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Coral Bleaching and Disease: Recovery and Mortality on Martinique Reefs following the 2005 Caribbean Bleaching Event

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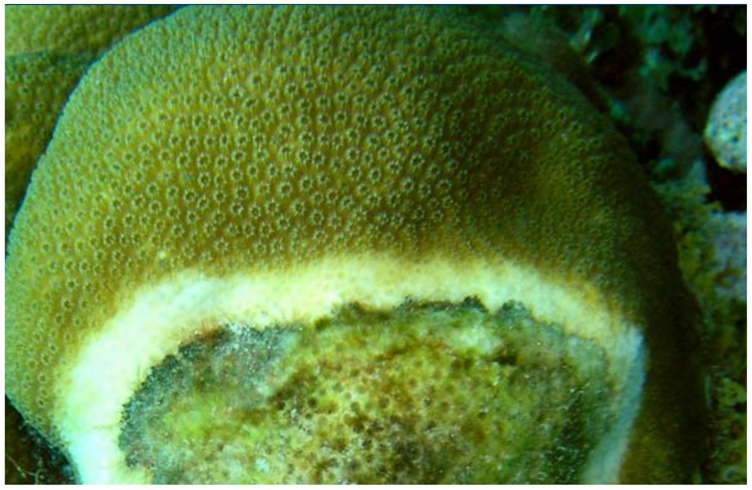

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Paper

Coral Bleaching and Disease: Recovery and Mortality on Martinique Reefs following the 2005 Caribbean Bleaching Event

C.A Cowan

Abstract

In the face of global warming, elevated seawater temperatures are predicted to cause an increased frequency and intensity of mass-bleaching events on a global-scale. Elevated sea surface temperatures in the western Atlantic from July to November, 2005 produced widespread bleaching of corals in the Caribbean. Martinique reefs experienced a total of 12 Degree Heating Weeks between mid-August and mid-October 2005, with seawater temperatures at monitored reef sites reaching temperatures of 30.4^{o}C in September, 2005. Underwater surveys of the reefs in November indicated that there was widespread total bleaching of coral colonies on the reefs. This paper presents the effects of the 2005 bleaching episode on Martinique reefs, detailing the recovery and mortality rates of coral species and addresses the impacts of a recent disease outbreak causing lesions characteristic of yellow band disease and white plague. It does not appear that bleaching confers a fitness value on Martinique reefs, as mortality rates on bleached colonies were significantly higher than on those that did not bleach. Disease outbreaks are likely to prevail during periods of elevated seawater temperature while corals are stressed and experience depleted energy reserved and impaired defence systems. Thus, mortality estimations following bleaching seasons should not be attributed solely to bleaching – it is probable that other factors are acting synergistically with bleaching. Frequent monitoring of bleached reef sites is required to ensure that synergistic disturbances, exacerbating the stresses of thermal bleaching do not go unnoticed. It may be impossible to shelter coral reefs from large-scale disturbances such as elevated seawater temperatures due to global warming, but by acting on factors which can be addressed by management on a smaller scale it may be possible to ameliorate the aftermath of coral bleaching.

1. Introduction

The frequency and severity of coral bleaching events is increasing throughout the world's oceans (Wilkinson, 1999; Douglas, 2003; Goreau & Hayes, 2005). Prolonged bleaching can cause extensive coral mortality (Burke et al. 2004; Yonge & Nichols, 1931; Harvell et al 1999) and coupled with disease and pollution, may have contributed to the loss of approximately 16% of the world's coral reefs within the past decade (Hoegh-Guldberg, 1999). Myriad factors have been associated with the bleaching process such as temperature extremes (McWiliiams et al. 2005; Buddemeier & Fautin, 1993; Brown, 1997; Glynn, 1996) high solar irradiance (Brown et al. 2002), prolonged darkness (Douglas, 2003), changes in salinity (Jokiel and Coles, 1990), epizootics (Brown, 2000; Rosenberg & Falkovitz, 2004) and heavy metal presence (Douglas, 2003). Recent mass-mortality bleaching events, such as the 1997-1998 El Nino Southern Oscillation-associated event have been closely linked to rising seawater temperatures, and in the face of projected global warming, it is likely we will see an increased frequency of mass-bleaching events (Hoegh-Guldberg, 1999; Risk, 1999; Douglas, 2003; Sheppard, 2003).

During bleaching, corals either extrude their endosymbiotic zooxanthellae (dinoflagellate algae of the genus *Symbiodinium*), or there is concomitant loss of photosynthetic pigments within each zooxanthellae. The loss of the coral host-zooxanthellae symbiosis terminates the process by which corals acquire sufficient energy to survive. The consequent energetic deficit means bleached corals have an impaired ability to cope with stresses, both natural and anthropogenic and may suffer partial or total mortality (Meesters et al. 1993; Wilkinson, 1999; Hughes et al. 2003; McClanahan et al. 2004). Stresses such as storm abrasion, sedimentation, eutrophication, freshwater runoff, epizootics and increased predation pressure on surviving corals can exacerbate the effects of bleaching (Borger, 2005). Chronic bleaching may eventually lead to reproductive failure and reduced growth, leading to a loss of physical integrity and net erosion of coral reefs (Schumacher et al. 2005). Substantial bleaching-induced physiological impairment and mortality coupled with anthropogenic factors on Caribbean reefs has allowed algae to outcompete corals and induce a coral-algal phase shift on many reef systems (Aronson & Precht, 2001; Gardner et al. 2005), eliciting greatly reduced species diversity and cover of hermatypic corals in some parts of the Caribbean.

Although there is speculation surrounding the future of coral reefs with projected climate change predictions, there is mounting evidence to suggest that corals do in fact possess adaptability to environmental stresses, and display patterns of susceptibility to bleaching and recovery which could lead to their persistence through projected climate change in the near future (Fitt et al. 2001; Brown et al. 2002; Fautin & Buddemeier, 2004). Variable susceptibility to temperature-induced coral bleaching can be due to variation in the resident *Symbiodinium* population. *Symbiodinium* types vary between coral species and geographic region and also in their physiological tolerances (LaJeunesse et al. 2004; McClanahan et al. 2004), and so variation in the relative abundance of *Symbiodinium* types within the host may influence bleaching susceptibility (Buddemeier & Fautin, 1993). Environmental parameters such as upwelling (Goreau et al. 2000; Salm et al. 1993), turbidity (Goreau et al. 2000), cloud cover (Mumby et al. 2001) and water flow (McClanahan et al. 2005; Nakamura & Yamasaki, 2005) may allow avoidance of bleaching conditions at a local scale, and coral host tissues may possess protective physiological mechanisms as described in table 1 to reduce the stresses leading to bleaching (Brown et al. 2002; Salih et al. 2000; Sharp et al. 1997).

Table 1 – Physiological mechanisms found in coral tissues and samples that are thought to ameliorate the temperature stress which may lead to bleaching.

Protective mechanism	Authors
High concentration of xanthophylls (xanthin and diatoxanthin) for use in the xanthophyll cycle to dissipate excess excitation energy via non-photochemical quenching	Fitt et al. 2001; Coles & Brown, 2003; Warner et al. 1996
High concentration of fluorescent pigments to fluoresce excess absorbed light	Salih et al. 2000; Brown et al. 2002
Efficient induction of heat shock proteins to protect damaged proteins and aid membrane transport	Sharp et al 1997; Downs et al. 2000; Brown et al. 2002;
Increased concentration of oxidative enzymes upon heat shock to prevent cellular damage from toxins	Lesser et al. 1990; Downs et al. 2000
Robust host-symbiont associations, possessing a high proportion of heat-tolerant *Symbiodinium*	Toller et al. 2001; Baker et al. 2001; Buddemeier & Fautin, 1993

Many biotic and abiotic pressures on recovering corals following bleaching events profoundly affect their chances of recovery. Among such pressures are coral disease outbreaks, predation pressures, pollution, and destructive fishing practices. The frequency of occurrence and geographic range of coral diseases has increased in the past decade (Borger, 2005; Goreau et al. 1998; Hayes & Goreau, 1998; Harvell et al. 2001). Disease outbreaks have been linked to impaired protection responses from corals undergoing or recovering from bleaching (Harvell et al, 2001) and in the face of climate change this confounding factor affecting coral recovery may lead to declines in coral species diversity (Aronson & Precht, 1997; Bruckner, 2002).

While interspecific variation in bleaching susceptibility has been identified (Brown et al. 2002; Rowan, 2004; Fitt et al. 2001; McClanahan et al. 2005; Rowan et al. 1997; Baird & Marshall, 2002) there have been relatively few studies that link bleaching susceptibility to mortality rates (Brown & Coles, 2003). Furthermore there have been even less studies in which specific coral colonies are tracked through their bleaching phase and recovery phase. During the recovery phase it is essential to quantify the spatial and temporal dynamics of additional stresses such as disease outbreaks (Borger, 2005).

Elevated sea surface temperatures in the western Atlantic from July to November, 2005 produced widespread bleaching of corals in the Caribbean (Jeffrey et al. 2006). Martinique reefs experienced a total of 12 Degree Heating Weeks (one week of seawater temperatures 1 degree C above mean summer maximum) between mid-August and mid-October 2005, with seawater temperatures at monitored reef sites reaching temperatures of 30.4°C in September, 2005. Underwater surveys of the reefs in November indicated that there was widespread total bleaching of coral colonies on the reefs. This paper presents the effects of the 2005 bleaching episode on Martinique reefs, its aims are to 1) investigate species-specific bleaching susceptibility on Martinique reefs 2) summarise the short-term recovery and mortality since the 2005 bleaching event 3) assess the impact of a recent coral disease outbreak on the southern bank reef which was first observed in spring, 2006.

2. Materials & Methods

2.1 Study Sites

The effects of the 2005 bleaching event were studied at three reef sites, two on the south coast and one on the western, Caribbean coast of Martinique. All three sites are part of the monitoring sites covered by the Observatoire du Milieu Marin Martinique (OMMM) biannual monitoring program. There is a permanent 60m transect used for benthic surveys at each site. The southern sites were located on the bank reef which extends the length of the southern coast of the island (figure 1). Pointe Borgnesse (14.45, 60.91) exhibits approximately 46% coral cover (J-P. Marechal – personal communication) and is close to the outflow of three major rivers and the extensive marina and moorings in La Marin bay (figure 1). Jardin Tropical (14.45, 60.92) exhibits up to 61% coral cover (J-P. Marechal – personal communication) and is far to the west of the river outflow. The site on the Caribbean coast, Fondboucher (14.66, 61.16) is a fringing reef exhibiting up to 25% coral cover (J-P. Marechal – personal communication) and is clear of major river outflows. All transect sampling was conducted between 10 and 12 metres depth at all sites.

There is a difference in land-based and anthropogenic factors affecting the water quality between Pointe Borgnesse and Jardin Tropical; namely the run-off from three major rivers which meet the reef area at Pointe Borgnesse and the presence of the extensive marina and tourist resorts within La Marin bay, with Pointe Borgnesse being located on the headland at the entrance to this bay. Bocquene and Franco (2005) conducted surveys of pesticide contamination in river plumes in Martinique. There is intensive agriculture in the form of sugar cane, banana, and pineapple plantations in Martinique thus there is extensive use of pesticides, with high concentrations being detected, one of which – chlordecone is bioaccumulating and carcinogenic. Although the rivers in proximity to the sites surveyed in this study were not covered, it remains a possibility that may be chemical stressors within the water column where river plumes meet the coral reef at Pointe Borgnesse. It may be that Pointe Borgnesse is of degraded water quality due to hyposalinity and chemical contamination associated with river runoff and a high load of human waste from the marina heightening the likelihood of pathogen presence in the water column.

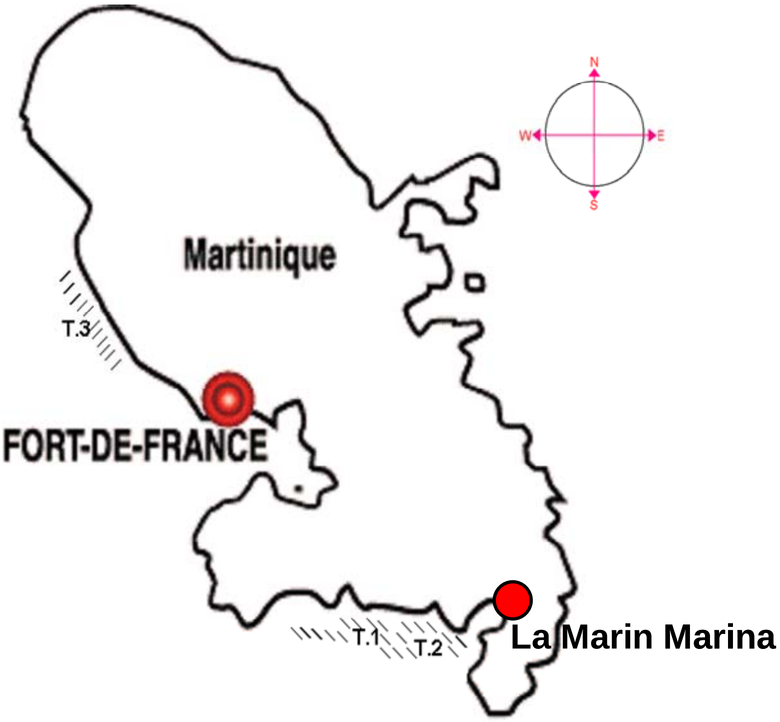

Figure 1 – Line map of Martinique showing the capital, Fort de France and the three permanent transect sites (T.1-T.3). T.1 = Jardin Tropical on the southern bank reef, T.2 = Pointe Borgnesse on the southern bank reef, T.3 = Fondboucher on the Caribbean coast fringing reef. Both T.1 and T.2 were also surveyed to determine the impacts of a recent coral disease outbreak using the 10 m transect method. The extensive marina and moorings at La Marin are indicated to the south.

2.2 Seawater temperatures

Seawater temperatures were monitored throughout the bleaching episode from June, 2005 until December 2005 using an EBRO EBI-85A temperature logger. The temperatures were recorded at the southern bank reef site at Pointe Borgnesse and at the northern fringing reef site, Fondboucher.

2.3 Survey method

Two distinct survey protocols were practiced to investigate different questions on the reefs of Martinique. Firstly, the consequences of bleaching were investigated at the three survey sites using video footage in order to track specific coral colonies (section 2.3.1). Secondly, 10 m transects were used to gain an insight into the recent mortality at the two southern sites and to assess the impacts of the recent coral disease outbreak (section 2.3.2).

2.3.1 The aftermath of the 2005 bleaching event

All sites were surveyed using SCUBA equipment. Video footage of the permanent 60 m monitoring transects was taken by the OMMM during the bleaching event in November 2005 at all three sites. Line intercept coral colonies on the video footage were identified to species level using benthic survey data from the OMMM biannual surveys and their condition was noted as 1) bleached, 2) pale and 3) healthy. These categories were sufficient as most colonies that did bleach were totally bleached, thus categories for percentage of colony bleached were not required. Pale colonies were defined as corals which were lighter than their habitual colour (as in Bruckner, 2002), but not displaying complete whiteness.

The permanent transects were revisited in April and May 2006 and video footage was once again obtained. The same colonies were identified on the April/May footage and their condition was noted as 1) dead, 2) partial mortality, 3) pale and 4) healthy. Dead colonies were defined as those displaying bare corallite structures or algal turf overgrowth, partial mortality was defined as those colonies in which part of the surface was overgrown with turf algae, pale colonies were identified as being paler than their habitual appearance and healthy colonies displayed no signs of morbidity or partial mortality, showing full recovery of their pigmentation.

2.3.2 Recent mortality and prevalence of disease following the 2005 bleaching event

Only the sites in the south were surveyed in detail to determine the level of recent and old mortality and the impact of a recent coral disease outbreak. This was due to the fact that the disease outbreak was first observed in the south, and to date, colonies at the northern sites have not shown signs of disease. It is also worth investigating any differences between the coral community health between Pointe Borgnesse and Jardin Tropical due to the fact that Pointe Borgnesse is a more heavily impacted site.

At each site, two buddy teams of divers haphazardly selected a start point for a 10 m transect. The AGRRA (Atlantic and Gulf Rapid Reef Assessment) monitoring protocol and apparatus was used to conduct 10 m transects – figure 2 (Kramer et al. 2005). The line intercept method was used, with all colonies intersecting the transect line being recorded.

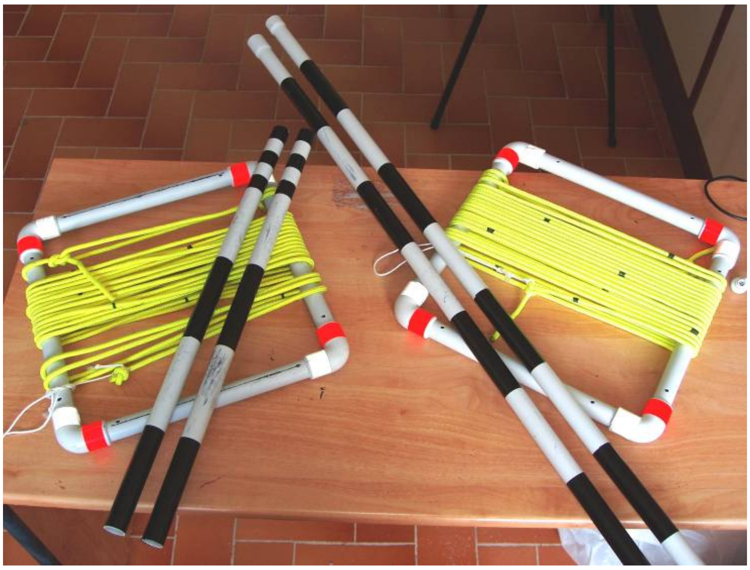

Figure 2 – AGRRA apparatus, 10 m long transect line wound around a 0.25 m^2 quadrat for convenience and transportation, 1 metre long measuring pole, marked at 10 cm intervals, and 0.5 cm long measuring pole marked at 10 cm and 2 cm intervals.

The following information was recorded for each intersecting colony: 1) species; 2) size (greatest length, perpendicular width, and greatest height); 3) percentage live tissues on outward facing surfaces; 4) percentage "recent" mortality and; 5) percentage "old" mortality. Where tissues were diseased, the percentage diseased surfaces and the type of disease were recorded. Percentage estimates were rounded to the nearest 1%. "Recent" mortality was defined as any non-living parts of the colony where the corallite structure was white and still intact or slightly eroded but still visible. Skeleton which was lightly covered in sediment or a thin layer of green turf algae was also classed as “recent” mortality. Where corallite structures had been destroyed by fish or snail predation and appeared as white lesions, there were also classed as “recent” mortality. “Old” mortality was defined as any non-living parts of the colony where the corallite structure had disappeared via erosion or was smothered by other organisms such as macroalgae or invertebrates. All diseases were identified using published descriptions in Bruckner (2002).

Other causes of mortality were noted e.g. algal overgrowth, predation, overtopping. Notably bleached surfaces were also noted. A 20 m^2 count of the long-spined sea urchin, *Diadema antillarum* was conducted over each 10m transect to assess the algal control potential at each site by counting the number of adult and juvenile *Diadema antillarum* within a 1m belt adjacent to either side of the 10 m transect. Ten transects were conducted at both sites, giving a total of 20 transects, with 273 coral colonies from 17 species being surveyed.

BLAGGRA (Bleaching Atlantic and Gulf Rapid Reef Assessment) surveys were conducted in January 2006 at 7 sites in Martinique to determine the “recent” and “old” mortality on the reefs following the bleaching event during the previous season (Lang et al. 2006). Comparison of the levels of recent and old mortality from the January and April/May surveys will be possible.

The majority of coral colonies on Martinique reefs are of an approximate hemispherical shape (e.g. *Montastrea spp. Colpophyllia sp. Porites sp*.) and thus the colony volume was calculated using the volume for a hemisphere ($2/3.\pi.r^3$) with radius as the sum of the length and width/2. The colony volume data was then log transformed to meet assumptions to allow parametric statistical testing (t-test) to determine whether disease prevalence was related to the size of the colonies.

Pointe Borgnesse was the site most affected by disease, so 6 colonies exhibiting signs of disease (tissue discolouration, distinct band of necrosis) were tagged in week two of the survey period and revisited after four weeks. Digital photographs of each tagged colony were taken upon initial tagging and after the four week interim period to determine the rate of disease advance on the colony.

3. Results

3.1 The aftermath of the 2005 bleaching event

In early 2005, before the sea temperature anomaly in the Caribbean and its associated coral bleaching, the reef sites of southern Martinique were estimated to exhibit up to 61% living coral cover (J-P. Marechal - personal communication), consisting of mainly the boulder coral - *Montastrea spp*. The temperature anomaly at the southern bank reef was monitored throughout the bleaching season at Pointe Borgnesse using a temperature data logger (figures 3). The temperature anomaly was also measured at the northern fringing reef site, Fondboucher (figure 4).

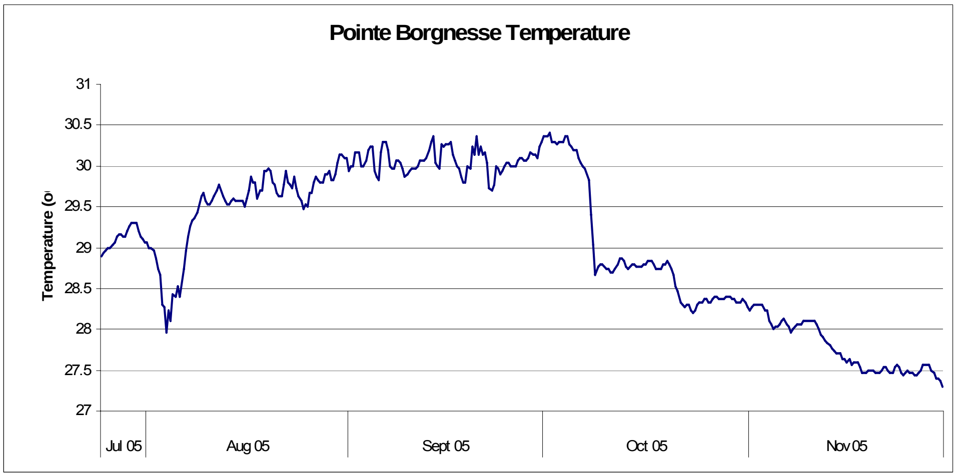

Figure 3 – Seawater temperatures recorded via datalogger during the 2005 summer months at the southern bank reef at Pointe Borgnesse, max temp = 30.4^{o}C during Sept, 2005.

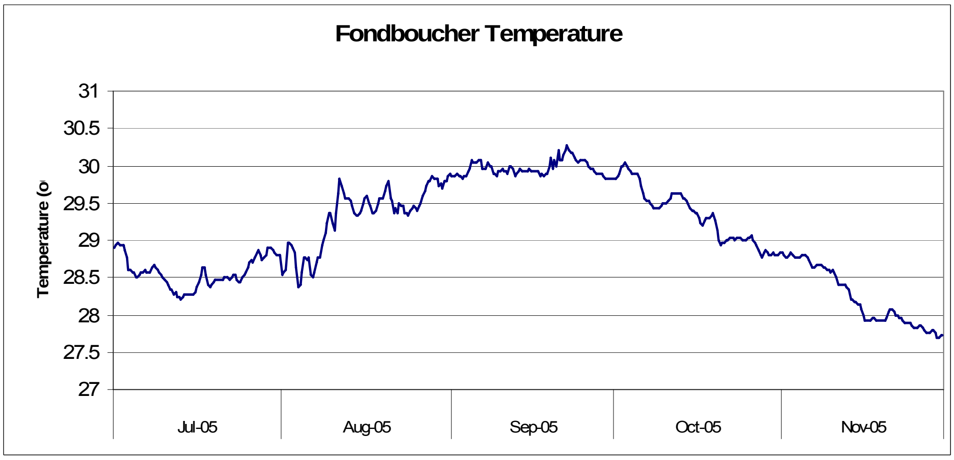

Figure 4 – Seawater temperatures recorded via datalogger during the 2005 summer months at the northern fringing reef at Fondboucher, max temp = 30.2^{o}C during Sept, 2005.

The sea temperature in Martinique waters was elevated to above 29.5^{o}C from mid-August 2005 until mid-October 2005. However, although this threshold is believed to herald a bleaching threat (NOAA, 2006), bleaching was observed earlier in the season on the reefs, as early as July (J-P. Marechal - personal communication) and the signs of coral bleaching were still observed during monitoring of the reefs in November 2005. An average of 12 degree heating weeks were recorded in Martinique, when sea surface temperatures of 1 degree C above the expected summer maximum were present (Lang et al. 2006).

Chi squared analysis of the permanent transect survey data determined that the colonies which did not bleach during the 2005 season suffered significantly less partial and total colony mortality the following spring at all three sites surveyed (Jardin Tropical: X^2 = 7.22, d.f = 2, p = 0.027, Pointe Borgnesse: X^2 = 21.8, d.f = 2, p<0.001, Fondboucher : X^2 = 23.81, d.f = 3, p<0.001). The health categories used in analyses were: dead, partial mortality, discoloured and healthy (table 2).

Thus, bleaching appears to have elicited a decline in health on the reefs surveyed, with instances of partial mortality and total colony mortality being widespread on colonies that bleached.

Table 2 – Colonies in each health category (assessed during April-May 2006 survey) at each site, grouped based on whether they bleached in November (Bleached) or were unaffected (Healthy) (sites are: JT = Jardin Tropical, PB = Pointe Borgnesse, FB = Fondboucher), data is number of colonies observed on the 60m permanent transects for each category.

Condition	Site	Dead	Partial mortality	Discoloured	Healthy
Bleached (in November, 2005)	JT	16	10	2	34
	PB	8	21	1	7
	FB	12	10	9	28
Healthy (in November, 2005)	JT	2	0	0	17
	PB	0	0	0	10
	FB	0	0	1	33

Bleaching appeared to be a very significant factor determining the health of corals the following spring at all three sites (figure 5), so the data for the sites was combined to investigate inter-species variability (table 3).

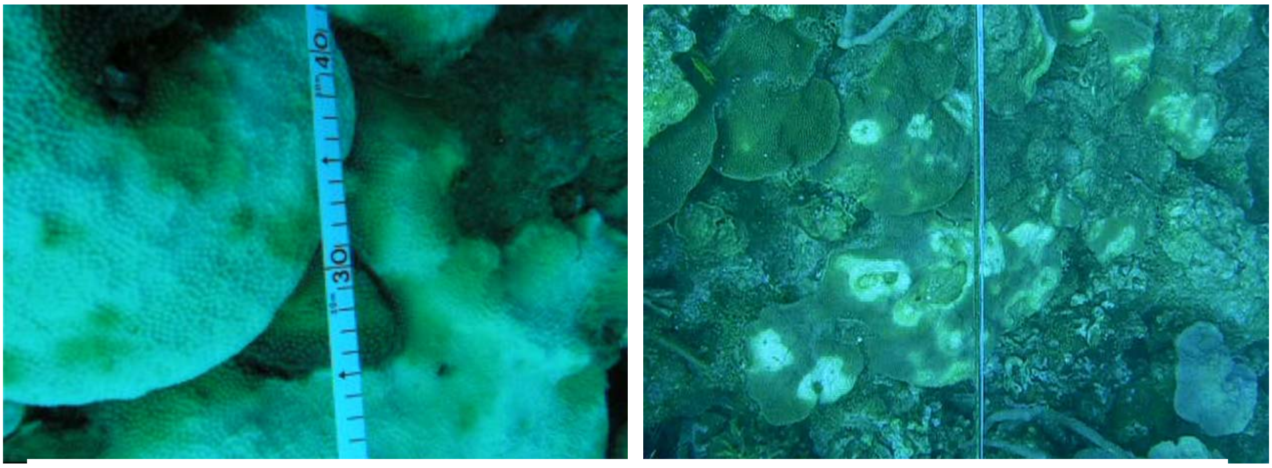

Figure 5 – Colony of *Montastrea faveolata* at Jardin Tropical. Left – Close up of bleached surfaces during November, 2005 surveys, Right – Entire colony in May, 2006 showing signs of Yellow Band disease and patchy necrosis.

Table 3 – Species response to bleaching from the April-May, 2006 survey period, data is combined from across the three sites with data indicating numbers of colonies showing total mortality, partial mortality, discoloured tissues, or good health.

	Dead	Partial mortality	Discoloured	Healthy
Agaricia agaricites	11	9	1	5
Colpophylla natans	1	0	1	1
Diploria labyrinthiformis	0	0	0	1
Diploria strigosa	1	1	0	1
Madracis mirabilis	0	0	0	9
Meandrina meandrites	0	0	2	3
Montastrea annularis	4	13	1	4
Montastrea faveolata	6	13	1	17
Porites astreoides	1	3	3	18
Porites divaricata	1	0	0	0
Porites porites	10	2	2	6
Siderastrea siderea	1	0	1	3
Stephanocoenia intercepta	0	0	0	1

The reefs of Martinique are dominated by the boulder coral, *Montastrea spp*. (see table 5 in section 3.2) with the detailed 10 m transect surveys of the reefs determining that *Montastrea spp*. accounts for 76.75% of total coral colonies at Pointe Borgnesse and 42.4% at Jardin Tropical. Therefore, species belonging to the *Montastrea spp*. family were grouped and tested against all other coral species combined in a category as "Others". It was determined that *Montastrea spp.* colonies appear to suffer relatively more partial mortality and there are proportionately less healthy colonies than in all other species grouped together – table 4 ($X^2 = 16.9$, d.f = 3, p = 0.001).

Table 4 – Condition of colonies that exhibited bleaching in November 2005, during the April/May, 2006 surveys for *Montastrea spp.* compared with all other species – data indicates the proportion of colonies observed on the 60 m permanent transects for each condition category.

	Dead	**Partial mortality**	**Discoloured**	**Healthy**
Montastrea spp	17	44.1	3.4	35.6
Others	26.3	15.2	10.1	48.4

"Recent" partial colony mortality and "Old" partial colony mortality of the two southern bank reef sites was calculated from the 10m transect data. "Recent" and "old" mortality were calculated as follows:

$$\% \text{ Recent Tissue Loss} = \frac{\text{Recent mortality}}{\text{Live tissue} + \text{Recent mortality}}$$

$$\% \text{ Old Tissue Loss} = \frac{\text{Old mortality}}{\text{Live tissue} + \text{Old mortality}}$$

Nonparametric Mann-Whitney tests determined that there was no significant difference between the recent mortality at Pointe Borgnesse and Jardin Tropical but there was a significant difference between the old mortality at the two sites, W = 74, p = 0.021 (figure 6).

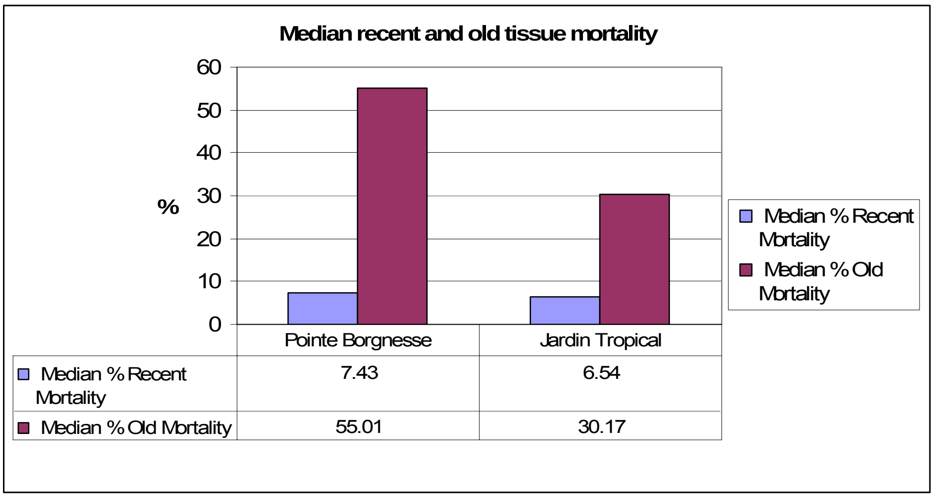

Figure 6 – Median % recent mortality and old mortality on coral colonies for each site surveyed during April-May, 2006.

During the January, 2006 BLAGRRA surveys it was determined that the "recent" mortality was on average 13% (±9%) on Martinique reefs (Lang et al. 2006), considerably higher than the percentage derived later in the season during April-May, 2006, thereby illustrating the requirement of regular monitoring of bleached sites to detect the recovery prospects of reefs.

The abundance of *Diadema antillarum* from the 20 m^2 belt transect counts at each site were analysed using a t-test. It was determined that there was a significant difference in *Diadema sp.* densities between Pointe Borgnesse and Jardin Tropical, T = 3.38, p = 0.004, d.f = 4. The mean density at Pointe Borgnesse was 10.2 individuals per 20 m^2 ±1.8(S.E) and the mean density at Jardin Tropical was 22.1 individuals per 20m^2 ±3(S.E). Therefore, there is a higher density of *Diadema sp*. at Jardin Tropical, and it can be postulated that this results in a higher rate of macroalgal herbivory.

3.2 Prevalence of disease following the 2005 bleaching event

During the 6 weeks survey period in April-May 2006, a total of 32 diseased coral colonies were recorded across the two southern sites. The 10 m transect surveys determined that *M.annularis* and *M.faveolata* were the most abundant species at the southern bank reef (table 5). Both yellow band disease and white plague affected the corals, with white plague being more prevalent (figures 7 and 8). The diseases affected colonies of *M.annularis, M.faveolata, C.natans* and *P.porites* with an overall prevalence of 11.1%. The relative prevalence of diseases on *M.annularis* and *M.faveolata* appears quite high, with over 25% of colonies being affected by signs of white plague. It is likely that this is not due to the dominance of *Montastrea spp*. at the sites, but by the overall large size of the colonies rendering them susceptible to chance disease infection.

Table 5- Coral population composition at each site, composition is indicated by prevalence percentage of recorded colonies across all 10 m transects.

Site	**Pointe Borgnesse**		**Jardin Tropical**	
Species (relative prevalence, %)	Colpophyllia natans	6.20	Acropora cervicornis	0.69
	Dichocoenia stokesi	0.78	Colpophyllia natans	7.64
	Diploria labyrinthyformis	1.55	Diploria labyrinthyformis	3.47
	Madracis decactis	1.55	Eusmilia fastigiata	0.69
	Madracis mirabilis	0.78	Madracis decactis	3.47
	Meandrina meandrites	0.78	Madracis mirabilis	15.97
	Montastrea annularis	36.43	Meandrina meandrites	4.17
	Montastrea cavernosa	0.78	Millepora alcicornis	2.08
	Montastrea faveolata	35.66	Montastrea annularis	11.11
	Montastrea franksi	3.88	Montastrea cavernosa	2.78
	Porites astreoides	10.08	Montastrea faveolata	23.61
	Porites porites	0.78	Montastrea franksi	4.86
	Stephanocoenia mechelini	0.78	Porites astreoides	13.19
			Porites porites	4.17
			Siderastrea siderea	1.39
			Stephanocoenia mechelini	0.69
Number of 10 m transects		10		10

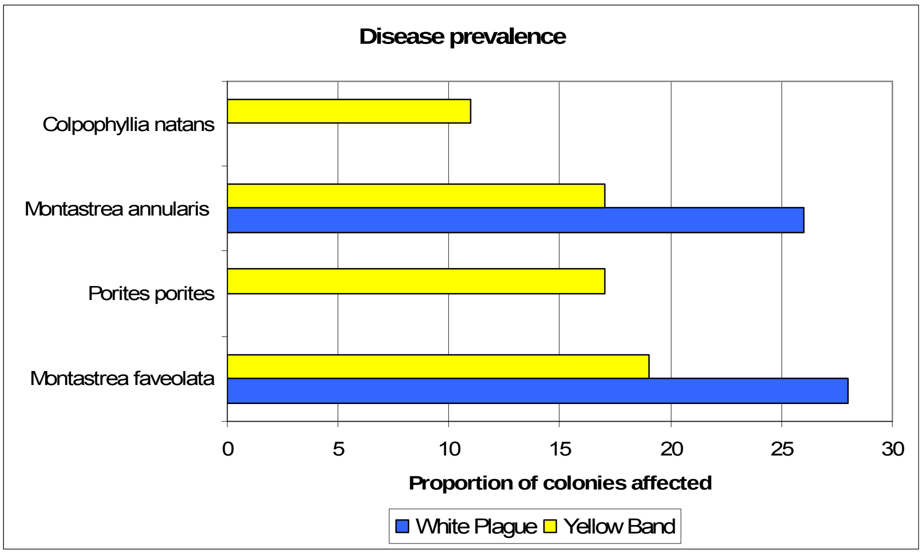

Figure 7 – Proportion of each species affected by each disease during the six week survey period (April-May, 2006), *C.natans* n = 9; *P.porites*, n = 6; *M.annularis*, n = 23; *M.faveolata*, n = 43.

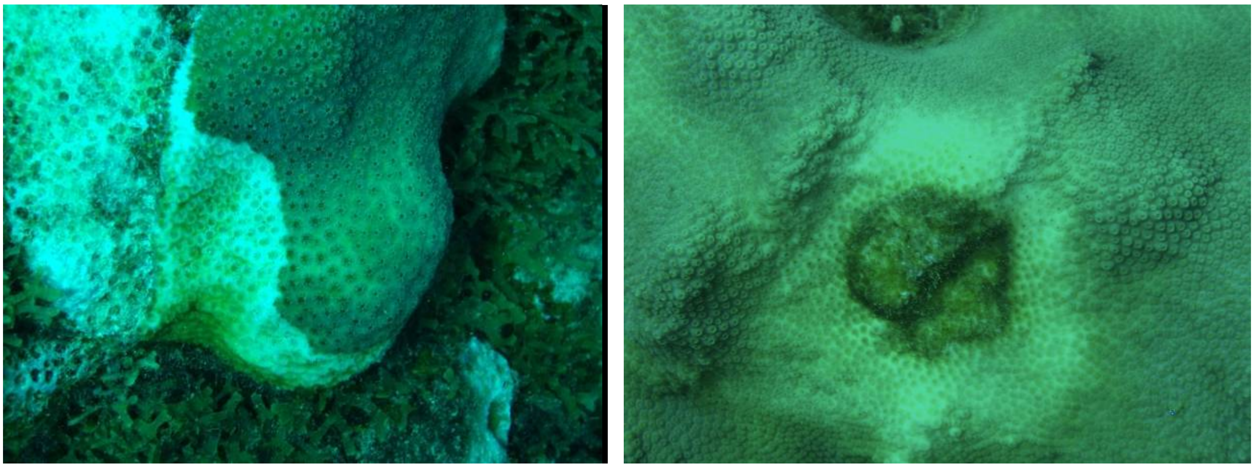

Figure 8 – Coral diseases observed on the Martinique reefs. Left – *Montastrea annularis* at Pointe Borgnesse showing signs of white plague. Right – *Montastrea faveolata* showing symptons of Yellow Band disease at Pointe Borgnesse.

Diseased corals colonies were of a significantly larger size at Jardin Tropical (t-test, T = 2.79, p = 0.011, d.f = 20). The mean colony volume for healthy corals was 0.13 m^3 ± 0.05(S.E), with the mean colony volume of diseased colonies being 0.16 m^3 ± 0.04(S.E). However, there was no significant difference in the size distribution of diseased and healthy colonies at the other site – Pointe Borgnesse, where the colonies are on average larger.

The total diseased colonies exhibiting signs of white plague and yellow band disease from both sites were combined and tested to determine whether the two types of disease appear to target different size classes of colonies. There was no significant difference between the size distributions of colonies affected with each disease type: Mann Whitney, W = 776, p > 0.05 (White Plague median = 0.042, n = 32 and Yellow Band median = 0.037, n = 14). Thus, it appears that yellow band disease and white plague follow similar opportunistic means of spread through coral communities.

Of the 6 tagged colonies at Pointe Borgnesse, only one colony showed signs of disease advancement. This suggests that many signs of disease could be signs of predation in one instance (figure 9A) or old, arrested disease spread (figure 9B). However, one *Montastrea faveolata* colony showed signs of white plague, with considerable tissue loss in the four week period between survey visits (figure 9C-F). Approximately 5% of the outward facing colony surfaces were killed by the advancing disease during the four weeks.

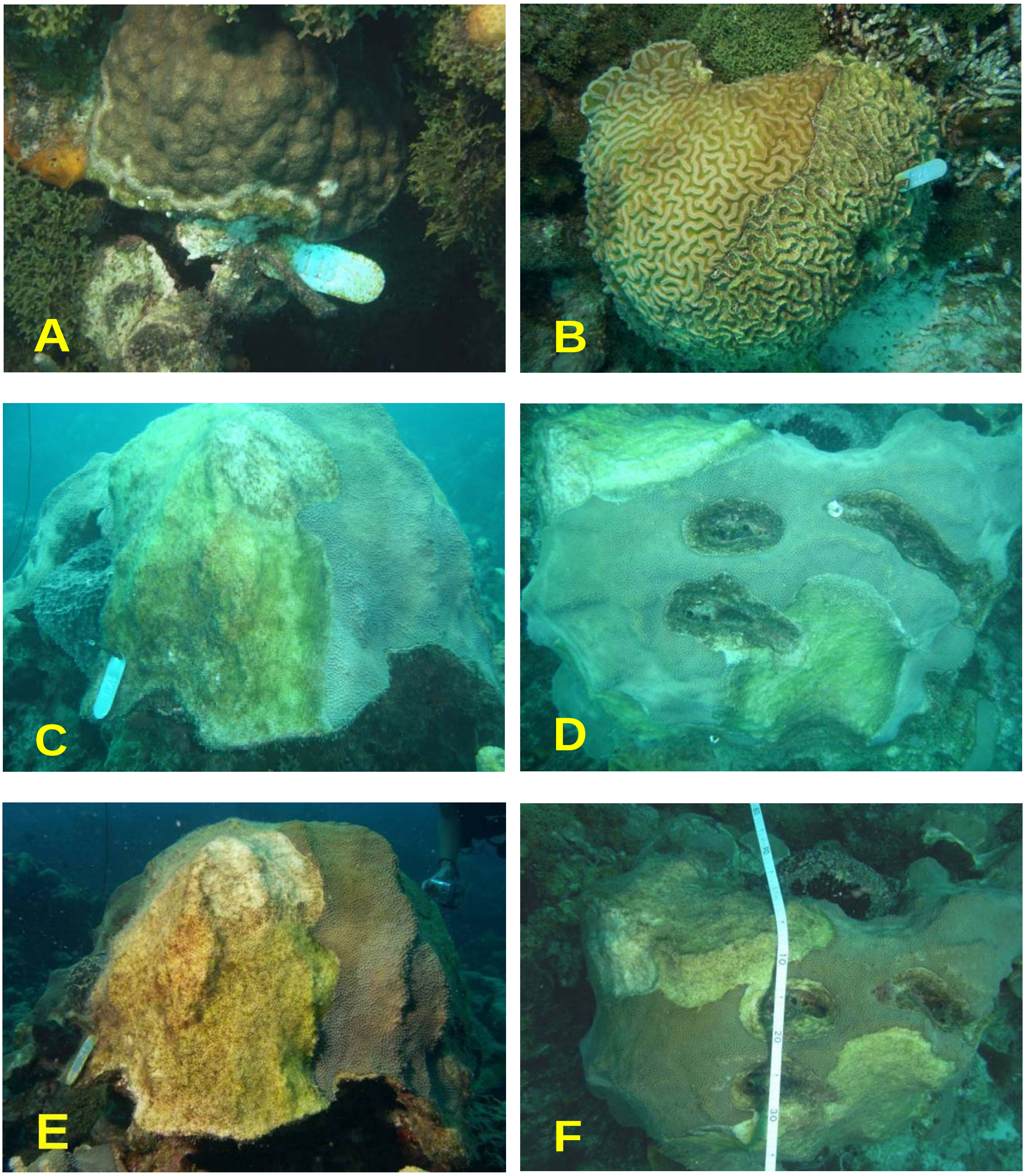

Figure 9 – Tagged coral colonies at Pointe Borgnesse. A = *Porites astreoides* showing signs of corallivore predation along the base, most likely predator is parrotfish. B = *Colpophyllia natans* showing signs of old disease and necrosis band, this band did not advance during the four week period between surveys. C = Side of *Montastrea faveolata* showing white plague symptoms in week 1. D = Same *Montastrea faveolata* from above during week 1. E-F = Same *Montastrea faveolata* colony taken after the four weeks, showing signs of white plague with an advancing band of necrosis acting on the upper and side faces of the colony.

4. Discussion

Despite accumulating knowledge of coral bleaching and mortality events (Burke et al. 2004; McClanahan et al. 2005; Schumacher et al. 2005; Jeffrey et al. 2006) there is still little known about the relationship between bleaching and mortality (Brown & Coles, 2003) or how they are causally linked (Harvell et al. 2001). Many studies to date have quantified bleaching prevalence and severity on coral reefs as an indicator of impact (Burke et al. 2004). There is much evidence to suggest that bleaching is not an impact in itself, but rather a sign of stress which may be overcome, with corals returning to their former health (Baker et al. 2001; Brown et al. 2002). Few studies have aimed to quantify bleaching-related mortality which is of greater significance ecologically and for management, and studies that do address this issue have largely focused upon quantifying dead tissue surfaces following thermal stress, attributing such mortality solely to bleaching (Burke et al. 2004; Schumacher et al. 2005). In this study, bleaching severity and species susceptibility has been directly linked to mortality following the bleaching event. It is essential to investigate such trends so that we can answer the question of whether bleaching is an advantageous response to environmental stress that is elicited to allow the coral to better cope with a fluctuating environment in the future (as stated in the adaptive bleaching hypothesis, Buddemeier & Fautin, 2004), or whether it is the reaction to stressful conditions that go beyond the tolerance threshold of corals and serves the purpose of removing damaged algal cells from the coral tissues.

Elevated sea water temperatures closely associated with coral bleaching events, and the 2005 Caribbean-wide event was no different. Temperatures were elevated to 1 degree Celsius above mean summer maxima for a period of 12 weeks in Martinique waters; this caused widespread bleaching on coral reefs, with many colonies experiencing total bleaching. During bleaching, a coral’s zooxanthellae density may be reduced by between 50-90% (Brown et al. 1995), with pigment loss noticeable to the human eye when zooxanthellae density is reduced 70-90% (Fitt et al. 2000). Thus, a bleached coral’s ability to exercise photoautotrophic metabolism is impaired and it cannot function optimally. Elevated water temperatures also cause physiological stresses other than bleaching which may lead to mortality if warm temperatures prevail for a prolonged period and may also favour the development of microbial pathogens in the water column (Harvell et al. 2002; Jones et al. 2004).

Although corals may begin to regain their pigmentation once temperatures have returned to normal, bleached corals are in a weakened state for an extended period following bleaching (Edmunds et al. 2003; Jones et al. 2004). This study shows that following the 2005 bleaching, a disease outbreak on southern Martinique reefs may be accelerating the rate of mortality among corals, thus the coral mortality since the bleaching was not caused by bleaching alone. It is likely that the synergistic effect of a stressed, susceptible host undergoing bleaching and an increase in the growth and reproduction of microbial pathogens during raised water temperatures elicited the disease outbreak which is exacerbating mortality rates.

4.1 Bleaching-related recovery and mortality

This study has demonstrated that over the three sites surveyed for the effects of bleaching in Martinique, bleached coral colonies generally showed a decline in health the following spring. Species which showed good recovery rates were *Madracis mirabilis, Meandrina meandrites*, and *Porites astreoides*. Species which showed high mortality rates were *Porites porites, Agaricia agarcites, Montastrea annularis* and *Montastrea faveolata*. Stimson et al. (2002) suggest that species with more tissue per square centimetre of coral surface show lower mortality rates, based on findings following the 1998 bleaching event in Okinawa. It is also suggested that species with higher densities of *Symbiodinium* and lower zooxanthellae release rates during bleaching exhibit low mortality. From outward appearance, species showing good recovery rates on Martinique reefs seem to have high tissue to surface area ratios, for example - the convoluted surfaces of *M.meandrites* and the pencil coral, *M.mirabilis*. Accordingly, the larger boulder corals, *Montastrea spp.* and the thin plate coral*, A.agaricites* have lower tissue to surface area ratios, thus they show poor recovery rates. However, although there is evidence of the coral host tissue determining bleaching susceptibility (Brown et al. 2002; Bhagooli & Hidaka, 2003) further examination of coral tissues beyond the scope of this study would be required to ascertain whether inter-specific differences in host tissues was a factor influencing bleaching susceptibility and recovery in Martinique.

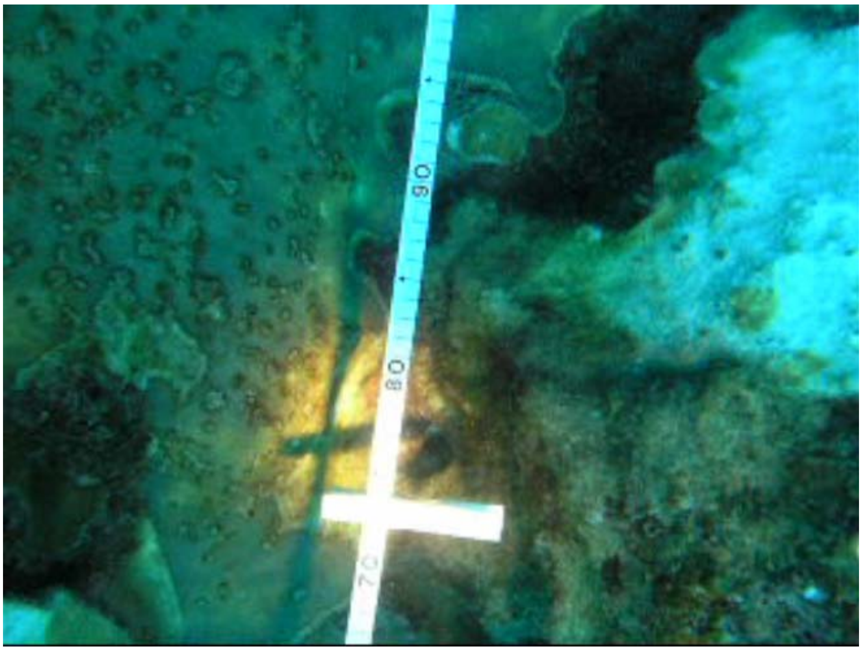

Figure 10 – Two separate colonies of *Montastrea faveolata* at Jardin Tropical. Right-hand colony is bleached and left-hand colony is healthy. This demonstrates high intra-specific bleaching susceptibility on the reefs surveyed. Macroalgal mat growth, most likely *Dictyota spp*. can be seen in the bottom right-hand corner.

There was also a high incidence of intra-specific variability in bleaching response and recovery between adjacent coral colonies belonging to the same species (for example - bleached and healthy colonies side by side – see figure 10). This suggests there is considerable genetic variation within the coral and *Symbiodinium* populations. There is increasing evidence that genetic variation in *Symbiodinium* "clades" (typed clade A- clade F) accounts for inter-specific bleaching susceptibility (McClanahan et al. 2005; Rowan et al. 1997; Baker et al. 2004; LaJeunesse et al. 2004; Lewis & Coffroth, 2004) and that by acquiring a novel population of *Symbiodinium* belonging to a more thermo-tolerant clade, bleached corals can actually acquire an adaptive fitness from bleaching in response to thermal stress (Baker, 2001; Buddemeier & Fautin, 1993).

Rowan et al. (1997) found that *Montastrea annularis* and *Montastrea faveolata* possess *Symbiodinium* of clades A, B and C with colonies dominated by clade B avoiding bleaching in response to elevated temperatures and colonies with high proportions of clade C exhibiting bleaching in 1995 on the Caribbean coast of Panama. Thus, it is postulated that clade B is heat-tolerant and clade C has a low heat-tolerance in Caribbean waters. Indeed, Toller et al. (2001) have shown that colonies of *Montastrea annularis* recovering after bleaching have down-regulated clade C *Symbiodinium* in favour of other clades. Thornhill et al. (2006) report that *Montastrea spp*. in the Caribbean have been found to possess clade D *Symbiodinium* (widely recognised as heat-tolerant – Baker et al. 2004; Rowan, 2004). Therefore, it is clear that there is much variation in *Symbiodinium* populations within *Montastrea annularis* and *Montastrea faveolata.* This may explain the variation in bleaching response and recovery success within these species and many others on the Martinique reefs.

The dominant coral species, *Montastrea annularis* and *Montastrea faveolata* were found to be the most susceptible to post-bleaching mortality (table 3). It has been repeatedly found that susceptible taxa are often dominant, such as *Acropora spp* and branching *Porites spp*. in the Indo-Pacific (McClanahan et al. 2004) with resultant large decreases in coral cover. It is possible that the loss of dominant *Montastrea spp.* colonies in Martinique may have repercussions for the reproductive potential of reefs and ultimately, their ability to replace lost coral cover over time to ensure reef degradation does not ensue (Baird & Marshall, 2002).

The “recent” mortality on Martinique reefs was estimated at approximately 13% in January (Lang et al. 2006), whereas it was lower by the April/May surveys at up to 7.43%. This is most likely due to rapid algal colonisation to form macroalgal mats during the interim period between surveys creating surfaces which were identified as “old” mortality in the April/May surveys that had been identified as “recent” in the January surveys. *Dictyota spp*. is very prolific on the Martinique reefs, colonising any bare surfaces on coral colonies and in some cases smothering live tissues. Furthermore, in situ observations indicated that most “recent” mortality on coral colonies was associated with diseased tissues and necrosis. Therefore, bleaching-related mortality may be undetectable by the time the study was undertaken and recent mortality was attributable to disease along with other mortality such as predation and smothering. This illustrates the necessity for regular monitoring of reefs affected by bleaching to distinguish the long term effects of discrete bleaching events by keeping track of mortality due to the bleaching and mortality attributable to other synergistic ecological and physical factors. The timescale and spatial extent of such factors is discussed in the conclusions where recommendations for reef monitoring are presented.

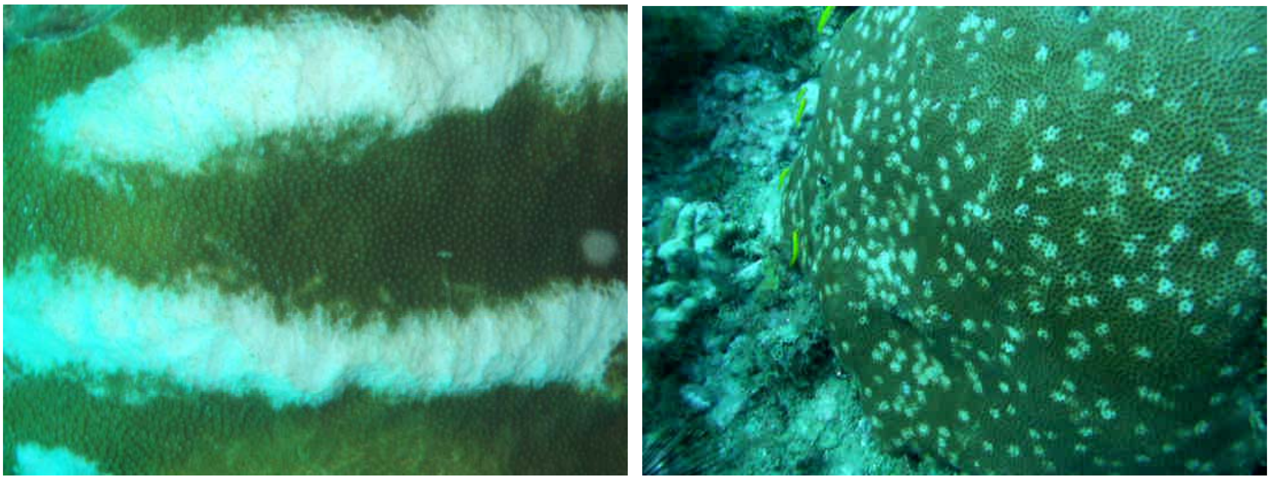

Figure 11 – Evidence of predation pressure on coral colonies following the bleaching season in Martinique. Left: *Montastrea faveolata* at Pointe Borgnesse with scars from parrotfish grazing. Right: *Siderastrea siderea* at Fondboucher showing scars which are likely from parrotfish “spot biting”. The short coral snail, *Coralliophila abbreviata* and the bearded fireworm, *Hermodice carunculata* are also prevalent corallivores on Martinique reefs.

It is thought that corals in high-flow environments display enhanced recovery rates following bleaching and otherwise susceptible species may avoid extensive bleaching (Nakamura & VanWoesik, 2001; Nakamura et al. 2005; Nakamura & Yamasaki, 2005), thus water-flow has been suggested as a mitigating factor for bleaching (Nakamura & Yamasaki, 2005) which may account for much of the intraspecies variability in bleaching and recovery seen on reefs. The most exposed site, Jardin Tropical on the southern bank reef showed the best recovery rates of the three sites studied and the lowest mortality (total dead surfaces) levels. This may be due to enhanced water-flow and other ecological factors such as high *Diadema antillarum* densities allowing competitive macroalgal species to be kept in check thereby enhancing the reefs potential to harbour new coral recruits and reducing the threat of smothering.

Another factor which may be influencing recovery rate discrepancies between the two sites is corallivore abundance. A No-Take area (NTA) was introduced in September, 1999 to the area surrounding Pointe Borgnesse, it was reopened to professional fisheries on April 1st 2006 for a period of 6 months. Thus, fish abundance and size has greatly increased recently at this site due to the absence of fishery pressures. Many targeted species are corallivores and were freed from top-down control by fisheries for two years, thus there are many scars from parrotfish predation on coral colonies at Pointe Borgnesse (figure 11). It is possible that reduced live tissue cover following the bleaching event has indirectly aided bioerosion rates due to fish grazing (Croquer et al. 2005) by placing more predation pressure on the surviving coral tissues, and consequently predation is contributing to mortality rates at both sites, in particular at Pointe Borgnesse, with observations suggesting *Montastrea annularis* is favoured by parrotfish.

4.2 Prevalence of disease following the 2005 bleaching event

This study deduced that the epizootic outbreak on the southern bank reef in Martinique was associated with signs of both white plague and yellow band disease in scleractinian corals. The disease prevalence over total coral colonies surveyed at the two sites was approximately 11%. In situ observations showed that white plague was causing the most tissue death. However, yellow band disease affected four species (*M.annularis, M.faveolata, P.porites, C.natans*), whereas white plague was found on only two species (*M.annularis* and *M.faveolata*). Recent studies of white plague prevalence on other Caribbean reefs have obtained different results, with *Dichocoenia stokesi* reported as most affected with white plague in the Florida Keys in 1995 and 1997 (Richardson et al. 1998), *Diploria clivosa* reported as most affected in Florida during 2001 and 2002 (Borger, 2005), and *Siderastrea siderea* reported as most affected in Dominica from 2000 to 2002 (Borger & Steiner, 2005). Thus, it is clear that coral susceptibility to epizootics can vary greatly both spatially and temporally (Borger, 2005).

Many authors stress the link between coral disease and temperature (Porter et al. 2001; Harvell et al. 2001; Jones et al. 2004; Rosenberg & Falkovitz, 2004). Alker et al (2001) showed that *Aspergillosis sydowii*, the causative agent of a Caribbean sea fan syndrome exhibits optimal growth at 30°C, which is above the thermal limit at which bleaching occurs. Harvell et al. (2001) postulate that high mortality rates in thermally stressed gorgonians, *Briarium asbestinum*, in the Florida Keys was caused by disease rather than directly via bleaching stress. It is believed that loss of zooxanthellae during bleaching weakened the host, increasing susceptibility to flourishing pathogen populations, thus the disease is an indirect effect on the coral, mediated through the coral bleaching response (Jones et al. (2004). Therefore it is likely that the epizootic in Martinique was a result of the elevated water temperatures of the 2005 summer which caused widespread coral bleaching and is acting as a secondary factor, exacerbating coral mortality rates following the bleaching.

It has been ascertained that white plague and yellow band disease show different epidemiological behaviours (Richardson et al. 1998) and that the loss of symbiotic zooxanthellae occurs via a different mechanism in corals suffering from diseases than in corals stressed from thermal bleaching (Cervino et al. 2004a). White plague type II is an area of great concern due to its rapid rate of tissue loss (Borger & Steiner, 2005), high virulence and spread rates, and wide host range (Richardson et al. 2001). It affects many dominant, slow-growing species (17 susceptible species have been recorded) so it may take a long time for reef recovery following an outbreak. It exhibits two 'types' – I and II. Type I is slower advancing, whereas type II has the ability to kill a small colony within a few days (Bruckner, 2002) with tissue death rates estimated at 2-3cm per day by Richardson et al. (1998) and almost 4 metres of living tissue loss in 12 months over 15 coral colonies was attributed to white plague-Type II by Croquer et al. (2005). As present, it is unclear which type is affecting Martinique reefs but long-term, frequent surveys of affected colonies may determine this in time.

A rod-shaped bacterium of the genus *Sphingomonas* has been identified as the main cause of white plague (Bruckner, 2002) with an Alphaproteobacteria - *Aurantimonas coralicida* recently identified as a possible cause in the Florida Keys (Denner et al. 2003). During infection the coral host tissues are attacked, this is different from yellow band disease, where the zooxanthellae cells are targeted within the gastrodermal tissues (Cervino et al. 2004a) - figure 12 illustrates some signs of zooxanthellae cell death associated with yellow band disease. Although zooxanthellae are thought to possess superior heat shock protein induction compared with their coral host tissues (Sharp et al. 1997), they are generally less heat-tolerant (Fitt et al. 1993; Cervino et al. 2004b). Virus-like particles (VLPs) have been noted in corals undergoing thermal bleaching (Wilson et al. 2001) and also in corals inoculated with yellow band disease (Cervino et al. 2004b). It is postulated that VLPs are inducted into coral tissues during elevated temperatures, thereby increasing the likelihood of thermally stressed corals developing yellow band disease (Cervino et al. 2004b). Corals, and in particular *Montastrea spp*. which have withstood thermal bleaching have been observed to succumb to yellow band infection with consequent colony death (Cervino et al. 2004b). It is probable that vulnerable, bleached corals in Martinique waters succumbed to infection by yellow band disease as a result of their impaired defensive responses, and will suffer high mortality rates.

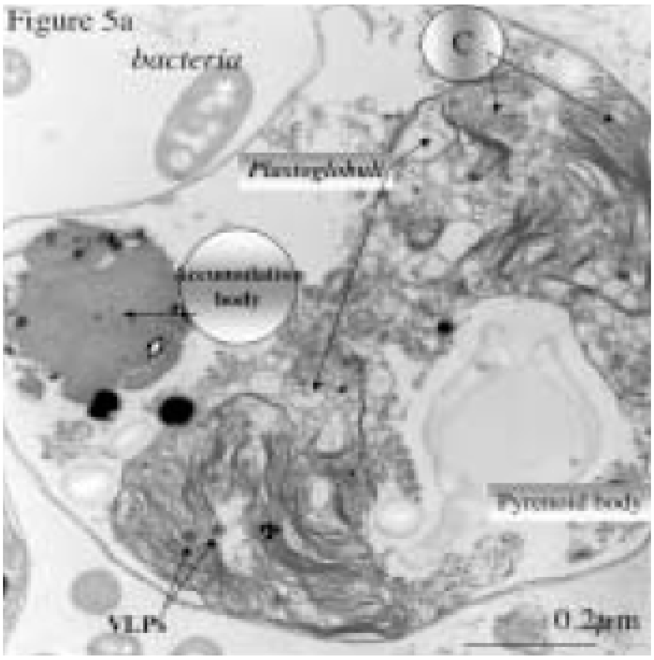

Figure 12 – Transmission electron micrograph image of *Symbiodinium* cell exposed to yellow band bacteria. Cell wall is degraded and cell is exhibiting vacuolation and cytoplasmic shrinkage. Chloroplasts have moved to the circumference of the cell with accumulation body swelling and fragmented pyrenoid body. C = chloroplasts. From Cervino et al. (2004a).

Observations of the tagged coral colonies displaying signs of disease lesions suggest that the current white plague-like epizootic in Martinique exhibits rapid progression rates. Of the 6 colonies tagged, four showed no extension of the necrosis band over a four week period. This is most likely due to cessation of the disease spread suggesting that the disease outbreak may be short-lived. One colony showing signs of white plague suffered extensive necrosis over the four week period (Figure 9) with approximately 5% of the total colony surface becoming necrosed in this period. Given such rates of advancement, it is likely the current epizootic on southern reefs of Martinique is a type-II-like white plague outbreak, with the potential to kill entire coral colonies while it is active. However, due to the fact that a low number of colonies tagged showed disease progression (1 out of 6) it is possible that the disease is entering quiescence and may not spread further on the reefs. Therefore, prospects for recovery following the epizootic disturbance are reasonable.

This study resolved that disease prevalence was higher on larger sized coral colonies at the southern bank reef of Martinique. Smaller coral colonies have been noted for displaying resistance to natural disturbances such as bleaching. Shenkar et al. (2005) showed that the Mediterranean coral, *Oculina patagonica* avoided bleaching where the colony was small with high bleaching-related mortality causing a shift in individual colony size throughout the population towards smaller colonies. It may that smaller colonies are able to place more energy reserves towards defence mechanisms such as anti-oxidative pathways as they do not have to place energy towards reproductive output. However, Bythell et al. (1993) studied chronic factors and hurricane impact on coral size-distributions in the U.S Virgin Islands. It was determined that the probability of being damaged by chronic factors – such as disease and bleaching increases with colony size, but the likelihood of the damage resulting in whole colony mortality decreases with size. Thus, it is likely that small colonies which were affected with disease and were killed were not included in the surveys and so were missed out, so it appears that disease favours larger sized colonies.

The *Diadema antillarum* density at Pointe Borgnesse was considerably lower than at Jardin Tropical on the southern bank reef. White plague-like disease was first observed at Pointe Borgnesse in early spring 2006, and it is possible that macroalgal mats, not held in check by urchin grazing may have harboured disease-causing pathogens. Nugues et al. (2004) found that *M.faveolata* colonies exposed to the macroalgae *Halimeda optunia* developed signs of white plague-type II, with the known bacterium, *Aurantimonas coralicida* identified as the causative agent of the disease. It is possible that macroalgae may act as reservoirs for disease-causing pathogens. Thus, proliferation of competitive macroalgae through a lack of top-down control by herbivores or eutrophication from river run-off (Bruno et al. 2003) at Pointe Borgnesse may have allowed pathogen densities to thrive, leading to the disease outbreak.

AGRRA surveys in the British Virgin Islands in January, 2006 established that there was a white plague-like epizootic on several southern reef sites (J.Lang – personal communication) and reefs of Dominica, to the immediate north of Martinique have been recorded showing epizootic signs in the past few years (Borger, 2005; Borger & Steiner, 2005). It is possible that pathogen spread occurred following prevailing currents southwards to Martinique as has been postulated for separate epizootics elsewhere (Bruckner & Bruckner, 1997). However, this is unlikely as disease appears to be localised on the southern reef sites so it is unlikely that pathogens have been carried from the north to the southern Martinique reef alone. It is far more probable that land-based factors such as agricultural contamination and river runoff and the presence of the La Marin marina provide stressors to corals rendering them susceptible to disease infection.

Conclusions

The reefs of Martinique are showing many signs of recovery following the 2005 Caribbean-wide bleaching event, with many species showing tolerance to thermal stress by regaining full health by the following spring (*M.mirabilis, P.astreoides, C.natans*). However, there is also a considerable level of recent mortality since the thermal bleaching event. From observations of individual coral colonies it is clear that bleaching does not confer a fitness value to corals as many species have been depleted as they failed to recover from bleaching or succumbed to secondary stresses such as epizootic presence. The disease outbreak involving white plague and yellow band disease appears to be exacerbating mortality rates as weakened coral hosts undergoing bleaching and recovery were susceptible to infection by microbial pathogens thriving during the elevated water temperatures.

This study demonstrates the necessity of frequent monitoring of bleached reef sites to ensure that synergistic disturbances such as disease outbreaks do not go unnoticed. If the extent of the bleaching event was quantified using an infrequent surveying program, the mortality due to epizootic presence may have been attributed solely to bleaching. This would miss out issues pertaining to epizootic presence which may be associated with human-induced stress that must be addressed to maintain the reefs in good health. Although bleaching events are visible for weeks to months on coral reefs, they act at far larger time scales and leave a legacy on the reef ecosystem long after the signs of bleaching have receded. Decreased coral cover, epidemic disease outbreak, intensified predation pressure on surviving corals and increased susceptibility to collapse following storm damage may all ensue a coral bleaching season. It may be impossible to shelter coral reefs from large-scale disturbances such as elevated seawater temperatures due to global warming, but by acting on factors which can be addressed by management on a smaller scale it may be possible to ameliorate the aftermath of coral bleaching.

During coral bleaching and recovery from thermal stress, it may be necessary to monitor affected reef ecosystems on a regular basis to determine whether management measures are required to maximise the reef resilience (Nystrom et al. 2000). Predation on coral tissues can fluctuate considerably at a scale of hours to days, whereas signs of disease outbreak may take months to become detectable from a monitoring perspective (Nystrom et al. 2000). Therefore, it is important to conduct quarterly, multi-year surveys of susceptible sites, increasing monitoring frequency during periods of heightened stress such as thermal bleaching events. In the case of Martinique, the future resilience of its coral reefs will depend on careful fisheries management and the assessment natural herbivorous control of macroalgae, and the implementation of intervention techniques to control algal dominance where necessary.

In the face of predicted climate change and increasing frequency and severity of bleaching events, Martinique reefs may experience a decreased dominance of *Montastrea annularis* and *Montastrea faveolata* which offer much of the topographical relief on the reefs and greatly enhance the niche space of the entire reef ecosystem for other trophic levels. Therefore, management efforts should focus on reef areas rich in susceptible, dominant *Montastrea spp*. and afford them high protection from controllable sources of stress and mortality such as river contaminants, eutrophication, and excessive fishing. There is currently scoping work being conducted in Martinique to assess the feasibility of designating the coral-rich southern bank reef site as a Marine protected area (MPA). This study has shown that these high coral cover reefs are susceptible to thermal stresses and are currently coping with a disease outbreak. Therefore, it is paramount that protection measures are put in place to afford the reefs the best chances of coping with and surviving through future thermal bleaching events.

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