ($-1.05 \pm 5.0\%$ yr$^{-1}$) from 2019 to 2020 and highest ($53 \pm 13.1\%$ yr$^{-1}$) from 2006 to 2007. *S. siderea* growth rate ranged from $-8.4 \pm 7.7\%$ yr$^{-1}$ from 2005 to 2006, to $45.8 \pm 12.8\%$ yr$^{-1}$ from 2010 to 2011. *M. cavernosa* growth rate from 2019 to 2020 exceeded that from 2015 to 2016 (Tukey, p = 0.02). *P. astreoides* and *S. siderea* growth rates did not significantly vary between any time points (Tukey, p > 0.05). Growth rates were negative (but not significantly so) for *M. cavernosa* from 2004 to 2005 (emmeans linear contrasts, estimate = $-7.4\%$ yr$^{-1}$, $t = -1.9$, p = 0.10) and strongly negative from 2015 to 2016 (emmeans linear contrasts, estimate = $-8.8\%$ yr$^{-1}$, $t = -2.4$, p < 0.05). *P. astreoides* growth rates were significantly higher than the mean from 2006 to 2007 (emmeans linear contrasts, estimate = $17.9\%$ yr$^{-1}$, $t = 3.2$, p = 0.03).

Growth rates were marginally lower than the mean for *S. siderea* from 2005 to 2006 and strongly negative from 2006 to 2007 (emmeans linear contrasts, estimate = $-17.1\%$ yr$^{-1}$, $t = -2.7$, p = 0.06 and $-20.1\%$ yr$^{-1}$, $t = -3.1$, p = 0.04).

Regionwide, *M. cavernosa* linear extension ranged from $-0.73 \pm 0.36$ cm yr$^{-1}$ (SE) from 2015 to 2016 to $0.20 \pm 0.08$ cm yr$^{-1}$ from 2019 to 2020. *P. astreoides* linear extension ranged from $-0.14 \pm 0.15$ cm yr$^{-1}$ from 2019 to 2020 to $0.54 \pm 0.12$ cm yr$^{-1}$ from 2006 to 2007. *S. siderea* linear extension ranged from $-0.22 \pm 0.16$ cm yr$^{-1}$ from 2005 to 2006 to $0.25 \pm 0.06$ cm yr$^{-1}$ from 2001 to 2002. *M. cavernosa* linear extension from 2003 to 2004, from 2009 to 2010 and from 2019 to 2020 was significantly higher than from 2015 to 2016 (Tukey, p < 0.05). *P. astreoides* linear extension from 2006 to 2007 and from 2010 to 2011 was significantly greater than from 2019 to 2020 (Tukey, p < 0.05). *S. siderea* linear extension was significantly lower from 2006 to 2007 than from 2019 to 2020 (Tukey, p = 0.04). In all 3 species, survey years with significantly lower linear extension had strong declining trends in linear extension with colony diameter (Fig. S3).

### 3.4. Realized vs. potential growth

Linear extension of 81 colonies tracked as juveniles (<5 cm diameter) declined with colony age for all 3 species, most noticeably in *P. astreoides* (Fig. 4). Mean maximum annual linear extension of juveniles

Table 2. Percentage of colonies which declined in arithmetic mean radius (AMR) during at least 1 interannual period by size class (colony diameter). Note: While some colonies declined in size multiple times, each unique colony is only counted once per size class; NA: not applicable, as no *S. siderea* colonies larger than 20 cm diameter were surveyed

| Species | Colony size class | | | |
| --- | --- | --- | --- | --- |
| | Juvenile: <5 cm (%) | Small: 5–10 cm (%) | Medium: 10–20 cm (%) | Large: >20 cm (%) |
| *Montastraea cavernosa* | 61 | 73 | 79 | 100 |
| *Porites astreoides* | 25 | 51 | 75 | 100 |
| *Siderastrea siderea* | 71 | 65 | 67 | NA |

Table 3. Mean colony diameter and minimum colony age during every interannual growth rate record, mean colony diameter (calculated from projected colony area) and mean minimum colony age during each increase or decrease in net arithmetic mean radius (AMR) per time period

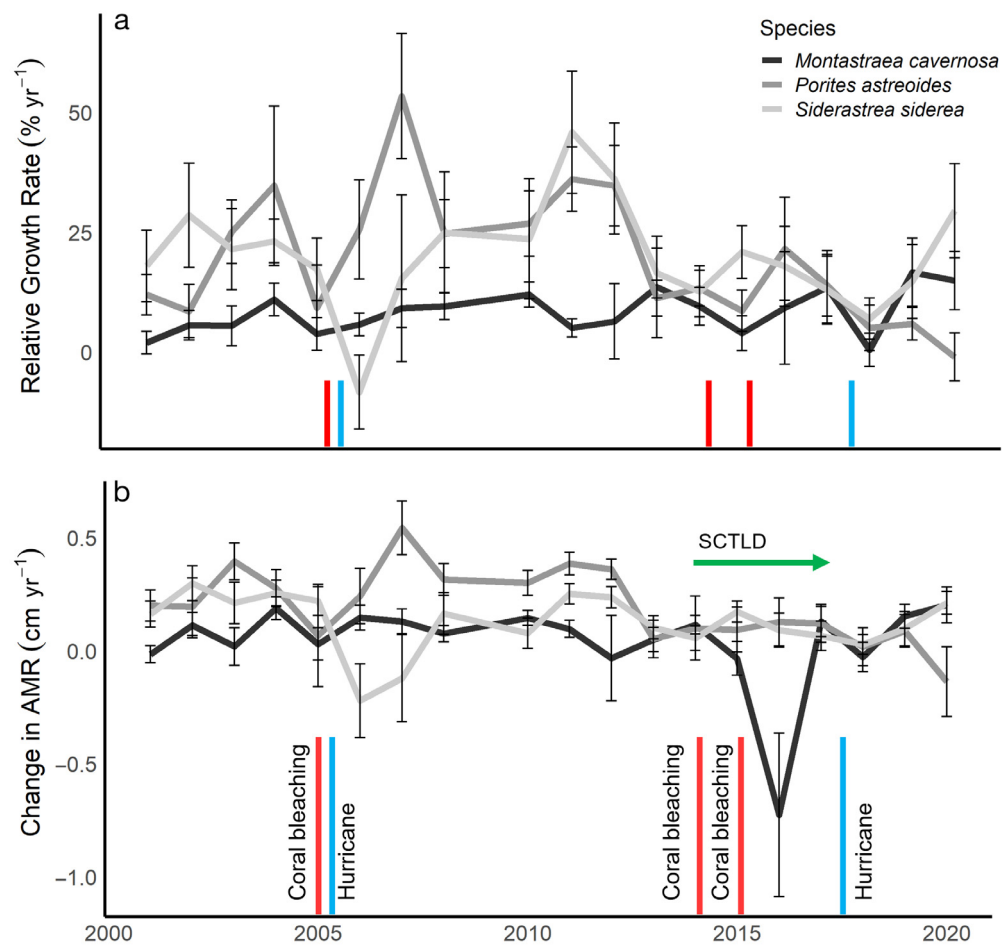| Species | All colonies (±SE) | | Diameter (cm ± SE) | | Minimum colony age (yr ± SE) | |
| --- | --- | --- | --- | --- | --- | --- |
| | Diameter (cm) | Minimum colony age (yr) | Increased AMR | Decreased AMR | Increased AMR | Decreased AMR |
| *Montastraea cavernosa* | 11.3 ± 0.4 | 8.8 ± 0.2 | 10.2 ± 0.5 | 13.8 ± 0.9 | 8.6 ± 0.3 | 9.3 ± 0.4 |
| *Porites astreoides* | 8.3 ± 0.2 | 7.8 ± 0.2 | 7.9 ± 0.2 | 9.5 ± 0.4 | 7.1 ± 0.2 | 10.4 ± 0.5 |
| *Siderastrea siderea* | 4.9 ± 0.1 | 7.7 ± 0.3 | 4.8 ± 0.2 | 5.2 ± 0.3 | 7.4 ± 0.3 | 8.7 ± 0.5 |

Fig. 3. Interannual growth pattern of the 3 coral species. (a) Mean relative growth rate ± SE, based on proportional change in planar area (% change $yr^{-1}$). (b) Mean ± SE change in arithmetic mean radius (AMR) (cm $yr^{-1}$). Major acute disturbances, namely bleaching (red lines) and hurricanes (blue lines), during the study period are noted. Multiple hurricanes impacted the Southeast Florida Coral Reef Ecosystem Conservation Area (ECA) in 2005, and Hurricane Irma impacted the ECA in 2017. Stony coral tissue loss disease (SCTLD; green arrow) was prevalent in the ECA from 2014 to 2017

(i.e. the mean of the maximum annual linear extension per colony, ±SE) was 0.46 ± 0.01, 0.72 ± 0.1 and 0.52 ± 0.01 cm $yr^{-1}$ for *M. cavernosa*, *P. astreoides* and *S. siderea*, respectively, but mean annual linear extension was substantially lower (0.13 ± 0.02, 0.23 ± 0.0 and 0.12 ± 0.02 cm $yr^{-1}$, respectively). After 20 yr, realized increases in colony size were 3 times lower than their potential growth (assuming isometric growth), such that after 20 yr, the mean AMR of juveniles was only 3.27 ± 0.6 cm (SE) for *M. cavernosa*, 5.0 ± 0.0 cm for *P. astreoides* and 3.7 ± 0.8 cm for *S. siderea*.

## 4. DISCUSSION

Coral growth recorded from 2000 to 2020 in the Southeast Florida Coral Reef ECA was very limited for *Montastraea cavernosa*, *Porites astreoides* and *Siderastrea siderea*, which are the 3 most abundant corals in this region. This was primarily due to exceptionally high prevalence and extent of partial mortality, particularly in larger or older colonies, which limited realized growth and constrained colony size. Aside from moderate rates (33%) of whole colony mortality, 61% of surviving colonies had partial mortality, and 85% of all colonies surveyed reduced in size during at least 1 interannual period. Every large colony (>20 cm diameter) reduced in size during at least 1 interannual period, and 12% of the colonies still alive in 2020 were smaller than at the start of monitoring. Of these, 19% of *S. siderea* had shrunk, and no colonies observed here grew into the largest size class (>20 cm diameter). As a result, there is a predominance of small colonies, and our findings suggest that under current conditions, few natural colonies, or those introduced through restoration, are
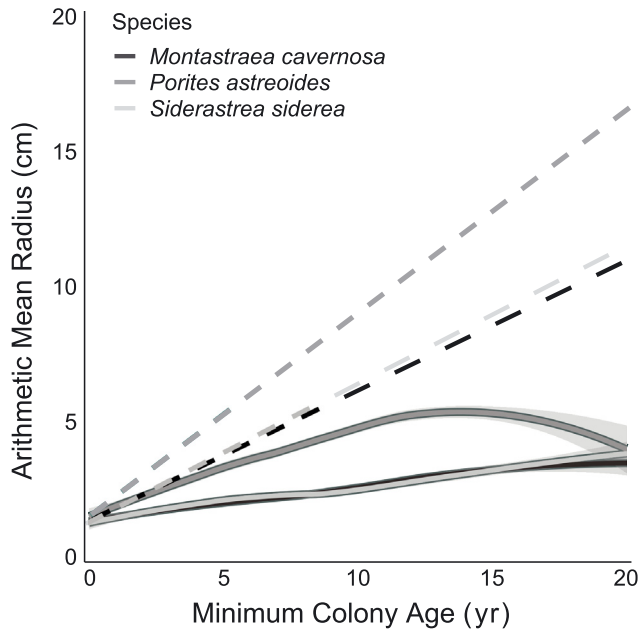
Fig. 4. Potential vs. realized size progression with minimum colony age of juveniles (colonies < 2.5 cm arithmetic mean radius [AMR] at first measurement). Dashed lines (potential AMR) represents mean maximum potential increase in AMR (mean of maximum change in AMR per colony; Table 1) with time. Solid lines represents mean measured AMR over time of juveniles (shading = ±1 SE)

going to attain large sizes (>20 cm diameter), meaning long-term recovery is unlikely.

Colony growth (measured as change in AMR) declined with size in all 3 species, most evidently during periods with acute disturbances. Small, relatively young *M. cavernosa* and *P. astreoides* colonies had generally less partial mortality than older, large colonies, giving them significantly increased growth capacity. This may lead to short-term increases in coral cover, but sustained increases in colony size appear to be prevented by cumulative stress and acute disturbances (Hughes & Jackson 1985, Pisapia & Pratchett 2014). Growth rates of *S. siderea* declined with colony size, but not minimum colony age, maintaining a population of small, potentially old colonies (Elahi & Edmunds 2007). This may explain the high abundance of small, fecund colonies found in southeast Florida (Moyer et al. 2003, St Gelais et al. 2016) but may prevent this species from contributing greatly to reef growth.

Whole and partial colony mortality were most prevalent following years with known acute disturbances or disease outbreaks, which effectively slowed the growth rate of the reef-building species *M. cavernosa* and *S. siderea*. This study spanned multiple acute disturbances that impacted the ECA: El Niño-related

bleaching in 2005, 2014 and 2015, major hurricanes in 2005 and 2017 and a severe disease outbreak, stony coral tissue loss disease, which peaked in 2016 (Hayes et al. 2022, Jones et al. 2022). Whole colony mortality was primarily observed rapidly after acute disturbance (i.e. the year of or after acute disturbance). Of the 45 colonies that died, 82% died from late 2013 to 2016, and *M. cavernosa* and *S. siderea* growth rates were lowest following acute disturbances.

Interspecific differences in growth rate suggest variable resilience to acute disturbances which align with their predicted life-history strategies (Darling et al. 2012) and susceptibility to temperature stress in the ECA (Jones et al. 2020). *M. cavernosa* linear extension was lowest from 2015 to 2016 and growth rate lowest from 2017 to 2018, with the greatest decline in live tissue planar area in the largest and oldest colonies. Heat stress in combination with local environmental stress has previously been suggested to limit *M. cavernosa* growth rate in the Florida Keys (Manzello et al. 2015) and coupled with disease has limited growth in the ECA (Walton et al. 2018). Despite this, *M. cavernosa* colonies that survived were growing faster at the end of the study period than at any point in the previous 20 yr. *M. cavernosa* growth rate was highest from 2018 to 2019, linear extension was highest from 2019 to 2020, and the growth rate from 2019 to 2020 was significantly higher than from 2015 to 2016. Potential explanations include that colonies resistant to heat stress and disease or recruited during the thermal stress event have intrinsic resilience (Darling & Côté 2018, Madin et al. 2020), or that environmental conditions are facilitating increased growth rate (Cooper et al. 2012). Mean and minimum sea surface temperature have risen in the ECA since 2007 (Jones et al. 2020), and with no extreme thermal stress events experienced since 2015, higher mean annual temperature may be facilitating increased growth (Lough & Barnes 2000, Cooper et al. 2012, Manzello et al. 2015). Whether this increase in growth and linear extension is resulting in increased calcification requires further investigation (Helmle et al. 2011), but this does suggest that *M. cavernosa* may have increased capacity to recover during inter-disturbance periods.

*S. siderea* growth rate and linear extension were lowest following heat stress from 2005 to 2006 and both remained low from 2006 to 2007. *S. siderea* is generally considered to be resistant to acute disturbance, often maintaining growth rates despite thermal stress (Darling et al. 2012, Kuffner et al. 2013, Rippe et al. 2018). Our evidence suggests that in the ECA, intense thermal stress may reduce *S. siderea*

growth rate and kill whole colonies, potentially accounting for mortality of 4 colonies in late 2013 to 2015, but most colonies persist and growth rate generally recovers within several years.

No clear effect of acute disturbance on *P. astreoides* growth rate was detected here, but 16% of colonies surveyed between 2015 to 2016 died and growth rates subsequently remained low, suggesting that despite initial increased thermal tolerance, repeated heat stress has negatively impacted the *P. astreoides* population (Grottoli et al. 2014, Manzello et al. 2015, Jones et al. 2020). Growth rates were highest for *P. astreoides*, increasing their recovery potential, but partial mortality was exceptionally high for larger colonies, suggesting the population will continue to be dominated by small colonies.

Acute disturbances correlated with some interannual declines in *M. cavernosa* and *S. siderea* growth rate and most instances of whole colony mortality, but low growth rates and high rates of partial mortality were observed even during supposed inter-disturbance periods, suggesting local pressures, either related to the high-latitude environmental conditions, or locally elevated sedimentation and eutrophication (Jones 2022), are contributing significantly to limited net growth (Hughes & Jackson 1980, Elahi & Edmunds 2007, Crabbe 2009, Ortiz et al. 2018). For instance, *P. astreoides* growth rate and linear extension were lowest during the inter-disturbance period from 2019 to 2020, when *M. cavernosa* and *S. siderea* growth rates were high. *P. astreoides* has an encrusting growth form, which increases its susceptibility to overgrowth interactions with macroalgae that increase in cover during periods devoid of major hydrodynamic action (Lirman 2000, Mumby et al. 2005).

Growth rates of *M. cavernosa* and *P. astreoides* were consistent across all locations studied, while *S. siderea* exhibited slight inshore–offshore variation. In the Florida Keys, the local climate has been suggested to buffer *S. siderea* from reduced growth in nearshore areas during heat stress events (Rippe et al. 2018). Our study suggested that *S. siderea* also grew faster at inshore sites in the adjoining high-latitude ECA, but 60% of the colonies alive in 2020 had still shrunk in at least 1 interannual period. *M. cavernosa* and *P. astreoides* growth rates were slightly lower on the inner reef and higher on the middle reef, but this is likely largely a function of colony size (Pratchett et al. 2015, Dornelas et al. 2017). Despite accounting for colony size in the model, most large *M. cavernosa* and *P. astreoides*, which experienced the greatest decline in live tissue planar area from partial mortality, are found on the

inner reef. Huston (1985) found *M. cavernosa* growth rates were highest at 16–25 m depth (linear extension = 0.36 to 1.1 cm yr$^{-1}$), and in our study, twice as many *M. cavernosa* and *P. astreoides* colonies died on the inner reef as on the outer reef (~18 m depth), suggesting there may be some depth-related stress resistance (Bongaerts & Smith 2019). No clear pattern in growth rate variation by sub-region was seen for any species, reflective of minimal difference in latitude within the ECA which may influence changes in growth rate (Cooper et al. 2012).

In conclusion, low net growth rates are primarily due to high partial colony mortality, which has further resulted in a preponderance of small colonies for each of the 3 most abundant coral species in the ECA. Maximum growth rates of *M. cavernosa*, *P. astreoides* and *S. siderea* in the ECA align with growth rates recorded in the tropical western Atlantic (e.g. Hughes & Jackson 1985, Huston 1985, Elahi & Edmunds 2007, Crabbe 2009), but these growth rates are rarely sustained long-term. This has important implications for natural recovery and assisted recovery via restoration, where the fragmentation of large colonies and subsequent reattachment to maximize growth has become commonplace (Page et al. 2018). Our findings suggest that while initial growth rates of small or juvenile corals may be high, these are rarely sustained due to acute disturbances and chronic pressures. Without significant change in the environmental conditions, high rates of partial mortality will persist, constraining growth and resulting in a coral assemblage dominated by small colonies with limited recovery capacity.

LITERATURE CITED

Anderson KD, Heron SF, Pratchett MS (2015) Species-specific declines in the linear extension of branching corals at a subtropical reef, Lord Howe Island. Coral Reefs 34: 479–490

Anthony KR, Connolly SR (2004) Environmental limits to growth: physiological niche boundaries of corals along turbidity–light gradients. Oecologia 141:373–384

Beger M, Sommer B, Harrison PL, Smith SD, Pandolfi JM (2014) Conserving potential coral reef refuges at high latitudes. Divers Distrib 20:245–257

Bongaerts P, Smith TB (2019) Beyond the 'Deep Reef Refuge' hypothesis: a conceptual framework to characterize persistence at depth. In: Loya Y, Puglise K, Bridge T (eds) Mesophotic coral ecosystems. Coral reefs of the world, Vol 12. Springer, Cham, p 881–895

Brito-Millán M, Vermeij MJA, Alcantar EA, Sandin SA (2019) Coral reef assessments based on cover alone mask active dynamics of coral communities. Mar Ecol Prog Ser 630:55–68

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304

Cacciapaglia C, van Woesik R (2016) Climate-change refugia: shading reef corals by turbidity. Glob Change Biol 22:1145–1154

Cantin NE, Lough JM (2014) Surviving coral bleaching events: *Porites* growth anomalies on the Great Barrier Reef. PLOS ONE 9:e88720

Carilli JE, Norris RD, Black B, Walsh SM, McField M (2010) Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. Glob Change Biol 16:1247–1257

Cooper TF, O'Leary RA, Lough JM (2012) Growth of Western Australian corals in the Anthropocene. Science 335:593–596

Crabbe MJC (2009) Scleractinian coral population size structures and growth rates indicate coral resilience on the fringing reefs of North Jamaica. Mar Environ Res 67:189–198

Crabbe MJC, Carlin JP (2007) Industrial sedimentation lowers coral growth rates in a turbid lagoon environment, Discovery Bay, Jamaica. Int J Integr Biol 1:37–40

Darling ES, Côté IM (2018) Seeking resilience in marine ecosystems. Science 359:986–987

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15:1378–1386

Dodge RE, Vaisnys JM (1977) Coral populations and growth patterns: responses to sedimentation and turbidity associated with dredging. J Mar Res 35:715–730

Dodge RE, Aller RC, Thomson J (1974) Coral growth related to resuspension of bottom sediments. Nature 247:574–577

Dornelas M, Madin JS, Baird AH, Connolly SR (2017) Allometric growth in reef-building corals. Proc R Soc B 284:20170053

Edmunds PJ, Bruno JF, Carlon DB (2004) Effects of depth and microhabitat on growth and survivorship of juvenile corals in the Florida Keys. Mar Ecol Prog Ser 278:115–124

Elahi R, Edmunds P (2007) Consequences of fission in the coral *Siderastrea siderea*: growth rates of small colonies and clonal input to population structure. Coral Reefs 26:271–276

Fong J, Todd PA (2021) Spatio-temporal dynamics of coral–macroalgal interactions and their impacts on coral growth on urbanised reefs. Mar Pollut Bull 172:112849

Gold Z, Palumbi SR (2018) Long-term growth rates and effects of bleaching in *Acropora hyacinthus.* Coral Reefs 37:267–277

Goldberg WM (1973) The ecology of the coral–octocoral communities off the southeast Florida coast: geomorphology, species composition, and zonation. Bull Mar Sci 23:465–488

Grigg R (1981) Coral reef development at high latitudes in Hawaii. Proc 4th Int Coral Reef Symp 1:687–693

Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD and others (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. Glob Change Biol 20:3823–3833

Hayes NK, Walton CJ, Gilliam DS (2022) Tissue loss disease outbreak significantly alters the Southeast Florida stony coral assemblage. Front Mar Sci 9:975894

Helmle KP, Dodge RE, Swart PK, Gledhill DK, Eakin CM (2011) Growth rates of Florida corals from 1937 to 1996 and their response to climate change. Nat Commun 2:215

Hughes TP, Jackson JBC (1980) Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. Science 209:713–715

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141–166

Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263

Huston M (1985) Variation in coral growth rates with depth at Discovery Bay, Jamaica. Coral Reefs 4:19–25

Jones NP (2022) Benthic community dynamics and stony coral demographics in Florida in relation to acute disturbances and chronic pressures. PhD dissertation, Nova Southeastern University, Fort Lauderdale, FL

Jones NP, Figueiredo J, Gilliam DS (2020) Thermal stress-related spatiotemporal variations in high-latitude coral reef benthic communities. Coral Reefs 39:1661–1673

Jones NP, Ruzicka RR, Colella MA, Pratchett MS, Gilliam DS (2022) Frequent disturbances and chronic pressures constrain stony coral recovery on Florida's Coral Reef. Coral Reefs 41:1665–1679

Kuffner I, Hickey T, Morrison J (2013) Calcification rates of the massive coral *Siderastrea siderea* and crustose coralline algae along the Florida Keys (USA) outer-reef tract. Coral Reefs 32:987–997

Lenth R (2019) Emmeans: estimated marginal means, aka least-squares means. R package version 1.3.2. https://CRAN.R-project.org/package=emmeans

Lirman D (2000) Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments. J Exp Mar Biol Ecol 251:41–57

Logan A, Tomascik T (1991) Extension growth rates in two coral species from high-latitude reefs of Bermuda. Coral Reefs 10:155–160

Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral *Porites.* J Exp Mar Biol Ecol 245:225–243

Madin JS, Baird AH, Baskett ML, Connolly SR, Dornelas MA (2020) Partitioning colony size variation into growth and partial mortality. Biol Lett 16:20190727

Manzello DP, Enochs IC, Kolodziej G, Carlton R (2015) Coral growth patterns of *Montastraea cavernosa* and *Porites astreoides* in the Florida Keys: the importance of thermal stress and inimical waters. J Exp Mar Biol Ecol 471:198–207

Mellin C, Matthews S, Anthony KRN, Brown SC and others (2019) Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. Glob Change Biol 25:2431–2445

Moyer RP, Riegl B, Banks K, Dodge RE (2003) Spatial patterns and ecology of benthic communities on a high-

latitude South Florida (Broward County, USA) reef system. Coral Reefs 22:447–464

Mumby PJ, Foster NL, Fahy EAG (2005) Patch dynamics of coral reef macroalgae under chronic and acute disturbance. Coral Reefs 24:681–692

Neal BP, Khen A, Treibitz T, Beijbom O and others (2017) Caribbean massive corals not recovering from repeated thermal stress events during 2005–2013. Ecol Evol 7:1339–1353

Nyström M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. Trends Ecol Evol 15:413–417

Ortiz JC, Wolff NH, Anthony KR, Devlin M, Lewis S, Mumby PJ (2018) Impaired recovery of the Great Barrier Reef under cumulative stress. Sci Adv 4:eaar6127

Page CA, Muller EM, Vaughan DE (2018) Microfragmenting for the successful restoration of slow growing massive corals. Ecol Eng 123:86–94

Pinheiro J, Bates D (2000) Linear mixed-effects models: basic concepts and examples. In: Mixed-effects models in S and S-Plus. Springer, New York, NY, p 3–56

Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S, Van Willigen B, Maintainer R (2017) Package 'nlme'. Linear and nonlinear mixed effects models. https://CRAN.R-project.org/package=nlme

Pisapia C, Pratchett MS (2014) Spatial variation in background mortality among dominant coral taxa on Australia's Great Barrier Reef. PLOS ONE 9:e100969

Pisapia C, Edmunds PJ, Moeller HV, Riegl BM, McWilliam M, Wells CD, Pratchett MS (2020) Projected shifts in coral size structure in the Anthropocene. Adv Mar Biol 87:31–60

Pratchett MS, Anderson KD, Hoogenboom MO, Widman E and others (2015) Spatial, temporal and taxonomic variation in coral growth–implications for the structure and function of coral reef ecosystems. Oceanogr Mar Biol Annu Rev 53:215–295

Pratchett MS, McWilliam MJ, Riegl B (2020) Contrasting shifts in coral assemblages with increasing disturbances. Coral Reefs 39:783–793

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Riegl B, Purkis S (2015) Coral population dynamics across consecutive mass mortality events. Glob Change Biol 21: 3995–4005

Riegl B, Cavalcante G, Bauman AG, Feary DA, Steiner S, Purkis S (2017) Demographic mechanisms of reef coral species winnowing from communities under increased environmental stress. Front Mar Sci 4:344

Rippe JP, Baumann JH, De Leener DN, Aichelman HE, Friedlander EB, Davies SW, Castillo KD (2018) Corals sustain growth but not skeletal density across the Florida Keys Reef Tract despite ongoing warming. Glob Change Biol 24:5205–5217

Schneider CA, Rasband WS, Eliceri KW (2012) NIH Image to Image J: 25 years of image analysis. Nat Methods 9:671–675

St. Gelais AT, Chaves-Fonnegra A, Brownlee AS, Kosmynin VN, Moulding AL, Gilliam DS (2016) Fecundity and sexual maturity of the coral *Siderastrea siderea* at high latitude along the Florida Reef Tract, USA. Invertebr Biol 135:46–57

Tanner JE (1995) Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. J Exp Mar Biol Ecol 190:151–168

Vega Thurber RL, Burkepile DE, Fuchs C, Shantz AA, McMinds R, Zaneveld JR (2014) Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. Glob Change Biol 20:544–554

Walton CJ, Hayes NK, Gilliam DS (2018) Impacts of a regional, multi-year, multi-species coral disease outbreak in southeast Florida. Front Mar Sci 5:323

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer Science & Business Media, New York, NY