

Convergent mortality responses of Caribbean coral species to seawater warming

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Citation: Smith, T. B., M. E. Brandt, J. M. Calnan, R. S. Nemeth, J. Blondeau, E. Kadison, M. Taylor, and P. Rothenberger. 2013. Convergent mortality responses of Caribbean coral species to seawater warming. *Ecosphere* 4(7):87. <http://dx.doi.org/10.1890/ES13-00107.1>

Abstract. Species-specific responses to disturbance are a central consideration for predicting the composition, dynamics, and function of future communities. These responses may be predictable based on species traits that can be analyzed systematically to understand those characteristics important in determining susceptibility and potential for recovery. Scleractinian coral communities of the Western Atlantic are experiencing increased frequency and severity of extreme thermal disturbance, coral bleaching, and mortality. A conceptual thermal bleaching response model developed in this study suggests multiple susceptibility pathways that can lead corals to partial mortality and the loss of biomass, or complete mortality and the loss of genotypes, with implications for species-specific persistence and recovery. Coral assessments from annual to semi-annual surveys at 18 sites in the U.S. Virgin Islands, northeastern Caribbean Sea, before, during, and after the catastrophic 2005 coral bleaching event and during the mild 2010 bleaching event were used to evaluate bleaching, disease, and mortality responses. Three convergent groupings of species emerged based predominantly on their responses to the 2005 event: Type I—high bleaching and initial mortality, no subsequent white disease, and severe losses of cover (exhibited by *Agaricia agaricites* and branching *Porites* species); Type II—moderate bleaching and initial mortality, high subsequent white disease prevalence, and severe losses of cover (exhibited by *Colpophyllia natans*, *Montastraea annularis* species complex, and *M. annularis* sensu stricto); Type III—moderate to low bleaching and paling, low to no subsequent white disease, and low to no loss of cover (exhibited by *Diploria strigosa*, *Montastraea cavernosa*, *Porites astreoides*, and *Siderastrea siderea*). Whole colony mortality was uncommon, even in the most susceptible species, suggesting a potential for recovery among the majority (19 of 27) of scleractinian corals studied. Type II species performed worse than predicted by species traits because of their susceptibility to disease, a factor that needs to be incorporated more fully in models of thermal stress response. Responses of all species to the milder 2010 event were less severe, with limited bleaching and no detectible mortality. Future community composition of Caribbean coral reefs under seawater warming will likely be increasingly dominated by resistant Type III species.

Key words: Caribbean bleaching event 2005; coral bleaching; coral disease; partial mortality; recovery; resistance; species traits; thermal stress; tolerance; United States Virgin Islands.

Received 26 March 2013; revised 31 May 2013; accepted 3 June 2013; **published** 26 July 2013. Corresponding Editor: D. P. C. Peters.

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INTRODUCTION

Disturbance affects communities by changing the relative abundance of constituent species, the strength of their interactions, and the feedbacks between organisms and the environment. Therefore, predicting the responses of individual species will be central to predicting the emergent properties of reorganized communities. This is particularly true for foundational species that, by virtue of their structure and function, have an inordinate influence on community and ecosystem processes and stability (Dayton 1972, Ellison et al. 2005). Light-dependent scleractinian corals are the foundational species of coral reefs, providing physical structure that influences most community processes. Thus, understanding the individual responses of coral species and their patterns of recovery during and after disturbance will increase our understanding of how coral reef community and ecosystem properties will also change with disturbance.

Thermally induced mass coral bleaching has become one of the most critical disturbances to coral reefs (Hoegh-Guldberg 1999, Baker et al. 2008) and may stimulate increasing global degradation of coral reefs even under optimistic global carbon emission and coral adaptation scenarios (Frieler et al. 2012). The major effects of mass coral bleaching are shifts in community structure of corals and their symbionts and, therefore, the ecological function of coral ecosystems (Loya et al. 2001, Brandt 2009). The bleaching response defined here is related not only to the visual manifestation of loss of symbionts, loss of chlorophyll in symbionts, or acute effects of mortality in bleached corals, but also the delayed mortality that occurs in corals during recovery, long after the apparent visual evidence of bleaching has disappeared (Glynn 1996). Short-term shifts in community structure will be guided by species-specific resistance to disturbance, as seen in patterns of mortality during the bleaching response (Marshall and Baird 2000, McClanahan 2000, Loya et al. 2001, McClanahan et al. 2001, Baird and Marshall 2002), while long-term shifts in community structure will be controlled by both species-specific resistance during disturbance and recov-

ery patterns after disturbance has passed (McClanahan 2008, van Woesik et al. 2011). In any given environment, species or community persistence over multiple disturbances may be due to endogenous processes where resistance is enhanced by partial colony survival that favors regrowth and both sexual and asexual reproduction. In addition, persistence may be favored by exogenous processes, such as the supply of larvae from connected populations.

Within a community, patterns of thermal stress response among species are governed by biological characteristics of the coral holobiont and secondary interactions between corals and other organisms or the environment. These aspects of the thermal stress response vary among species and can result in the species-specific patterns of bleaching, mortality, persistence, and recovery. The thermal susceptibility of the coral animal, apart from its relationship with *Symbiodinium*, is not well understood. Most non-symbiotic organisms have much higher thermal tolerance limits than the coral symbioses, suggesting that thermal susceptibility is strongly related to the partial or complete breakdown of symbiosis (Baird et al. 2009). However, although Indo-Pacific coral species do demonstrate a pattern whereby increased bleaching severity and subsequent mortality have been shown to be related (Baird and Marshall 2002), the relationship can be nuanced, with some species bleaching and showing low mortality and other species not bleaching but showing high mortality (McClanahan 2004). The latter species may be directly susceptible because of host vulnerability to thermal stress. In practice, host and holobiont responses are hard to separate in the context of species-specific responses to high thermal stress and in most cases the thermal response can be considered integrated among host and symbiont.

In contrast to host susceptibility to thermal stress, the susceptibility of coral symbiosis to bleaching is highly related to numerous biological traits of corals (see Gates and Edmunds 1999, Baker et al. 2008, van Woesik et al. 2012). Since bleaching is typically a light mediated response to thermal stress (Lesser 1997), factors that reduce light or heat stress, or increase resistance to light and heat stress can buffer the effects of

thermal stress. Both Baker et al. (2008) and van Woesik et al. (2012) summarized known colony traits that imparted higher tolerance in a thermally fluctuating environment, including massive morphology (versus branching morphology), thick tissues, large inter-corallite spacing, low growth rates, large colony size, large corallite size, association with *Symbiodinium* Clade D, and a porous skeletal structure. Each of these characteristics can impart resistance to bleaching and also resistance to thermally induced mortality. This may include limiting mortality on colonies to partial, rather than whole colony (genet). For example, perforate corals (e.g., *Porites*) have intra-skeletal refuges of tissue that may survive over severe thermal stress and regrow after stress has subsided (Baker et al. 2008). Also, heterogeneous symbiont associations have been shown to protect coral species that can support thermally resistant symbiont types (e.g., *Symbiodinium* Clade D) as long as these symbionts are in high abundance within the coral colony at the time of thermal stress (Baker 2001, Baker et al. 2004). In the Western Atlantic, large faviids have been shown to host a diversity of symbiont clades (Rowan et al. 1997), including Clade D (LaJeunesse 2002). Colonies possessing unequal distributions of symbionts with differing susceptibilities to thermal stress may show intra-colony variation of bleaching, favoring partial mortality over total colony mortality (Baker et al. 2008). Although there is strong evidence to support traits that impart thermal resistance, when colony traits conflict in their potential for resistance to thermal stress (e.g., branching *Porites* species with perforate skeletons), it is unclear a priori whether a species will show high or low resistance.

Thermally stressed and/or bleached corals are in a precarious position for maintaining their energy balance. Lowered densities of zooxanthellae lead to decreasing photosynthesis to respiration ratios and the possibility of declining energy reserves to maintain metabolism (Porter et al. 1989, Anthony et al. 2007, Rodrigues and Grottoli 2007). For some Western Atlantic coral species there is a positive relationship between colony energy and resistance to mortality among conspecifics (Thornhill et al. 2011), and this may apply more broadly between coral species (van Woesik et al. 2012). If the latter is true, then

species that can maintain higher energy stores may be more successful at resisting mortality if bleached, while those species that tend to fall into negative energy states may be at an increased risk of starvation (Grottoli et al. 2004). Positive, or less negative, energy states could be favored through greater species-specific tissue mass ratios or increased capability for heterotrophic subsidy during thermal stress (Grottoli et al. 2006).

A stressed and starved coral may also show increased susceptibility to secondary agents of stress. Abiotic stressors such as physical damage, excess nutrients, and toxins, which may normally be tolerated, can have greater impacts on corals already thermally stressed. For example, dissolved inorganic nutrients may cause cascading effects that increase the severity of bleaching (Wooldridge 2009a) by decreasing the availability of dissolved inorganic carbon to symbionts (Wooldridge 2009b) and by increasing symbiont densities prior to bleaching, which may increase reactive oxygen production at the initiation of thermal stress (Cunning and Baker 2012). Secondary biological stressors, such as predation, competition, parasitism, and disease, may also have greater effects on corals that are already thermally stressed, particularly if the effects of thermal stress cause a weakening of coral defense mechanisms.

Recently there have been an increasing number of studies demonstrating a link between thermal stress and coral disease. For example, thermal stress was related to increased white diseases prevalence on the Great Barrier Reef when coral cover was high (Bruno et al. 2007). In addition, Muller et al. (2008) showed that Caribbean acroporids had increased disease prevalence when bleached or thermally stressed, and had increased disease severity when corals were bleached. Furthermore, Brandt and McManus (2009) showed that Caribbean *Montastraea faveolata* colonies with higher bleaching extent had higher incidence of white plague disease after thermal stress, *Siderastrea siderea* with dark spots disease later had a greater extent of bleaching, and *Colpophyllia natans* showed an association between the incidence of black band disease and bleaching. Thus, thermal stress can increase the prevalence and extent of disease in corals; however, because corals show species-specific

patterns of susceptibility to various diseases (Calnan et al. 2008), increased susceptibility to disease with thermal stress may also have species-specific patterns.

Recovery from disturbance may also show species-to-species variability. Recovery after thermal disturbance, bleaching, and mortality is facilitated by resistance to the disturbance and rapid reestablishment within the environment. Biological processes that might favor recovery include broadcast spawning (Glynn and Colley 2008) and high recruit density, strong potential for regrowth after partial mortality, and high colony growth rates (Darling et al. 2012, van Woesik et al. 2012). In the Indo-Pacific, rapid recovery has been seen in many species with these characteristics. For example, recovery from 4% to 47% coral cover ten years after thermal disturbance on a reef flat in Sesoko Island, Japan was led by resistant massive and encrusting species, resistant small (<4 cm), fast-growing acroporids, and the nonresistant but fast asexually recruiting species *Montipora digitata* (van Woesik et al. 2011). In the Western Atlantic, recovery after mortality has tended to be slower, even in coral colonies that persisted through disturbance (Rogers and Miller 2006). This may relate to a higher influence of chronic secondary stressors (e.g., land-based sources of pollution and overfishing) that interact with acute disturbance in the Western Atlantic (Connell 1997), and the changing demographics of dominant reef building species, such as *Montastraea annularis* (Edmunds and Elahi 2007). However, some species (e.g., sub-massive *Porites astreoides* and massive *Diploria strigosa*) have shown high resistance to thermal and storm disturbances and in some locations have been steadily increasing in abundance over the last few decades (Green et al. 2008, Edmunds 2010).

The growing body of literature on coral's response to thermal stress makes it clear that thermal stress and bleaching can impact multiple aspects of coral physiology and survival. We propose a conceptual thermal bleaching stress response model that can be separated into four physiological stress components encompassing host susceptibility, holobiont susceptibility (bleaching), susceptibility to starvation, and susceptibility to secondary stressors (Fig. 1). In the model, the components of physiological

stress can increase susceptibility to other components within the same vertical column. For example, increased thermal susceptibility leading to increased bleaching can increase susceptibility to disease, and vice versa (Brandt and McManus 2009). The severity of the thermal response in any physiological component can also lead to partial mortality (the loss of coral biomass) or genet mortality (the loss of biomass and genotype), with consequences for recovery. This model provides a conceptual framework for understanding how coral species with their respective traits respond to thermal stress and highlights different pathways that can lead to different outcomes of physiological stress, partial mortality, and genet mortality.

High thermal stress and coral bleaching events affected the northeastern Caribbean in 2005 and 2010 and provided the opportunity to examine species-specific responses of corals to thermal stress. These events had contrasting signatures in the United States Virgin Islands. The year 2005 was the most severe high sea surface temperature (SST) event on record for the northeastern Caribbean (Eakin et al. 2010). In the Virgin Islands, satellite SST records registered a peak of 10.25 degree heating weeks (DHW) and a period of approximately 59 days above the local bleaching threshold of 29.5°C (Aug. 20–Oct. 18); a level of thermal stress accumulation associated with severe coral bleaching and some mortality (NOAA 2012). The warm season of 2010 started as warm or warmer than 2005, with the bleaching threshold surpassed for 21 days between August 12 and September 2. In a clear example of ameliorative storm cooling (Manzello et al. 2007), the passing of the storm center of Hurricane Earl on August 30th, approximately 100 km to the northeast of the St. Thomas-St. John, caused a rapid decline in SST's below the bleaching threshold to 29.3°C. Then from October 5–8, the passage of Hurricane Otto caused windy and cloudy weather that further reduced SST below 29.1°C (see Fig. 1 in Brandt et al. 2013). Total DHW accumulated in 2010 began to decrease after the beginning of October, when it had reached 5.1 DHW; a level associated with some bleaching and limited mortality.

This study presents six years of bleaching response and recovery data for 27 Western Atlantic coral species over catastrophic 2005

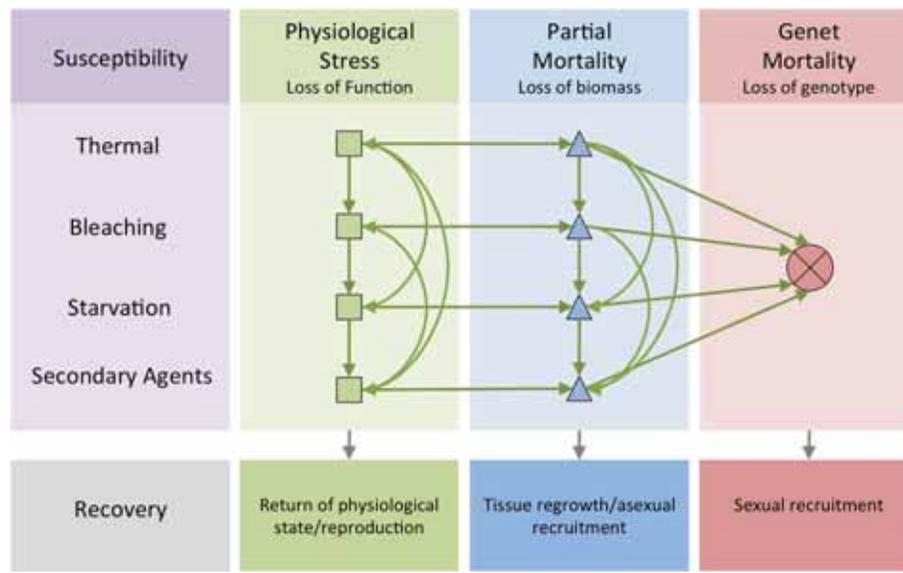


Fig. 1. A conceptual model of the thermal bleaching stress response in any given environment with respect to corals, coral species, and community change. The negative impacts at the community level increase from left to right. Thermal stress is a function of susceptibility at four levels, including thermal stress on the coral animal, the bleaching response, starvation, and secondary agents that affect survival. Stress can lead to partial mortality and the loss of cover, but retention of extant genotypes. Partial mortality can include whole colony mortality if the colony is part of a larger genet that is not linked by tissue. In the most severe case, genet mortality can cause the loss of genotypes. Recovery is governed by the speed and completeness of return in each stress and mortality component, and becomes increasingly difficult with loss of biomass and genotypes.

and mild 2010 thermal stress events. The responses of Western Atlantic coral species to large magnitude thermal stress events, particularly those as strong as 2005, are not well documented. In addition, this study investigated multiple aspects of colony response, including partial mortality and disease; at a resolution able to capture the major proximate drivers of coral cover change and recovery. Our specific aim was to examine the empirical response of coral species across these thermal disturbances to determine if species traits predicted response pathways that predisposed taxa to greater susceptibility, greater resistance, or greater recovery. We hypothesized that in 2005 all species would show severe bleaching (>50% prevalence), but that branching and foliose species would be more highly affected. We also hypothesized that species-specific patterns of coral bleaching, disease, and partial mortality could be characterized by the thermal bleaching stress response model and would be strong predictors of cover loss within species. Those species with

higher physiological susceptibility at any level of the model or with interactions between components of physiological susceptibility should be more predisposed to partial or total mortality. The potential for recovery among Western Atlantic corals was also investigated using both empirical observations and mortality characteristics that may promote future resilience. Lastly, we examined species groupings or trait groupings that can be used to predict the response of these or similar communities to future disturbance and used this information to assess which Caribbean species may be “winners” or “losers” under the influence of increasing thermal stress events.

METHODS

The U.S. Virgin consists of three major islands, St. Croix, St. John, and St. Thomas, surrounded by shelves with widths varying from 0.2–25 km (Fig. 2). St. Thomas and St. John lie adjacent on the wide Puerto Rican shelf, whereas St. Croix

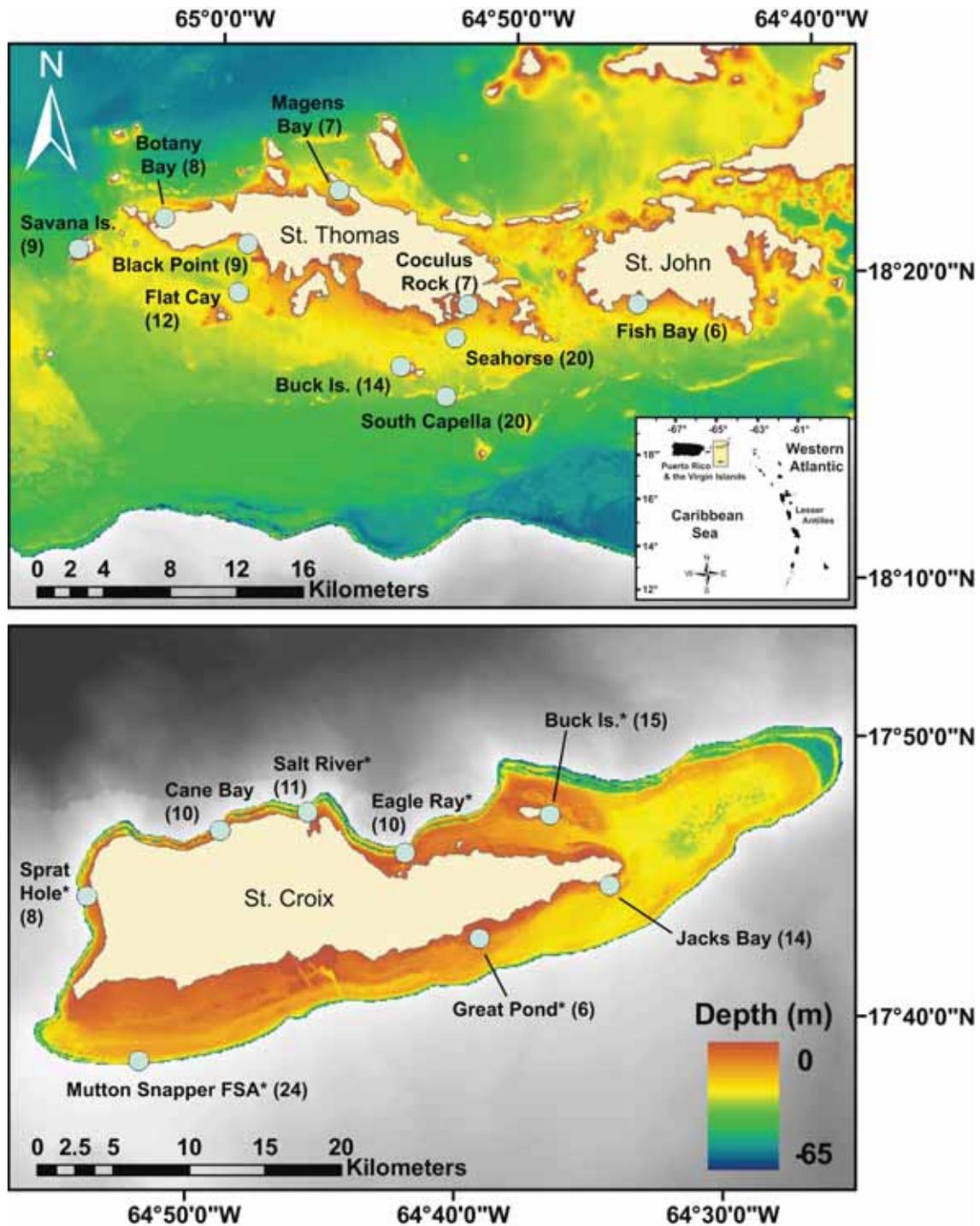


Fig. 2. Study sites around St. Croix, St. Thomas, and St. John, U.S. Virgin Islands. Numbers in parentheses are the mean site depths in meters. Sites marked with an asterisk were not sampled during the 2010 thermal stress event and were not used in statistical comparisons for 2010 bleaching prevalence and extent. Yellow box in inset indicates the U.S. Virgin Islands in relation to the eastern Caribbean. Gray shaded bathymetry indicates seafloor deeper than 65 m.

lies on its own narrow platform about 60 km to the south and separated by the Anegada Passage with depths greater than 4000 m. A total of 18 sites on all three major islands of the U.S. Virgin Islands were surveyed annually or semi-annually between the years 2004 to 2010 as part of the Territorial Coral Reef Monitoring Program (TCRMP; Fig. 2). Here we consider sites less than 25 m in depth in an effort to understand the response of species within the ocean surface mixed layer of the northeastern Caribbean. In addition, sites dominated by acroporid corals were not assessed, but their response to the 2005 bleaching event in the US Virgin Islands has been reported elsewhere (Muller et al. 2008). Each site consisted of six permanent 10 m long transects marked by steel rods and separated by 3–5 m distance. However, prior to 2007 transects at seven sites in St. Thomas were laid in random directions with the same spacing and in the same area of reef as where permanent transects were established in 2007. These sites were Black Point, Buck Island (St. Thomas), Flat Cay, Savana Island, Seahorse Cottage Shoal, and South Capella. It is likely that this had the effect of increasing the year-to-year variability in coral cover estimates from prior to bleaching through 2006, and decreasing variability after 2007. However, there were no significant differences in species-specific coral cover from 2006 to 2007, with the exception of *Colpophyllia natans*. This suggested that increased variability from random transects caused no spurious differences in year-to-year coral cover that was unrelated to the bleaching event; however, *C. natans* cover patterns between these periods should be treated with some caution. Sampling consisted of direct visual observation of coral health and video-based recording of benthic cover (methods described below).

Sites were assessed at least once as a baseline prior to the 2005 mass bleaching event (2004–May 2005), during the mass bleaching event (September–December 2005), in early recovery (health sampling only; January–May 2006), after bleaching (June–December 2006), annually between 2007 and 2009, and then during the 2010 bleaching event (subset of 12 sites, Fig. 2). The 2010 bleaching event was relatively minor in severity; thus, only data from the height of the event are reported to investigate the differences

in the bleaching and paling response among species between 2005 and 2010.

Coral cover

Video sampling was conducted along 10 m transects following standard methodologies (Rogers and Miller 2001, Smith et al. 2008). A SCUBA diver swam at a uniform speed (3–5 min. per transect), pointing a video camera perpendicular to the substrata and following the vertical contour of the reef at the approximate height of a guide wand, 0.4 m in length. Non-overlapping captured images represented a planar area of reef approximately 0.31 m² (0.64 m × 0.48 m). Ten randomly located points were superimposed on each captured image and the benthic cover under each point was then identified to the lowest identifiable taxonomic level and used in calculation of percent cover. For coral species in the *Montastraea annularis* species complex (*M. annularis*, *M. faveolata*, and *M. franksi*) there was difficulty in assigning species, particularly after the 2005 bleaching event where partial mortality often led to small tissue patches without discernable taxonomic characteristics. This was not usually the case with *M. annularis*, whose macro-morphology tended to remain obvious. Therefore, two taxonomic categories of the *M. annularis* species complex are considered in this study: *M. annularis* and the *Montastraea annularis* species complex (MX), which hereafter refers to a combination of *M. faveolata* and *M. franksi*, with the likelihood of small numbers of amorphous *M. annularis*. This lumping of *M. faveolata*, *M. franksi*, and small *M. annularis* could mask some of the variation in individual species responses, such as susceptibility to disease. In addition, branching poritids, including *Porites divaricata*, *Porites furcata*, and *Porites porites* were combined under the species designation branching *Porites* spp. to avoid confusion in species assignment. However, from in situ observations on health transects, 92.4% of branching poritids were identified as *P. porites*.

Coral health

All scleractinian coral and hydrocoral colonies greater than 10 cm in largest diameter and intersected by the transect line were assessed in situ. Prior to 2008, only colonies greater than 10 cm in largest diameter were evaluated. Starting

in 2008, all colonies, regardless of size were recorded, although the analyses were constrained to colonies greater than 10 cm to match the pre-2007 data set. This resulted in a sample size of 9,989 coral colonies. Colonies were assessed for signs of bleaching, disease, and mortality following a modified Atlantic and Gulf Rapid Reef Assessment protocol (Kramer et al. 2005, Calnan et al. 2008, Smith et al. 2008). Variables measured were colony longest horizontal length (including dead colony portions), bleaching (prevalence and extent), white diseases (prevalence), recent partial and total mortality (prevalence), and old partial mortality (prevalence and extent). Prevalence represents the number of individuals in the population affected, while extent represents the proportion of the colony affected and takes into account only affected individuals.

Abnormal lightening of the colony color was assessed by experienced observers and categorized as bleaching (colony areas with a stark white appearance), or paling. Visual estimates of bleaching have been used extensively in the literature, with good correlations to symbiont chlorophyll concentration, and order of magnitude reductions in symbiont density from normal conditions to those indicated by stark or skeletal white coloration (McClanahan et al. 2007). When bleaching or paling was present on a colony, the extent (proportion) of white or paling tissue on the colony affected was estimated. For colonies that had both bleached and pale tissue, the colony was scored as bleached for prevalence calculations and only the extent of the bleached tissues was used in comparisons, giving greater weight to the most severe signs of poor coral health. Some level of low prevalence and low extent bleaching and paling (combined prevalence <20%, or 40% for *S. siderea*) was common in the focal species before the bleaching event in the period prior to bleaching and in periods that preceded the study (T. Smith, *unpublished data*). Although this was not specifically controlled for, bleaching and paling associated with thermal stress in 2005 and 2010 was typically many times greater than background bleaching.

Diseases were conservatively categorized into recognized Western Atlantic scleractinian diseases and syndromes (following Bruckner 2007). Only the diseases characterized as white disease,

including white plague, were examined in this study as these had disproportionate impacts on coral tissue loss after bleaching (Miller et al. 2009). We use the more general term of white disease (Bythell et al. 2004) as it is not clear that the etiologies were specifically related to characterized white plague types in all cases. In general, we defined white disease lesion signs as multifocal to coalescing areas of recent tissue loss that appeared to have originated basally or peripherally on colonies and proceeded as a solid to discontinuous band (Appendix B). Background white disease levels were not specifically controlled for, as levels of white disease in the focal species at the study sites from 2002–2004 (0.5%, $N = 2018$ colonies) were many times lower than seen in our study (T. Smith, *unpublished data*).

Recent mortality was defined as areas of skeleton recently denuded of living tissue with very little to no filamentous algae colonization on non-eroded coral skeleton. Old mortality was identified as areas of the colony with no living tissue with thick turf or macroalgae growth on top of eroded coral skeleton. Complete colony mortality was scored where there was evidence of recent mortality and no indication of any living tissue anywhere on the colony.

Data analysis

The prevalence of bleaching and paling, and the change of coral cover were assessed for all coral species sampled and presented as summary statistics. Nine focal scleractinian coral species with the highest abundances on the reefs sampled were chosen for comparative analysis because their sample size was amenable to parametric statistical comparisons. These species were *Agaricia agaricites*, *Colpophyllia natans*, *Diploria strigosa*, *Montastraea annularis*, *Montastraea annularis* species complex, *Montastraea cavernosa*, *Porites astreoides*, branching *Porites* spp., and *Siderastrea siderea*. In addition, these species represented a range of traits, facilitating evaluation of the performance of different biological characteristics during and after bleaching. For variables that represented chronic responses to the bleaching event and were therefore linked between time periods, such as old partial mortality and coral cover, a statistical model was used that incorporated the nine focal species and time. For variables that were acute and not

necessarily linked across time periods, such as bleaching/paling, white disease, and recent mortality, the pattern among the nine focal species was assessed within a specific time period or using the mean values at the height of the response.

Comparisons among species for the bleaching response were carried out at time periods that represented the maximum response during height of the bleaching event and, separately, for the first time period of recovery after the 2005 thermal stress event (Jan.–May 2006). Bleaching prevalence and extent was compared among the nine focal species for surveys conducted at the height of the 2005 thermal stress event. Bleaching among species was also tested at the height of the 2010 thermal stress event at a subset of 12 sites surveyed between August and November. Paling was tested within the 2005 and 2010 thermal stress events, when they had the potential to covary with the bleaching response, and an additional comparison was made among species in the 2005 bleaching recovery period (Jan.–May 2006). When significant differences were found among species, the difference between species was compared with a Tukey's HSD post-hoc test. With the exception of principal components analysis, all statistical comparisons were conducted in JMP v9 (SAS Institute).

The prevalence of white disease and recent mortality among coral species was tested in the two sampling periods just subsequent to bleaching in 2005. The purpose was to determine the peak prevalence among species of white disease or recent mortality stimulated by catastrophic bleaching in 2005. For each species the peak prevalence of white disease and recent mortality was taken from the early 2006 sampling period (Jan.–May) or the late 2006 period (Jun.–Dec.), whichever value was higher for the species. Species were compared with a Kruskal-Wallis test due to violations of parametric analysis and pair wise differences between species were then tested with a Tukey's HSD post-hoc test. For white disease only the six focal species that exhibited these disease signs were used to compare peak prevalence (*C. natans*, *M. annularis*, *M. annularis* species complex, *M. cavernosa*, *P. astreoides*, and *S. siderea*). Within each species the temporal pattern of recent partial mortality was also examined with individual Kruskal-Wallis

tests followed by Tukey's HSD post-hoc tests. White diseases were not tested over time because of frequent periods with zero values, and the comparisons were made with visual inspection of the temporal pattern.

Old partial mortality was tested among the nine focal species and time periods using a repeated-measures analysis of variance (RM-ANOVA). Pairwise post-hoc comparisons between species and time periods were performed using a Tukey's HSD test.

Coral cover was tested among the nine focal species and time periods using a RM-ANOVA after an arcsine transformation. The pattern of individual species over time was then tested with a separate RM-ANOVA with a Bonferroni adjustment procedure or a Kruskal-Wallis test when data did not meet assumptions for parametric analysis. Post-hoc comparisons among times were performed using a Tukey's HSD test.

The change in coral colony abundance caused by the 2005 bleaching event was tested for each species. The abundance of colonies greater than 10 cm maximum length was calculated from coral health intercept transects prior to bleaching in 2005 and after the cessation of the response to bleaching in 2007. The relative change was calculated for each species on each transect and used to test the hypothesis that the change in abundance was significantly different than zero using a Wilcoxon test on ranks.

Live tissue size frequencies of the focal coral species were compared among length size categories; small (10–15 cm), medium (16–30 cm), and large (>30 cm) and the years 2005, 2007, and 2010. Data was not available on multiple size dimensions (length, width, height) prior to the 2005 bleaching event and a reliable estimate of the actual total and living area of a colony could not be calculated. Instead, live tissue lengths were calculated as the total colony length, inclusive of dead colony portions, multiplied by the percent of colony living (1 minus the extent of partial mortality). Since the extent of partial mortality is an areal measure and live length is linear measure, the live length calculated in this study provided a mutually consistent, but not exact, estimate of longest length of living tissue. As a caveat, this estimate of live tissue length underestimates the true live length for colonies with a high degree of partial mortality, since, all

other things equal, the percent area decreases by the square while the percent length decreases linearly. Thus, there may have been an overestimation of the downward size class transition frequencies. As a check against undue bias, the direct change of maximum length (living and dead colony portions) was tested between the same time periods and results were robust for all species except MX ($\chi = 4.2$, $p = 0.376$). MX have very distinct individual skeletal structure and very dense skeletons that were readily identifiable even after a high degree of partial mortality (see Appendix B), thus, they only showed size frequency changes when an estimate of live tissue length was used. Frequencies of live lengths in size classes were tested among time periods with a contingency table and χ^2 analyses. The species *A. agaricites*, *C. natans*, and *P. astreoides* had low expected frequency in some cells that should lead to cautious interpretation of the χ^2 analysis. For example, *A. agaricites* and *C. natans* both had no representative colonies in some size classes over some years.

Relationships between the response variables for the 2005 and 2010 bleaching events among the focal coral species were explored with a correlation matrix. Principal component analysis (PCA) was then used to analyze the pattern of response to the 2005 bleaching event among the nine focal species. For each species the following variables were included in the analysis: (1) mean colony abundance change between 2005 and 2007, (2) mean coral cover change between 2005 and 2007, (3) peak of mean bleaching prevalence during the 2005–2006 event, (4) mean paling prevalence between January and May 2006 (recovery), (5) peak of mean disease prevalence following the 2005–2006 event, (6) peak of mean recent mortality prevalence in 2006, and (7) peak of mean old mortality prevalence following the 2005–2006 event. All data were normalized and the correlation matrix was used as the basis for the analysis using the PCA routine in the statistical software package PRIMER (v. 6).

The ranking of coral species responses the 2005 bleaching event recorded in this study were compared to a trait-based ranking of coral genera responses to thermal stress (van Woesik et al. 2012). Thermal responses in van Woesik et al. (2012) were based on the consensus opinion of 10 coral reef scientists, who produced a list of eight

coral traits associated with tolerance to thermal stress (Appendix A). Coral genera responses were evaluated by the same scientists against a hypothetical +3°C thermal stress anomaly during the solar insolation maximum. From the present study, coral cover change was chosen as the response metric as it is an integrated measure of coral response that is the most commonly used in studies of coral community disturbance. Scores for each trait and overall trait rankings of van Woesik et al. (2012) were used as published but evaluated against published quantitative information (Appendix A). Ties in rank within traits or cover loss were assigned the mean value of the rank slots that would have been taken by the tied ranks if arbitrarily assigned higher or lower (e.g., two species with a tie in ranks over slots 3 and 4 would have each been assigned a value of 3.5). The differences between hypothetical rankings from van Woesik et al. (2012) and empirical rankings of coral cover change from this study were used as the comparative metric.

RESULTS

The extreme thermal disturbance event in 2005 initiated a distinct sequence of coral responses across the shallow and intermediate depth coral reefs monitored from 2004 to 2010 (Fig. 3). Overall, the coral stress responses showed a lagged pattern; with a high mean prevalence of bleaching from September through December 2005 preceding the highest recorded mean prevalence of white diseases by three months to a year. The response of coral cover was closely associated with the onset of white diseases, suggesting that disease lesions and their associated recent partial mortality were responsible for cover loss. Recent partial mortality spiked within three months to a year after bleaching, concurrent with a 48% loss of relative coral cover, and the rapid and pervasive accumulation of signs of old partial mortality. These responses are evaluated below for the 27 individual species recorded and the nine focal species.

Bleaching

All of the nine focal coral species were affected by bleaching during the 2005 thermal stress event. The combined prevalence of stark white bleaching and paling on these species was

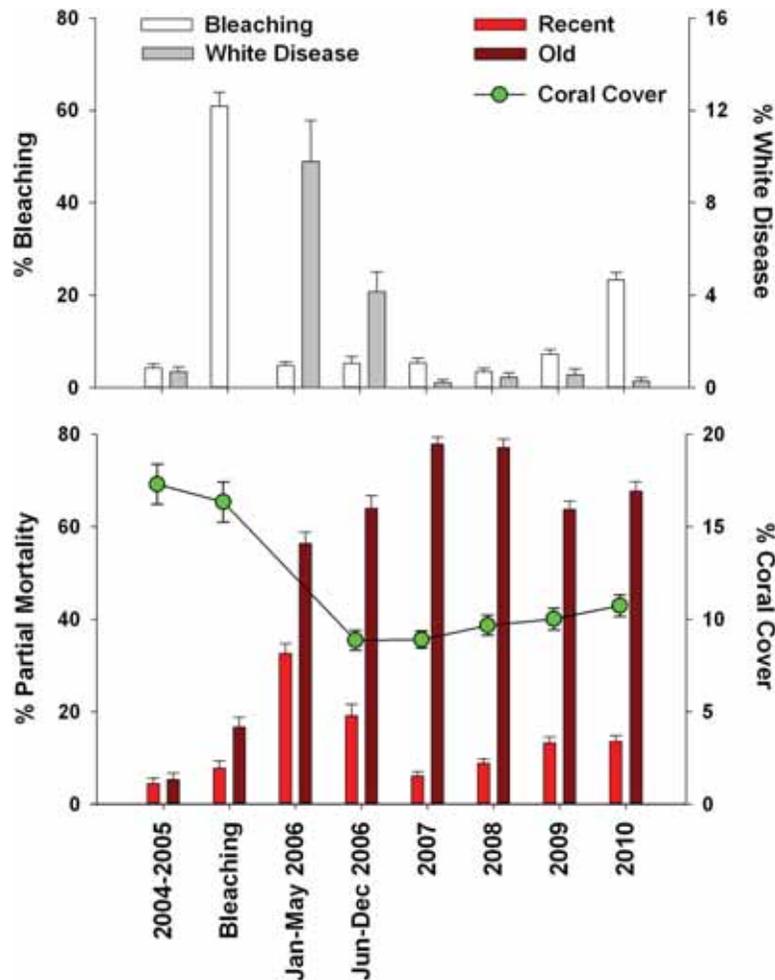


Fig. 3. Summary of total community response for all scleractinian coral species to bleaching across sites and time periods. Upper panel, the prevalence of the coral stress responses stark white bleaching (left-axis) and white diseases (right-axis). Lower panel, the prevalence of recent and old partial mortality (left-axis) and total hard coral cover (right-axis). Error bars are \pm SE.

greater than 70% during the bleaching period (Fig. 4). However, the prevalence of coral bleaching and paling during the height of the bleaching event and during the recovery period was significantly different among coral species (Table 1). During the height of the bleaching event, *Agaricia agaricites* had the highest prevalence of stark white bleaching (90%) and the highest extent of bleaching (92%). Paling prevalence was relatively low in *A. agaricites* largely because most colonies were almost entirely bleached. With paling included, only 3% of sampled *A. agaricites* colonies showed no bleaching or paling. Branching *Porites* spp., which had a

high prevalence of bleached colonies (78%) at a high extent (87%), with 11% of prevalence of colonies showing no bleaching or paling. Non-focal species with fewer sampled colonies that also showed a strong response to the 2005 thermal stress event included *Agaricia grahamae*, *Isophyllia* spp., *Madracis decactis*, *Madracis mirabilis*, *Millepora complanata*, *Mycetophyllia* spp. and *Stephanoceaonia intercepta* (Table 2).

Species showing an intermediate bleaching response during the 2005 thermal stress event included *Colpophyllia natans*, *Siderastrea siderea*, and the two taxonomic divisions of the *Montastraea annularis* species complex (Fig. 4). Bleaching

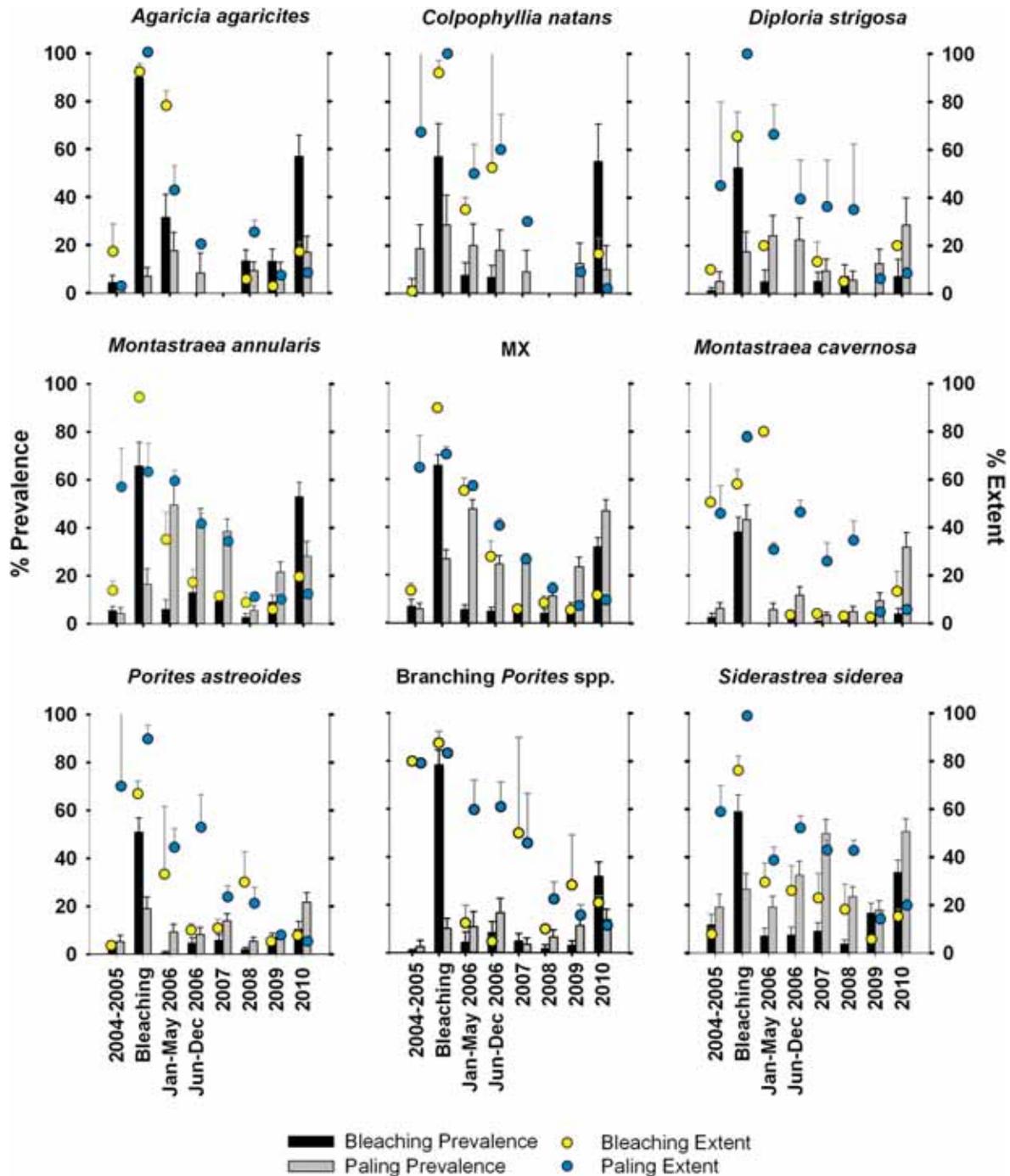


Fig. 4. The prevalence and extent of coral bleaching and paling (\pm SE) for nine focal coral species across eight periods spanning 2004–2010. MX = *Montastraea annularis* species complex.

prevalence for these species was between 55% and 70%, but when bleaching was present it affected the majority of the colony (bleaching extent >75%). Few colonies of *C. natans*, *M. annularis*, *M. annularis* species complex, and *S. siderea* escaped impact, as the number of colonies showing no bleaching or paling was 14%, 18%, 8%, and 14%, respectively. A non-focal species

Table 1. Statistical comparison of the prevalence and extent of bleaching among nine focal species during height of bleaching in 2005.

Test	F/ χ^2	df	Prob.	AA	CN	DS	MA	MX	MC	PA	BP	SS
Prevalence												
BL 2005	38.8†	8	<0.0001	A	ABC	BC	ABC	AB	C	BC	AB	BC
PA 2005	30.3†	8	0.0002	B	AB	AB	AB	AB	A	B	B	AB
BL 2006	32.8†	8	<0.0001	A	B	B	B	B	B	B	B	B
PA 2006	87.1†	8	<0.0001	C	BC	ABC	AB	A	C	C	C	C
BL 2010	13.0	8/337	<0.0001	AB	AB	CD	A	BC	D	D	BC	BC
PA 2010	5.9	8/337	<0.0001	C	BC	ABC	ABC	AB	ABC	C	C	A
Extent												
BL 2005	18.4	8/476	<0.0001	A	AB	BC	AB	A	C	C	AB	AB
PA 2005	5.6	8/256	<0.0001	AB	AB	AB	AB	B	A	AB	AB	A
BL 2006	4.0	8/57	0.0011	A	AB	AB	AB	AB	AB	AB	B	B
PA 2006	2.8	8/283	0.0050	AB	AB	AB	A	A	AB	AB	AB	B
BL 2010	2.1	8/273	0.0358	A	A	A	A	A	A	A	A	AB
PA 2010	6.6	8/274	<0.0001	ABC	ABC	ABC	AB	BC	BC	C	AB	A

Notes: Test code abbreviations are: BL = bleached, PA = pale. Species code abbreviations are: AA = *Agaricia agaricites*, CN = *Colpophyllia natans*, DS = *Diploria strigosa*, MA = *Montastraea annularis*, MX = *Montastraea annularis* species complex, MC = *Montastraea cavernosa*, PA = *Porites astreoides*, BP = branching *Porites* species, SS = *Siderastrea siderea*.

† Wilcoxon χ^2 statistic for non-parametric comparisons.

that also showed an intermediate response was *Diploria labyrinthiformis* (Table 2).

The focal species with the lowest levels of bleaching in 2005 were *D. strigosa*, *M. cavernosa*, and *P. astreoides* (Fig. 4). The species *D. strigosa* and *P. astreoides* had a similar response, with

about half of colonies bleached to an extent of 66% of tissue surface, and with a relatively large proportion of colonies that showed no bleaching or paling (~30%). *M. cavernosa* had fewer colonies that showed no bleaching or paling during the height of bleaching (18%), and among

Table 2. Response summaries of 27 stony coral species for mean prevalence of bleaching and paling during the height of the 2005 bleaching event (Sep.–Dec. 2005) and the 2010 bleaching event (Sep.–Oct. 2010).

Species	2005 BL % (SE, N)	2005 PA % (SE)	2010 BL % (SE, N)	2010 PA % (SE)
<i>Agaricia agaricites</i>	89.8 (4.5, 36)	7.0 (3.5)	66.6 (10.6, 18)	18 (8.5)
<i>Agaricia grahamae</i>	78.5 (14.8, 7)	7.1 (7.1)	0 (0, 2)	100 (0)
<i>Agaricia lamarcki</i>	59 (14.7, 11)	9 (9)
<i>Colpophyllia natans</i>	57.1 (13.7, 14)	28.5 (12.5)	50 (15, 11)	9 (9)
<i>Dendrogyra cylindrus</i>	33.3 (33.3, 3)	66.6 (33.3)	0 (0, 3)	0 (0)
<i>Dichocoenia stokesii</i>	0 (0, 3)	66.6 (33.3)
<i>Diploria clivosa</i>	11.1 (11.1, 3)	66.6 (33.3)	0 (0, 0)	0 (0)
<i>Diploria labyrinthiformis</i>	61.1 (11.8, 18)	27.7 (10.8)	16.6 (16.6, 6)	33.3 (21)
<i>Diploria strigosa</i>	52.5 (11.1, 20)	17.5 (8.3)	0 (0, 13)	30.7 (12)
<i>Eusmilia fastigiata</i>	33.3 (33.3, 3)	66.6 (33.3)	16.6 (16.6, 6)	33.3 (21)
<i>Helioseris cucullata</i>	0 (0, 1)	100 (0)	0 (0, 1)	100 (0)
<i>I. sinuosa/I. rigida</i>	100 (0, 3)	0 (0)
<i>Madracis decactis</i>	100 (0, 5)	0 (0)	0 (0, 9)	22.2 (12.1)
<i>Madracis mirabilis</i>	50 (50, 2)	0 (0)	0 (0, 1)	100 (0)
<i>Meandrina meandrites</i>	0 (0, 13)	25.6 (12)	0 (0, 9)	5.5 (5.5)
<i>Millepora alcicornis</i>	63 (12.3, 14)	9.5 (7.3)	9 (6.2, 22)	9 (6.2)
<i>Millepora complanata</i>	53.3 (22.6, 5)	6.6 (6.6)
<i>Montastraea annularis</i>	65.7 (9.8, 21)	16.4 (6.5)	58 (6.5, 35)	27.8 (6.1)
<i>Montastraea annularis</i> spp. cpx.	65.6 (4.6, 72)	26.6 (3.8)	34.7 (4.2, 56)	46.5 (4.7)
<i>Montastraea cavernosa</i>	38.1 (6.1, 53)	43.3 (6.2)	3.8 (2.3, 48)	31 (6.2)
<i>Mycetophyllia</i> spp.	100 (0, 1)	0 (0)	8.3 (8.3, 6)	0 (0)
<i>Porites astreoides</i>	50.7 (6, 52)	18.9 (4.8)	10.7 (3.1, 61)	21.3 (4.1)
Branching <i>Porites</i> spp.	78.3 (6.2, 32)	10.1 (4.2)	35.2 (6.4, 40)	12.6 (4.1)
<i>Scolymia</i> spp.	0 (0, 1)	100 (0)
<i>Siderastrea siderea</i>	58.9 (7, 45)	26.6 (6.4)	36.3 (5.5, 51)	51.8 (5.5)
<i>Stephanocoenia intercepta</i>	100 (0, 3)	0 (0)	5.8 (5.8, 17)	52.9 (12.4)

Notes: Abbreviations are: BL = bleached; PA = paling; *I. sinuosa* = *Isophyllia sinuosa*; *I. rigida* = *Isophyllastrea rigida*; Cpx. = complex. An ellipsis (...) indicates no data.

the focal species it exhibited the lowest prevalence of bleaching (38%), but the highest prevalence of paling (43%). Some non-focal species that were also less responsive to bleaching included *Dendrogyra cylindrus*, *Diploria clivosa*, *Dichocoenia stokesii*, *Eusmilia fastigiata*, *Helioseris cuculata*, *Meandrina meandrites*, and *Scolymia* spp. (Table 2).

In the recovery period from January to May 2006 there were also species-specific differences in prevalence of bleaching and paling that corresponded to prolonged signs of stress. The phenomena of “apparent recovery” may have affected species that showed low prevalence of bleaching or paling in the recovery period. In this case tissues or colonies that were severely bleached may have been more prone to mortality during and just after the bleaching event, leading to fewer bleached colonies and tissues in the recovery period. This is a caveat to interpreting the data for species that appeared to recover more rapidly but had a high prevalence of recent partial mortality, such as branching *Porites* species. In contrast, the highly bleached species *Agaricia agaricites* maintained a significantly higher prevalence of bleaching into the recovery period, indicating a failure of colonies to recover their symbionts (Fig. 4, Table 1). In addition, the two large faviids *M. annularis* and the *M. annularis* species complex both exhibited a prolonged recovery period with significantly higher prevalence of paling into early 2006.

Species-specific bleaching and paling responses to the 2010 thermal stress event showed some differences and similarities to the 2005 event. In 2010 all species had a prevalence of bleaching or paling that was elevated above background bleaching levels in non-bleaching periods (prior to 2005, 2007–2009). However, the extent of bleaching and paling on colonies was low and similar among species (Table 1), indicating spotty and partial bleaching, in contrast to 2005 when the extent of bleaching was severe and affected the majority of the colony. In 2010, the most severely affected species were *A. agaricites*, *C. natans*, and *M. annularis*, in contrast to 2005, when *A. agaricites* and branching *Porites* spp. were the most severely affected. Also in contrast to 2005, the *M. annularis* species complex and *S. siderea* were lightly affected in 2010, with a moderate prevalence of bleaching and paling at a low extent. The most bleaching resistant species

in 2005 were also the most resistant in 2010; *D. strigosa*, *M. cavernosa*, and *P. astreoides* showed a moderate prevalence of paling at a low extent, but no apparent increase in bleaching prevalence.

White disease

Identifiable white diseases after the 2005 bleaching event only affected six of the nine focal species within transects, including *C. natans*, *M. annularis*, *M. annularis* species complex, *M. cavernosa*, *P. astreoides* and *S. siderea* (Fig. 5). White disease also affected an additional three of 18 non-focal species (Table 3), although sample sizes were low. The prevalence of white diseases on affected species in 2006 was the highest recorded for any period at these sites between 2001 and 2012 (Calnan et al. 2008, Smith et al. 2008). The massive faviids, *C. natans* and *M. annularis* species complex tended to have the greatest prevalence of white disease in 2006 (Fig. 5, Table 4). However, the occurrence of bleaching or paling that was common for these species in 2006 (delayed recovery) was not related to the occurrence of white disease on a colony basis (contingency analysis, $n = 912$, $\chi^2 = 2.2$, $p = 0.323$), suggesting that recovery of algal pigmentation did not prevent the later development of disease signs. Although not recorded as susceptible to white disease in sampled transects, marked *D. strigosa* colonies at a subset of five of the sites assessed in a separate project showed signs of white disease between Dec. 2005 and Apr. 2006 ($N = 25$, prevalence = 8.0%). Of note is the fact that no cases of white disease were recorded during the bleaching period in 2005 on any species of coral.

Partial mortality

Recent and old partial colony mortality showed a strong response to the 2005 bleaching event with a pattern that differed among species. Recent partial mortality varied across time among and within species (Table 4, Table 5), lagging behind bleaching and peaking in 2006 for some species (Fig. 6). In general, recent partial mortality patterns followed patterns of bleaching severity across species, with the highest prevalence in *A. agaricites* and branching *Porites* spp. Recent partial mortality also occurred earlier in *A. agaricites*, starting in the 2005 bleaching period and peaking in Feb.–Apr. 2006 (Fig. 6). However,

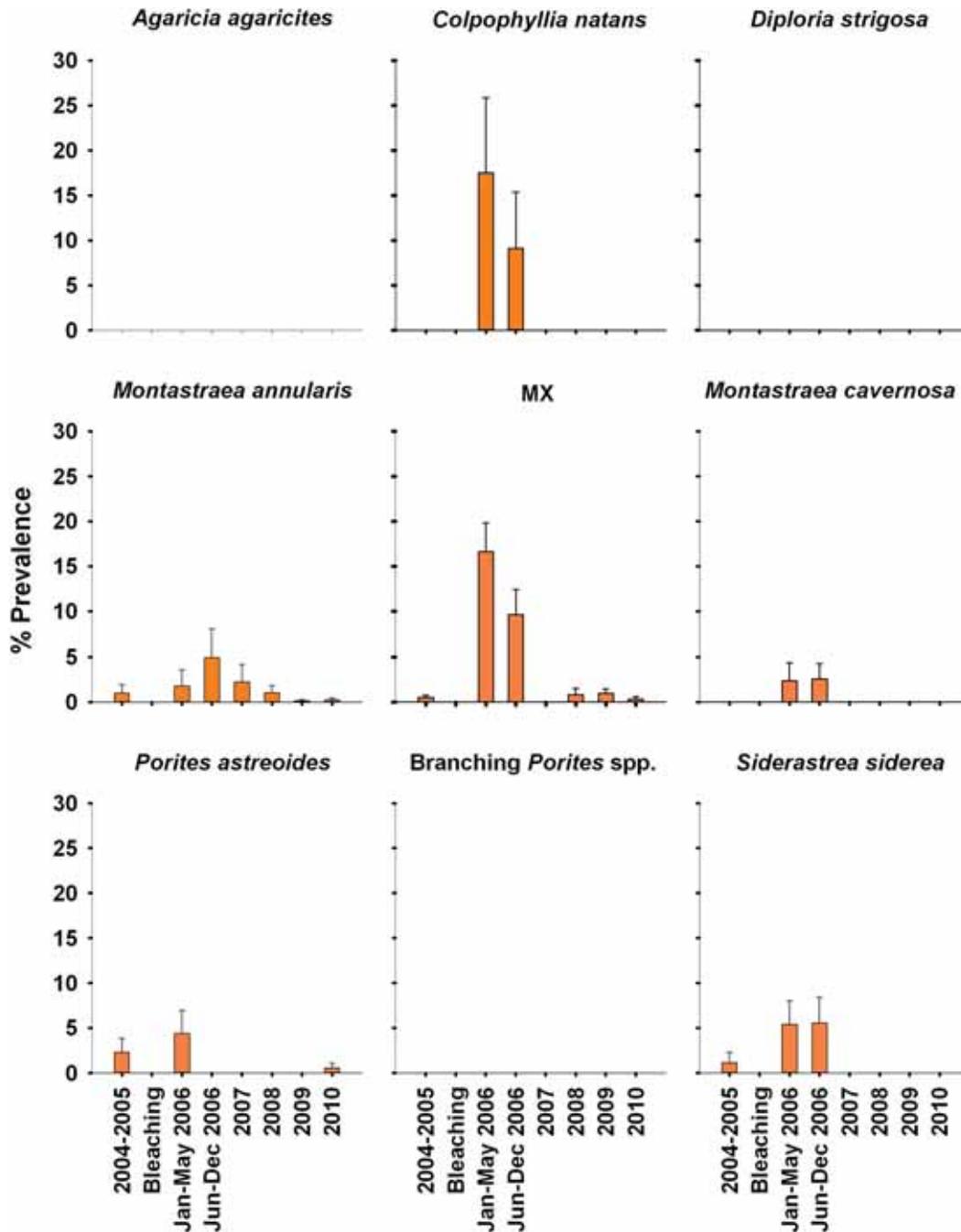


Fig. 5. The prevalence of white disease (\pm SE) for nine focal coral species across eight periods spanning 2004–2010. Species with no data indicate that disease was not seen in those species. MX = *Montastraea annularis* species complex.

few *A. agaricites* were sampled in the later part of 2006 ($N = 13$), as the abundance of colonies greater than 10 cm in diameter had already declined by 81%. Other species that had signif-

icantly elevated recent partial mortality after the peak of bleaching in 2005 included; *C. natans*, *M. annularis* species complex, *M. cavernosa*, and *S. siderea*, whereas there was no significant eleva-

Table 3. Response summaries of 27 stony coral species for mean prevalence of peak white disease (2006), percentage of total colony mortality (bleaching period to 2007), coral cover before bleaching in 2005, and the change in coral cover after the 2005 bleaching event (bleaching period to 2007).

Species	M	N	WD		Mortality %	2005 cover %	Cover change %
			% (SE, N)				
<i>Agaricia agaricites</i>	F	434	0 (0, 22)		15.9	0.7	-91.8
<i>Agaricia grahamae</i>	F	35	0 (0, 22)		8.0	0.0	-100.0
<i>Agaricia lamarcki</i>	F	31	0 (0, 2)		0.0	0.004	-87.0
<i>Colpophyllia natans</i>	M	154	17.5 (8.3, 20)		6.7	0.2	-81.1
<i>Dendrogyra cylindrus</i>	C	26	0 (0, 5)		7.1	0.04	22.0
<i>Dichocoenia stokesii</i>	M	14	100 (0, 2)		0.0	0.02	25.8
<i>Diploria clivosa</i>	M	34	0 (0, 2)		0.0	0.1	-55.3
<i>Diploria labyrinthiformis</i>	M	119	5.8 (5.8, 17)		5.3	0.3	-73.5
<i>Diploria strigosa</i>	M	284	0 (0, 20)		2.0	0.4	-35.2
<i>Eusmilia fastigiata</i>	B	44	0 (0, 5)		0.0	0.02	-5.9
<i>Helioseris cucullata</i>	P/S	5	0 (0, 3)		0.0	0.0	-100.0
<i>I. sinuosa</i> / <i>I. rigida</i>	M	4	0 (0, 1)		0.0	0.0	-14.6
<i>Madracis decactis</i>	N	92	0 (0, 4)		0.0	0.01	-14.2
<i>Madracis mirabilis</i>	B	43	12.5 (12.5, 8)		3.7	0.3	-96.1
<i>Meandrina meandrites</i>	Sm	141	0 (0, 11)		0.0	0.1	21.9
<i>Millepora alcicornis</i>	B	269	0 (0, 20)		0.0	0.3	16.8
<i>Millepora complanata</i>	VP	90	0 (0, 2)		3.7	0.2	-76.3
<i>Montastraea annularis</i>	M	1074	4.9 (3, 37)		0.0	2.6	-60.4
<i>Montastraea annularis</i> spp. complex	M	2704	16.6 (3.2, 82)		0.8	7.2	-58.7
<i>Montastraea cavernosa</i>	M	1140	2.5 (1.7, 65)		0.4	1.2	2.8
<i>Mycetophyllia</i> spp.	P/S	15	0 (0, 1)		...	0.1	-60.0
<i>Porites astreoides</i>	M	1428	4.3 (2.5, 57)		0.7	1.5	-14.6
Branching <i>Porites</i> spp.	B	610	0 (0, 36)		3.9	1.2	-63.3
<i>Scolymia</i> spp.	S	9	...		0.0	0.0	...
<i>Siderastrea siderea</i>	M	900	3.7 (2.5, 54)		0.0	0.7	24.4
<i>Stephanocoenia intercepta</i>	M	139	0 (0, 8)		0.0	0.03	34.2

Notes: Abbreviations are: M = morphology; N = number of colonies; Mortality = total colony mortality; Cover = coral cover; *I. sinuosa* = *Isophyllia sinuosa*; *I. rigida* = *Isophyllastrea rigida*; B = branching; C = columnar; F = Foliose; M = massive; N = Nodular; P/S = plating/sheeting; S = solitary; Sm = Sub-massive; and VP = vertically plating. An ellipsis (...) indicates no data.

tion of recent partial mortality in the species *D. strigosa*, *M. annularis*, and *P. astreoides* (Fig. 6).

The prevalence of old partial mortality had the same general pattern among all coral species. The pattern of old partial mortality was not significantly different among species, as indicated by a non-significant species \times time interaction term (Table 6). Therefore, post hoc comparisons are shown separately among species and time in Table 6. Old partial mortality increased significantly and rapidly with time starting in early 2006, following the height of bleaching in 2005 and the onset of white diseases and recent mortality (Fig. 7). The prevalence of old partial

mortality continued to build into 2007 followed by a leveling of prevalence in 2007 and 2008. By 2009 the prevalence of old partial mortality on all species began to decline; however, prevalence values were still much higher than pre-disturbance levels. Although the pattern of old partial mortality was similar among species over time, species such as *M. annularis* and the *M. annularis* species complex had the highest overall prevalence, while species *A. agaricites*, *D. strigosa*, and *P. astreoides* had lower overall prevalence (Table 6).

Complete colony mortality that occurred during and after bleaching was moderate to low in

Table 4. Statistical comparison of the peak prevalence of white disease and recent partial mortality among coral species in 2006 during recovery from bleaching in 2005. For white disease only data for affected species were tested.

Test	χ^2	df	Prob.	AA	CN	DS	MA	MX	MC	PA	BP	SS
White disease	38.3	5	<0.0001	...	AB	...	AB	A	B	B	...	B
Recent partial mortality	123.0	8	<0.0001	A	BCD	E	CDE	C	DE	E	AB	DE

Notes: Species codes as in Table 1. An ellipsis (...) indicates white disease did not occur for these species on transects.

frequency, despite the severity of the bleaching response for some species, the strong increase in partial mortality, and the frequent health monitoring after bleaching in 2005 (Table 3). Total colony mortality ranged from 0 to 15.9% for all species, with the highest loss in *A. agaricites* followed by *Millepora complanata*. Branching *Porites* spp. had low total colony mortality (3.9%) although they were highly susceptible to bleaching and partial mortality.

Coral cover, colony abundance, and size frequencies

Coral cover declined after the 2005 coral bleaching event in most of the focal species but remained unchanged in *D. strigosa*, *P. astreoides*, and *S. siderea* (Fig. 8, Table 7). In addition, *M. cavernosa* had a declining pattern of coral cover that was not significantly different after Bonferroni adjustment of p-values and appeared to be unrelated to the 2005 bleaching event. For those species that lost coral cover there was little indication of recovery in the five years following the mortality related to 2005 bleaching, with the possible exception of a slight increase in cover for the *M. annularis* species complex. The majority of non-focal species also showed losses of coral cover over the 2005 bleaching event (Table 3); however, these species had very low coral cover initially and were represented by a small number of transects, therefore change values should be treated with caution. From observations in 2011, the mild 2010 bleaching event did not have any appreciable effect on coral cover at these study reefs (T. Smith, unpublished data).

The change in abundance for colonies greater than 10 cm among the focal species was variable (Fig. 9, Table 8). The only species to have a significant loss in abundance was *A. agaricites*, while four species showed a significant increase in abundance (*M. annularis* species complex, *M. cavernosa*, *P. astreoides*, and *S. siderea*). The remainder of the focal species had no detectable change in abundance, including species that showed large decreases in coral cover (*C. natans*, *M. annularis*, *M. annularis* species complex, and branching *Porites* spp.).

The live length size frequencies of most focal species declined between 2005, 2007, and 2010 (Table 9, Fig. 10). For most species, colonies in the 10–15 cm size class increased while corals greater

Table 5. Statistical comparison of recent partial mortality prevalence across sampling time periods for individual species.

Source	χ^2	df	Prob.
Total	222.9	7	<0.0001
AA	84.0	7	0.0001
CN	27.4	7	0.0003
DS	6.4	7	0.490
MA	9.0	7	0.256
MX	134.3	7	<0.0001
MC	21.3	7	0.0034
PA	12.1	7	0.100
BP	66.5	7	<0.0001
SS	24.1	7	0.0011

Notes: Post hoc comparisons shown in Fig. 6. Species codes as in Table 1.

than 30 cm decreased. While some of the change may have resulted from recruitment into the smallest size classes, a more parsimonious explanation is that living tissue on large colonies regressed in size due to partial mortality. As with other indications of response to the 2005 bleaching event, *A. agaricites* was the most negatively affected species, with a loss of all colonies in the largest size class; however, the *M. annularis* species complex, *M. cavernosa*, and *S. siderea* also lost a large proportion of colonies in the largest size class. Only branching *Porites* spp. had live length size frequencies that did not significantly change among years.

Comparison of the coral species response

The species to species correlations among the major bleaching response variables showed strong relationships between many variables (Table 10). The among species 2005 bleaching prevalence was highly negatively correlated with the 2005 paling prevalence and the change in abundance (higher bleaching was related to a decrease in abundance), and highly positively correlated with the peak of recent mortality in 2006. Coral cover change and abundance change were highly positively correlated, such that species that lost the most cover also lost the greatest number of colonies. Cover and abundance change were also highly negatively correlated with peak of recent mortality in 2006, indicating high recent mortality was associated with loss of tissue and colonies. The 2010 bleaching prevalence was positively correlated with 2005 bleaching prevalence as well as the

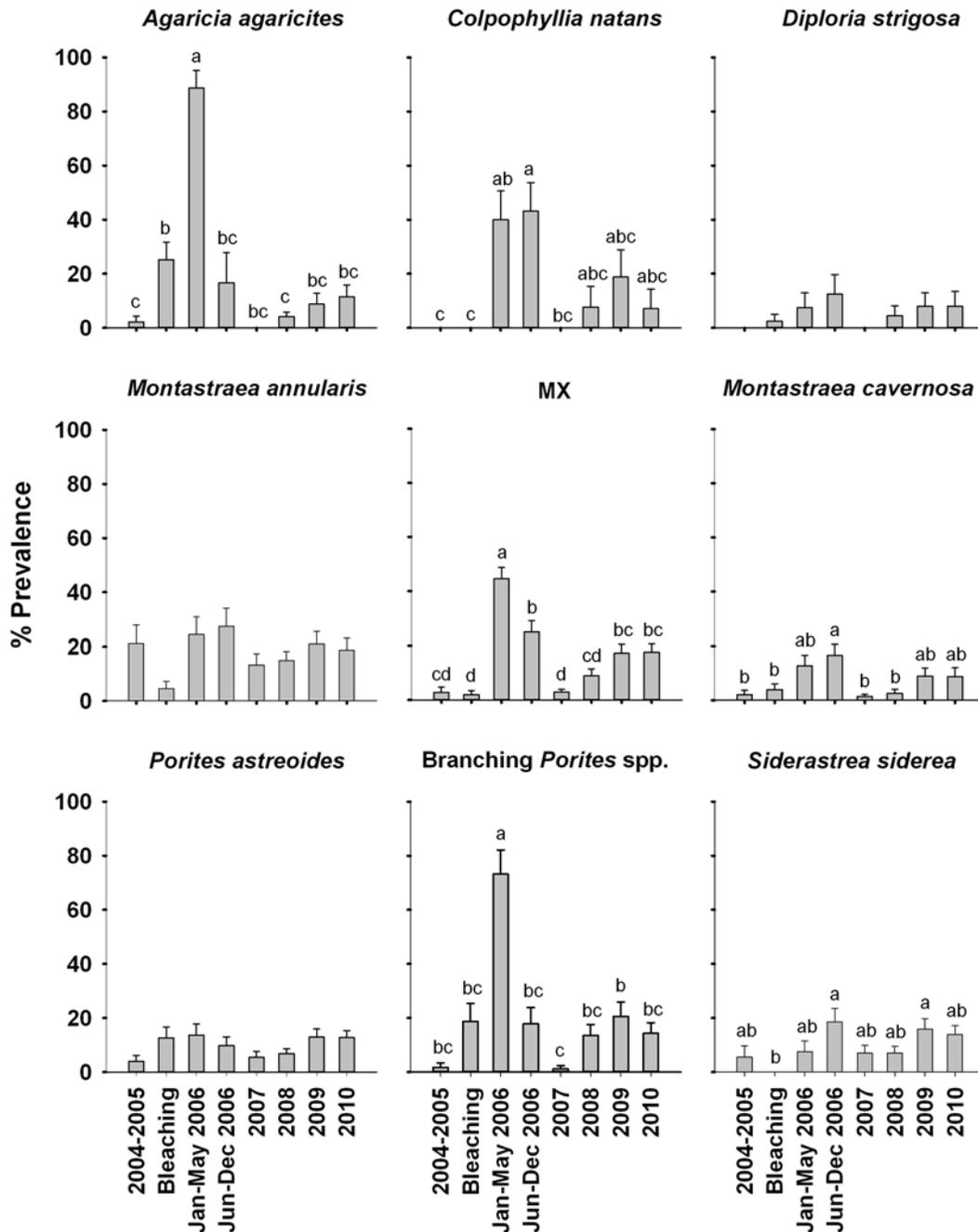


Fig. 6. The prevalence of recent partial mortality (\pm SE) for nine focal coral species across eight periods spanning 2004–2010. Post-hoc comparisons are Tukey's HSD across time periods. MX = *Montastraea annularis* species complex.

peak prevalence of old mortality after 2005. Additionally, 2010 bleaching prevalence was negatively correlated with the abundance change after 2005 bleaching; thus, species that responded

negatively to the 2005 bleaching event tended to be more susceptible to bleaching in 2010. The exception was *S. siderea*, which had relatively high bleaching in 2010 but showed no cover loss

Table 6. Statistical comparison of the prevalence of old partial mortality between the nine focal coral species and eight time periods.

Source	F	df	Prob.	JP/MA	BL/MX	2006a/BP	2006b/MC	2007/CM	2008/SS	2009/AA	2010/DS	PA
Time	20.8	7/45	<0.0001	D	D	C	BC	A	A	B	BC	
Species	5.14	4/51	0.0015	A	AB	ABC	BC	BC	C	D	D	D
Species × Time	1.26	28/164	0.1861									

Notes: Abbreviations are: JP = just prior to bleaching in 2004 and 2005; BL = 2005 bleaching event; 2006a = Jan.–May 2006; 2006b = Jun.–Dec. 2006. Tukey's HSD post hoc comparisons are shown between species (combined periods) and between time periods (combined species). Species codes as in Table 1.

and an increase in colony abundance after 2005.

The first two axes of the PCA were the only axes with eigenvalues greater than 1 and together these axes comprised 81% of the variation in the multivariate dataset, while axes 3, 4 and 5 comprised the remaining variation (Table 11). Therefore, axes 1 and 2 adequately characterized the multivariate space, justifying the presentation of just these two axes (Fig. 11). Along the first axis, the eigenvector values for coral cover change and coral abundance change were of the largest magnitudes and were comparable but opposite to bleaching prevalence and recent mortality (e.g., in those species where coral cover change was negative, indicating a loss of coral cover, bleaching prevalence was higher in 2010; Table 10). When plotted along this first axis, there is a clear separation between those species that experienced high bleaching and high levels of recent mortality along with larger declines in coral cover (*M. annularis*, *M. annularis* species complex, *C. natans*, branching *Porites* spp. and *A. agaricites*) and those species less affected by bleaching and recent mortality which experienced little to no change in densities and cover (*P. astreoides*, *M. cavernosa*, *S. siderea*, and *D. strigosa*) (Fig. 11). In addition, *A. agaricites* stood farther out to the right on axis 1 because this species also had a large decline in abundance.

In axis 2, the eigenvector values were far greater for disease prevalence and paling than for any other factor (Table 11). Along this axis, three distinct groups of species can be discerned: (1) *A. agaricites* and branching *Porites* spp. which experienced no disease and low post-event paling, (2) *P. astreoides*, *M. cavernosa*, *S. siderea*, and *D. strigosa* which experienced some disease and some post-event paling, and (3) *C. natans*, *M. annularis*, and *M. annularis* species complex which experienced high levels of disease and high levels of paling after the bleaching event.

Thus, we can produce roughly three groupings of species corresponding to the response variables: Type I species had large initial response during bleaching that included high bleaching prevalence, high recent mortality, and a large decline in coral cover (*A. agaricites* and branching *Porites* species); Type II species had a high to moderate initial response of bleaching prevalence, followed by delayed recovery of normal coloration, high disease prevalence, high recent mortality, a large decline in coral cover, and stable or increasing colony abundance (*C. natans*, *M. annularis*, and the *M. annularis* species complex); and Type III species had a moderate initial response of bleaching prevalence, low to no disease increase after bleaching, low to no increase in recent mortality, low to no decline in coral cover, and stable or increasing colony abundance (*D. strigosa*, *M. cavernosa*, *P. astreoides*, and *S. siderea*).

Comparison of hypothetical responses based on species traits (Appendix A) showed that many of the focal species had different empirical response (cover change) ranks (Table 12). Over performing species, where coral cover loss rank was less than the trait grouping rank, included the Type III species *P. astreoides* and *S. siderea*. Underperforming species included the Type II species *C. natans*, *M. annularis*, and *M. annularis* spp. complex.

DISCUSSION

Species performance over the 2005 bleaching event

As predicted, the responses of corals to the 2005 high thermal stress and mass coral reef bleaching event were highly species-specific, ranging from high tissue mortality and decreasing adult abundance to undetectable loss of cover and colonies. Bleaching of corals during 2010 was

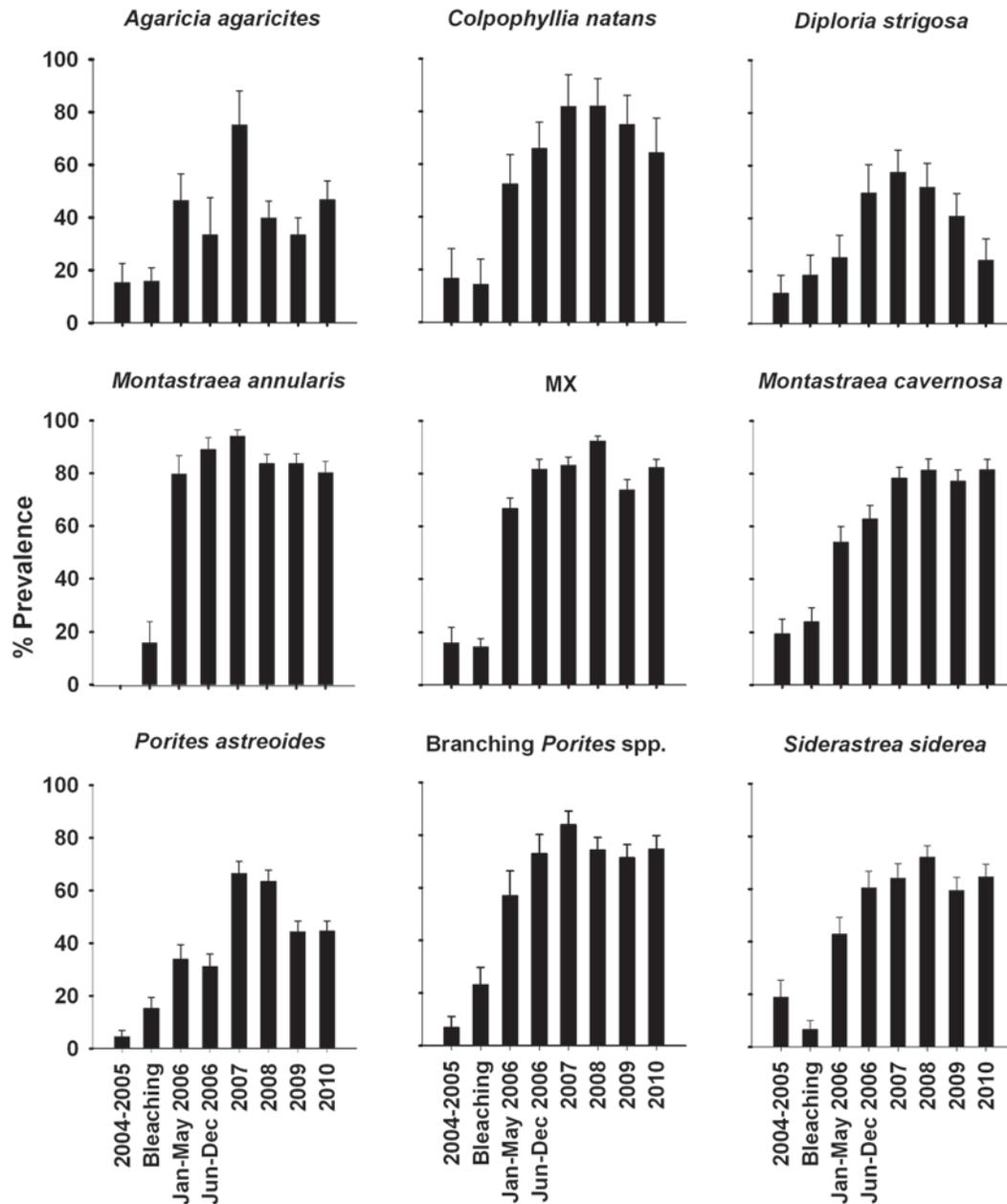


Fig. 7. The prevalence of old partial mortality (\pm SE) for nine focal coral species across eight periods spanning 2004–2010. MX = *Montastraea annularis* species complex.

much less severe than in 2005, but also showed species-specific rankings of susceptibility. These results underscore the species-specific variability seen in the thermal stress and bleaching responses in studies from the Indo-Pacific (Marshall and Baird 2000, Loya et al. 2001, Baird and Marshall 2002, McClanahan 2004, van Woesik et al. 2011),

eastern Pacific (Glynn et al. 2001), and Western Atlantic (Lasker et al. 1984, Gates 1990, Lang et al. 1992, McField 1999, Oxenford et al. 2008, Villamizar et al. 2008, Brandt 2009). However, this study showed that species characteristics favored different outcomes to thermal stress reflected in patterns of bleaching, disease, and

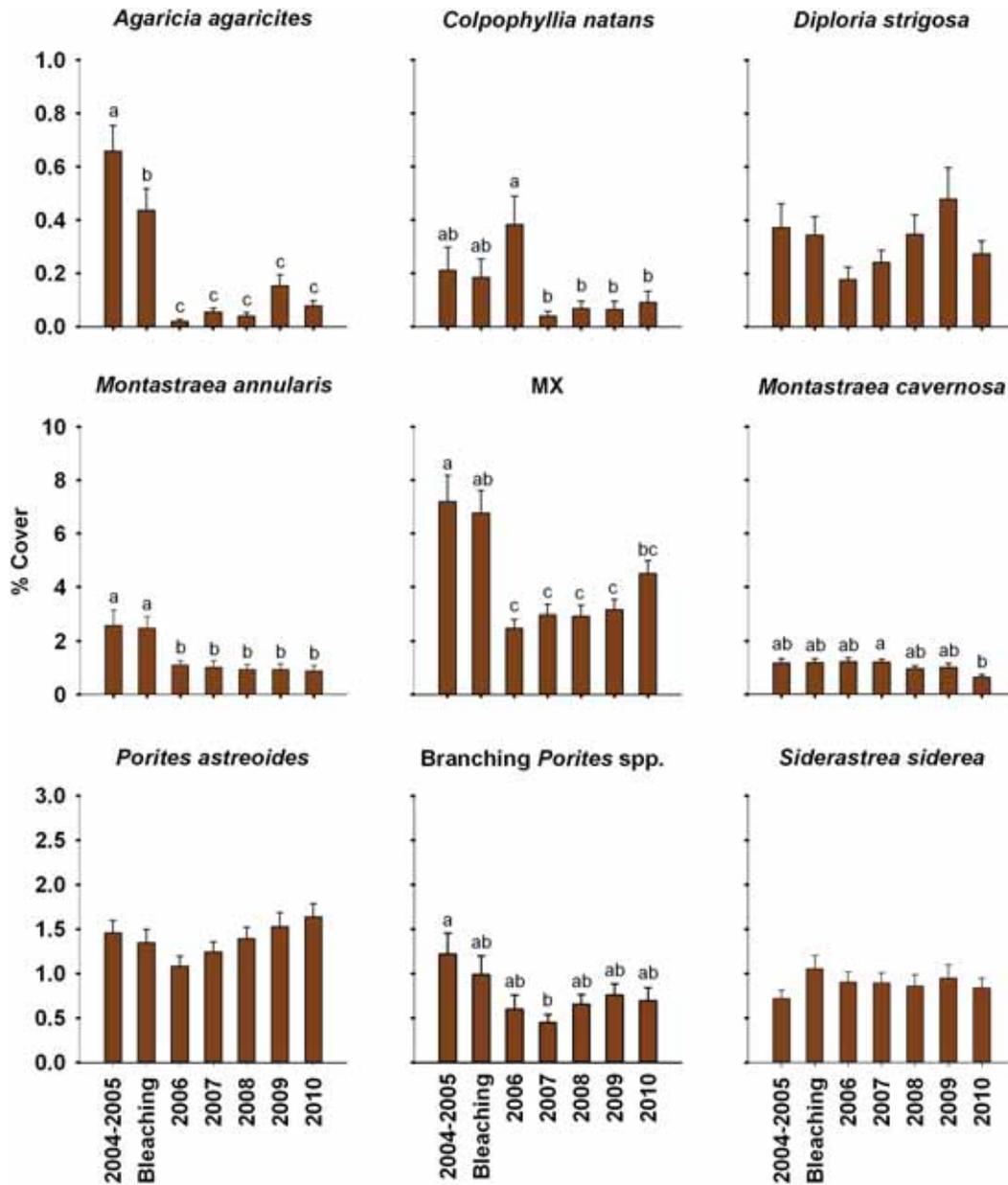


Fig. 8. Coral cover (\pm SE) for nine focal coral species across seven periods spanning 2004–2010. Post-hoc comparisons are Tukey's HSD across time periods. Note the changing y-axis scale among the different rows. MX = *Montastraea annularis* species complex.

partial to total mortality. These patterns converged to the three types of response: Type I species, with high bleaching and initial mortality, no subsequent white disease, and severe losses of cover; Type II species, with moderate bleaching and initial mortality, high subsequent white disease prevalence, and severe losses of cover;

and Type III species, with moderate to low bleaching and paling, low to no subsequent white disease, and low to no loss of cover.

Non-resistant Type I and Type II species whose cover decreased by half or more arrived at the loss of cover by two different routes. Type I species most susceptible to the visual manifesta-

Table 7. Statistical results of a repeated-measures ANOVA of coral cover among the nine focal coral species and seven time periods and the individual tests of coral cover within species over time.

Source	F/ χ^2	df	Prob.
Among species			
Species	65.9	8/963	<0.0001
Time	18.1	6/958	<0.0001
Species \times Time	6.1	48/4718	<0.0001
Within species			
AA	113.1†	6/748	<0.0001
CN	21.3†	6/748	0.0016
DS	1.7	6/748	0.115
MA	36.6†	6/748	<0.0001
MX	22.8†	6/748	0.0009
MC	2.3	6/748	0.035
PA	1.8	6/748	0.104
BP	2.5	6/748	0.017
SS	0.7	6/748	0.664

Note: Species codes as in Table 1.

† Indicates a non-parametric Kruskal-Wallis test.

tion of coral bleaching, *A. agaricites* and branching *Porites* spp., were also the most susceptible to early and high mortality during the peak of bleaching. This pattern has been noted previously for *Agaricia* spp. in the Western Atlantic (Lasker et al. 1984). In contrast to Type II species, this mortality was not associated with white disease. Within the thermal bleaching response model, Type I species have high thermal and bleaching susceptibility that leads directly to

partial or genet mortality (Fig. 1).

As predicted by species traits, Type I *A. agaricites* and branching *Porites* spp. were the least tolerant to thermal stress. These species showed the lowest a priori tolerance scores based on traits and ranked among the species with the greatest cover loss in this study. Type I species were small foliose and branching species, morphological characteristics that are predicted to predispose corals to high mortality under thermal stress (Gates and Edmunds 1999, Baird and Marshall 2002, van Woesik et al. 2012). Branching and foliose morphologies may be a good trait predictor of susceptible Type I species, whilst other traits need further scrutiny. There is little background trait information available for *A. agaricites*; however, this species does seem to be slow growing (linear extension) relative to other Atlantic coral species (Huston 1985), and this may impart tolerance to thermal stress. It is likely that branching *Porites* spp., like *Porites porites* (Edmunds and Davies 1986), shows fast calcification rates relative to other species (Edmunds et al. 2011), potentially making them less tolerant. On the other hand, branching *Porites* spp. have traits associated with tolerance, including a perforate skeleton and deep skeletal tissue reservoirs, high biomass per area (Edmunds and Davies 1986, Edmunds et al. 2011), and the ability to feed heterotrophically to offset loss of

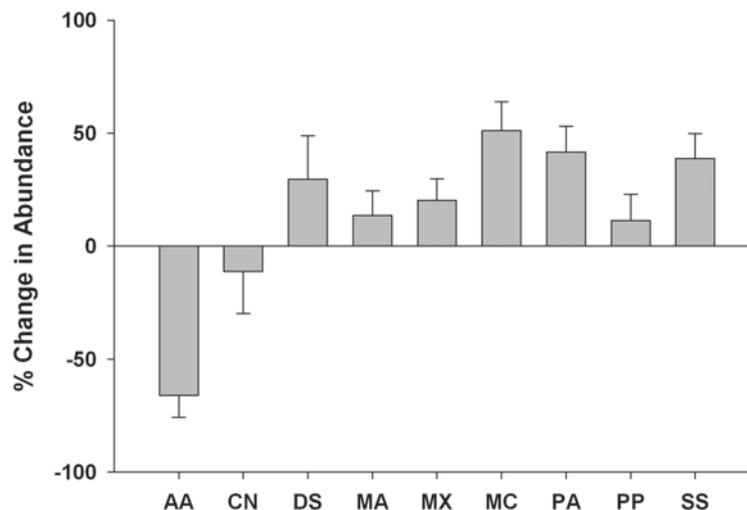


Fig. 9. The change in abundance (\pm SE) of focal species for colonies greater than 10 cm maximum length over the 2005 bleaching event. Periods were prior to bleaching (2004–2005) and after thermal stress mortality in 2007. Species codes in Table 1.

Table 8. Statistical results of a Wilcoxon signed-ranks test for the hypothesis of relative colony abundance change greater than zero for the nine focal coral species between time periods prior to bleaching in 2005 and after the response to bleaching 2007.

Source	Signed-rank value	df	Prob.
AA	-286.5	42	<0.0001
CN	-19.5	26	0.559
DS	96.5	40	0.123
MA	205.0	67	0.152
MX	389.5	89	0.044
MC	539.5	79	<0.0001
PA	786.5	95	<0.0001
BP	115.5	59	0.229
SS	433.0	69	0.0004

Note: Species codes as in Table 1.

energy (Seemann et al. 2012). These traits may have contributed to the low relative levels of total colony mortality and maintenance of colony abundance, even though the species experienced the third highest loss of cover. Thus, there may be different trait combinations in Type I species that lead to different degrees of tolerance to the more immediate effects of thermal stress.

Type II species possess traits that may have made them more resistant to thermally induced pigment loss (van Woesik et al. 2012); however, they lost far more cover than was predicted a priori by species traits. *Colpophyllia natans*, *M. annularis*, and the *M. annularis* spp. complex are all large faviids, possessing the traits of tolerance: massive morphologies, thick tissues, large colony sizes, and low calcification rates. Furthermore, *M. annularis* and *M. annularis* spp. complex host *Symbiodinium* Clade D in higher abundances after thermal disturbance (Thornhill et al. 2006), whereas this has not been demonstrated for *C. natans*. Hosting Clade D may have contributed to greater heterogeneity in bleaching across colony surfaces (Rowan et al. 1997, Baker et al. 2008) (Appendix B), and greater levels of partial versus whole colony mortality. Yet resistance to direct bleaching induced mortality was negated to some degree by susceptibility to disease. During recovery from the 2005 bleaching event white disease was also noted on both *C. natans* and *M. annularis* in shallow marine protected areas of the U.S. Virgin Islands (see Miller et al. 2006, Whelan et al. 2007, Miller et al. 2009), but not in Barbados (Oxenford et al. 2008). In this study, the occurrence of disease led to the relatively high losses of

Table 9. Size frequency analysis of focal coral species, with sample sizes for each period indicated.

Species	N 2005	N 2007	N 2010	χ^2	Prob.
AA	61	14	46	30.9†	<0.0001
CN	14	15	17	15.4†	0.0039
DS	37	43	31	12.8	0.012
MA	124	180	173	42.4	<0.0001
MX	381	339	360	236.8	<0.0001
MC	125	167	129	32.7	<0.0001
PA	145	185	246	18.3†	0.0011
BP	49	69	102	2.9	0.576
SS	70	113	146	55.1	<0.0001

Notes: Contingency table analysis was conducted between years 2005, 2007, 2010 and the colony live tissue size classes 10–15 cm (small), 16–30 (medium), and >30 (large). Species codes as in Table 1.

† Indicates size bins without corals and expected frequencies were <5 in more than 20% of cells, suggesting a cautious interpretation of χ^2 results.

tissue as coral cover did not decrease until after the bleaching event and incidence of disease was not related to bleaching, paling, or normal pigmentation in the recovery period of early 2006. This suggests that disease incidence was not related to delayed recovery from bleaching, but was related to some aspect of the colony or community response during the height of the bleaching.

The bleaching response pattern for Type II species suggested a path in the bleaching response model of progression from bleaching susceptibility to starvation susceptibility directly to susceptibility at the level of secondary agents (disease). We hypothesize that susceptibility to disease was increased due to negative energy states in the colonies as the result of the reduction of photosynthate transfer from *Symbiodinium*, followed by a depletion of colony tissue energy reserves. *Montastraea annularis* can lose half its energy content during bleaching stress (Porter et al. 1989) and, although tissue energy was not measured in this study, we can assume that severely bleached colonies in this study were similarly affected. Energy reserves can take many months to years to recover after bleaching (Rodrigues and Grottoli 2007), thus, even normally pigmented colonies may have been susceptible. The post-bleaching white disease outbreak has been suggested as appearing similar to White Plague Type II (Whelan et al. 2007, Miller et al. 2009); however, it was not clear if white disease signs indicated an infectious disease (Richardson et al. 1998), an environmen-

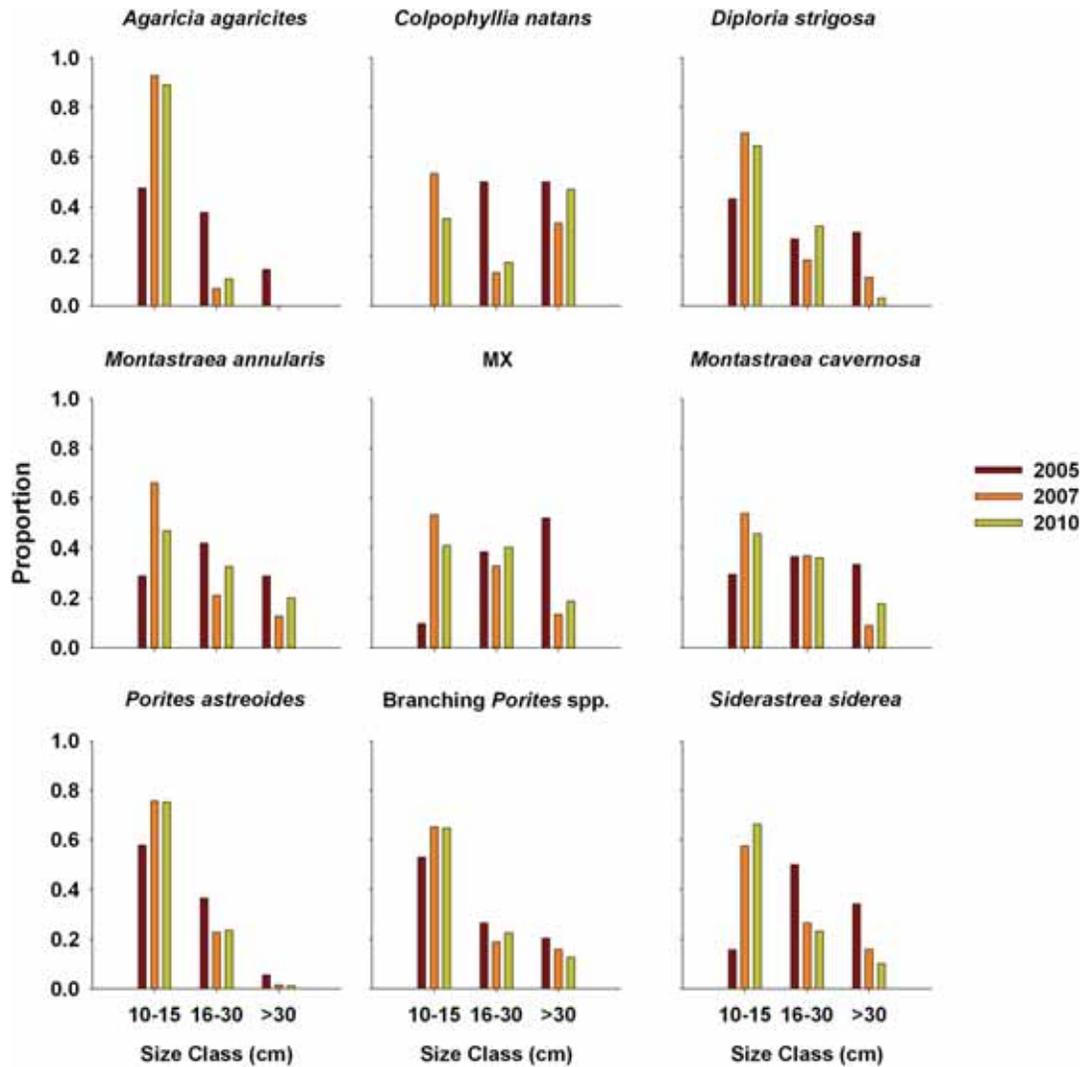


Fig. 10. Size frequencies of live tissue length for small (10-15 cm), medium (16-30 cm) and large (>30 cm) colonies of the focal coral species across years 2005, 2007, 2010. MX = *Montastraea annularis* species complex.

Table 10. Correlations among focal coral species for major bleaching response variables.

Measure	2005 BL	2006 PA	Peak WD	Peak recent	Peak old	Abundance change	Cover change	2010 BL
2005 BL	1.000							
2006 PA	0.212	1.000						
Peak WD	-0.146	0.446	1.000					
Peak recent	0.900	-0.022	-0.044	1.000				
Peak old	0.477	0.589	0.413	0.519	1.000			
Abundance change	-0.813	-0.097	-0.024	-0.841	-0.488	1.000		
Cover change	-0.689	-0.337	-0.268	-0.751	-0.606	0.817	1.000	
2010 BL	0.704	0.418	0.322	0.628	0.758	-0.774	-0.679	1.000

Notes: Bleaching (BL) values represent mean prevalence for each species during the 2005 or the 2010 bleaching event, or paling (PA) prevalence between January and May 2006. Peak white disease (WD), peak recent mortality, peak old mortality represent the maximum average mean prevalence in 2006, after 2005 bleaching event. Abundance change and cover change represent change between prior to the 2005 bleaching event to 2007. Significant correlations are bolded ($\alpha = 0.05$).

Table 11. Eigenvalues and percentage variation explained by the five principal components axes using coral condition and status indices for each of the nine species. Eigenvectors for each of the five measurement indices are also presented.

Measure	Principal component				
	1	2	3	4	5
Eigenvalues	3.91	1.74	0.635	0.339	0.22
Variation explained (%)	55.9	24.9	9.1	4.8	3.1
Cumulative variance explained (%)	55.9	80.8	89.9	94.7	97.9
Eigenvectors					
Cover change (2005–2007)	−0.457	0.044	−0.209	−0.398	−0.515
Abundance	−0.452	−0.201	−0.17	−0.241	−0.215
Peak disease	0.099	−0.61	0.655	0.063	−0.417
Paling 2006 (recovery)	0.189	−0.574	−0.612	0.359	−0.09
Peak old	0.376	−0.35	−0.151	−0.759	0.304
Peak bleaching 2005	0.444	0.238	−0.287	0.084	−0.564
Peak recent	0.449	0.277	0.14	−0.261	−0.309

tal response (Lesser et al. 2007), or an epidemiological response that combined environmentally induced susceptibility and infectious transmission (Bruno et al. 2007, Brandt et al. 2013). The susceptibility to disease increased the empirical response above that predicted by species traits, making Type II species that were apparently somewhat resistant to bleaching less tolerant to thermal stress overall. Models of species traits used to predict response to thermal disturbance should also investigate the possibility of traits that decrease tolerance to thermally linked diseases.

Type III species were moderately resistant to bleaching, but tended to be very tolerant of thermal stress. This tolerance included less partial mortality, smaller reductions in size and cover, and low genet mortality relative to the other focal species. The low loss of cover indicated low susceptibility to thermal stress, bleaching, starvation, or secondary agent components of the thermal bleaching response model. Primary tolerance of thermal stress may also have prevented interactions with bleaching, starvation, and disease that would have led to greater partial or total mortality, as seen in Type II species. Type III species all share some characteristics that fit concepts of thermal tolerance, including a massive to sub-massive morphology and high calcification rates. In addition, all of these species have some capacity for heterotrophy (Mills et al. 2004, Mills and Sebens 2004). However, other traits are not consistent among species. *M. cavernosa* and *D. strigosa* had the most traits associated with tolerance, with the

exception that both possess an imperforate skeleton and *D. strigosa* has not been associated with *Symbiodinium* Clade D at a level perceived to confer tolerance. The empirical response of these two species was very close to that which was predicted by their trait rankings.

On the other hand, *P. astreoides* and *S. siderea* over performed relative to predictions based on

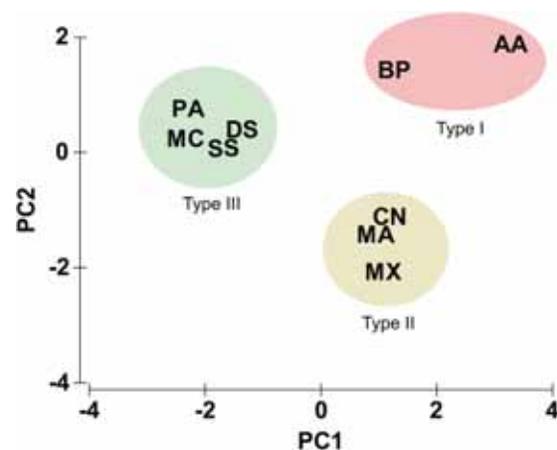


Fig. 11. Multivariate comparison of focal species' response to 2005 bleaching event. Represented are the first two principal components of the nine species using the indices maximum 2005 bleaching prevalence, paling prevalence (PA during the recovery period (Jan.–May 2006), coral cover change (prior to 2005 bleaching to 2007), coral abundance change (prior to 2005 bleaching to 2007), and the peak prevalence of white disease, recent partial mortality and old partial mortality after the 2005 bleaching period. Species codes as in Table 1.

Table 12. Comparison on species performance rank predicted based on species traits (van Woesik et al. 2012) and empirical performance from this study based on cover loss.

Species	Trait score	Trait rank	Cover loss	Cover loss rank	Trait-cover rank difference
<i>Agaricia agaricites</i>	-4	8.5	92	9	-0.5
<i>Colpophyllia natans</i>	2	5.5	81	8	-2.5
<i>Diploria strigosa</i>	4	3	35	4	-1
<i>Montastraea annularis</i>	4	3	60	5.5	-2.5
<i>Montastraea annularis</i> spp. complex	4	3	60	5.5	-2.5
<i>Montastraea cavernosa</i>	5	1	-3	1	0
<i>Porites astreoides</i>	0	7	15	2	5
Branching <i>Porites</i> spp.	-4	8.5	63	7	1.5
<i>Siderastrea siderea</i>	2	5.5	25	3	2.5

Note: Ties in rank were assigned the mean value of the rank slots that would have been taken by the tied ranks if arbitrarily assigned higher or lower.

species traits, as they each possessed only half the traits considered to confer tolerance, but were still very tolerant of thermal stress. This was particularly true for *P. astreoides*, which had many traits that may make them more susceptible to thermal stress (e.g., small distance between corallites, small colonies, and a lack of *Symbiodinium* Clade D; van Woesik et al. 2012). Large distance between corallites, large colonies, and possession of Clade D are perceived to allow partial, versus total, mortality and increased energy storage. However, the perforate skeleton of *P. astreoides* and *S. siderea* may outweigh the lack of other traits that provide these mechanisms of tolerance by facilitating partial mortality and energy storage in deep skeletal tissue reservoirs. The influence of traits such as a perforate skeleton that cover a range of possible mechanisms for thermal tolerance may need additional weighting in trait based coral susceptibility models.

Impacts of partial mortality

Although the 2005 coral bleaching event was severe by multiple measures and unprecedented for the Caribbean (Eakin et al. 2010), the majority of cover loss among even the most severely affected coral species was the result of partial mortality rather than genet mortality. With the exception of *A. agaricites* and *C. natans*, seven of the nine focal species showed little change in abundance of colonies greater than 10 cm length and had few cases of complete colony mortality. Also, with the exception of branching *Porites* spp., all species after 2005 exhibited significant transitions of live length size frequencies away from large colonies to small colonies, suggesting

a high-degree of partial mortality rather than total colony mortality (for examples see Appendix B). It also seems unlikely that in the five-year time frame of recovery in this study that there would have been any substantial sexual recruitment and growth of colonies into the >10cm size classes that would have been detectable in our study design. Increases in colony abundance in this study were therefore the result of fission, not sexual recruitment (Hughes and Jackson 1980, Loya et al. 2001).

The impact of partial mortality on the resilience of Western Atlantic corals depends on how size class transitions affect overall demographic rates. Demographic feedbacks within adult mortality, fission, and downward size transitions that are not well represented in abundance changes can trump recruitment and lead to losses of colonies and cover (Hughes and Tanner 2000, Edmunds and Elahi 2007). For populations of *M. annularis* where demographic models have been applied, no reasonable amount of recruitment restored the largest size classes of corals and prevented ultimate population extinction when positive size transition probabilities were low, including a model parameterized with data from a study site within the US Virgin Islands (Edmunds and Elahi 2007). In addition, a demographic model parameterized with *M. annularis* population data from eastern Puerto Rico over the 2005 thermal stress event showed very low cover or extirpation with thermal stress events of 2005 level severity recurring at a frequency of less than every 17 years (Hernández-Pacheco et al. 2011). Consequently, partial mortality in large framework building corals may be a short-term step on a downward trend

ending in low abundance or extirpation. This susceptibility may be increased if low cover inhibits positive feedbacks that facilitate coral recruitment and growth (Bozec et al. 2013). However, none of these models parameterized with empirical data included the ability for *M. annularis* populations to adapt to recurring stresses, which might occur with selection for resistant coral genotypes or adaptive bleaching (Buddemeier and Fautin 1993, Baker 2001). The latter involves the ability of corals to associate with different clades of algal endosymbionts (e.g., Clade D) with increased tolerance of thermal stress and resistance to bleaching. These considerations may be important in assessing the long-term potential for large faviids to endure repeated thermal stress.

Regrowth of extant genotypes may speed the pace and scale of recovery (van Woesik et al. 2011). There has been only slight restoration of total coral cover in the five years after the thermal stress in 2005; however, by 2010 the *M. annularis* species complex, *P. astreoides*, and branching *Porites* spp. have shown evidence of increasing cover. Genotypes that survived the disturbance should buffer the genetic diversity within species, including the genotypes of corals that are centuries old. In addition, an increase in the relative abundance of resistant algal endosymbiont genotypes that may occur with adaptive bleaching might be preserved within the system for a window of time (Thornhill et al. 2006). In this case, surviving tissues possess a “memory” of high thermal disturbance that could lead to greater tolerance over future events, although the long-term costs of reversion to previous host-symbiont combinations or maladaptive combinations need to be considered (Jones 2008). Some of the species-specific differences in response to the 2005 and 2010 thermal stress events could be consistent with a shift to greater thermal tolerance through selection of resistant coral genotypes and adaptive bleaching. For example, relative to other species and their response in 2005, the *M. annularis* species complex and branching *Porites* spp. had a lower bleaching response in 2010, and this could be taken as evidence of adaptation to thermal stress after 2005. However, colony-specific monitoring is necessary to determine the potential for adaptation when comparing two very different stress

events, particularly without consideration of spatial variation in the stress (e.g., environmental variation around *M. annularis* versus *M. annularis* species complex dominated reefs).

The susceptible Type I species *A. agaricites* provides a good example of the potential for partial mortality to influence long-term recovery. As the most thermally sensitive species, *A. agaricites*, had a 66% decrease of colonies greater than 10 cm length and the greatest prevalence of complete colony mortality (15.9%). Thus, 50% of colonies either transitioned to size classes smaller than 10 cm or suffered complete mortality. While some whole colony mortality was likely to have been missed in the sampling that occurred within the time frame that recent mortality transitioned to old mortality, approximately three months (Smith et al. 2008), much of the abundance decrease may have represented partial mortality and a transition to size classes less than 10 cm. Between 2008 and 2010, when all sizes of colonies were assessed, 80% of *A. agaricites* colonies were less than 10 cm in maximum diameter (N = 499), indicating there was no shortage of small colonies that could represent colonies that survived through 2005 and regressed in size. Despite the susceptibility of *A. agaricites* to the direct effects of thermal and bleaching stress, surviving colonies often had intra-colony refuges of tissue within the cryptic and shaded environments where small tissue patches (<10 cm) often survived (Appendix B). The sheeting to foliose morphology of *A. agaricites* may create heterogeneous light environments across the colony surface that act as intra-colony refuges from thermal-light induced bleaching. Observations suggest that these tissue patches are beginning to regrow out of these intra-colony refuges (Appendix B). A similar pattern of susceptibility and recovery can be seen in branching *Porites* spp. Within the expert ranking of physical and biological traits that favor tolerance and recovery conducted by van Woesik et al. (2012), *A. agaricites* and branching *Porites* spp. may be extremely intolerant of thermal stress (i.e., foliose morphology, high calcification rate, small size, low symbiont diversity, or non-porous skeleton), but resilient in the long-term because of high recovery potential (i.e., high recruit density, colony regrowth from surviving tissue, and high colony growth rates). Thus, these taxa may not

be stress-resistant but could be classified as weedy due to a high capacity for recovery favored by brooding reproduction and high growth rates (Darling et al. 2012).

Conclusions

The results of this study support the concept that there will be winners and losers among coral species in response to a future of increasing frequency and intensity of thermal stress events. Many species traits predicted to influence increased tolerance to thermal stress performed well for Caribbean coral species over the 2005 stress event, with perforate skeleton seeming to have a relatively large positive influence on some Type III species. On the other hand, in Type II species some combinations of traits predicted for tolerance (massive morphology, thick tissues, large distance between corallites, large colony size, and the ability to host populations of *Symbiodinium* Clade D) were superseded by the susceptibility to disease. Large faviids seem very susceptible to long-term population declines because they fare poorly over the whole stress response, when bleaching, disease, and mortality are considered. In addition, *M. annularis* and the *M. annularis* spp. complex are likely less equipped for the recovery phase because they tend to grow slowly and have lower fecundity and greater susceptibility to mortality when small (Edmunds and Elahi 2007). While faviids may be considered “losers”, Type III species are likely the clear “winners” because they are resistant to thermal stress and may be capable of recovery on short time scales when disturbed. Type I species are losers in the short-term, but may show long-term persistence due to their high potential for recovery. A key component of persistence, versus continued decline, for Type I species may be the return frequency of thermal disturbance. Continued monitoring of these communities will determine if initial recovery trajectories result in a restoration of community components prior to the next disturbance. We predict that future thermal stress events are likely to generate a community of diminutive, fast-growing colonies with higher proportions of Type III species.

In summary, we found that there were species-specific differences in the bleaching response that corresponded to different traits among species

and, as predicted, the most highly affected species possess branching and foliose colony morphologies. There was also a significant correlation between species-specific bleaching prevalence during the 2005 thermal stress event and subsequent recent partial mortality and cover change, indicating that bleaching responses and mortality were linked within species. Those species that had a higher prevalence of bleaching in 2005 also tended to have a higher prevalence of bleaching in 2010, with the exception of the *M. annularis* species complex and branching *Porites* spp., suggesting that for most species tolerance is similar over catastrophic and mild bleaching events, but that for some species there may have been limited adaption to thermal stress, warranting further investigation. Finally, because of the preponderance of partial mortality among coral species, the ultimate resilience and future trajectory of reefs in the Caribbean will be intimately tied to the demographics of surviving, smaller colonies and the recurrence of future disturbance.

ACKNOWLEDGMENTS

We thank G. Bosire, L. Carr, G. Gentius, S. Herzleib, C. Loeffler, A. Paul, L. Allen-Requa for field assistance, S. Prosterman for diving support, and M. Henderson and C. Joseph for administrative support. We thank K. Baltzer, P. Edmunds, P. Glynn, L. Henderson, and J. Lang for helpful comments on the manuscript. This manuscript benefitted through interactions among the Future Reefs workgroup of the NSF National Center for Ecological Analysis and Synthesis, grant #EF-0553768 to P. Edmunds and R. Gates. The Virgin Islands Department of Planning and Natural Resources, Division of Coastal Zone Management and the NOAA Coral Reef Conservation Program funded this work. The Virgin Islands Experimental Program to Stimulate Competitive Research (NSF award # 346483 & 0814417) and the Lana Vento Charitable Trust provided equipment support. Views and opinions expressed in this manuscript do not reflect those of the funding agencies. This is contribution #89 from the Center for Marine and Environmental Studies, University of the Virgin Islands.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Traits of thermal tolerance for the nine focal species taken from van Woesik et al. (2012). To corroborate expert consensus, quantitative assessments of species traits from data published in Edmunds et al. (2011) were used to generate a median value among species and compared against the value for the species, when available. Values for *A. agaricites* were taken from the congener *A. tenuifolia*, as this was the closest available species with quantitative trait information. Quantitative trait information from Edmunds et al. (2011) was available for tissue thickness, distance between corallites, and calcification rate. Other traits were evaluated from the literature as referenced in the article text, or taken as given from expert consensus. Cover loss taken from this study (Table 3). Ties in rank were assigned the mean value of the rank slots that would have been taken by the tied ranks if arbitrarily assigned higher or lower. Morphology abbreviations as in Table 3.

Trait	Morph.	Tissue thick./ mass	Distance between corallites	Calcification rate	Colony size	Corallite size	Clade D	Skeletal structure	Trait score
<i>Agaricia agaricites</i>									
Description	F	thin (4.8†)	small (11.5†)	fast	medium	small	yes	non-porous	
Score	0	-1	-1	-1	0	-1	1	-1	-4
<i>Colpophyllia natans</i>									
Description	M	thick (4.8)	large	Slow	large	large	no	non-porous	
Score	1	1	-1	1	1	1	-1	-1	2
<i>Diploria strigosa</i>									
Description	M	thick	large (2)	Slow	large	large	no	non-porous	
Score	1	1	1	1	1	1	-1	-1	4
<i>Montastraea annularis</i>									
Description	M	thick (8.5)	large (6.4)	low (0.48)	large	small	yes	non-porous	
Score	1	1	1	1	1	-1	1	-1	4
<i>Montastraea annularis</i> spp. complex									
Description	M	thin (6.5)	large	low	large	small	yes	non-porous	
Score	1	1	1	1	1	-1	1	-1	4
<i>Montastraea cavernosa</i>									
Description	M	thick	large (1.25)	low	medium	large	yes	non-porous	
Score	1	1	1	1	0	1	1	-1	5
<i>Porites astreoides</i>									
Description	M, E	thick	small (18)	low	small	small	no	porous	
Score	1	1	-1	1	-1	-1	-1	1	0
Branching <i>Porites</i> spp.									
Description	B	thick (17.1)	small (23.8)	low (0.46)	small	small	no	porous	
Score	-1	1	-1	-1	-1	-1	-1	1	-4
<i>Siderastrea siderea</i>									
Description	M	thin	small (9)	low	medium	medium	yes	porous	
Score	1	-1	-1	1	0	0	1	1	2

Note: Tissue thick./mass refers to tissue thickness and biomass.

†Values from *Agaricia tenuifolia*.

APPENDIX B

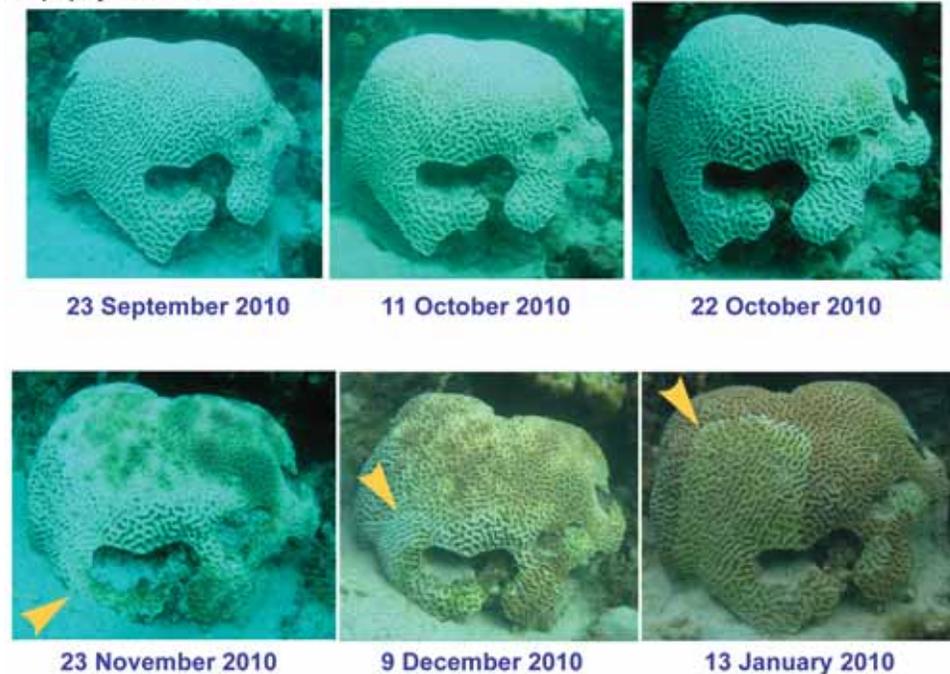
Agaricia agaricites*Colpophyllia natans*

Fig. B1. Photographic time course of two of the nine focal species, with examples of different phases of the response to the 2005 or 2010 high thermal stress events affecting the U.S. Virgin Islands. *Agaricia agaricites*: These corals showed severe bleaching and mortality early in the 2005 bleaching event. Surviving tissue remnants had begun to grow out of refuges and recolonize skeletons by 2009, with more robust recovery by 2012. Note that these are not the same colony. *Colpophyllia natans*: The response of bleached *C. natans* to the 2005 and 2010 event was typified by this marked colony followed over 2010 and 2011. Severe bleaching persisted during the height of the thermal disturbance. During restoration of colony pigmentation, white disease lesions (orange arrows) started from colony bases or margins and caused a high degree of partial mortality.

Diploria strigosa

12 November 2005



17 December 2005



17 December 2005



15 April 2006



26 November 2006 (a & b)



Fig. B2. Photographic time course of *Diploria strigosa*, with examples of different phases of the response to the 2005 high thermal stress event affecting the U.S. Virgin Islands. Colonies marked with an asterisk represent the same marked colony that was followed over time. Unmarked colonies are ad hoc examples of thermal stress response. The majority of *D. strigosa* bleached in 2005 recovered with relatively little loss of tissue. However, a subset of colonies marked and followed between 2005 and 2006 showed the development of white disease during recovery and high loss of tissue. Mortality was partial, with sparse patches of living tissue remaining (orange arrows).

Montastraea annularis

27 September 2005



13 November 2005



11 November 2005



30 April 2006



25 July 2006



26 August 2006

Fig. B3. Photographic time course of *Montastraea annularis* with examples of different phases of the response to the 2005 high thermal stress event affecting the U.S. Virgin Islands. Colonies are ad hoc examples of thermal stress response. Colonies of *M. annularis* bleached at moderate levels in 2005, with high intra-colony heterogeneity that ranged from unbleached to severely bleached tissue. Many colonies developed white disease in the recovery period, with high prevalence of partial mortality. Evidence of paling on surviving tissues often lasted for a year or more.

Montastraea annularis species complex

05 October 2005



13 November 2006



25 July 2006



28 April 2006



17 August 2008

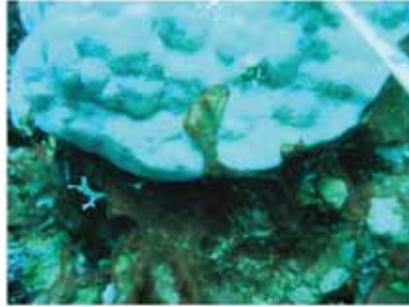


10 October 2011

Fig. B4. Photographic time course of *Montastraea annularis* species complex with examples of different phases of the response to the 2005 high thermal stress event affecting the U.S. Virgin Islands. Colonies marked with an asterisk represent the same marked colony that was followed over time. Unmarked colonies are ad hoc examples of thermal stress response. The response of the *Montastraea annularis* species complex was similar to *M. annularis*, except that white diseases tended to be more severe on *M. annularis* species complex. Active or recently active lesions are denoted in middle photos with orange arrows. A marked colony of *M. faveolata* that was impacted by severe bleaching (top left) had partial mortality that covered approximately 90% of the colony surface by 2006. This colony had shown relatively little recovery by 2011 (pink areas denote living tissue in bottom right image).



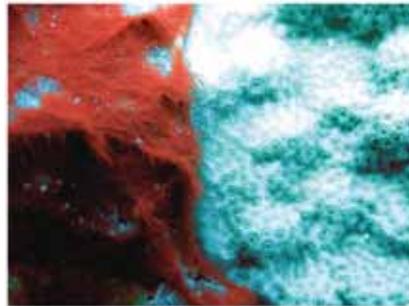
Fig. B5. Photographic time course of *Montastraea cavernosa* with examples of different phases of the response to the 2005 high thermal stress event affecting the U.S. Virgin Islands. Colonies are ad hoc examples of thermal stress response. Colonies of *M. cavernosa* showed a very weak bleaching response during thermal stress in 2005, with mostly colonies presenting no bleaching or partial paling. Nonetheless, some colonies lost tissue in patches that rarely led to whole colony mortality.

Porites astreoides

27 September 2005



06 December 2005



28 June 2006



07 December 2005



27 April 2006

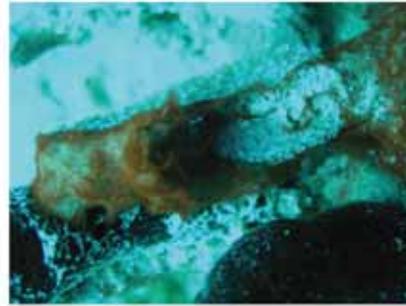


25 October 2006

Fig. B6. Photographic time course of *Porites astreoides* with examples of different phases of the response to the 2005 high thermal stress event affecting the U.S. Virgin Islands. Colonies marked with an asterisk represent the same marked colony that was followed over time. Unmarked colonies are ad hoc examples of thermal stress response. Some colonies of *P. astreoides* showed severe bleaching in 2005. Many colonies that were bleached became susceptible to algal overgrowth, although that was not directly measured in this study. One marked colony recovered pigment by 2006, but showed small losses of tissue (<25% of colony surface).

Branching *Porites* species

05 October 2005



27 September 2005



22 November 2005



30 January 2006



13 April 2006



30 April 2006

Fig. B7. Photographic time course of branching *Porites* spp. with examples of different phases of the response to the 2005 high thermal stress event affecting the U.S. Virgin Islands. Colonies of branching *Porites* spp. were severely bleached in 2005, with the majority of partial mortality occurring by January 2006. Algal overgrowth was common on bleached and recovering colonies.

Siderastrea siderea

06 October 2005



12 November 2005



09 December 2005



31 January 2006



16 September 2006



14 April 2007

Fig. B8. Photographic time course of *Siderastrea siderea* with examples of different phases of the response to the 2005 high thermal stress event affecting the U.S. Virgin Islands. Colonies marked with an asterisk represent the same marked colony that was followed over time. Unmarked colonies are ad hoc examples of thermal stress response. Colonies of *S. siderea* were moderately bleached in the 2005 bleaching event. A marked colony showed a typical pattern of pigment recovery with little loss of living tissue.