The role of background algal symbionts as drivers of shuffling to thermotolerant symbionts following bleaching in three Caribbean coral species

Seasonal changes in algal symbionts in three Caribbean coral species and their influence on symbiont shuffling following bleaching recovery

Daisy Buzzoni1,2\*, Ross Cunning3, Andrew C. Baker1

**Author Affiliations**

1. Department of Marine Biology and Ecology, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy., Miami, FL 33149, USA
2. Current address: Department of Biology, University of Victoria, Canada
3. Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium, USA

**Communicating Author**

Daisy Buzzoni: daisybuzzoni@gmail.com

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**Abstract**

Reef-building corals host diverse dinoflagellate algal symbionts (Family Symbiodiniaceae) whose identity can influence host thermotolerance and whose relative abundance can be dynamic. Heat-induced coral bleaching can accelerate changes in symbiont communities in favour of thermotolerant types, particularly in the genus *Durusdinium.* We employed experimental bleaching to manipulate the algal symbiont communities of three common Caribbean reef-building species, (*Montastraea cavernosa*, *Orbicella faveolata*, and *Siderastrea siderea*), and tested whether seasonal differences in their symbiont communities at time of collection from the reef affected their responses to manipulation. In *O. faveolata* and *S. siderea*, background levels of *Durusdinium trenchii* prior to bleaching led to recovery with a higher proportion of *Durusdinium* compared to corals without background *Durusdinium*. In contrast, in *M. cavernosa*, *Durusdinium* became highly dominant after recovery even when it was undetectable prior to bleaching, reflecting differences among coral species in the tendency for *D. trenchii* to become dominant following bleaching. Seasonal differences were also detected in *M. cavernosa*, which hosted more symbionts per host cell and was more susceptible to bleaching in October (following annual temperature maxima) compared to the previous April (following temperature minima). These results demonstrate how background symbionts and seasonal differences in symbiont density can affect the disturbance and recovery dynamics of algal symbiont communities in different coral species and prompt further research into how seasonal changes in algal symbiosis can add complexity into predictions of bleaching response, which are increasingly relevant in light of predicted winter warming and prolonged warm summer temperatures under climate change.

**Introduction**

Coral reef bleaching is the loss of photosynthetic algal symbionts (Family Symbiodiniaceae) from reef-dwelling invertebrate hosts (exemplified by the loss of symbionts from reef-building scleractinian corals) [(Glynn, 1996; LaJeunesse et al., 2018)](https://paperpile.com/c/2qJvT7/q31R+jluL). This dysfunctional symbiosis (‘dysbiosis’, [(Palmer, 2018)](https://paperpile.com/c/2qJvT7/LbWY) is typically driven by photoinhibition of the algal symbionts, due to environmental stress (most commonly sustained periods of anomalously high temperature, [(Gustafsson et al., 2014; Smith et al., 2005)](https://paperpile.com/c/2qJvT7/6wtP+hrkb), further modulated by the capacity of the coral host to reduce or mitigate that stress [(Baird et al., 2009; Berkelmans & van Oppen, 2006)](https://paperpile.com/c/2qJvT7/zmrp+0qHp). Heat-induced bleaching is now the principal driver of scleractinian coral (‘coral’ hereafter) mortality worldwide, as bleaching events are becoming more frequent and more intense [(Hughes et al., 2018)](https://paperpile.com/c/2qJvT7/86gx/?prefix=Hughes%20et%20al.%2C&noauthor=1). Annual severe bleaching is expected on 90% of the world’s coral reefs by 2055 [(van Hooidonk et al., 2014)](https://paperpile.com/c/2qJvT7/B2XM) as rising sea surface temperatures increase the duration and frequency of marine heatwaves [(Fordyce et al., 2019; Oliver et al., 2018)](https://paperpile.com/c/2qJvT7/pEtx+q0Sn). Exploring the drivers of thermal tolerance and the recovery of these symbioses following disturbance is therefore of paramount importance for the future of coral reefs.

Adult corals of some species can be flexible in their symbiotic associations [(Baker, 2003; Putnam et al., 2012; Ziegler et al., 2015)](https://paperpile.com/c/2qJvT7/YJKs+Sdur+6NAk/?prefix=Baker%2C,,&noauthor=1,0,0), often hosting multiple different symbionts simultaneously, at least at background levels (comprising <1% of the symbiont community) [(Boulotte et al., 2016; Correa et al., 2009; Silverstein et al., 2012)](https://paperpile.com/c/2qJvT7/EYbv+hVLi+4NW3). The loss of symbionts during bleaching may provide an opportunity for corals to recover with different symbiont communities [(Baker, 2003; Buddemeier & Fautin, 1993)](https://paperpile.com/c/2qJvT7/S3cM+YJKs/?noauthor=0,1&prefix=,Baker%2C). Changes in algal symbiont community composition within a coral colony following bleaching and recovery can result from the uptake and proliferation of exogenous symbionts, or by the proliferation of residual symbionts that remain in bleached coral tissue, typically referred to as ‘switching’ and ‘shuffling’ respectively [(Baker, 2003; Buddemeier & Fautin, 1993; Silverstein et al., 2012)](https://paperpile.com/c/2qJvT7/S3cM+YJKs+hVLi/?noauthor=0,1,0&prefix=,Baker%2C,). Different Symbiodiniaceae may confer different thermal tolerance to their hosts [(Berkelmans & van Oppen, 2006; Swain et al., 2017)](https://paperpile.com/c/2qJvT7/zmrp+gMCE), which can result in shifts in favour of thermotolerant algal symbionts on reefs following high temperature anomalies [(Baker, 2004)](https://paperpile.com/c/2qJvT7/CT1g/?prefix=Baker%2C&noauthor=1), particularly *Durusdinium trenchii* on Caribbean reefs [(Kemp et al., 2014; LaJeunesse et al., 2009; Thornhill et al., 2006)](https://paperpile.com/c/2qJvT7/qptf+prnj+KV2a).

Algal symbiont communities can also undergo seasonal fluctuations in composition independently of bleaching [(Chen et al., 2005; Ziegler et al., 2015)](https://paperpile.com/c/2qJvT7/aygv+6NAk), for example summertime increases in relative abundance of *Durusdinium* in *Leptoria phrygia* in Taiwan [(Huang et al., 2020)](https://paperpile.com/c/2qJvT7/VSMT) and transient increases in the proportion of *D. trenchii* in the summer preceding a bleaching event [(LaJeunesse et al., 2009)](https://paperpile.com/c/2qJvT7/prnj), with communities generally reverting to their pre-disturbance composition over months-years in the absence of further heat stress [(LaJeunesse et al., 2009; Thornhill et al., 2006)](https://paperpile.com/c/2qJvT7/qptf+prnj).

In addition to differences in the identity of symbionts, total symbiont densities in corals also undergo seasonal fluctuations. Multi-year studies of Caribbean and Indo-Pacific coral species have shown increases in symbiont density and photochemical efficiency (Fv/Fm) during winter, and decreases during the summer. These decreases occur even in years with no visible signs of bleaching, suggesting an acclimatisation response to lower temperature and irradiance during the winter [(Fagoonee et al., 1999; Fitt et al., 2000; Stimson, 1997; Thornhill et al., 2011; Warner et al., 2002)](https://paperpile.com/c/2qJvT7/Z7UJ+Z4Lc+Av17+5eWV+B6ag). In the Caribbean, annual peaks in coral tissue biomass occur in the spring, potentially reflecting accumulated photosynthate transfer following winter symbiont density peaks, which then decrease during the summer [(Fitt et al., 2000; Thornhill et al., 2011)](https://paperpile.com/c/2qJvT7/Z4Lc+5eWV).

Higher symbiont densities have also been implicated in decreased thermal tolerance, supposedly due to carbon limitation of photosynthesis (reduced autotrophic capacity) [(Wooldridge, 2009, 2020)](https://paperpile.com/c/2qJvT7/9xXU+4YSM), and/or increased production of reactive oxygen species in response to stress [(Cunning & Baker, 2014; Weis, 2008)](https://paperpile.com/c/2qJvT7/VarN+BHHr). Low host biomass, and lipid content in particular, has also been linked to reduced bleaching resilience [(Hughes & Grottoli, 2013)](https://paperpile.com/c/2qJvT7/P0Kd/?prefix=Hughes%20%26%20Grottoli%2C&noauthor=1) and perhaps also resistance [(Wooldridge, 2014)](https://paperpile.com/c/2qJvT7/zU2Y). Symbiont to host cell ratios may be useful proxies that unify metrics of symbiont density and host tissue biomass, and are predictive of thermotolerance [(Cunning & Baker, 2013)](https://paperpile.com/c/2qJvT7/AUTK). However, they have not yet been monitored over seasonal timescales, despite the fact that there is evidence of seasonal differences in bleaching sensitivity [(Cunning et al., 2021; Scheufen et al., 2017)](https://paperpile.com/c/2qJvT7/xLyI+Bnhw), short-term acclimatisation response to warmer summer temperatures [(Berkelmans & Willis, 1999)](https://paperpile.com/c/2qJvT7/36gJ) also remains unresolved. Thus, the first aim of the current study was to study the effects of seasonal changes in symbiont to host cell ratio and community composition on coral bleaching resistance.

The second aim of the current study was to investigate how seasonal changes in algal symbiont communities affected their ability to recover with different symbionts following bleaching. Although many factors, such as coral species [(Baker & Romanski 2007; Goulet, 2006)](https://paperpile.com/c/2qJvT7/SsuZ+dJH5/?noauthor=0,1&prefix=,Baker%20%26%20Romanski), duration of heat stress and recovery temperature [(Cunning et al., 2015)](https://paperpile.com/c/2qJvT7/8Eg3) have been tested in assessing the tendency for corals to change symbionts following bleaching, the effect of background symbionts in driving these changes has not been explicitly investigated. Competitive trials of *Durusdinium* versus other common genera inside octocoral hosts have suggested that population sizes following disturbance affect competitive outcomes between symbionts with priority effects facilitating the initial proliferation of *Durusdinium* under stressful environmental conditions before they are excluded by photochemically superior competitors [(McIlroy et al., 2019)](https://paperpile.com/c/2qJvT7/r3gs). Consequently, the question of whether seasonal changes in the abundance of *Durusdinium* affect the propensity for later shuffling/switching in favour of these symbionts may be key to understanding recovery trajectories of corals following bleaching events.

Here, we compared seasonal differences in symbiont to host cell ratio and the proportion of *Durusdinium trenchii* in three common Caribbean reef-building coral species following annual temperature minima and maxima) . We then subjected these corals to experimental bleaching and tested whether seasonal differences in algal symbiont communities affected either the thermal tolerance or the proportion of *Durusdinium* that the corals recovered with following bleaching. Given the predicted increase in marine heatwaves, their prolonged duration over multiple seasons [(Pörtner et al., 2019; van Hooidonk et al., 2020)](https://paperpile.com/c/2qJvT7/zvly+hVVe), and the increasingly important role of heat-tolerant symbionts in warming oceans, developing our understanding of seasonal variation in thermotolerance and tendency of corals to recover with heat tolerant symbionts at different times of the year, understanding symbiont community dynamics following bleaching recovery has never been more pressing.

**Materials and Methods**

*Colony selection and core collection*

To select colonies for study, we sampled 54 colonies (all > 30 cm in diameter) of *Montastraea cavernosa*, *Orbicella faveolata*, and *Siderastrea siderea* at depths of 7.5-8.5 m depth from Emerald Reef (25.406 to 25.407 N, 80.058 to 80.060 W), off Key Biscayne, SE Florida, USA. We then characterised the algal symbiont communities in these colonies (see *DNA extraction and analyses,* below) and selected the 10 colonies of each species containing the lowest proportions of *Durusdinium* (30 colonies in total). Although genotypes were not explicitly identified in this study, selected colonies were at least 5 m apart to decrease the chances of sampling clonemates [(Baums et al., 2006)](https://paperpile.com/c/2qJvT7/FoYL). From each colony, two cores, each 2.5 cm diameter and 2 cm deep, were removed using a submersible drill (Nemo Power Tools Ltd.) fitted with a diamond core drill bit (Montana Brand Tools). Cores (N=60 in total) were extracted from the uppermost surfaces of colonies to standardise irradiance and minimise variation in symbiont communities due to intra-colonial niche partitioning [(Rowan et al., 1997)](https://paperpile.com/c/2qJvT7/bj8Z). Holes in colonies resulting from coring were filled with a two-part epoxy putty to promote healing. Cores were collected in March-April 2019 (hereafter referred to as the ‘April’ batch), and another set of 60 cores was collected from the same 30 colonies in October 2019 (referred to as the ‘October’ batch).

*Laboratory maintenance of corals*

Cores were attached to ceramic plugs using cyanoacrylate ‘Reef Glue Gel’ (Boston Aqua Farms) and maintained in plastic egg-crates. From each batch of 60 cores, 1-2 cores of each colony (N=45 cores total, across 3 species) were assigned to the bleaching treatment, and the remaining 5 cores of each species (N=15 total) were used as non-bleached controls (Table S1). Corals were maintained in ~300L indoor, flow-through, fiberglass tanks in the Marine Technology and Life Science Seawater (MTLSS) complex at the University of Miami’s Rosenstiel School of Marine,Atmospheric, and Earth Science, supplied with seawater at 27°C (+/- 1°C) from nearby Bear Cut that had been sand-filtered to 10 microns (which removes larger particles but does not remove Symbiodiniaceae, [(Littman et al., 2008)](https://paperpile.com/c/2qJvT7/Wb7j). The 45 heat-stressed cores from each batch were kept in one tank and the 15 control cores in another, with cores rotated within tanks during each weekly cleaning to reduce any potential confounding effects of tank position. Two 500 gph pumps were used to circulate water within each tank, and corals were maintained on a 12h:12h light:dark cycle using three Hydra 52HD lights (Aqua Illumination, C2 Development Inc.) at 20% intensity across all wavelengths, which delivered approximately 125 µEinsteins m-2 s-1 PAR, measured using an Apogee MQ-210X light metre) across each tank. Corals were fed twice weekly with 4g of resuspended zooplankton and phytoplankton (‘Reef-Roids’, Polyplab, Kansas USA).

*Heat stress*

After 3-5 weeks of acclimation to laboratory conditions, experimental cores were exposed to a heat stress protocol. On day 1 of heat stress the temperature was raised (using in-tank heaters) to 32°C (+/- 0.5°C); this rapid temperature increase was developed from previous methods for successful symbiont manipulations in these species [(Cunning et al., 2015)](https://paperpile.com/c/2qJvT7/8Eg3). After 15 days of heat stress, photochemical efficiency measurements were taken using an imaging pulse amplitude modulated (I-PAM) fluorometer (Walz, Effeltrich, Germany). Corals were dark-adapted for 30 minutes [(Warner et al., 2002)](https://paperpile.com/c/2qJvT7/Av17), then delivered a saturating pulse at 2,800 µmol photons m-2 s-1 at 460 nm for 800 ms. The maximum quantum yield of symbionts’ PSII was quantified as Fv/Fm [(Warner et al., 1996)](https://paperpile.com/c/2qJvT7/mTvD). I-PAM measurements were always taken in the early evening to control for diel variation in photochemical efficiency [(Warner & Berry-Lowe, 2006)](https://paperpile.com/c/2qJvT7/DqSW). After 15 days, if Fv/Fm was either <0.25 or <50% of the coral’s pre-heat stress Fv/Fm, corals were placed into a glass ‘recovery’ aquarium within the fiberglass tank, which was maintained at 29°C (+/- 0.5°C), to promote shifts toward *Durusdinium* dominance [(Cunning et al., 2015)](https://paperpile.com/c/2qJvT7/8Eg3). Corals that maintained Fv/Fm values above these thresholds were maintained under heat stress and I-PAM measurements were taken every two days until Fv/Fm thresholds were met. After 25 days (April batch) or 22 days (October batch) in heat stress, the temperature was raised to 33°C (+/- 0.5°C) to induce sufficient Fv/Fm declines in any remaining corals. In total, the mean Degree Heating Weeks (DHW) to which all heat-stressed corals were exposed [(Liu et al., 2014)](https://paperpile.com/c/2qJvT7/jDgm)) was 8.6 DHW (April batch) and 9.8 DHW (October batch).

During this controlled bleaching protocol, small (~2 mm diameter) tissue biopsies were preserved in 1% SDS (​​sodium dodecyl sulphate) in DNAB [(Baker & Cunning 2016)](https://paperpile.com/c/2qJvT7/9jwT/?prefix=Baker%20%26%20Cunning&noauthor=1) at four time points: ‘Before heat stress’ (cores of both treatments were sampled just before the onset of heat stress), ‘After heat stress’ (experimental cores were sampled when they were removed from heat stress and control cores were sampled when heat stress had ended for all cores), ‘1 month recovery’ (bleached cores were sampled one month after they had been taken out of heat stress), and ‘2 month recovery’ (all cores were sampled at the end of the experiment, on average one month after the ‘1 month Recovery’ sampling).

*DNA extraction and analyses*

Aliquots of tissue samples were subjected to a modified organic extraction protocol [(Baker 1997)](https://paperpile.com/c/2qJvT7/zdTQ/?prefix=Baker&noauthor=1) and quantitative PCR was performed using Taqman Environmental Master Mix (QuantStudio 3, Applied Biosystems) and symbiont genus-specific primers and probes targeting the actin gene [(Cunning et al., 2015; Cunning & Baker, 2013)](https://paperpile.com/c/2qJvT7/8Eg3+AUTK). To date, the only species of *Durusdinium* that has been reported in the Caribbean and western Atlantic is *D. trenchii* [(Correa et al., 2009; Pettay et al., 2015)](https://paperpile.com/c/2qJvT7/EYbv+lbcL) but we specify *Durusdinium* to the genus level in the figures presented only to maintain consistency with other symbiont genera (of which there are multiple local species [(LaJeunesse et al., 2003)](https://paperpile.com/c/2qJvT7/8vlp). VIC dye was used for the *Cladocopium* probe, whilst all other probes used a FAM dye. *Cladocopium* and *Durusdinium* targets were multiplexed together in the same well. Data were corrected for differences in DNA extraction efficiency, actin gene copy number, and dye fluorescence (Table S2) using the stepOneR package [(Cunning, 2020)](https://paperpile.com/c/2qJvT7/LVTW). Amplifications were filtered to include only those in which both technical replicates amplified with Ct values < 40.

Whilst the use of genus-level assays does not allow for finer-scale symbiont identification, qPCR methods were used in this study to rapidly and cheaply quantify changes in the relative abundances of symbiont genera. Other studies have estimated very high sensitivities of qPCR methods for detecting the presence of extremely low abundance ‘background’ symbionts at proportions as low as 0.003% (for *Durusdinium*) [(Correa et al., 2009; Mieog et al., 2007)](https://paperpile.com/c/2qJvT7/x749+EYbv), which are of specific interest for this study.

*Statistical analyses*

Data were analysed in RStudio V4.2.1 [(R Core Team, 2022)](https://paperpile.com/c/2qJvT7/EUz1). Linear mixed effects models with colony as a random effect, and batch as a fixed effect, were fit to pre-heat stress S:H data and also to post-heat stress S:H data (for which dominant symbiont genus was also included as an additional fixed effect for *O. faveolata* and *S. siderea*) using the ‘lme4’ package [(Bates et al., 2015)](https://paperpile.com/c/2qJvT7/MsSv). Generalised mixed effects models with binomial error distributions, including colony as a random effect and pre-heat stress proportion *Durusdinium*, were fit to post-heat stress proportion *Durusdinium* data (with batch included as an additional fixed effect in some models), also using the ‘lme4’ package [(Bates et al., 2015)](https://paperpile.com/c/2qJvT7/MsSv). Parameter estimates and associated confidence intervals were estimated from mixed effects models using the ‘emmeans’ package [(Lenth, 2022)](https://paperpile.com/c/2qJvT7/qxbV), whilst the significance of fixed effects in models was tested using partial F-tests in the ‘lmerTest’ package [(Kuznetsova et al., 2017)](https://paperpile.com/c/2qJvT7/tC69).

By fitting a predictive quasibinomial model of the change in proportion *Durusdinium* hosted after heat stress relative to the initial proportion *Durusdinium* hosted, a shuffling metric was derived to represent the magnitude of shuffling (or switching) to *Durusdinium* [(Cunning et al., 2018)](https://paperpile.com/c/2qJvT7/gybJ/?prefix=Cunning%20et%20al.%2C&noauthor=1). No *Durusdinium* was detected in any *M. cavernosa* cores before heat stress, so this shuffling metric was calculated as the change in the proportion of *Durusdinium*. All data and statistical analyses are available at github.com/DaisyBuzzoni/seasonal\_shuffling.

**Results**

*Symbiont to host cell ratios and bleaching resistance in April vs. October*

The mean number of symbionts per coral cell (S:H ratio) increased in *Montastraea cavernosa* between April 2019 (after the seasonal temperature minimum in January/February, Fig. 1a) and October 2019 (after the seasonal maximum in August/September, Fig. 1a) (*t* = 3.54, *p* = 0.0011\*\*, Fig. 1b). However, S:H ratios did not change from April to October in *O. faveolata* (*t* = 0.079, *p* = 0.938) and only a marginal decrease was observed in *S. siderea* colonies (*t* = 2.07, *p* = 0.048\*) (Fig. 1b). No change was detected in the proportion of *Durusdinium* in cores of *M. cavernosa* (*z* = 0, *p* = 1), *O. faveolata* (*z* = 1.19, *p* = 0.235) or *S. siderea* (*z* = 1.69, *p* = 0.091) between April and October (Fig. 1c).

After heat stress exposure, *M. cavernosa* collected in October lost more symbionts than those collected in April, despite smaller declines in photochemical efficiency (Fig. 1d), a difference seen only in *M. cavernosa*. Post heat-stress S:H was significantly lower in the October *M. cavernosa* corals (*t* = 3.50, *p* = 0.002\*\*), and no difference in pre-heat stress Fv/Fm was detected between April and October *M. cavernosa* cores (*t* = 1.27, *p* = 0.216). No such difference in post heat-stress S:H was seen in O*. faveolata* (*t* = 0.067, *p* = 0.949) or *S. siderea* (*t* = 0.538, *p* = 0.600).

*Shifts in favour of Durusdinium depend on coral species but not on season*

The proportion of *Durusdinium* before bleaching and after recovery differed between coral species, when corals collected in April and October were pooled (Figs. 1c & 2). The shuffling index for experimental corals was 0.927 for *M. cavernosa*, 0.938 for *O. faveolata* and 0.760 for *S. siderea* (Fig. 3a). For corals not subjected to heat stress (controls), shuffling indices were 0.009, 0.017 and -0.170 respectively. However, there was no significant difference in the magnitude of shuffling between April and October for *M. cavernosa* (*t* =1.668, p=0.107), *O. faveolata* (*t* =0.415, *p* = 0.683), or *S. siderea* (*t* = 0.029, *p* = 0.977), (Fig. S1).

*Initial presence or absence of Durusdinium drives magnitude of symbiont shifts, depending on coral species*

By the end of heat stress, some shuffling toward *Durusdinium* had already occurred in *O. faveolata* and *S. siderea,* but not *M. cavernosa* (Fig. 3a)*.* However, despite the delay in shifts towards higher proportions of *Durusdinium* in *M. cavernosa*, the magnitude of the shift two months after heat stress was only very slightly less than that of *O. faveolata* (Fig. 3a). In order to better distinguish the role of background *Durusdinium* on the timing and trajectory of symbiont shuffling, corals were grouped by species and by initial *Durusdinium* proportion (Fig. 3b). No significant species-level effects were found between *O. faveolata* and *S. siderea*, on the change in proportion *Durusdinium* following recovery (*t* = 0.971, *p* = 0.333,), and these two species were therefore pooled in Fig. 3b due to small group sample sizes. *M. cavernosa* and *O. faveolata/S. siderea* corals that initially hosted no *Durusdinium* only started to gain *Durusdinium* during the recovery period (Fig. 3b). Yet after two months of recovery, proportion *Durusdinium* was significantly higher in *M. cavernosa* than in *O. faveolata/S. siderea* corals (*z* = 2.324, *p* = 0.020). In *O. faveolata* and *S. siderea*, cores that initially hosted some *Durusdinium* (<50%, mean ~10%) recovered with significantly more *Durusdinium* than those that initially hosted no (0%) *Durusdinium* 0% (*z* = 2.284, *p* = 0.022\*).

**Discussion**

*Seasonal coral-symbiont associations and bleaching resistance*

Corals colonies from April 2019 were collected at cool temperatures (25°C) during the spring warming phase), while colonies from October 2019 were collected at a warmer temperature (29°C) but during an autumnal cooling phase (Fig. 1). These seasonal temperature changes are also accompanied by variation in irradiance, both in terms of maximum intensity and duration (daylight hours). Measurements of photosynthetically active radiation (PAR) just south of the Emerald reef collection site have shown that the additional irradiance in July, compared to December, translates into increased net and gross primary productivity in reef-building corals [(Owen et al., 2021)](https://paperpile.com/c/2qJvT7/QtAV), with implications for symbiont population dynamics. Moreover, dissolved inorganic nitrogen (DIN) also shows significant seasonal variation on Florida’s Coral Reef , typically with higher DIN in January-June compared to July-December [(Lapointe et al., 2004)](https://paperpile.com/c/2qJvT7/fMsf). This is relevant to algal symbiont densities which are typically increased by elevated DIN [(Dubinsky et al., 1990; Marubini & Davies, 1996; Muller-Parker et al., 1994; Muscatine et al., 1989)](https://paperpile.com/c/2qJvT7/7oeV+2TQ2+6Xg1+WJ6b). Consequently, the differences in *M. cavernosa* symbiont communities (Fig. 1b) in April and October is unlikely to be attributable solely to temperature, but rather a combination of co-varying environmental factors.

The symbiont:host cell ratios reported here reflect the relative abundance of host and symbiont cells, whereby the increased S:H observed in *M. cavernosa* from April and October (Fig. 1b) reflects increased symbiont numbers and/or reduced host cell numbers. Interpreting this result as an April-to-October relative decrease in host cells would be consistent with previous studies’ reports of host tissue biomass minima in Floridian late summer/early fall (around October), and symbiont density minima during Floridian summer [(Fitt et al., 2000; Warner et al., 2002)](https://paperpile.com/c/2qJvT7/Z4Lc+Av17). The lack of significant difference in S:H seen from April to October in both *O. faveolata* and *S. siderea* may be explained by relatively higher symbiont cell loss and/or relatively smaller host cell loss during summer warming, in comparison to *M. cavernosa*. These three coral species have broadly the same mounding/massive morphologies, yet smaller scale morphological differences such as corallite arrangement and host tissue thickness shape the photic microenvironment within colonies, influencing the loss and proliferation of symbionts [(Loya et al., 2001; Wangpraseurt et al., 2012)](https://paperpile.com/c/2qJvT7/OQmY+9PeR). Furthermore, coral species-specific metabolic differences, and symbiont resource provisioning could influence S:H changes [(Allgeier et al., 2020; Wooldridge, 2014)](https://paperpile.com/c/2qJvT7/zU2Y+LctS), in addition to the type of algal symbionts hosted, given differences in the baseline *in hospite* densities of different symbiont genera (specifically with higher densities of *Durusdinium* observed compared to *Cladocopium* [(Cunning & Baker, 2013)](https://paperpile.com/c/2qJvT7/AUTK)).

While the proportion of *Durusdinium* symbionts differed between coral species at the time of collection (Fig. 2), there were no differences in this metric between April and October in any species. Experimental bleaching has revealed that more severe heat stress can induce larger shifts in favour of *Durusdinium* following recovery [(Cunning et al., 2015)](https://paperpile.com/c/2qJvT7/8Eg3), and this has been documented (including in *M. cavernosa* and *S. siderea*) during a natural bleaching event in the Caribbean [(LaJeunesse et al., 2009)](https://paperpile.com/c/2qJvT7/prnj). However, we observed only sporadic paling (3 to 6 on a visual colouration scale [(Siebeck et al., 2006)](https://paperpile.com/c/2qJvT7/yoON)) of corals at Emerald Reef between April and October 2019, which was not considered a bleaching year in Florida. Consequently, although *Durusdinium* may have a photochemical advantage, compared to other symbionts,at high temperatures [(Carballo-Bolaños et al., 2019; Cunning et al., 2018)](https://paperpile.com/c/2qJvT7/gybJ+JFEC/?prefix=Cunning%20et%20al.%2C,&noauthor=1,0), it would appear that conditions at Emerald reef in 2019 were not severe enough for *Durusdinium* to proliferate, at least in the three coral species we studied.

Given that reductions in S:H indicate bleaching and reduced Fv/Fm indicates symbiont photochemical impairment, Fig 1d could suggest lower thermotolerance in October compared to April. Pertinent to this is the difference in heat stress exposure described in the methods above wherein temperatures were raised from 32 to 33°C three days earlier for the October batch. Since we controlled for heat stress response via Fv/Fm we cannot discount the possibility that this result is due to a decoupling of Fv/Fm and symbiont loss in response to this earlier temperature increase. Yet measures of symbiont abundance relative to host cells (S:H) provide a more ecologically relevant metric of the state of the coral-algal symbiosis, compared to absolute host cell or symbiont densities alone [(Cunning & Baker, 2014)](https://paperpile.com/c/2qJvT7/BHHr) because an increase in the number of symbionts *per coral cell*, as seen between April and October in Fig. 1b, could theoretically result in a faster accumulation of reactive oxygen species (ROS) during heat stress [(Cunning & Baker, 2013)](https://paperpile.com/c/2qJvT7/AUTK). This could explain the larger decrease in S:H seen in *M. cavernosa* in October compared to in April (Fig. 1d), but further studies to directly measure intracellular ROS production or oxidative damage [(Gardner et al., 2017)](https://paperpile.com/c/2qJvT7/fYeh) are needed to substantiate the role of S:H in the rate of ROS accumulation. Alternatively, some coral species seem to acclimate to warmer summer temperatures with wider or higher thermal tolerance margins [(Jurriaans & Hoogenboom, 2020)](https://paperpile.com/c/2qJvT7/le7c), which may preadapt corals to resist bleaching [(Kenkel & Matz, 2016)](https://paperpile.com/c/2qJvT7/SNNM), yet other populations have revealed phenotypes with increased bleaching susceptibility in the summer [(Scheufen et al., 2017)](https://paperpile.com/c/2qJvT7/xLyI).

These results suggest that some species of coral may be more susceptible to bleaching during certain months of the year, specifically at the end of the typical warm season. Many coral bleaching predictive models are based on bleaching events occurring during the summer [(Grottoli et al., 2014; van Hooidonk et al., 2020)](https://paperpile.com/c/2qJvT7/u8CS+hVVe). Whilst the majority of marine heatwaves do indeed occur during the summer (of each hemisphere), the duration of marine heatwaves is increasing so much so that they may extend beyond the summer [(Sen Gupta et al., 2020)](https://paperpile.com/c/2qJvT7/M00j) (as seen in the most recent global mass bleaching event from 2014-17, during which heat stress on many reefs was sustained over typically ‘warm’ and ‘cool’ seasons [(Hughes et al., 2018; van Hooidonk et al., 2020)](https://paperpile.com/c/2qJvT7/86gx+hVVe/?prefix=Hughes%20et%20al.%2C,&noauthor=1,0)). Indeed, coral thermal tolerance under shifting temperature seasonality has recently been highlighted as an area in need of further research, on the basis of predicted winter warming and extended warm summer temperatures [(Ziegler et al., 2021)](https://paperpile.com/c/2qJvT7/bZ18).

*Consistency in host species-specific symbiont shuffling/switching propensity at different times of the year*

The results shown in Fig. 3a support previous evidence that symbiont flexibility varies predictably with coral species [(Putnam et al., 2012; Ziegler et al., 2015)](https://paperpile.com/c/2qJvT7/Sdur+6NAk), in that a hierarchy can be constructed from least to most likely to host *Durusdinium* after bleaching recovery [(Cunning et al., 2018)](https://paperpile.com/c/2qJvT7/gybJ/?prefix=Cunning%20et%20al.%2C&noauthor=1). While a large number of experimental *O. faveolata* and *S. siderea* corals hosted at least some *Durusdinium* at time of collection, *M. cavernosa* were either dominated by *Durusdinium*,or hosted no Durusdinium at all (and were subsequently selected for experimental bleaching, Fig. 2). This suggests that, although *Durusdinium* is readily able to proliferate within *M. cavernosa* following bleaching (Fig. 3a), background populations of *Durusdinium* may not persist long-term under non-stressful conditions.

The species-specific tendencies to recover from bleaching with *Durusdinium* did not change between corals collected in April and those collected the following October (Fig. S1). This suggests that any changes in host physiology, symbiont or microbiome physiology, or holobiont community changes that may have occurred between April and October did not significantly affect the relative abundance of *Durusdinium* and co-occurring symbionts two months into recovery. *Durusdinium* is clearly so readily able to proliferate inside the bleached *M. cavernosa* microenvironment (Fig. 2, 3a), that neither an elevated abundance of *Cladocopium* per host cell prior to bleaching in October (Fig. 1b), nor the retention of additional *Cladocopium* per host cell (Fig. 1d) at the end of heat stress in April, caused significant reductions in *Durusdinium* dominance upon recovery.

*Host species-specific effects of background Durusdinium on symbiont shifts upon bleaching recovery*

By the end of heat stress, *O. faveolata* and *S. siderea* were already hosting more *Durusdinium* relative to co-occurring symbionts (Fig. 3a). We are unable to distinguish whether this post-heat stress shift in *O.faveolata* and *S. siderea* is indicative of exogenous uptake or proliferation of *Durusdinium*, or simply the differential loss of non-*Durusdinium* symbionts during heat stress. However, due to the harsh photic microenvironment (linked to reduced symbiont self-shading and to skeletal light-scattering) in bleached corals [(Swain et al., 2016; Wangpraseurt et al., 2014)](https://paperpile.com/c/2qJvT7/3M2c+kVmi), it is likely that this increase in the proportion *Durusdinium* hosted between the start and the end of heat stress largely represents the preferential loss of non-*Durusdinium* symbionts in these two species. Although *Durusdinium* has been documented to colonise and/or proliferate in bleached corals while still under heat stress [(Claar et al., 2020)](https://paperpile.com/c/2qJvT7/g0vz), *Durusdinium* outnumbered co-occurring symbionts sooner in recovery in *O. faveolata* and *S. siderea* compared to *M. cavernosa* (Fig. 3a). This is perhaps unsurprising, given that *Durusdinium* was absent (or present at undetectable levels) prior to heat stress.

The large shift towards hosting *Durusdinium* seen in *M. cavernosa* after two months of recovery suggests that its initial absencedid not inhibit this species from switching to hosting almost exclusively *Durusdinium* (Figs. 2, 3a). When comparing the proportion *Durusdinium* recovered by *O. faveolata* and *S. siderea* corals two months into recovery, corals that initially hosted background levels of *Durusdinium* recovered with significantly more *Durusdinium* on average than those in which *Durusdinium* was initially undetectable (Fig. 3b), with extensive variation between individuals. This implies a role of background symbionts in shaping the dynamics of post-bleaching symbiont recovery in these coral species, perhaps for example reflecting priority effects at play during bleaching recovery, as suggested by McIlroy *et al*. [(2019)](https://paperpile.com/c/2qJvT7/r3gs/?noauthor=1) following experiments on octocoral recruits whereby residual symbionts are able to exclude incoming symbionts despite competitive inferiority.

Although the ecological and physiological role of background symbionts on host phenotypes remains unclear, there is recent evidence of possible holobiont functions for low abundance symbionts. The presence of background symbionts may pose an energetic cost to the host, supposedly by introducing competitive instability into holobionts [(Kenkel & Bay, 2018)](https://paperpile.com/c/2qJvT7/K5hG). In contrast, network analyses of Red Sea coral holobionts found that the presence of low abundance symbionts increased holobiont stability during disturbance [(Ziegler et al., 2018)](https://paperpile.com/c/2qJvT7/5TD3). Field surveys of *Acropora millepora* on the Great Barrier Reef have also documented that corals hosting background levels of *Durusdinium* (> 0.3%) had higher survivorship through bleaching and recovery than those with no detectable *Durusdinium* [(Bay et al., 2016)](https://paperpile.com/c/2qJvT7/XAoa). Our findings contribute to the growing body of evidence for a role of background symbionts in shaping coral climate resilience, although this may be limited to only those symbionts capable of becoming dominant in hosts, such as *Durusdinium* [(Lee et al., 2016)](https://paperpile.com/c/2qJvT7/bxwv).

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**Figure Legends**

**Fig. 1** Seasonal differences in initial symbiont communities and bleaching resistance. **a** Temperature data from Emerald Reef measured with a Hobo logger (Onset Computer Corporation) deployed on the reef from August-December 2019, and approximated for previous months from NOAA temperature data measured at Fowey Rocks (9km south of Emerald) between 2015 and 2019 . Line width indicates standard error of mean daily recorded temperatures. **b** October 2019: April 2019 ratio of symbionts per host cell for each coral colony shown on a log10 scale. Small points represent individual colonies while large points and error bars represent predicted October:April odds ratios and 95% confidence intervals.**c** Points represent the proportion of *Durusdinium* in each coral core after collection from the reef, binned into 0.033 increments in proportion. Violin plots represent probability density distributions. **d** Post heat-stress Fv/Fm plotted against post heat-stress S:H, with each point representing an *M. cavernosa* core. Larger points and error bars represent the mean +/- SE for April and October batches of *M. cavernosa*

**Fig. 2** Proportion of symbionts that were identified as *Durusdinium* in cores (April and October batches combined) before heat stress and after two months of recovery following heat stress in **a** *Montastraea cavernosa*, **b** *Orbicella faveolata,* and **c** *Siderastrea siderea*. Data are grouped into 0.02 (proportion *Durusdinium*) bins

**Fig. 3** Symbiont shuffling magnitude and timing. **a** Shuffling metrics (for April and October bleached corals combined) were calculated at each of three sampling time-points after heat stress, with error bars representing 95% confidence intervals of predicted values. For non-bleached controls, the magnitude of predicted shuffling is shown only for the final post-heat stress time-point **b** Proportion *Durusdinium* detected at each of the four sampling time-points (bleached corals only, April and October corals combined), with small points representing individual cores. Larger points and error bars represent the mean +/- SE for each group, categorised by pre-heat stress proportion *Durusdinium* with *Orbicella faveolata* and *Siderastrea siderea* corals grouped together