Coral community bleaching response on a highly urbanised reef

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Abstract

Projected increases in the magnitude and frequency of sea surface temperature anomalies present a significant threat to the persistence of tropical coral reefs, however, detailed studies of community level responses to thermal stress are needed if its effect on reef resilience are to be understood. While many studies report on broad, regional scale responses to thermal stress (e.g., proportion of corals bleached), far fewer examine variation in susceptibility among taxa and change in coral community structure, before, during and after bleaching on individual reefs. Furthermore, relatively few studies of bleaching response come from highly urbanised reefs that experience chronic disturbances such as elevated sedimentation and turbidity. Here we report in detail on the bleaching response of corals at a highly urbanised reef site south of mainland Singapore during (June, July) and immediately after (October) a major thermal coral bleaching event in 2010. To estimate the capacity for resistance and resilience to thermal stress, we report on a) the overall bleaching severity during and after the event, b) differences in bleaching susceptibility among taxa during the event and c) the response of the reef in terms of taxonomic community structure before (2009) and after (2012) bleaching. Despite severe bleaching in 2010 (66% of colonies bleached), post-bleaching recovery appeared to be relatively rapid and coral taxa that are usually highly susceptible (e.g., *Acropora* and *Pocillopora*) were relatively unaffected, i.e., either they did not bleach or they bleached and recovered. Although there was no significant change in coral taxonomic community structure among years, taxa that bleached most severely tended to have the greatest reductions in relative cover. Several factors may have contributed to the overall high resistance of this site to bleaching including turbidity, symbiont affiliation and heterotrophy. A parsimonious explanation for the reversed pattern of bleaching susceptibility among taxa is

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that these coral populations have adapted and/or acclimatised to thermal stress. Despite ongoing chronic anthropogenic impacts, we suggest that this site has potential for rapid recovery of coral cover due to the dominant coral taxa and growth forms being capable of rapid regrowth from remnant colonies.

Introduction

Coral bleaching refers to the paling or whitening of shallow water reef corals that results from the loss of symbiotic dinoflagellate algae (known as zooxanthellae) or their algal pigments (Douglas 2003). Bleaching is a stress response, leading to sub-lethal damage and/or partial or whole colony mortality for the coral host, and can be induced by several factors (Baird et al., 2009). Large-scale bleaching episodes, however, are strongly correlated with elevated sea temperatures and may be exacerbated by high irradiance (Glynn 1993; Brown 1997). Major bleaching events driven by thermal anomalies have caused widespread and catastrophic mortality of corals and are considered one of the main drivers of global reef degradation (Hoegh-Guldberg et al., 2007). Bleaching severity, at the level of the coral assemblage, varies substantially as a consequence of the severity of thermal stress (Kleypas et al., 2008), the thermal history of the site (e.g., Thompson & van Woesik 2009), local environmental factors that affect irradiance (e.g., cloud cover or turbidity) (Mumby et al., 2001; Dunne & Brown 2001) and the type and diversity of symbiotic algae present in the coral host tissue (Baker et al., 2004).

One of the strongest drivers of variation in bleaching at a reef scale, however, is the taxonomic composition of the coral assemblage (Marshall & Baird 2000). This is because, until recently, there were found to be consistent differences in the susceptibility of coral taxa to bleaching (Brown 1997; Marshall & Baird 2000; Loya et al., 2001; McClanahan et al., 2004; but see Guest et al., 2012). For example, in most studies to date, branching colonies of the genera *Acropora* and *Pocillopora* tended to bleach much more severely relative to other growth forms and coral genera, particularly slow growing massive species (Marshall & Baird 2000; Loya et al., 2001; McClanahan et al., 2004). This observation has led to the widespread classification of fast growing branching species as “losers” in the face of global warming (Loya et al., 2001), at least in the short term (van Woesik et al., 2011). The classification of corals as winners or losers does not, however, take into consideration the capacity for normally susceptible species to adapt and/or acclimatise to thermal stress (Maynard et al., 2008 a; Maynard et al., 2008 b; Baird & Maynard 2008).

Not only do different coral taxa vary in their bleaching responses, but they also differ in their ability to recover from bleaching. For example, in a study of individually tagged colonies of four species on the Great Barrier Reef (GBR) following bleaching, 88% of *Acropora hyacinthus* and 32% of *A. millepora* colonies (both fast growing branching species) died compared to whole colony mortality in only 13% of *Platygyra daedalea* and 0% of *Porites lobata* (both slow growing massive species)(Baird & Marshall 2002). Most surviving *P. daedalea* and *P. lobata* colonies lost some tissue through partial colony mortality but this was rare in the *Acropora*, and colonies either survived intact or died completely (Baird & Marshall 2002). The physiological mechanism that normally leads to greater susceptibility among fast growing branching species is unknown, but has been associated with metabolic rate (Gates & Edmunds 1999), tissue thickness (Loya et al., 2001), mass transfer rates (Nakamura & van Woesik 2001), fluorescent proteins (Bou-Abdallah et al., 2006), light absorbing capacities (Fabricius 2006), heterotrophy (Grottoli et al., 2006), and symbiont association (Baker 2004).

Differential bleaching severity among taxa has important ecological implications because it influences the potential of species to adapt to future thermal stress by natural selection (Baird & Maynard 2008). Susceptible taxa, such as *Acropora* and *Pocillopora*, have relatively fast growth rates (Harriott 1999) and become sexually mature within two to three years (Baria et al., 2012; Stimson 1978), life history traits which predispose these genera to adapt more rapidly (Baird & Maynard 2008). Thus, one might expect a more rapid adaptive response on reefs dominated by fast growing susceptible species (providing that the coral population recovers following bleaching) (Maynard et al., 2008 b). The incidence of partial versus full colony mortality within a coral community following bleaching also has implications for the rate at which a reef recovers following a disturbance. Reefs dominated by corals that tend to suffer partial coral mortality may recover coral cover rapidly via regrowth of remnant colonies, rather than relying on recruitment of new colonies from larvae (e.g., Golbuu et al., 2007; Diaz-Pulido et al., 2009).

Understanding the potential of reef assemblages to recover from disturbances (such as bleaching) is becoming increasingly important as the frequency and magnitude of anthropogenic impacts affecting reefs increase (Pandolfi et al., 2003). Temperature induced mass coral bleaching events are predicted to become more frequent (Hoegh-Guldberg 1999; Donner et al., 2005; Eakin et al., 2009) and reef coral assemblages will undoubtedly change in terms of their taxonomic composition over the next few decades (Pandolfi et al., 2003).

While many studies report on broad, regional scale responses to thermal stress during bleaching events (e.g., proportion of corals bleached)(e.g., Wilkinson 1998) fewer examine variation in susceptibility among taxa and change in coral community structure, before, during and after bleaching on individual reefs (e.g., Loya et al., 2001; Brown et al., 2002; Maynard et al., 2008 a; van Woesik et al., 2011; McClanahan 2014; Pratchett et al., 2013). Such detailed studies are needed if we are to understand the effect that repeated thermal anomalies will have on community structure and reef resilience. Furthermore, less is known about the capacity for resistance and recovery on urbanised reefs that experience severe chronic disturbances such as elevated sedimentation and turbidity (although see Brown et al., 2002). It is often assumed that these reefs will be less resilient to additional disturbances than reefs that are effectively managed or reefs far from anthropogenic influences (West & Salm 2003; Golbuu et al., 2007; Nystrom & Folke 2001).

In 2010, corals throughout the Indian Ocean and Southeast Asia experienced higher than normal water temperatures leading to extensive coral bleaching at many reef sites (http://coralreefwatch.noaa.gov/satellite/bleachingoutlook/index.html). Severe bleaching was reported in Singapore and Malaysia (Thomas & Heron 2011; Guest et al., 2012), Thailand (Hoeksema & Matthews 2010; Phongsuwan and Chansang 2012; Sutthacheep et al., 2012), Indonesia (Wilson et al., 2012; Maynard et al., 2012), Brunei, Cambodia, Philippines and Vietnam (Tun et al., 2010). In an earlier publication Guest et al. (2012) reported an unusual reversal in bleaching susceptibility among coral taxa and contrasting bleaching responses among sites in Singapore, Malaysia and Sumatra during 2010. To further examine the capacity for resistance of heavily urbanised Singaporean reefs, here we examine the bleaching responses of corals at a reef site south of mainland Singapore during (June, July) and immediately after (October) the 2010 bleaching event. The aims of this study were to a) estimate the capacity for resistance to thermal stress by quantifying overall bleaching severity during and after the event, b) compare relative bleaching susceptibility among taxa during and after the event, and c) examine the effect of the bleaching event on coral cover and coral taxonomic community structure.

Methods and materials

Study site

All work was conducted at a fringing reef on the western side of Pulau Satumu (Raffles Lighthouse, 1°09′35.09″N, 103°44′24.09″E). Pulau Satumu is situated approx. 13 km from mainland Singapore and is the southernmost reef within Singapore's territorial waters. The western fringing reef at Pulau Satumu is approx. 250 m long and 20-30 m wide (i.e., from shore to the base of the reef slope). Singapore's marine environment is characterised by high levels of sedimentation, turbidity and eutrophication as a result of extensive historical coastal development and ongoing dredging of shipping channels (Chou 1996; Gin et al., 2000). Although heavily impacted, most of Singapore's islands have fringing reefs with relatively diverse coral communities with over 250 scleractinian species (Huang et al., 2009). Due to its distance from the mainland, Pulau Satumu has the lowest rates of sedimentation and suspended solids of studied Singaporean reefs (Low & Chou 1994; Todd et al., 2004; Dikou & van Woesik 2006). This site also has the highest hard coral cover (~50 to 70% in the present study) and greatest coral species richness among Singaporean reefs (Dikou & van Woesik 2006; Huang et al., 2009). While it is one of the least impacted sites in Singapore, levels of sedimentation (~15 mg cm^2 d^{-1}) and suspended solids (~10 mg l^{-1}) (Todd et al., 2004) still exceed values considered normal for coral reefs (Rogers 1990). This, and other sites in Singapore, are dominated in terms of coral cover by foliose, encrusting, massive and submassive coral growth forms, particularly from the genera *Montipora*, *Merulina*, *Platygyra*, *Echinopora* and *Pachyseris* (Guest et al., unpublished data). However, Pulau Satumu was selected as it has one of the only accessible reefs within Singapore's territorial waters possessing an assemblage of *Acropora* and *Pocillopora* (primarily *P. damicornis*) corals suitable for meaningful ecological studies (Guest et al., 2005).

Surveys of bleaching susceptibility

Extensive bleaching of corals and other zooxanthellate taxa (e.g., anemones, zooanthids) at multiple sites south of Singapore was first recorded in May 2010 (Tun et al., 2010). Coral bleaching is triggered when sea surface temperatures (SST) exceed a climatological maximum monthly mean (MMM) for extended periods. The extent of thermal stress is typically expressed in terms of degree heating weeks (DHW) (Liu et al., 2003). In Singapore, remotely sensed data derived from the Pathfinder dataset of the US National Oceanic and Atmospheric Administration (Casey et al., 2010; Kilpatrick et al., 2001) indicated that SSTs rose above the climatological MMM of 29.86°C in mid-April 2010 and remained elevated until at least mid-August 2010 (Guest et al., 2012). During this period, maximum DHW of 12.02°C weeks (i.e., accumulation of thermal anomalies at temperatures >29.86°C) occurred in mid-July (Guest et al., 2012), although this was based on a slightly modified version of the most commonly used DHW method (i.e., when thermal anomalies begin to accumulate at ≥1°C above MMM). The level of thermal stress reported for Singapore was similar to that of other sites in Southeast Asia, including Malaysia and Sumatra (Guest et al., 2012). For the present study, surveys of bleaching susceptibility were carried out on June 15, July 5 and October 4 2010, i.e., approximately +8, +12 and + 25 weeks after sea temperatures exceeded MMM in Singapore.

On survey occasions in June and July, coral colonies within four haphazardly placed 30 m × 1 m belt-transects were surveyed at depths between ~2 and 5 m along the reef flat and upper reef slope on the western side of Pulau Satumu. Survey data in October were collected using methods described in (Guest et al., 2012). Ten replicate two-metre radius survey plots were selected haphazardly and all colonies within each plot were surveyed. Although the survey methods in June/July and October differed, the total area survyed was similar (120 m^2 in June/July and 126 m^2 in October). In addition to the transects and survey plots, in July and October a wider survey of the genus *Acropora* was carried out during a 40-minute random swim, in which all *Acropora* colonies encountered were surveyed. Following the scheme described by (Marshall & Baird 2000) all colonies within each transect or survey plot were identified to genus level and bleaching status was recorded as follows: 1) healthy=no bleaching; 2) moderately bleached=colony pale or less than 50% of surface area bleached and; 3) severely bleached=colony greater than 50% bleached. A bleaching index (BI) was estimated following methods described by McClanahan et al. (2004) as follows:

$$BMI = \frac{0c1 + 1c2 + 2c3}{2}$$

Where c1 to c3 are the three coral status categories expressed as the proportion of colonies (%) surveyed arranged in order from not bleached to severely bleached. This differs from the bleaching and mortality index described by (McClanahan et al., 2004) as it does not include recently dead colonies.

Coral cover and taxonomic community structure were characterized by SCUBA divers using the line intercept method (English et al., 1997) in September 2009, 2010 and 2012 (i.e., one year before bleaching, during bleaching and two years after bleaching). During each survey, five replicate 20 m transects were laid parallel to the reef crest at a depth of ~3 to 4 m and each transect was separated by a distance of approximately 5 m. The genera and growth forms of all hard coral colonies encountered along each transect were recorded. Non-metric multidimensional scaling (nMDS) ordinations and one-way ANOSIM based on Bray-Curtis similarities of square-root transformed data were produced in PRIMER v6 (Clarke & Gorley 2006) to examine changes in coral community structure among years.

Results

A total of 597, 542 and 491 colonies were surveyed in June, July and October 2010 respectively. Surveys of taxa susceptibility of all genera carried out in June and July revealed that an estimated 66% and 58% respectively of colonies surveyed were bleached (Fig. 1). In June an estimated 36% of colonies were moderately bleached and 30% were severely bleached, whereas in July there was already some evidence of recovery with only 33% and 25% moderately and severely bleached respectively (Fig. 1). In contrast, in October only 18% of colonies surveyed were bleached, with only 4% severely bleached and 14% moderately bleached (Fig. 1). A total of 30 taxa were surveyed during all three sampling occasions in 2010. Bleaching severity varied greatly among populations within each sampling occasion, within populations and among sampling occasions. The proportion of colonies bleached within genera varied from 0% to 100% among genera in all survey months, however, for most taxa, bleaching severity declined markedly between June and October (Table 1). For example, in June and July, 22 of 30 taxa surveyed had ≥50% of colonies bleached, whereas in October only 4 taxa had ≥ 50% of colonies bleached (Table 1).

Considering only taxa for which at least 5 colonies were sampled on all 3 occasions, 4 coral genera had consistently low susceptibility to bleaching (i.e., BI < 30) throughout the study period (Table S1, Fig. 2). These included *Acropora*, *Galaxea*, *Pavona* and *Merulina* (Table S1, Fig. 2). The genus *Acropora* was the least affected among all genera, with 82% of colonies surveyed in July (at least 13 species surveyed) unaffected by bleaching with the remainder either pale or partially bleached and none severely bleached (Table 2, Fig. 2, 3a-c). A further 7 genera had relatively moderate susceptibility to bleaching (i.e., BI from 30 to 59) in both June and July, but of these, all but one (*Porites*) had low severity (BI <30) by October (Table S1, Fig. 2). All colonies of *Porites* surveyed in June and July were massive (primarily *P. lutea* and *P. lobata*) or submassive (*P. rus*). Only one colony of branching *Porites* (possibly *P. cylindrica*) was surveyed in October and this had suffered severe partial mortality (80% of colony), suggesting it had experienced bleaching related mortality. A further 8 genera had relatively high bleaching susceptibility (i.e., BI ≥60) in June and/or July, but again, all had low severity (i.e., BI <30) by October (Table S1, Fig. 2). For example, all *Pocillopora* colonies (predominantly *P. damicornis*) were bleached, with 80% moderately and 20% severely bleached in July, but by October only 15% remained moderately bleached (Table S1, Fig. 2, Fig. 3d). The massive taxa *Porites*, on the other hand recovered less quickly with 43% of colonies moderately or severely bleached in October, compared to 53% in July (Table S1, Fig. 2, Fig. 3e).

Average coral cover at Pulau Satumu declined from 72.2 ± 11.1% (mean ± SD) in 2009 to 50.7 ± 8.4% in 2010, but had partly recovered to 56.0 ± 9.1% by 2012. A total of 36 coral genera were surveyed before, during and after the bleaching event in 2009, 2010 and 2012 (Table S2). While there were changes in relative cover of certain taxa before and after bleaching, there was no significant shift in coral taxonomic community structure among years at Pulau Satumu (One-way ANOSIM, Global R -0.08) suggesting that most differences in relative cover of taxa among years were a result of natural temporal variation. It is worth noting, however, that of the 8 taxa that had high susceptibility to bleaching in June/July, five showed decreases in relative abundance after bleaching (*Pachyseris*, *Fungia*, *Pectinia*, *Hydnophora* and *Montipora*) (Table S1). In contrast, only one of the four taxa (*Pavona*) that showed low bleaching susceptibility had declined in relative abundance between 2009 and 2012 (Table S2). The taxa that had the highest bleaching index in October (*Porites*) also had the greatest decrease in relative abundance between 2009 and 2012 (Table S2). Relative cover of *Acropora* remained unchanged before and after bleaching, while relative cover of *Pocillopora* increased nine-fold (Table S2).

Discussion

Between May and August 2010 Singapore's reefs were reported to be severely bleached (i.e., >50% of colonies bleached) as a result of the thermal anomaly (Tun et al., 2010). Despite severe bleaching at one Singaporean site (Pulau Satumu) in 2010, post-bleaching recovery appeared to be rapid and coral taxa that are usually highly susceptible (e.g., *Acropora* and *Pocillopora*) were relatively unaffected (also reported in Guest et al., 2012). Surveys of four other sites around Singapore's Southern Islands found similar reef-scale bleaching responses, suggesting that Pulau Satumu was representative of the broader community (Tun et al., 2010). Surveys to estimate bleaching associated coral mortality carried out in October 2010 at Pulau Satumu revealed that an estimated 4% of colonies had died recently (Guest et al., 2012). The majority of the change seen in the proportion of bleached and healthy colonies between June and October was, therefore, due to colonies recovering from bleaching and not as a result of colonies bleaching and subsequently dying. Bleaching associated mortality on other Singaporean reefs (reported to be <10% of corals) was much lower than reported at other locations in Southeast Asia, particularly at sites in the Andaman Sea and Gulf of Thailand where close to half of colonies surveyed were reported to die following bleaching (Bridge et al., 2013, Phongsuwan & Chansang 2012, Sutthacheep et al., 2013, Tun et al., 2010), but similar to reports from sites in Peninsular Malaysia (Tioman Island) Indonesia (e.g., Wakatobi, Bali), Brunei, Sabah and Sarawak (Tun et al., 2010) .

In addition to relatively high overall resistance of corals at Pulau Satumu to bleaching, the taxonomic hierarchy of susceptibility among coral genera was unprecedented. In all studies prior to 2010 there has been a consistent pattern of susceptibility among coral taxa, with branching *Acropora* and *Pocillopora* being more susceptible to thermal stress than massive growth forms (Baird & Marshall 2002; Loya et al., 2001; Marshall & Baird 2000;

McClanahan et al., 2004). In contrast, in the present study, *Acropora* were the least affected of all taxa, with 5, 18 and 4% of colonies moderately bleached in June, July and October. In contrast, most surveyed colonies of *P. damicornis* were bleached in June and July (83 and 100% respectively), however, only 15% of colonies remained moderately bleached in October. No recently dead colonies of *Pocillopora* and only one recently dead colony of *Acropora* were recorded during surveys in October 2010 (data from Guest et al., 2012) thus we can conclude that these, normally susceptible, genera were largely resistant to bleaching associated mortality at this reef during the 2010 thermal anomaly. On the other hand, massive species and other growth forms and taxa behaved normally, i.e., they tended to bleach moderately and recover relatively slowly (Baird & Marshall 2002). For example a high proportion of surveyed *Porites* colonies (43%) were still moderately or severely bleached in October. Surveys of coral benthic structure showed decreases in overall coral cover after the bleaching event; however, taxonomic community structure did not change significantly. There were no decreases in relative abundance of *Acropora*, but there were increases in relative abundance of *Pocillopora* and decreases in relative abundance of *Porites*. For *Porites*, this was not as a result of species with branching morphologies bleaching and dying as the majority of *Porites* surveyed at Pulau Satumu were either massive or submassive morphologies (e.g., *P. lutea*, *P. rus*). A similar pattern, i.e., relatively low susceptibility to bleaching of *Acropora* corals, was also reported for sites in Indonesia (e.g., Wakatobi) (Wilson et al., 2010) and Malaysia (e.g., Tioman Island) (Guest et al., 2012), indicating this unusual taxonomic reversal in susceptibility was not restricted to the reef at Pulau Satumu. To the best of our knowledge, this is the first time such a response has been reported for these usually highly susceptible taxa during a major thermal bleaching event. In light of these results, there is a clear need to re-evaluate the current paradigm regarding winners and losers among corals in the face of climate change.

Several possible explanations exist for the overall high resistance to bleaching at Pulau Satumu in 2010. Firstly, Singapore's corals may host relatively thermally tolerant symbiont clades. Currently published accounts of symbiont association from Singaporean reefs only exist for five species of zoanthid which host C1/C3, C15/C91 and clade D derived *Symbiodinium* (Reimer & Todd 2009). Work is currently in progress to identify zooxanthellae clade types for a range of Singaporean coral species using next generation sequencing approaches and initial results suggest that most coral taxa host predominantly clade C derived symbionts (B. Wilson, unpublished data). Secondly, high turbidity, which characterises Singapore's coastal waters (e.g., average Secchi depth ~2 m) (Guest et al., 2007) may provide a degree of protection from light stress during thermal anomalies. In combination with high temperatures, elevated levels of irradiance can lead to coral bleaching (Brown 1997; Dunne & Brown 2001) and it has been shown that when irradiance is lowered during thermal anomalies (e.g., by cloud cover) corals bleach less severely (Mumby et al., 2001). Thirdly, it is conceivable that high concentrations of suspended particulate matter (SPM) present in Singapore's coastal waters, e.g., ranging from 9 to 16 mg l^{-1} (Todd et al., 2004), which can be an important source of food for corals on turbid reefs (Anthony 2000), may have provided an opportunity for corals to obtain a higher proportion of their energy requirements from heterotrophy during periods of thermal stress (Grottoli et al., 2006). If the latter two explanations are true, they provide examples of an "ecological surprise" (Paine et al., 1998), where two disturbances (elevated turbidity and thermal anomalies) act antagonistically to prevent high bleaching-associated mortality.

A final plausible explanation for the level of bleaching resistance at Pulau Satumu is that corals at this site possess greater tolerance to acute temperature fluctuations due to prior acclimatisation, i.e., phenotypic changes by an individual organism in response to fluctuations in natural conditions (Coles & Brown 2003). It is well established that bleaching is induced when temperature increases significantly above the long-term mean annual maximum (Coles & Brown 2003 and references within) and that corals living at higher average ambient temperatures have higher thermal tolerances than those living at lower temperatures (Coles et al., 1976). On reefs with similar mean temperatures but differences in overall temperature fluctuations (i.e., differences in standard deviation around the mean), corals that experience the larger fluctuations may also have greater thermal tolerance (McClanahan & Maina 2004; McClanahan et al., 2007; Oliver & Palumbi 2011). Support is provided for this explanation by the fact that annual SST variability (i.e., standard deviation of the mean) is ~40 - 52% higher at sites in the South China Sea where overall bleaching severity was lower in 2010 compared to sites in the Andaman Sea (this is despite similar levels of thermal stress in 2010 and similar long term average SSTs) (Guest et al., 2012).

While the above may explain the overall resistance of corals at Pulau Satumu to bleaching, they do not explain the unprecedented hierarchy of taxa susceptibility (e.g. low susceptibility for *Acropora* and *Pocillopora*) seen at this and other sites in Southeast Asia (Guest et al., 2012; Wilson et al., 2010). A parsimonious explanation for the reversal in susceptibility at certain sites in 2010 is that removal of susceptible individuals from populations that bleached during previous episodes, followed by reproduction and successful recruitment of the remaining, more thermally tolerant individuals, has led to adaptation through natural selection within an ecological time frame. High variability within populations in response to thermal stress provides a very strong selective pressure. Due to the life history traits of *Acropora* and *Pocillopora* - i.e., fast growth rates (Harriott 1999), onset of sexual maturity within 2 to 3 years (Stimson 1978; Baria et al., 2012) and high rates of whole colony mortality following thermal stress (Baird & Marshall 2002) - these taxa are the most likely to adapt in a rapidly changing environment (Baird & Maynard 2008). This hypothesis is supported by the observation that these genera were generally less susceptible to bleaching at sites in Southeast Asia that bleached during the last major episode in 1998, whereas they suffered high levels of bleaching associated mortality in 2010 at sites that did not bleach in 1998 (Guest et al., 2012). Furthermore, studies carried out on reefs over successive bleaching events that have documented increasing thermal tolerance and declining rates of bleaching induced mortality in usually susceptible taxa over successive bleaching events (Glynn et al., 2001; Maynard et al., 2008 a; Pratchett et al., 2013). Unfortunately, nothing is known about differences in taxa susceptibility for the reef at Pulau Satumu during 1998, however, at Indonesian sites close to Singapore, *Acropora* was reported to be the most affected taxa in 1998, suffering extensive mortality (Suharsono 1999). Clearly, repeated surveys at individual sites over successive bleaching events, coupled with detailed environmental data are necessary to accurately assess the potential for adaptation among scleractinians.

The response of corals to thermal stress at Pulau Satumu has important implications for resilience. Surveys of benthic community structure carried out in 2009 and 2010 showed a reduction in overall cover of corals from ~73 to 51% at this site, however, there was no significant change in coral taxonomic community structure before and after the bleaching event in 2010. In the present study, decreases in relative cover (%) at Pulau Satumu were greatest for the coral taxa *Porites*, *Pavona*, *Pachyseris*, *Montipora* and *Echinopora* between 2009 and 2012. With the exception of *Porites*, which predominantly has massive growth forms at Pulau Satumu, these taxa typically have foliose or encrusting growth forms. Considering that there was little evidence of whole colony mortality following the 2010 bleaching (i.e., ~4% of colonies surveyed) (Guest et al., 2012) but that partial colony mortality of bleached colonies was noted for several taxa during surveys (e.g., *Montipora*, Fig. 3f), it is likely that the observed loss of coral cover in 2010 was primarily due to partial colony mortality. Singapore does not experience typhoons and major coral predators (e.g., *Acanthaster plancii*) have not been documented locally, thus the 2010 bleaching event was the only major natural disturbance affecting Singaporean reefs during the study period. We cannot, however, rule out the possibility that other anthropogenic disturbances such as boat groundings and anchor damage (both of which are common in Singapore) also contributed to changes in coral cover between 2009 and 2012. The processes of regrowth of remnant colonies and recruitment of larvae both contribute to the time taken for coral cover to recover to pre-disturbance levels on reefs, but recovery rates vary among habitats and are highly dependent on the composition of surviving coral communities (Golbuu et al., 2007). Measured linear extension rates for foliose and massive species (e.g., *Merulina ampliata* ~25 mm yr^{-1} , *Porites lutea* ~18mm yr^{-1}) (Dikou 2009, Tanzil et al., 2013) at Pulau Satumu are within the normal range for other scleractinians elsewhere (Harriott 1999, Lough & Barnes 2000). In contrast, estimated rates of settlement of new coral spat at this site are relatively low (Bauman et al., unpublished data) compared to published settlement rates for other Indo-Pacific reef sites (Glassom et al., 2004). Surveys of benthic community structure before and after the 1998 coral bleaching event at this site revealed that coral cover returned to pre-disturbance levels within 10 years (JR Guest, unpublished data). Considering the low levels of coral settlement and the fact that most bleaching related mortality appeared to be as a result of partial colony mortality, it seems likely that the primary mechanism for rapid recovery of coral cover at Pulau Satumu was regrowth of remnant colonies rather than sexual recruitment.

In this study we show a remarkable level of resistance to, and recovery from, a major thermal coral bleaching event at a chronically impacted Indo-Pacific reef site. Furthermore, we document a reversed pattern of bleaching susceptibility where usually highly susceptible taxa were relatively unaffected by bleaching. These results suggest an underappreciated resilience in urbanized, impacted reef systems and that corals that have been classified as losers in the face of climate change may have a greater capacity for adaptation and/or acclimatization than previously supposed. While this does not mean that threats to reefs have been exaggerated, it provides hope that, if measures are taken to reduce global impacts, many Indo-Pacific coral reefs may show a greater capacity for resilience than expected.

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Table 1. Proportion of colonies bleached in all taxa that were surveyed in June, July and October. *Additional surveys of *Acropora* in July and October were carried out by random swims to increase number of colonies surveyed.

		June		**July**		**October**	
Family	**Genus**	**Bleached (%)**	**n**	**Bleached (%)**	**n**	**Bleached (%)**	**n**
Faviidae	*Diploastrea*	0	3	33	3	0	3
Siderastreidae	*Psammocora*	0	1	100	2	20	5
Faviidae	*Caulastrea*	0	1	0	1	100	1
Acroporidae	*Acropora*	5	21	18	62*	4	83*
Merulinidae	*Galaxea*	6	17	20	10	0	14
Agariciidae	*Pavona*	21	24	21	14	0	14
Poritidae	*Goniopora*	25	4	50	4	25	4
Faviidae	*Cyphastrea*	40	5	33	3	0	2
Merulinidae	*Merulina*	46	54	35	43	8	25
Acroporidae	*Astreopora*	50	2	0	3	0	1
Poritidae	*Porites*	53	15	53	17	43	23
Faviidae	*Platygyra*	58	38	61	18	25	24
Faviidae	*Echinopora*	59	22	71	14	36	11
Faviidae	*Favites*	60	20	62	26	20	25
Euphyllidae	*Euphyllia*	60	5	60	5	100	1
Faviidae	*Goniastrea*	66	41	54	54	11	35
Acroporidae	*Montipora*	75	146	64	105	8	64
Mussidae	*Symphyllia*	75	12	83	12	33	12
Faviidae	*Favia*	78	9	75	12	22	9
Fungiidae	*Podabacia*	80	5	86	7	44	9
Pocilloporidae	*Pocillopora*	83	12	100	10	15	40
Fungiidae	*Ctenactis*	83	6	60	5	29	7
Fungiidae	*Fungia*	84	25	81	27	20	25
Merulinidae	*Hydnophora*	88	8	90	10	25	8
Agariciidae	*Pachyseris*	89	35	93	27	44	9
Pectinidae	*Pectinia*	89	54	76	41	33	27
Pectinidae	*Oxypora*	100	2	100	1	0	2
Turbinaria	*Turbinaria*	100	1	50	2	0	3
Euphyllidae	*Plerogyra*	100	6	100	2	100	3
Mussidae	*Lobophyllia*	100	3	100	2	100	2

Fig. 1. Overall coral bleaching severity in June, July and October in terms of proportion (%) of colonies not bleached, moderately bleached and severely bleached (categories 1, 2 and 3 respectively).

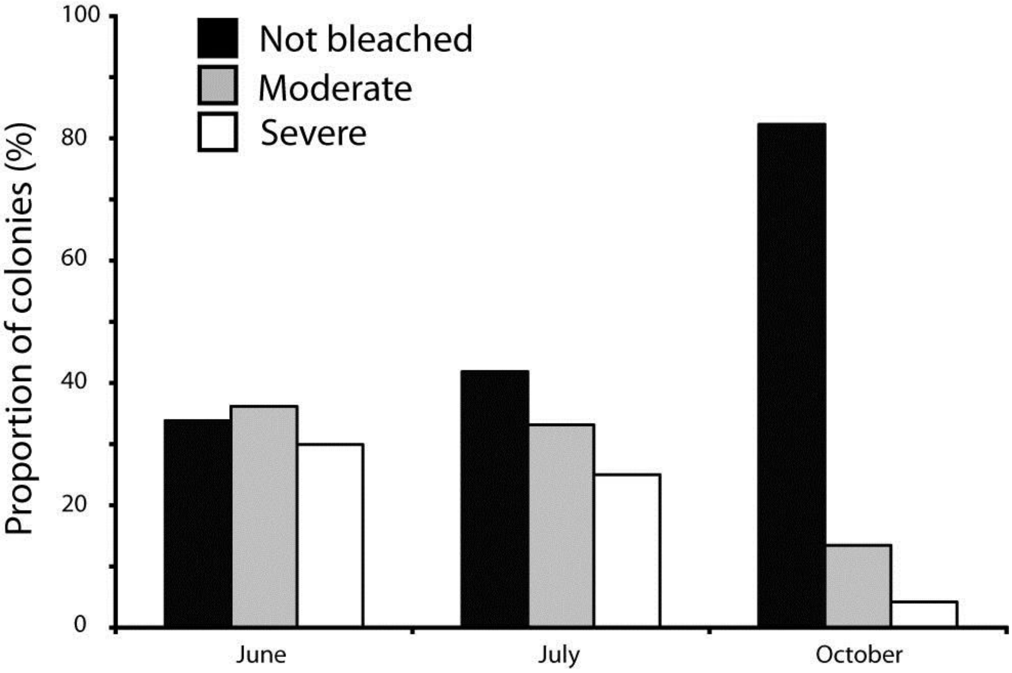

Fig. 2. Proportion (%) of colonies not bleached (black bars), moderately bleached (gray bars) and severely bleached (white bars) for all genera that had at least 5 colonies surveyed on all three survey occasions.

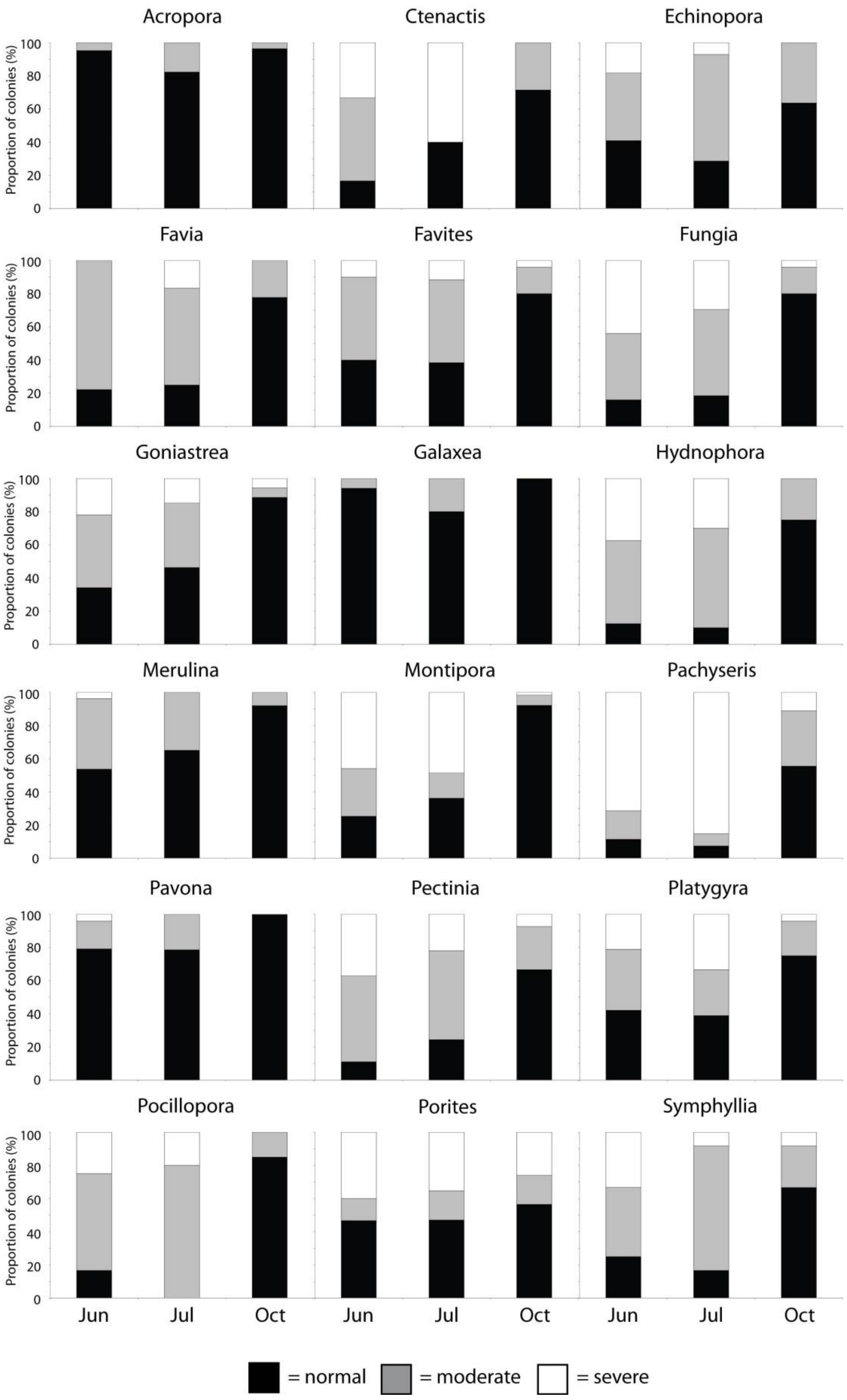

Fig. 3 Bleaching at Pulau Satumu in July 2010: a) healthy colony of *Acropora tenuis* next to severely bleached colony of *Montipora*, b) healthy colony of A. tenuis next to severely bleached colony of *Platygyra* sp., c) healthy colony of *A. hyacinthus* with severely and partially bleached massive and encrusting corals, d) severely (left) and partially (right) bleached colonies of *Pocillopora damicornis*, e) severly bleached colony of *Porites* (massive) and f) partial mortality and disease in bleached colony of *Montipora* sp. Photos: JR Guest.