THE ROLE OF COLONY SIZE IN THE RESISTANCE AND TOLERANCE OF SCLERACTINIAN CORALS TO BLEACHING CAUSED BY THERMAL STRESS

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ABSTRACT

In 2005 and 2010, high sea surface temperatures caused widespread coral bleaching on Jamaica's north coast reefs. Three shallow (9m) reef sites were surveyed during each event to quantify the prevalence and intensity of coral bleaching. In October 2005, 29-57% of the colonies surveyed were bleached. By April 2006, 10% of the corals remained pale/partially bleached. Similarly, in October 2010, 23-51% of corals surveyed at the same sites were bleached. By April 2011, 12% of the colonies remained pale/partially bleached. Follow-up surveys revealed low coral mortality following both events, with an overall mean of 4% partial colony mortality across all species and sites observed in April 2006, and 2% in April 2011. Mixed effects models were used to quantify the relationship between colony size and (a) bleaching intensity, and (b) bleaching related mortality among coral species. The bleaching intensity model explained 51% of the variance in the bleaching response observed during the two events. Of this 51%, fixed effects accounted for ~26% of the variance, 17% of which was attributed to species-specific susceptibility to bleaching , 5% to colony size, <1% colony morphology and 4% to the difference in bleaching intensity between the two events. The random factor (site) accounted for the remaining ~25% of the variance. The mortality model explained 16% of the variance in post bleaching mortality with fixed effects, including colony size, morphology and species explaining ~11% of the variance, and the random effect (site) explaining 5%. On average, there was a twofold difference in bleaching intensity between the smallest and the largest size classes. Modelling the relationship between colony level characteristics and site-specific environmental factors on coral species' susceptibility to thermal stress can shed light on community level responses to future disturbances.

RÉSUMÉ

En 2005 et 2010, l'élévation des températures de surface a entraîné un blanchiment à grande échelle des récifs coralliens de la côte nord de la Jamaïque. Trois de ces récifs peu profonds (9m) ont fait l'objet d'une étude visant à quantifier l'étendue et l'intensité du blanchiment. En octobre 2005, 29-57% des colonies étudiées étaient blanchies. Cinq mois plus tard, 10% des coraux restaient pâles ou partiellement blanchis. En octobre 2010, 25-51% des colonies étaient blanchies et, cinq mois plus tard, 12% d'entre elles restaient pâles ou partiellement blanchies. Les levés subséquents de ces sites d'étude ont révélé un taux réduit de mortalité, avec un taux moyen de 4% de mortalité partielle sur l'ensemble des colonies en avril 2006, et de 2% en avril 2011. Une modélisation à effets mixtes a été choisie pour analyser la relation entre la taille d'une colonie et : a) son degré de blanchiment et b) son taux de mortalité, et ce pour l'ensemble des espèces présentes. Le modèle du degré de blanchiment explique 51% de la variance dans la réponse au blanchiment entre les deux épisodes. De ces 51%, les effets fixes expliquent ~26% de la variance de la réponse au blanchiment, dont : 17% attribuables à la particularité de l'espèce, 5% à la taille de la colonie, <1% à la morphologie et 4% à la différence d'élévation thermique entre les deux événements. 25% de la variance est attribuable au facteur aléatoire, soit le site même du levé. Le modèle de mortalité explique 16% de la variance de mortalité post-blanchiment, tandis que les effets fixes (espèce, taille et morphologie des colonies) représentent ~11% de la variance et le facteur aléatoire (site) 5%. Le degré de blanchiment des colonies était deux fois plus élevé dans les colonies plus massives comparé à celui des colonies de taille plus menue. La modélisation de la relation entre les caractéristiques d'une colonie corallienne et sa sensibilité au stress thermique devrait permettre de mieux mesurer l'impact de futures perturbations thermiques.

1 GENERAL INTRODUCTION

Coral reefs, frequently referred to as rainforests of the sea (Davidson 1998), are among the most biologically diverse and economically valuable ecosystems on the planet. Most of the coral reef systems are found in the tropical waters, between 30°N and 30°S of the equator, where they fringe coastal areas or form offshore barrier reefs and atolls (Veron 2000). Coral reefs cover less than 1% of the ocean floor, yet support 25% of all marine species, including more than 4,000 species of fish and 800 hard coral species (Paulay 1997; Spalding et al. 2001). Along with biodiversity, coral reefs also provide invaluable ecosystem services at local and global scales including coral reef fisheries, coastal protection, and tourism. In 2010 the annual benefits from corals reefs for the Caribbean region alone were estimated at US $395 million for coral reef fisheries, up to US $2.8 billion for shoreline protection, and US $2.7 billion from tourism (Burke et al. 2011). Coral reefs have endured millennia of natural change, however, the unprecedented loss of coral cover and coral diversity over the last century give rise for concern (Hughes et al. 2003).

Seventy-five percent of world's coral reefs are estimated to be under direct threat from a combination of natural and anthropogenic factors (Burke et al. 2011). The main threats to coral reefs include: (1) overfishing and destructive fishing practices, (2) overdevelopment of coastal areas and the resulting habitat destruction / fragmentation, (3) watershed and marine based pollution, (4) disease and (5) climate change. In 2008, the International Union for Conservation of Nature listed 27% of reef-building corals, including the two critically endangered Caribbean *Acropora* species, to the Red List of Threatened Species. According to The Status of Coral Reefs of the World (Wilkinson 2008), approximately 20% of reefs have been destroyed, 35% are threatened or at a critical stage, and the remaining healthy reefs are under impending threat of climate change. Climate change has been linked to increase in coral diseases (Ruiz-Moreno et al. 2012), and reduced coral calcification due to ocean acidification (Hoegh-Guldberg et al. 2007). However, the main climate-related threat to coral reefs is coral bleaching caused by the heat-induced disruption of the symbiotic relationship between corals and their algal endosymbionts (Coles and Brown 2003; Eakin et al. 2009).

In order to evaluate the impact of high temperatures on corals, it is necessary to understand the fundamental nature of hermatypic corals. Scleractinian corals (Phylum: Cnidaria, Class: Anthozoa, Order: Scleractinia) are considered the foundation species of coral reefs because they generate raw material for the reef framework, and provide the three dimensional complexity that underlies the niche diversity of coral communities (Hoegh-Guldberg 2011). This diverse group of hermatypic or stony corals differs from other members of the Class Anthozoa because they secrete hard aragonite exoskeletons (i.e. crystaline calcium carbonate, $CaCO_3$) that serve as building blocks of reef ecosystems (reviewed by Harrison in Dubinsky and Stambler 2011).

Hermatypic corals form a symbiotic relationship (obligate mutualism) with unicellular algae of the genus *Symbiodinium* (Class: Dinophyceae), commonly referred to as zooxanthellae. Zooxanthellae are photosynthetically active and transfer up to 90% of the photosynthate to the coral host (Muscatine et al. 1984), thus playing a vital role in the light enhanced calcification of scleractinian corals (Barnes and Chalker 1990). In exchange, the coral host provides shelter, nutrients (e.g. nitrogenous wastes) and an ideal environment for photosynthesis (Pearse and Muscatine 1971). Once considered to be a single species, *Symbiodinium microadriaticum* (Freudenthal 1962), the genus *Symbiodinium* is divided into eight phylogenetic clades (A-H), each of which is further subdivided into subclades (LaJeunesse 2001). Coral-zooxanthellae associations are highly intricate with algal endosymbionts contributing significantly to physiological attributes and the overall fitness of the coral holobiont (Little et al. 2004). The ‘photosymbiosis’ between coral hosts and zooxanthellae has been essential to the successful evolution and proliferation of zooxanthellate scleractinians in oligotrophic tropical seas (Stanley Jr. and Schootbrugge 2009); anything that disturbs this association can be detrimental to the coral colony.

Bleaching is a stress response characterized by the disruption of the coral-algal symbiosis due either to the degradation of algal pigments or to partial or complete expulsion of zooxanthellae from the coral host (Douglas 2003). Various mechanisms of zooxanthellae expulsion from corals have been reported, including exocytosis, apoptosis (or programmed cell death), necrosis, and host detachment (Coles and Brown 2003). Zooxanthellae contain chlorophyll a and carotenoids, in particular the peridinins, which give corals their brown colour. Once the zooxanthellae are expelled, the tissue of the coral host becomes translucent with the white calcium carbonate skeleton visible, giving the coral its bleached appearance (Jones et al. 1998).

Bleaching can occur in response to various stressors including sedimentation (Rogers 1990), changes in salinity (Goreau 1964), cold sea water temperatures (Glynn and D’Croz 1990), and land-based sources of pollution (Keller et al. 2009). However, bleaching has been most frequently associated with elevated sea temperatures (Hoegh-Guldberg and Smith 1989) and high solar radiation (Sandeman 1988).

Elevated sea surface temperatures (SST) alone, or in combination with excessive solar irradiance can cause photoinhibition or light-induced reduction of photosynthetic capacity in zooxanthellae (Hoegh-Guldberg and Smith 1989; Gleason and Wellington 1993). Photoinhibition occurs in response to the reduction in photosynthetic electron transport, combined with the continued high absorption of excitation energy leading to damage at photosystem II (PSII) reaction centers (Long et al. 1994). In the bleached symbiosis, the algal cells are metabolically compromised, with a diminished capacity to provide the animal with photosynthetic carbon (Perez et al. 2001).

When temperatures exceed a certain threshold, light levels exacerbate the damage caused by thermal stress resulting in the production of reactive oxygen radicals that damage cellular structures (Jones et al. 1998). The production of reactive oxygen species (ROS) causes the host to expel the zooxanthellae through detachment of host cells with the complement of zooxanthellae (Sandeman 2006). Because of the low tolerance of the photosynthetic processes to high temperatures, even normal levels of sunlight are enough to damage the photosynthetic system of the zooxanthellae (Coles and Brown 2003). The relationship between temperature and light in causing coral bleaching explains why bleaching is frequently lower on shaded parts of the colonies or shaded reef areas (Hoegh-Guldberg 1999; Baird and Marshall 2002). At the reefscape level, the bleaching responses may be influenced by factors such as cloud cover (Mumby et al. 2001), shading from nearby landforms, and natural variations in turbidity that influence the amount of light to which corals are exposed (Marshall and Schuttenberg 2006).

While small scale bleaching occurs in response to local stressors (Oliver et al. 2009; Burke et al. 2011), large-scale bleaching events are associated with periods of exceptionally warm sea surface temperatures (SST), coupled with high solar radiation and calm ("doldrums") weather conditions (Hoegh-Guldberg 2011). Past global bleaching events have coincided with El Niño Southern Oscillation (ENSO) suggesting that large-scale bleaching cycles are caused by the combination of increased seawater temperatures due to anthropogenic climate change (Eakin et al. 2010), compounded by cyclic warming events such as ENSO and seasonal warming (Williams and Bunkley-Williams 1990). In the last three decades mass bleaching events have affected coral reefs globally (Oliver et al. 2009; Burke et al. 2011).

In the Caribbean, mass bleaching events were documented in 1982/3 (Jaap 1985), 1987/88, 1990 (Williams and Bunkley-Williams 1988; Lang et al.1992; Fitt and Warner 1995), 1995/6 (Woodley et al. 1997) and 1997/98 (Kramer and Kramer 2000) - each with increasing severity (Goreau 1990; Goreau et al. 2000) and variable mortality (Miller et al. 2006). Although bleaching due to thermal anomalies is not the only cause of reef decline in the Caribbean (Hughes 1994), the increased frequency and intensity of these large-scale, temperature-induced bleaching events since the 1980s (Goreau and Hayes 1994) presents a serious threat to coral reefs throughout the basin (Obura and Grimsditch 2009).

Coral bleaching is detrimental to coral health (Douglas 2003). Immediate effects of thermal stress on the coral host include reduction in zooxanthellae densities, loss of chlorophyll pigments, increase in respiration rate and declines in coral proteins, lipids and carbohydrates (Glynn 1993). Delayed, non-lethal effects of bleaching include diminished rates of skeletal growth, calcification and tissue regeneration (Meesters and Bak 1993; Mendes and Woodley 2002), impaired reproduction (Szmant and Gassman 1990), and decreased resistance to disease

(Lesser 2007). The overall reduction in coral fitness due to bleaching can lead to delayed mortality, and to subsequent decrease in coral abundance and diversity (Loya et al. 2001). Reduced growth rates can aggravate any injurious processes already underway, and decrease the capacity of corals to compete favorably for space with other reef benthos like macroalgae and sponges. The diminished capacity of bleached corals to reproduce has negative impacts on coral recruitment rates in the year following the bleaching event (Glynn and D'Croz 1990; Szmant and Gassman 1990). Bleached colonies can regain their pre-bleaching symbiont densities after mild bleaching episodes, as temperatures return to their normal seasonal values (Szmant and Gassman 1990). Widespread and prolonged bleaching, however, can result in extensive coral mortality and even lead local extinction or extirpation of thermally susceptible species (Glynn and D'Croz 1990; Glynn 1996).

Bleaching is highly variable at the colony and community level because corals differ in their response to thermal stress between species, between bleaching events and between locations. Variation in the bleaching response between species and within species can be attributed to (1) differences in host specific traits including tissue thickness, size and morphology (Siebeck et al. 2006), (2) presence of genetically different types of zooxanthellae with different host-specific environmental tolerances (van Oppen et al. 2009), or (3) coexistence of diverse symbionts (clades) within a host (Rowan et al. 1997).

At the reefscape level, physical factors including local currents, bathymetry (Glynn and D'Croz 1990; van Woesik 2001), water quality (Miller et al. 2011), depth (Lang et al. 1988), the three-dimensional complexity of the habitat, and weather conditions can act synergistically to influence coral susceptibility to thermal stress and high irradiance (Brown 1997). Given that bleaching events are highly variable in duration and in magnitude, and that coral assemblage responses are variable, research efforts today are focused on identifying factors and attributes that contribute to the resistance and tolerance of corals to thermal stress.

The most common metrics used to describe and to quantify the impact of thermal stress are percent of corals, or percent of coral cover bleached, and percent of recent mortality. Other metrics (which may span across scales) that are of interest include differential survivorship among species, identification of resistant assemblages or sites, and environmental factors which can explain site specific patterns of bleaching and bleaching avoidance (Spalding 2009). Follow-up surveys are used to assess recovery (tolerance), bleaching related mortality and the persistence of bleaching among certain coral species (Lang et al. 1992). Analyzing these metrics across different reef sites can differentiate patterns of impact and survival within and among sites, and identify areas which may serve as refugia or areas of adaptation and recovery.

Bleaching patterns at the colony level may indicate variable exposure to environmental factors. Variability in bleaching among different colony size classes can provide insight into the immediate impacts of thermal stress by identifying susceptible species and size-classes; this information can be used to infer potential impacts of frequent bleaching events on population dynamics of coral assemblages, including shifts in species dominance or changes in the size frequency distribution of corals (Obura and Grimsditch 2009). In some systems bleaching was more prevalent among larger colony sizes (Brandt 2009), while in other systems smaller corals appeared to be more susceptible (Obura 2001). Some authors claim that there is no relationship between coral colony size and bleaching sensitivity (Ortiz et al. 2009). Other authors, however, predict that an increase in the frequency of bleaching events will likely result in shifts in dominance from branching to massive corals, with a co-occurant loss of coral abundance and diversity (Loya et al. 2001; West and Salm 2003; Brandt 2009) as well as loss of structural complexity (Aronson et al. 2002).

High SSTs and high irradiance cause oxidative stress (Sandeman 1988, 1999) resulting in the accumulation of damaging superoxides and other oxygen radicals in coral tissues (Jones et al. 1998; Downs et al. 2002). Therefore, the capacity of corals to efficiently remove metabolic toxins, superoxides and free radicals may allow colonies to survive or recover from the stress. At the colony level the hydrodynamics of flow over complex surfaces determine mass transfer (Monismith 2007). Flow-mediated mass transfer describes the uptake of nutrients by corals and may also play a role in how corals respond to thermal stress (Nakamura and van Woesik 2001). Given the geometric complexity of corals, the surface-to-volume ratio determines the amount of surface area across which mass transfer can occur (Falter et al. 2005). Nakamura and van Woesik (2001) examined the theoretical relationship between mass transfer, colony size and water velocity as a possible mechanism for size-specific differential in bleaching responses among coral colonies. They found that mass transfer was greater for small colonies and as such, small coral colonies would be more likely to withstand thermal and irradiation stress than large coral colonies.

In this study, the relationship between colony size and intensity of the bleaching response was investigated to determine if colony level characteristics such as size and morphology could be used to help model susceptibility of coral species to thermal stress. Colony size was selected as a variable since many colony-level processes (e.g. growth, reproductive capacity) are related to colony size rather than age (Hughes 1984). Disruptions of these processes can have direct implications for long term health of coral communities affected by bleaching events.

2 The Role of Colony Size in the Resistance and Tolerance of Scleractinian Corals to Bleaching Caused by Thermal Stress

2.1 Introduction

Climate change, rising sea temperatures and the resulting mass bleaching events are recognized as the greatest threats to coral reefs globally (Obura and Grimsditch 2009). Coral bleaching is a stress response characterised by the disruption of the symbiosis between a coral host and its endosymbiotic algae or zooxanthellae (*Symbiodinium* sp.). Coral bleaching can be triggered by various environmental stressors, but is primarily associated with unusually high sea-surface temperatures (Hoegh-Guldberg 1999) and increased solar radiation (Lesser and Shick 1990). Since the 1980s the frequency of large-scale bleaching events has been on the rise (Goreau and Hayes 2005). Changes in global weather patterns and increased sea surface temperatures (SST) are leading to dire predictions that bleaching events will become chronic disturbances (Hoegh-Guldberg et al. 2007; Wilkinson and Souter 2008).

Coral bleaching can result in reduced skeletal growth and reproductive output (Szmant and Gassman 1990; Mendes and Woodley 2002), decreased resistance to disease (Lesser 2007) as well as loss of abundance and diversity (Loya et al. 2001). The severity of bleaching impacts is highly variable because corals differ in their response to thermal stress among species, bleaching events and regions. Corals depend on zooxanthellae for up to 95% of their energy and face starvation once they are bleached. As sea temperatures return to more seasonal values, bleached corals which have survived thermal stress have the capacity to gradually repopulate their tissues with zooxanthellae and recover (Szmant and Gassman 1990). Bleached corals may regain their symbionts through uptake of new cells from the water column, or more likely, through the proliferation of surviving zooxanthellae that remain in the bleached coral's tissues at very low levels (Hoegh-Guldberg et al. 1987). Prolonged exposure to thermal stress, however, can lead to extensive mortality resulting in species and phase shifts, which can alter the composition and the function of reef communities (Gardner et al. 2003). Where bleaching related mortality is high, physical and biological erosion can then break down the three-dimensional reef framework, impeding community recovery. In such cases, it may take decades to restore former levels of coral cover, species diversity and topographic relief, if at all (Baker et al. 2008).

Given that bleaching events are highly variable in duration and magnitude, and that coral assemblage responses are therefore variable, research efforts today are focused on identifying the factors and attributes that contribute to the resistance and tolerance of corals to thermal stress. Resistance is the ability of individual corals to endure thermal stress without bleaching, while tolerance is the ability of corals to survive once bleached (West and Salm 2003). Resistance to thermal bleaching, coral tolerance and reef recovery determine whether a system is resilient and can recover from impacts of a disturbance without changing its core functions and services (Carpenter et al. 2001; Nyström et al. 2008).

Quantifying resistance and tolerance requires the use of indicators. Bleaching indices, coral cover, diversity indices and relative abundance (evenness) are common measures used to estimate coral resistance and tolerance (Nyström et al. 2008). These indicators, however, provide limited information on the relative contribution of individual species to the observed community patterns. Coral size-frequency distributions, on the other hand, convey demographic information ranging from individual colony growth to population dynamics, including recruitment and mortality (partial/total) (Bak and Meesters 1998). Colony size data provide insight into population responses to environmental changes or past events, and may therefore, allow prediction of population dynamics following a disturbance (Crabbe 2009).

The role of colony size in the response of corals to thermal stress is key to understanding and predicting the potential impacts of recurring bleaching events on population dynamics of coral assemblages (Obura and Grimsditch 2009). Variable observations have been made with respect to colony size and bleaching sensitivity. In some studies bleaching is more prevalent among larger colony sizes (Brandt 2009), in others smaller corals appear to be more susceptible (Obura 2001), and yet in others there appears to be no relationship between coral colony size and bleaching sensitivity (Ortiz et al. 2009). The precise combination of factors and mechanisms underlying the variable bleaching responses remain elusive. Some authors predict, however, that an increase in the frequency of bleaching events will likely result in shifts in dominance from branching to massive coral, loss of coral abundance and diversity (Loya et al. 2001; West and Salm 2003) as well as loss of structural complexity due to reduced vertical accretion of skeletal carbonates (Aronson et al. 2002).

Nakamura and van Woesik (2001) examined the theoretical relationship between mass transfer, colony size and water velocity as a possible mechanism for size-specific differential in bleaching responses among coral colonies. The interaction of photosynthetically active radiation (PAR), UV radiation and temperature (SSTs) can cause an accumulation of damaging superoxides and other oxygen radicals in coral tissues which can lead to photoinhibition in zooxanthellae, and to subsequent bleaching of the host (Lesser 1997; Sandeman 2006). Higher water flow rates decrease the likelihood of bleaching by increasing mass transfer of oxygen radicals and their derivatives from coral tissue, thus averting the accumulation of these deleterious compounds in thermally stressed colonies. Based on Newton's law of viscosity and Reynold's number which incorporates the dimensional characteristics of the colony, Nakamura and van Woesik (2001) demonstrated that mass transfer, within a certain surface area, was greater for small colonies than for large colonies. According to the mass transfer model, small coral colonies would be at an advantage during periods of thermal and irradiation stress.

Specific objectives of this study were to (1) quantify and compare bleaching prevalence (percent of colonies bleached) and intensity (percent of colony bleached) during the 2005 and 2010 bleaching events on three reefs located on Jamaica's north coast, and (2) to examine the relationship between colony size, morphology, and species across these two bleaching events, by testing (*in-situ*) the prediction based on the mass transfer model, (Nakamura and van Woesik 2001) that bleaching due to thermal stress is positively related to colony size.

2.2 Methodology

2.2.1 Bleaching surveys

Quantitative surveys of coral bleaching were conducted in 2005/06 and 2010/11 on three reefs near Discovery Bay, Jamaica (Figure 2.2.1, Table 2.2.1). The timing of the surveys corresponded to the estimated peak of each bleaching event, when sea surface temperatures were at their highest (September/October 2005 and 2010), in order to capture the maximum bleaching response, and approximately five months following the onset of bleaching (March/April 2006 and 2011) to assess the recovery from bleaching, and to quantify bleaching-related mortality.

Five to ten randomly placed 10 m^2 transects (CARICOMP 2001) were surveyed and photographed at each site in 2005, 2006, 2010 and 2011. Phototransects were obtained by taking non-overlapping photographs (photoquadrats) along the length of the transect while maintaining a camera-to substrate distance of 1m, to generate ~ 70 x 80 cm photoquadrats of the substrate. Each transect comprised approximately 20 photoquadrats. Corals were photographed perpendicular to the main growth axis of the colony, with a reference scale included in the frame for image scaling/calibration. Transects were photographed with a Canon EOS 20D, 8 megapixel digital SLR camera set in an Ikelite housing, and equipped with an external flash to ensure consistent illumination in the images.

2.2.2 Study Sites

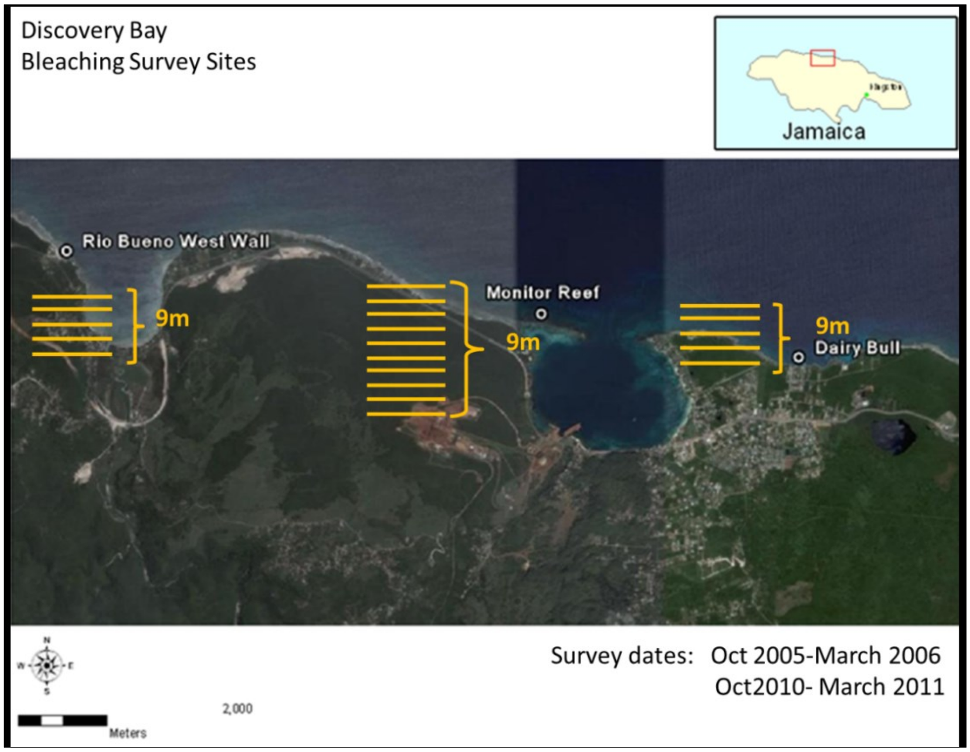
1. Monitor Reef is part of the classic spur and groove reef system located on Discovery Bay's West Fore Reef (WFR), (18.472897°N; -77.413928°W). The vertical profile, zonation and substrate composition of the reef have been extensively documented (Goreau 1959; Goreau and Goreau 1973; Liddell and Ohlhorst 1981, 1987; Cho 2004; Gayle 2009). Monitor Reef is comprised of a reef flat that gives way to an *Acropora palmata* rubble zone, *Diadema* zone, mixed zone, *Acropora cervicornis* rubble zone and a fore reef escarpment (Cho 2004). Coral cover at 9 m was approximately 12% (Table A.4).

2. Dairy Bull reef is located 2.5 km east of Discovery Bay (18.468055°N, -77.388441° W). The terrace is approximately 300 m long and 100 m wide supporting a healthy coral community (Idjadi et al. 2006). Dairy Bull faces a steep rocky shore that maintains relatively high bi-directional wave surge in all but the calmest of weather conditions. Coral cover at 9 m was 27% (Table A.4).

3. The West wall at Rio Bueno site is located on the outer edge of the Rio Bueno embayment (18.479451°N; -77.460042°W). The area is characterized by low level riverine input which contributes to fluctuating salinity levels (0-3m depth) and periodic sediment plumes (Mallela et al. 2004). In 2005/2006, coral cover along the wall at 9 m was approximately 20%, and increased to 28% in 2011 (Table A.4).

Table 2.2.1 Summary of the survey protocol. Random phototransects (1m x 10m) were used to quantify bleaching along the 9m depth contour at three reef sites. Temperature loggers were deployed at each site. Bleaching prevalence (% colonies bleached) was quantified for each reef. Bleaching intensity (% of colony surface area bleached, cm^2) was measured for colonies encountered along transects.

Latitude (N)	Longitude (W)	Reef Site	Survey Year	Reef Type	Reef Slope	Depth (m)	Transects (#)	Transect length (m)	Total area surveyed (m^2)
18.472897°	-77.413928°	MONITOR REEF	2005	Fringing Reef	Gentle	9	10	10	100
18.472897°	-77.413928°	MONITOR REEF	2006	Fringing Reef	Gentle	9	10	10	100
18.472897°	-77.413928°	MONITOR REEF	2010	Fringing Reef	Gentle	9	10	10	100
18.472897°	-77.413928°	MONITOR REEF	2011	Fringing Reef	Gentle	9	10	10	100
18.468055°	-77.388441°	DAIRY BULL	2005	Fringing Reef	Gentle	9	5	10	50
18.468055°	-77.388441°	DAIRY BULL	2006	Fringing Reef	Gentle	9	5	10	50
18.468055°	-77.388441°	DAIRY BULL	2010	Fringing Reef	Gentle	9	5	10	50
18.468055°	-77.388441°	DAIRY BULL	2011	Fringing Reef	Gentle	9	5	10	50
18.479451°	-77.460042°	RIO BUENO	2005	Fringing Reef	Wall	9	5	10	50
18.479451°	-77.460042°	RIO BUENO	2006	Fringing Reef	Wall	9	5	10	50
18.479451°	-77.460042°	RIO BUENO	2010	Fringing Reef	Wall	9	5	10	50
18.479451°	-77.460042°	RIO BUENO	2011	Fringing Reef	Wall	9	5	10	50



Survey dates: Oct 2005-March 2006
Oct2010- March 2011

Figure 2.2.1. Bleaching monitoring sites located on the north-central coast of Jamaica (Google Earth, 2011).

2.2.3 Temperature data

In 2005 and 2010, NOAA issued bleaching alerts during the summer months warning of rising Sea Surface Temperatures (SSTs) and the formation of HotSpots in the Caribbean basin. Coral Bleaching Hotspots highlight regions where SSTs have reached 1.0 °C above the maximum mean summertime temperature (Glynn and D'Croz 1990; Goreau and Hayes 1994). A HotSpot value of 1.0 °C is the threshold for thermal stress leading to coral bleaching. Degree Heating Weeks (DHW) index provides a measure of sustained thermal stress or SSTs above the mean summertime temperatures during a 12 week period. There is a correlation between coral bleaching and DHW values ≥ 4 °C-weeks (Eakin et al. 2010). By the time DHW values reach 8 DHW weeks, widespread bleaching is likely and bleaching related mortality can be expected (Marshall and Schuttenberg 2006; Eakin et al. 2010).

Regional Sea Surface Temperatures (SSTs), the formation of HotSpots in the Caribbean, and degree heating weeks (DHW) were obtained from NOAA/NESDI's Coral Reef Watch Satellite Monitoring website which monitors current reef environmental conditions to identify areas at risk of thermal stress (http://coralreefwatch.noaa.gov/satellite/baa/index.html).

Sea water temperature on Monitor Reef, at Dairy Bull and at Rio Bueno was tracked during both bleaching events using HOBO (Onset Corp) and STAR-Oddi remote data loggers (http://www.onsetcomp.com/products/data-loggers/ua-002-64). The loggers were enclosed in waterproof casings and attached to the reef substrate where temperature data were recorded at 15 min intervals. Temperature data were collected from January through December in 2005 and 2006, and from February 2010 through to April 2011.

2.2.4 Image analysis and surface area calculation

Photoquadrats were analysed using the Coral Point Count (CPCe v 3.6) image analysis software designed for performing image calibration, and planar area and length calculations of benthic features (Kohler and Gill 2006). For the purpose of this study, the sampling unit was a single coral colony, defined as any individual free standing coral skeleton with living tissue. Image scaling/calibration was based on the reference scale contained within each photoquadrat. Coral colonies were classified according to species and morphology, and colony sizes estimated by measuring the planar surface area (cm^2), including the proportion of the colony bleached (fully or partially), and/or the proportion of the colony showing bleaching related mortality (recent mortality) (Figure 2.2.2). Recent mortality was recognized as any non-living tissue on the colony surface where the corallite structure could still be distinguished and identified to the genus level, and were white or overgrown by a thin layer of filamentous turf algae (Lang et al. 2010).

The bleaching response for each colony was characterized by the intensity of the colouration as:

> **NB** = normal colouration. The tissue is unaltered and shows no sign of bleaching.
>
> **P/PB** = pale or partially bleached. The “pale” category refers to tissue that appears pale relative to what is considered “normal” for the species, depth and habitat. Pale colouration can be further defined as the colour of the tissue having retained its usual hue but having lost some of its colour saturation. Partially bleached refers to areas that are fully bleached or a colony that is mottled in appearance.
>
> **BL** = fully bleached. The tissue of the entire colony is completely white. Some fully bleached corals may appear pale purple, blue, or pink, in addition to being transparent.

Severely bleached corals appear transparent, but the polyp tissue above the skeleton can still be seen.

RD = recently dead. Corallite structures are intact but exposed and devoid of living tissue. The corallite structures may also be slightly eroded but still visible beneath sediment, turf algae or cyanobacteria.

Coral colonies were classified into five morphology categories according to (Humann and DeLoach 2002):

1 - Massive: boulder, mounding, columnar

2 - Encrusting

3 – Encrusting: keeled (thick, bifacial upright extensions)

4 - Leaf, plate, sheet corals

5 - Branching, digitate

Figure 2.2.2. CPCe (Coral Point Count with Excel extensions) program provides a tool for image calibration and area analysis of benthic features. The traced circumference of a colony was used to calculate the planar colony surface area. Subareas within a colony area were used to estimate proportion of colony surface area that was fully bleached (BL), partially bleached or pale (PB/P), or recently dead (RM).

2.2.5 Statistical Analysis

2.2.5.1 Bleaching and Mortality

According to the Global Protocol for Monitoring of Coral Bleaching (Oliver *et al.* 2004) the most important variable to monitor in all bleaching surveys is the percentage of the total living coral cover that is bleached. Since bleaching assessment is based on standard set of bleaching categories, percent bleaching values can subsequently be used for spatial and temporal comparison of sequential bleaching events.

The bleaching response and the subsequent mortality were quantified for the 12 most common species, which represented ~90% of all colonies surveyed at each site (Table A.1). *Acropora cervicornis* and *Millipora* species were excluded from the colony size analysis due to low abundance of the former, and due to challenges in estimating planar colony size measurement for these branching and blade-like morphologies.

The bleaching response and bleaching related mortality were quantified at two different resolutions. First, bleaching prevalence was calculated for each site during each of the bleaching events. Bleaching prevalence was defined as percent (%) of colonies surveyed along random transects that showed some degree (>10% of colony) of bleaching. Secondly, colony bleaching intensity (extent), defined as proportion of colony surface area affected by bleaching, was calculated for individual colonies. Prevalence and extent of (recent) mortality were quantified based on post-bleaching surveys conducted in March/April of 2006 and 2011. Mortality occurring at the onset of a bleaching event is likely to be associated with a disease or causes other than bleaching; however, when mortality is delayed, occurring several weeks to months after the onset of bleaching, then it can most likely be attributed to (a) starvation, or (b)"bleaching-related" mortality (Jones 2008). One- and two-way permutation ANOVAs (10,000 iterations) were used to compare the bleaching/mortality prevalence and intensity (extent) between bleaching and post-bleaching surveys 2005/06 and 2010/11, and between 2005 and 2010 events.

2.2.5.2 Model Selection

Bleaching intensity, measured at the colony level as proportion of colony area that was bleached, was used to ascertain if, and to what extent, the intensity of the bleaching response to thermal stress was related to physical attributes such as colony size and morphology of individual colonies, and to what extent this relationship varied between species.

Two mixed effects models were developed to quantify (a) bleaching intensity and (b) bleaching related mortality as a function of colony surface area (Size), conditional upon species and morphology, observed at the three study sites during the 2005/06 and 2010/11 bleaching events. Models were fitted using R’s (V. 2.15.3) library lme4, given its suitability for large observational data sets with unbalanced designs and nested random effects (Bates 2010; R Development Core Team 2010).

2.2.5.3 Bleaching Model

The response variable in the first model was bleaching intensity BLI (adapted from McClanahan 2004) where proportions of colony surface area that were fully bleached (BL), pale (P), and partially bleached (PB) were added to obtain a single bleaching intensity value. Bleaching categories were weighted according to bleaching intensity such that the fully bleached category was assigned a value of 1, and pale and partially bleached categories a value of 0.5. Bleaching intensity (BLI) for each colony was calculated using the following equation:

Equation(1): $BLI = 0.5*P+0.5*PB +1.0*BL$

Bleaching intensity (BLI) was the response variable in the model, with colony size (Size, cm^2), survey date (Date), species (Species) and morphology (Morphology) treated as fixed effects. Given the spatial nature of the data set, Site (reef) was treated as a random factor, with transects and quadrats as nested terms (Table 2.2.2). Colony size data were log transformed ($\log_{10}(Size+1)$) to address the skewed nature of the data. Bleaching intensity (BLI) data were transformed using the logit function for proportional data (Warton and Hui 2011).

Table 2.2.2. Description of main variables used in developing the mixed effect bleaching model.

Variables	**Description**	**Type**
BLI	*Proportion of colony area bleached (weighted by intensity of bleaching)*	*Continuous response variable*
rMORT	*Proportion of colony area recently dead*	*Continuous response variable*
SIZE	*Colony area*	*Continuous explanatory variable*
SPECIES	*Species name*	*Categorical explanatory variable (12 levels)*
MORPHOLOGY	*Colony morphology type*	*Categorical explanatory variable (5 levels)*
DATE	*Date of survey*	*Categorical explanatory variable*
SITE/TRANSECT/QUAD	*Location/reef site*	*Categorical grouping variable*

The first step in the model building process was to determine the random effects structure. Although the effect of individual sites on bleaching was not of primary interest, the between-site variation might explain some of the variation observed in the bleaching data. Treating Site and the nested Transects/Quadrat as random terms was based on the assumption that the three reef sites were a random sample from a larger number of sites, and that the variation between them was inherently random.

To determine the best structure of the random effects term, the response variable (BLI) was fitted against the intercept and a random term in order to assess which random effect structure performed best. Starting with the null model (Model#1-intercept only model), a set of candidate models with different random structures were compared (Table 2.2.3). Model comparison was based on Akaike Information Criterion (AIC). AIC is a measure of the relative quality of a statistical model, addressing the trade-off between the goodness of fit of the model and the complexity of the model (Akaike 1974). The best random effect structure, with the lowest AIC (Δ AIC= -1,232.71), included the Site term with nested Transect and Quadrat terms (Model #5).

Table 2.2.3. Models used in evaluating the optimal random effect structure of the model.

	Model	**AIC (BLI)**	**Δ AIC**
1	glm (BLI ~ 1)	25,224	0
2	lmer (BLI ~ 1 +(1| SITE)	24,724	-500
3	lmer (BLI ~ 1 +(1| SITE / TRANSECT)	24,543	-681
4	lmer (BLI ~ 1+(1| SITE / TRANSECT / QUAD)	24,299	-924
5	lmer (BLI ~1+(SIZE |SITE/TRANSECT/QUAD)	23,991	-1,233

In the second step, the optimal mixed effects model was selected using the dredge function in the MuMin R package (Barton 2012). The dredge function was used to generate a set of models with all possible combinations (subsets) of the explanatory (fixed) terms and relevant interaction terms provided in the "global model". The global bleaching model included all main fixed effects (Table 2.2.2) and their interaction terms, and the random effects structure identified in the previous step (Table 2.2.3, Model #5).

The global bleaching model is described by the following equation:

Equation (2): BLI ~ SIZE + DATE + SPECIES + MORPHOLOGY + SIZE: DATE + SIZE: SPECIES + SIZE: MORPHOLOGY + DATE: SPECIES + DATE: MORPHOLOGY + SPECIES: MORPHOLOGY + SIZE: DATE: SPECIES + (SIZE|SITE/TRANSECT/QUAD)

The third step entailed selecting the best model. Corrected Akaike Information Criterion (AICc) was used to choose between competing models generated by the dredge function in R (Burnham and Anderson 2002). The AICc selects models with high likelihood, while penalizing for additional parameters, such that the best model has the smallest AICc. To evaluate the degree of support for the best model, AIC differences were calculated between the best model and each competing model. These differences were summarized as an AIC weight, quantifying the probability that the selected model was the best model among compared models (Burnham and Anderson 2002). Large AIC weights (>0.3) indicate considerable support for a model, while small weights (<0.2) indicate very little support for the model. The three top models had similar AICc values and were further compared with analysis of deviance (Quinn and Keough 2002).

The r.squared GLMM function in the MuMIn package (Nakagawa and Schielzeth 2013) was used to describe the goodness-of-fit of the model by calculating the marginal and conditional R^2 values. The *marginal* R^2 describes the proportion of variance explained by the fixed factor(s) alone and the *conditional* R^2, describes the proportion of variance explained by both the fixed and random factors.

2.2.5.4 Mortality Model

The model selection process (Steps 1-3) was repeated in developing the second mixed effect model for describing the relationship between (recent) mortality due to bleaching as a function of colony size, species, morphology and event.

The global mortality model used in the selection process is described by the following equation:

Equation (3): rMORT ~ SIZE + DATE + SPECIES + MORPHOLOGY + SIZE: DATE + SIZE: SPECIES + SIZE: MORPHOLOGY + DATE: SPECIES + DATE: MORPHOLOGY + SPECIES: MORPHOLOGY + SIZE: DATE: SPECIES + (SIZE|SITE/TRANSECT/QUAD)

The random component structure of the model was the same as was used in the bleaching model. The optimal mixed model describing bleaching related mortality corrected for size, species, morphology and survey date, and relevant interaction terms was selected using the iterative MuMin function (Barton 2012) and corrected AICc values referenced in selecting the top model.

The selected models were assessed graphically by examining the distribution of the standardized residuals to check for normality and by plotting the residuals versus the predicted values. Given that the assumption of homogeneity of variance and normality were violated, we used conservative threshold values ($\alpha < 0.001$) in selecting fixed effect terms for inclusion in the models.

2.3 Results

2.3.1 Temperature Data

In 2005, sea surface temperature anomalies caused extensive coral bleaching across the Caribbean basin (Wilkinson and Souter 2008). Satellite sea surface temperature data indicated that thermal stress associated with these temperature anomalies was the highest recorded in 20 years (Figure 2.3.1) (Clark et al. 2009). NOAA satellite regional sea surface temperature (SST) data for the Caribbean, including Jamaica, pointed to hot spot formation (SSTs in excess of 1°C above the maximum expected temperatures) in the Caribbean basin in June and July. The hotspot persisted throughout the summer months, spreading from the lesser Antilles, passing north-west through the Caribbean basin, reaching Jamaica in August where it remained until it dissipated in late October (Figure 2.3.1 a). The conditions were made worse by the doldrums on Jamaica's north coast which lasted throughout the summer. Accumulated heat stress for Jamaica was at 3-4 Degree Heating Weeks (DHW) by the end of the summer and reached a maximum of 7 DHWs by late October (Figure 2.3.1 b, Table 2.3.1).

In early summer of 2010, NOAA satellites again showed hotspot activity developing in the south-eastern Caribbean and expanding north-west toward Jamaica and Cuba (Figure 2.3.1 c). A major thermal anomaly was reported for the Caribbean with temperatures rising steadily throughout the summer. On average, temperatures in 2010 were 0.010 degrees Celsius higher than in 2005. By the end of the summer, the accumulated heat stress on the north coast of Jamaica was at 2 DHW and reached a maximum of 5 DHW by late October (Figure 2.3.1 d, Table 2.3.1). In Jamaica, initial signs of bleaching in 2010 were reported at the end of August.

Table 2.3.1. Degree heating weeks (DHW) index calculates the magnitude and duration of SST above mean temperatures during 12 week intervals. DHWs were tracked through the summer months in 2005 and 2010. The accumulated thermal stress was notably higher in 2005 and persisted through to the end of December.

	15th 2005	30th 2005	15th 2010	30th 2010
January	0	0	0	0
	..	..	..	..
June	0	0	0	0
July	0	0	0	0
August	2	2-3	0	2
September	4	5-6	4-5	4-5
October	6	7	4-5	4-5
November	6	5-6	4	0
December	5	2	0	0

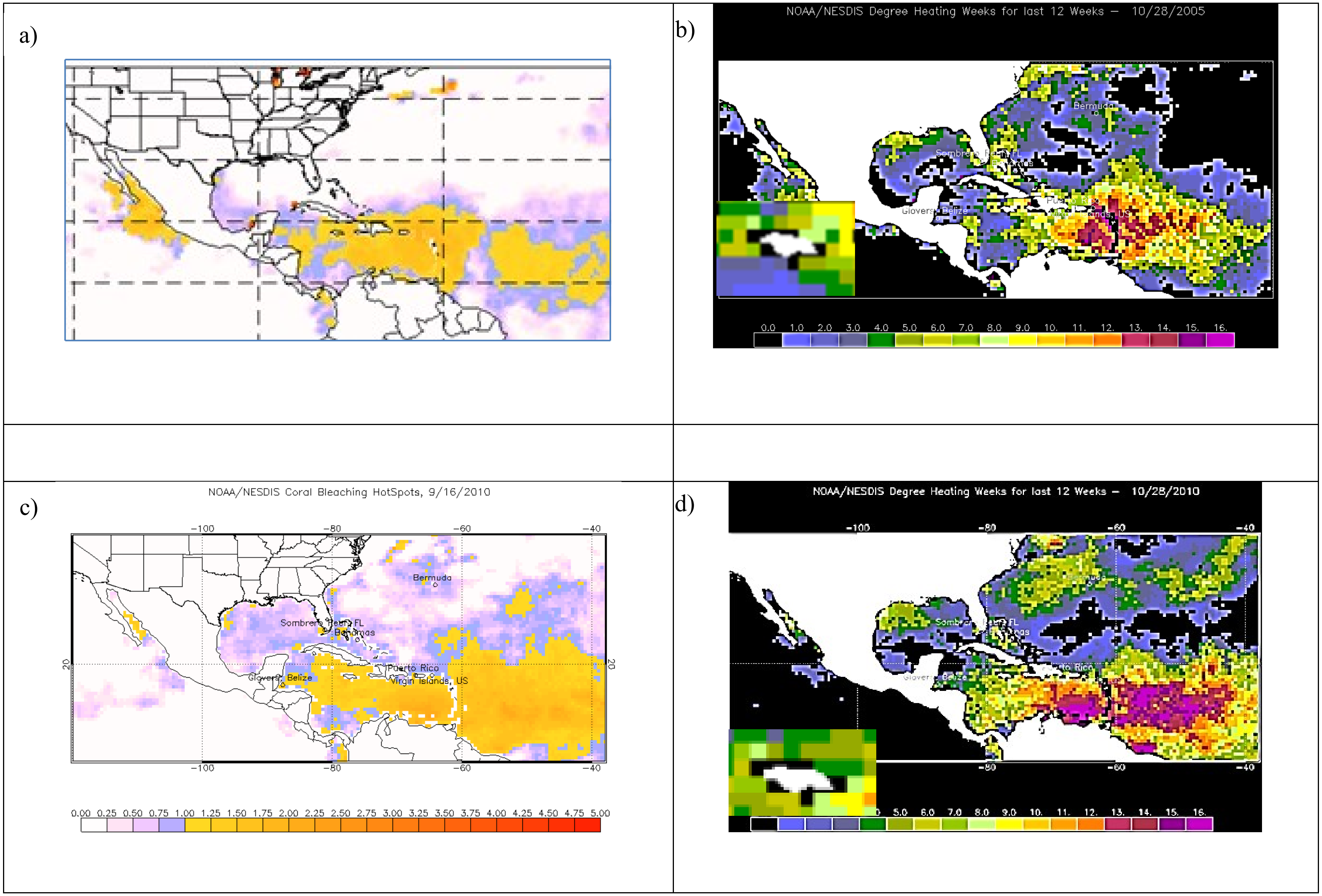


Figure 2.3.1. NOAA coral bleaching hotspot schematics shown as yellow to orange gradient for the Caribbean basin in (a) September of 2005 (http://www.ospo.noaa.gov/Products/ocean/cb/hotspots/2005.html) and (c) in September of 2010 (http://www.ospo.noaa.gov/Products/ocean/cb/hotspots/2010.html). Corresponding schematics for accumulated thermal stress over a 12 week period, shown in Degree Heating Weeks (DHW), for the Caribbean at the end of (b) October 2005 (http://www.ospo.noaa.gov/data/cb/dhw/2005/dhwa.9.30.2005.gif), and (d) October of 2010 (http://www.ospo.noaa.gov/Products/ocean/cb/dhw/2010.html).

In-situ sea data loggers for the Discovery Bay West fore reef recorded a steady increase in temperature from June to October of 2005. The average daily temperature rose from 28.4°C in June to 30°C in August, peaking at 30.4°C by end of October. The average monthly summer temperatures in 2005 were 1°C higher relative to those recorded for previous years (2000-2004) during which no bleaching was observed (Figure 2.3.2).

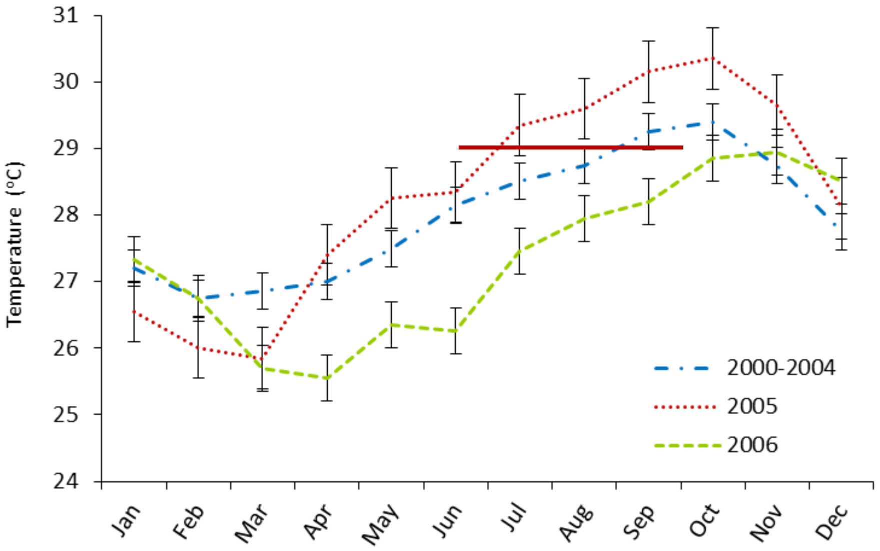


Figure 2.3.2 . Average monthly sea temperature (^{o}C +/- SE) at 9m on the Discovery Bay West Fore-Reef. (From DBML /CARICOMP data record). The (red) line represents the average summertime (June-September) temperature for the three sites.

Similar *in-situ* sea water temperature trends were observed during the summer of 2010 (Figure 2.3.3). Temperatures which rose above the seasonal average (~29 ºC) in June persisted through the summer months, peaking at 30.6ºC in October, before returning to more seasonal values following Hurricane Tomas in early November.

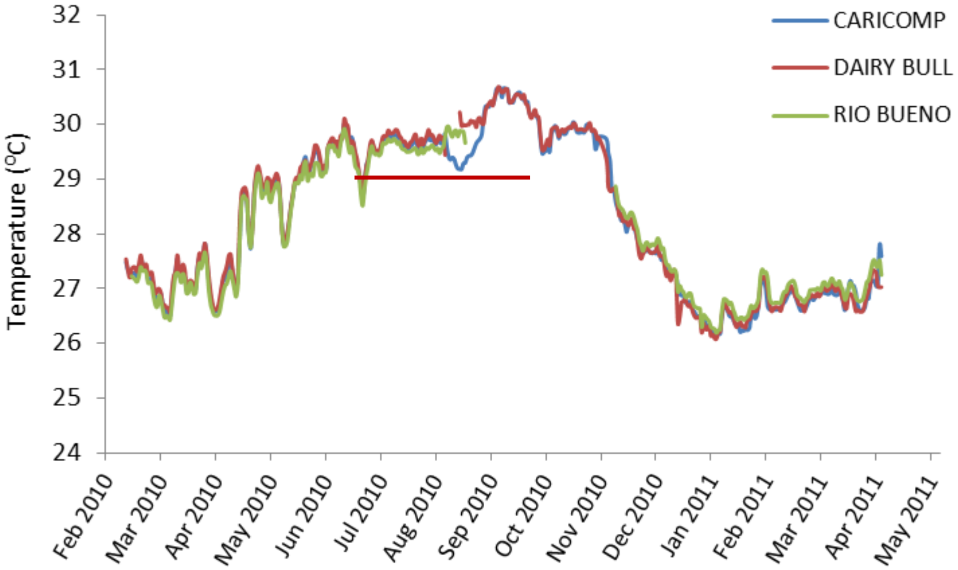


Figure 2.3.3. Daily seawater temperatures recorded by loggers deployed at a depth of 9m at the Monitor Reef, Dairy Bull and Rio Bueno sites reached a maximum of 30.6 ºC and remained elevated through to October of 2010 (unpublished DBML-CARICOMP data). The (red) line represents the average summertime temperature (June-September) for the three sites.

2.3.2 Bleaching - 2005 and 2010

A total of 11,327 colonies were assessed for bleaching status across three reef sites: 2,078 in 2005, 2,462 in 2006, 3,486 in 2010 and 3,301 in 2011 (Table 2.3.2).

Table 2.3.2. Bleaching prevalence and bleaching intensity observed at the three study sites during the peak and five months after the 2005 and 2010 bleaching events. Bleaching prevalence was defined as mean % of surveyed colonies affected by bleaching. Bleaching intensity was defined as mean proportion of colony surface area bleached.

Date	Site	Total # colonies/ 50 m^2 (100 m^2*)	# colonies BL	BL prevalence (%)	+/- SE	BL intensity (proportion)	+/- SE
2005	Monitor Reef	644*	366	56.8	2.0	0.47	0.018
2006	Monitor Reef	672*	105	15.6	1.4	0.08	0.009
2010	Monitor Reef	1125*	504	44.8	1.5	0.28	0.012
2011	Monitor Reef	1069*	41	3.8	0.6	0.02	0.003
2005	Dairy Bull	688	270	39.2	1.86	0.23	0.014
2006	Dairy Bull	983	86	8.7	0.9	0.03	0.004
2010	Dairy Bull	1063	534	50.2	1.53	0.22	0.01
2011	Dairy Bull	978	141	14.4	1.12	0.03	0.004
2005	Rio Bueno	746	218	29.2	1.67	0.14	0.01
2006	Rio Bueno	807	42	5.2	0.78	0.02	0.004
2010	Rio Bueno	1298	301	23.2	1.17	0.06	0.005
2011	Rio Bueno	1254	210	16.7	1.05	0.05	0.005

In 2005, the first reports of coral bleaching in September coincided with sea temperatures rising above 30°C. High temperatures persisted throughout October and abated by mid-November. Surveys were carried out at Monitor Reef, Dairy Bull and Rio Bueno study sites from mid-October through to early November.

The bleaching response in 2005 varied significantly between the three study sites, both in terms of prevalence (% of colonies surveyed that showed some degree of bleaching) (ANOVA, F_{site}=58.16, p=0.0001) and intensity (proportion of colony surface area bleached) (ANOVA,

F_{site}=143.4, p=0.0001) (Table 2.3.2). At the peak of the bleaching event in late October 2005, 57% of the coral colonies surveyed at the Monitor Reef site presented some degree of bleaching with 32% completely bleached, and the remaining 25% partially bleached. At Dairy Bull, 39% of all colonies surveyed were bleached, 10% were fully bleached and 29% were partially bleached. At Rio Bueno, 29% of the colonies were bleached, of which 4% were fully bleached and the remaining 25% were partially bleached (Figure 2.3.4).

By March-April of 2006, as the temperatures returned to their seasonal normal range (~26°C, Figure 2.3.2), the recovery from bleaching was significant at all the sites, both in terms of prevalence (ANOVA, $F_{site|date}$= 17.61, p=0.0001) and intensity (ANOVA, $F_{site|date}$= 91.97, p=0.0001) (Table 2.3.2). Most coral colonies on Monitor Reef recovered from bleaching, with only 1% remaining fully bleached. The remaining 14% were pale or partially bleached. At Dairy Bull and Rio Bueno reefs, 9% and 5% of all surveyed colonies were still pale or partially bleached, respectively (Figure 2.3.4).

Similarly in 2010, first anecdotal accounts of bleaching were reported by late summer and also coincided with temperatures rising above 30°C (~2DHW, Figure 2.3.2). Surveys were conducted in October 2010. Despite similar temperature trends between the two events, bleaching prevalence and intensity were lower in 2010 on Monitor reef and at Rio Bueno, whereas at Dairy Bull, the prevalence was higher but the intensity was comparable to 2005 (Tukey HSD p=0.91).

At the peak of the 2010 bleaching event, bleaching prevalence varied between the three sites (ANOVA, F_{site}=111.27, p=0.0001). On Monitor Reef 45% of the corals were bleached, of which 12% were fully and 33% partially bleached. At Dairy Bull, 50% of the corals were bleached, of which 5% were fully and 45% partially bleached. Bleaching at Rio Bueno was moderate at 23% (<1% of the colonies were fully bleached).

The rain and the cooling temperatures that accompanied Hurricane Tomas in early November caused a drop in sea surface temperatures. When the sites were resurveyed in April 2011, bleaching prevalence (ANOVA, $F_{date|site}$=126.9, p=0.0001) and intensity ($F_{date|site}$=164.0, p=0.0001) had decreased significantly across all sites except for Rio Bueno (Tukey HSD, p=0.73), where 1% of the colonies remained fully bleached and 16% partially bleached. At Monitor Reef, only 4% of the colonies remained pale or partially bleached, and at Dairy Bull, ~1% remained fully bleached and 13% pale or partially bleached (Figure 2.3.4).

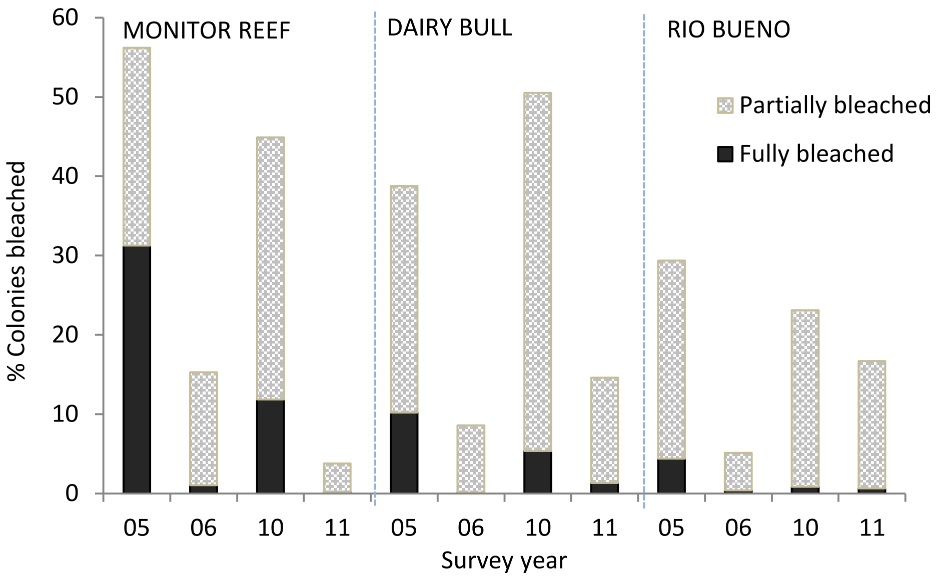


Figure 2.3.4. Bleaching prevalence observed at each study site at the peak of the bleaching event (2005 and 2010) and recovery observed five months later (2006 and 2011). Bleaching was more intense (fully bleached colonies) in 2005 than in 2010.

The decrease in bleaching prevalence and intensity between bleaching and recovery surveys pointed to a level of tolerance among coral species to thermal stress. After both bleaching events, as sea surface temperatures abated, most bleached corals recovered their zooxanthellae and gradually regained their normal colour. The slower recovery in 2006 corresponded to the slower decrease in sea temperature.

2.3.3 Species Abundance and Bleaching

Although the number of individual coral colonies surveyed varied between the survey years, the relative abundances of species were generally consistent (Figure 2.3.5). Monitor Reef and Dairy Bull were similar in terms of species diversity (26 species) and community composition with fast growing species including *Agaricia* spp., *Porites astreoides,* slower growing *Montastraea annularis, Siderastrea siderea* followed by *Madracis* spp., *Helioceris cucullata, Agaricia* *lamarcki*, branching *Porites porites, Agaricia humilis, Montastraea faveolata* and *Stephanocoenia intersepta* , dominating the assemblages. Out of 25 species identified at Rio Bueno *Agaricia* spp*., Madracis* spp., *Porites astreoides,* and *Siderastrea siderea* were the most common species encountered on the reef.

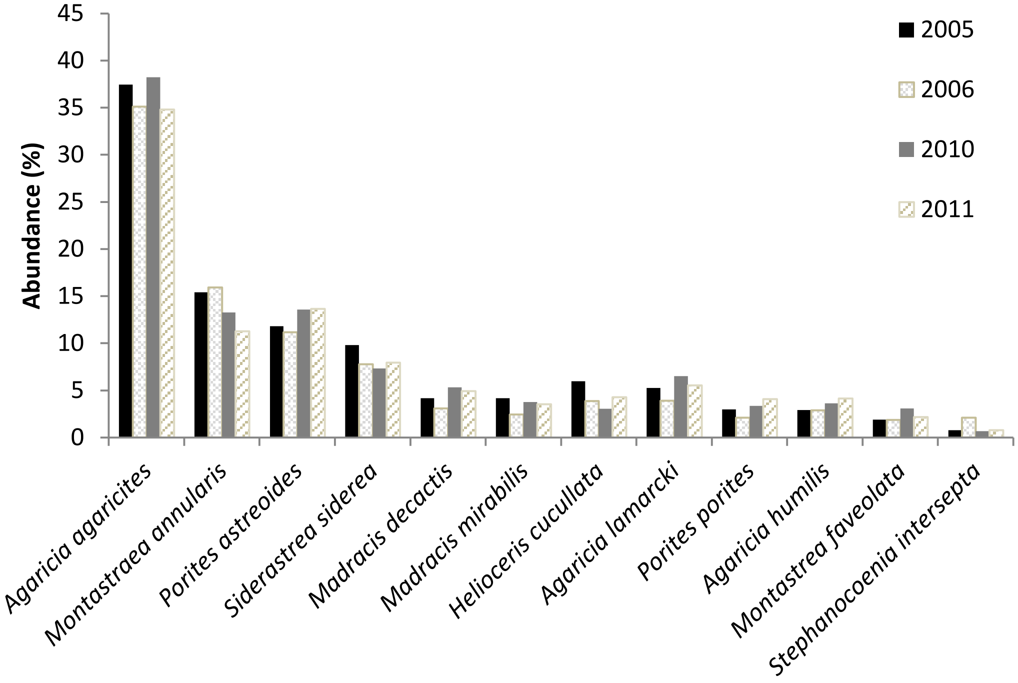


Figure 2.3.5. Relative abundance of 12 most common coral species encountered at the study sites for each survey year.

On Monitor and at Dairy Bull reefs (Figure 2.3.6 a and b) bleaching during both bleaching events was most prevalent for *A. agaricites, M. annularis, A. humilis,* followed by *M. faveolata, A. lamarcki* and *H. cucullata*. Branching *Porites* spp. and *S. siderea* exhibited mild to moderate bleaching. At Rio Bueno, *A. agaricites*, *H. cucullata* were most susceptible to bleaching, whereas *Madracis* spp, *P. astreoides* and *S. intersepta* showed consistent resistance to thermal stress (Figure 2.3.6 c, Table A.1).

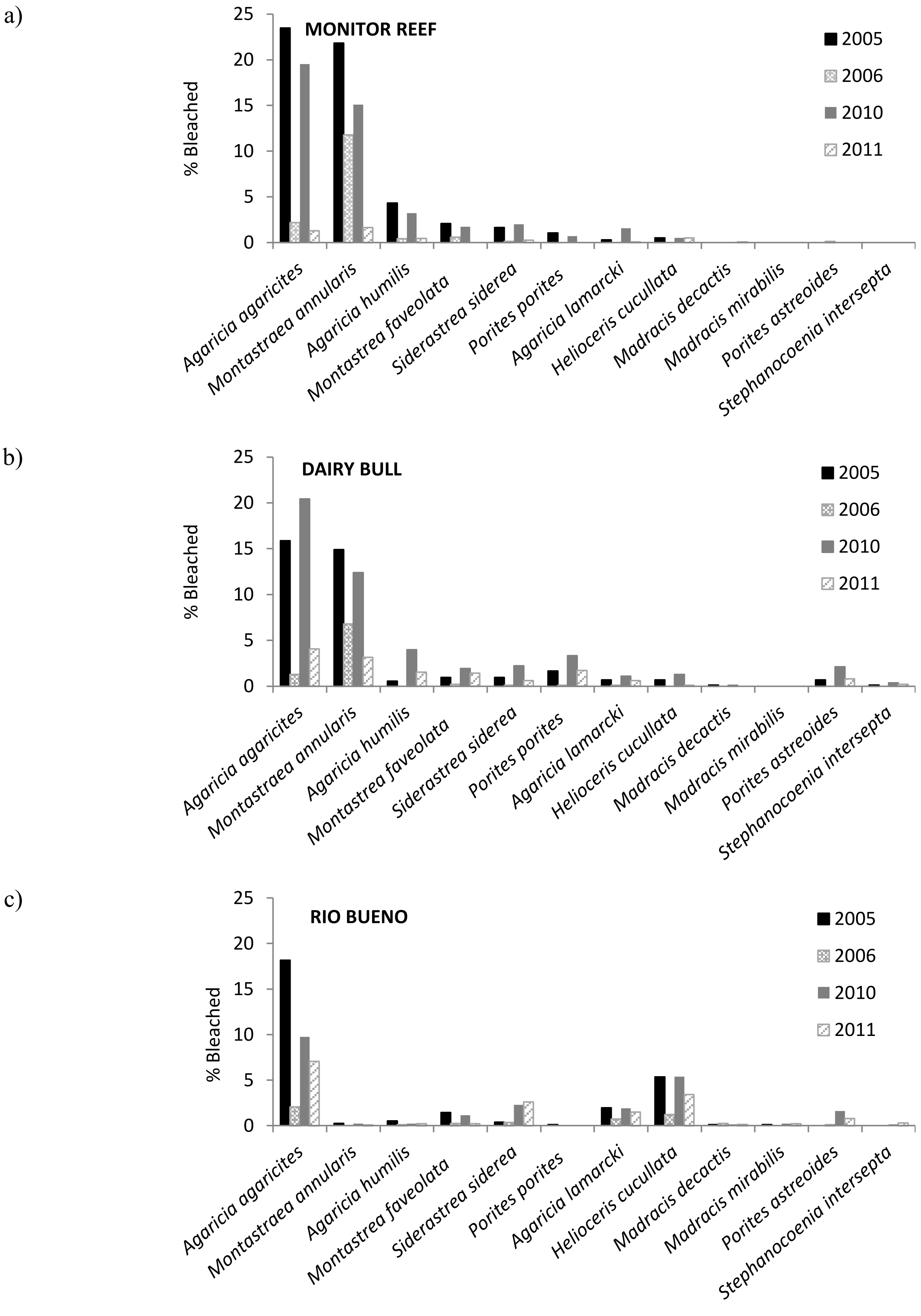


Figure 2.3.6. Bleaching prevalence (% colonies bleached) across all species observed during each survey at: a) Monitor Reef, b) Dairy Bull and (c) Rio Bueno sites.

2.3.4 Bleaching and Colony Size

The relationship between bleaching intensity and colony size was similar for colonies surveyed at Monitor Reef and Dairy Bull during both bleaching events, but was less evident at Rio Bueno (Figure 2.3.7). The relationship between bleaching intensity and colony size varied among species (Figure 2.3.8) and growth forms (Figure 2.3.9). A positive relationship between bleaching and colony size was observed for several species, including *A. agaricites*, *A. humilis*, *H. cucullata*, *M. faveolata* and *P. porites*. Bleaching intensity among *M. annularis* colonies was consistent across the range of colony sizes, confirming the high susceptibility of the species to thermal stress. Bleaching was more pronounced among the larger *M. faveolata* and to a lesser extent among *S. siderea* colonies. *M. mirabilis, M. decactis, P. astreoides* and *S. intersepta* appeared to be consistently resistant to thermal stress, regardless of colony size. The relationship between bleaching and colony size was more evident in 2005 when bleaching intensity was higher. In terms of colony growth forms, bleaching as a function of size was most evident for the massive colonies and to a lesser extent for the encrusting, branching, keeled and plating/foliose morphologies (Figure 2.3.9).

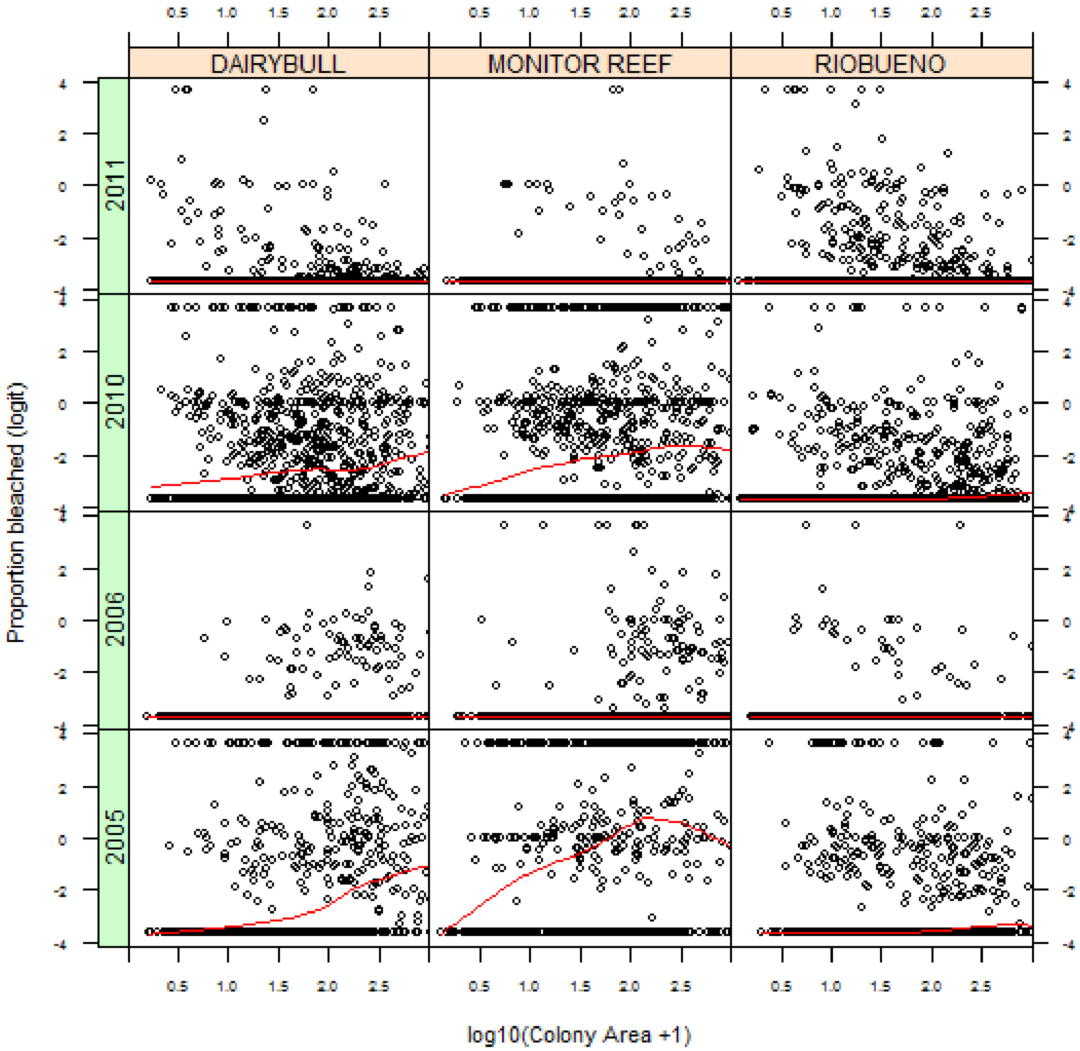


Figure 2.3.7. Logit transformed bleaching intensity as a function of colony size observed at the three study sites during the bleaching and recovery surveys in 2005/06 and 2010/11. A loess smoother line was added for ease of visual interpretation.

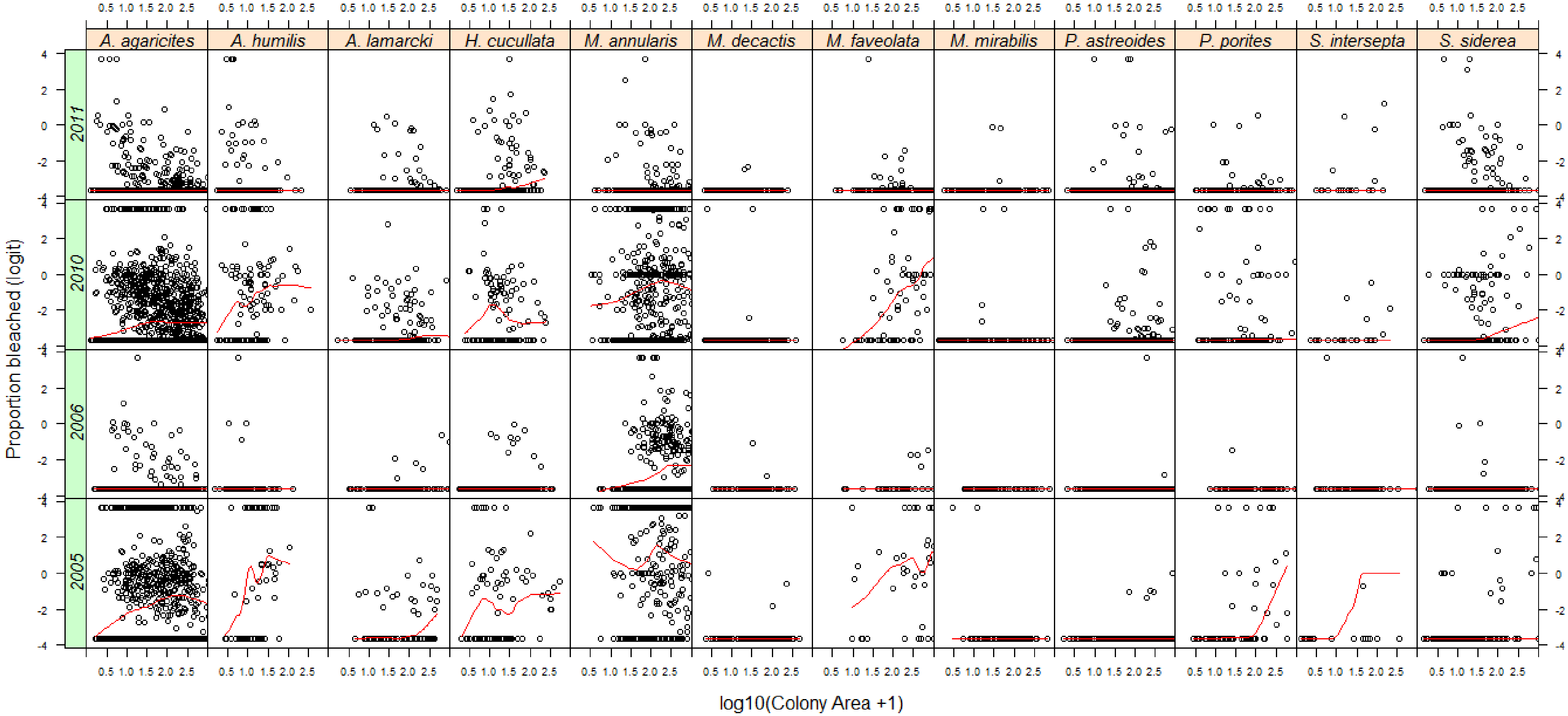


Figure 2.3.8. Bleaching intensity measured as logit transformed proportion of the colony surface area bleached, as a function of colony size, for the twelve common species observed during the 2005 bleaching survey and the subsequent recovery (2006), and during the 2010 bleaching survey and the subsequent recovery (2011). A loess smoother line was added for ease of visual interpretation.

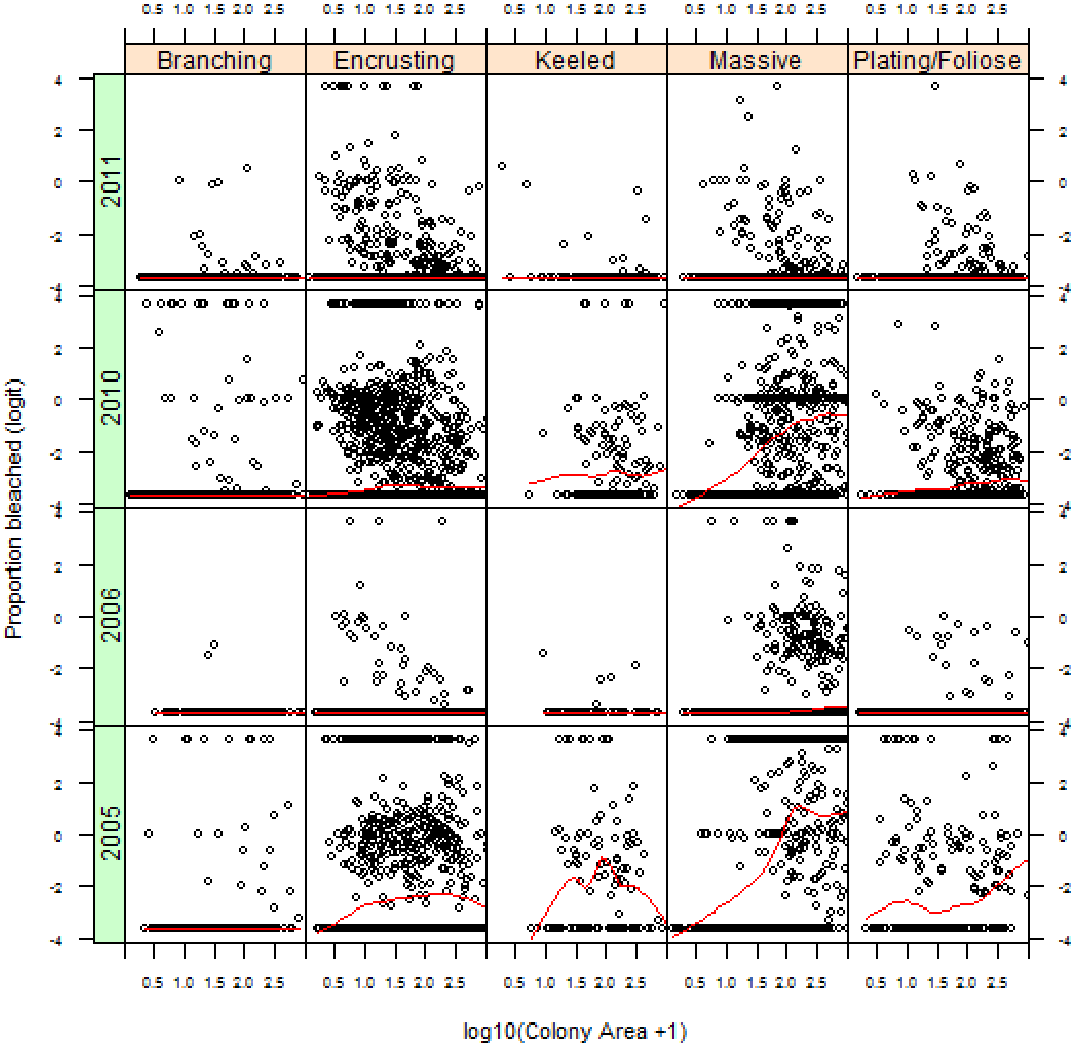


Figure 2.3.9. Bleaching intensity as a function of colony size for 5 morphologies.: branching/digitate, encrusting, keeled, massive and plating/foliose. The relationship between colony size and colony morphology was most evident for the massive and encrusting growth forms. A loess smoother line was added for ease of visual interpretation.

2.3.5 Bleaching Model

The mixed effects statistical model developed was based on the premise that the intensity of the bleaching response (BLI) was influenced by colony size, colony morphology, species, and the interaction of these terms for each bleaching event (Date). All the main fixed effects variables and relevant interactions listed in the global model, *Equation (2)*, were used to identify the component models within 4 AIC units of the best model. The best model predicting the bleaching response included Colony Size, Morphology, Species, and the Date main terms, as well as Size: Species, Size: Date, Date: Species and Date: Size: Species interaction terms, as independent variables having a significant effect on the proportion of colony bleached (Table 2.3.3). Four models were selected, however only the first one with an AIC weight >0.2 was considered.

Table 2.3.3. Model inference selection outcome for best component models predicting bleaching intensity as a function of colony size, species morphology and survey date.

Model#	**Component models**	**df**	**logLik**	**AICc**	**Delta**	**Weight**
1	BLI ~ SIZE+ DATE + SPECIES+ MORPHOLOGY + SIZE:SPECIES+ DATE:SIZE + DATE:SPECIES + DATE:SIZE:SPECIES + (SIZE|SITE/TRANSECT/fQUAD)	62	-11,316.55	22,702.03	0.0	0.89
2	BLI ~ SIZE+ DATE + SPECIES+ MORPHOLOGY+SIZE:SPECIES+ DATE:SIZE + DATE:SPECIES + DATE:MORPHOLOGY + DATE:SIZE:SPECIES + (SIZE|SITE/TRANSECT/fQUAD)	66	-11,315.57	22,706.46	4.73	0.09
3	BLI ~ SIZE+ DATE + SPECIES + MORPHOLOGY + DATE:SIZE + DATE:SPECIES + SIZE:SPECIES	51	-11,334.06	22,710.70	8.68	0.01
4	BLI ~ SIZE+ DATE + SPECIES+MORPHOLOGY + fDATE:SPECIES +SIZE:SPECIES	50	-11,334.73	22,712.15	10.12	0.01

All the terms included in Model 1were significant at a threshold level of $\alpha < 0.001$ except for the main effect Date (Analysis of Deviance DF=1, p= 0.4), and the interaction terms Size: Date (Analysis of Deviance, df=1, p=0.0024) and Date: Species (Analysis of Deviance, df=11, p 0.0022).

Excluding both Size: Date and Date: Species interaction terms from the model (Model 1), or the Date: Species term alone, did not improve the goodness of fit of the model (Δ AIC = 22.22). As such, only the Size: Date interaction term was excluded from the model (Δ AIC=0), however, the main effect (Date) was retained in the model given its relative importance and inclusion in interaction terms which were significant (Table 2.3.4).

The final model is described by the following equation:

Equation (3)

$$\mathrm{BLI} \sim \mathit{SIZE} + \mathit{DATE} + \mathit{SPECIES} + \mathit{MORPHOLOGY} + \mathit{SIZE}{:}\ \mathit{SPECIES} + \mathit{DATE}{:}\ \mathit{SPECIES} + \mathit{DATE}{:}\ \mathit{SIZE}{:}\ \mathit{SPECIES} + (\mathit{SIZE} | \mathit{SITE/TRANSECT/QUAD})$$

Table 2.3.4. Analysis of deviance was carried out to determine the statistical significance of the fixed effect variables and the interaction terms in the optimal model. All the terms included in the optimal model were significant at a threshold level of $\alpha<0.001$ except for Date: Species interaction term (df=11, p=0.002), and the main effect Date (df=1, p= 0.4) which was retained given its relative importance and its inclusion in two interaction terms. The relative importance of each term is included.

Response variable :	BLI			
Fixed Effects	Chisq	Df	p-value	Relative Importance
(Intercept)	34.94	1	3.41 e-09 ***	-
3 SIZE	26.91	1	2.13 e-07 ***	1.0
1 DATE	0.70	1	0.40	1.0
4 SPECIES	107.38	11	2.20 e-16 ***	1.0
2 MORPHOLOGY	32.15	4	1.78 e-06 ***	1.0
8 SIZE : SPECIES	58.81	11	1.54 e-08 ***	1.0
7 DATE : SPECIES	29.11	11	0.0022 **	1.0
9 SIZE : DATE : SPECIES	34.48	12	0.0006 ***	0.98

*Signif. codes: *** 0.001 ** 0.01 * 0.05 . 0.1 1*

The effect size of bleaching intensity in the bleaching model was calculated for the individual main fixed effect variables in the model using the plotLMER.fnc (Figure 2.3.10). A positive relationship between bleaching intensity and colony size (effect size =0.63) indicated that bleaching intensity was twofold higher for larger colonies (>1000 cm^2) compared to smaller colonies (<100 cm^2) (Figure 2.3.10 a). While the relationship between bleaching intensity and colony size appeared to be quite strong, the colony size variable in the model explained only ~5% of the variability observed in the data set (Table 2.3.5).

Bleaching intensity varied between the 2005 and 2010 bleaching events (effect size=0.26), (Figure 2.3.10 b). Despite similar temperature patterns observed during the summers of 2005 and 2010, the magnitude and duration (DHW) of thermal stress was greater in 2005, as was the magnitude of the bleaching intensity which was ~2 times higher in 2005 than in 2010 (Figure

2.3.10 b). The recovery from both bleaching events was evident (Figure 2.3.4). The variability in bleaching intensity between the survey dates explained ~4% of the variability in the data.

The magnitude of bleaching intensity was highly variable among species (effect size=0.73) (Figure 2.3.10 c). The observed variation in bleaching can be attributed to species-specific physiological characteristics not included in our model. During both bleaching events, *Agaricia* and *Montastraea* species showed highest susceptibility to bleaching. Conversely, *Porites astreoides, Madracis* spp. and *Stephanocoenia intersepta* colonies were resistant to thermal stress. Dissimilarity in bleaching intensity among species explained 17% of the observed variability.

The effect size for morphology was relatively low at 0.25. The intensity of the bleaching response was highest among the massive/columnate and encrusting colonies, and lowest among plating growth forms (Figure 2.3.10 d).

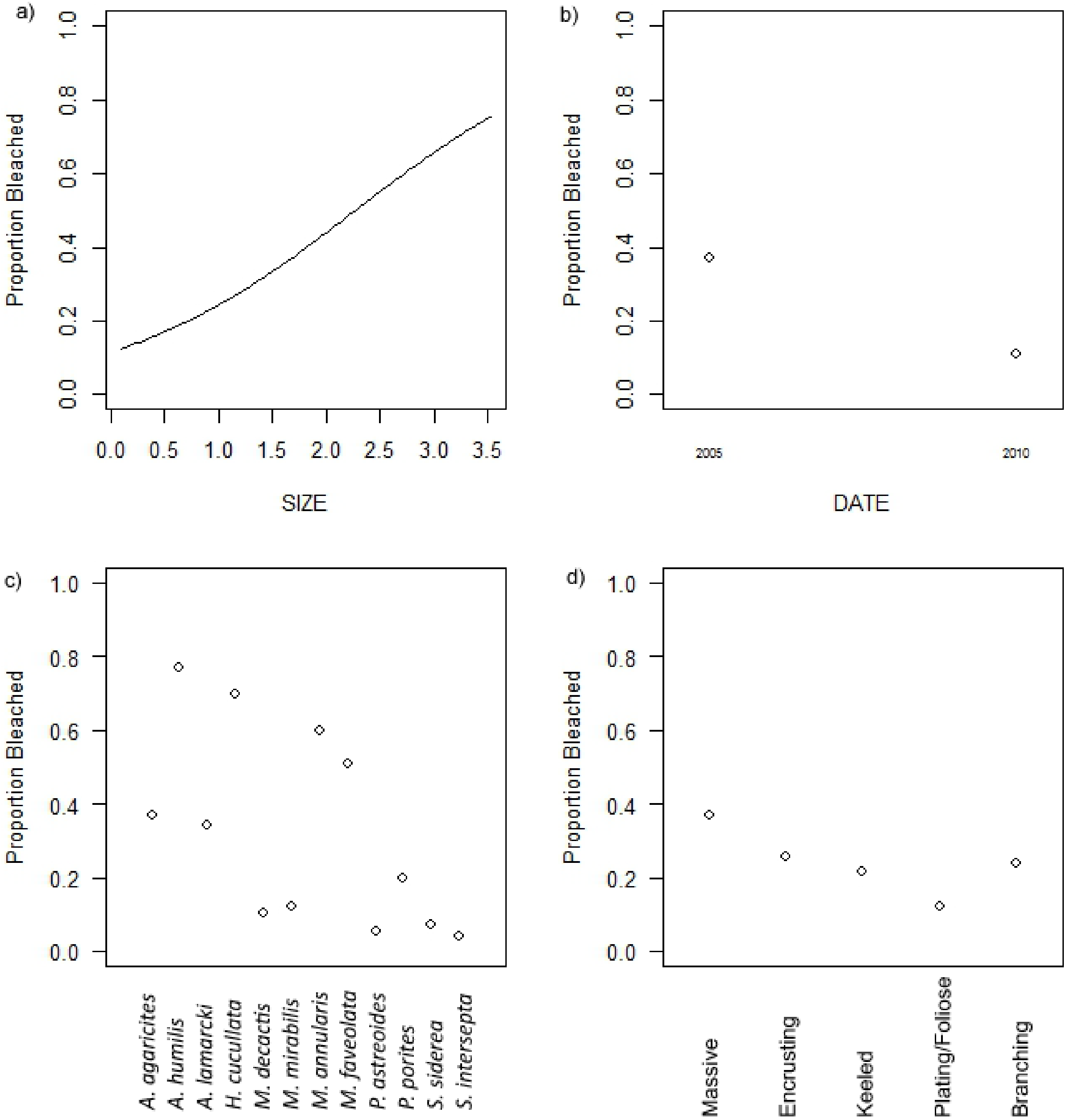


Figure 2.3.10. Effect size of bleaching intensity explained by the main fixed effects variables included in the bleaching model: (a) bleaching intensity as a function of log colony surface area (Size); (b) bleaching intensity effect size for the 12 individual species included in the model: (c) effects size of bleaching intensity observed during the 2005 and 2010 surveys; (d) effect size of bleaching intensity for the five colony morphologies.

The bleaching model, accounting for colony size, species, morphology and survey date, explained 51% of the variance in the bleaching response observed during 2005 and 2010 bleaching events (Table 2.3.5). The fixed terms in the model accounted for 26% of the variance, of which colony size explained 5%, differences among species susceptibility to bleaching 17%, colony morphology <1%, and an additional 4% due to differences in bleaching intensity between the two bleaching events.

Table 2.3.5. Marginal and conditional R^2 values were calculated to assess the overall model fit by calculating how much of the variance in the bleaching response was explained by the bleaching model, and how much of the variance was explained by the component terms (main fixed effects) in the model. The main fixed effects terms were removed one by one and the resulting marginal R^2 value subtracted from the Model Marginal R^2 value of the complete model to calculate the contribution of each fixed effect in explaining the observed variance.

	Marginal R^2	Conditional R^2	Component contribution
Model 1	0.255	0.51	0.25*
Model 1- SIZE	0.2		0.05
Model 1 - MORPHOLOGY	0.252		0.003
Model 1- SPECIES	0.08		0.17
Model 1- DATE	0.2		0.04

** Component contribution of the random term in the model.*

The relative contribution of the random effect to the overall model accounted for an additional 25% (Conditional R^2 – Marginal R^2) of the observed variability in the bleaching response.

The bleaching model coefficients are presented in (Table 2.3.6) and the graphs based on model coefficients for each fixed effect in Figure 2.3.11 and Figure 2.3.12.

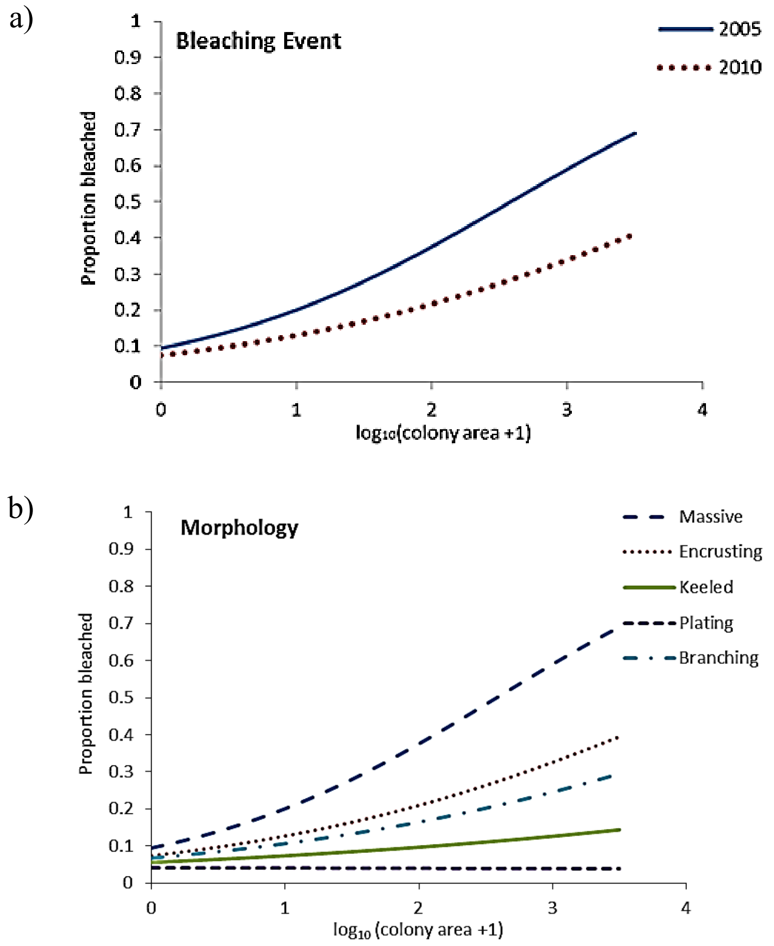


Figure 2.3.11. The relationship between bleaching intensity and colony size based on the bleaching model coefficients. According to the model (a) larger colonies are more susceptible to thermal stress. The difference in the bleaching intensity reflects the difference in DHW between 2005 and 2010. (b) Bleaching intensity as a function of colony size was higher for massive/columnate and encrusting growth forms.

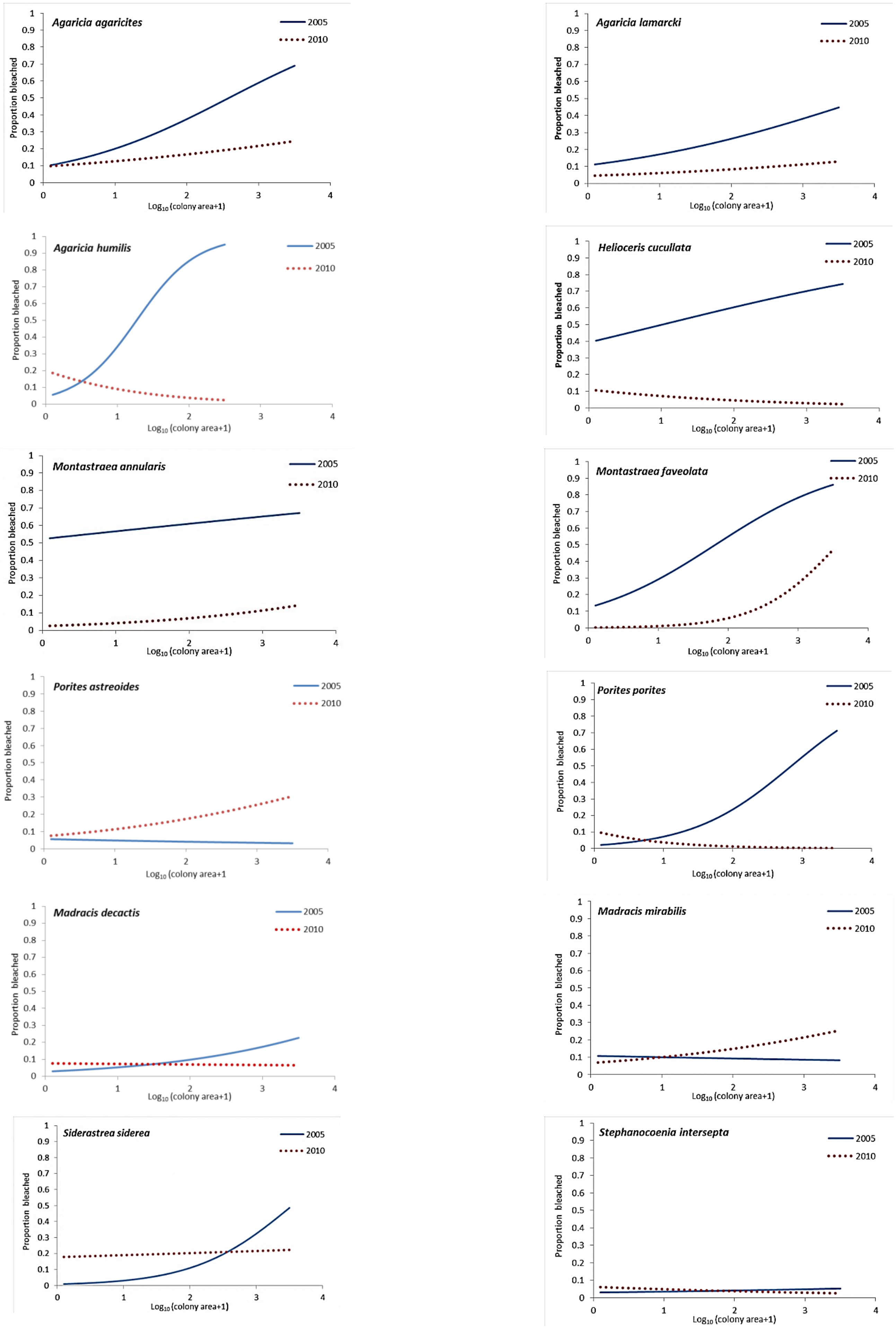


Figure 2.3.12. Species-specific bleaching intensity to different levels of thermal stress (2005 vs. 2010) as a function of colony size for 12 coral species common to the three study sites based on the bleaching model coefficients.

Table 2.3.6. Estimated coefficients for bleaching intensity based on the best model predicting the bleaching response as a function of colony size, species morphology and bleaching event.

	Dependent variable: Proportion of colony bleached (BLI)					
	Estimate	Std. Error	t value	lower	upper	p
Constant	-2.26	0.38	-5.91	-3.00	-1.51	0.000
SIZE	0.87	0.17	5.19	0.54	1.20	0.000
DATE 2010	-0.26	0.31	-0.84	-0.86	0.34	0.402
SPECIES *Agaricia humilis*	-0.82	0.79	-1.03	-2.37	0.74	0.303
SPECIES *Agaricia lamarcki*	0.14	0.78	0.18	-1.39	1.66	0.860
SPECIES *Helioceris cucullata*	1.82	0.55	3.31	0.74	2.90	0.001
SPECIES *Madracis decactis*	-1.28	0.60	-2.15	-2.46	-0.11	0.032
SPECIES *Madracis mirabilis*	0.14	0.78	0.19	-1.39	1.67	0.854
SPECIES *Montastraea annularis*	2.35	0.51	4.56	1.34	3.36	0.000
SPECIES *Montastraea faveolata*	0.29	1.08	0.26	-1.83	2.41	0.792
SPECIES *Porites astreoides*	-0.56	0.40	-1.41	-1.34	0.22	0.158
SPECIES *Porites porites*	-1.69	0.65	-2.60	-2.96	-0.41	0.010
SPECIES *Siderastrea siderea*	-2.55	0.39	-6.47	-3.33	-1.78	0.000
SPECIES *Stephanocoenia intersepta*	-1.22	0.88	-1.39	-2.94	0.50	0.166
MORPHOLOGY Encrusting	-0.27	0.16	-1.73	-0.58	0.04	0.085
MORPHOLOGY Keeled	-0.57	0.20	-2.82	-0.97	-0.18	0.005
MORPHOLOGY Plating	-0.89	0.20	-4.53	-1.28	-0.51	0.000
MORPHOLOGY Branching	-0.37	0.26	-1.45	-0.87	0.13	0.147
SIZE: SPECIES *Agaricia humilis*	1.54	0.64	2.41	0.29	2.80	0.017
SIZE: SPECIES *Agaricia lamarcki*	-0.33	0.42	-0.79	-1.15	0.49	0.432
SIZE: SPECIES *Helioceris cucullata*	-0.44	0.38	-1.18	-1.19	0.30	0.240
SIZE: SPECIES *Madracis decactis*	-0.21	0.35	-0.61	-0.90	0.47	0.543
SIZE: SPECIES *Madracis mirabilis*	-0.96	0.42	-2.30	-1.78	-0.14	0.022
SIZE: SPECIES *Montastraea annularis*	-0.69	0.24	-2.87	-1.17	-0.22	0.005
SIZE: SPECIES *Montastraea faveolata*	0.21	0.45	0.47	-0.66	1.09	0.636
SIZE: SPECIES *Porites astreoides*	-1.05	0.21	-5.04	-1.45	-0.64	0.000
SIZE: SPECIES *Porites porites*	0.51	0.38	1.36	-0.22	1.25	0.173
SIZE: SPECIES *Siderastrea siderea*	0.48	0.25	1.92	-0.01	0.98	0.055
SIZE: SPECIES *Stephanocoenia intersepta*	-0.70	0.63	-1.11	-1.95	0.54	0.268
DATE 2010: SPECIES *Agaricia humilis*	0.87	0.92	0.94	-0.94	2.68	0.347
DATE 2010: SPECIES *Agaricia lamarcki*	-0.79	0.92	-0.86	-2.60	1.02	0.392
DATE 2010: SPECIES *Helioceris cucullata*	0.17	0.78	0.22	-1.35	1.69	0.825
DATE 2010: SPECIES *Madracis decactis*	1.05	0.71	1.48	-0.34	2.44	0.138
DATE 2010: SPECIES *Madracis mirabilis*	-0.39	0.84	-0.46	-2.03	1.26	0.647
DATE 2010: SPECIES *Montastraea annularis*	-1.42	0.65	-2.20	-2.70	-0.15	0.028
DATE 2010: SPECIES *Montastraea faveolata*	-4.07	1.44	-2.82	-6.90	-1.24	0.005
DATE 2010: SPECIES *Porites astreoides*	-0.30	0.51	-0.58	-1.31	0.71	0.562
DATE 2010: SPECIES *Porites porites*	2.13	0.85	2.51	0.47	3.79	0.013
DATE 2010: SPECIES *Siderastrea siderea*	0.72	0.49	1.47	-0.24	1.69	0.143
DATE 2010: SPECIES *Stephanocoenia intersepta*	-0.45	1.27	-0.35	-2.93	2.04	0.726
SIZE: DATE 2010: SPECIES *Agaricia agaricites*	-0.55	0.18	-3.03	-0.91	-0.19	0.003
SIZE: DATE 2010: SPECIES *Agaricia humilis*	-1.25	0.75	-1.67	-2.72	0.22	0.095
SIZE: DATE 2010: SPECIES *Agaricia lamarcki*	0.00	0.51	0.01	-0.99	1.00	0.994
SIZE: DATE 2010: SPECIES *Helioceris cucullata*	-0.80	0.56	-1.44	-1.89	0.29	0.152
SIZE: DATE 2010: SPECIES *Madracis decactis*	-0.71	0.46	-1.56	-1.60	0.18	0.120
SIZE: DATE 2010: SPECIES *Madracis mirabilis*	0.12	0.49	0.25	-0.83	1.08	0.799
SIZE: DATE 2010: SPECIES *Montastraea annularis*	0.22	0.30	0.72	-0.37	0.81	0.469
SIZE: DATE 2010: SPECIES *Montastraea faveolata*	1.45	0.61	2.36	0.25	2.65	0.019
SIZE: DATE 2010: SPECIES *Porites astreoides*	0.17	0.26	0.65	-0.34	0.68	0.514
SIZE: DATE 2010: SPECIES *Porites porites*	-1.47	0.50	-2.95	-2.44	-0.49	0.004
SIZE: DATE 2010: SPECIES *Siderastrea siderea*	-0.24	0.32	-0.76	-0.87	0.38	0.446
SIZE: DATE 2010: SPECIES *Stephanocoenia intersepta*	0.59	0.90	0.65	-1.18	2.35	0.515

Groups	Name	Variance	Std.Dev.
QUAD:(transect:SITE)	(Intercept)	0.89	0.94
SIZE		0.23	0.48
transect:SITE	(Intercept)	0.32	0.57
SIZE		0.12	0.35
SITE	(Intercept)	0.20	0.44
SIZE		0.03	0.16
Residual		2.97	1.72

Log Likelihood	- 11,654.21
Akaike Inf. Crit. (Corrected)	22,702.03
Bayesian Inf. Crit.	23,167.80
Observations	5,564

Note: **p<0.1; **p<0.05; ***p<0.01*

2.3.6 Mortality – 2005 and 2010

Recovery from bleaching was assessed by quantifying the persistence of bleaching (Figure 2.3.4) along with signs of recent mortality (necrotic tissue, exposed skeleton not yet overgrown by macroalgae). Mortality was quantified both as prevalence (number of colonies showing signs of recent mortality) and severity of mortality (proportion of total coral surface area showing recent mortality). The former can inflate the overall estimate of mortality because it does not account for the degree of the response. As such, quantifying the proportion of colony affected by recent mortality provided a more accurate estimate of recent (bleaching related) mortality. Post-bleaching surveys conducted following both bleaching events revealed that most colonies survived the bleaching, and a small percentage remained pale (Figure 2.3.4). The prevalence and the severity of recent mortality varied between sites (Table 2.3.7).

By April 2006, 17% (SE =0.75) of colonies surveyed across all three sites showed signs of recent mortality. The severity of recent mortality across all three sites was estimated at 4% (SE= 0.3). For the affected colonies, the mean recent mortality per colony was 23% (SE= 1.0). Similar mortality patterns were observed in April 2011 with 18% (SE=0.66) of the surveyed colonies showing signs of partial mortality. Mean recent mortality across all three sites was estimated at 2% (SE=0.66). For affected colonies, the mean recent mortality per colony was 10% (SE=0.69). Partial mortality was highest at the Dairy Bull site (Figure 2.3.13, Table 2.3.7) where ~29% of the colonies showed recent mortality occurring mostly at the edges of colonies (8%, SE=0.78, mean recent mortality per colony). Total mortality was observed in <1% of the colonies.

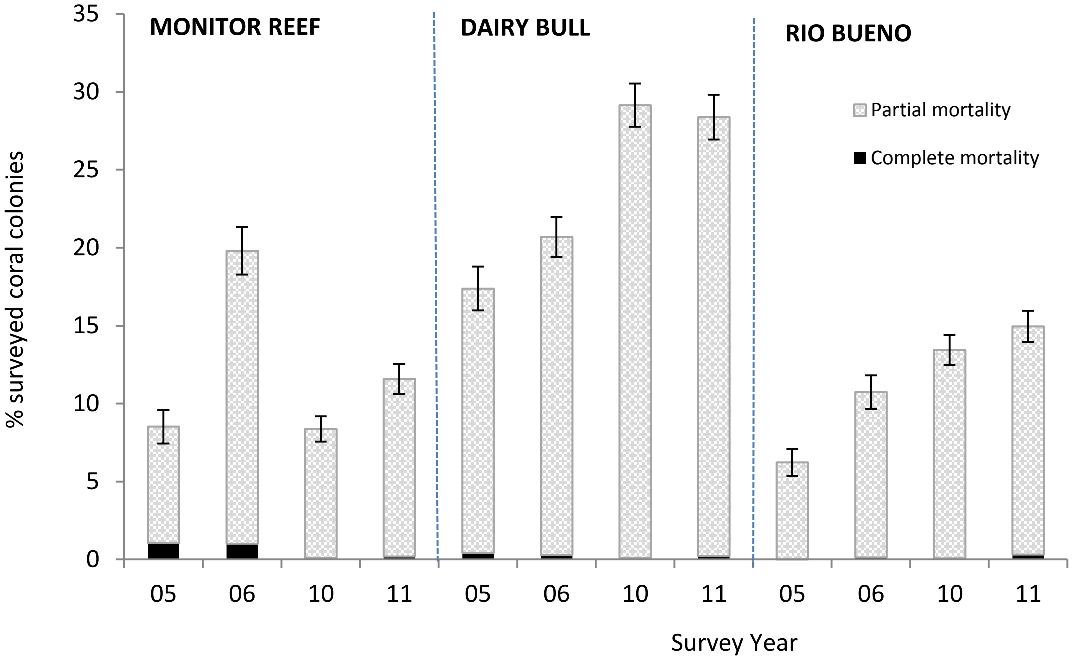


Figure 2.3.13. Percent of surveyed colonies with signs of recent mortality observed at each study site at the peak of the bleaching event (2005 and 2010) and five months later (2006 and 2011).

During both events *A. agaricites* experienced highest relative partial mortality at all three reef sites, followed by *M. annularis* on Monitor and Dairy Bull reefs (Figure 2.3.14). In 2010, 5-11% of *A. agaricites* and 6% of *M. annularis* presented signs of partial mortality, whereas for other species the recovery was strong with <4% showing signs of recent mortality.

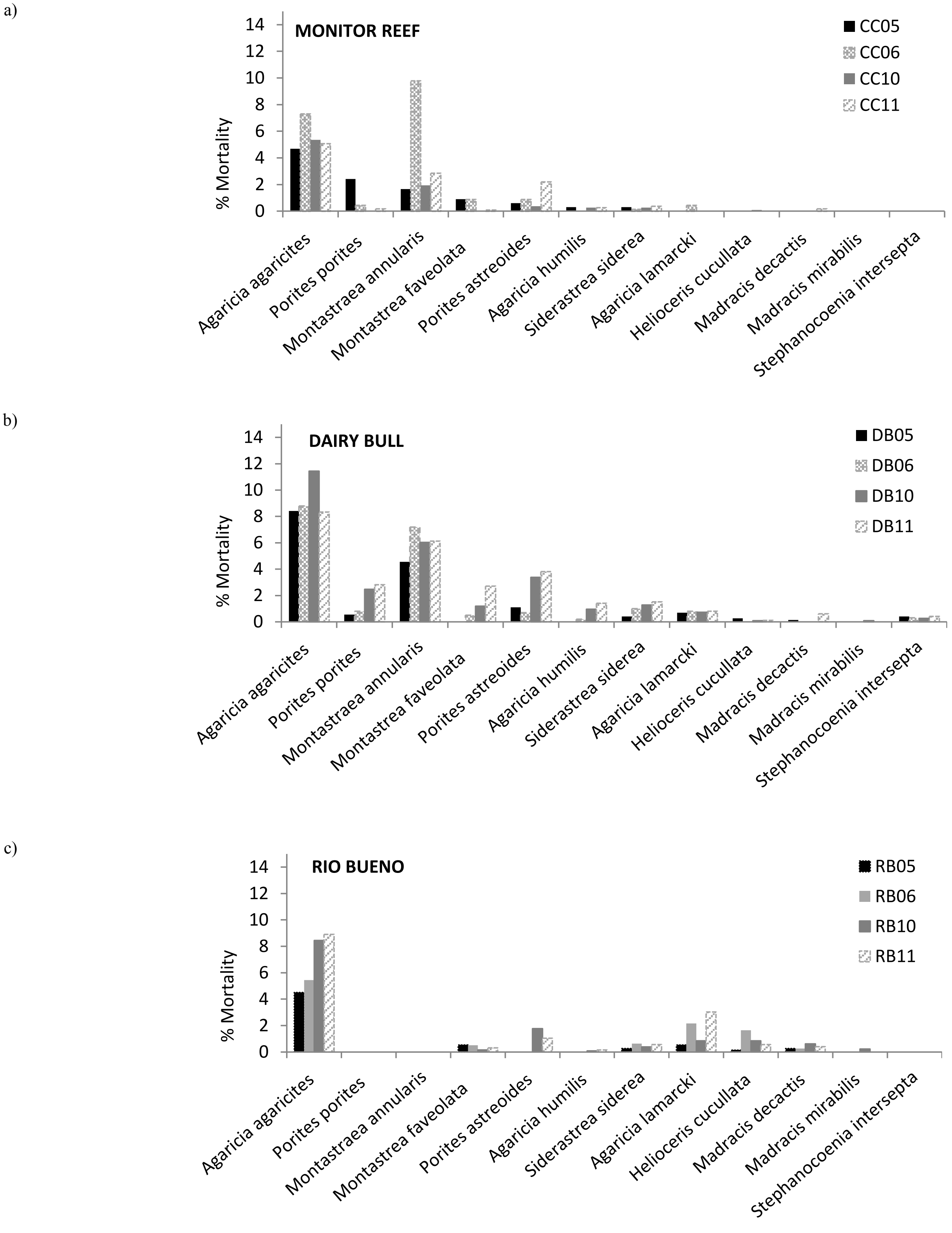


Figure 2.3.14. Percentage of colonies with partial mortality for the most common species observed during each survey year at (a) Monitor Reef, (b) Dairy Bull and (c) Rio Bueno reef sites.

2.3.7 Mortality and Colony Size

The evidence in support of a relationship between colony size and bleaching related mortality was weak across all sites and surveys (Figure 2.3.15). Except for the relatively higher prevalence of recent mortality among *A. agaricites* and *M. annularis,* there was a notable lack of trend between mortality and colony size between coral species (Figure 2.3.16). There was no obvious relationship between mortality and colony size for the five morphology types (Figure 2.3.17).

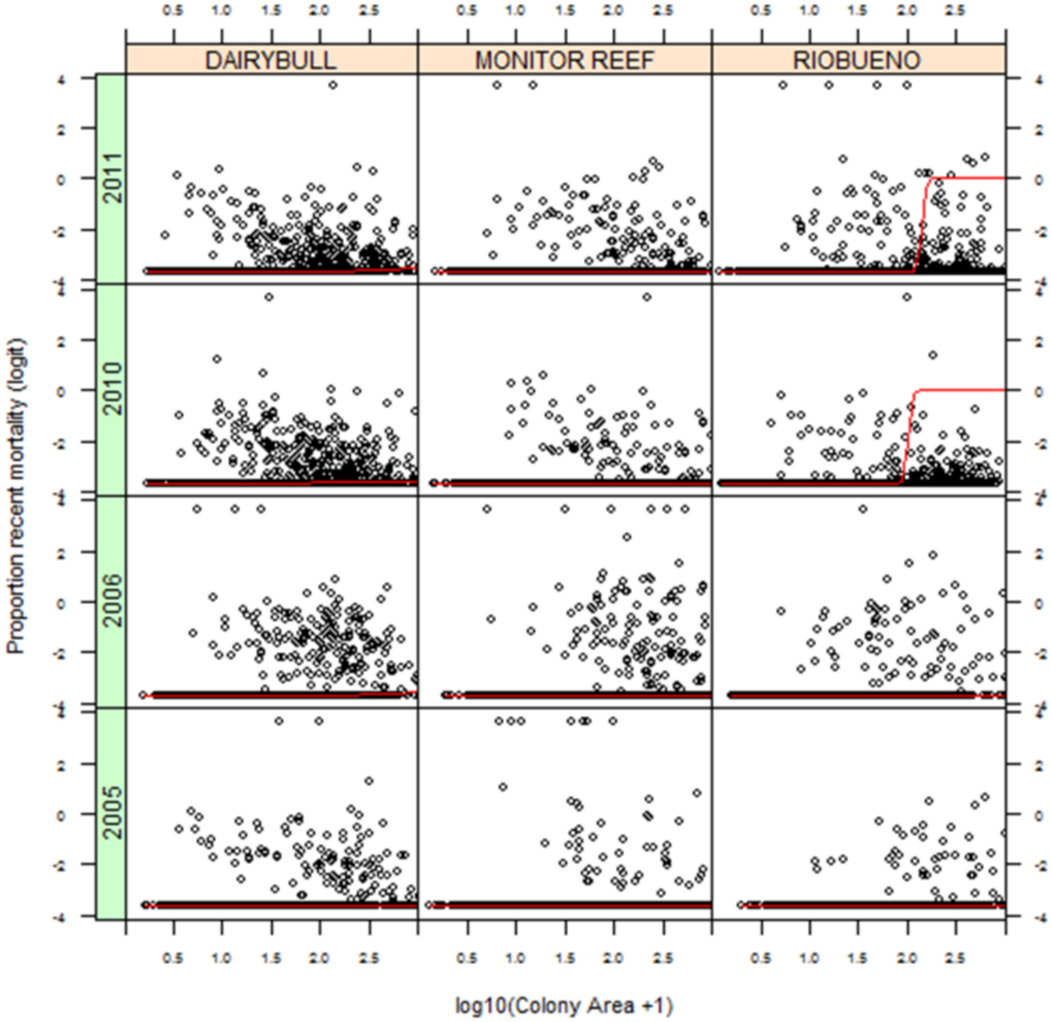


Figure 2.3.15. Recent mortality as a function of colony size observed at the three study sites during the bleaching and recovery surveys in 2006 and 2011. A loess smoother line was added for ease of visual interpretation.

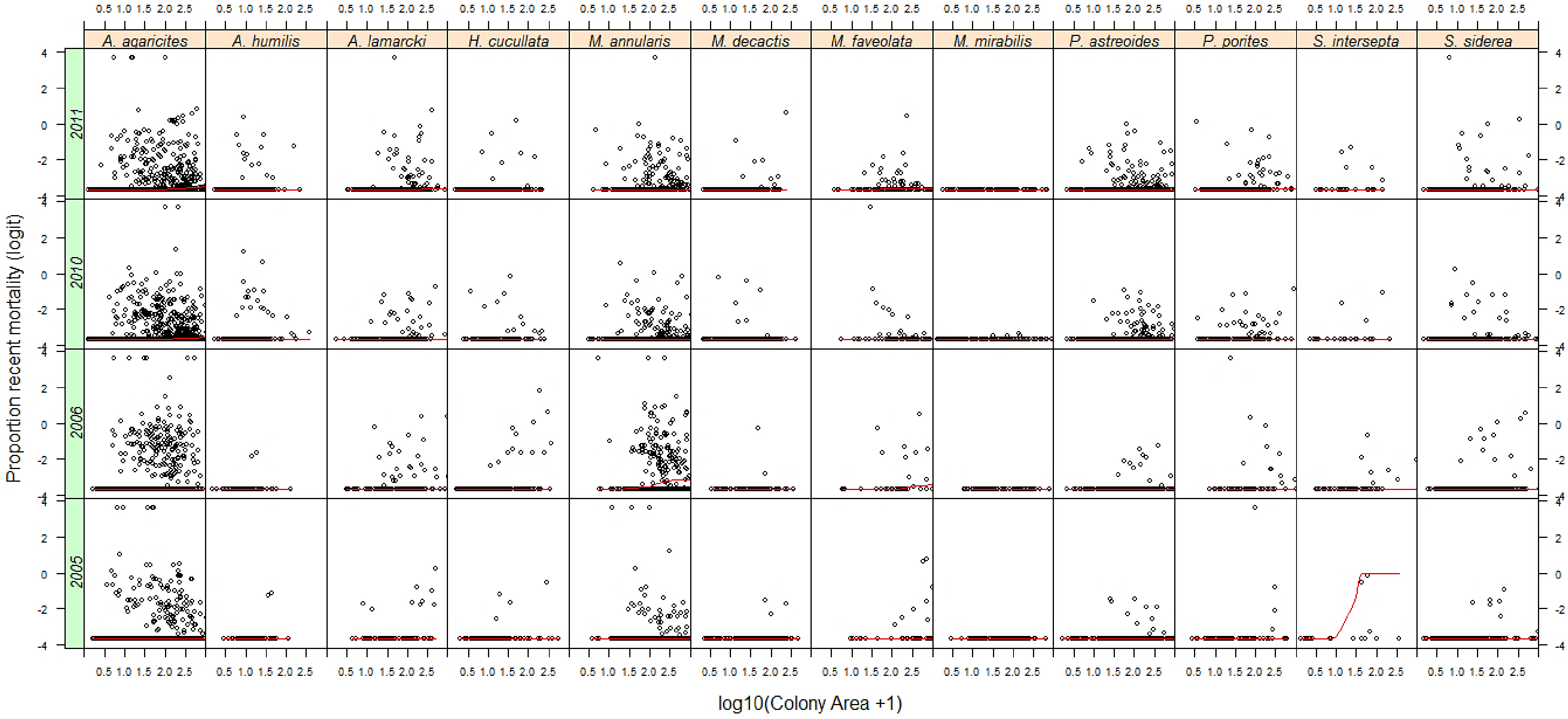


Figure 2.3.16. Recent mortality measured as proportion of the colony surface area, showing recent mortality as a function of colony size for the twelve common species observed during the 2005 and 2010 bleaching surveys, and the follow-up surveys conducted in 2006 and 2010. A loess smoother line was added for ease of visual interpretation.

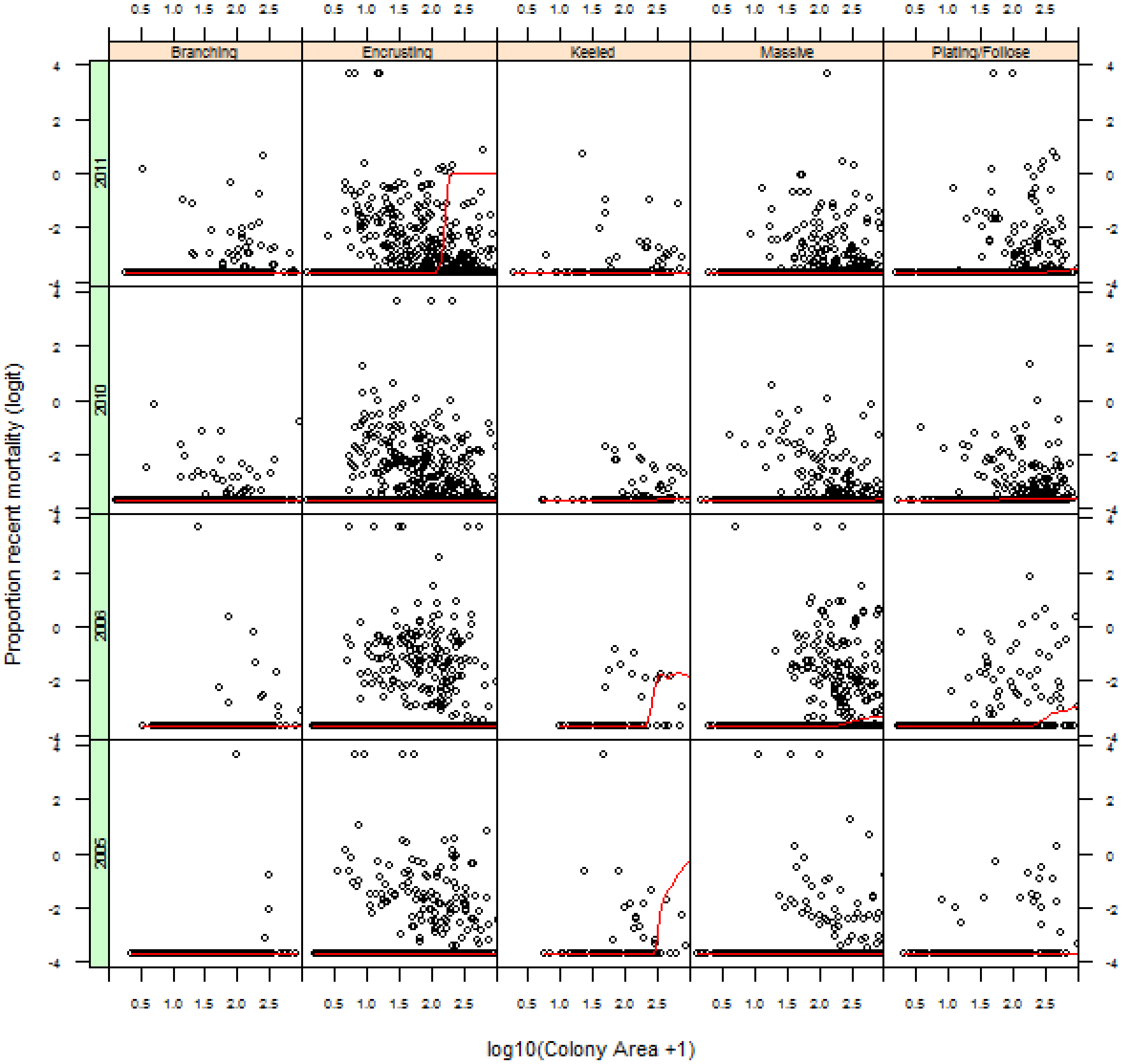


Figure 2.3.17. Recent mortality as a function of colony size for 5 morphologies: branching, encrusting, keeled, massive, and plating/foliose. A loess smoother line was added for ease of visual interpretation.

Table 2.3.7. Summary of recent mortality, including the number of colonies affected by recent mortality as well as the mean proportion of colony surface area showing recent mortality at each of the study sites for all the survey years.

MONITOR REEF	Total # Colonies	No Mortality	Recent Mortality	Colonies With Recent Mortality (%)	SE	Mean proportion of colony surface recently dead	SE	Total mortality (recent + old) (proportion)	SE
2005	669	612	57	8.5	0.01	0.026	0.01	0.040	0.006
2006	687	551	136	19.8	0.02	0.059	0.01	0.125	0.009
2010	1147	1051	96	8.4	0.01	0.012	0.01	0.028	0.003
2011	1088	962	126	11.6	0.01	0.015	0.01	0.052	0.004

DAIRY BULL	Total # Colonies	No Mortality	Recent Mortality	Colonies With Recent Mortality (%)	SE	Mean proportion of colony surface recently dead	SE	Total mortality (recent + old) (proportion)	SE
2005	725	599	126	17.38	0.01	0.030	0.004	0.045	0.005
2006	1001	794	207	20.68	0.01	0.040	0.004	0.064	0.005
2010	1081	766	315	29.14	0.01	0.023	0.002	0.055	0.004
2011	987	707	280	28.37	0.01	0.022	0.002	0.063	0.005

RIO BUENO	Total # Colonies	No Mortality	Recent Mortality	Colonies With Recent Mortality	SE	Mean proportion of colony surface recently dead	SE	Total mortality (recent + old) (proportion)	SE
2005	756	709	47	6.22	0.01	0.011	0.002	0.033	0.004
2006	820	732	88	10.73	0.01	0.024	0.003	0.047	0.005
2010	1302	1127	175	13.44	0.01	0.008	0.001	0.060	0.004
2011	1257	1609	188	10.46	0.01	0.018	0.003	0.100	0.006

2.3.8 Mortality Model

A second model was developed to examine the relationship between mortality and coral colony size. Due to the delayed nature of bleaching related mortality, only post bleaching mortality data (2006 and 2011) were used in the model. Since the precise cause of mortality among corals can be difficult to determine (Eakin et al. 2010), only recent mortality was assumed to be due to thermal stress.

As with the bleaching response model, the saturated mortality model included colony size, species, morphology, survey date and all relevant interaction terms. Reef sites were treated as random effects. A single best component model was identified through the model-inference process (Table 2.3.8). Other models had ΔAIC > 4 and weight <0.2 suggesting poor support for the models. The best model is described by the following equation:

Equation (4) MORT ~ SIZE + DATE + SPECIES+ MORPHOLOGY +

SIZE: SPECIES+DATE: SIZE + DATE: SPECIES + DATE: MORPHOLOGY+

(SIZE|SITE/TRANSECT/QUAD)

Table 2.3.8. Model inference selection outcome for the single best component model predicting colony mortality as a function of colony size, species, morphology and survey date.

	df	logLik	AICc	Delta	Weight
MORT ~ SIZE+ DATE + SPECIES+ MORPHOLOGY+SIZE:SPECIES+DATE:SIZE + DATE:SPECIES+DATE:MORPHOLOGY	55	-6972.52	13908.24	0	0.98

All the fixed effect terms and selected interaction terms for the best model were significant (Table 2.3.9) except for Species (p=0.24) and Date (p=0.032) terms which were retained in the model because of their relative importance and inclusion in interaction terms.

Table 2.3.9. Analysis of deviance for the fixed effect variables and the interaction terms predicting mortality as a function of colony size, species and morphology across all the survey dates, retained in the final model. The relative importance of each term is included.

Fixed Effects	Chisq	Df	p-value	Relative variable importance
Intercept	918.1316	1	<2.2e-16	-
Size	211.7208	1	<2.2e-16	1.0
Date	4.6231	3	0.0315449	1.0
Species	13.9061	11	0.2382347	1.0
Morphology	36.9768	4	1.821e-07	1.0
Size:Species	53.4694	11	1.475e-07	1.0
Size:Date	54.2491	1	1.766e-13	1.0
Date:Species	72.3386	11	4.379e-11	1.0
Date:Morphology	20.5362	4	0.0003913	0.98

Effect size was calculated for the individual main fixed effect variables in the model using the plotLMER.fnc (Figure 2.3.18). The effect of colony size on bleaching related mortality (proportion of colony area exhibiting partial mortality) was positive but low (effect size=0.11). The degree of recent mortality did not vary significantly among species (effect size =0.03) or among morphologies (effect size =0.02). Low levels of bleaching related mortality were observed during the recovery surveys (5 months after the onset of bleachign) for both bleaching events (effect size = .01).

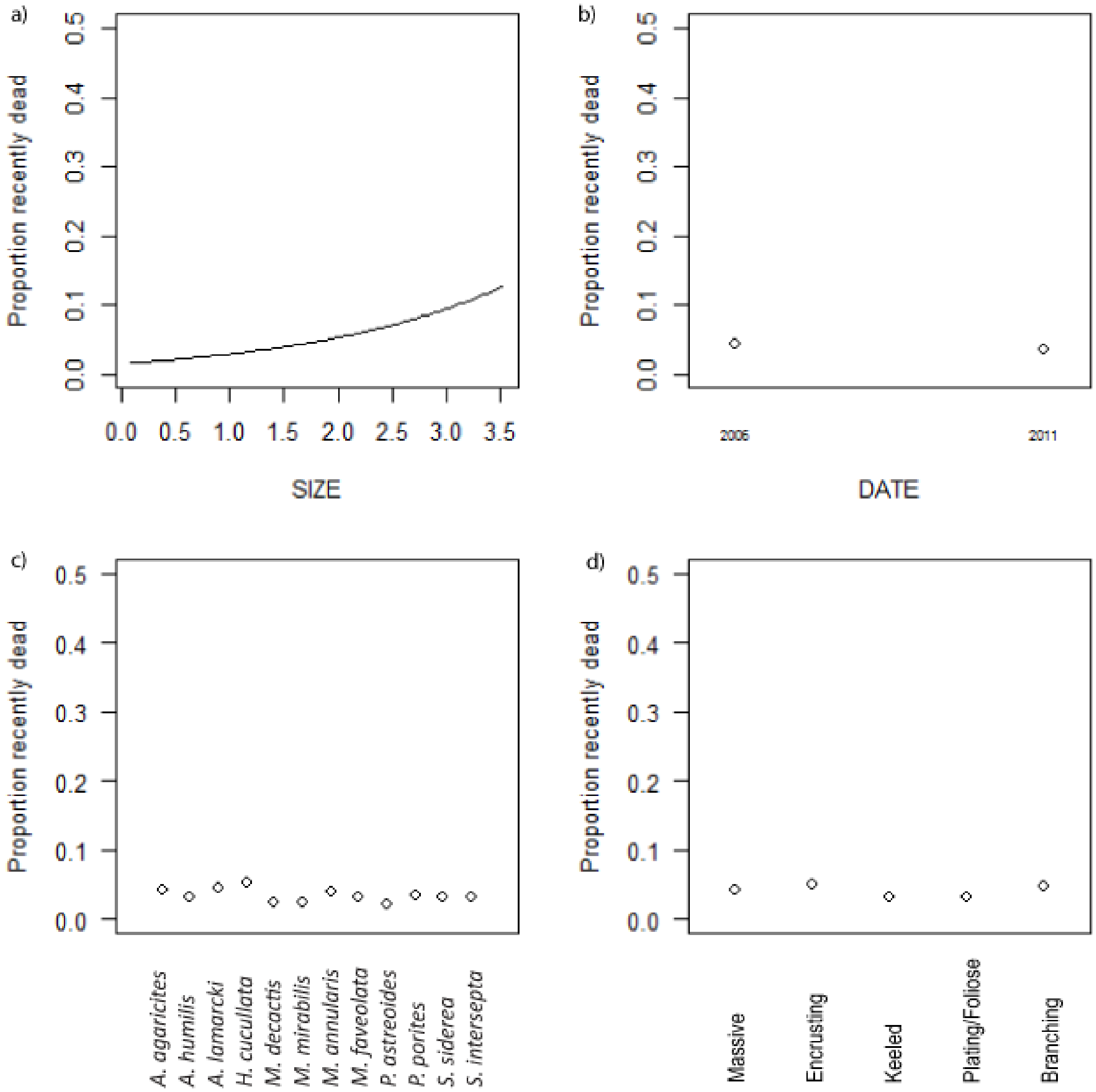


Figure 2.3.18. Effect size for recent mortality (partial mortality) explained by the main fixed effects variables included in the mortality model: (a) the effect size for recent mortality as a function of colony surface area; (b) effect size for differences in recent mortality between 2006 and 2011 surveys; (c) effect size for recent mortality of the 12 dominant species included in the model; (d) effect size for differences in recent mortality for the 5 main colony morphology types.

The model explained 16% of the variance in the observed mortality data between bleaching events. Size explained 6%, morphology 0.001%, species 3% and date 3% of the variance. The random effect (Site) explained 5% of the variance.

Table 2.3.10. Marginal and conditional R^2 values were calculated to assess the overall model fit of the mortality model.

	Marginal R^2	Conditional R^2	Component contribution
Model 1	0.11	0.16	0.05*
Model 1- SIZE	0.04		0.06
Model 1 - MORPHOLOGY	0.102		0.001
Model 1- SPECIES	0.07		0.03
Model 1- DATE	0.07		0.03

** Component contribution of the random term in the model.*

Coefficients for the mortality model are presented in Table 2.3.11, and the corresponding graphs for each fixed effect in the mortality model are presented in Figure 2.3.19, Figure 2.3.20 and Figure 2.3.21.

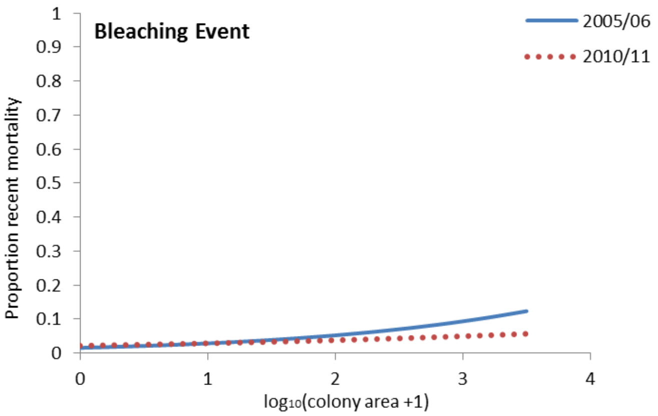


Figure 2.3.19. The relationship between recent mortality and colony size was weak but positive. Larger colonies are more likely to experience partial mortality due to bleaching.

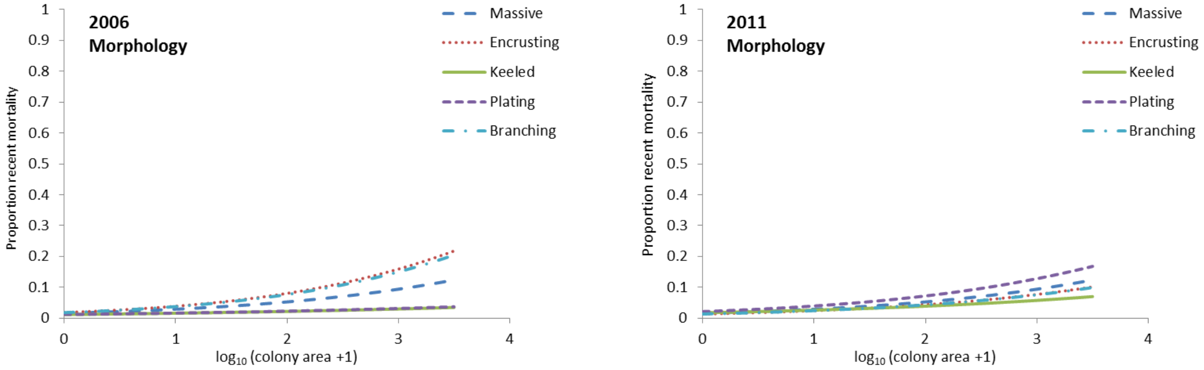


Figure 2.3.20.The relationship between recent mortality and colony morphology. In 2006 mortality was higher among encrusting, branching and massive colonies, whereas in 2011 plating and massive colonies suffered more partial mortality.

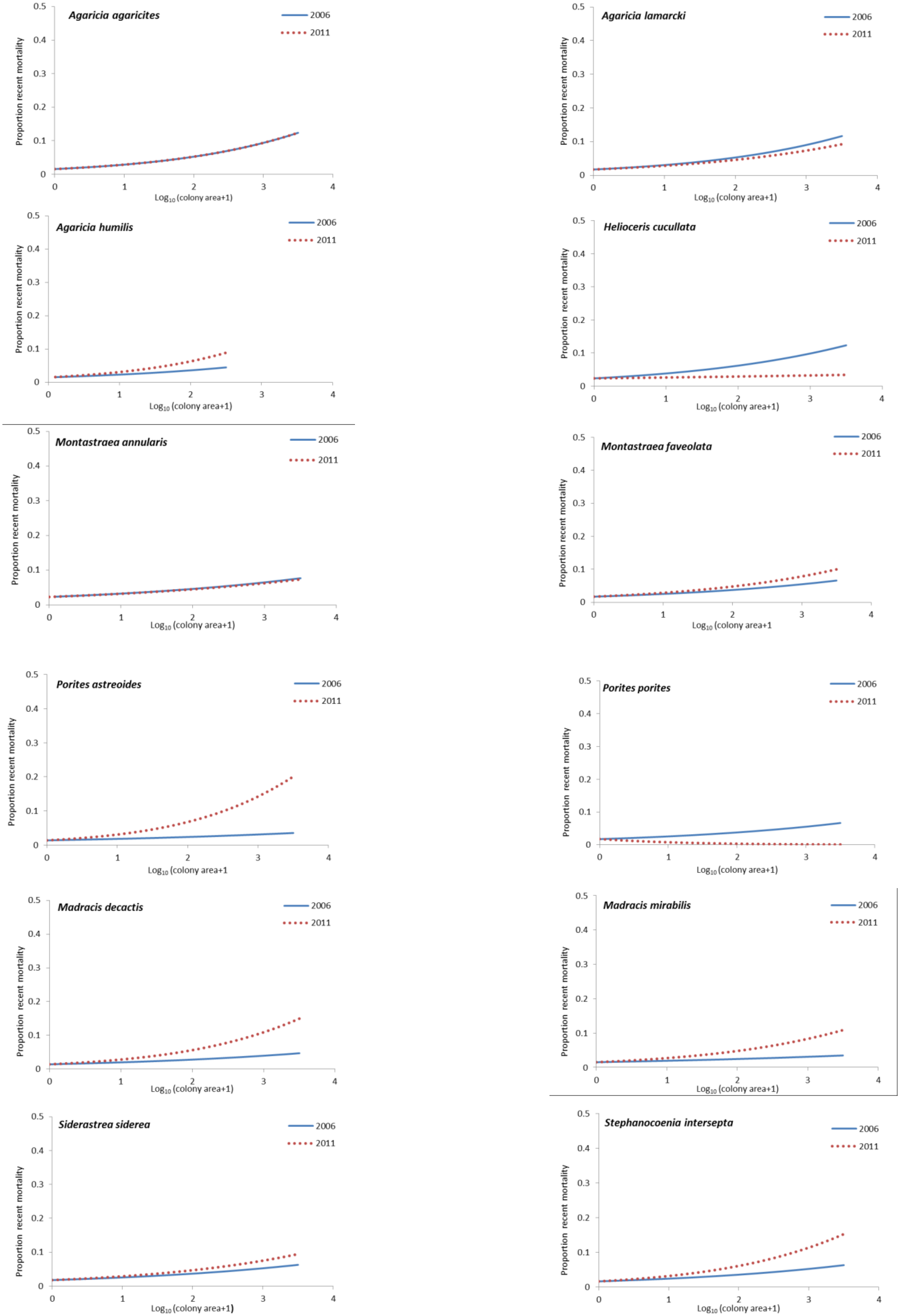


Figure 2.3.21. The relationship between proportion of recent mortality and colony size for the 12 species common to the three study sites based on the mortality model coefficients.

Table 2.3.11. Estimated coefficients for bleaching related mortality based on the best model (MM.7) describing mortality as a function of colony size, species morphology and bleaching event.

	Dependent variable: Recent Mortality (MORT)					
Fixed Effects	Estimate	Std.Error	t -value	lower	upper	p-value
CONSTANT	-4.13	0.14	-30.30	-4.40	-3.87	0.000
SIZE	0.62	0.04	14.55	0.54	0.71	0.000
DATE2011	0.35	0.16	2.15	0.03	0.66	0.032
SPECIES *Agaricia humilis*	-0.07	0.17	-0.38	-0.40	0.27	0.702
SPECIES *Agaricia lamarcki*	0.12	0.18	0.66	-0.23	0.46	0.511
SPECIES *Helioceris cucullata*	0.41	0.16	2.50	0.09	0.73	0.013
SPECIES *Madracis decactis*	-0.15	0.22	-0.67	-0.59	0.29	0.504
SPECIES *Madracis mirabilis*	-0.04	0.26	-0.16	-0.54	0.46	0.875
SPECIES *Montastraea annularis*	0.38	0.19	2.00	0.01	0.75	0.046
SPECIES *Montastraea faveolata*	0.10	0.29	0.34	-0.47	0.66	0.737
SPECIES *Porites astreoides*	-0.15	0.12	-1.24	-0.39	0.09	0.215
SPECIES *Porites porites*	0.11	0.28	0.38	-0.43	0.65	0.701
SPECIES *Siderastrea siderea*	0.11	0.15	0.74	-0.19	0.42	0.462
SPECIES *Stephanocoenia intersepta*	0.04	0.29	0.12	-0.53	0.60	0.901
MORPHOLOGY Encrusting	0.15	0.12	1.25	-0.09	0.39	0.213
MORPHOLOGY Keeled	-0.30	0.16	-1.92	-0.61	0.01	0.055
MORPHOLOGY Plating	-0.29	0.15	-1.91	-0.59	0.01	0.057
MORPHOLOGYBranching	0.13	0.20	0.65	-0.27	0.53	0.516
SIZE :SPECIES *Agaricia humilis*	-0.17	0.14	-1.19	-0.44	0.11	0.236
SIZE :SPECIES *Agaricia lamarcki*	-0.05	0.08	-0.61	-0.22	0.11	0.541
SIZE :SPECIES *Helioceris cucullata*	-0.12	0.10	-1.24	-0.30	0.07	0.215
SIZE :SPECIES *Madracis decactis*	-0.26	0.11	-2.41	-0.47	-0.05	0.016
SIZE :SPECIES *Madracis mirabilis*	-0.38	0.11	-3.50	-0.59	-0.17	0.0005
SIZE :SPECIES *Montastraea annularis*	-0.26	0.07	-3.65	-0.40	-0.12	0.0003
SIZE :SPECIES *Montastraea faveolata*	-0.22	0.12	-1.88	-0.46	0.01	0.060
SIZE :SPECIES *Porites astreoides*	-0.34	0.06	-5.84	-0.46	-0.23	0.000
SIZE :SPECIES *Porites porites*	-0.22	0.11	-2.06	-0.44	-0.01	0.040
SIZE :SPECIES *Siderastrea siderea*	-0.25	0.07	-3.63	-0.38	-0.11	0.0003
SIZE :SPECIES *Stephanocoenia intersepta*	-0.22	0.18	-1.24	-0.57	0.13	0.215
SIZE :DATE 2011	-0.34	0.05	-7.37	-0.43	-0.25	0.000
DATE 2011:SPECIES *Agaricia humilis*	0.29	0.12	2.43	0.06	0.53	0.016
DATE 2011:SPECIES *Agaricia lamarcki*	-0.07	0.13	-0.56	-0.33	0.18	0.574
DATE 2011:SPECIES *Helioceris cucullata*	-0.39	0.14	-2.85	-0.67	-0.12	0.005
DATE 2011:SPECIES *Madracis decactis*	0.37	0.20	1.83	-0.03	0.76	0.067
DATE 2011:SPECIES *Madracis mirabilis*	0.35	0.25	1.41	-0.14	0.83	0.158
DATE 2011:SPECIES *Montastraea annularis*	-0.01	0.15	-0.08	-0.32	0.29	0.933
DATE 2011:SPECIES *Montastraea faveolata*	0.13	0.18	0.71	-0.23	0.48	0.477
DATE 2011:SPECIES *Porites astreoides*	0.55	0.08	7.21	0.40	0.70	0.000
DATE 2011:SPECIES *Porites porites*	0.14	0.25	0.56	-0.35	0.63	0.576
DATE 2011:SPECIES *Siderastrea siderea*	0.13	0.15	0.87	-0.16	0.41	0.385
DATE 2011:SPECIES *Stephanocoenia intersepta*	0.28	0.22	1.29	-0.14	0.71	0.196
DATE 2011:MORPHOLOGY Encrusting	-0.17	0.14	-1.20	-0.44	0.11	0.232
DATE 2011:MORPHOLOGY Keeled	0.10	0.19	0.52	-0.27	0.46	0.606
DATE 2011:MORPHOLOGY Plate	0.30	0.18	1.71	-0.04	0.65	0.087
DATE 2011:MORPHOLOGY Branching	-0.16	0.25	-0.62	-0.66	0.34	0.534

Random Effects	***Variance***	***Std.Dev.***
QUAD: TRANSECT: SITE	0.037	0.193
SIZE	0.058	0.240
TRANSECT: SITE	1.21e-12	1.10e-06
SIZE	0.002	0.045
SITE	0.00e+00	0.00e+00
SIZE	4.15e-05	0.006
Residual	0.599	0.774

Log Likelihood	- 6,972.52
Akaike Inf. Crit. (Corrected)	13,908.24
Bayesian Inf. Crit.	14,421.85
Observations	5,763.00

2.4 Discussion

The response of corals to elevated sea surface temperatures is decidedly complex and variable (Lang et al. 1992; Kramer and Kramer 2000). In the present study, which spanned two bleaching events, bleaching patterns indicated that some coral species were more likely to bleach than others, that conspecifics exposed to the same thermal stress conditions had dissimilar responses, and that even within a single colony bleaching could be distinctly uneven or mottled. Understanding the underlying mechanisms for the observed disparity in the coral bleaching response between reef areas and between bleaching events is essential to being able to predict potential impacts on coral assemblages and community trajectories in response to the anticipated increase in the frequency of thermal stress events.

2.4.1 2005 and 2010 Bleaching Events

Summer sea surface temperature patterns and the hotspot formation in 2005 and 2010 led to warnings and predictions of extensive bleaching throughout the Caribbean. In 2005, accumulated heat stress values were at 3 DHW by the end of the summer, and peaked at 7 DHW by late October. In 2010, the accumulated heat stress during the summer months was somewhat mitigated by storms but still reached 5 DHW by October. A noteworthy difference between the 2005 and 2010 bleaching events were the storms. Despite being one of the most active hurricane seasons on record (Wilkinson and Souter 2008), the summer of 2005 was remarkable on Jamaica's north coast due to doldrums. Minimal wind activity and lack of summer storms meant no relief from the constant summer heat. High SSTs lasted into late November and started to return to more seasonal values by January. In contrast, the hot summer months in 2010 were punctuated by storms. In September tropical storm Nicole brought diluvial rains to much of

Jamaica resulting in a temporary drop in sea surface temperatures. In early November, more rain came with Hurricane Tomas (a Category 2 event) which grazed the eastern tip of Jamaica en route to Haiti. In 2010, the stormy conditions played an important role in bringing the sea surface temperatures rapidly back into their normal seasonal range by mid-November. The passage of the hurricane and the resulting vertical mixing of the water column alleviated thermal stress on coral reefs and accelerated recovery for bleached corals (Manzello et al. 2007).

In 2005 and 2010, high sea surface temperatures caused widespread bleaching on Jamaica's north coast reefs. Both events were characterized by extensive coral bleaching but relatively low mortality. In October 2005, 28-57% of the colonies surveyed along the 9 m contour at the three study sites were bleached. By April 2006, 10% of the corals remained pale/partially bleached and recent mortality due to bleaching was 4%. In October 2010, 23-50% of corals surveyed at the same sites were bleached. By April 2011, 12% of the colonies remained pale/partially bleached and mortality due to bleaching was estimated at 2%. Although the bleaching prevalence was similar between the two events, bleaching intensity in 2005 was higher than in 2010, corresponding to the higher accumulated thermal stress (DHW) observed in 2005.

2.4.2 Bleaching model interpretation

The mixed effects bleaching model, describing the bleaching response as a function of colony size conditional on species, morphology and survey date, explained 51% of the variance observed in the data that spanned two bleaching events. Collectively, the main fixed effects in the model accounted for 26% of the variance, 17% of which was attributed to species-specific susceptibility to bleaching, 5% to colony size, 4% to differences in bleaching intensity between the two bleaching events, and <1% to colony morphology. The random factors in the model (site/transect/quadrat) explained the remaining 25% of the variance in the bleaching response.

Within random effects, most of the variability in bleaching intensity was detected at the quadrat level which reflects spatial differences in exposure to stress. The component variability in the bleaching model attributed to the nested site term (site/transect/quadrat) was relatively high but consistent with other studies which also attributed a large portion of explained variance in bleaching to random terms, including location and time. Yee (2008) examined the relationship between the bleaching response and various environmental variables and found that random variables, namely location and time, explained much more of the variance than the environmental (fixed) variables under consideration. Assuming there were no local "historical" mechanisms or other site-specific random processes at play, the results suggest that there were other environmental (fixed) factors, which were not included in the bleaching model, and which could explain some of the residual variance. For example, water velocity, a rate-determining factor in mass transfer may influence the intensity of bleaching, and may therefore explain some of the variance observed in the bleaching prevalence and intensity among sites. Nakamura and van Woesik (2001) demonstrated that coral colonies growing in high-water flow habitats were more resistant to the combination of thermal stress and high irradiance than colonies in low water-flow habitats.

In the bleaching model, the temporal factor was treated as a fixed effect to determine how much of the variance could be explained by the difference in bleaching intensity between the two bleaching events. Each of the fixed effects and the corresponding interaction terms in the model are discussed in turn.

2.4.3 Colony Size and Bleaching

Although colony size alone explained a small percent (5%) of the variability in bleaching intensity observed during the two events, it was a statistically significant predictor of bleaching. The effect size of bleaching intensity (proportion of colony bleached) for small (2-100 cm^2) colonies was 0.3, 0.43 for small to medium colonies (100-350 cm^2), 0.53 for medium to large colonies (350-1000 cm^2), and 0.63 for the largest colonies (> 1000 cm^2) (Figure 2.3.10). On average, there was a twofold difference in bleaching intensity between the smallest and the largest size classes. Size-modulated bleaching patterns observed in the current study provide further evidence that physical characteristics of coral colonies, including size and shape, influence colony-level response to thermal stress. The higher bleaching intensity observed among larger coral colonies was consistent with predictions made by Nakamura and van Woesik (2001) who hypothesized that under the same water flow regime, smaller colonies would fare better under thermal stress conditions than larger ones due to higher mass transfer to and from smaller colonies.

2.4.4 Species, Colony Size and Bleaching

Despite similar summer temperature patterns between the 2005 and 2010 bleaching events, the differences in the duration of sustained thermal stress (DHW) were reflected in the bleaching prevalence and intensity observed for each coral species (Table A.2, Table A.3). Of the 12 dominant species common to the study sites some were clearly more susceptible to thermal stress than others. *Montastraea annularis, Montastraea faveolata, Agaricia agaricites, Agaricia humilis, and Helioceris cucullata* were most sensitive to high temperatures, exhibiting the highest bleaching intensity, and remaining bleached for months after the thermal stress had abated.

The effect of colony size on bleaching was most evident when examined in the context of individual species. Like colony size, the Species main effect term in the final model was significant (p=0.001) as was the Size: Species interaction term (p=0.001) indicating that the relationship between bleaching and colony size varied among species (Figure 2.3.12).

Agaricids were among the first species to bleach and showed high susceptibility to thermal stress during both events (Figure 2.3.6). 51% of *A. agaricites* and 59% of *A. humilis* colonies bleached in 2005, and 46% and 63% in 2010, respectively (Table A.2). Bleaching intensity for the Agaricids was higher in 2005 (Table A.3), with colonies more likely to bleach fully, compared to 2010 when most colonies presented variegated bleaching patterns. The differences in bleaching intensity corresponded to differences in DHW between the two events. The positive relationship between bleaching intensity and colony size observed for *A. agaricites, A. humilis, A. lamarcki* and *H. cucullata* in 2005 (Figure 2.3.12), was less notable in 2010, indicating that at least for these species, larger colonies were more susceptible when exposed to sustained thermal stress (7 DHW) as was the case in 2005.

For *Montastraea* species bleaching prevalence (Table A.2) and intensity (Table A.3) were also high during both events. The mean bleaching intensity for *M. annularis* varied between events, (0.63 in 2005 and 0.51 in 2010), but the effect size of bleaching intensity as a function of colony size varied only marginally for each event (Figure 2.3.12). In contrast, *M. faveolata* colonies showed a very strong relationship between bleaching intensity and colony size. *Montastraea* species are highly susceptible to thermal stress (Oxenford et al. 2008; Brandt and McManus 2009), and suffered high rates of mortality in other parts of the Caribbean during the 2005 bleaching event (Rogers et al. 2009). Since the demise of *A. cervicornis* in the 1980s (Alvarez-Filip et al. 2009), *M.annularis* become the main reef building species, providing much of the remaining topographical complexity on many Jamaican reefs (Aronson and Precht 2001). Especially at Dairy Bull, *M. annularis* colonies maintained the architectural complexity of the reef and served as the foundation taxon in the phase shift reversal observed at the site (Idjadi et al. 2006). The bleaching susceptibility of *M. annularis* is of concern in the short-term because of the potential for widespread bleaching-related mortality, and in the long-term due to latent negative impacts on coral growth and reproductive potential (Munday et al. 2009); both can negatively impact the resilience of the reefs.

The most thermally resistant species were *Madracis* spp., *Porites astreoides* and, *Stephanocoenia intersepta. P. astreoides* did not present any bleaching in 2005; however, in 2010 "partial bleaching" was observed along colony edges and around lesions, a pattern more consistent with disease or other environmental stressors than bleaching. For the branching *P. porites,* bleaching intensity as a function of colony size differed between events (Figure 2.3.12). In 2005, bleaching among smaller colonies was observed primarily on the tips of branches, whereas larger colonies tended to bleach completely. The relationship between bleaching intensity and colony size for *P. porites* was not apparent in 2010.

Siderastrea siderea colonies presented signs of mild bleaching during both events (Table A.3). In 2005, larger colonies were more affected than smaller ones, whereas in 2010 colonies of all sizes exhibited low intensity bleaching (Figure 2.3.12). Bleaching appeared as blotchiness or pale blue colour across a colony's surface area. Among larger *Siderastrea siderea* colonies bleaching was confined to colony tops while the sides (shaded surfaces) retained their normal brown colouration; this bleaching pattern is indicative of solar irradiance acting synergistically with elevated sea temperature to cause bleaching (Eakin et al. 2009). *Madracis* and *Stephanocoenia* species showed consistent resistance to thermal stress during both bleaching events. *Madracis* morphospecies are strongly associated with a single clade of zooxanthellae (clade B) across different habitats, and hardly ever bleach (Fitt and Warner 1995; Diekmann et al. 2002).

In terms of differential species susceptibility to thermal stress, field observations from the current study were consistent with other studies in the region, which documented species-specific variability in the response to thermal stress, with individual taxa showing different degrees of bleaching and recovery. In St. Croix, USVI the elevated summer SSTs in 2005 resulted in 51% of the live coral cover bleaching (Clark et al. 2009). *M. annularis* and *Agaricia sp*. experienced the highest degree of bleaching while *Dedndrogyra cylindrus, Eusmilia fastigiata, Mussa angulosa, Mycetophyllia aliciae* and *Scolymia* spp. did not present any signs of bleaching. In Barbados, where the 2005 bleaching event was deemed to be the most severe bleaching episode documented on the island, 71% of coral colonies were bleached (Oxenford et al. 2008). The most severely bleached species were *Agaricia* spp. followed by *Favia fragum*, *Dendrogyra cylindricus*, and *Millepora spp.* The most resistant species were *Colpophyllia natans* and

Madracis decactis with less than 10% of colonies bleached. By contrast, Brandt (2009) reported that among the scleractinian corals found on inshore patch reefs in the Florida Keys, *Colpophyllia natans* and *Diploria strigosa* were most susceptible to bleaching while *Stephanocoenia intersepta* colonies were most resistant.

Although *Colpophyllia natans, Diploria labyrinthiformis* and *Diploria strigosa* colonies were not abundant in our surveys, 30% of the colonies of these species (pooled across all sites, n=19) experienced partial bleaching in 2005. Bleaching prevalence among the massive brain coral species was lower in 2010 with ~ 18% of colonies showing partial bleaching (n=38). A larger sample size of these massive coral species would be required to determine their susceptibility to thermal stress.

The relationship between colony size and susceptibility to thermal bleaching was investigated in other studies where they found greater resistance to bleaching among smaller colonies (Mumby 1999; Loya et al. 2001; Shenkar et al. 2005). Higher resistance/tolerance among smaller colonies and recruits under high thermal and high irradiance conditions has been attributed to higher rates of passive diffusion (Nakamura and van Woesik 2001), and to the presence of photo-protective fluorescent proteins (Papina et al. 2002) which are found in higher concentrations in small colonies than in larger ones. Bena and van Woesik (2004) observed that planula and newly settled recruits tend to have higher concentrations of photo-protective pigments which may confer protection to this size group during prolonged periods of high thermal and irradiance stress. Other physiological mechanisms, including antioxidant systems (Richier et al. 2005) and

UV-absorbing mycosporine-like amino acids within the coral tissue (Shick and Dunlap 2002) may also contribute to coral acclimatization to thermal stress .

Along with the species effect, colony size partially explained the differential bleaching among and within species. The residual variance in the bleaching response not explained by the bleaching model suggests that there are other causal factors at play. While there is no consensus as to the dominant or primary factors that determine bleaching susceptibility of the holobiont (coral + algae), variable bleaching has been attributed to the host-symbiont combinations, and the inherent physiological tolerances of zooxanthellae clades to thermal stress (Fitt and Warner 1995). Corals have been shown to respond differently to elevated temperatures depending on clade of *Symbiodinium* present (Abrego et al. 2008). Clades A-D are dominant among reef building corals and greatly influence the physiology and the overall fitness of the holobiont (Császár et al. 2010). For example, the coral algal associations including clade D are more thermally tolerant (Rowan 2004) and have been observed to become more prevalent in scleractinian corals following major bleaching events (Glynn et al. 2001; Baker et al. 2004). Baker (2004) examined corals from five locations in the Indo-Pacific that exhibited different responses during the 1997-98 El-Nino-Southern Oscillation (ENSO) bleaching event. The findings of the study suggested that corals populated by thermally tolerant *Symbiodinium* clade D became dominant on reefs that had previously experienced severe bleaching and mortality, and that the resulting symbioses resembled those found in high-temperature environments. Scleractinian corals exhibit variable degrees of symbiont specificity, with some taxa establishing symbioses with a wider range of symbionts, while others are highly specific (Goulet 2006). Polymorphic symbiosis, such as have been documented for *M. annularis, M. faveolata,* and *M.*

franksi in the Caribbean (Rowan and Knowlton 1995; Rowan et al. 1997; Toller et al. 2001), may underlie some of the unexplained within-species and within-colony variability in responses to thermal stress observed in the present study.

2.4.5 Bleaching and Morphology

In the bleaching model, the colony morphology term was significant but explained only ~1% of the variance in the observed bleaching response. Bleaching intensity was more evident among the larger massive and encrusting colonies and less so among the keeled, branching and plating forms. The effect size for bleaching intensity among large massive colonies was 0.25, 0.16 for encrusting colonies, and < 0.14 for the keeled, plating, and branching forms (Figure 2.3.10 d). The patterns of bleaching among the growth forms observed during the 2005 and 2010 bleaching events were consistent with results reported for preceding bleaching events, with massive and encrusting forms experiencing higher bleaching intensity and remnant bleaching (Lang et al. 1992).

Although the Species:Morphology interaction term in the bleaching model was not significant, and given that not all species surveyed had different growth forms, it is important to consider the impact of morphology on bleaching in the context of individual species. Encrusting and massive growth forms were represented primarily by *Agaricia* and *Montastraea* species which were the most abundant species at the study sites. In the case of *Agaricia* species, which have amorphous encrusting, keeled (bifacial), and unifacial plating/foliose growth forms (Helmuth and Sebens 1993), some of the variability in the bleaching response may be explained by colony morphology. Among the *Porites* species, which have branching, encrusting, massive, and plate-like growth forms, the branching *Porites porites* experienced greater bleaching than the thermally–resistant massive and encrusting Porites *astreoides* (Figure 2.3.12).

The observed differences in bleaching susceptibility between hemispherical (massive and encrusting) and cylindrical (branching and digitate) growth forms can be explained, in part, by shape-related differences in thermal properties. Jimenez *et al.* (2008) described the coral heat budget by summarizing the coral surface temperature as a function of heat fluxes between the coral tissue, its skeleton and the ambient water. They measured colony surface temperature in response to increased irradiance and water temperature, and found that the (1) hemispherical corals reached higher temperatures than branching corals and (2) that the response for both hemispherical and cylindrical growth forms increased proportionately to the coral radius. Their results suggest that large hemispherical colonies experienced higher temperatures than smaller colonies and that size, more than shape, accounted for the difference in surface warming between branching and massive growth forms. For branching corals, heat transfer over and through the colony is determined by spacing between branches, which can cause large variations in heat and mass transfer (Monismith 2007).

According to the bleaching model, plating growth forms were least susceptible to bleaching during both bleaching events **(**Figure 2.3.10 d). van Woesik et al. (2012) tested the hypothesis that conspecifics of different size and shape have different mass transfer capacities and consequently, respond differently to thermal stress. Using coral-gypsum model experiments, they demonstrated that diffusion was dependent on the size and morphology of the models, and on the water-flow speeds; small models had higher diffusion rates than large models which was contrary to the notion that mass transfer rates scale in direct proportion to the size of the organism (Patterson 1992). The study showed that the efficiency of mass transfer was inversely proportional to size for (flat) encrusting growth forms. Furthermore, in low-flow conditions, which often accompany thermal anomalies, it was more beneficial for colonies to be small (whether flat or branching) than large and branching. In the present study, massive and encrusting forms exhibited a positive relationship between colony size and increased susceptibility to bleaching during the 2005 and 2010 events. However, for the branching growth forms (*P. porites*), bleaching intensity increased with colony size only during the 2005 event which was marked by doldrums and sustained thermal stress (Figure 2.3.12).

Variable bleaching susceptibility among coral taxa has been linked to colony size and growth form, and also to coral tissue thickness (Loya et al. 2001). Although tissue thickness was not included in the bleaching model, it may be another factor underlying the unexplained variability in the bleaching response to thermal stress. Species with deeper tissues may be more resistant to the synergistic effect of high irradiance and high SSTs due to the photo-protective capacity of the tissue which modulates the amount of PAR (Photosynthetically Active Radiation) through shading of zooxanthellae within the host tissue (Hoegh-Guldberg 1999; Brown et al. 2002). For example, *Porites* spp. are less susceptible to bleaching than the thinner tissued *Acropora* spp. (Glynn 1993). Coral species with thinner tissue may have limited energy stores which may impede recovery from bleaching unless the host can meet energy requirements through heterotrophy (Grottoli et al. 2006). If size, morphology and tissue thickness influence susceptibility to thermal stress under severe light intensities, then small, encrusting and thick-tissued colonies are more likely to survive abnormal environmental conditions, presumably due to high mass transfer capacity and the protective capacity of their tissue (Loya et al. 2001).

2.4.6 Location

Bleaching prevalence and intensity varied among reef sites during both bleaching events. The Site term (random), with nested Transect and Quadrat terms, explained 25% of the variance in the overall bleaching model. Variation in coral bleaching response among reefscapes during a bleaching event can be attributed to the composition and the condition of the coral community (Marshall and Baird 2000; McClanahan et al. 2007), and to the spatial variation in the physico-chemical conditions known to bring about coral bleaching (Edmunds 1994). In addition to elevated sea surface temperatures, site-specific environmental factors such as localized currents, proximity to upwelling, shading, turbidity, and depth may all contribute to the variability in the bleaching response of corals to thermal stress within and among individual reef sites (Berkelmans et al. 2004).

Despite the differences in the intensity of bleaching among sites, the relative abundance of the most common species remained unchanged between the years (Figure 2.3.5). Monitor and Dairy Bull reefs had similar coral species composition, however the coral cover at Dairy Bull was twice that found on Monitor Reef (Table A.4). Coral assemblages at these sites were dominated by *Agaricia* and *Montastraea* species. At Rio Bueno the species composition was dominated by *Agaricia* species. Bleaching intensity at Rio Bueno during both bleaching events was lower in comparison to the other sites. A partial explanation for this difference may stem from differences in habitat characteristics. Transects at Rio Bueno were located along the edge of a wall where scleractinian corals may benefit from the shading effect as well as from upwelling currents which may temper the effect of high SSTs by mixing with the warmer surface layers (West and Salm 2003). In addition, turbidity due to intermittent sediment plumes common to this site (Mallela et al. 2004) may provide additional protection by reducing light penetration (Jokiel and Brown 2004).

Certain coral species are capable of tolerating thermal stress and thriving in environments where temperatures exceed the average temperature of tropical waters (~28° C). Understanding why some habitats or regions escape bleaching is as important as understanding why others bleach. For example, thermal stress can vary on small spatial scales where localized currents and high degree of water mixing, cold water upwelling, or high water-flow rates may mitigate the impacts of thermal and irradiance stress, and keep coral colonies from bleaching. Such localized environmental variability can create a large, seemingly random source of variability in the bleaching response (corrected for species, size and morphology). Of interest is whether certain habitats might serve as refugia where coral assemblages can thrive and act as reservoirs for nearby reefs, and whether these refugia warrant protection from other stressors (i.e. anthropogenic) (Riegl et al. 2009).

2.4.7 Mortality

In spite of moderate to severe bleaching observed at the study sites during the 2005 and 2010 bleaching events, post-bleaching mortality did not rise above the “significant mortality” threshold of 8% defined by Eakin et al. (2010) which was based on the 2005 pan-Caribbean bleaching and mortality data. The overall mean of recent morality across all species was estimated at 4% for 2005/06 and 2% for 2010/11, values which are considered normal background mortality levels during periods without any major disturbance (Eakin et al. 2010). Mortality patterns varied between the bleaching events due to differences in the duration of thermal stress (DHW), and among sites presumably due to variation in local conditions.

Most of the mortality observed during the bleaching event was partial mortality. Only a small number (~1%) of colonies experienced full mortality. *A. agaricites* experienced highest relative partial mortality at all three reef sites, followed by *M. annularis* at Monitor and Dairy Bull reefs (Figure 2.3.14). For encrusting and plating Agaricids, lesions were observed mostly along the edges of colonies. Such lesions are typically associated with bottom related processes, especially algal overgrowth (Vermeij et al. 2010). Turf algae are dense, short (< 1cm), multi-species assemblages of filamentous benthic algae and cyanobacteria (Steneck and Dethier 1994) which can overgrow and kill coral tissue through allelopathic effects, by causing hypoxia and changes in pigmentation of the coral (Barott et al. 2009). Lesions formed on top or middle of colonies were more frequent among *M. annularis* colonies. Such lesions are vulnerable to species-specific pathogens, or overgrowth by algae and boring sponges.

Partial mortality or lesions are common among coral colonies that have been subjected to biotic or abiotic disturbances including abrasion due to storms, sedimentation (Crabbe and Carlin 2007), bleaching, disease, predation and others. The ability of corals to survive or recover from partial mortality is essential to their survival (Meesters et al. 1996). Failed lesion regeneration can result in patches of bare skeleton surrounded by healthy tissue, which over time, can lead to colony fragmentation (Edmunds 1994; Meesters et al. 1996). Lesions overgrown by algae or colonized by boring sponges can eventually lead to full colony mortality. Small colonies exposed to bottom processes are more likely to suffer full mortality compared to larger colonies which may have the benefit of height or "escape in height" (Meesters et al. 1996).

Sites selected in the study are typical of coral reefs found along Jamaica's north coast. The reefscape at Dairy Bull, however, is noteworthy for its topographic complexity, species diversity, coral cover (Idjadi et al. 2006) and in particular, for the presence of *A. cervicornis* stands intermingled with other species. Although *Acropora cervicornis* colonies were not included in the analysis of the current study (because this species was not present at all study sites), there was high prevalence of bleaching within that species at the Dairy Bull site (personal observations). High post-bleaching mortality among *Acroporids* was reported in other studies (Quinn and Kojis 2008) with mortality patterns attributed to the preferential survival of thick-tissued species, which in cases of significant mortality, can lead to structural shifts with an increase in the relative abundance of massive and encrusting coral species (Loya et al. 2001).

Mortality among corals is generally size specific, with full-colony mortality more likely to occur among smaller size classes than larger ones (Hughes and Jackson 1980; Sakai 1998). Under various types of stressors, larger colonies tend to have higher survivorship probability than smaller colonies (Shenkar et al. 2005). Bleaching related mortality, on the other hand, tends to be independent of colony size (Baird and Marshall 2002), which is in contrast to the results of the current study where the amount of recent mortality increased marginally with colony size. This weak relationship between colony size and bleaching related mortality differentiates mortality due to thermal stress from many other sources of mortality on reefs such as pollution, sedimentation, competition, injury from predation or damage from storms (Jackson and Hughes 1985). Mortality due to thermal stress is correlated with the duration and intensity of the thermal anomaly, species-specific tolerance to thermal stress, and with local environmental factors. The results of the current study indicate that although bleaching related mortality observed during the course of the two bleaching events was related to colony size, the effect size was low.

Species/ size-specific bleaching responses and changes in colony size frequency distributions serve as indicators of impacts caused by thermal stress episodes because they reflect changes in demographic processes such as growth and mortality. Due to their modular nature coral colonies have the ability to survive partial tissue death (Hughes and Jackson 1980; Babcock 1991). Partial mortality plays an important role in the size regulation of coral colonies (Hughes 1984). Partial mortality and fission of larger colonies into physiologically separate but genetically identical colonies (Highsmith 1982) can influence the size frequency distribution of coral assemblages. For example, changes in size-frequency distributions of coral communities may signal selective mortality among specific size classes or it may indicate low recruitment which can be indicative of reduced reef resilience (Bak and Meesters 1999). Even though age and size of colonies may not always be correlated (Hughes 1984), they determine the reproductive maturity and output of corals, with larger or older colonies having greater reproductive potential (Kojis and Quinn 1985). Tracking appropriate indicators over time can signal potential shifts to dominance by small, less-fecund coral colonies (Done 1992; Brandt 2009) or to a population dominated by larger colonies (Edmunds 2005).

There were no major shifts in the size frequency distribution of coral colonies at the reef sites (Figure A.1, Table A.5) following the 2005 and 2010 bleaching events. Moreover the size frequency distributions for the 12 most abundant species at the three sites also remained relatively constant (Figure A.2). For the 2005 bleaching event, the results of the current study are consistent with observations made by Crabbe (2011) who used size-frequency distributions as a community level metric to measure resilience following the 2005 bleaching event and also found that the community structure remained unchanged with smaller sized colonies dominating the reefscape.

Bleaching related mortality is frequently associated with outbreaks of disease. Following the 2005 event in the Florida Keys, Brandt (2009) observed white plague, black band, and dark spot on some colonies of *M. faveolata, C. natans,* and *S. siderea* respectively. Similar observations were made in the US Virgin Islands (Miller et al. 2006) where extensive bleaching (>90% of coral cover) was accompanied by signs of white plague disease, resulting in 26-48% loss in coral cover. In the current study, disease was not observed during the 2005/6 surveys. During the 2010/11 surveys, however, Yellow Band Disease (YBD) was observed on some *M. annularis* colonies at the Dairy Bull site. The progression of YBD is often slow but persistent and requires long-term monitoring to determine if the occurrence represents a pulse or a chronic presence.

2.4.8 Acclimatization and post-bleaching succession

While the patterns of susceptibility among coral genera were similar between the two bleaching events, the lower bleaching intensity observed in 2010 suggests that the thermal stress did not surpass the threshold level known to cause extensive bleaching, but it might also provide circumstantial evidence for the influence of prior exposure to bleaching (i.e. the 2005 or earlier events) during which less resilient colonies would have already been lost.

The recovery from bleaching and the low bleaching related mortality following both bleaching events indicate a level of tolerance of surveyed coral assemblages to thermal stress. Crabbe (2011) examined post-bleaching coral size frequency distribution, colony growth and rates of recruitment as metrics for coral resilience on the fringing reefs around Discovery Bay following the 2005 bleaching event. He concluded that recruitment was returning after the major bleaching event of 2005, indicating good levels of coral resilience, but found that larger corals were not necessarily resilient, presumably due to reduced post-bleaching growth among the lager colony size classes.

It is difficult to discern whether the lower intensity of bleaching observed in 2010 was due primarily to the shorter duration of the thermal anomaly or if there was acclimatization among coral species. Proposed mechanisms for coral adaptation and acclimatization to thermal stress range from physiological adaptation (Gates and Edmunds 1999) to symbiont "shuffling" and "switching" (Baker 2003; Baker et al. 2004). Resilience of coral colonies depends on their capacity to repopulate their tissues with more thermally resistant clade(s) of zooxanthellae (Jones et al. 2008) and also on their capacity to meet their energy requirements through heterotrophy and from stored energy reserves (Grottoli et al. 2006).

At the colony level the mechanisms underlying acclimatization and adaptation are obscured by the different life histories of the host and its symbionts (Obura 2009). The question that has been of interest to scientists is whether the observed shifts in symbiont communities following bleaching or stress events represents an adaptive mechanism for coping with environmental change or if is it a temporary acclimatization. According to the Adaptive Bleaching Hypothesis (Buddemeier and Fautin 1993), the loss of zooxanthellae during bleaching provides the coral host with an opportunity to re-establish a symbiosis with a different dominant zooxanthellae, resulting in a new, more thermally resistant holobiont. Some consider symbiont shuffling as a mechanism by which some coral species can increase their thermal tolerance (Berkelmans and van Oppen 2006) and which may explain why the same coral species may respond differently from one bleaching event to another. The Coral Probiotic Hypothesis (CPB) expands the definition of the holobiont to include the host, the endosymbiotic zooxanthellae and also pools of metabolically active bacteria. According to CPB, coral colonies can adapt to changing environmental stress conditions by fluctuating the relative amounts of certain bacterial species that are already present within the colony tissues (Reshef et al. 2006). “Adaptation” in the case of CPB, is attributed to bacteria and can take place in days or weeks, instead of years or decades required for adaptation through natural selection, for more thermally tolerant host genotypes. The bacteria-facilitated adaptation may allow a bleached holobiont to assimilate nutrients more efficiently, prevent pathogen infections and provide alternative sources of carbon and energy from photosynthetic prokaryotes.

Bleaching prevalence and intensity among coral colonies are influenced by the interaction of local biotic and abiotic factors, and by the duration of thermal stress. Some authors have suggested that, in addition to the usual causal factor of bleaching, previous exposure to high temperature may also influence coral susceptibility to thermal stress (Mumby et al. 2001; Carilli et al. 2012; Guest et al. 2012). Some studies showed that coral colonies which survived previous bleaching events were less likely to bleach during subsequent events (Baker et al. 2004; McClanahan et al. 2007), suggesting that the capacity for acclimatization and adaptation exists (Maynard et al. 2008). If acclimatization to thermal stress was in fact occurring during the course of our study, it might partially explain the difference in the overall bleaching response between the 2005 and 2010 bleaching events.

The increased frequency of bleaching events similar to 2005/06 and 2010/11 raises concerns about immediate and long-term impacts of repeated bleaching events on coral reef communities on Jamaica`s north coast. Despite enduring decades of anthropogenic stressors, ranging from poor coastal land use practices, to overfishing (Jackson et al. 2001), hurricanes (Woodley 1989), disease (Weil 2004) and climate change, the reefs near Discovery Bay, showed signs of gradual recovery with strong evidence of localized phase shift reversal (Idjadi et al. 2006). Increased frequency and magnitude of mass bleaching events could impede this recovery. Disturbances such as mass bleaching events have the potential to trigger shifts and shape coral assemblages over time through gradual replacement of historically dominant species by more opportunistic “weedy” species which can persist and thrive under, what are for other species, unfavorable environmental conditions (Knowlton 2001; McClanahan et al. 2007; van Woesik et al. 2011).

Life history strategies of opportunistic “weedy” species are characterized by fast growth and high reproductive rates (brooders). The high energy demand for the “weedy” life history strategy can make species like *A. agaricites* vulnerable during periods of high thermal stress, which explains the high bleaching intensity and mortality observed for this species during both events.

However, higher growth and reproductive rates among these weedy species offset their susceptibility to stress (i.e. mortality due to thermal stress) (Obura 2009). On the opposite end of the spectrum are life history strategies of the stress-tolerant, long-lived species (e.g. *Montastraea, Siderastrea*) which have greater ability to withstand (resist or tolerate) stress by being able to survive low metabolic rates during stress (Obura 2009). The trade-offs among the stress-tolerant species are lower growth and reproductive rates.

The species most susceptible to bleaching were also the most abundant species, namely *Agaricia* and *Montastraea* species. Although *Montastraea* spp. were more tolerant than *Agaricia* spp., recurring bleaching events could result in a gradual decline of this massive species, which is the main frame builder on many of Jamaica's north coast reefs (Goreau and Macfarlane 1990). Assemblages exposed to recurrent thermal stress are more likely to become dominated by persistent, thermally resistant species (e.g. *P. astreoides, Madracis* spp.) (Green et al. 2008), and by weedy species (*A. agaricites*), which despite their susceptibility to thermal stress, have high reproductive rates.

For species that exhibit a positive relationship between colony size and bleaching, frequent exposure to thermal stress has the potential to diminish the resilience of larger colonies and reduce their fecundity. Change in the abundance of larger colonies can alter the population size structure which in turn can lead to changes in population dynamics, more specifically to changes in recruitment patterns (Hughes and Tanner 2000).

The present day abundance of weedy species, especially *Agaricia* and *Porites*, and the persistence of massive species (*Montastrea* spp.) on the reefs surveyed suggests that in addition to colony traits, life-history strategies also play an important role in determining which species are more likely to withstand climate change (Edinger and Risk 2000; van Woesik et al. 2011; Darling et al. 2012).

The size-modulated bleaching patterns observed in the current study provide evidence that physical characteristics of coral colonies, specifically size and shape, influence colony-level responses to thermal stress differently among coral species. Susceptibility to thermal stress varied among species and among sites, suggesting that bleaching and mortality are influenced by local environmental conditions. For example, elevated sea surface temperatures can interact with other local environmental factors to exacerbate (excessive solar irradiation or sedimentation) or mitigate (strong water currents, upwelling, storm activity, shading, etc.) coral response to thermal stress. The higher bleaching intensity observed among larger coral colonies (*Montastraea* and *Agaricia* species) was consistent with predictions made by Nakamura and van Woesik (2001) who postulated that under the same water flow conditions, smaller colonies would fare better under thermal stress conditions than larger ones due to higher mass transfer to and from smaller colonies. Despite the moderate to severe bleaching observed among coral colonies, resulting mortality rates were low following both bleaching events, suggesting that the assemblages at the study sites showed a degree of tolerance given the magnitude and duration of thermal stress during the 2005/06 and 2010/11 bleaching events. Individual coral taxa displayed varying degrees of resistance and tolerance to thermal stress; most were able to survive the bleached state, in whole or in part, and recover.

Mixed effects models can be an effective tool for assessing the impact of thermal stress on individual species, and for quantifying the influence of specific colony traits which may confer resistance or tolerance to thermal stress. Given the amount of variance explained by the Site term, the power of bleaching models could be improved by incorporating local or site-specific environmental variables known to influence bleaching:

- temperature and (DHW) measuring the duration of thermal stress;
- irradiance (PAR) - radiation fluctuations can be both beneficial and dangerous for the persistence of the coral holobiont depending on duration and intensity (Dunne and Brown 2001);
- turbidity CDOM (Coloured Dissolved Organic Matter) which absorbs the radiation and decreases the stress (West & Salm 2003);
- local water current data;
- depth.

2.5 General Conclusions

According to climatic projections, global temperature is estimated to increase by 2-4 °C by the end of this century (Hughes et al. 2003; Donner et al. 2009). The impending threat of climate change has fueled the search to identify factors that influence coral susceptibility to thermal stress and those that enable corals to acclimatize in the short-term, and adapt in the long-term. Predictions that bleaching events will occur with greater frequency have also brought to the forefront the need for effective tools that allow reef managers to assess the impact of thermal stress on individual species and on coral assemblages, and to predict the likely consequences of future bleaching episodes.

In 2005 and 2010, increased sea surface temperatures caused widespread coral bleaching on Jamaica's north coast reefs. Despite similar temperature patterns between the events, the differences in the duration of accumulated thermal stress (DHW) were reflected in the bleaching prevalence and intensity observed among coral species. Both events were characterized by significant and extensive coral bleaching but relatively low mortality (~4% post bleaching).

In this study, mixed effects models were used to quantify bleaching response and bleaching related mortality as a function colony size, morphology and species across three sites. The bleaching model explained 51% of the variance in bleaching observed across the two bleaching events. As expected, most of the variance was explained by the Site random term and the Species fixed term, confirming that species-specific susceptibility to thermal stress is further influenced by local environmental conditions. While colony size provided partial (5%) explanation for the variability in coral susceptibility to thermal stress, it is a significant indicator of colony level responses to thermal anomalies. More specifically, the results of this study demonstrate that bleaching as a function of colony size shows the immediate impact of thermal stress on colony size-classes, especially among the more susceptible species such as *A. agaricites* and *M. annularis*. The relationship between colony size and bleaching was more apparent in 2005 than in 2010, which indicates that larger colonies may be at greater risk than smaller colonies during periods of thermal stress exceeding 6 DHW.

The higher susceptibility among larger colonies and the preferential bleaching-related survival of coral colony size-classes observed during the two bleaching events may have long-term community level implications due to potential impacts on demographic processes such growth, (partial) mortality and fission, and recruitment (Hughes 1984). Given that reproduction in corals is size dependent, with larger and presumably older colonies having greater reproductive potential (Hoegh-Guldberg 2011), bleaching may have a more intense effect on the reproductive output of populations than other types of disturbances. Lack of resilience or reduced fitness among larger colonies due to bleaching implies reduced reproductive output and a potential shift to dominance by smaller and less fecund size classes.

The mortality model explained 16% of the variability in mortality data from the two bleaching events. Similar to the bleaching model, the colony size and species fixed terms explained 6% and 3% of the variability, respectively. The results indicate that colony size was a weak, albeit positive, predictor of bleaching related mortality for the 2005/06 and 2010/11 bleaching events.

The results of this study show that mixed effects models can be valuable tools for identifying susceptible and tolerant species, and for quantifying the influence of various colony traits on temperature-induced bleaching response. As the threat of further bleaching events looms, models that can help describe and even predict species’ responses to thermal anomalies in function of their duration and intensity, can be used as a tool by reef managers in formulating management strategies. This study provides a scalable model that can be used to describe the bleaching response at the colony as well as at the community level. It provides the foundation for hybrid models that could further refine the assessment an event’s local outcome by incorporating community composition and local environment variables, such as depth, water flow, SSTs, DHW and solar radiation.

APPENDIX

Table A.1. Coral species observed at survey sites showing the total number of colonies surveyed per species group and number and % of colonies bleached per species. Only data for the 12 most common species are listed: a) Monitor Reef, b) Dairy Bull, and c) Rio Bueno

a)

MONITOR REEF	Total colonies	No. bleached colonies	relative % colonies bleached	Total colonies	No. bleached colonies	relative % colonies bleached	Total colonies	No. bleached colonies	relative % colonies bleached	Total colonies	No. bleached colonies	relative % colonies bleached
Survey date	2005	2005	2005	2006	2006	2006	2010	2010	2010	2011	2011	2011
Agaricia agaricites	215	155	24.1	198	15	2.2	389	224	19.9	370	13	1.2
Agaricia humilis	34	29	4.5	18	3	0.4	50	37	3.3	44	6	0.6
Agaricia lamarcki	5	2	0.3	9	0	0.0	57	18	1.6	52	1	0.1
Helioceris cucullata	1	0	0.0	2	0	0.0	1	0	0.0	2	0	0.0
Madracis decactis	8	1	0.2	3	0	0.0	7	1	0.1	10	0	0.0
Madracis mirabilis	2	1	0.2	1	0	0.0	1	0	0.0	2	0	0.0
Montastraea annularis	163	146	22.7	203	81	12.1	225	173	15.4	191	16	1.5
Montastrea faveolata	18	14	2.2	22	4	0.6	31	20	1.8	27	0	0.0
Porites astreoides	89	0	0.0	116	1	0.1	182	0	0.0	171	2	0.2
Porites porites	16	7	1.1	18	0	0.0	38	8	0.7	43	0	0.0
Siderastrea siderea	85	11	1.7	78	1	0.1	137	23	2.0	146	3	0.3
Stephanocoenia intersepta	8	0	0.0	4	0	0.0	7	0	0.0	11	0	0.0
Total common species	644	366	56.8	672	105	15.6	1125	504	44.8	1069	41	3.8
Total all species	715			729			1229			1201		
Common species as % of all colonies surveyed	90			92			92			89		

b)

DAIRY BULL	Total colonies	No. bleached colonies	relative % colonies bleached	Total colonies	No. bleached colonies	relative % colonies bleached	Total colonies	No. bleached colonies	relative % colonies bleached	Total colonies	No. bleached colonies	relative % colonies bleached
Survey date	2005	2005	2005	2006	2006	2006	2010	2010	2010	2011	2011	2011
Agaricia agaricites	239	115	16.7	401	13	1.3	348	216	20.3	297	38	3.9
Agaricia humilis	17	4	0.6	26	0	0.0	71	41	3.9	72	19	1.9
Agaricia lamarcki	21	5	0.7	45	1	0.1	31	12	1.1	33	4	0.4
Helioceris cucullata	20	5	0.7	10	0	0.0	16	12	1.1	16	1	0.1
Madracis decactis	16	1	0.1	11	0	0.0	6	1	0.1	5	0	0.0
Madracis sp	6	0	0.0	21	0	0.0	10	0	0.0	4	0	0.0
Montastraea annularis	165	108	15.7	195	68	6.9	240	164	15.4	183	30	3.1
Montastrea faveolata	8	7	1.0	14	2	0.2	29	18	1.7	63	14	1.4
Porites astreoides	107	5	0.7	123	0	0.0	167	20	1.9	162	12	1.2
Porites porites	44	12	1.7	35	1	0.1	80	29	2.7	89	16	1.6
Siderastrea siderea	38	7	1.0	83	1	0.1	56	18	1.7	44	6	0.6
Stephanocoenia intersepta	7	1	0.1	19	0	0.0	9	3	0.3	10	1	0.1
Total common species	688	270	39.2	983	86	8.7	1063	534	50.2	978	141	14.4
Total all species	737			1055			1205			1087		
Common species as % of all colonies surveyed	93			93			88			90		

c)

RIO BUENO	Total colonies	No. bleached colonies	relative % colonies bleached	Total colonies	No. bleached colonies	relative % colonies bleached	Total colonies	No. bleached colonies	relative % colonies bleached	Total colonies	No. bleached colonies	relative % colonies bleached
Survey date	2005	2005	2005	2006	2006	2006	2010	2010	2010	2011	2011	2011
Agaricia agaricites	351	143	19.2	281	17	2.1	612	179	13.79	492	90	7.2
Agaricia humilis	12	4	0.5	28	1	0.1	7	2	0.2	22	3	0.2
Agaricia lamarcki	44	15	2.0	94	5	0.6	71	19	1.5	132	19	1.5
Helioceris cucullata	64	38	5.1	135	10	1.2	91	45	3.5	125	42	3.3
Madracis decactis	66	1	0.1	63	2	0.2	175	1	0.1	149	2	0.2
Madracis sp	82	1	0.1	39	0	0.0	122	3	0.2	111	3	0.2
Montastraea annularis	3	2	0.3	1	0	0.0	3	0	0.0	1	1	0.1
Montastrea faveolata	15	11	1.5	11	2	0.2	13	11	0.8	16	3	0.2
Porites astreoides	58	0	0.0	41	1	0.1	130	17	1.3	122	10	0.8
Porites porites	4	1	0.1	0	0	0.0	0	0	0.0	4	0	0.0
Siderastrea siderea	45	2	0.3	84	3	0.4	66	22	1.7	75	33	2.6
Stephanocoenia intersepta	2	0	0.0	30	1	0.1	8	2	0.2	5	4	0.3
Total common species	746	218	29.2	807	42	5.2	1298	301	23.2	1254	210	16.7
Total all species	811			896			1458			1302		
Common species as % of all	92			90			89			96		

Table A.2. Mean (+/-SE) bleaching prevalence (proportion of colonies surveyed displaying bleaching response) for each species and survey date.

DATE	SPECIES	BL	std.error
2005	*Agaricia agaricites*	0.51	0.02
2006	*Agaricia agaricites*	0.05	0.01
2010	*Agaricia agaricites*	0.46	0.01
2011	*Agaricia agaricites*	0.12	0.01
2005	*Agaricia humilis*	0.59	0.06
2006	*Agaricia humilis*	0.06	0.03
2010	*Agaricia humilis*	0.63	0.04
2011	*Agaricia humilis*	0.20	0.03
2005	*Agaricia lamarcki*	0.31	0.06
2006	*Agaricia lamarcki*	0.04	0.02
2010	*Agaricia lamarcki*	0.31	0.04
2011	*Agaricia lamarcki*	0.11	0.02
2005	*Helioceris cucullata*	0.52	0.05
2006	*Helioceris cucullata*	0.07	0.02
2010	*Helioceris cucullata*	0.54	0.05
2011	*Helioceris cucullata*	0.30	0.04
2005	*Madracis decactis*	0.03	0.02
2006	*Madracis decactis*	0.03	0.02
2010	*Madracis decactis*	0.02	0.01
2011	*Madracis decactis*	0.01	0.01
2005	*Madracis mirabilis*	0.02	0.02
2006	*Madracis mirabilis*	0.00	0.00
2010	*Madracis mirabilis*	0.03	0.01
2011	*Madracis mirabilis*	0.03	0.01
2005	*Montastraea annularis*	0.77	0.02
2006	*Montastraea annularis*	0.37	0.02
2010	*Montastraea annularis*	0.73	0.02
2011	*Montastraea annularis*	0.13	0.02
2005	*Montastraea faveolata*	0.78	0.07
2006	*Montastraea faveolata*	0.17	0.06
2010	*Montastraea faveolata*	0.67	0.06
2011	*Montastraea faveolata*	0.16	0.04
2005	*Porites astreoides*	0.02	0.01
2006	*Porites astreoides*	0.01	0.01
2010	*Porites astreoides*	0.08	0.01
2011	*Porites astreoides*	0.05	0.01
2005	*Porites porites*	0.31	0.06
2006	*Porites porites*	0.02	0.02
2010	*Porites porites*	0.31	0.04
2011	*Porites porites*	0.12	0.03
2005	*Siderastrea siderea*	0.12	0.03
2006	*Siderastrea siderea*	0.02	0.01
2010	*Siderastrea siderea*	0.24	0.03
2011	*Siderastrea siderea*	0.16	0.02
2005	*Stephanocoenia intersepta*	0.06	0.06
2006	*Stephanocoenia intersepta*	0.02	0.02
2010	*Stephanocoenia intersepta*	0.21	0.08
2011	*Stephanocoenia intersepta*	0.19	0.08

Table A.3. Mean (+/-SE) bleaching intensity (proportion of colony bleached) for each species and survey date.

DATE	SPECIES	BL	std.error
2005	*Agaricia agaricites*	0.29	0.01
2006	*Agaricia agaricites*	0.01	0.00
2010	*Agaricia agaricites*	0.15	0.01
2011	*Agaricia agaricites*	0.02	0.00
2005	*Agaricia humilis*	0.45	0.06
2006	*Agaricia humilis*	0.05	0.02
2010	*Agaricia humilis*	0.34	0.03
2011	*Agaricia humilis*	0.10	0.02
2005	*Agaricia lamarcki*	0.10	0.03
2006	*Agaricia lamarcki*	0.01	0.00
2010	*Agaricia lamarcki*	0.06	0.01
2011	*Agaricia lamarcki*	0.03	0.01
2005	*Helioceris cucullata*	0.27	0.04
2006	*Helioceris cucullata*	0.02	0.01
2010	*Helioceris cucullata*	0.19	0.02
2011	*Helioceris cucullata*	0.10	0.02
2005	*Madracis decactis*	0.02	0.01
2006	*Madracis decactis*	0.00	0.00
2010	*Madracis decactis*	0.01	0.01
2011	*Madracis decactis*	0.00	0.00
2005	*Madracis mirabilis*	0.02	0.02
2006	*Madracis mirabilis*	0.00	0.00
2010	*Madracis mirabilis*	0.02	0.01
2011	*Madracis mirabilis*	0.01	0.01
2005	*Montastraea annularis*	0.63	0.02
2006	*Montastraea annularis*	0.20	0.02
2010	*Montastraea annularis*	0.51	0.02
2011	*Montastraea annularis*	0.04	0.01
2005	*Montastraea faveolata*	0.58	0.06
2006	*Montastraea faveolata*	0.03	0.01
2010	*Montastraea faveolata*	0.46	0.05
2011	*Montastraea faveolata*	0.02	0.01
2005	*Porites astreoides*	0.01	0.00
2006	*Porites astreoides*	0.00	0.00
2010	*Porites astreoides*	0.02	0.01
2011	*Porites astreoides*	0.02	0.01
2005	*Porites porites*	0.20	0.05
2006	*Porites porites*	0.00	0.00
2010	*Porites porites*	0.21	0.04
2011	*Porites porites*	0.02	0.01
2005	*Siderastrea siderea*	0.10	0.02
2006	*Siderastrea siderea*	0.01	0.01
2010	*Siderastrea siderea*	0.17	0.02
2011	*Siderastrea siderea*	0.05	0.01
2005	*Stephanocoenia intersepta*	0.04	0.04
2006	*Stephanocoenia intersepta*	0.02	0.02
2010	*Stephanocoenia intersepta*	0.03	0.02
2011	*Stephanocoenia intersepta*	0.09	0.04

Table A.4. Substrate composition for the three reef sites surveyed during and after the 2005 and 2010 bleaching events. Included are the major substrate categories (Gayle and Charpentier unpublished data).

Latitude (N)	Longitude (W)	Reef Site	Survey Year	Depth (m)	Coral Cover (%)	SE	Macroalgal Cover (%)	SE	Coralline Algae (%)	SE	Gorgonians (%)	SE	Zoanthids (%)	SE	Sponges (%)	SE	Other Living (%)	SE	Other Substrate (%)	SE
18.472897°	-77.413928°	MONITOR REEF	2005	9	9.31	1.59	54.42	7.68	16.22	1.46	0.28	0.06	0.06	0.03	5.88	0.94	0.00	0.00	8.47	5.88
18.472897°	-77.413928°	MONITOR REEF	2006	9	7.28	0.78	52.26	3.70	20.43	1.44	0.27	0.14	0.01	0.01	1.86	0.42	0.13	0.05	13.53	3.28
18.472897°	-77.413928°	MONITOR REEF	2010	9	12.25	0.53	47.53	3.22	15.79	1.13	0.30	0.07	0.03	0.02	1.64	0.74	1.67	0.37	12.72	1.06
18.472897°	-77.413928°	MONITOR REEF	2011	9	11.43	1.06	36.30	3.04	21.13	1.48	0.55	0.19	0.03	0.02	0.45	0.19	0.53	0.10	18.73	1.15
18.468055°	-77.388441°	DAIRY BULL	2005	9	26.17	5.93	14.25	7.36	28.01	0.50	0.05	0.05	0.48	0.13	3.07	0.34	0.52	0.20	22.76	2.61
18.468055°	-77.388441°	DAIRY BULL	2006	9	27.21	5.61	17.74	10.01	21.40	3.16	0.38	0.07	0.55	0.22	3.17	0.87	1.33	0.61	24.26	1.58
18.468055°	-77.388441°	DAIRY BULL	2010	9	27.80	4.14	9.85	3.60	28.49	2.42	1.36	0.37	0.38	0.25	3.27	0.86	0.97	0.25	15.52	0.89
18.468055°	-77.388441°	DAIRY BULL	2011	9	27.69	3.38	12.15	4.76	31.68	2.37	0.75	0.09	0.55	0.26	4.25	0.75	0.76	0.54	12.09	1.82
18.479451°	-77.460042°	RIO BUENO	2005	9	18.00	2.06	5.60	1.51	39.60	2.04	3.00	1.15	0.20	0.20	2.40	0.77	1.20	0.52	27.20	2.93
18.479451°	-77.460042°	RIO BUENO	2006	9	19.20	2.88	16.40	1.95	37.00	1.66	0.60	0.33	0.20	0.20	1.60	0.69	1.00	0.50	23.80	3.35
18.479451°	-77.460042°	RIO BUENO	2010	9	26.83	3.82	3.76	1.11	26.28	2.75	1.48	0.43	0.08	0.06	4.87	1.22	0.10	0.07	27.44	3.95
18.479451°	-77.460042°	RIO BUENO	2011	9	28.47	3.04	22.59	2.24	41.50	2.19	1.68	0.65	0.79	0.19	2.74	0.70	1.14	0.41	1.16	0.59

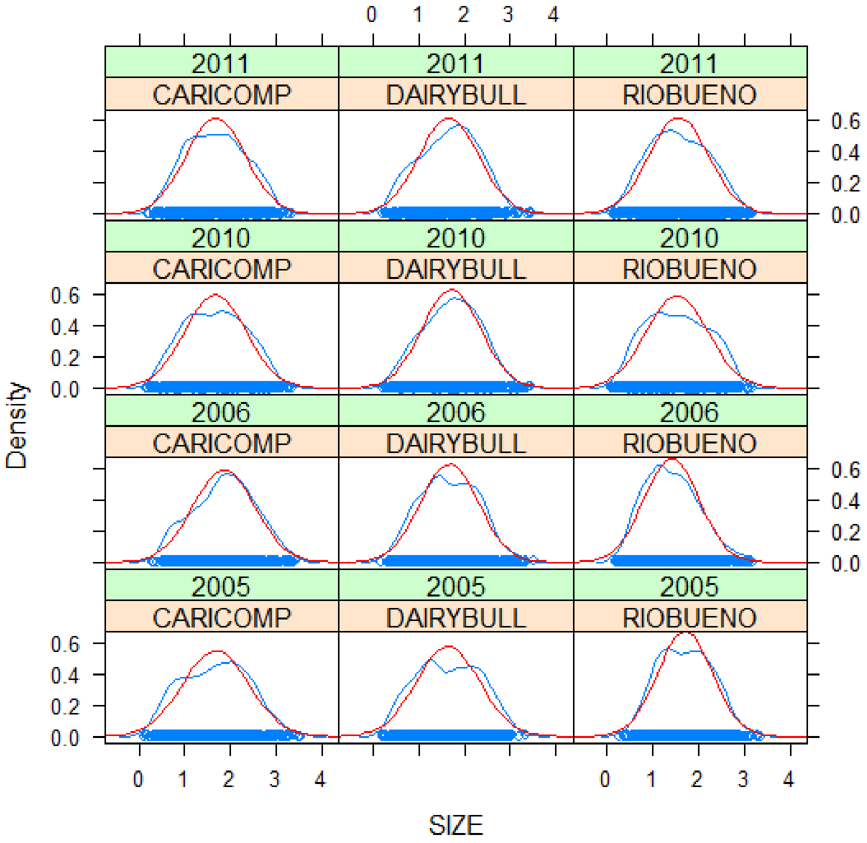


Figure A.1. Log transformed colony size frequency distributions (blue lines) observed at the study sites during the bleaching and post-bleaching surveys conducted in 2005/06 and 2010/11, compared to normal distribution curve (red line). Two-way ANOVA was used to compare the mean colony size during and post bleaching for each survey and each site.

Table A.5. Results of the Tukey multiple comparisons of log transformed colony size means with 95% family-wise confidence level, for each reef site, and survey dates. At Dairy Bull there were no significant changes in the mean colony sizes during and after the bleaching events, as well as between the bleaching events. On Monitor Reef (CARICOMP) there was a change in the mean colony size following the 2005 bleaching event, but not following the 2010 event. Similarly at Rio Bueno, there was a significant change in mean colony size after the 2005 event but not after the 2010 event. Moreover, there were significant changes in the mean colony size at Rio Bueno between the events, which also coincides with the increase in coral cover between the events

	diff	lwr	upr	p adj
DAIRYBULL:2005-DAIRYBULL:2006	0.02	-0.09	0.13	1.00
DAIRYBULL:2005-DAIRYBULL:2010	0.07	-0.04	0.17	0.60
DAIRYBULL:2010-DAIRYBULL:2011	-0.06	-0.15	0.04	0.69
MONITORREEF:2005-MONITORREEF:2006	0.17	0.06	0.29	0.00
MONITORREEF:2005-MONITORREEF:2010	-0.02	-0.12	0.09	1.00
MONITORREEF:2010-MONITORREEF:2011	0.01	-0.08	0.10	1.00
RIOBUENO:2005-RIOBUENO:2006	-0.30	-0.41	-0.19	0.00
RIOBUENO:2005-RIOBUENO:2010	-0.18	-0.28	-0.08	0.00
RIOBUENO:2010-RIOBUENO:2011	0.04	-0.04	0.13	0.93

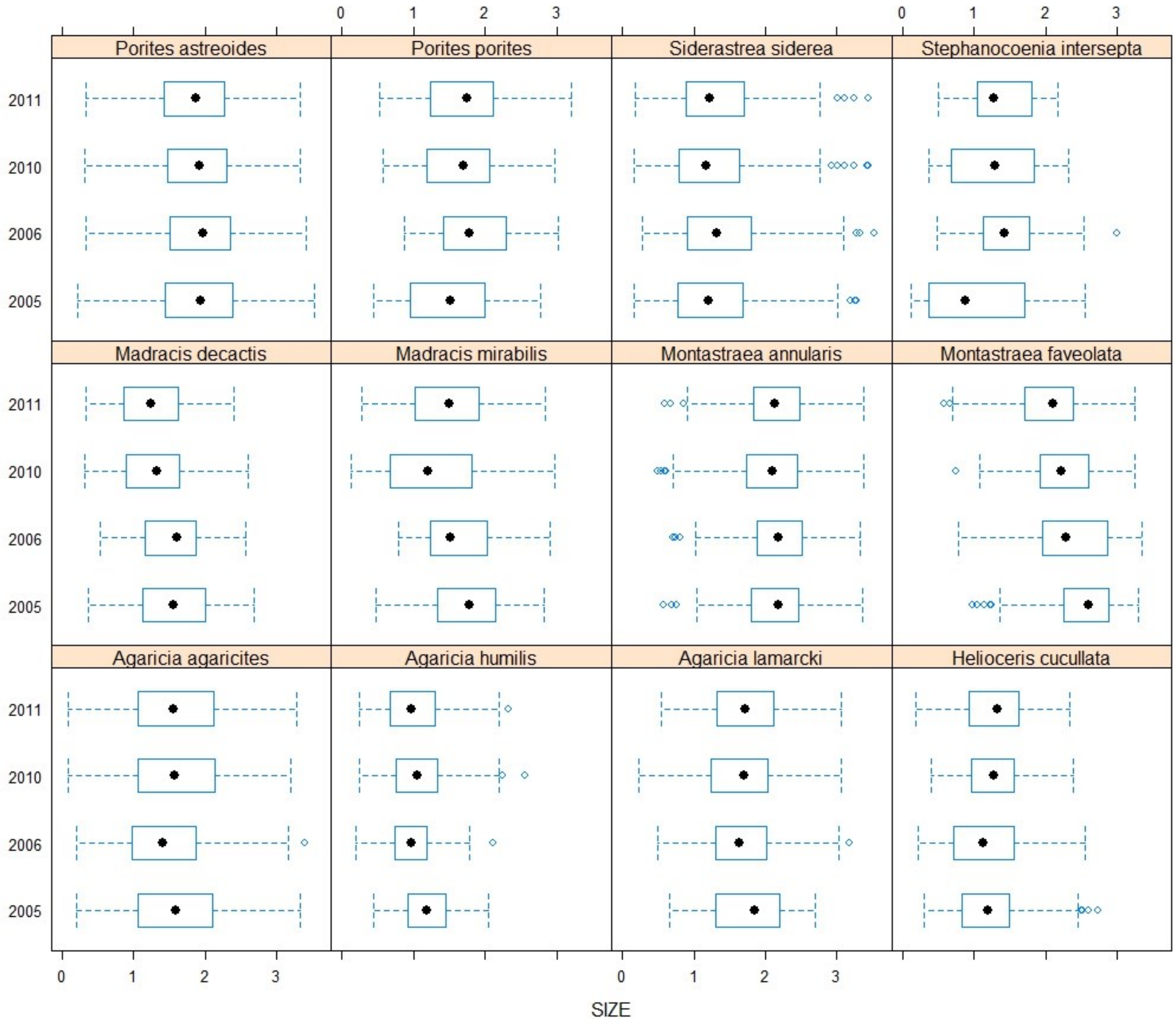


Figure A.2. Box-and-whisker plot comparing log transformed colony size for the 12 common species. Displayed are the median, the first and third quartiles, and the extreme values for colony sizes.

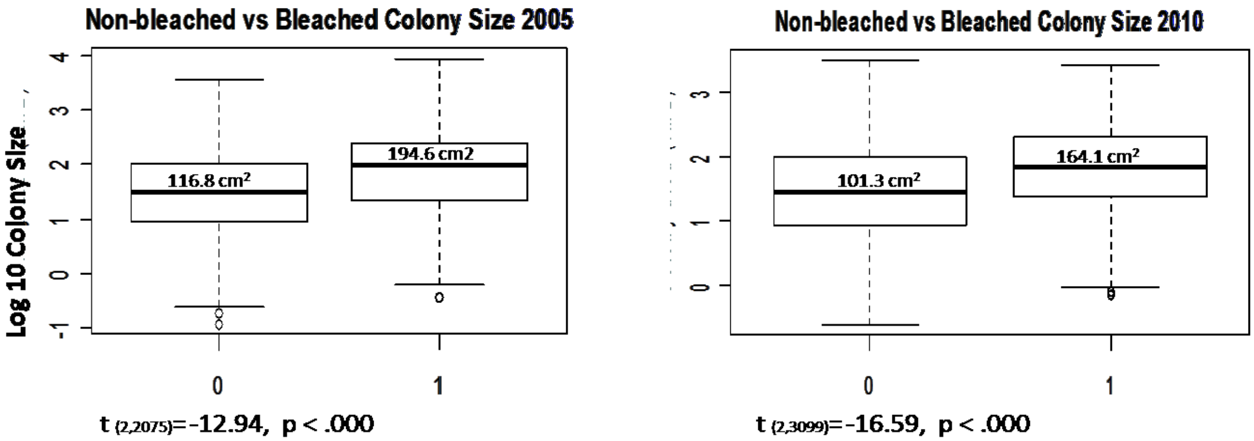


Figure A.3. The mean colony size of bleached and unbleached colonies pooled across the three study sites in 2005 and 2010.

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