

# Disease incidence is related to bleaching extent in reef-building corals

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**Abstract.** Recent outbreaks of coral bleaching and disease have contributed to substantial declines in the abundance of reef-building coral. Significant attention has been paid to both phenomena in order to determine their effect on reef trajectories. Although each is positively correlated with high temperatures, few studies have explored the potential links between bleaching and disease. A longitudinal study of corals in the Florida Keys was therefore conducted during the 2005 Caribbean bleaching event to quantify bleaching extent and disease incidence in corals, and to determine whether they were related or if they acted as discrete phenomena. These data indicated that overall, a positive correlation exists between bleaching extent and disease incidence. However, the specific interactions between these two phenomena varied among disease bleaching combinations. *Montastraea faveolata* colonies with greater bleaching intensities later developed white plague (WP) infections. Meanwhile, *Siderastrea siderea* colonies with dark spot disease (DS) bleached more extensively than apparently healthy colonies. Finally, bleaching and black band disease (BB) co-occurred on *Colpophyllia natans* throughout the bleaching event. WP, BB, and bleaching are each independently capable of changing the structure of coral populations through loss of living tissue, and DS is an important indicator of reef health. Understanding the dynamics of how these mortality sources interact is critical to understanding mortality patterns and predicting how reef communities will respond to future events.

**Key words:** black band disease; coral bleaching; coral disease epizootiology; coral white plague disease; dark spot syndrome; 2005 mass bleaching event.

## INTRODUCTION

Large-scale “mass” bleaching events (the loss of symbiotic algae from coral colonies over large reef tracts) have been associated most commonly with abnormally elevated water temperatures (Jokiel 2004). Higher prevalences of coral-mortality-causing diseases have also been correlated with warmer temperatures (e.g., Gil-Agudelo and Garzon-Ferreira 2001, Kuta and Richardson 2002, Boyett et al. 2007, Bruno et al. 2007), which may increase pathogen virulence or decrease host disease resistance (Harvell et al. 2002). It is not surprising therefore that mass bleaching events and disease outbreaks have been linked temporally during thermal anomalies (Jones et al. 2004, Miller et al. 2006). The drivers behind these events have received significant research attention (Voss and Richardson 2006, Sampayo et al. 2008), but little is known about whether (and if so, how) these mortality sources interact (Muller et al. 2008). Recent evidence suggests, however, that bleaching and some diseases may act synergistically when they co-occur (Muller et al. 2008). The dynamics of these

synergisms are poorly understood, yet critical to our understanding of how coral communities will respond as the extent and frequency of mass bleaching events and disease outbreaks increase with warming temperatures (Hayes and Goreau 1998, Hoegh-Guldberg 1999, Ward and Lafferty 2004, Donner et al. 2007).

Mass bleaching events and coral disease outbreaks have each destroyed extensive amounts of live coral cover throughout the world (Hoegh-Guldberg 1999, Harvell et al. 2004), driving shifts from coral-dominated to macroalgae dominated reefs (Lesser 2007). The potential synergisms between them are therefore cause for great concern (Jones et al. 2004, Miller et al. 2006, Muller et al. 2008). However, investigating relationships between bleaching and disease has been difficult due to the challenges of monitoring for the incidence of disease in individual colonies. Coral disease occurrence is typically low and can be patchy. Coral reef monitoring usually occurs on an annual basis, due to the logistical difficulties and costs inherent to frequent resurveying of reef sites (Jones 2008). This makes understanding disease or bleaching incidence in relationship to the specific health histories of colonies difficult (Green and Bruckner 2000). It also reduces the probability of detecting short-duration epizootics (Harvell et al. 2001), and may mean that observed events are assessed

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after their peak, at which time distinguishing the relative impacts of disease vs. bleaching is difficult or impossible (Harvell et al. 2004, Jones 2008).

In summer and fall of 2005, a thermally induced mass bleaching event affected coral populations of the north and northeastern Caribbean region (Donner et al. 2007). This event was followed by outbreaks of coral disease that had devastating impacts in many parts of this region (Miller et al. 2006; see other examples in Wilkinson and Souter 2008). Frequent monitoring of coral colonies in the Florida Keys, USA before, during, and after this event afforded the opportunity to document dynamic interactions between bleaching extent and coral disease within individual colonies. More extensive bleaching on colonies of *Montastraea faveolata* was associated with the incidence of white plague, and dark spot infection on colonies of *Siderastrea siderea* was correlated with more extensive bleaching. The specifics of these interactions and their potential implications are reported here.

#### MATERIALS AND METHODS

In order to quantify the incidence and impact of coral disease on inshore patch reefs of the Florida Keys, USA, intensive monitoring was undertaken at two sites, Cheeca Rocks (24°53'50" N, 80°36'57" W) and Coral Gardens (24°50'9" N, 80°43'39" W), between the fall of 2004 and the spring of 2006. At each site, all colonies >10 cm in maximum diameter within five randomly located and permanently installed 16-m<sup>2</sup> quadrats (numbers and size distributions of colonies are described in Appendix A) were monitored for bleaching and disease. The sampling was designed in particular to investigate differences in coral status when water temperatures were high vs. low (e.g., summer to fall and winter to spring, respectively). Sites were surveyed approximately every other week in time periods between October and November 2004 and February and April 2005. When bleaching alerts were issued for the Florida Keys in July of 2005, surveying was instituted in August and continued until November 2005. Gaps in surveying during this period represent times when weather prevented access to the sites. Final surveys were executed twice more in April and May 2006.

For each colony on each site visit, the extent of bleaching exhibited by a colony was recorded based on visual inspection as the observed percentage (to the nearest 5%) of the colony's total living tissue area experiencing complete loss of pigment. Black band disease (BB) was identified as a black mat that delineated live tissue from recently denuded skeleton (Fig. 1), dark spot disease (DS) was identified as discolored dark areas of tissue, and white plague disease (WP) signs were identified as a sharp line separating live tissue from recently denuded skeleton where the tissue loss originated from the base or margin of the colony. Water temperature was recorded at the tops of reef structures at each site on each visit using a YSI 30M

salinity, conductivity, and temperature meter (YSI, Yellow Springs, Ohio, USA) with an accuracy of  $\pm 0.1^\circ\text{C}$ .

Prevalence of bleaching was calculated as a population-level index, as the total proportion of corals of each species that exhibited bleaching on  $\geq 10\%$  of their living tissue area. Similarly, prevalence of disease for each species was calculated as the proportion of all colonies of that species showing signs of disease on a survey date. Mean bleaching extent was calculated as a colony-level index, as the mean percentage of bleached tissue area across all coral colonies of each species. Disease incidence ("no. new" in Fig. 2) was the number of colonies which showed disease signs on a survey date that had not shown disease signs on any previous survey date. Recovery ("no. recovered" in Fig. 2) was the number of colonies which showed disease signs on the previous survey date, but no longer showed signs on that date. Our use of the word "recovery" does not indicate that tissue healed or grew back, as no re-growth of tissue lost due to disease or bleaching was noted during this study. Reinfection ("no. re-infected") was the number of colonies that showed disease signs on a survey date that had previously shown disease signs and recovery.

Bleaching extent data were arc-sine-transformed to achieve approximate normality and were examined independently for each primary host species: *Montastraea faveolata*, *Siderastrea siderea*, and *Colpophyllia natans*. Site and quadrat within a site had no effect on bleaching extent in initial analyses (Appendix B), and therefore all monitored colonies were pooled for the analysis of each species. Bleaching extent data for each species were then examined for temporal differences using a repeated-measures analysis of covariance (RM-ANCOVA), with survey date as the within-subjects factor and "disease outcome" as a between-subjects factor (Sokal and Rohlf 2001). For each colony, "disease outcome" was either positive (the colony was diseased at the start of the bleaching event or became diseased at some point during the event) or negative (it remained apparently disease free throughout the bleaching event). The effect of colony size was tested and included in the model as a covariate, because colony size may play a role in the extent of bleaching experienced by a colony or the occurrence of disease on it.

#### RESULTS

Beginning in August 2005, abnormally high temperatures ( $>30^\circ\text{C}$ ) were recorded for the Florida Keys, USA reef tract (Manzello et al. 2007) and at monitoring sites (Fig. 2a). Bleaching was noted on colonies of each of the three primary host species, *Montastraea faveolata*, *Siderastrea siderea*, and *Colpophyllia natans* (Fig. 2b–d), although colony bleaching extent was low (Fig. 3a–c). By September, bleaching affected  $>75\%$  of each species (Fig. 2b–d), and significant increases in colony bleaching extent were recorded between August and 1 September (Fig. 3a–c, Table 1). Bleaching prevalence and extent

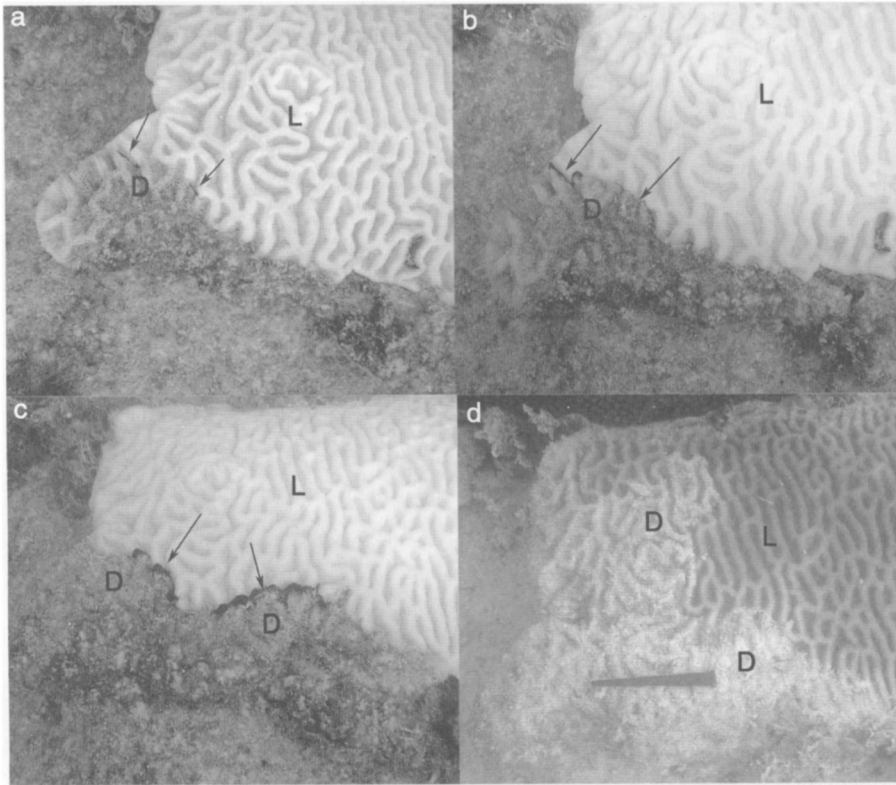


FIG. 1. Bleaching *Colpophyllia natans* colony affected by black band disease. (a) Two small areas of black band (indicated by arrows) are visible separating (L) living, bleaching tissue from (D) dead, recently denuded skeleton (photo taken 1 September 2005). (b) The areas of black band have progressed slightly and the band on the left has thickened (photo taken 6 September 2005). (c) The black band areas have thickened and progressed further, and (D) the region of dead coral has expanded and started to erode (photo taken 12 October 2005). (d) No black band is visible, and some pigment had returned to (L) the living tissue, although (D) significant mortality and some erosion had occurred (photo taken 9 November 2005). The nail was 8.3 cm long.

remained high through September. Significant decreases in bleaching extent were finally recorded between September and October in *M. faveolata* and *S. siderea* (Fig. 3a, b, Table 1) and between October and November in *C. natans* (Fig. 3c, Table 1), corresponding with a decline in temperature (Fig. 2a). Bleaching continued to affect colonies of *C. natans* into the spring of 2006 (Fig. 2d), although bleaching extent was low (Fig. 3c).

Disease prevalence increased during the bleaching event, but differed temporally by disease (Fig. 2b–d). White plague (WP) that was previously active on colonies was not present when sites were first surveyed in August (Fig. 2b, “no. recovered WP”), and only one newly affected colony and two reinfected colonies were noted in August and September (Fig. 2b). Instead, WP disease prevalence increased in October and November, corresponding with a significant decrease in bleaching extent (Fig. 3a, Table 1). This increase in disease prevalence was due to the appearance of WP signs on many previously unaffected colonies (Fig. 2b, “no. new WP”) as well as the reappearance of WP signs on previously affected colonies (Fig. 2b, “no. re-infected WP”). Colony size did not significantly affect bleaching extent in *Montastraea faveolata*, nor was there a

significant interaction effect between disease outcome and colony size (Table 2). However, bleaching extent on colonies of *M. faveolata* was significantly affected by disease outcome (Table 2). Colonies that became diseased experienced greater bleaching extent through the bleaching event than colonies that did not become diseased (Fig. 3a).

New dark spot (DS)-affected colonies were observed at the start of monitoring in August 2005 (Fig. 2c) and before bleaching extent on *Siderastrea siderea* significantly increased in September (Fig. 3b, Table 1: “16 Aug vs. 1 Sep”). On 1 September, new DS-affected colonies were noted (Fig. 2c, “no. new DS”) but some colonies previously affected no longer showed DS signs (Fig. 2c, “no. recovered DS”). After 1 September, no new cases of DS were observed, and by the end of the monitoring period DS was no longer prevalent (Fig. 2c). Colony size had a significant effect on bleaching extent in *S. siderea*, but there was no significant interaction effect between size and disease outcome (Table 2). Disease outcome had a significant effect on bleaching extent on colonies of *S. siderea* (Table 2). Diseased colonies experienced greater bleaching extent than colonies that were not diseased (Fig. 3b).

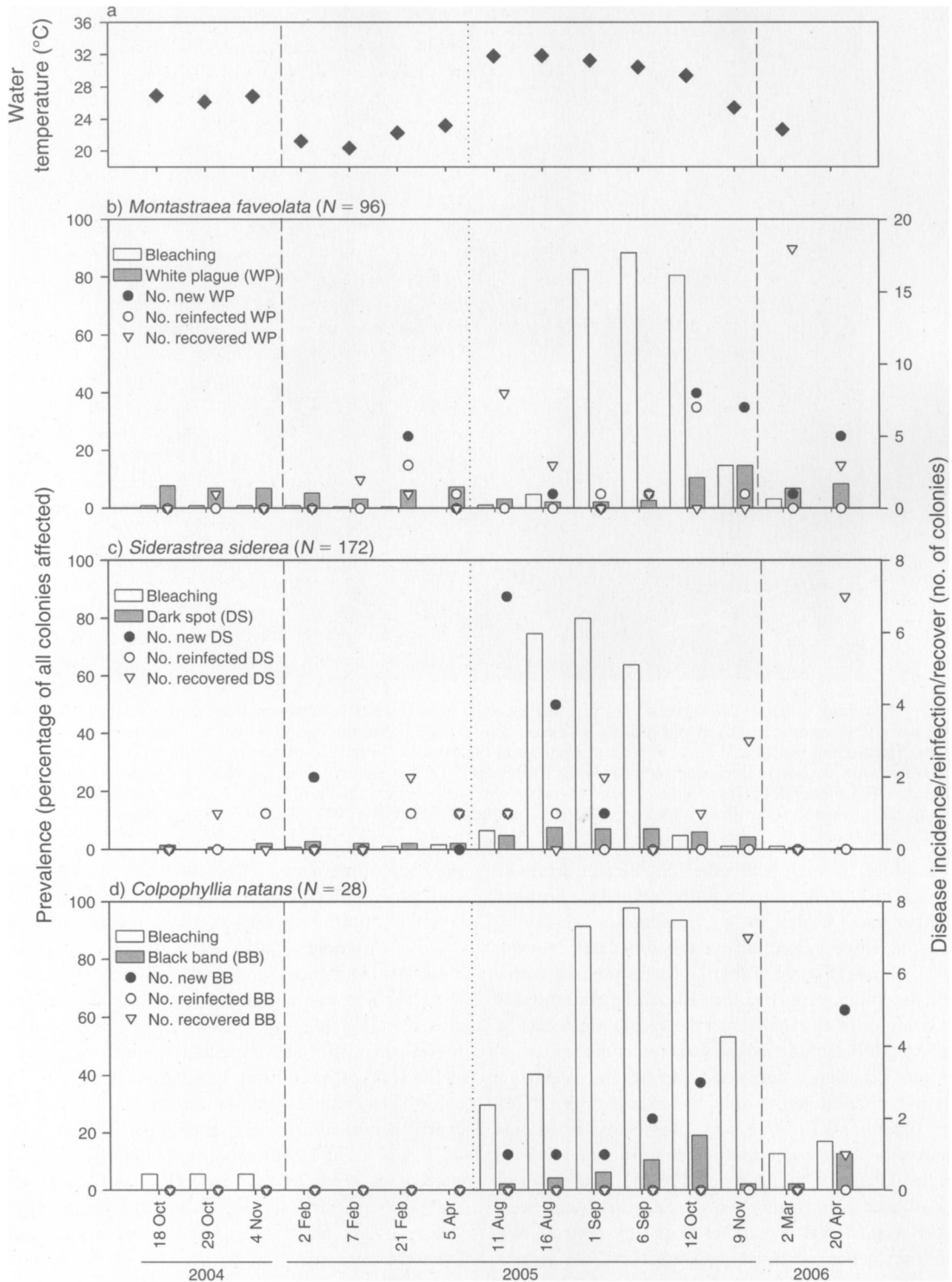


FIG. 2. (a) Mean water temperature recorded at the tops of reef structures at both sites. (b–d) Bleaching and disease prevalence, reported as the percentage of affected colonies in the total population of monitored colonies, and disease incidence, reinfection, and recovery as the number of colonies showing new disease signs (no. new), re-occurrence of disease signs (no. reinfected), or no disease signs when signs had been present on the previous date (no. recovered), respectively, on colonies of (b) *Montastraea faveolata*, (c) *Siderastrea siderea*, and (d) *Colpophyllia natans*. Dashed lines separate different years, and dotted line indicates transition from spring to summer.

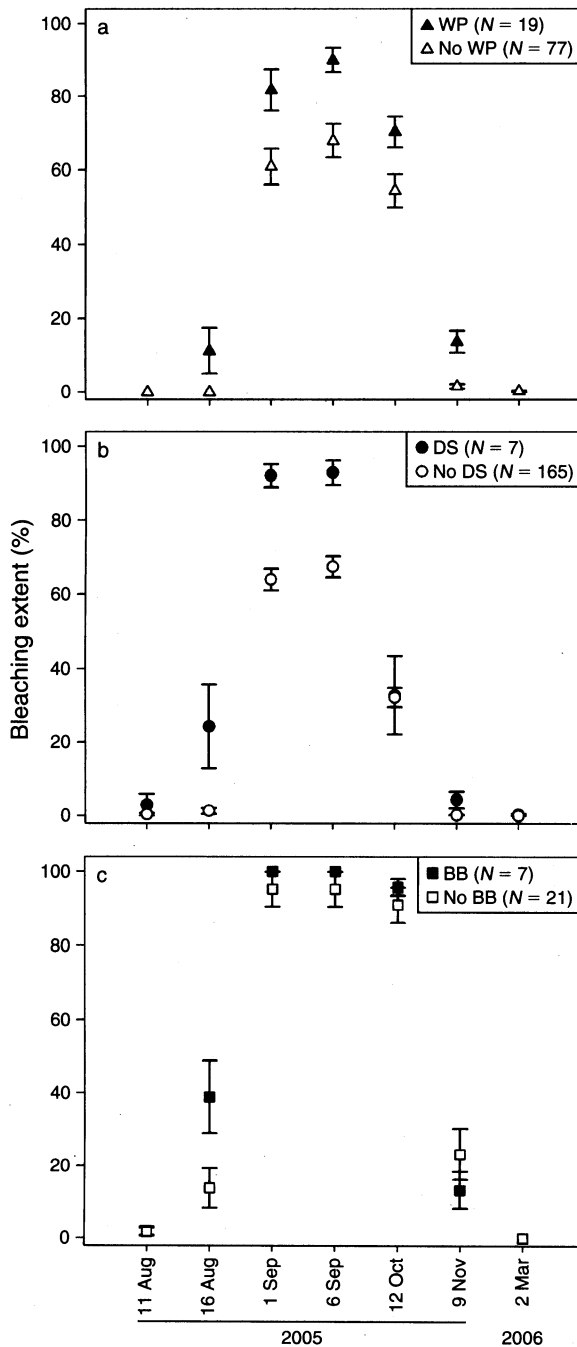


FIG. 3. Percentage of tissue area bleached (bleaching extent; mean  $\pm$  SE) on colonies that showed disease at some point during the bleaching event (white plague [WP], dark spot [DS], and black band [BB]) and on colonies that did not (no WP, no DS, and no BB) for (a) *Montastraea faveolata*, (b) *Siderastrea siderea*, and (c) *Colpophyllia natans*. Bleaching extent differed significantly through time on all three species, and disease status had a significant effect on bleaching extent for *M. faveolata* and *S. siderea*, but not for *C. natans* (Table 2).

New cases of black band (BB)-affected *Colpophyllia natans* colonies were observed continuously beginning in August through September and October (Fig. 2d, “no. new BB”). In November, all but one colony no longer showed BB signs (Fig. 2d, “no. recovered BB”), concurrent with a significant decrease in bleaching severity (Fig. 3c, Table 1: “12 Oct vs. 9 Nov”). Bleaching continued in the spring of 2006, and new BB cases were once again noted in April of 2006 (Fig. 2d, “no. new BB”). Colony size significantly affected bleaching extent on colonies of *C. natans*, but there was no significant interaction between size and disease outcome (Table 2). No significant effect of disease outcome on *C. natans* bleaching extent was detected by the RM-ANCOVA (Table 2). However, before the onset of major bleaching, bleaching extent was greater on colonies that developed BB than on those that did not (Fig. 3c, 16 August).

Mortality due to disease could have inflated the estimates of bleaching extent by decreasing the total area of live tissue with pigment. However, disease-related mortality on colonies never exceeded 5% of the colony’s surface area for WP or BB and never exceeded 1% for DS (data not shown). The only exception was on 9 November 2005, when two WP-affected colonies experienced a loss of >5% of their total tissue area from the subsequent survey date. The difference in bleaching extent between colonies that became diseased and colonies that did not should therefore be interpreted cautiously for this date. Excluding these colonies from

TABLE 1. Results of Tukey hsd post hoc comparisons after repeated-measures ANCOVAs of colony bleaching extent through time.

Species, consecutive date comparison	Post hoc comparisons		
	95% confidence interval		P
	Upper bound	Lower bound	
<i>Colpophyllia natans</i>			
11 Aug vs. 16 Aug	0.39	-2.58	0.602
16 Aug vs. 1 Sep	-1.88	-4.84	0.000***
1 Sep vs. 6 Sep	0.62	-1.18	1.000
6 Sep vs. 12 Oct	1.27	-0.49	1.000
12 Oct vs. 9 Nov	4.79	2.39	0.000***
9 Nov vs. 1 Mar	2.33	0.26	0.002**
<i>Montastraea faveolata</i>			
11 Aug vs. 16 Aug	0.07	-0.41	0.727
16 Aug vs. 1 Sep	-3.80	-4.94	0.000***
1 Sep vs. 6 Sep	0.40	-0.96	1.000
6 Sep vs. 12 Oct	1.56	0.18	0.001***
12 Oct vs. 9 Nov	4.10	2.93	0.000***
9 Nov vs. 1 Mar	0.68	0.16	0.000***
<i>Siderastrea siderea</i>			
11 Aug vs. 16 Aug	0.18	-0.45	1.000
16 Aug vs. 1 Sep	-3.17	-4.49	0.000***
1 Sep vs. 6 Sep	0.57	-1.04	1.000
6 Sep vs. 12 Oct	2.56	1.01	0.000***
12 Oct vs. 9 Nov	3.01	1.89	0.000***
9 Nov vs. 1 Mar	0.17	-0.04	0.983

Note: Date comparisons span from 11 August 2005 to 1 March 2006. \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

TABLE 2. Results of repeated-measures ANCOVAs of colony bleaching extent through time with disease outcome (either became or was diseased or was not diseased) as a factor and colony-size class as a covariate.

Species	Date			Colony size class		
	F	df	P	F	df	P
<i>Colpophyllia natans</i>	11.7	4, 22	<0.001***	4.985	1, 25	<0.05*
<i>Montastraea faveolata</i>	15.7	5, 93	<0.001***	3.428	1, 97	=0.067
<i>Siderastrea siderea</i>	22.8	5, 93	<0.001***	11.765	1, 169	<0.01**

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

the analysis, however, did not change the significance of the results.

#### DISCUSSION

##### *White plague as a possible result of decreased disease resistance relative to bleaching extent*

Incidence of white plague (WP) in *Montastraea faveolata* was highest at the end of the bleaching event, when thermal stress was declining and when colonies began to show recovery of pigment. But this observation of increased incidence of disease following bleaching events is not new (Harvell et al. 2002, Weil et al. 2006). The abundance of potential pathogens is known to increase under conditions that promote bleaching and may amplify the probability of infection in the population as a whole (Harvell et al. 2002). However, this study documents for the first time that colonies that developed WP experienced more extensive bleaching during the event, suggesting a significant relationship between bleaching extent and disease incidence beyond common occurrence.

Physiological changes associated with coral bleaching suggest that it represents a compromised health state for the host and may result in opportunities for pathogen invasion (Ritchie 2006). These changes include some that result in decreased disease resistance, including a loss of antimicrobial activity in the surface mucus layer (Ritchie 2006), reduced energy reserves (Rodrigues and Grottoli 2007), and a loss of regenerative ability (Meesters and Bak 1993). This loss of disease resistance may occur relative to the extent of bleaching experienced by a colony, thus creating opportunities for WP pathogen invasion in colonies that experience more extensive bleaching. However, diverse coral-associated microbial communities are clearly different between diseased and non-diseased corals (Pantos et al. 2003), and they are also known to change in response to environmental stress and during bleaching (Ritchie and Smith 1995, 2004). Normally benign members of the microbial community may increase in abundance relative to the extent of bleaching, and become opportunistic pathogens resulting in WP signs on more extensively bleached colonies (Lesser et al. 2007). Loss of disease resistance, opportunistic infection, or both may have occurred relative to bleaching extent in the corals monitored in this study. Explaining the significant relationship

between WP and bleaching extent discovered in this study will take more research, both through field monitoring efforts and experimental studies, but is necessary for understanding how WP incidence will respond to future mass bleaching events.

##### *The potential role of dark spot in enhancing bleaching*

The dynamics and greater bleaching extent of dark spot (DS)-affected *Siderastrea siderea* colonies also indicated a significant association between disease and bleaching in corals, but with different implications. In this study, the majority of DS infections were recorded before the onset of major bleaching and when thermal stress was high. DS-affected colonies subsequently experienced more extensive bleaching than unaffected colonies. In this case, having DS may have increased bleaching extent on affected colonies through some physiological mechanism, possibly through an adverse effect on hosted *Symbiodinium* populations, the algal endosymbionts that are expelled or degraded resulting in bleaching.

Studies suggest Caribbean DS is the result of coral tissue invasion by endolithic fungi (Galloway et al. 2007, Work and Aeby 2008). In the other known coral-fungal pathogen system, *Aspergillosis* in sea fans, the *Symbiodinium* are not affected by fungal invasion (Kirk et al. 2005). Yet, some physiological impacts to the endosymbionts of *Siderastrea siderea* have been observed in relation to DS infection (Cervino et al. 2001, Galloway et al. 2007). These adverse impacts may have led to more *Symbiodinium* being expelled or degraded when thermal stress was high, resulting in a greater bleaching extent of DS-affected colonies. However, more extensive bleaching on DS-affected colonies may have instead been due to an association between DS and the composition of *Symbiodinium* hosted by colonies. *Siderastrea siderea* can host a diversity of *Symbiodinium*, including four "clades" (A–D) or subgenera, and several taxa within these clades ("types;" LaJeunesse 2002, Thornhill et al. 2006). Recently, Correa et al. (2009) found that DS incidence was negatively correlated with *Symbiodinium* diversity and with hosting *Symbiodinium* ITS-2 type D1a. Some members of *Symbiodinium* clade D are relatively thermo-tolerant (Rowan 2004), and in some cases, hosting these symbionts can increase the heat tolerance of a coral colony by 1.5°C (Berkelmans and van Oppen 2006, but see Abrego et al. 2008). Therefore,

TABLE 2. Extended.

Disease outcome			Disease outcome × colony-size class		
F	df	P	F	df	P
0.500	1, 25	0.486	0.006	1, 24	0.941
10.308	1, 97	<0.01**	0.085	1, 96	0.772
6.425	1, 169	<0.05*	0.094	1, 168	0.760

hosting a greater endosymbiont diversity and/or hosting clade D prior to the bleaching event may have provided resistance to both DS infection and subsequently to bleaching (Correa et al. 2009). Or, physiological interactions between DS and *Symbiodinium* populations may have resulted in a more bleaching-susceptible community of endosymbionts in DS-affected colonies. Understanding the significant relationship between DS and bleaching extent documented in this study would benefit from further longitudinal studies of colonies in situ that incorporate sampling for *Symbiodinium* community changes and physiological impacts.

#### *Black band incidence coincident with bleaching*

Finally, this study corroborates other findings that black band (BB) incidence is highest during periods of elevated temperatures (Kuta and Richardson 2002, Boyett et al. 2007). BB emerged for the first time during monitoring at the start of the bleaching event and expanded through the event consistent with continued thermal stress. Although no significant relationship was detected between BB infection and the bleaching extent experienced by colonies of *Colpophyllia natans* in this study, its dynamics paralleled those of bleaching in this species. The slightly greater bleaching extent experienced by infected colonies on one date early on in the bleaching event may have proved significant with a larger sample size. The relationship between BB and bleaching may therefore warrant further investigation.

This study reports for the first time significant relationships between disease and the extent of bleaching experienced by individual corals. This work emphasizes the importance of understanding synergistic interactions among seemingly independent responses of organisms to environmental factors, especially those affected by climate change.

Investigating these interactions is critical to understanding the origins of mortality patterns caused by large-scale events such as mass bleaching. Coral colonies are capable of recovering from bleaching once the causative stressor is removed, and they may sustain little to no partial mortality depending on the stressor type and length of exposure (Anthony et al. 2007). Yet, mortality stemming from mass bleaching events has often been attributed to bleaching alone (Glynn 1994). In contrast, WP and BB diseases are always associated with rapid tissue loss (Rutzler et al. 1983, Richardson et al. 1998), and tissue lost due to disease often remains

absent of new coral growth (Edmunds 2000, Nugues 2002, Borger 2005). Both WP and BB have demonstrated a capacity to alter the structure of coral populations at large scales (e.g., Edmunds 1991, Bruckner and Bruckner 1997, Richardson and Voss 2005, Page and Willis 2006, Francini et al. 2008), and although DS typically causes little mortality to the corals it infects, its abundance on dominant reef-building species makes it an important indicator of reef health (Gochfeld et al. 2006). In this study, the positive relationships uncovered between disease and more extensively bleached colonies suggest that resulting mortality patterns were the result of dynamic synergisms between bleaching and disease and not the impact of one or the other independently or alone.

These results have provided greater insight into linkages between physiological responses of reef-building corals to thermal stress, and shed light on how bleaching and disease may interact during future anomalous thermal events. Warmer temperatures associated with a changing climate will likely generate higher frequencies of bleaching (Hoegh-Guldberg et al. 2007) and disease (Harvell et al. 2002). This, combined with other impacts has prompted dire predictions of an impending future devoid of reefs (Carpenter et al. 2008). But like most ecological communities, coral communities are diverse across multiple scales, and they can vary in their bleaching tolerance (Coles and Brown 2003) and disease susceptibility (Sutherland et al. 2004). Therefore, predictions should be made cautiously, and emphasis placed on understanding the dynamics and interactions of these types of coral responses and how they may change under changing climate conditions (Maynard et al. 2008). This type of understanding is necessary for predicting the occurrence and consequence of future events.

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#### APPENDIX A

Number of monitored colonies for each primary host species and for all species combined within quadrats at sites (*Ecological Archives* E090-202-A1).

#### APPENDIX B

Effect of site and quadrat on colony bleaching extent from repeated-measures ANOVAs for each of the three primary host species (*Ecological Archives* E090-202-A2).