Long-term changes in the susceptibility of corals to thermal stress around Phuket, Thailand

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The bleaching susceptibility of 28 coral taxa around southern Phuket was examined in four natural major bleaching events, in 1991, 1995, 2010, and 2016. Surveys were conducted by line intercept and belt transect methods. All coral colonies were identified to genus or species-level and their pigmentation status was assessed as: (1) fully pigmented (i.e. no bleaching), (2) pale (loss of colour), (3) fully bleached, and (4) recently dead as a result of bleaching-induced mortality. Bleaching and mortality indices were calculated to compare bleaching susceptibility among coral taxa. In 2016 some of the formerly bleaching susceptible coral taxa (e.g. *Acropora*, *Montipora, Echinopora*, *and Pocillopora damicornis*) showed far greater tolerance to elevated sea water temperature than in previous years*.* In *P. damicornis* the higher bleaching resistance encompassed all sizes from juveniles (<5cm) to adults (>30cm). In contrast, some of the formerly bleaching-resistant corals (e.g. the massive *Porites, Goniastrea, Dipsastraea, and Favites*) became more susceptible to bleaching over repeated thermal stress events. Our results support the hypothesis that some of the fast-growing branching corals (*Acropora*, *Montipora*, and *Pocillopora*) may have life-history traits that lead to more rapid adaptation to a changed environment than certain growing massive species.

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Abstract

Methods. The bleaching susceptibility of 28 coral taxa around southern Phuket was examined in four natural major bleaching events, in 1991, 1995, 2010, and 2016. Surveys were conducted by line intercept and belt transect methods. All coral colonies were identified to genus or species-level and their pigmentation status was assessed as: (1) fully pigmented (i.e. no bleaching), (2) pale (loss of colour), (3) fully bleached, and (4) recently dead as a result of bleaching-induced mortality. Bleaching and mortality indices were calculated to compare bleaching susceptibility among coral taxa.

Results. In 2016 some of the formerly bleaching susceptible coral taxa (e.g. *Acropora*, *Montipora, Echinopora*, *and Pocillopora damicornis*) showed far greater tolerance to elevated sea water temperature than in previous years. In *P. damicornis* the higher bleaching resistance encompassed all sizes from juveniles (<5cm) to adults (>30cm). In contrast, some of the formerly bleaching-resistant corals (e.g. the massive *Porites, Goniastrea, Dipsastraea, and Favites*) became more susceptible to bleaching over repeated thermal stress events.

Discussion. Our results support the hypothesis that some of the fast-growing branching corals (*Acropora*, *Montipora*, and *Pocillopora*) may have life-history traits that lead to more rapid adaptation to a changed environment than certain growing massive species.

Introduction

Coral bleaching is a phenomenon involving the breakdown of the coral-alga1 symbiosis, resulting in the loss of symbiotic algae and/or their pigments (Brown 1997; Jokiel 2004). The symptoms of bleaching include a gradual loss of colour which may culminate in death if environmental stresses persist. Various physical parameters account for bleaching such as low salinity(Coles & Jokiel 1978; Scott et al. 2013), high light intensity(Dunne & Brown 2001), increased and decreased sea water temperature (Brown et al. 1996; Lesser 1996; Lirman et al. 2011; Rodríguez-Troncoso et al. 2014), and high CO_2 (Anthony et al. 2008). Elevated temperature and light have been regarded as the major agents triggering bleaching and it is well accepted that they cause widespread bleaching events (Berkelmans & Oliver 1999; Bruno et al. 2001; Eakin et al. 2010; van Hooidonk et al. 2012).

Not all coral taxa are equally susceptible to bleaching under the same stress and not all corals are able to recover to the same extent after bleaching (Baird & Marshall 2002; McClanahan 2004; Obura 2005). In general, slow growing coral taxa with massive or columnar morphologies are less susceptible to bleaching than fragile, fast growing taxa with branching or plating morphologies (Furby et al. 2013; Hongo & Yamano 2013; Loya et al. 2001; Marshall & Baird 2000; McClanahan 2004). Nevertheless, bleaching susceptibility of a coral species can change over time. There are studies documenting an improved bleaching tolerance in corals that previously experienced thermal/light stresses (Bellantuono et al. 2012; Fang et al. 1997; Maynard et al. 2008; Middlebrook et al. 2008; Schoepf et al. 2015). But there are also reports showing a decrease in bleaching tolerance in corals after repeated thermal/light stress (Brown et al. 2014; Hongo & Yamano 2013). The bleaching responses of corals to combined heat/light stressors will depend very much on the intensity of each stressor and their prior exposure to these stressors in the period leading up to bleaching (Brown et al. 2002a).

The capacity of corals to adapt to elevated temperatures has received increased attention in recent years. Adaptation can involve both host and/or symbiont. Different symbiont types are known to confer different thermal tolerance to a given coral host. In corals associating with more than one symbiont type, the switching and/or shuffling of symbionts differentially adapted to thermal and/or light stress may increase the proportion of thermally tolerant symbionts and improve the bleaching tolerance of the coral holobiont (Berkelmans & van Oppen 2006; Oliver & Palumbi 2011; Ulstrup et al. 2006). Selection for temperature tolerance in algal symbionts is well documented along environmental gradients from the scale of the colony (LaJeunesse et al. 2007) to the coral community scale (Jones et al. 2008). In addition to the symbionts, the coral host can play an important role in thermal tolerance through physiological acclimatization, e.g. by enhancing cellular antioxidant defence pathways in response to stress (Bellantuono et al. 2012; Brown et al. 2002b; Wicks et al. 2012).

In 2016, a relatively moderate bleaching event took place in the Andaman Sea in response to temperature anomalies above the bleaching threshold, which affected about 50% of coral cover and led to very limited bleaching-induced mortality as a result. Bleaching occurred across the area from May to early July. Interestingly, during this event we observed contrasting bleaching patterns to those observed in earlier bleaching years. Unexpectedly, we found the previously bleaching-susceptible branching corals *Acropora* and *Pocillopora* to show very limited bleaching, whereas the formerly bleaching-resistant massive *Porites* corals bleached extensively. Here, we investigate the bleaching susceptibility of various coral taxa around the southern Phuket sea area, by comparing recent coral bleaching patterns with those identified in the historical bleaching events of 1991, 1995, and 2010.

Materials and methods

Study site

Bleaching surveys were conducted around southeastern Phuket (Fig. 1) during peak periods of major bleaching events when degree heating weeks (DHW) initially reached the maximum in 1991, 1995, 2010 and 2016, respectively. Mass coral mortality followed the 2010 bleaching event, the largest so far on record (Phongsuwan & Chansang 2012). Minor to moderate bleaching events, defined as events where bleaching affects about 10% and 50% of coral cover, respectively, (Oliver et al. 2004) were observed in 1998, 2003, 2005, and 2007. Survey methodologies included permanent line intercept transects and belt transects. For the line intercept transects, a 100m measuring tape was laid out at each site at about 5 m depth. The corals below the transect line were identified to the genus or species level (total 28 taxa) and the corresponding section of each taxon intercepting the transect line was measured to the nearest centimeter (Loya 1972). Coral taxa and corresponding morphologies are provided in Table S1. For the belt transects, three 30 × 1m areas were investigated at each site by laying out a 30m measuring tape at about 5 m depth and recording the corals located within 0.5m left and right of the tape. The change from line transects (before 2016) to belt surveys (only in 2016) was necessary to accommodate the strongly reduced coral cover after the mass mortality following the 2010 bleaching event. In all surveys, the bleaching status of coral colonies was classified according to the following categories: (1) fully pigmented or no bleaching, (2) pale (loss of colour), (3) fully bleached, and (4) recently dead as a result of bleaching-induced mortality. In addition to the taxon-specific differences in bleaching susceptibilities, we determined the size-specific bleaching susceptibilities for one of the species (*Pocillopora damicornis*) at one of the sites (Tang-khen Bay). The size classes were categorized as follows: (1) primary polyp (~2mm) to small colony (5cm), (2) juvenile colony (6-10cm), (3) subadult colony (11-30cm), and (4) large colony (>30cm diameter). A bleaching and mortality index (BMI) was used to assess the bleaching susceptibilities of different coral taxa and sizes. BMI was calculated by weighting the proportion of colonies that bleached by the severity of bleaching and adding bleaching-induced mortality as follows: BMI = (0c1+1c2+2c3+3c4)/3 where c1 is fully pigmented; c2 is pale; c3 is fully bleached; and c4 is recently dead, all calculated as percent per year (McClanahan 2004).

To account for differences in the number and location of sites between survey years (Table 1), bleaching susceptibilities were computed for each survey separately, acknowledging that spatial variability in coral communities between sites may have biased the results (cf. Supplementary Information).

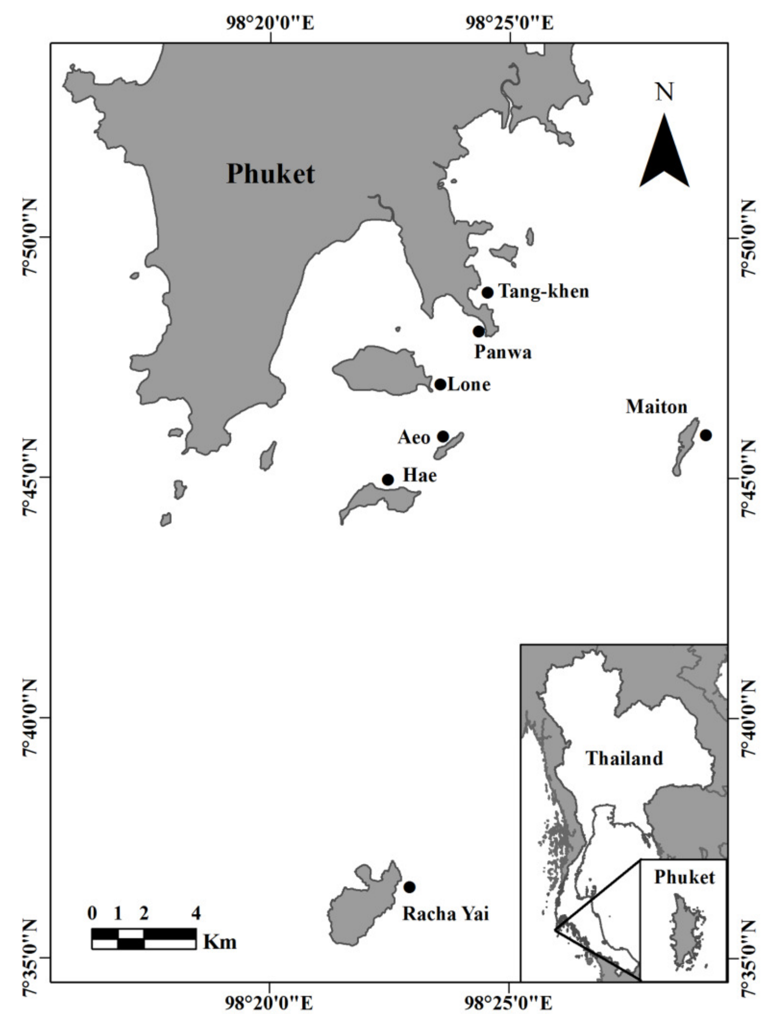

Figure 1 The location of Phuket Island in the Andaman Sea, Thailand (inset), and positions of bleaching survey sites.

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Table 1 Number of sites, surveying methods, and surveying periods in different bleaching years.

Year	Station Location	Method	Surveying Period
1991	Panwa 1, Lone, Hae, Racha Yai	Permanent line intercept transect	Jun
1995	Panwa 1, Panwa 2, Aeo, Hae 1, Hae 2		Jun
2010	Panwa 1, Aeo, Lone, Hae, Racha Yai		May
2016	Panwa 1, Tang-khen, Aeo, Lone, Hae, Racha Yai, Maiton	Belt transect	May

Note: the distance between Panwa 1and Panwa 2, Hae 1 and Hae 2 was about 100 meters and 500 meters, respectively

Thermal history and stress

Daily mean sea surface temperature (SST) was derived from the 4km^2 NOAA High Resolution SST AVHRR (1981-2016), data provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their Web site at http://www.esrl.noaa.gov/psd/. To assess the thermal stress level, degree heating weeks (DHW) were calculated using the NOAA Coral Reef Watch (CRW) methodology (Liu et al. 2006) for major bleaching years in this area, in 1991, 1995, 2010, and 2016. Briefly, the average maximum of the hottest month (maximum of the monthly mean SST climatology, or MMM climatology) served as a basis for the calculation of coral bleaching HotSpots (HS), defined as the temperature exceeding the MMM climatology (Liu et al. 2003). DHW was calculated by accumulating daily HS as follows:

$$DHW = \frac{1}{7}\sum_{i=1}^{84} HS_i, if\ HS_i \geq 1℃$$

where HS_i is the sea surface temperature (°C) above MMM for each day i over a 84 day (or 12 week) rolling window. As HS values less than 1 °C were found to be insufficient to cause bleaching stress on corals, only HS_i values larger than 1 °C were accumulated (Liu et al. 2003).

Results and discussion

Several bleaching events have taken place in the Andaman Sea over the last 25 years (Phongsuwan & Chansang 2012). The thermal conditions in terms of DHW in bleaching years that bleaching surveying data were available from 1991 to 2016 are shown in Figure 2. DHW initially reached the maximum at the different times of the years, i.e. late June in 1991 and 1995, and mid May in 2010 and 2016. The heat stress in 2010 was the highest ever encountered, when DHW was over

8°C-weeks, resulting in extensive bleaching across the Andaman Sea and subsequent mass coral mortality (Phongsuwan & Chansang 2012). In 2016, DHW were higher than 1991 and 1995, but the actual bleaching response was lower than expected from the levels of temperature stress. Bleaching susceptibility varied among coral taxa and also in different years (Fig. 3). In 2016 some coral taxa appeared to show increased thermal tolerance than previously, other taxa showed the reverse pattern. Corals that appeared to be bleaching resistant in 2016 included *Acropora*, *Echinopora*, *Montipora*, and *P. damicornis*. Corals that bleached extensively in 2016 included *Hydnophora*, *Fungia*, *Pectinea*, *Goniastrea*, *Herpolitha*, *Dipsastraea* (formerly known as *Favia*), *Merulina*, *Platygyra*, and *Podabacia.* Moreover, *P. damicornis* appeared to be bleaching resistant across all size classes measured, with 92-99% of colonies exhibiting no bleaching (Fig. 4).

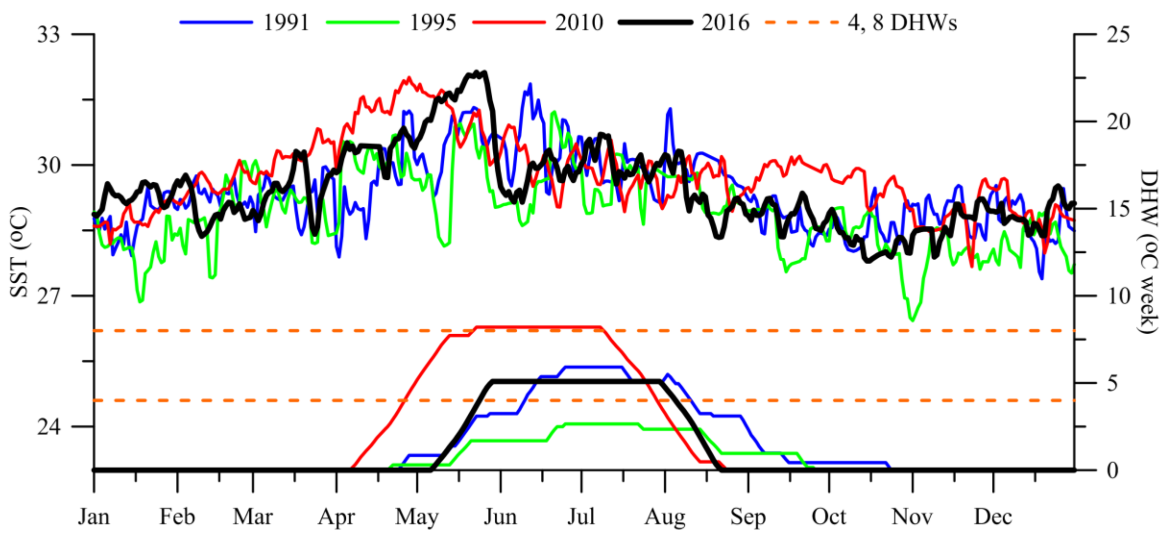

Figure 2 Daily sea surface temperature and degree heating week (DHW) at Panwa, southern Phuket in bleaching years 1991 (blue), 1995 (green), 2010 (red), and 2016 (black). Orange hatched lines indicate where DHW is 4 and 8°C-weeks which results in widespread bleaching and subsequent mortality, respectively.

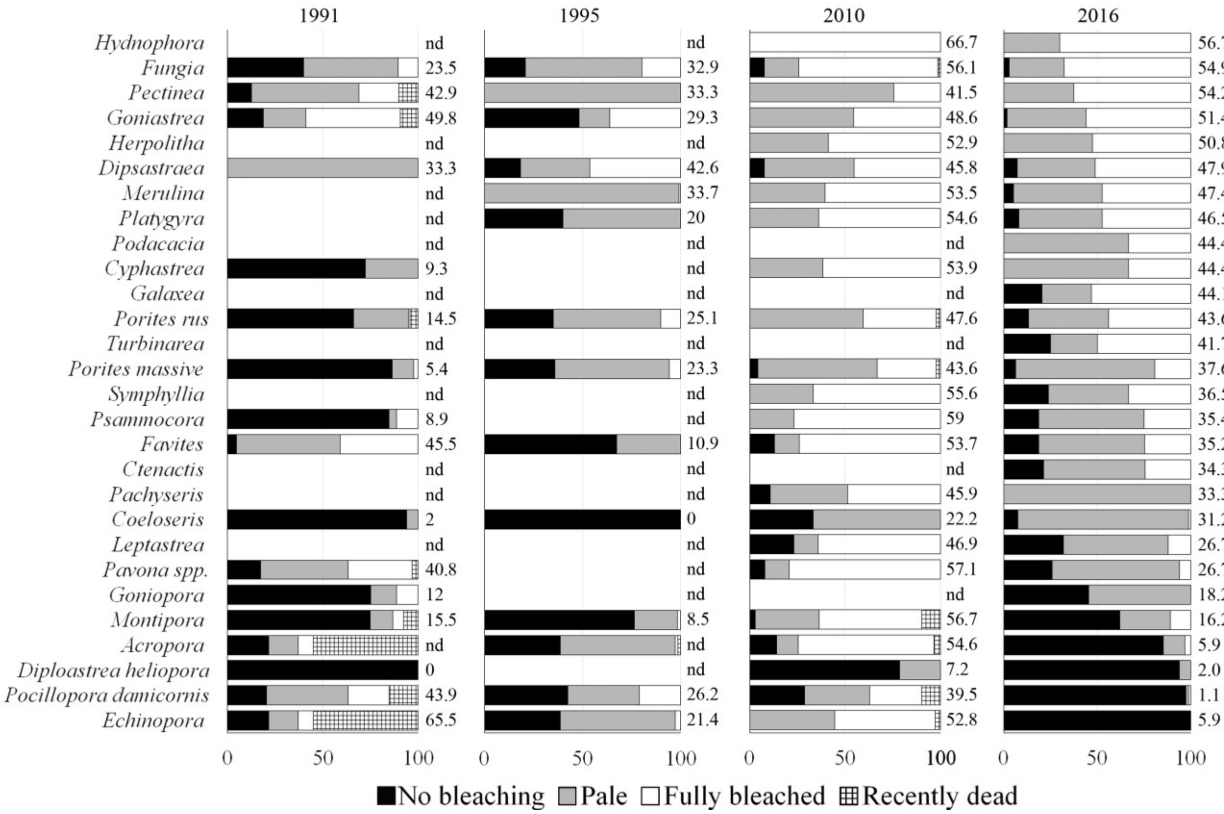

Figure 3 Bleaching susceptibility of coral taxa in 1991, 1995, 2010, and 2016 around the southern Phuket sea region, displayed as percent cover of four categories of bleaching status: unbleached (black), pale (gray), bleached (white), and recently dead (black stripe). Number to the right of each bar indicates bleaching and mortality indices of each taxon. Bleaching susceptibility of coral taxa is arranged from top to bottom with highest to lowest bleaching and mortality indices in 2016. Data presents only species represented by 5 or more colonies/representatives. nd indicates where no data are available.

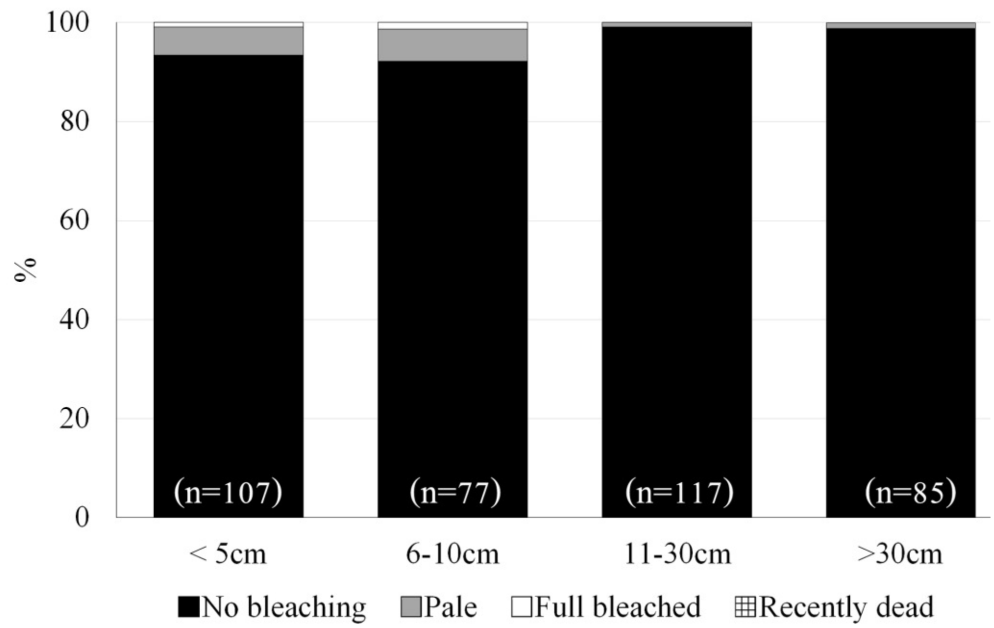

Figure 4 Bleaching susceptibility of *Pocillopora damicornis* at Tang-khen Bay during elevated sea water temperatures in 2016, displayed as percent cover of four categories of bleaching status: unbleached (black), pale (gray), bleached (white), and recently dead (black stripe) for four different size classes (maximum diameters) of corals. Number in brackets indicate colony numbers monitored in four different size classes.

Corals that showed decreased bleaching susceptibility in 2016 were branching or plating morphologies. These corals are commonly considered to be some of the most bleaching sensitive taxa (Furby et al. 2013; Marshall & Baird 2000; McClanahan 2004) suffering extensive mortality at the study sites after the 2010 bleaching event (Fig. S1). Results suggest that these coral taxa were more resistant to bleaching in 2016 than other typical bleaching-resistant coral taxa (Fig. 5). This is the first report of reduced bleaching susceptibility in formerly bleaching susceptible coral taxa in the Andaman Sea. Similar results have previously been observed in Singapore and Peninsular Malaysia during a bleaching event in 2010 (Guest et al. 2012; Guest et al. 2016) and also in 2016 (J. T. I. Tanzil, pers. comm.), during the 2002 bleaching event in Sir Abu Nuair, Arabian Gulf (Riegl 2003) and on the Great Barrier Reef (Maynard et al. 2008). A recent analysis of repeatedly surveyed reefs in the Great Barrier Reef indicates, however, that effects of prior bleaching may be masked by the severity of the event (Hughes et al. 2017). Many factors may affect the environmental adaptation of coral taxa through historical temperature stresses, including

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changes in the symbiotic associations with coral hosts (Baird et al. 2007; Baker 2003), natural selection adjusting the frequency of genes that code for traits resisting thermal stress (Weis 2010), age of corals (Brown et al. 2014), physiological acclimatization (Bellantuono et al. 2012) and previous environmental experience (Brown et al. 2002a)

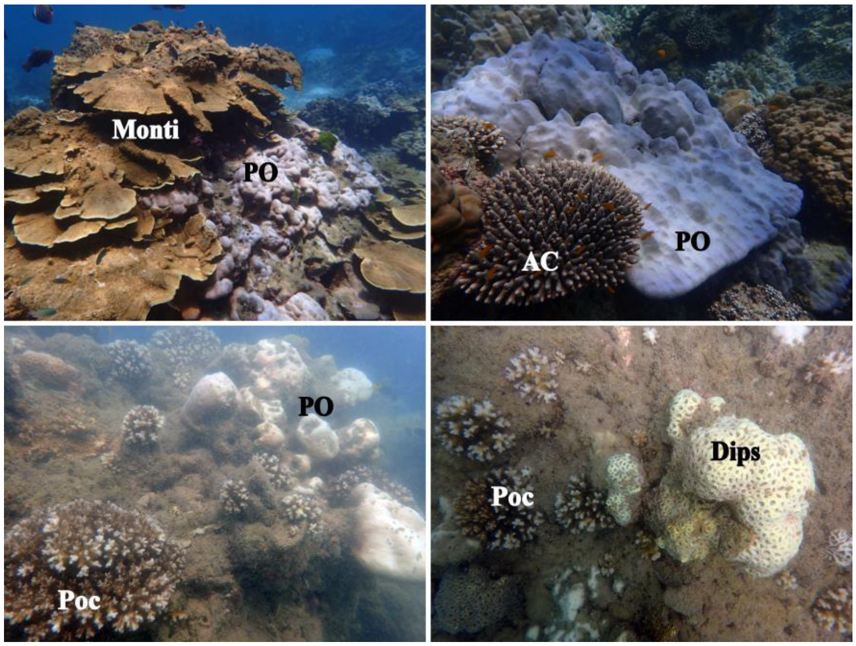

Figure 5 Unusual bleaching responses to increased temperature in May 2016. Bleached *Porites* (Po) and *Dipsastraea* (Dips) adjacent to colonies of *Acropora* (Ac), *Montipora* (Monti), and *P. damicornis* (Poc), which appear unaffected.

Prior to the rise in SST in early 2016, there were two significant factors that may have affected the responses of corals at the study site. First, was the severe thermal stress in 2010 followed by widespread coral mortality (Phongsuwan & Chansang 2012). Lower bleaching susceptibility in some taxa may have been the result of acclimatization as reported by Maynard et al. (2008), where prior major bleaching events can lead to increased thermal tolerance in corals. Second, was the astronomically low tide associated with the 19 year tidal cycle noted in early 2015 followed by a positive Indian Ocean Dipole (IOD) (Webster et al. 1999) from August to December in late 2015. As a result of lowered sea levels during these times, corals on the shallow reef front would have experienced high light levels during low spring tides, a factor previously shown to have had an important impact on coral thermal tolerance in similar circumstances in this region prior to the

1998 bleaching (Dunne & Brown 2001). It seems possible that symbionts which had photoacclimated to high light radiation were more easily able to counter photoinhibition than nonacclimated symbionts (Brown et al. 2002a). This was further supported by the finding of (Schoepf et al. 2015), who showed higher bleaching tolerance of corals inhabiting highly fluctuating environments (solar radiation and temperature). However, such thermal tolerance was not exhibited by all coral taxa in our study.

Observed changes in bleaching susceptibility may relate to coral life history traits and evolutionary potential. Species with “competitive” life history traits such as Acropora tend to bleach and suffer high whole-colony mortality, whereas stress tolerant and generalist species tend to suffer partial mortality and take a long time to bleach and recover. Colonies of stress tolerant and generalist species will remain in the population while susceptible genotypes of competitive species will be selected out of the population much more efficiently (Day et al. 2008). One such example is *P. damicornis*, which was absent from some surveying sites for many years after the 2010 severe bleaching event, before observing the re-appearance of juveniles in 2014 (L. Putchim, unpublished data). Our study shows that the present *P. damicornis* population was bleaching resistant across all size classes in 2016, including the adults that survived from the last bleaching. It is possible that the new resistant recruits may never have experienced bleaching, but may have inherited thermal tolerance from their parents (Dixon et al. 2015). Since the growth rate of a juvenile colonies of *P. damicornis* is about 1.5- 3cm/year (Jerker 2002; Richmond 1987; Trapon et al. 2013), 5 cm corals are approximately one to three years old depending on the environmental conditions.

Another factor improving the thermal tolerance of competitive species could be their association with diverse genetic varieties of their *Symbiodinium* symbionts. Different *Symbiodinium* genotypes have been found to respond differently to thermal stress (Kinzie et al. 2001; Sampayo et al. 2008). *Pocillopora* and *Acropora* in the Indian Ocean were found to associate with 6-7 types of *Symbiodinium*, while *Porites* displayed a much higher symbiont fidelity with only 2 types of *Symbiodinium* (LaJeunesse et al. 2010). *Pocillopora* showed different bleaching responses in relation to *Symbiodinium* types during a thermal stress event in the southern Gulf of California (LaJeunesse et al. 2007), and the high proportion of stress-resistant clade D *Symbiodinium* in

Andaman Sea corals was taken as an indication of an adaptive response in the coral community to previous thermal stress events (LaJeunesse et al. 2010). The eroding resilience of the massive *Porites* over the 25 year period, by contrast, may reflect the lower adaptive potential of corals that, for good or evil, enjoy only one or two symbiont options.

Our findings underscore the importance of long-term and fine-grain monitoring of local and regional bleaching responses to underpin appropriate management action to conserve coral reefs in the face of recurrent thermal stress events.

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