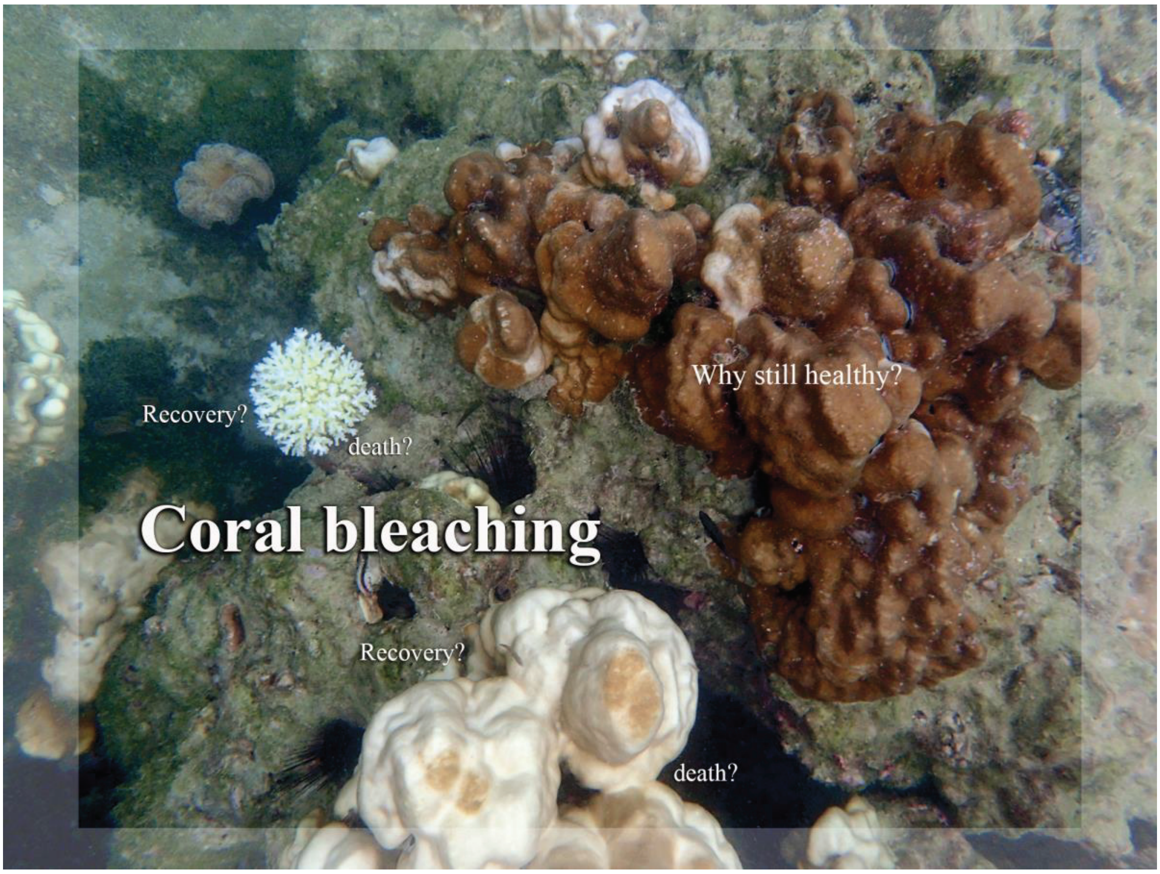
CORAL BLEACHING AND RECOVERY IN THE THAI ANDAMAN SEA



Lalita Putchim

Deutscher Akademischer Austausch Dienst
Servicio Alemán de Intercambio Académico
Bremen International Graduate School for Marine Sciences
Universität Bremen

CORAL BLEACHING AND RECOVERY IN THE THAI ANDAMAN SEA

Dissertation submitted by

Lalita Putchim

In partial fulfilment of the requirements for the degree of doctor of natural sciences (Dr. rer. nat.)
Faculty of Biology/Chemistry, University of Bremen

September 28th, 2017

PHUKET MARINE BIOLOGICAL CENTER
DEPARTMENT OF MARINE AND COASTAL RESOURCES
AWI
DAAD
Deutscher Akademischer Austausch Dienst
Servicio Alemán de Intercambio Académico
GLOMAR
Bremen International Graduate School for Marine Sciences

Universität Bremen

The present study was conducted at the Alfred Wegener Institute Helmholtz Center for Polar and Marine Research (AWI) in Bremerhaven and the Phuket Marine Biological Center (PMBC) in the frame of the Thai-German cooperation in marine sciences.

Funding was provided by the German Academic Exchange Service (DAAD), the Marie Curie ITN CalMarO (FP7-PEOPLE-2007-1-1-ITN, grant number 215157), the German Federal Ministry of Education and Research (BMBF) project BIOACID (Grant Number 03F0608B, Bioacid 3.2.3 Coral calcification in marginal reefs), the AWI and PMBC.

Support was also given by the Bremen International Graduate School of Marine Sciences 'Global Change in the Marine Realm' (GLOMAR), funded by the German Research Foundation (DFG) within the frame of the Excellence Initiative by the German federal state governments to promote science and research at German universities.

The thesis was reviewed by

Prof. Dr. Claudio Richter
Bentho-Pelagic Processes, Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research (AWI), Bremerhaven, and University of Bremen, Germany

Prof. Dr. Barbara E. Brown
School of Biology, Newcastle University, Newcastle NE1 7RU, UK; and Environmental Research Institute, University of the Highlands and Islands, Thurso KW14 7EE, UK.

SUMMARY

Severe coral bleaching in response to increasing sea temperatures threatens coral reefs in many regions of the world, including the Andaman Sea, Thailand. Coral bleaching involves the breakdown of the coral-algae symbiosis, resulting in the loss of the intracellular microalgal dinoflagellates of the diverse genus *Symbiodinium,* also called 'zooxanthellae'. Elevated temperatures and high solar irradiation are considered to be the primary factors causing widespread coral bleaching.

In the Andaman Sea, bleaching events have occurred in the years 1991, 1995, 1998, 2003, 2010, and 2016 following abnormally high sea-surface temperatures (SST). The 2010 SST anomaly was the hottest on record with unprecedented bleaching and mortality of corals. However, corals showed different responses to thermal stress and important spatial differences, both between and within reefs.

Manuscript I highlights the importance of the physico-chemical environment in alleviating thermal stress during periods of elevated SST. We found that corals exposed to internal waves (IW) suffered considerably less bleaching and mortality than reefs away from the influence of IW. The recurrence of IW not only provides pulses of cool and nutrient-rich water, the environmental variability also appears to acclimate (or adapt) corals enhancing bleaching tolerance and survival.

Manuscript II shows, however, that enhanced thermal tolerance of corals due to acclimatization (or adaptation) to fluctuating environments (IW) is taxon-dependent. Allegedly heat-sensitive genera such as *Pocillopora* or *Acropora* appear to benefit less from acclimation in thermally fluctuating environments than genera considered thermally robust, such as *Porites*. The magnitude of bleaching thus depends on both environmental factors (e.g. IW) and the taxonomic composition of the coral community.

Manuscript III shows that the thermal history is also important and may hold some unexpected surprises. In this study, we investigated the species-specific bleaching responses of 28 near-shore coral taxa during four major mass bleaching events around Phuket (Andaman Sea) in 1991, 1995, 2010, and 2016. Remarkably, we found that the bleaching susceptibilities of corals can change with time: following a number of bleaching events where branching corals showed severe bleaching and massive corals showed little bleaching, the latest 2016 bleaching showed a startling reversal in the bleaching pattern – bleaching in the massive corals and pigmented colonies in the few remaining branching corals. Obviously, strong selective forces on the declining population of fast-growing corals appear to have improved their capacity to cope with thermal stress, while most of the slow-

growing massive corals appear to have lost their resistance and have become more susceptible to bleaching. Acclimatization (or adaptation) may play an important role in explaining these striking changes in thermal tolerance.

Manuscript IV moves from the coral community to the species level and explores the connection between thermal history, mortality and colony size in an intertidal coral. While the thermal stress events in the 1990's caused only low mortality in *Goniastrea aspera*, the 2010 mass bleaching event was followed by large mortality affecting the large colonies but not the smaller ones. This surprising finding suggests that the older colonies that had experienced bleaching before have not been able to bolster their thermal resistance, either due to senescence, or perhaps because the large colonies invest proportionally more into reproduction, saving them less energy for surviving a thermal stress event.

The relative roles of coral host and zooxanthellae in stabilizing the photosymbiosis of the holobiont (i.e. the ensemble of host and *Symbiodinium*) is still under debate. While it is now widely acknowledged that both host factors and the diversity of the microalgal symbionts play important roles in thermal tolerance, there are limited studies on *Symbiodinium* diversity and host fidelity in Thai waters. **Manuscript V** presents the results of a comparative study on *Symbiodinium* diversity in *Porites lutea* from different sites in the Andaman Sea and the Gulf of Thailand. In spite of the regional differences, we found similar *Symbiodinium* populations, based on the ITS1 and ITS2 sequences. Most *Porites lutea* (78%) hosted *Symbiodinium* type C15, while 20% contained clade C1 and few percent contained C17 and D1a. While it is generally accepted that different *Symbiodinium* types confer different heat tolerances, future studies are required to assess the spatio-temporal dynamics of the *Symbiodinium* communities and their relation to the bleaching response in *Porites*.

While there have been intense surveys of bleaching occurrences when SST increases, only a few observations are available for the fate of bleached coral colonies in the aftermath of a bleaching event. It is well known that not all bleached corals die. But the factors governing recovery versus demise of the corals are currently only poorly understood. In **Manuscript VI** fully bleached corals were individually marked, re-visited, and the levels of recovery and mortality recorded over a 5-month period. The results show that re-pigmentation of bleached corals largely depends on their available energy stores. Corals with the highest biomass, i.e. the free-living fungid corals (*Ctenactis, Fungia* and *Herpolitha*) also showed the highest recovery rate.

Besides direct effects, bleaching may influence coral fitness and also make corals more vulnerable to other stressors such as microbial pathogens. It is thus not surprising that coral bleaching events are often followed by the outbreak of coral disease. In **Manuscript VII,** the tagging of colonies allowed us to follow disease in *Porites lutea* after the 2010 bleaching event. While Pink Syndromes

were common, we found higher abundances of Ulcerative White Syndrome compared to the years before the 2010 mass bleaching event.

This thesis explores the causes and consequences of coral bleaching events in the Andaman Sea of Thailand on the coral community, organismal and sub-organismal (symbiont) scale. Physico-chemical factors as well as species-specific responses of corals to thermal stress contribute to complex patterns of bleaching and mortality, revealing large differences in acclimatization and adaptation in space and time. Understanding the species-specific bleaching responses in their particular environment provides a promising tool for management, as the identification of bleaching-tolerant corals and the factors enhancing coral tolerance may help improve the design of appropriate rehabilitation techniques. This study highlights potential refuge areas for corals which are necessary to protect and facilitate quick post-bleaching recovery. The protection of reef areas harbouring coral communities tolerant to thermal stress, along with the rehabilitation of degraded coral reef ecosystems with bleaching tolerant species, is a promising approach to improve the success of reef conservation management in a warming ocean.

ZUSAMMENFASSUNG

Weltweit steigen die Meerwassertemperaturen und dadurch kommt es immer häufiger zu massiven Korallenbleichen, die global auftreten. Diese bedrohen die Integrität der Korallenriffe, wie es auch in der Andamanen See zu beobachten ist. Verantwortlich für das ‘Bleichen’ der Korallen ist der Verlust ihrer Symbionten (intrazelluläre Mikroalgen der Gattung *Symbiodinium*). In erster Linie wird dieses Bleichen durch erhöhte Temperatur, aber auch durch starke Sonneneinstrahlung verursacht.

In der Andamanen See konnten in den letzten Jahrzehnten mehrere durch abnormal hohe Meeresoberflächentemperaturen (SST) verursachte Korallenbleichen beobachtet werden (1991, 1995, 1998, 2003, 2010 und 2016). Die Korallenbleiche im Jahr 2010 war die stärkste, die in der Region beobachtet wurde und zog hohe Korallenmortalitäten nach sich. Allerdings reagierten die Korallen stark unterschiedlich auf Hitzestress und es konnten auch wichtige räumliche Unterschiede in Bezug auf Bleiche und Mortalität der Korallen (sowohl innerhalb eine Riffs als auch zwischen Riffen) festgestellt werden.

Manuskript I befasste sich mit der Rolle von physikalisch-chemischen Umweltbedingungen, die zu einer Abmilderung von Hitzestress während Phasen erhöhter Meeresoberflächentemperatur führten. Wir konnten beobachten, dass Korallen, die in Riffen wachsen, die dem Einfluss von Internen Wellen (IW) ausgesetzt waren, weniger stark gebleicht wurden und niedrigere Mortalitäten aufwiesen als Riffe, die nicht unter dem Einfluss von IW standen. Interne Wellen bringen nicht nur kurze, wiederkehrende Pulse von kaltem nährstoffreichem Tiefenwasser in die seichten Korallenriffe, sondern die durch sie verursachte starke Umweltvariabilität trägt dazu bei, dass Korallen sich an Stressbedingungen akklimatisieren (anpassen) und ihre Toleranz und Überlebensfähigkeit gegenüber Extremereignissen erhöht.

Manuskript II ging der Frage nach, ob diese erhöhte Stresstoleranz, die durch eine stark variable Umgebung bedingt ist, für alle Arten gleichermaßen gilt. Vermeintlich hitze-sensitive Korallengattungen wie *Pocillopora* oder *Acropora* profitierten nicht im gleichen Maße wie hitze-tolerante Korallen z.B. der Gattung *Porites*. Das ließ darauf schließen, dass das Ausmaß einer Bleiche sowohl von Umweltfaktoren (z.B. dem Einfluss von IW), als auch von der Zusammensetzung der Korallenarten eines Riffes abhängt.

Zusätzlich zeigten wir im **Manuskript III,** dass auch vergangene Hitzeereignisse eine wichtig Rolle spielen, mit oft unerwarteten Folgen für die Stresstoleranz von Korallen. In dieser Studie, untersuchten wir in küstennahen Riffen um Phuket (Andamanen See) die artspezifischen Reaktionen von insgesamt 28 Korallenarten während vier vergangener Korallenbleichen (1991,

1995, 2010 und 2016). Bemerkenswerterweise stellten wir fest, dass sich die artspezifische Sensitivität gegenüber Hitzestress verändern kann: für gewöhnlich reagieren verzweigt wachsende Arten mit früher einsetzendem und stärkerem Bleichen im Vergleich zu massiv wachsenden Arten. Während der letzten Korallenbleiche im Jahr 2016 stellte sich ein überraschend anderes Bild ein: Verzweigt wachsende Arten bleichten gar nicht, massiv wachsende Arten taten dies jedoch. Offensichtlich wirkte die vorausgehende extreme Korallenbleiche in 2010 als starkes Selektionsereignis und die wenigen verzweigten Korallen, die dieses überlebten, waren nun Hitzestress gegenüber toleranter. Im Gegensatz dazu scheinen die massiven Arten ihre hohe Stressresistenz verloren zu haben und vergleichsweise sensitiver geworden zu sein. Dies zeigt, dass Akklimatisierung und evolutive Anpassung eine wichtige Rolle spielen können und zu bemerkenswerten Änderungen der Stressresistenzen führen können.

Im **Manuskript IV** veränderten wir unseren Blickwinkel und betrachteten den Effekt von Hitzestress auf der Artebene. Wir untersuchten den Zusammenhang von vorausgegangenem Hitzestress, Mortalität und Koloniegröße bei einer Korallenart, die in der Gezeitenzone vorkommt. Während Korallenbleichen in den 1990er Jahren nur geringe Mortalität bei der Korallenart *Goniastrea aspera* verursachten, kam es in Folge der Korallenbleiche im Jahre 2010 zu hohen Mortalitäten bei großen Kolonien, nicht jedoch bei kleinen Kolonien. Bei dieser Art erwarben die ‘Erwachsenenkolonien’ keine erhöhte Stressresistenz durch vorangegangene Korallenbleichen. Dies deutet daraufhin, dass in ältere Kolonien der Alterungsprozess die Stresstoleranz verringert, oder diese verhältnismäßig mehr Energie in die Reproduktion stecken, wodurch weniger Energie während Hitzestressperioden zur Verfügung steht.

Neben Umweltfaktoren, Korallenart und –größe können auch der Korallengenotyp, sowie der Genotyp des Symbionten (als auch die Kombination aus beiden) zur Stabilität der Symbiose unter Hitzestress beitragen. Trotz der wichtigen Rolle der beiden Symbiosepartner ist noch wenig über die Diversität von *Symbiodinium* und die Spezifizität zu ihren Korallenwirten in den thailändischen Korallenriffen bekannt. **Manuskript V** stellte ein erste Vergleichsstudie von verschiedenen Riffen, sowohl in der Andamanen See, als auch im thailändischen Golf und der Diversität der Symbionten bei der Art *Porites lutea* dar. Trotz der großen räumlichen Distanz wiesen die Korallen eine ähnliche Symbiontenpopulation auf (basierend auf der ITS1 und ITS2 Sequenz). Der Hauptsymbiosepartner der Koralle *Porites lutea* war *Symbiodinium* Typ C15 mit 78%, gefolgt von Typ C1 mit 20%. Nur wenige Korallen enthielten *Symbiodinium* der Typen C17 und D1a. Unterschiedliche *Symbiodinium* Typen sind ebenfalls bekannt für ihre unterschiedliche Hitzestressresistenz. Inwiefern diese Unterschiede in der Stressresistenz zur Heterogenität von Korallenbleichen in der Region beitragen können, muss noch untersucht werden. Zudem stellt sich auch die Frage, wie dynamisch Symbionten-Populationen zeitlich als auch räumlich sein können und Selektion durch vorangegangene Hitzestressereignisse unterlagen und somit die Stresstoleranz der Koralle beeinflussen können.

Das Auftreten von Korallenbleichen führt oft zu einem intensiven Monitoring am Höhepunkt der Hitzewelle, die Folgen dieser Bleichen werden jedoch oft weniger rigoros verfolgt. Tatsache ist, dass nicht alle Korallen an den Folgen von Korallenbleichen sterben. Welche Faktoren ausschlaggebend sind, ob eine Koralle sich erholt oder stirbt, ist nicht bekannt. In **Manuskript VI** beobachteten wir komplett gebleichte individuell markierte Korallen über 5 Monate und protokollierten das Ausmaß an Erholung oder Mortalität. Wir zeigten, dass das Wiedererlangen von Symbionten und Pigmenten hauptsächlich von den Energiereserven abhing. Korallen die an sich schon eine hohe Biomasse aufwiesen (wie freilebende Pilzkorallen z.B. *Ctenactis*, *Fungia* und *Herpolitha*), zeigten die höchste Erholungsrate vom Hitzestress.

Neben unmittelbaren Effekten von Hitzestress auf Korallen, können Korallenbleichen auch indirekte Effekte nach sich ziehen. Diese machen Korallen anfälliger für zusätzliche Stressoren, wie Krankheiten. In **Manuskript VII** wurden markierte Korallen auf eine erhöhte Anfälligkeit für Krankheiten nach der extremen Korallenbleiche in 2010 hin beobachtet. In ein paar Gebieten konnte ein leichter Anstieg an 'Ulcerative White Syndrom' bei *Porites lutea* festgestellt werden. Das „Pink Syndrom" stellte eine allgemein verbreitete Krankheit dar, die aber auch schnell wieder verschwand. Insgesamt konnte jedoch kein deutlicher Anstieg von Korallenkrankheiten als Folge der Korallenbleiche in 2010 verzeichnet werden.

Zusammenfassend untersuchte die Arbeit Korallenbleichen in der Andamanen See in Thailand, ihre Ursachen und Folgen für die Zusammensetzung der Korallenarten, die Korallen selbst sowie ihre Symbionten. Sowohl physikalisch-chemische Faktoren, als auch artspezifische Reaktionen auf Hitzestress trugen sowohl zu einem komplexen Muster an Intensitäten in der Korallenbleiche, als auch Korallensterblichkeit bei. Es zeigten sich starke Unterschiede in Akklimatisierung, als auch Anpassung von Korallen an Extremereignisse in Raum und Zeit.

Erst wenn wir das Zusammenspiel von artspezifischen Unterschieden in der Hitzeresistenz und der Umwelt in der sie vorkommen verstehen, können wir gezieltere Schutzmaßnahmen für Korallenriffe ergreifen. Zum Beispiel können stresstolerante Korallen identifiziert werden und auch die Faktoren, die zu verbesserter Stresstoleranz führen, unterstützend eingesetzt werden. Hier untersuchten wir potentielle „Zufluchtsstätten" für Korallen, welche notwendig sind, um diese vor starkem Hitzestress zu schützen und ein schnelles Erholen zu ermöglichen. Um Korallenriffe in einem prognostizierten, wärmeren Ozean zu erhalten, wird es, neben der Umsetzung von geeigneten Restaurierungsmaßnahmen für degradierte Korallenriffe, zunehmend wichtig sein, solche Zufluchtsstätten zu schützen.

ACKNOWLEDGEMENTS

I would like to thank my supervisor, Claudio Richter, for the encouragement and advice he has provided throughout my time as his student. His careful editing contributed enormously to the production of this thesis, and I am lucky to have him as my supervisor. Thanks so much for never giving up on me – and for a lot of cheese and wine!

I would like to express my great appreciation to Barbara Brown. Thank you for helping me to experience research with various interesting topics and scientists, and for all your kind support. I have learned a lot from you.

I must express my gratitude to Marlene Wall and Getraud Maria Schmidt, both provided very useful comments and criticisms relating to several aspects of this work. Completing this work would have been all the more difficult were it not for the support and friendship provided by them.

I would like to express the deepest appreciation to Somkiat Khokiattiwong, who initially pushed me towards PhD study and always stayed beside me. Also, Niphon Phongsuwan and Nalinee Thongtham, who offered endless support in many ways: including with data, knowledge, and suggestions. Working under you is a pleasure and an experience that I will truly treasure. Thank you bosses.

I would like to show my appreciation to my examination committee: Andreas Kunzmann and Mirta Teichberg, who agreed to act as my examiners on relatively short notice. I also want to thank Luisa Federwisch and Kristina Beck, my student committee members.

I owe my deepest gratitude to Christoph Held, who advised me on genetic issues, and also Andrea Eschbach, whose laboratory work provided me with the preliminary genetic results.

The successful completion of all my field components would not have been possible without the involvement of a large number of people. I would like to take this opportunity to thank the staff at the Phuket Marine Biological Center; Chaimonkol Yaearunpattana (p′Bee), Anupong Charoenphol (p′Noom), Suwit Laemka, Wirat Sinbosakorn (Bang Air), Boonchui Koyirattanakul (Na Chui), Perasak Mano (p′Meaw), and Aumnauy Saetan (p′Jun).

Special thanks to all the readers for giving outside comments and checking grammar, namely Joy Smith, Kathryn Bimson, Angkana Rawichutiwan (Toon), Louise Anderson, and Houston Batteh Brown.

Special thanks also to Ursula Liebert, AWI staff, for her warm support and friendship.

During the period of five years, many friends have helped to colour my life. I have to acknowledge all my colleges in ‘international student room D-2400’. They are Marlene Wall, Joy Smith, Chen Wang, Shobhit Agrawal, and Charlotte Havermans. Thanks also to AWI friends Laura Fillinger (my cheese trainer), Claudi Matjes, Carlita de Aranzamendi, and Sylke Wohlrab. You guys are AWESOME!

Finally, there are many people who I would very much like to thank, who have cared about me, and have provided very important personal encouragement. These people have helped me to keep everything in perspective, so that I have enjoyed life and enjoyed doing my research. Very special thanks to my parents and family. Special thanks also to Ole for Grapher program, and Arm for providing me some map pictures. I would also especially like to thank p′Hunt, Jew, Wit, Au, Plearn, Praew, Eak, Jaa, Ohm, p′Aum, p′Dear for their friendship, kindness and invaluable personal support and encouragement, particularly when it was most needed.

CONTENTS

APPENDICES

CHAPTER 1 GENERAL INTRODUCTION

Coral reefs are among the most valuable ecosystems on Earth in terms of their biological diversity and importance to humans and other organisms (Costanza et al., 1997; Cesar et al., 2003), but at the same time they are also one of the most delicate and vulnerable ecosystems to anthropogenic threats (Burke et al., 2011). Overfishing, eutrophication, sediment run-off, global warming and ocean acidification are major causes of reef degradation (Jackson et al., 2001) and the situation is likely to get worse if trends continue (Hoegh-Guldberg et al., 2007; Burke et al., 2011). Because of this, reef degradation is increasing at rapid rates across the world. There is no shortcut to understanding the nature and consequences of bleaching. Numerous scientific studies have investigated the bleaching phenomenon. Physical and biological factors that disrupt the photosymbiosis between the coral host and its microalgal symbionts and induce bleaching have been identified at different temporal and spatial scales. To mitigate the impacts of bleaching, we must identify and protect specific areas where conditions are more likely to ensure relatively low bleaching impacts or mortality, as well as improve coral recovery by fostering optimal conditions for new coral recruitment and enhance reef conservation and management.

1.1 Coral reefs and corals

Coral reefs and ecosystem services

Coral reefs are one of the most biologically diverse ecosystems on Earth and are often equated with rainforests as their terrestrial counterpart (Reaka-Kudla, 1997). Although coral reefs cover less than 0.2% of the ocean floor, or about 284,300 km^2 (Spalding et al., 2001), they contain about 800 coral species and over a million other species that depend directly on the coral reef ecosystem. Coral reefs are also the most valuable ecosystems on the planet, providing important resources and services, both direct and indirect. Direct uses of coral reef goods include fisheries, coastal protection, tourism/recreation, and biodiversity. Indirect values include the provision of goods given for job opportunities, the pharmaceutical industry, the aquarium market, and information services such as long-term data records of metal levels in seawater (Moberg and Folke, 1999). Globally, the value of coral reefs is estimated to be about US$30 billion/year in goods and services, with greatest value received in Southeast Asia (42%) (Cesar et al., 2003). The net benefits from the tourism/recreation sector are the largest share of this total (~32%), followed by coastal protection (30%), and fisheries and biodiversity (18%-19%).

Biology of corals

Hermatypic (or reef-building) stony corals (phylum Cnidaria, class Anthozoa, order Scleractinia) build large aragonitic calcium carbonate skeletons beneath a thin layer of living tissue (Fig. 1.1). Although there are a few solitary groups, most corals are colonial, where the individual polyps on top of the cup-shaped calices in the skeleton measure usually only a few millimetres in diameter and remain connected via living tissue (coenosteum) between the polyps. The polyp is tube-shaped and bears a mouth surrounded by tentacles (Fig. 1.1) (Veron, 2000).

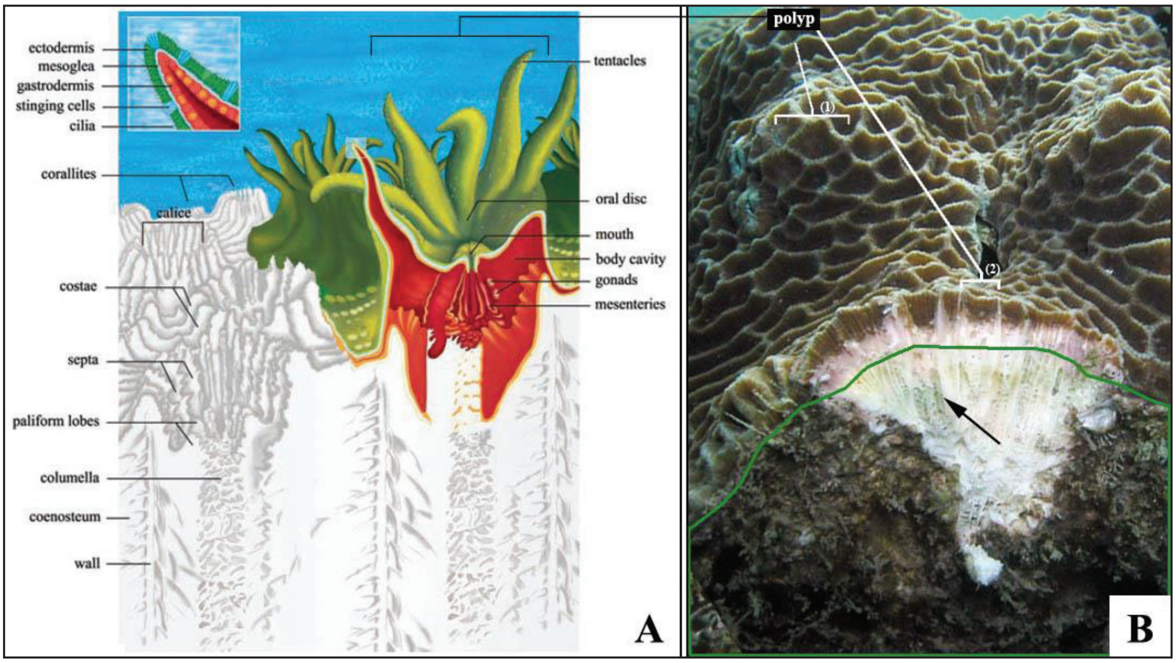


Figure 1.1 The structure of coral tissue and calcium carbonate skeleton. (A) A schematic drawing of a cross-section illustrating the polyp and skeleton features. (B) A living coral colony shown from the top view (1) and cross section of polyps (2) with the exposed thin layer of living tissue growing on top of the skeleton (area above green line). A second layer of calcium carbonate skeleton underneath covered by sediment and filamentous algae (below the green line) with a diverse community of boring endolithic algae is often found in the deeper parts of the coral skeleton (black arrow). Tentacles in the living colony here are retracted which is a normal diurnal behavior of many corals. Image A from Veron (2000).

Coral reefs are broadly distributed between 20°N and 20°S, covering tropical and subtropical regions with temperatures between 20°C and 30°C (UNEP-WCMC et al., 2010). They live in fully marine conditions with salinities generally ranging between 33-36 psu but up to 50 psu in the Red Sea and the Persian Gulf (Coles, 2003; Guan et al., 2015). Because of their photosynthetic symbionts (zooxanthellae, *Symbiodinium* spp.) corals require high light, but some low-light specialists are able to grow near the lower reaches of the euphotic zone to about 150-metres depth (Hinderstein et al., 2010). Particles in the water column such as sediment or plankton can reduce the water transparency and can be detrimental to reef growth.

Reproduction

Scleractinian corals have four patterns of sexual reproduction, depending on their sexuality (hermaphroditic or gonochoric) and developmental mode (brooding or broadcast spawning) (Szmant, 1986; Harrison and Wallace, 1990). There are:

- hermaphroditic followed by broadcast spawning
- hermaphroditic followed by brooding
- gonochoric followed by broadcast spawning
- gonochoric followed by by brooding

Colonies of broadcast spawners typically release the gametes into the water column for external fertilisation and larval development, whereas with brooders the development of planula larvae occurs within the parental polyps. Larvae from broadcasting spawning spend substantial time in the plankton before settlementment, allowing for long-distance dispersal. Some of the broadcast-spawned larvae settle within a few days after spawning (Miller and Mundy, 2003), while some can survive for up to a maximum range of 195 to 244 days after spawning (Graham et al., 2008). Brooding requires a substantial reproductive cost on the parent in order to successfully rear planula; however, the planula have a relatively higher probability of settlement and recruitment success (Jan, 1999; Nozawa and Harrison, 2005).

Morphology and ecological physiology of corals

After the settlement of a planula larvae on a hard substrate, the formation of the calcareous basal disk takes place within one day (Babcock et al., 2003). The circular flat corallites can be distinguished at the genus level after about 4 – 8 weeks (Babcock et al., 2003). When they grow, corals develop into one of seven main observable morphotypes of colonies: branching, massive, foliaceous, columnar, laminar, encrusting, or free-living (Fig. 1.2) (Veron, 2000). In particular, some morphotypes can be further differentiated. For example, branching corals, include subcategories of staghorn, bushy, bottlebrush, corymbose, and digitate. Besides genetic controls, the variety of shapes and sizes of coral colonies depend also on their surrounding environment. *Pocillopora damicorni*s, for example, demonstrates variable colony morphotypes along environmental gradients with thinner and finer branches in areas of low water movement compared to those growing under high water movement (Fig. 1.3) (Veron, 2000).

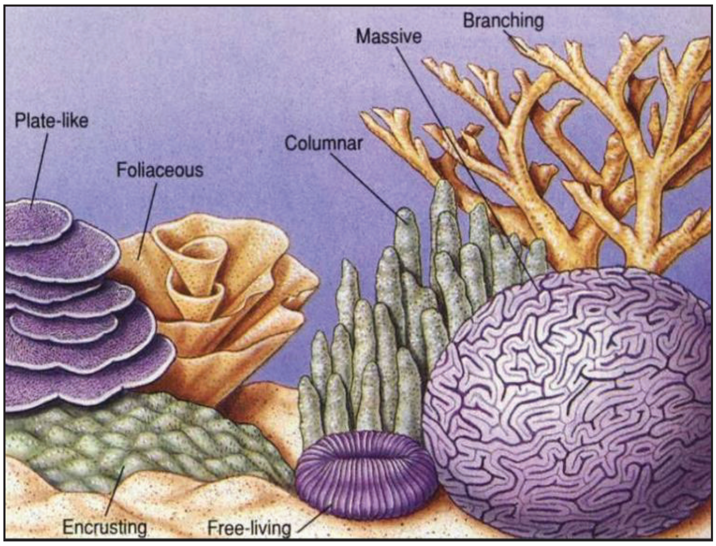


Figure 1.2 Example of the 7 typical coral colony morphotypes: plate-like, foliaceous, columnar, massive, branching, encrusting, and free-living.

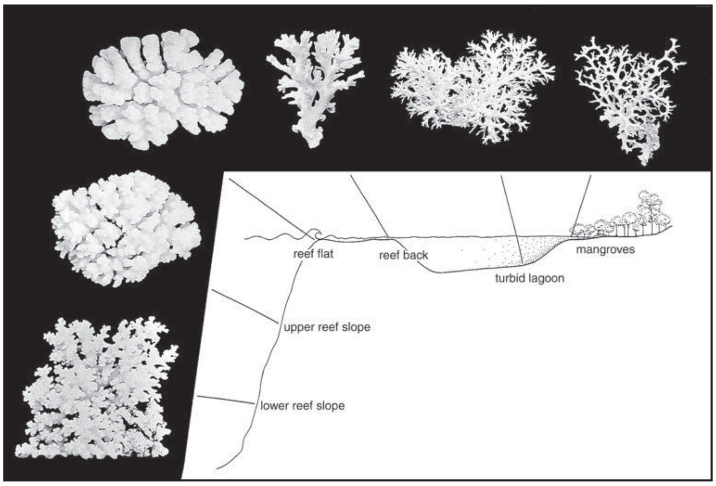


Figure 1.3 Variation in coral colony morphologies of *Pocillopora damicornis* grown under different environmental conditions (Veron and Pichon, 1976).

Different morphotypes can be attributed to other traits, such as tissue thickness (Loya et al., 2001). The tissue layers in massive corals have been found to be more than 3-fold thicker than in branching corals (Table 1.1). Differences in physiology determine the ability of corals to reject sediment and transfer particles across the coral-sea interface (Stafford-Smith, 1993; Riegl et al., 1996; Thomas and Atkinson, 1997; Reidenbach et al., 2006; Falter et al., 2007). van Woesik et al. (2012) indicated that colony size and volume of space between colony branches control the ability of mass transfer (the exchange of biogeochemical compounds between water and corals), including the removal of reactive oxygen generated in the process of photoinhibition, leading to an increase in the coral's ability to resist thermal stress. In branching *Acropora*, small colonies are likely more efficient in maintaining mass transfer than large colonies (van Woesik et al., 2012).

Table 1.1 Tissue thickness of massive and branching coral species (after Loya et al., 2001).

Species	Growth from	Tissue thickness (mm)
Favites chinensis	Massive	9.4 ± 0.174
Platygyra rukyuensis	Massive	4.0 ± 0.096
Goniastrea aspera	Massive	3.6 ± 0.006
Favia pallida	Massive	3.1 ± 0.011
Goniastrea retiformis	Massive	2.8 ± 0.195
Porites lutea	Massive	2.6 ± 0.009
Porites rus	Massive	1.9 ± 0.300
Mean		**3.9 ± 0.110**
Acropora digitifera	Branched	1.9 ± 0.105
Acropora gemmifera	Branched	1.9 ± 0.018
Stylophora pistillata	Branched	1.5 ± 0.279
Porites sillimaniani	Branched	1.3± 0.135
Porites cylindrica	Branched	1.3 ± 0.180
Acropora aspera	Branched	1.0 ± 0.329
Moontopora digitata	Branched	0.9± 0.0.006
Porcillopora damicornis	Branched	0.9 ± 0.043
Pocillopora veruucosa	Branched	0.4 ± 0.006
Mean		**1.2 ± 0.120**

Coral-algae association

In the corals' gastrodermal layer, there are millions of single-celled, golden-brown algae called 'zooxanthella', which is the common name of the broader dinoflagellate genus *Symbiodinium* (Fig. 1.4). Depending on the species, corals either acquire zooxanthellae in the days or months after their settlement ('horizontal transfer'), or obtain them from their mother ('vertical transfer') before fertilization (Shlesinger and Loya, 1991; Hirose et al., 2000; Abrego et al., 2012). These symbiotic algae are crucial for coral health. The host corals and the symbiotic zooxanthellae each benefit from their symbiotic relationship. The algae receive carbon dioxide and nitrogenous waste from the coral host. During daylight they convert these substances into carbohydrates and oxygen through the process of photosynthesis. The majority (78%-90%) of the photosynthetic products, consisting mostly of carbohydrates and lipids, are transferred directly to the coral host (reviewed in Leletkin, 2000). In return, the coral provides the zooxanthellae with protection and the compounds needed for photosynthesis. Zooxanthellae are also responsible for the rapid calcification and high growth rates observed among most reef-building corals. For this reason, zooxanthellate corals are restricted to shallow water, while non-zooxanthellae corals are dominant in deeper waters (Veron, 2000).

Symbiodinium are genetically very diverse. Nine clades (A-I) have been identified, each including a range of sub-clades which exhibit different ecological and biogeographical distributions. Among the divergent lineages of *Symbiodinium*, clade C is the most abundant and diverse in scleractinian corals (Baker, 2003). Although clade C is generally dominant in scleractinian corals, clade D has been found in significant proportions in putatively stressful turbid and/or hot environments (LaJeunesse et al., 2010b; Oliver and Palumbi, 2011b; Keshavmurthy et al., 2014). The thermal resistance of zooxanthellae has also been found to vary not only within clades but also among subcladal types (Sampayo et al., 2008).

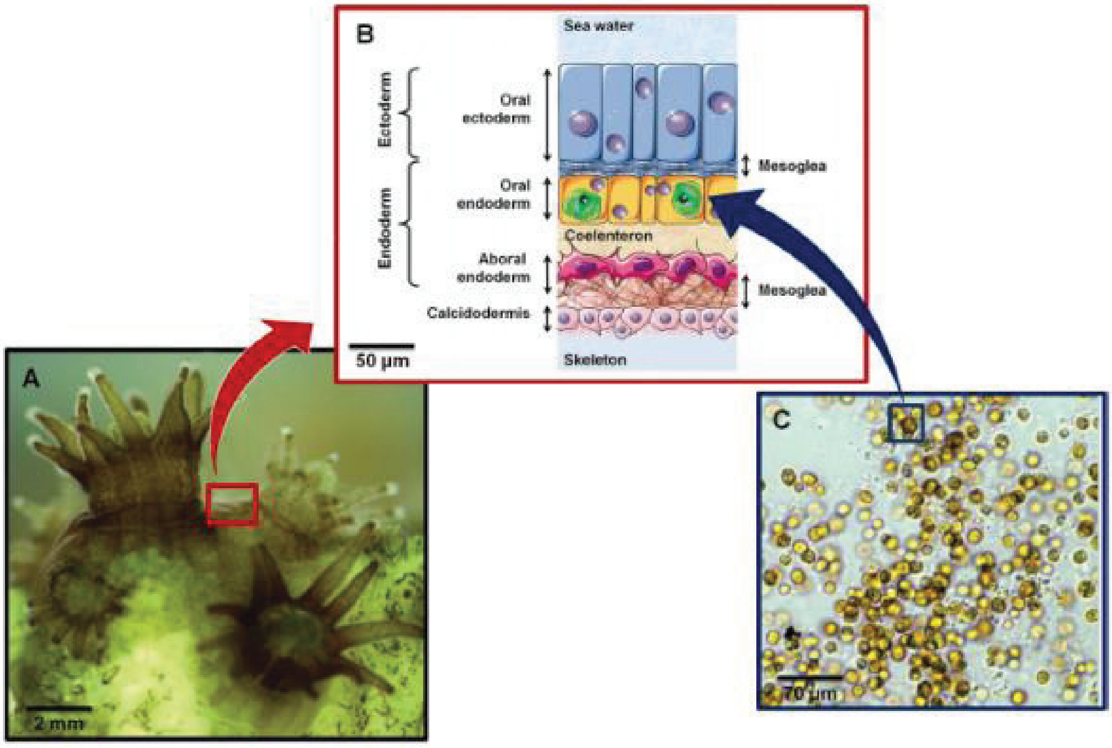


Figure 1.4 (A) Close up of coral polyps. (B) Cross section showing histological organization of a symbiotic and calcifying Anthozoan. Anthozoa are composed of two cell layers: ectoderm (epidermis) and endoderm (gastrodermis). *Symbiodinium* (represented as green structures in oral endoderm) are found in peri-vacuolar host membranes (symbiosome) in the gastrodermal cells. (C) *Symbiodinium kawagutii* under a light microscope. Image from Fournier (2013).

Energy allocation

Corals (holobionts) harvest energy from photoautotrophic and heterotrophic sources. Under normal conditions, the autotrophic zooxanthellae provide more than 90% of the energy needed by their hosts. The density of the zooxanthellae in the coral tissue is about one million cells/cm^2 (Muscatine and Pool, 1979). Corals are also able to feed heterotrophically by catching plankton with their nematocysts-laden stinging tentacles (Goreau et al., 1971). The mixotrophically acquired energy is invested into metabolism (excretion, respiration), tissue growth, development and reproduction, mucus production and calcification (Davies, 1991). Only if the daily requirements for basic metabolic needs are met (either from autotrophy or heterotrophy), corals allocate energy to other biological processes like tissue growth and calcification. If energy resources are limited due to either decreased light or plankton, corals can alter their biochemistry and physiology to maintain fitness (Fig. 1.5). For example, energy limitation can often cause a decline in tissue growth and reproduction, but coral growth or calcification may be maintained (Anthony et al., 2002; Baird and Marshall, 2002; Leuzinger et al., 2012).

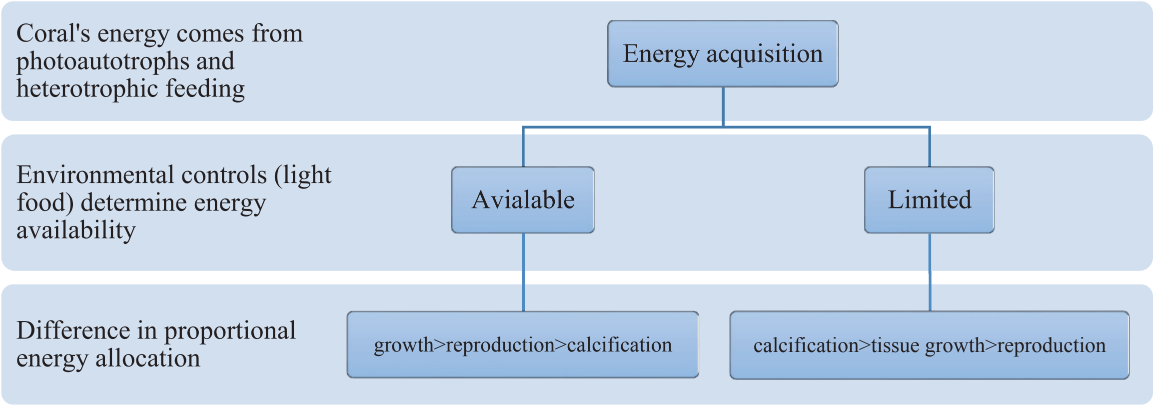


Figure 1.5 Energy allocation and use in coral under energy available and limited.

1.2 Coral reefs under climate change

Major causes of coral reef degradation

Over recent decades there has been serious concerns about the global decline of coral reefs due to a variety of disturbances, both natural and anthropogenic (Bruno and Selig, 2007; Burke et al., 2011; Jackson et al., 2014) (Fig. 1.6). They include small- and regional disturbances such as smothering by space-competing macroalgae or outbreaks of predatory crown-of-thorn starfish (Birrell et al., 2008; Phongsuwan et al., 2008), as well as regional to global impacts of climate change such as coral bleaching and ocean acidification. Natural physical disturbances are predominantly the result of strong wind or water movement caused by big storms including hurricanes and cyclones, or tsunamis such as the 2004 Indian Ocean Tsunami (Blakeway, 2005; Foster et al., 2006). Anthropogenic disturbances are exacerbated by the size of growing human population along the coastlines. Human activities impact coral reef health in a number of ways. Deforestation, agriculture, construction and industry lead to run-off of sediments, nutrients and pollutants causing siltation and eutrophication in coastal waters. Other human-induced physical disturbances to coral reefs are shipping-, fishing- and tourism-related activities like anchoring, snorkelling, diving or boat groundings (Cesar, 2000; reviewed in Chabanet et al., 2005; Phillips, 2014).

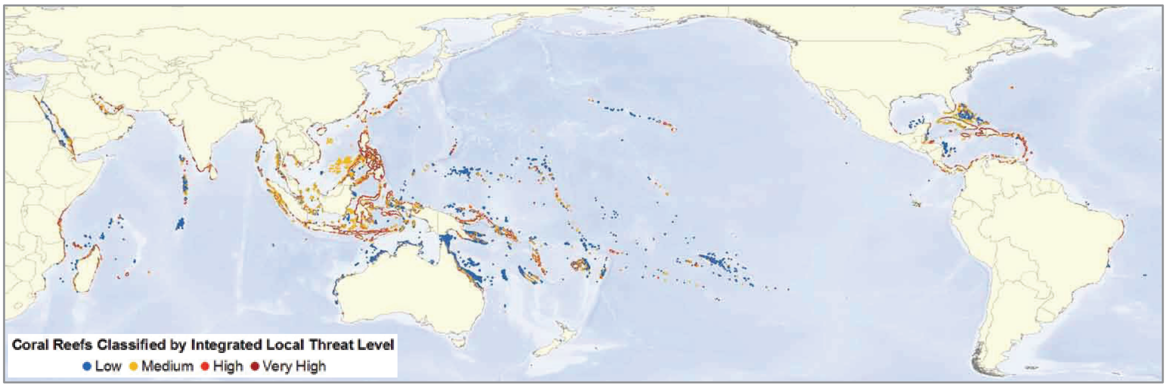


Figure 1.6 Map of the world's coral reefs showing the local risks affecting them. Present threats include overfishing, coastal development, watershed-based pollution, marine-based pollution and damage. Image from (Burke et al., 2011).

Recovery of degraded reef ecosystems depends on the timing and type of disturbance. Connell et al. (1997) indicated that the recovery of corals from acute (short-term) disturbances occurs faster than the recovery from chronic (long-term) disturbances. Some reefs weakened by chronic disturbances, such as overfishing and coastal development, fail to recover from large acute disturbances such as a major storm or a strong El Niño. Although intermediate levels of natural disturbances have been shown to increase diversity, the increase in anthropogenic disturbances leads to a reduction in species richness, abundance and diversity (Connell et al., 1997; Kuo et al., 2012) and a change in reef community composition (XiuBao et al., 2013).

Over the last decades thermal stress has become the most devastating coral reef disturbance, causing widespread mass bleaching and mortality in all coral reef provinces (Marshall and Schuttenberg, 2006; Oliver et al., 2009; GDRMN, 2010). The mass mortality of coral communities has been observed following severe bleaching events in 1998, 2010, and 2016. Bleaching events are closely linked to global climate change and have become stronger, more widespread and more frequent (Hoegh-Guldberg, 1999; Collins et al., 2013; van Hooidonk et al., 2013; Logan et al., 2014; Hughes et al., 2017). Bleaching events have already caused declines in coral cover in many areas (Wilkinson, 2008; Eakin et al., 2010) and will continue to cause a decline in the world's coral reefs along with the synergistic effects of ocean acidification (Fig. 1.7). This will directly affect the diversity of reef communities around the world **(**Hoegh-Guldberg et al., 2007). Very few carbonate reef structures will remain in sea temperatures that have been raised +2°C relative to today's values, leading to vast losses of biodiversity including loss of coral-associated organisms (Fig. 1.8). Coral bleaching is therefore becoming one of the major threats for global reefs.

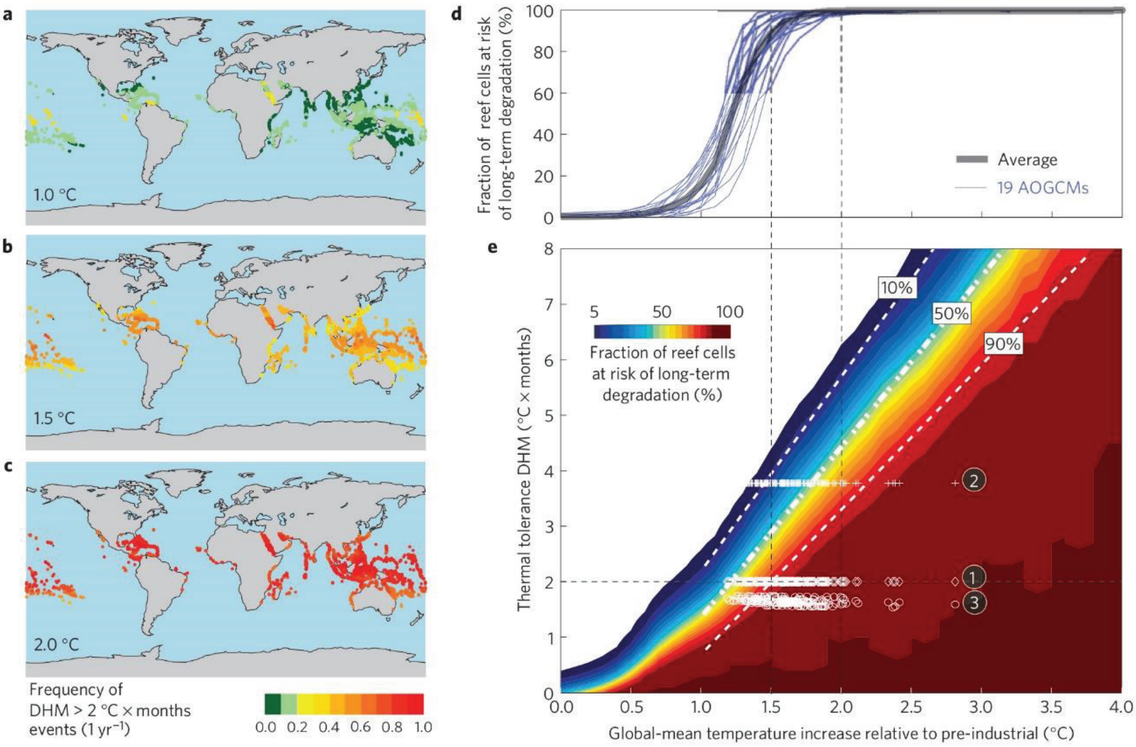


Figure 1.7 Thermal stress (Degree Heating Month, DHM) at different levels of global warming (a-c). Prediction of reefs under risk of long-term degradation due to thermal stress at DHM = 2°C (d) and fraction of the world's coral reef cells (coloured areas) at risk of long-term damage depending on frequency of coral bleaching event (e) (Frieler et al., 2012).

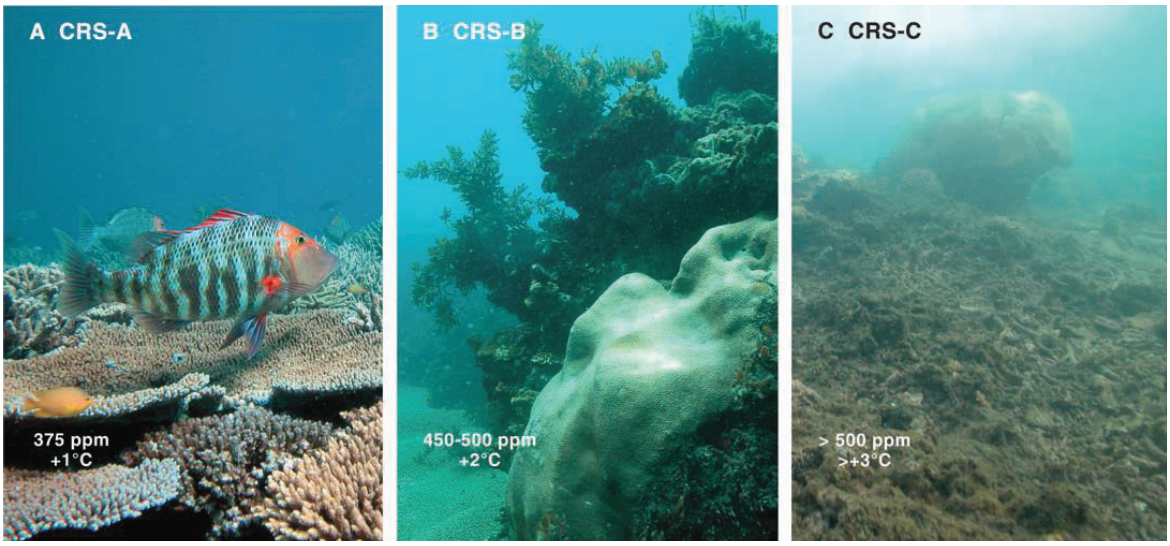


Figure 1.8 Different coral reef scenarios under seriously increasing levels of temperature and atmospheric carbon dioxide concentration $[CO_2]_{atm}$: (A) At the present condition of $[CO_2]_{atm}$ = 380 ppm, coral reefs will continue to change but will remain coral dominated and calcifying. (B) Under condition at $[CO_2]_{atm}$ = 450 to 500 ppm, reef erosion will exceed calcification. (C) When $[CO_2]_{atm}$ > 500, coral-associated fauna is expected to become rare or extinct given their dependence on living corals and the coral reef framework (Hoegh-Guldberg et al., 2007).

Coral Bleaching

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, 1997b; Jokiel, 2004). Without zooxanthellae, corals lose their colour and the underlying calcium carbonate skeleton shines through the translucent tissue turning the coral white (Fig. 1.9). When corals are stressed due to elevated temperatures and photosynthetically active radiation (PAR) (see other possible factors below), the damage may occur sequentially or in parallel to coral host and/or symbiont zooxanthellae. Heat stress can cause some corals to produce chemically reactive oxygen (ROS) and nitrogen species (RNS) (Dunn et al., 2004). The resulting oxidative stress causes damage of membranes, proteins, and DNA, the rapid decrease of PSII function, ATP, and protein synthesis, and, ultimately, the expulsion of the dysfunctional zooxanthellae (Dunn et al., 2004).

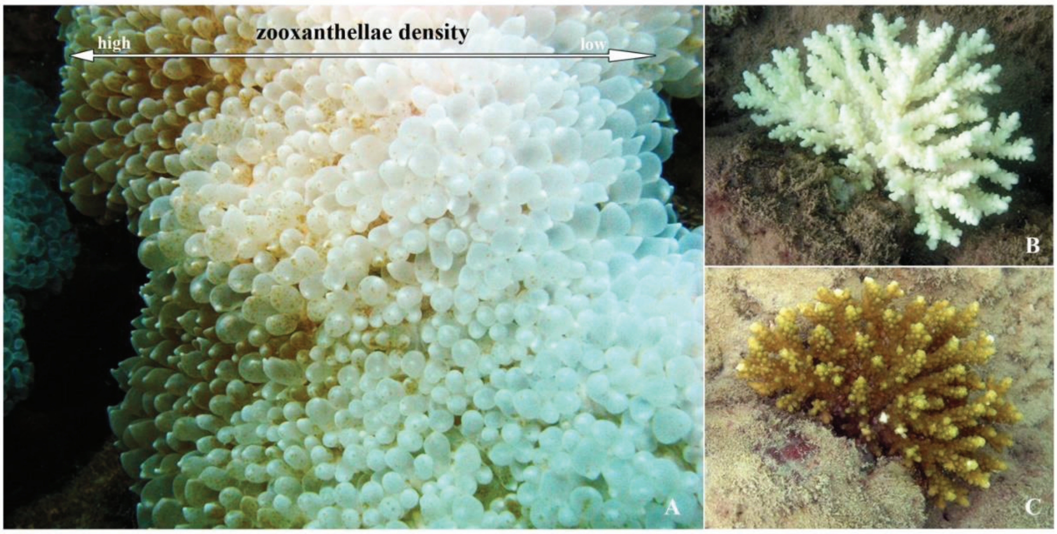


Figure 1.9 Different colours of coral colonies: (A) partial bleaching or bleaching in progress, showing a variation of zooxanthellae densities within a single colony, (B) full bleaching, and (C) full pigmentation.

Many studies have investigated ROS, which have been proposed to play an important role in bleaching (breakdown of the coral-algae symbiosis) (Brown, 1997b; Lesser, 2004; Smith et al., 2005). ROS include hydrogen peroxide (H_2O_2), superoxide radicals (O_2^-), singlet oxygen ($^1O_2$), and hydroxyl (OH^-) (Lesser, 2006), which can damage DNA, proteins, and lipids (Kirkland, 1991; Martins and Meneghini, 1994). Under natural conditions, cells have a sufficient capacity to detoxify those compounds. Under heat stress or excess light, production rates are higher than detoxification rates and the subsequent accumulation of ROS can result in damage to the photosystems and the photosynthetic membranes (Fig 1.10). ROS can further diffuse into the host cell and tissue where the host response may ultimately lead to the expulsion of the zooxanthellae and result in coral bleaching (Lesser, 1997).

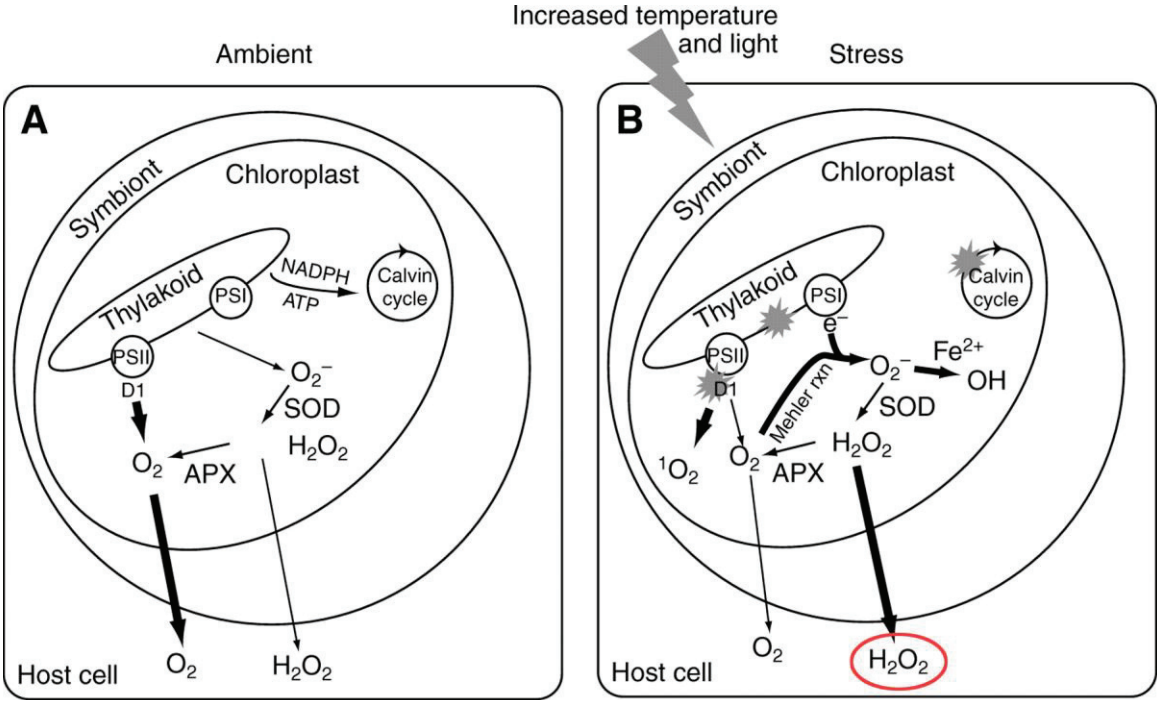


Figure 1.10 Schematics showing mechanisms of oxygen handling pathways in symbiont and host cells under normal conditions (A), and under light and thermal stress (B). Under themal stress, the excess production of the reactive oxygen species (ROS, red circle) trigger zooxanthellae expulsion, result in coral bleaching. Image from Wooldridge (2013).

Factors contributing to bleaching susceptibility

Corals respond differently to heat stress. During the same heat stress event, some corals may pale and bleach while others may retain their pigmentation. Corals that show no bleaching are defined as *bleaching resistant* corals, whereas corals that bleach more easily are referred to as *bleaching sensitive* or *bleaching susceptible*. The *bleaching susceptibility* of a given coral is assessed as a percentage of the total population undergoing bleaching (Marshall and Baird, 2000; McClanahan, 2004). Bleaching may or may not lead to coral mortality. *Bleaching tolerant* corals show survival and recovery after bleaching. *Bleaching tolerance* is assessed as a percentage of the total population surviving after a bleaching event (Obura, 2005).

In principle, bleaching severity primarily depends on the magnitude of stress, which can be caused either biotically or abiotically. The factors include temperature (Lesser, 1996; Heron et al., 2016; Hughes et al., 2017), light intensity (Dunne and Brown, 2001; Chen et al., 2005), salinity (Ailsa and Ross, 2003; Berkelmans et al., 2012), pH (Anthony et al., 2008), or sedimentation (Ineke et al., 1999). Temperature and light, however, have been regarded as the major agents triggering bleaching and it is well accepted that they cause widespread bleaching events (Bruno et al., 2001; Eakin et al., 2010; van Hooidonk et al., 2012).

In general, slow growing taxa with basic structures such as massive or columnar morphotypes, are less resistant to bleaching than fragile, fast growing taxa with branching or plating morphologies.

This is likely because the different morphologies can be attributed to different physiologies. Within a single species, extenuating factors such as colony size (Brown et al., 2014), antioxidant systems of the host (Brown et al., 2002c; Baird et al., 2009), genetic differences of symbionts (LaJeunesse et al., 2007; Oliver and Palumbi, 2011b), the symbiont and host microbiome (Reshef et al., 2006) or adaptation (Baker et al., 2004; Rowan, 2004) are all important in determining bleaching susceptibility of corals.

An interesting area of research is how corals respond to recurrent bleaching events. Some corals show the ability to adapt to heat stress through genetic adaptation, acclimatization, and symbiont shuffling. The Adaptive Bleaching Hypothesis (ABH) proposes that corals may adapt to thermal stress through bleaching-associated changes in their symbiont composition, where heat-sensitive *Symbiodinium* types are replaced by heat-resistant types (Buddemeier and Fautin, 1993). Two sorts of host-symbiont recombinations have been found: 'switching', where the existing symbiotic community was exchanged for a more suitable symbiont from the environment (Boulotte et al., 2016), and 'shuffling', where the relative proportions of the existing types within the community have been changed (Buddemeier and Fautin, 1993; Baker, 2003). Recent research has emphasized the importance of *Symbiodinium*-coral flexibility in withstanding changes in global climate, such as temperature-induced bleaching (Boulotte et al., 2016). While it has been suggested that the ABH provides a large potential for improved thermal tolerance, the majority of corals (77%) may host a single symbiont type and therefore cannot engage in symbiont switching or shuffling (Goulet, 2006), and there is so far only limited evidence (Brown et al., 2002a; Lopez-Maury et al., 2008; Kenkel et al., 2013; Smith et al., 2017)

Aftermath of bleaching

Besides direct effects on corals, disturbances may influence coral fitness making corals more vulnerable to other stressors such as bleaching or disease (Wagner et al., 2010; Erftemeijer et al., 2012). Raymundo et al. (2008) define coral disease as 'any impairment to health resulting in physiological dysfunction'. Under this definition disease agents can range from biotic agents such as bacteria, fungi, viruses, or protists to abiotic environmental stress like temperature, salinity, sedimentation, oxygen concentrations, and currents (Jones et al., 2004; Bruno et al., 2007; Harvell et al., 2007; Erftemeijer et al., 2012). Coral disease outbreaks can cause a serious decline in coral populations as exemplified in Florida and in the Caribbean (Goreau et al., 1998; Richardson et al., 1998). More than 30 different coral diseases have been described by scientists around the world (Hughes and Connell, 1987; Harriott and Banks, 1995; Goreau et al., 1998; Richardson et al., 1998; Kenkel, 2008; Williams, 2011; Putchim et al., 2012; Barkley et al., 2015; Pinzón et al., 2015). Coral diseases are known to be one of the most critical factors responsible for the decline of coral populations in coral reefs worldwide. Thus far, there has not been a serious situation with regard to coral disease in Thailand. However, the increased rates of disease throughout the world has led to increased attention to this topic in Thailand and elsewhere, though some causes remain to be elucidated.

1.3 Coral reef refugia

The places where corals have been noted to experience lower susceptibility to certain stressors have been referred to as refugia. The underlying factors in these environments that promote differences in interspecific susceptibility can be manifold, i.e. depth, turbidity or water quality (Marshall and Baird, 2000; Bruno et al., 2001; Wagner et al., 2010; Williams et al., 2010; Bridge et al., 2013b). The main trigger of bleaching is elevated sea temperature, therefore factors that involve heat reduction will promote coral resistance to temperature-related bleaching. Heat stress can be naturally reduced in areas where there is exposure to upwelling or internal waves (Bayraktarov et al., 2013; Wall et al., 2015; Schmidt et al., 2016). Reduced water temperatures are also caused by water currents (Nakamura and van Woesik, 2001; Oliver and Palumbi, 2011a; Wall et al., 2015), decreasing light levels from natural landscape, shading (Marshall and Baird, 2000), depth (Golbuu et al., 2007; Bridge et al., 2013a), sedimentation (Erftemeijer et al., 2012; Furby et al., 2013), or cloudy conditions (Mumby et al., 2001).

1.4 The Thai Andaman Sea

Climate

The Thai Andaman Sea is located in the easternmost Indian Ocean. The area is bounded by the Thai-Malay peninsula on the east and the Andaman-Nicobar Island chain on the west. Seasonal changes in wind influence the climate in the Andaman Sea and Southeast Asia. The Northeast monsoon is active from December to February causing dry and calm weather. From May to September, the Southwest monsoon leads to strong southwesterly winds and high rainfall over most of Southeast Asia. The data on rainfall in this study was recorded at Phuket station (Southern Meteorological Centre West Coast, unpublished data). The average monthly rainfall was between 126 and 325 mm, and reached a maximum of 384±107 mm around August and September (Fig. 1.11).

Water quality

Marine water quality along the coastline of the Andaman Sea, Thailand is regularly assessed by the Phuket Marine Biological Center (PMBC). The parameters collected include transparency, total suspended solids (TSS), dissolved inorganic nitrogen (DIN), and phosphate (Fig. 1.12). The important cross-shore differences reveal the influence of terrestrial run-off to the coastal area.

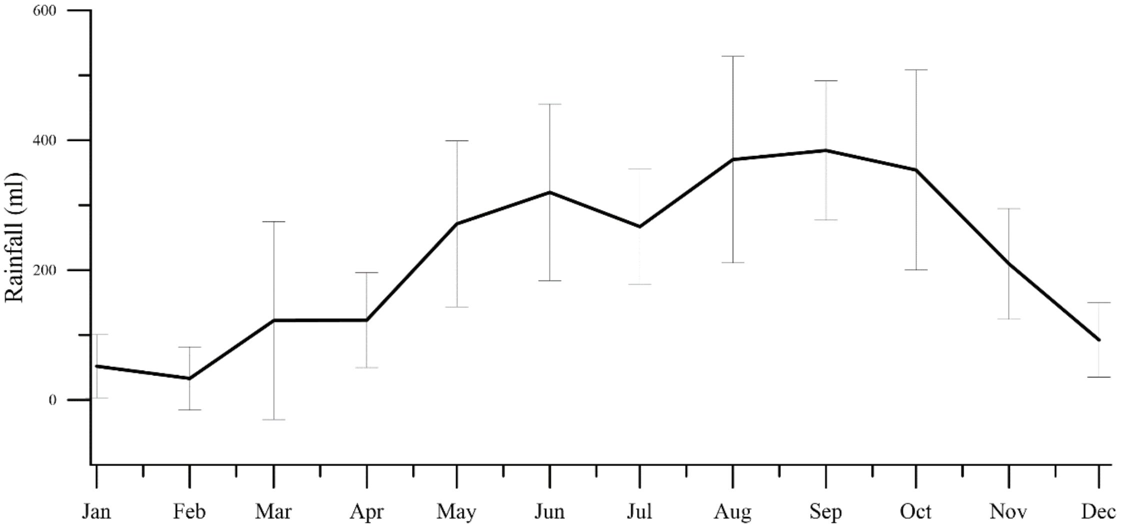


Figure 1.11 Long-term monthly average rainfall at Phuket station between 2001 and 2016. Data compiled by Southern Meteorological Centre West Coast.

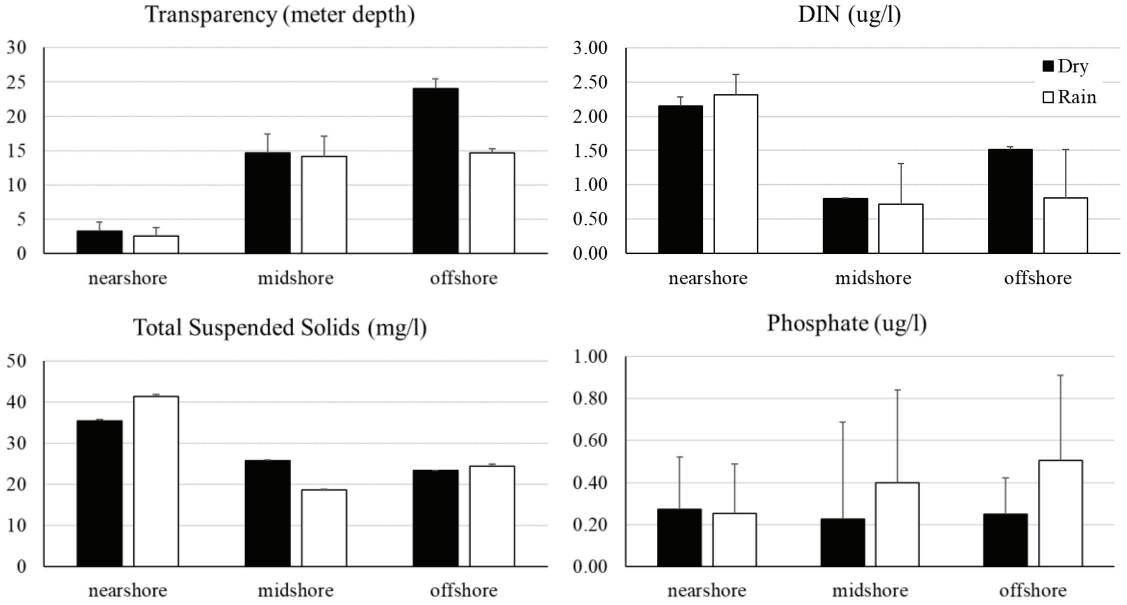


Figure 1.12 Water parameters at nearshore (Panwa), midshore (Racha Island), and offshore (Similan Island) in the Andaman Sea: transparency, total suspension solid, dissolved inorganic nitrogen (DIN), and phosphate (TP). Water parameters were measured once during dry season (December to February) and wet season (May to September) between 2013 and 2016. Bars display average value with standard deviation (PMBC, unpublished data).

Coral reefs

Inshore and offshore coral reefs on the Thai Andama Sea shelf cover a total area of approximately 120 km^2 (PMBC, 2015). Coral diversity (269 scleractinian species) is relatively high compared to other locations in the Indian Ocean (reviewed in Brown, 2007; DMCR, 2013). Massive *Porites lutea* is the dominant species in the entire area. Earlier studies have shown that the Andaman Sea was only moderately affected by the 1997/98 global mass bleaching event and highlighted the potential importance of the Andaman Sea for future of coral reefs in a warming world (Brown, 2007; van Hooidonk et al., 2013). Over the years, however, living corals have been declining with a sharp reduction after the mass mortality following the 2010 bleaching event (Fig. 1.13). The impact was variable, with up to 90% bleaching-related mortality in many areas (Phongsuwan and Chansang, 2012). Currently, 78% of Andaman's coral reefs are in poor conditions (live coral : dead coral <1) (PMBC, 2015). The remaining reefs are subjected to the threat of anthropogenic activities.

The Thai government through its Department of Marine and Coastal Resources (DMCR) is raising public awareness for corals reefs and has established a number of preventive actions to avoid damage from human impacts since 1994 (Yeemin et al., 2006; Thongtham and Phongsuwan, 2012). Several rehabilitation projects have shown the improvement of coral reef conditions through increasing local coral population via coral transplantation, coral propagation, coral nursery, and providing artificial substrates into degraded reefs for new coral recruits (Fig. 1.14) (Thongtham, 2010). However, in spite of efforts, the rehabilitated corals (transplanted corals, nursed corals) were also affected by the severe 2010 bleaching event (Fig. 1.15).

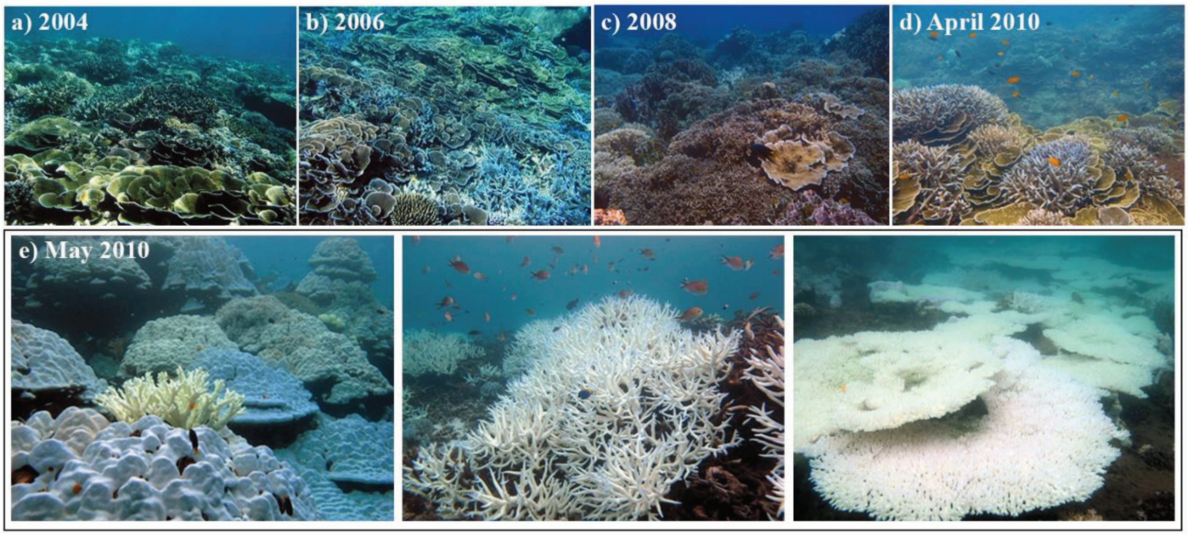


Figure 1.13 Examples of coral reefs in the Andaman Sea. Non-bleaching reef in 2004, 2006, 2008 and, 2010 (a-d) and bleaching reefs in May 2010 (e).

Figure 1.14 Coral rehabilitation in the Andaman Sea: coral floating nursery (left), providing artificial substrate for new recruits (upper right) coral transplantation (lower right).

Figure 1.15 Bleaching occurred in the Andaman Sea on the floating nursery (left), the artificial substrates (upper right), and transplanted corals (lower right) in 2010.

1.5 Research questions

Based on the information above, I addressed the following research questions in the present thesis:

- What are the reasons for the observed spatial variability in bleaching, mortality and recovery between colonies and reefs?
- What are the reasons for the observed temporal variability in bleaching between recent and earlier stress events?
- How does bleaching affect the fitness of corals (e.g. their susceptibility to disease)?

CHAPTER 2 SCOPE OF THESIS *AND PUBLICATION OUTLINE*

The present thesis is based on seven manuscripts - three publications in peer-reviewed journals, one manuscript in review and three manuscripts in preparation, as listed below. The specific contributions of the authors on the study idea, concept, data acquisition and analysis, as well as the writing of the manuscript are explained. The order of the chapters corresponds to the design of the thesis and the level of knowledge described in the introduction.

1. Wall M, **Putchim L**, Schmidt GM, Jantzen C, Khokiattiwong S, and Richter C. 2015. Large-amplitude internal waves benefit corals during thermal stress. Proceedings of the Royal Society B: Biological Sciences 282: 20140650. Doi: 10.1098/rspb.2014.0650

   Contributions: The idea of a project on the influence of internal waves on coral reefs was initiated by C Richter. The particular idea of this study was developed by M Wall. Sampling and sample analysis were mainly conducted by M Wall and L Putchim. Data analysis was conducted by M Wall, L Putchim, C Jantzen, and GM Schmidt with support from C Richter. Reagents/materials/analysis tools were contributed by S Khokiattiwong and C Richter. The manuscript was written by M Wall with improvements by C Jantzen, GM Schmidt and C Richter.

2. **Putchim L,** Wall M, Schmidt GM, Phongsuwan N and Richter C (in preparation). Living in a highly fluctuating environment: how does it shape thermal tolerance across coral taxa?

   Contributions: The idea of a project on different bleaching responses of coral between exposed and sheltered areas of internal waves was conceived by M Wall and developed by M Wall and L Putchim. Sampling and sample analysis were conducted by L Putchim and M Wall. Data analysis was conducted by L Putchim with support of M Wall and C Richter. The manuscript was written by L Putchim with improvements by M Wall, GM Schmidt and C Richter.

3. **Putchim L,** Phongsuwan N, Yaemarunpattana C, Thongtham N, Richter C (in review). Long-term changes in the susceptibility of corals to thermal stress around Phuket, Thailand

   Contributions: The idea of the project was conceived by L Putchim. Sampling and analysis were conducted by N Phongsuwan, L Putchim and C Yaemarunpattana. Data analysis was conducted by L Putchim with support of C Richter. The manuscript was written by L Putchim and C Richter.

4. Brown BE, Dunne RP, Phongsuwan N, **Putchim L**, and Hawkridge JM. 2014. The reef coral *Goniastrea aspera*: a 'winner' becomes a 'loser' during a severe bleaching event in Thailand. Coral Reefs 33:395-401. Doi:10.1007/s00338-013-1120-3

   Contributions: The idea of the project was conceived by BE Brown. Sampling was conducted by BE Brown, N Phongsuwan, JM Hawkridge, and RP Dunne. Laboratory analysis was done by L Putchim. Data analysis was conducted by RP Dunne and BE Brown. The manuscript was written by BE Brown with contributions by RP Dunne, JM Hawkridge, N Phongsuwan and L Putchim.

5. **Putchim L**, Pootakham W, Yoocha T, and Thongtham N (in preparation). Preliminary studies on genetic diversity of corals symbiont in the Thai Andaman Sea and Gulf of Thailand

Contributions: The idea of the project was conceived by L Putchim. Sampling was conducted by L Putchim and N Thongtham. Laboratory analysis was done by W Pootakham and T Yoocha. Data analysis was conducted by L Putchim and W Pootakham. The manuscript was written by L Putchim and W Pootakham.

6. **Putchim L**, Phongsuwan N, Wall M, Schmidt GM and Richter C (in preparation). Coral species recovery after whole colony bleaching in the Andaman Sea

Contributions: The idea of the project was conceived by N Phongsuwan and developed by L Putchim with input from C Richter. Sampling and analysis were conducted by L Putchim. Data analysis was conducted by L Putchim with support of C Richter. The manuscript was written by L Putchim with improvements by GM Schmidt, M Wall and C Richter.

7. **Putchim L**, Yamarunpattana C, and Phongsuwan N. 2012. Observations of coral disease in *Porites lutea* in the Andaman Sea following the 2010 bleaching. Phuket Marine Biological Center Research Bulletin 71: 57-62 ISSN 0858-1088

Contributions: The idea of the project was conceived by N Phongsuwan and developed by L Putchim. Sampling was conducted by L Putchim and C Yamarunpattana. Data analysis was conducted by L Putchim with support of N Phongsuwan. The manuscript was written by L Putchim with improvements by N Phongsuwan.

CHAPTER 3 MANUSCRIPTS

3.1 Manuscript I

Large-amplitude internal waves benefit corals during thermal stress

Wall M[1,2], **Putchim L[1,3]**, Schmidt GM[1], Jantzen C[1], Khokiattiwong S[3] and Richter C[1]

[1]*Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research,*
Am Alten Hafen 26, 27568 Bremerhaven, Germany

[2]*GEOMAR, Helmholtz Center for Ocean Research, Marine Geosystems,*
Wischhofstraße 1-3, 24148 Kiel, Germany

[3]*Phuket Marine Biological Center,*
51 Sakdidet Road, 83000 Phuket, Thailand

Wall M, **Putchim L**, Schmidt GM, Jantzen C, Khokiattiwong S, and Richter C. 2015. Large-amplitude internal waves benefit corals during thermal stress. Proceedings of the Royal Society B: Biological Sciences 282: 20140650. Doi: 10.1098/rspb.2014.0650

Abstract

Tropical scleractinian corals are particularly vulnerable to global warming as elevated sea surface temperatures (SSTs) disrupt the delicate balance between the coral host and their algal endosymbionts, leading to symbiont expulsion, mass bleaching and mortality. While satellite sensing of SST has proved a reliable predictor of coral bleaching at the regional scale, there are large deviations in bleaching severity and mortality on the local scale that are poorly understood. Here, we show that internal waves play a major role in explaining local coral bleaching and mortality patterns in the Andaman Sea. Despite a severe region-wide SST anomaly in May 2010, frequent upslope intrusions of cold sub-pycnocline waters due to breaking large-amplitude internal waves (LAIW) mitigated coral bleaching and mortality in shallow waters. In LAIW-sheltered waters, by contrast, bleaching-susceptible species suffered severe bleaching and total mortality. These findings suggest that LAIW benefit coral reefs during thermal stress and provide local refugia for bleaching-susceptible corals. LAIW are ubiquitous in tropical stratified waters and their swash zones may thus be important conservation areas for the maintenance of coral diversity in a warming climate. Taking LAIW into account can significantly improve coral bleaching predictions and provide a valuable tool for coral reef conservation and management.

Introduction

Global warming and ocean acidification are recognized as the major threats to coral reefs (Bellwood et al., 2004; Hoegh-Guldberg et al., 2007). The thermal optimum for most scleractinian corals is very close to their upper thermal temperature limit, and therefore moderate increases in sea surface temperatures (SSTs) of 1–2°C can become stressful to corals (Hoegh-Guldberg, 1999; Fitt et al., 2001). Such stressful conditions are known to disrupt the photosymbioses between corals and the unicellular algae *Symbiodinium*, thus causing symbiont loss, coral bleaching and mortality (Glynn, 1991; Hoegh-Guldberg, 1999; Fitt et al., 2001). A series of global mass bleaching events has led to a marked decline in coral cover and species diversity over recent decades (Hoegh-Guldberg et al., 2007; De'ath et al., 2012), and concerns over the projected increase in frequency and intensity of bleaching events with the eventual demise of coral reefs (Donner et al., 2005) has fostered the search for natural refugia (Glynn, 1996; Riegl, 2003).

Reef refugia maintain higher coral cover and species diversity, and are target areas for reef conservation. Both extrinsic and intrinsic factors may contribute to coral reef resistance to thermal stress (Glynn, 1996; West and Salm, 2003). Several studies in various environmental settings have confirmed that extrinsic environmental factors such as mixing and advection of cooler water (e.g. in upwelling regions or offshore reefs) can alleviate heating and provide refuge from bleaching (Riegl, 2003; Manzello et al., 2007; Riegl et al., 2009; Chollett and Mumby, 2013). More recently, high-frequency step changes in temperature were observed in Indian Ocean and Andaman Sea coral reefs (Sheppard, 2009; Schmidt et al., 2012; Wall et al., 2012), most probably due to breaking large-amplitude internal waves (LAIW) (Osborne and Burch, 1980; Vlasenko and Hutter, 2002). LAIW are particularly strong during periods of maximum thermal stratification and SSTs (Schmidt et al., 2012), ubiquitous in the world ocean (Jackson, 2007), and observed to reach into many coral reef environments (Wolanski and Pickard, 1983; Wolanski and Delesalle, 1995; Leichter et al., 2005; Leichter and Salvatore, 2006; Wang et al., 2007; Leichter et al., 2012; Schmidt et al., 2012; Wall et al., 2012; Storlazzi et al., 2013). However, their potential role in mitigating thermal stress has not yet been investigated.

LAIW are generated when strong tidal flows interact with topographic features and travel along the density gradient in the water column. In the Andaman Sea, the Andaman– Nicobar Island arc and shallow Dreadnought Bank generate internal waves with extraordinary large amplitudes of up to 80 m that travel eastwards with speeds of approximately 2 m s^{-1}(Perry and Schimke, 1965; Osborne and Burch, 1980). When they approach the Thai continental slope and shelf, they transform into secondary wave trains (Vlasenko and Stashchuk, 2007). These waves of elevation with trapped recirculating cores may propagate for considerable lengths across the shelf bottom (Klymak and Moum, 2003) and carry parcels of cold subpycnoline water into shallower coral reef areas (Schmidt et al., 2012). The temperature drops are sudden (within minutes), large (up to 10°C), short (15–30 min duration), intermittent (several per cycle) and confined to the sea bed, rarely extending to the sea surface, so that they are largely invisible to remote temperature sensing by satellites (Leichter et al., 2006; Sheppard, 2009).

A monsoonal climate dominates the Andaman Sea. April/May marks the transition from northeast (NE) to southwest (SW) monsoon with peak annual temperatures (Khokiattiwong and Yu, 2012). During the dry NE monsoon season, when the pycnocline shoals, LAIW are strongest (January through March). During the SW monsoon season, by contrast, the pycnocline is generally deeper. Southwesterly winds pile up surface water and depress the pycnocline so that fewer LAIW propagate upslope and reach into shallow reef areas (Schmidt et al., 2012; Wall et al., 2012). Around July/August, the SW monsoon reaches its full intensity with advection and turbulent mixing, increasing resuspension of sediments in shallow water (Wall et al., 2012). Both LAIW and the SW monsoon act from the same westerly direction so that west island sides are exposed to both internal and surface waves, albeit at different times, whereas eastern sides remain sheltered. Weak LAIW and monsoon mixing may overlap during transition seasons.

Although the Andaman Sea has experienced major coral bleaching events in 1991, 1995 and 2003, the 2010 mass bleaching event was the most severe on record. It caused high loss of live coral cover, but showed pronounced local differences in bleaching extent and subsequent mortality, which may be attributed in part to local differences in coral community composition (intrinsic factor) with more or less bleaching susceptible species (Phongsuwan and Chansang, 2012; Yeemin et al., 2012). Part of the variability may also be speculated to be due to internal waves (Phongsuwan and Chansang, 2012; Yeemin et al., 2012), but a test of this hypothesis is lacking. Thus, the 2010 severe bleaching event provides an excellent opportunity to test the underlying hypothesis: can LAIW benefit reefs during mass bleaching?

We took advantage of the natural setting of the Thai continental shelf (i.e. coral-fringed islands with differential exposure to LAIW (Wall et al., 2012); Figure 3.1.1a) and we took into account species-specific differences in coral susceptibility to heat stress. We hypothesize that differences in bleaching response (BR) are inversely related to LAIWexposure and a function of differences in community composition. If LAIW are able to reduce heat stress andmitigate coral bleaching, this would have important implications for reef health in the future and should be considered in coral reef conservation and management.

Material and methods

(a) Study sites

Seven islands were chosen for this study located on the continental shelf west of Thailand in the Andaman Sea. From north to south, the islands were Surin, Tachai, Bon, Similan, Miang, Payang and Racha (Fig. 3.1.1a). Twelve sites were selected; seven sites facing west (W) were exposed to LAIW and SW monsoon impact (Racha, Payang, Miang, Similan, Bon, Tachai and Surin), whereas five other sites were located on the LAIW and SW monsoon sheltered east (E) island sides (Racha, Payang, Miang, Similan and Surin).

(b) Environmental background

In situ temperature was recorded with Onset HOBO temperature loggers (Tidbits; resolution: +0.28C). They were deployed in 15 m water depth at Racha W, Miang E, Miang W, Bon W, Tachai W and Surin W, logging at 3 min intervals for the entire year 2010 (Wall et al., 2012). At Racha E, loggers were deployed at 20 and 10 m with a logging interval of 20 min and recorded the temperature from March 2010 until the end of July 2010. For Surin E, a temperature record was available from 15 m water depth ranging from March 2010 to December 2010 with a logging interval of 20 min (data courtesy of the Phuket Marine Biological Center from their Andaman Sea Monitoring Programme). Temperature data are unavailable for Payang and Similan, but previous work has shown only marginal temperature differences between similarly exposed sides of the Similan Islands (Fig. 3.1.1a), so that the temperature records available for the east and west sides of the central Similan Island Miang can be taken as representative (Schmidt et al., 2012).

(c) Bleaching survey

At each of the 12 sites, photo frame (50 X 50 cm) images were taken at the study depth of 15 m with 31–70 quadrats per site during the May 2010 (high temperature anomaly) and 27–80 quadrats per site during the December 2010 sampling (recovery phase). The sampling procedure involved placing the frames randomly into the reef following the 15 m isobaths over a distance of 25–50 m and taking photographs perpendicular to the substrate with the frame in the centre of the image. Photos were taken with Canon Powershot G12 cameras with underwater housing (resolution: minimum 3648 × 2736 pixels per image).

(d) Data analyses

(i) Temperature analyses

We used both satellite-derived degree heating weeks (DHW_S) from the National Oceanographic and Atmospheric Administration (NOAA) and in situ field data to calculate degree heating weeks

(DHW_f) according to NOAA (see the electronic supplementary material for more details). We used regression models to compare the ability of both satellite and in situ records to predict bleaching in the Andaman Sea. LAIW cooling intensities were quantified for each site by calculating cumulative degree-day cooling values according to Leichter et al. (2006) (see the electronic supplementary material for more detail).

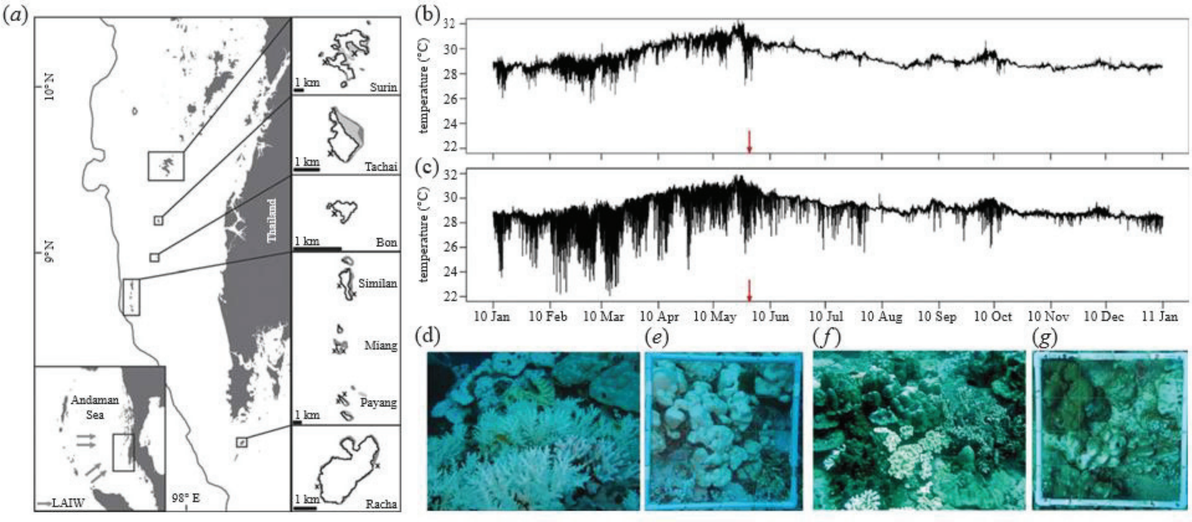


Figure 3.1.1 Study sites, temperature and BR at exposed and sheltered island sides in the Andaman Sea, Thailand. (a) Study sites on the Thai continental shelf beyond the breaking zone of LAIW near the 200 m isobath (line). Lower left inset shows the Andaman Sea with the direction of LAIW propagation (and monsoon winds). Right insets show close-ups of the islands with locations of the of study sites on opposing (exposed and sheltered) sides of the islands (sources of maps: mainland, Wessel and Smith (1996); bathymetry, Smith and Sandwell (1997) ; study islands: UNEP Coral Millennium Project). (b – g) Temperature and BR observed on the (b,d,e) sheltered and (c,f,g) exposed island sides of Miang. (b,c) The red arrow in the temperature graphs marks the time of bleaching monitoring. (d – g) Images display the observed difference in BR between (d,e) sheltered and (f,g) exposed island sites.

(ii) Photoframe analyses

Photoframe images were processed with the coral point count method (CPCe; cf. (Kohler and Gill, 2006)) to determine the percentage live and dead coral cover, coral community composition and bleaching status of the corals. A uniform grid of 15 X 15 points was superimposed on each frame and the presence of live or dead corals beneath each point recorded. The bleaching status of the coral at each point was assessed on an ordinal scale ranging from ‘healthy’ (with usual pigmentation) to ‘pale’ (reduced pigmentation), ‘bleached’ (completely white tissue), ‘recently dead’ (where the bare white skeleton was visible and already started to be overgrown by fresh green algae) and ‘dead’ (non-white carbonate structure that is still recognizable as former coral colony; see the electronic supplementary material, Fig. 3.1.S1). With the exception of the last category, we distinguished between the following coral groups: *Porites* spp. branching, *Porites* spp. massive, Pocilloporidae (*Pocillopora* spp. and *Stylophora* spp.), *Acropora* spp., *Diploastrea heliopora* and ‘other’ (all remaining taxa). The most dominant genera were selected (note: *Diploastrea* is a genus that only consists of one species) and all other genera were grouped together due to their relatively low abundances. These recorded coral groups were used to estimate differences in bleaching susceptibility for the coral communities at the different sites.

(iii) Site-specific community bleaching susceptibility index

A community bleaching susceptibility index (CBSI) was calculated by ranking the six recorded coral groups (see above) according to their reported susceptibility (Wessel and Smith, 1996; Smith and Sandwell, 1997; Marshall and Baird, 2000; Kohler and Gill, 2006; Phongsuwan and Chansang, 2012; Yeemin et al., 2012) into three bleaching susceptibility groups (0–2): very low susceptibility (*Diploastrea heliopora* (s1)), moderate susceptibility (*Porites* spp. massive (s2) and other (s3)) and high susceptibility (*Acropora* spp. (s4), *Porites* spp. branching (s5) and Pocilloporidae (s6)). This index was calculated as

$$\mathrm{CSBI} = \frac{(0 \times s_1 + 1 \times (s_2 + S_3) + (c_4 + c_5 + c_6)}{2}.$$

The coral group occurrences (i.e. percentage coral cover excluding ‘dead’ coral category) were multiplied by their susceptibility score and the resulting sum was normalized to a scale from 0 to 100 by dividing it by 2.

(iv) Site-specific bleaching response

The BR was quantified for each site (McClanahan et al., 2004). This evaluation is based on the photoframe data and calculated as

$$\mathrm{BR} = \frac{(0 \times c_1 + 1 \times c_2 + 2 \times c_3 + 3 \times c_4)}{2},$$

with the status-categories c1=healthy, c2=pale, c3=bleached and c4=recently dead (excluding ‘dead’ coral as mortalities cannot be derived from the particular bleaching event), all given as percentage cover for each site. The percentage coral of each category (c1–c4) was multiplied by a score (0–3) to weigh the different categories according to their bleaching intensity: no weight (0) for healthy (not bleached) and highest weight (3) for recently dead corals (i.e. mortality as a consequence of heat stress). The resulting sum was normalized to a scale from 0 to 100 by dividing it by 3. As some corals still showed signs of bleaching during the December survey, the same categories as in May were applied (‘healthy’, ‘pale’, ‘bleached’, ‘recently dead’ and ‘dead’; see electronic supplementary material, Fig. 3.1.S1b1–2; ‘recently dead’ are corals with white tissue and/or bare skeleton overgrown by algae). This allowed calculating BR values for December that quantified the progress in recovery of the remaining corals. For both indices, the multipliers were chosen following McClanahan et al. (2004). Different multipliers affect the absolute but not the relative values, and have a negligible effect on the statistical results. In the December surveys, it was not possible to assess the time of mortality (i.e. to differentiate between the corals that had died in May and those that had already died before the bleaching event). Hence, to determine post-bleaching mortality, the ‘dead’ corals from the May survey were subtracted from the total mortality (‘dead’ and ‘recently dead’) in December.

(v) Bleaching response as a function of extrinsic and intrinsic variables

The ability of different extrinsic and intrinsic factors (i.e. DHW and CBSI, respectively) to predict the observed site-specific BR was tested using simple and mixed multiple linear regression models, labelled (a) to (f) (Faraway, 2005). They were calculated across all study sites using single predictors or a combination of predictors. Significant regression models were tested for error normal distribution (Anderson–Darling test for regression model: (b) $p=0.523$, (c) $p=0.739$, (e) $p=0.971$, (f) $p=0.864$) and homoscedasticity of errors (Breusch–Pagan test for regression model: (b) $p=0.153$, (c) $p=0.788$, (e) $p=0.223$, (f) $p=0.209$). Independence of errors (Durbin–Watson statistic for regression model: (b)=0.300, $p=0.523$; (c)=0.233, $p=0.739$; (e)=1.88, $p=0.526$; (f)=2.04, $p=0.634$; all no autocorrelation) and correlation between predictors (Spearman correlation calculated for regression model: (e) $p=0.17$, $p=0.589$, (f) $p=0.20$, $p=0.552$; both no correlation) were tested for all significant models and the multiple linear models, respectively. The best-fit multiple model (regression model (e)) was further tested for influential cases using outlier tests and Cook’s statistics. Tachai W was identified for both tests as a potential influential case (outlier test: Tachai W rstudent=2.05, $p=0.892$; Cook’s statistic: Tachai W has the highest value of 0.22, but is below the critical value of 0.44). Tachai W was colonized by a high percentage of corallimorpharian compared with the other sites (see the electronic supplementary material, Table 3.1.S1) that could have been additionally stressful to the corals (see Results and discussion). Thus, a new model (model (f)) was fitted with the omission of this point. The software package R (version 3.0.1) was used for all statistical analyses.

Results and discussion

In situ temperature data show that internal waves coincided with a period of anomalously warm SSTs in the Andaman Sea in May 2010, leading to intermittent periods of cooling near the neabed in shallow (15 m) reef areas (Fig. 3.1.1b, c; supplementary material, Fig. 3.1.S2). The temperature dropped down to a minimum value of 22.1°C measured at the exposed side of Miang during the heat stress period (Fig. 3.1.1b and Table 3.1.1). LAIW cooling intensity differed between exposed sites and was stronger for Miang and Tachai (degree-days cooling of -19.2 and -16.8°C d, respectively) compared with Surin (-10.6°C d, Table 3.1.1). These differences in cooling and their potential to alleviate heat stress are not reflected in degree heating weeks derived from satellite temperature data (DHW_s, Table 3.1.1). By contrast, LAIW resulted in remarkable differences in heat stress when calculated from in situ temperature data (DHW_f, Table 3.1.1). These data revealed a 40–80% higher heat stress on the sheltered east sides. This is consistent with a significantly reduced BR at LAIW exposed compared with sheltered sites (Table 3.1.2 and Fig. 3.1.1d–g, 2a; two-tailed t-test: t=22.3794, d.f.=9.97, p=0.039) and suggest that LAIW abate heating and mitigate coral bleaching. Hence, satellite-derived temperature data were not able to predict the observed BR across all study sites (regression slopes not different from 0; Table 3.1.3). By contrast, $\mathrm{DHW_f}$ explained 40% of the observed BR (Fig. 3.1.2b; F=6.70, p=0.027, d.f.=10; Table 3.1.3).

Table 3.1.1 Temperature conditions during the high temperature anomaly in 2010 summarized for the exposed west (W) and sheltered east (E) sites; Tachai W (TW), Payang W (PW), Miang W (MW), Similan W (SiW), Racha W (RW), Surin W (SuW), Bon W (BW), Racha E (RE), Payang E (PE), Miang E (ME), Similan E (SiE) and Surin E (SuE). Temperature values include mean, maximum (max) and minimum (min) temperature recorded during this period. LAIW cooling intensities are calculated as degree-day cooling (DDC) below the NOAA bleaching threshold (30.62°C). Degree heating weeks (DHW) derived from satellite ($\mathrm{DHW_s}$) and field data ($\mathrm{DHW_f}$) reflect differences in heat anomaly observed at the sea surface and in 15 m water depth.

	exposed							sheltered				
sites	TW	PW[a]	MW	SiW[a]	RW	SuW	BW	RE[b]	PE[b]	ME	SIE[b]	SuE
mean [°C]	30.3	-	30.3	-	30.3	30.5	30.6	30.7	-	30.6	-	30.8
max [°C]	32.1	-	31.9	-	31.8	32.2	32.3	32.3	-	32.4	-	32.2
min [°C]	22.1	-	22.1	-	24.5	23.9	23.4	25.7	-	26.3	-	27.6
DDC	-17.0	-	-16.4	-	-12.1	-9.7	-6.9	-5.5	-	-3.0	-	-1.9
$\mathrm{DHW_s}$	5.2	4	4	4	5.7	6.8	5.2	5.7	4	4	4	6.8
$\mathrm{DHW_f}$	2.4	2.3	2.3	2.3	1.2	5.4	6.2	6	7.8	7.8	7.8	9

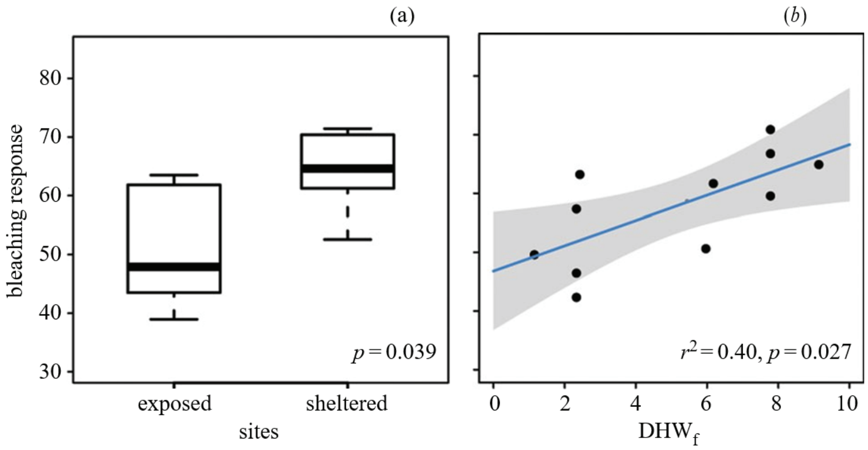


Figure 3.1.2 Coral reef community BR to the thermal stress in May 2010. (a) Boxplots display the BR ($\mathrm{BR_M}$) observed for exposed and sheltered island sites (two-tailed t-test, p = 0.039; central boxes show median and 25th and 75th percentiles, and whiskers the min. and max. range). (b) $\mathrm{BR_M}$ plotted as a function of heat stress (as degree heating weeks from field data $\mathrm{DHW_f}$) for each site (solid line represents the linear regression model: r^2 = 0.40, p = 0.027; the grey area denotes the 95% CI). (Online version in colour.)

Remote sensing has considerably advanced the predictability of coral mass bleaching over recent decades (Maynard et al., 2008b), despite challenges and limitations, particularly regarding spatial and temporal resolution (Leichter et al., 2006; Gove et al., 2013), as well as a general underestimation of temperature values in southeast Asia (Dunne, 2012; Tanzil et al., 2013). A notable shortcoming with SST remote sensing is its restriction to the uppermost skin of the ocean surface and, hence, its inability to detect subsurface processes acting on the seabed surrounding the corals. Short-term temperature fluctuations at the study sites and elsewhere are thus not adequately assessed (Leichter et al., 2006; Sheppard, 2009).

Here we were able for the first time to quantify the strong discrepancy between satellite and in situ data during an unprecedented bleaching event. This challenges the applicability of satellite temperature data alone to predict bleaching intensity and patterns in this region and regions with similar variation in temperature regime (Leichter et al., 2006; Sheppard, 2009). Even though remotely sensed SST measurements do not capture subsurface LAIW cooling, surface rip bands associated with LAIW can be tracked from space using synthetic aperture radar (SAR) and optical sensors such as MODIS (Moderate Resolution Imaging Spectrometer), allowing the generation of a global LAIW atlas (Jackson, 2007). So far it is not possible, however, to assess the magnitude of LAIW and associated mixing from SAR or MODIS data. The implementation of an in situ temperature monitoring system is consequently essential to quantify the magnitude of LAIW-associated cooling. Such information can be used to model the reliability of LAIW reef refugia in a warming ocean (Chollett and Mumby, 2013; Carrigan and Puotinen, 2014). Given the ubiquity of LAIW Jackson (2007), they may rival or exceed the importance of coastal upwelling in mitigating heat stress in corals.

Owing to its intermittent nature, LAIW cooling is not expected to completely nullify heat stress. Thus, bleached corals were observed at all sites during this severe heat stress and only a small percentage of corals remained healthy two months after the temperature had started to exceed the bleaching threshold. However, a greater percentage of healthy and pale corals were observed at the LAIW-exposed sites while the percentage of bleached and recently dead corals was higher at the LAIW-sheltered sites (Fig. 3.1.3). This was particularly apparent when comparing exposed with sheltered sites of the same island (e.g. BR differences sheltered versus exposed: Racha=52.6 versus 39.0, Miang=71.4 versus 41.8 and Surin=61.2 versus 45.2; Table 3.1.2).

Table 3.1.2 BR and CBSI calculated for all exposed west (W) and sheltered east (E) island sides (abbreviations are same as in Table 3.1.1) for the bleaching monitoring in May (BRM, CBSIM) and December 2010 (CBSID, BRD)

	exposed							sheltered				
sites	TW	PW	MW	SiW	RW	SuW	BW	RE	PE	ME	SIE	SuE
BMI bleaching	63.5	47.9	41.8	62.1	39	45.2	61.4	52.6	64.6	71.4	70.4	61.2
BMI recovery	36.9	20.6	22.7	21.7	27.1	15.6	23.5	21.2	21.9	26.3	20.1	27.2
CBSI bleaching	60.4	62.5	59.1	68.7	41.1	36	59.5	63.4	69	68.2	59.1	53.4
CBSI recovery	51.2	42.9	52.5	51.3	39.8	17.3	50.7	42.6	49.2	44.1	49	46.4

As coral species differ in their susceptibility to bleaching, coral community composition is a crucial parameter to explain small-scale bleaching variability (Marshall and Baird, 2000; Phongsuwan and Chansang, 2012). Therefore, we quantified for each site a CBSI to rank sites according to their intrinsic bleaching susceptibility. Bleaching vulnerable coral communities were found on both exposed and sheltered sites (e.g. exposed side of Similan and the sheltered sides of Payang and Miang; Table 3.1.2). However, some susceptible groups like branching *Porites* were almost exclusively observed at the sheltered island sides (see the supplementary material, Fig. 3.1.S3a). Individual coral groups showed strong differences in the extent of bleaching in May 2010 with milder bleaching on the exposed sites even within the most susceptible group (Fig. 3.1.3). Community inherent differences in bleaching susceptibility alone explained 39% of the observed BR (F=6.364, *p*=0.030, d.f.=10; Table 3.1.3) and already provide an estimation of how severe a BR will be for different reef communities. However, it is still unknown whether susceptibility patterns undergo substantial changes after this bleaching event, which has not been observed so far on the Thai coast of the Andaman Sea (Phongsuwan and Chansang, 2012), but has been shown for other locations in southeast Asia (Guest et al., 2012).

Extrinsic (environmental conditions) and intrinsic factors (community assemblage) are quite well able to predict differences in bleaching severity. Incorporating both extrinsic and intrinsic factors in models proved essential for increasing bleaching prediction accuracy (McClanahan et al., 2007; Yee et al., 2008). The predictability of our models increased markedly, explaining 67% of the BR by taking both $\mathrm{DHW_f}$ and $\mathrm{CBSI_M}$ into account (F=9.267, *p*=0.007, d.f.=9; Table 3). Our combined linear regression model provides some key messages: first of all, it highlights the potential of LAIW to provide protection from mass bleaching, and second it underlines the need to monitor temperature as well as community composition at the reef scale.

Variability in BR has been further attributed to other extrinsic (e.g. turbulence, light) and intrinsic factors (e.g. energy reserve, thermal history). At the study sites, both LAIW and the SW monsoon increase currents, which are known to reduce the BR (Shashar et al., 1996; Nakamura and van Woesik, 2001; Finelli et al., 2006). Previous thermal history, in particular exposure to substantial temperature fluctuations, can render corals more stress-resistant (Castillo and Helmuth, 2005; Oliver and Palumbi, 2011a; Putnam and Edmunds, 2011). While most of these studies investigated warm temperature anomalies, the negative anomalies observed here on the exposed sites might have a similar effect on the BR. Variations in content, composition and acquisition of energy reserves can allow corals to better cope with heat stress (Grottoli et al., 2006; Anthony et al., 2009). LAIW exposure affects the energetic status of corals (Roder et al., 2010; Roder et al., 2011) by the delivery of plankton and nutrients into the reef (Roder et al., 2010; Schmidt et al., 2012). This additional energy supply may also account for a reduced BR. Bleaching intensity is also a matter of exposure to the intensity of solar radiation with increased light levels to cause bleaching (Brown et al., 2002a). Both the arrival of LAIW and the impact of the SW monsoon waves increase turbidity and sedimentation in shallow water areas (Pomar et al., 2012), resulting in reduced light levels at the western LAIW-exposed sites. However, increased sedimentation can also be stressful to corals (Riegl and Brancha, 1995; Philipp and Fabricius, 2003). Hence, the corals themselves might be more robust against thermal stress and may benefit from increased water currents in addition to LAIW cooling, but may be negatively affected by the increased SW monsoon sedimentation rate.

Table 3.1.3 (a – c) Simple and (d – f) multiple linear regression models were calculated with (BR_M) as response variable and degree heating weeks derived from satellite (DHW_s) and calculated from in situ field data (DHW_f) as well as $CBSI_M$ during heat stress in May 2010 as predictive variables. Significance of p-values is denoted by asterisks.

parameter	BR_M				
	r^2	F-statistic	d.f.	t-value (slope)	p-value
(a) DHW_s	0.11	1.176	10	-0.86	0.304
(b) DHW_f	0.4	6.703	10	2.59	0.027*
(c) $CBSI_M$	0.39	6.364	10	2.52	0.030*
(d) $DHW_s + CBSI_M$	0.43	3.382	9		0.08
DHW_s				0.796	0.447
$CBSI_M$				2.259	0.05
(e) $DHW_f + CBSI_M$	0.67	9.267	9		0.007**
DHW_f				2.8	0.021*
$CBSI_M$				2.74	0.023*
(f) $DHW_f + CBSI_m^a$	0.78	14	8		0.002**
DHW_f^a				3.74	0.006**
$CBSI_M^a$				2.91	0.019*

$**p < 0.01$, $*p > 0.05$.

[a] Refit of model (e) by omitting the site Tachai W from the model calculations (see Material and methods section for justification).

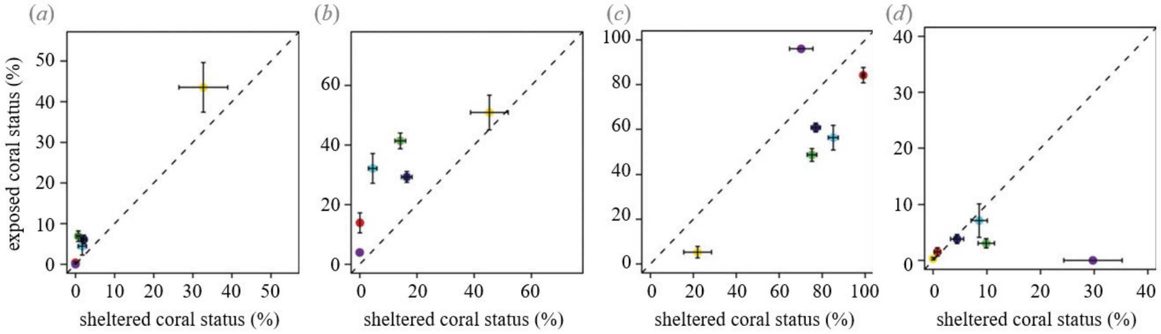


Figure 3.1.3 Coral group status during the bleaching event in May 2010, for Pocilloporidae (red), *Acropora* spp. (cyan), *Porites* spp. massive (green), *Porites* spp. branching (purple), other (blue), *Diploastrea heliopora* (yellow). Coral group status recorded as (a) healthy, (b) pale, (c) bleached and (d) recently dead and displayed as a fraction of total coral group cover for the sheltered versus exposed island sides during the bleaching event in May 2010.

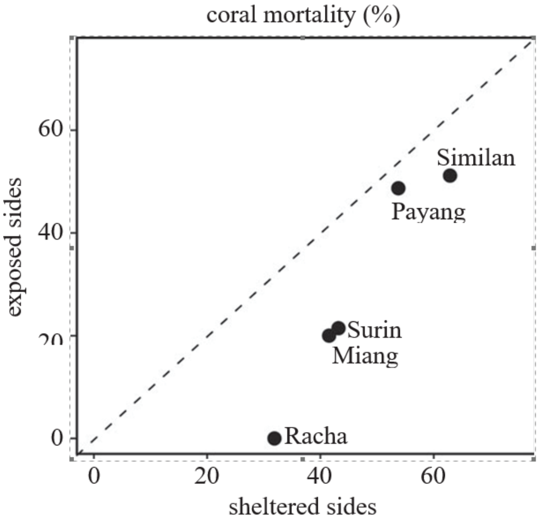


Figure 3.1.4 Scatter plot of coral mortality observed in December 2010 on sheltered compared with the respective exposed site.

Surveys carried out half a year after the bleaching monitoring (December 2010) revealed that the surviving corals had started to recover, but were not fully recovered yet (BR is not 0; Table 3.1.2; corals still showed signs of bleaching; supplementary material, Fig. 3.1.S1b1–2). Despite the strong LAIW-related differences in bleaching mitigation during the thermal stress period, recovery of the remnant coral community was not very different between exposed and sheltered sites (two-tailed t-test BR exposed versus sheltered sites: t=0.2332, d.f.=9.081, p=0.82). This suggests that LAIW and monsoon exposure on the W sides of the islands may play an antagonistic role (i.e. mitigating bleaching during the dry season but delaying recovery during the SW monsoon). The SW monsoon is characterized by increased sedimentation rates on the exposed sites at the height of the wet season (Wall et al., 2012). Sediment removal is energetically expensive for the corals, potentially diverting a higher fraction of the available energy away from regeneration and repair. Coral photosynthesis is also reduced in turbid waters (Riegl and Brancha, 1995; Philipp and Fabricius, 2003). Both the reduced energy from photosynthesis and the reallocation of energy to remove the sediment is likely to have hampered the recovery process on the exposed reefs.

By contrast, mortality at exposed and sheltered sites showed strong differences, with higher post-bleaching mortality on sheltered compared with the respective exposed site (Fig. 3.1.4). In addition, mortality varied strongly between species, resulting in post-bleaching coral communities with a higher proportion of resilient taxa at all sites (Table 3.1.2; $CBSI_D$ during recovery phase: 44.8+3.0 versus $CBSI_M$ during the thermal stress period: 58.4+2.8). This caused a shift in the dominance of coral taxa across sites, resulting in coral communities that are more bleaching-resistant (i.e. that have a lower CBSI). Whether such a shift represents an alternative state or a long-lasting condition strongly depends on the frequency and intensity of bleaching events.

The coral community at Tachai W showed severe bleaching and the slowest recovery (Table 3.1.2) despite both strong LAIW cooling (Table 3.1.1; see the supplementary material, Fig. 3.1.S2) and moderate sedimentation rates (Wall et al., 2012). This discrepancy can only partly be explained by the high percentage of bleaching-susceptible species found at this site (Table 3.1.2). High densities of corallimorpharians were observed at Tachai W accounting for 42% of the benthic cover (see the supplementary material, Table 3.1.S1). Corallimorpharians have been described as aggressive space competitors, which may kill corals at early stages of succession following disturbance events (Kuguru et al., 2004). Corallimorpharians were already present at this site during the thermal anomaly and were observed to compete for space with *Porites lutea* (see the supplementary material, Fig. 3.1.S4). This may have exacerbated the physical stress conditions (high temperature during the thermal anomaly and sedimentation during the SW monsoon), which highlights the complexity of factors and interactions governing the reef ecological responses to a changing environment. Multiple stressors are well known to additionally reshape coral reef communities (Carilli et al., 2010; Darling et al., 2013), and therefore need careful consideration when monitoring reef condition and predicting future reef trajectories (McClanahan et al., 2009; Ban et al., 2012). It has been predicted that bleaching events will occur annually or biannually by 2050 (Donner et al., 2005), with critical consequences for reef health and distribution (Hoegh-Guldberg et al., 2007). The observed community shift towards more heat-tolerant species composition potentially renders coral communities more resistant to the predicted future bleaching scenarios (Côté and Darling, 2010). However, this may occur at the expense of species diversity (Darling et al., 2013). Bleaching susceptible species survived at the exposed sites (see the supplementary material, Fig. 3.1.S3b) and may survive under the predicted future scenario in such natural resilient areas. This enhances their chance to recolonize the sheltered E sites and potentially can help to maintain biodiversity and reef integrity. Both the selection of heat-resistant species on the sheltered sites and the maintenance of coral biodiversity on the exposed sites may prove essential for sustaining coral reefs in the Andaman Sea and other semi-enclosed tropical basins in the face of climate change.

LAIW benefit corals during unprecedented bleaching and LAIW-exposed coasts may provide local refugia for corals. Because LAIW are ubiquitous in tropical areas, they may play a major role in sustaining coral diversity and cover in a warming climate. LAIW exposure is, however, a ‘mixed blessing’, as it hampers reef development (Schmidt et al., 2012; Wall et al., 2012) and coral growth (Schmidt and Richter, 2013), but promotes high diversity (Schmidt et al., 2012) and coral fitness (Roder et al., 2010; Roder et al., 2011) under prevailing conditions (i.e. non-bleaching) that might prove essential for reef persistence in this area. While LAIW have proved beneficial in alleviating thermal stress, sedimentation caused by increasing monsoon swell appears to retard the recovery process. While both processes are spatially coupled (both act from a westerly direction), they are temporally decoupled. In other non-monsoonal settings, the situation may be simpler and coral recovery will probably be faster. Internal wave-induced temperature variations were observed in tropical reefs to range from 1–3°C (Wolanski and Pickard, 1983; Wolanski and Delesalle, 1995; Leichter et al., 2006; Storlazzi et al., 2013) up to 10°C (Leichter et al., 2005; Leichter et al., 2006; Wang et al., 2007; Sheppard, 2009), and differ in frequency and duration. In the Caribbean, for instance, internal tides yield cold-water periods that are not as sudden and short lived (Leichter et al., 2006; Leichter and Salvatore, 2006) as in the Andaman Sea. Consequently, the effects on coral growth, reduced reef development (Leichter and Salvatore, 2006) and potentially species diversity appear much less pronounced. However, additional stressors that lead to a dramatic decline in coral health (Gardner et al., 2003) might represent the bottleneck for coral resistance to future changes. Our study highlights how a complex suite of environmental and biological factors interact to explain coral bleaching and recovery at the local scale. Understanding the physical dynamics and ecological responses is instrumental to understand the resilience of corals in a changing climate. LAIW may play an important, yet understudied role in providing local refugia for corals in a warming world.

Supplementary data is given in Appendix 1

3.2 Manuscript II

Living in a highly fluctuating environment: how does it shape thermal tolerance across coral taxa?

Putchim L[1,2], Wall M[1,3], Schmidt GM[1], Phongsuwan N[2] and Richter C[1]

[1]*Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research,*
Am Alten Hafen 26, 27568 Bremerhaven, Germany

[2]*Phuket Marine Biological Center,*
51 M.8 Vichit, Muang, 83000 Phuket, Thailand

[3]*GEOMAR, Helmholtz Center for Ocean Research, Marine Geosystems,*
Wischhofstraße 1-3, 24148 Kiel, Germany

In preparation

Abstract

Coral bleaching represents one of the major threats to coral reefs. Natural resistant areas where corals can maintain their health during stressful conditions, like heat stress, may ensure that coral diversity will be conserved in the future. Certain environmental settings can mitigate coral bleaching, like upwelling areas or high latitude reefs. In addition, corals exposed to high natural fluctuations (strong daily swings in temperature or short-term pulses of cold-temperature) improve coral fitness, and hence, their stress tolerance. So far these studies are limited to a few taxa (e.g. massive *Porites, Acropora*) and do not investigate whether such acclimation is similar for different taxa. Here we address these questions in the Andaman Sea. The west sides along the off-shore Similan Islands are exposed to both large amplitude internal waves (LAIW) and SW-monsoons, both of which contribute to a large range in temperature fluctuations. These phenomena are nonexistent in the sheltered eastern sides of offshore islands of the Andaman Sea. During the extreme heat event in 2010, LAIW abated the heat stress and mitigated the coral community response on the western regions of the Andaman Sea. We monitored 15 common taxa in the west and east and compared their bleaching response. In most cases corals were more likely to survive bleaching events in the western regions compared to the east and we found that some genera (e.g. *Porites, Dipsastraea, Favites*) profited even more than others. No case of bleaching was substantially stronger on the west than on the east. However, well known non-tolerant taxa, such as *Pocillopora* and *Acropora*, were still the most susceptible even with their improved thermal tolerance. Hence, acclimatization to fluctuating environments induced by LAIWs enhance thermal tolerance for corals, albeit with tolerances varying between species.

Introduction

Average global temperatures are rapidly increasing over the past century and continue to warm the atmosphere and the world's oceans. As a consequence, coral bleaching events associated with increasing ocean temperatures are giving rise to global concerns regarding the future of corals reefs and are seen as a major threat (Baker et al., 2008; WMO, 2010). In particular, massive coral bleaching events affected reefs worldwide and caused extensive coral die offs. Approximately 90% of corals have been killed during the 1998 bleaching event in the Indian Ocean (Wilkinson, 2000) and 40% in 2005 in the Caribbean Sea (Eakin et al., 2010). Recently the Great Barrier Reef experienced a severe bleaching event caused by the last El Nino with so far unprecedented consequences for its future (Climate Council of Australia, 2016; GBRMPA, 2016). The severity is much greater than in earlier bleaching events in 2002 or 1998. Over a thousand kilometres of reef have been affected, and bleaching-induced mortality was more than 50% in some areas. However, there are many regions less susceptible than the other locations. Different regions/reefs show different patterns in their susceptibility or tolerance with some varying from year to year. Many people are searching for potential places of refuge for coral reefs, and are trying to understand reasons for its success. One of the main factors driving the survival of corals is acclimatization.

Improved tolerance to heat stress is known as acclimatization (Brown, 1997a; Gates and Edmunds, 1999). Fluctuating temperatures can enhance thermal tolerance for corals and occur during natural bleaching events (Maynard et al., 2008a; Guest et al., 2012), but have also been replicated under experimental laboratory conditions (Fang et al., 1997; Oliver and Palumbi, 2011a; Bellantuono et al., 2012b). Few studies have explored the tolerance of corals under cooling temperatures. So far, the experimental evidence suggests that corals react similarly to cooling as they do under heat stress, with cooler temperatures also causing photoinhibition, bleaching and mortality (Saxby et al., 2003; Roth et al., 2012; Rodríguez-Troncoso et al., 2014).

In the Andaman Sea region, large-amplitude internal waves (LAIW) flush cool water over corals and reduces bleaching in corals. In particular, LAIW represent an important oceanographic feature that structures the coral reefs landscape on off-shore islands. Recent attention has observed environmental variations caused by LAIWs and their influence on corals and coral reefs (Roder et al., 2010; Roder et al., 2011; Schmidt et al., 2012; Pacherres et al., 2013; Schmidt and Richter, 2013; Schmidt et al., 2016). LAIWs are generated around Sumatra and the Andaman-Nicobar Islands and then travel towards the Andaman Sea coast (Osborne and Burch, 1980). In shallow reef areas, LAIWs consist of short pulses of seawater with increased nutrient concentrations and reduced water temperature, pH, and oxygen (Schmidt et al., 2012). As a result, corals inhabiting LAIW-exposed areas need to cope with these strong environmental fluctuations, which result in reduced growth rates (Schmidt and Richter, 2013), reef development (Schmidt et al., 2012; Wall et al., 2012), and an adjustment of their metabolic traits (Roder et al., 2011). Also as a consequence, improved thermal tolerance was shown in LAIW-exposed *Porites* and *Pocillopora* corals by increasing survival and recovering rates from severe bleaching (Buerger et al., 2015; Schmidt et al., 2016). LAIW-influenced fluctuating environments can render coral reefs more thermally tolerant. Yet, no study explores whether it is true across coral taxa. He we observe acclimatization of several coral species exposed to LAWIs and qualitatively measure their responses to fluctuating temperature stress.

Materials and methods

(a) Study sites

Reef surveys were conducted at three islands belonging to the Similan Islands chain: Similan Island, Miang Island, and Payang Island, located from north to south (Fig. 3.2.1). These islands are characterized by strong environmental differences forming two distinct habitats. The western sides are exposed to the influence of large amplitude internal waves (LAIW) during the dry season until the beginning of the wet season (December - May). The western sides of the islands are also subjected to southwest monsoons during the dry season (April - November). The east sides are sheltered from both these phenomena. As a consequence, the exposed west reefs are characterized by a higher species diversity but with minimal carbonate reef framework compared to the complex reef structures in the east mainly dominated by massive *Porites* (Schmidt et al. 2012). In total three replicates of each habitat (exposed west- and sheltered east-shore reefs) were monitored for the present study (Fig. 3.2.1).

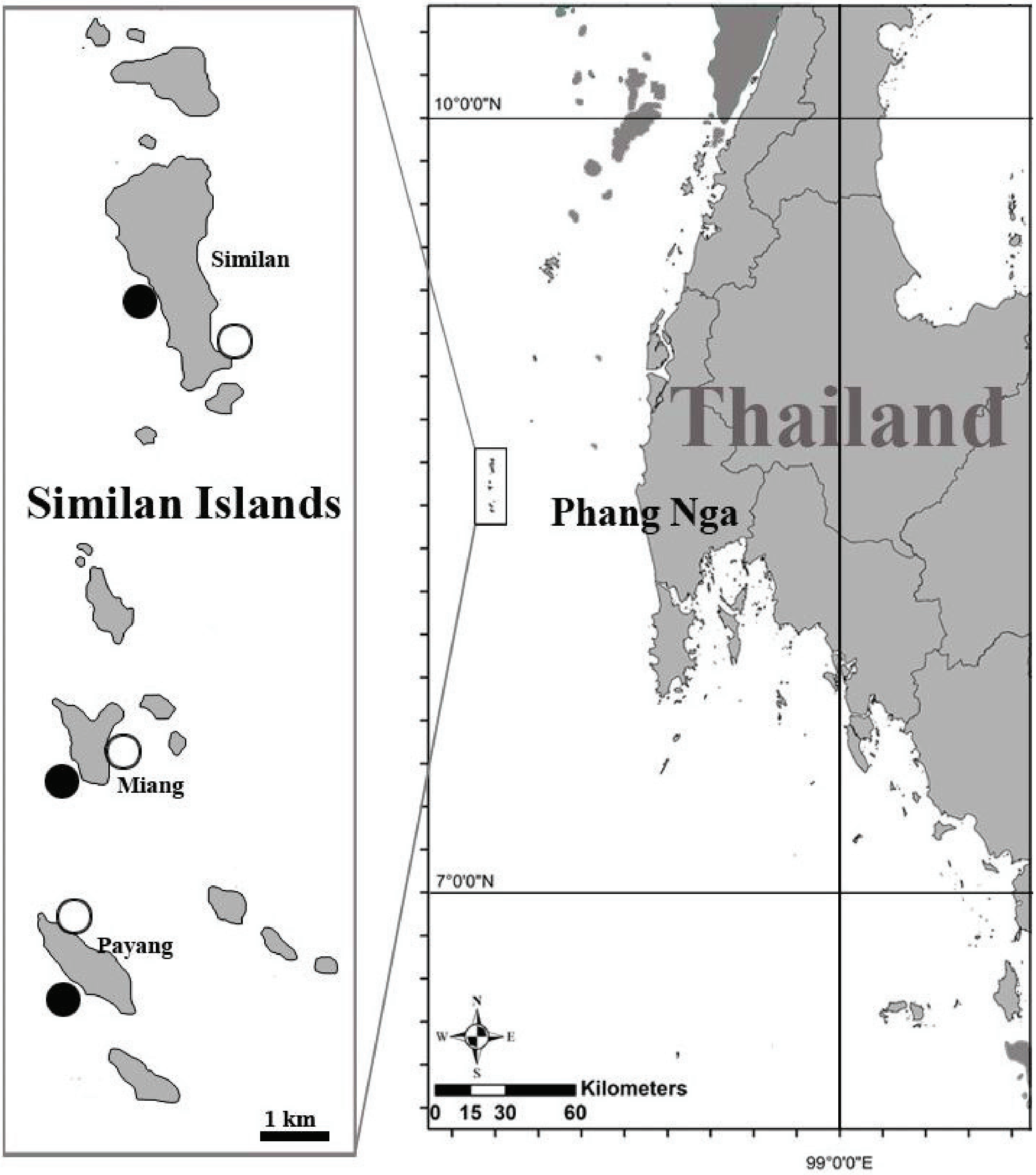


Figure 3.2.1 Map showing the study sites in the Andaman Sea, Thailand with insert close-up map of the sites in the east (white circles) and west (black circles) along the Similan Islands chain.

(b) Sea temperature during the 2010 bleaching event

In general, environmental conditions differed strongly between exposed west and sheltered east habitats along the Similan Islands mainly due to strong fluctuations of physical and chemical water parameters entrained by LAIWs and monsoons in the west (for more details see Schmidt et al. 2012). During the study period – the heat stress event between March and May, 2010 - water temperature was recorded in the east and west side of Miang Island (Fig.3.2.1). Temperature loggers (Tidbit v2, Onset computers; resolution 0.2°C within a range of 0 to 50°C) were attached to the bottom in about 15m water depth logging at 3min intervals from January to December 2010. The east and west sides showed remarkable differences (see supplementary info) and in average reduced heat stress at the exposed west. While in the sheltered east the mean temperature during the heat stress period (time during which the average daily temperature exceeded the bleaching threshold of 30.1°C (Brown et al. 1996) was 30.6°C (max temperature was 32.4°C) and lasted for 85 days; in the west sides, an average temperature of 30.3°C (max. temperature of 31.9°C) prevailed and the heat stress period lasted only for 73 days (Wall et al. 2014). A more detailed description of the temperature conditions is provided in Wall et al. (2015).

(c) Coral surveys

To compare the response of different coral taxa to the elevated temperature in the two different habitats (exposed west and sheltered east reefs), photo quadrats were taken at all sites during the bleaching event (in May and July) as well as post-bleaching event in December (post-bleaching conditions). Photo quadrats (50 x 50 cm) were taken randomly right above the reefs at a depth contour of 15 m. A minimum of 28 pictures was taken per site. The camera was held about 1m above the seafloor. Any colony located within each frame (>50% of colony area), was analyzed. This resulted 1740 colonies analysed at the sheletered reefs and 1389 at the exposed reefs (Table 1). Each individual was identified to genus level and the tissue condition was recorded. Coral tissue conditions were classified into one of four categories exhibited by the major part of the colony area (>50% colony area): fully pigmented (healthy), pale, bleached, and recently dead (Wall et al. 2015). The highly similar genera *Favites* and *Goniastrea* were difficult to differentiate from images and were thus pooled together. Since the two dominant genera, *Acropora* (branching, corymbose, table) and *Porites* (massive, encrusting, and branching), exhibited various growth forms a more detailed differentiation was applied within themBoth during and shortly after the heat stress period (May and July) were considered as bleaching periods in order to also account for taxa known for delayed heat stress responses (e.g. *Cyphastrea*, (McClanahan, 2004)). To derive trajectories of the different coral taxa (recovery from heat stress versus deterioration of the coral condition), we compared their immediate response to heat stress (May and July) with the longer-term consequences (conditions six months after the heat event in December).

(d) Data analysis

Coral community composition was determined from the photo frames for the different islands, sites and time periods (bleaching and post-bleaching). Since the lag time between bleaching and mortality is about 4-6 months (Brandt, 2009; Alemu and Clement, 2014), the coral community sampled during the bleaching event (1-2 months after the initial report of bleaching) is expected to represent the pre-bleaching coral community composition. This composition was compared to the post-bleaching coral community composition in December. Multivariate redundancy analysis (RDA; citation) was conducted to examine the coral community composition between sampled sites and to illustrate whether habitat and time accounted for the observed patterns in species composition. Habitat and time were regarded as explanatory factors. Prior to the analysis the coverage data were transformed ($x^{1/3}$) to reduce weight of dominant or absent taxa. We used Permanova with interaction (maximum permuation = 999) to examine whether coral composition differed significantly between habitat (exposed west and sheltered east) and time (bleaching and post-bleaching).

The coral health status was calculated as bleaching and mortality index (BMI) for each taxon. It is based on the four tissue status categories described above and calculated as follows:

$$\mathrm{BMI} = \frac{(0 \times c_1 + 1 \times c_2 + 2 \times c_3 + 3 \times c_4)}{3},$$

where c_1 is fully pigmented; c_2 is pale; c_3 is bleached; and c_4 is recently dead, all calculated as percent for each site. Then the percent of each recorded bleaching category was multiplied by a score from 0 to 3, according to the heat effect from fully pigmented to dead. The sum was normalized to a scale from 0-100 by dividing it by 3. We calcuated a bleaching and post-bleaching coral tissue condition as well as an average taxon specific BMI for both periods combined. Spatial patterns in the average bleaching response were analyzed by a Two-way ANOVA with habitat (exposed west versus sheltered east) and island (Miang, Payang and Similan) as independent explanatory variables (Anova Model: BMI ~ Habitat * Island). The tests were only performed for taxa present at minimum two islands within both habitats. Other taxa were omitted from further comparison. Comparison of habitat specific bleaching responses with time was done for all taxa occurring with at least 10 individuals per habitat (both sites and time periods were pooled per habitat; Table 3.2.1).

Table 3.2.1 Total number of surveyed coral colonies of the most common taxa in the exposed west and sheltered east study sites along the Similan Islands.

Taxa	**# of surveyed colonies**	
	exposed	**sheltered**
Acropora	**106**	**259**
branching	50	204
corymbose	13	26
table	43	29
Cyphastrea	27	43
Diploastrea	16	39
Dipsastraea	72	28
Favites	131	108
Hydnophora	59	10
Leptastrea	45	23
Pavona	105	73
Pocillopora	122	65
Porites	**486**	**869**
branching	37	232
encrusting	100	307
massive	349	330
Other	220	181
Grand Total	**1389**	**1740**

Results

Coral community composition differed between sheltered east and exposed west reefs (PERMANOVA: F = 5.25, p = 0.001) but did not significantly change with time (PERMANOVA: F = 2.13, p = 0.057). The redundancy analysis plot (Fig. 3.2.2) shows that 28.3% of the variation is explained by island exposure (first axis, RDA1; habitat) and 11.3% by time (second axis, RDA2; bleaching versus post-bleaching). Most of the community composition variation remained unexplained leaving other factors to contribute to the observed differences. Overall, the coral communities were dominated by few taxa common at both exposure sites: primarily *Porites* contributing with ~50% in the sheltered east and 35% in the exposed west to the coral community composition and *Acropora* with ~15% in east and ~8% in west. All other taxa were rather rare with <8% cover. Most taxa occurred at both exposure sites and only few showed significant preference for either exposed west or sheltered east sites (Fig. 3.2.S1, Table 3.2.S1).

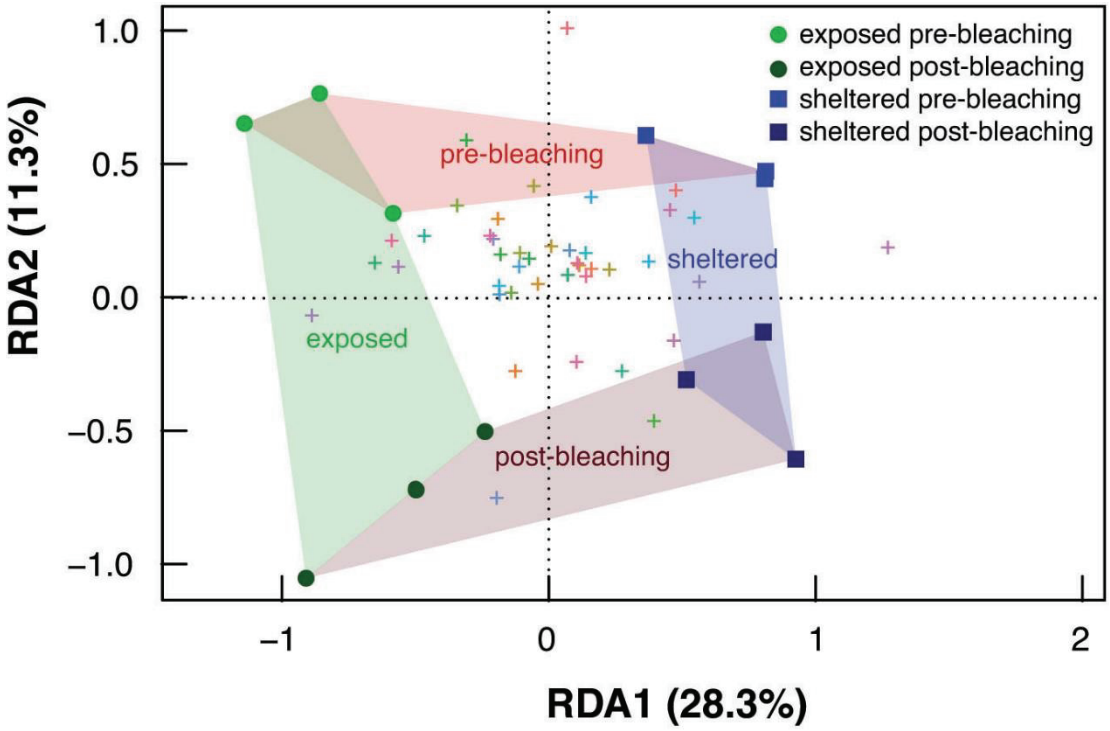


Figure 3.2.2 Redundancy analysis (RDA) of coral community changes as a function of exposure (exposed west versus sheltered east reefs) and time (bleaching versus post-bleaching composition). Circles mark exposed site communities and squares sheltered community ordination during the different time periods. Crosses represent taxa ordination (colour-code as in Fig. 3.2.S1).

The bleaching response calculated as bleaching and mortality index (BMI) was higher in the exposed west than in the sheltered east, but not affected by islands (Table 3.2.2). Many taxa, in particular dominant taxa such as *Porites*, *Acropora*, and *Favites*, received a positive influence from LAIW (Fig. 3.2.3). For 4 genera, however, the overall coral health condition was similar or slightly higher in the exposed west compared to the sheltered reefs i.e. *Hydnophora*, *Diploastrea heliopora*, *Cyphastrea*, and *Leptastrea* (Fig. 3.2.3).

Table 3.2.2 ANOVA results on the effect of island (Similan, Miang, Payang) and site (exposed west versus sheltered east) on the bleaching response calculated as bleaching and mortality index (BMI) of the coral community.

Source of Variation	*n*	**Analysis of variance**			**comparison**
		df	*F-ratio*	*p*	
Site	22 genera	1	10.728	0.0013 **	East > West
Island	22 genera	2	0.521	0.47	

** indicated a significant effect at *p*<0.01

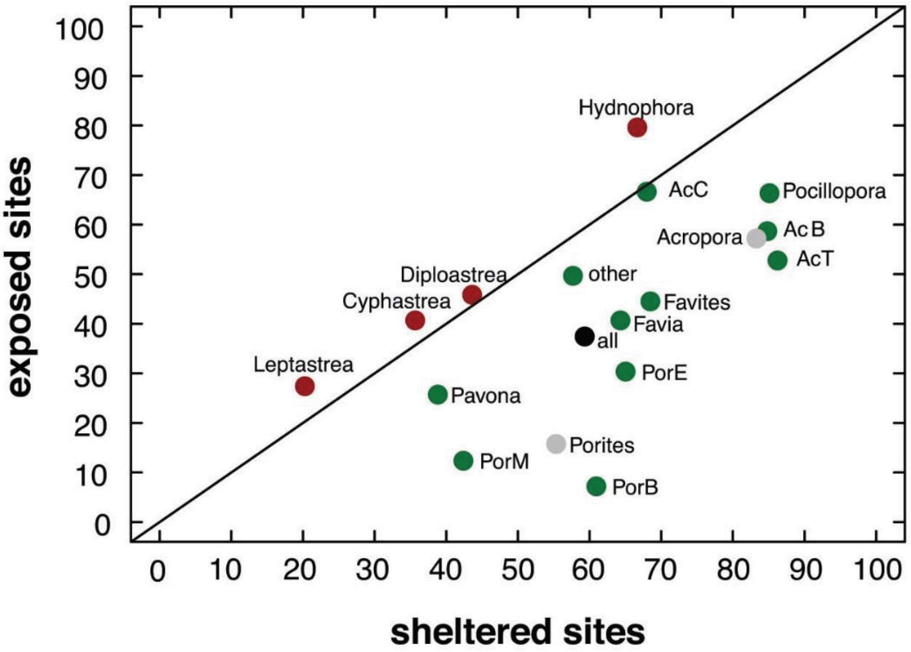


Figure 3.2.3 *Acropora*: AcT = table, AcC = corymbose, AcB = branching; *Porites*: PoM = massive, PoE = encrusting, PoB = branching; genus *Favites* also includes genus *Goniastrea*). Black line indicates 1:1 relationship between exposed west and sheltered east bleaching response. Red dots denote genera responding similarly or slightly stronger to heat stress in exposed west sites compared to sheltered east counterparts. Grey dots mark pooled data of various growth forms from the same genera: *Acropora* and *Porites*. Green dots denote genera benefiting from lowered heat stress and fluctuating conditions in exposed west sites.

Discussion

Previous studies eventually indicated that LAIW conditions enhance thermal tolerance and reduce bleaching-induced mortality in corals. Here, we provide a qualitative understanding of the implications of the acclimatization in a fluctuating thermal environment on the community response. The effect of environmental fluctuations on the acclimatization of corals was demonstrated in many different contexts. The increased tolerance of corals in previous studies mostly resulted from repeated heat experiences such as the exposure to photosynthetically active radiation (PAR) or heat stress in intertidal reef zones (Brown et al., 2002a; Schoepf et al., 2015), the experience of severe bleaching events (Maynard et al., 2008a; Guest et al., 2012), or pre-heat treatments before simulating a bleaching event in the laboratory (Fang et al., 1997; Middlebrook et al., 2008; Bellantuono et al., 2012a). In contrast, the fluctuating environment in LAIW-influenced areas offers the possibility to analyse the effect of repeated cooling stress. Temperature fluctuations at the Simiulan Islands can reach up to 10°C, with temperature dropping within a minute (Wall et al., 2015). Unlike to studies focussing on heat stress only, investigations on the response of corals to cooling stress are very limited. Based on the current knowledge though, the effect of cold stress to coral physiology is comparable to heat stress, i.e. corals exposed to low temperatures show a decline in metabolic activity, respiration, energy reserve, and photosynthetic proteins (Saxby et al., 2003; Rodríguez-Troncoso et al., 2014). Similarly, prolonged cooling stress can cause bleaching in corals and subsequently died as well as prolonged heat stress (Hoegh-Guldberg et al., 2005; Lirman et al., 2011). However, within short period of time, cooling stress can create more stress to corals. Roth et al. (2012) found that corals in 5-day cooling treatment have significantly lower linear extension and photoinhibition compare to heat stress. Not only variation in temperature, pH, inorganic nutrient, water current, and sedimentation rate are also suddenly following change (Roder et al., 2010; Wall et al., 2015). By that mean, fluctuating environment could be mean various variation of physical environment, which was also able to enhance thermal tolerance. However, the advantage of LAIW condition was not enhance only thermal tolerance to corals but also the fact that reducing of heat stress during bleaching event. Based on experimental evidence from Buerger et al. (2015), who indicated that corals inhabiting LAIW-exposed areas are able to tolerate to heat experimental treatment better than corals inhabiting in LAIW-shelter areas, regardless heat stress variation. However, we found that the improved thermal tolerant varied among coral taxa under natural heat stress.

It is well known that bleaching susceptibility differ among coral taxa, with some varying from place to place. This is the first study examining bleaching susceptibility under LAIW influence across coral taxa. In general, bleaching response from our results were consistent with previous bleaching reports resulted from heat stress, where *Porites* corals were among the most robust to environment change, and well known non-tolerant taxa as *Pocillopora* and *Acropora* were still the most susceptible even with background experience of LAIW. Capacity of improved thermal tolerance was coral taxa specific. In particular, coral taxa that were relatively high bleaching tolerance with BMI < 50, included *Leptastrea, Cyphastrea, Diploastrea, Pavona,* and massive *Porites*. Bleaching response of those taxa were not constant across places, but most of the time they were reported as a bleaching tolerance species (Marshall and Baird, 2000; McClanahan, 2004; Guest et al., 2012; Phongsuwan and Chansang, 2012). However, not all of them showing benefit from LAIW, where BMI value was similar between exposed and sheltered sites. It was quite surprise for *D. heliopora* participating in no benefit group from LAIW. Since *D. heliopora* was found relatively high plastic metabolic changes, where able to increase their energy reserve following LAIW intensity (Roder et al., 2011). This may explain by the fact that *D. heliopora* has a large size of polyp with thick tissue layer, slower growth rate (Bagnato et al., 2004), possibly allowing them to better maintain energy reserves throughout the bleaching regardless LAIW intensity. This suggest that thermal tolerance coral taxa do not acquire the benefit from LAIW as much as non-tolerance coral taxa. However, the most susceptibility found in improved thermal tolerance of non-tolerant coral taxa. So, we support the finding from Schoepf et al. (2015), who underline the limitation of improved tolerance to thermal stress. Living in a higher thermal tolerance as intertidal zone potential to improve thermal tolerance to corals than those living in subtidal zone. However, the powerful may not enough to survive, when stress exceed the upper limit of coral's tolerant capacity.

A clearly winner in our study, *Porites*, who was one of the most tolerance and acquire more benefit from LAIW. This was consistent with the results from experiment laboratory, where showing that LAIW-exposed *Porites* corals are able to resist increased seawater temperature than those form LAIW-sheltered side (Buerger et al., 2015). High environmental tolerance of *Porites* approve by the fact that they are the dominant reef-building corals in the Andaman Sea (Phongsuwan and Chansang, 1992; Changsang, 1999), and also in Indo-Pacific region (Potts et al., 1985). However, their status may be facing the risk, since they were also reported as one of the most highly susceptible to bleaching where else in the Andaman Sea during the 2010 bleaching event (Phongsuwan and Chansang, 2012). In inshore reefs, *Porites* was highly bleached, while *D. heliopora* was noted as resistant species with very limited bleached colonies. This contrast may explain by the fact of habitat difference between inshore and offshore areas. Inshore areas have naturally higher in nutrient, suspension solid, and sediment, and lower in light penetrate, water quality, water current, and turbidity, which those condition offer both ecological advantage and disadvantage to corals. Eventually, it was benefit to *D. heliopora* but not for other coral taxa (Phongsuwan and Chansang, 2012). Another important factor determining thermal tolerance is genetic differentiation of coral host and /or symbionts. Many studies showed the potential of harbouring resistant type of symbiont but sufficient data of genetic database was limited in the Andaman Sea.

Since thermal tolerance varied among coral taxa, Coral community composition in Similan Islands was different between east and west sides (Schmidt et al., 2012). Reef that dominate by thermal tolerant coral species play the important role for bleaching tolerant to the reef (Wall et al., 2015). However, tolerant reefs could compose by various thermal tolerant species and proportion. When considering in a given taxon, only few taxa showed the habitat preference. Most were prevalence either side or no significant difference between exposed and sheltered side and not change after this mass bleaching disturbance. Although, six months after bleaching mortality in the east was 50% higher than the west, almost all coral taxa are still sharing a similar proportion of the reef community for each side (Fig. 3.2.S2). Lower bleaching susceptibility at the LAIW-exposed sides indicated that LAIW has a potential to improve thermal tolerance to corals. However, when consider variation of coral community composition by side, almost all coral taxa were reduced by similar percentage composition at each side. Non-tolerant coral taxa were still the most suffer with their improved thermal tolerance, leading to no shifts in coral community composition through the time.

Considering about historical disturbance, the major threatening factor to coral reefs in the Andaman Sea was the 2010 mass bleaching event (Phongsuwan and Chansang, 2012), with the highest heat stress over last 35 years (Fig. 3.2.S3). So, the advantage from acclimatization may not have been obviously presented until then. Acclimatization can happen through various environment conditions. LAIW-influenced fluctuating environment is the one condition able to enhance the thermal tolerance to most coral taxa, while typically non-tolerance thermal taxa are still the most vulnerable with high mortality. We conclude with an examination of the limited capacity for acclimatization to protect corals from thermal stress as the ongoing global warming with continuing trends.

Supplementary data is given in Appendix 2

3.3 Manuscript III

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

Putchim L[1, 2, 3], Phongsuwan N [3], Yaemarunpattana C [3], Thongtham N [3], Richter C [1, 2]

[1] *Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Science, Bentho-Pelagic Processes, Bremerhaven, Germany*

[2] *University of Bremen, Bremen, Germany*

[3] *Phuket Marine Biological Center, Phuket, Thailand*
51 Sakdidet Road, 83000 Phuket, Thailand

In review at PeerJ#17893

Abstract

The bleaching susceptibility of 28 coral taxa around southern Phuket was examined in 2016, and compared to the last three major bleaching events in 1991, 1995, and 2010. 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. Size-specific bleaching susceptibility was studied only in *P. damicornis* at the given site, and found that 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. Increased thermal tolerance suggested that some of the fast-growing corals (*Acropora*, *Montipora*, and *Pocillopora*) might have life-history traits that lead to more rapid adaptation to a warming environment than certain slow-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, 1997b; 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 and Jokiel, 1978; Scott et al., 2013), high light intensity (Dunne and 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 and Oliver, 1999; Bruno et al., 2001; Eakin et al., 2010; van Hooidonk et al., 2012; Hughes et al., 2017).

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 and Marshall, 2002; McClanahan, 2004; Obura, 2005). In general, slow growing coral taxa with massive or columnar morphologies are less susceptible to bleaching-induced mortality than fragile, fast growing taxa with branching or plating morphologies (Marshall and Baird, 2000; Loya et al., 2001; McClanahan, 2004; Furby et al., 2013; Hongo and Yamano, 2013). Nevertheless, bleaching susceptibility can change over time. Numerous studies document an increased bleaching tolerance in corals that previously experienced thermal/light stresses (Fang et al., 1997; Maynard et al., 2008a; Middlebrook et al., 2008; Bellantuono et al., 2012b; Schoepf et al., 2015), while others showed a decrease in bleaching tolerance in corals after repeated thermal/light stress (Hongo and Yamano, 2013; Brown et al., 2014). Ultimately, the bleaching responses of corals to combined heat/light stressors depend upon the intensity and longevity of each stressor, however prior exposure to these stressors also influences susceptibility (Hoegh-Guldberg and Ross, 1999; Gorbunov et al., 2001; Brown et al., 2002a).

The capacity of corals to adapt to elevated temperatures has received increased attention in recent years (Császár et al., 2010; Weis, 2010; Bay and Palumbi, 2014; Schoepf et al., 2015). Adaptation can involve both host and/or symbiont (Császár et al., 2010; Leggat et al., 2011). Different symbiont types are known to confer differential thermal tolerance to a given coral host. For example, host *Symbiodinium* type D is recognized as the most thermally tolerant (Berkelmans and van Oppen, 2006; LaJeunesse et al., 2010b; Oliver and Palumbi, 2011b). In corals associating with more than one symbiont type, the switching and/or shuffling of symbionts improve the bleaching tolerance of the coral holobiont (Berkelmans and van Oppen, 2006; Ulstrup et al., 2006; Oliver and Palumbi, 2011b). 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). On the other hand, some coral species have been observed to harbour specific symbiont types that show a difference in environmental tolerance (Thomas et al., 2014; Thomas et al., 2017). 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 (Brown et al., 2002c; Bellantuono et al., 2012b; Wicks et al., 2012; Thomas et al., 2017), or through changing the genetic structure (Bay and Palumbi, 2014). Recent evidence has also demonstrated that some corals experience size-selective bleaching extent and subsequently mortality (Shenkar et al., 2005; Brandt, 2009; Brown et al., 2014). Larger coral colonies often display more extensive bleaching. An increase vulnerability to stress may exhibit in response to the decrease in physiological capacity with increasing colony size or coral age (Rinkevich and Loya, 1986; Meesters and Bak, 1995).

In the Andaman Sea, coral bleaching events occurring over the last few decades have had different affecting conditions and resulted in various subsequent outcomes. Minor to moderate bleaching events, defined as events where bleaching affects about 10% and 50% of coral cover, respectively (Oliver et al., 2004), were in 1998, 2003, 2005, and 2007. Records of mass coral bleaching following the 2010 bleaching event are the largest so far on record within the region (Phongsuwan and Chansang, 2012). Most recently, a relatively moderate bleaching event occurred in 2016 in response to temperature anomalies above the bleaching threshold, where the highest monthly mean temperature is exceeded by 1°C (Glynn and D'Croz, 1990). About 50% of coral cover was affected with a very limited bleaching-induced mortality. During field surveys examining the extent of the bleaching, it was noticed that not all coral species were bleached to the same extent and some displayed bleaching resistance, suggesting the potential for adaptation. 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

(a) Study sites and methods

Bleaching surveys were conducted around southeastern Phuket (Fig. 3.3.1) during peak periods of major bleaching events when degree heating weeks (DHW) initially reached the maximum heat stress in 1991, 1995, 2010 and 2016, respectively. To qualify the extent of bleaching, permanent line intercept transects and belt transects were surveyed. For the line intercept transects, a 100m measuring tape was laid out at each site at about 5 m depth around the upper reef slope, where corals are more abundant. We took advantage of this long-term data to advance our understanding of bleaching responses of corals over time. The corals below the transect line were identified to the genus or species level (total 28 taxa) and the corresponding section of each colony intercepting the transect line was measured to the nearest centimetre (Loya, 1972). 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 for the strongly reduced coral cover after the mass mortality following the 2010 bleaching event. However, these two methods provide comparable results (Nadon and Stirling, 2006; Jokiel et al., 2015). The additional 2 sites in 2016, Tang-khen and Maiton, were selected to cover over the area. These sites were also strongly affected by the 2010 bleaching event (L. Putchim, unpublished data; Fig. 3.3.S1). Heat stress conditions during average SST exceeded the coral bleaching threshold (see the supplementary material for more details), which was similar across the studied sites (Fig. 3.3.2). Range of mean temperature is about 0.5°C (Table 3.3.1). We further examined site-specific differences in bleaching susceptibility, and found no significant differences of eight sharing coral taxa between sites in 2016 (Table 3.3.S1), and pooled the data from all transects to calculate bleaching and mortality index for each coral species each year.

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) because of survey-limiting conditions. The size classes were categorized as follows: (1) primary polyp (~2mm) to small colony (5cm), (2) juvenile colony (6-10cm), (3) adult 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:

$$\mathrm{BMI} = \frac{(0 \times c_1 + 1 \times c_2 + 2 \times c_3 + 3 \times c_4)}{3}$$

where c_1 is fully pigmented; c_2 is pale; c_3 is fully bleached; and c_4 is recently dead, all calculated as percent per year (McClanahan et al., 2004). BMI is a measure of bleaching extent and subsequent mortality, so as BMI increases, susceptibility increases.

Bleaching susceptibility in terms of subsequent mortality in different coral species at the different sites during the past bleaching events in the Andaman Sea has been reported by Phongsuwan and Chansang (2012). In this paper, the focus is, therefore, of the bleaching response pattern of the corals during the 2016 bleaching event, and compared those patterns during past bleaching events.

To account for different locations of sites and stress conditions that differ among bleaching years, susceptibility level of the given coral taxon was assigned to the one of three categories: low moderate, and high, based on the difference between the highest and lowest BMI scores divided into 3 levels. This allows for interpretation of the temporal patterns of bleaching susceptibility between taxa, acknowledging that spatial variability in coral communities between sites may have biased the results (cf. Supplementary Information, Fig. 3.3.S2).

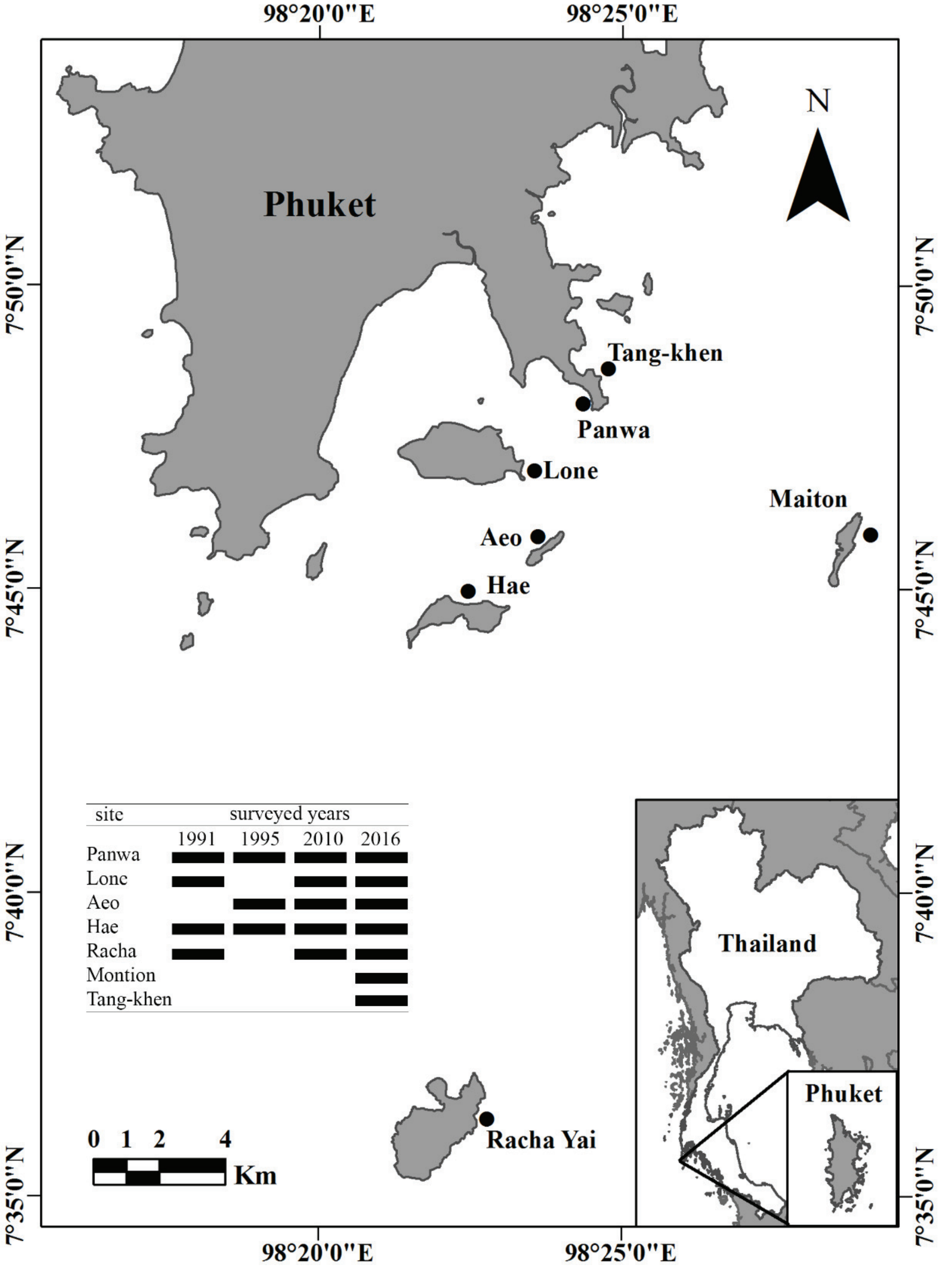
Statistical analyses were performed with the program SPSS 15.00 trial version for Windows. One-way ANOVA was used to test the differences in the bleaching and mortality index (BMI) between sites during the 2016 bleaching event and between colony size categories. Non-parametric Kruskal-Wallis Test were used when the requirements for parametric analyses were not met (Levene's test for homogeneity of variances, $p < 0.05$). A non-parametric Freidman test was used to compare the bleaching susceptibility among years.

(b) Thermal history and stress

Daily mean sea surface temperature (SST) data was derived from the 4km^2 NOAA High Resolution SST AVHRR (1981-2016), provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA (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 (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 an 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).



site	surveyed years			
	1991	1995	2010	2016
Panwa	▬	▬	▬	▬
Lone	▬		▬	▬
Aeo		▬	▬	▬
Hae	▬	▬	▬	▬
Racha	▬		▬	▬
Montion				▬
Tang-khen				▬

Figure 3.3.1 The location of Phuket Island in the Andaman Sea, Thailand (right inset), and positions of bleaching survey sites by belt transect method in 2016. The insert table at the left shows the bleaching surveying sites by line transect method during historical bleaching events in 1991, 1995, and 2010s.

Table 3.3.1 Basic summary statistics for SST at the seven study sites between 16 March and 2 August 2016, when daily SST exceeded the coral bleaching threshold.

Statistics	Panwa	Tang-khen	Lone	Aeo	Hae	Maiton	Racha
Minimum	27.96	28.26	27.57	27.53	27.86	27.37	25.32
Maximum	33.11	32.81	33.01	32.87	32.5	32.81	32.54
Range	5.15	4.55	5.45	5.33	4.64	5.44	7.22
Median	30.56	30.46	30.46	30.14	30.15	30.36	29.99
Mean	30.68	30.59	30.19	30.2	30.35	30.61	30.13
95% CI upper	30.67	30.57	30.17	30.19	30.34	30.6	30.11
95% CI lower	30.7	30.6	30.21	30.22	30.36	30.63	30.14
Std error	0.01	0.01	0.01	0.01	0.01	0.01	0.01
Std deviation	0.85	0.81	0.92	0.92	0.7	0.7	0.79
Variance	0.72	0.66	0.85	0.84	0.49	0.49	0.63

Results and discussion

Several bleaching events have taken place in the Andaman Sea over the last 25 years (Phongsuwan and 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 3.3.2. 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. DHW is a 12-week accumulation of thermal stress, which is quantified using two parameters: a cumulative SST above bleaching threshold and duration (Liu et al., 2006). The Andaman reefs experienced an 8°C-heating week, meaning that they have experienced eight weeks of temperatures 1°C higher than the bleaching threshold, four weeks of temperatures 2°C higher than the bleaching threshold, or other combinations. Such high thermal stress resulted in extensive bleaching across the Andaman Sea and subsequent mass coral mortality (Phongsuwan and 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 temporally (Fig. 3.3.3). Analysis of bleaching and mortality index (BMI) of 12 coral taxa where bleaching impact was recorded across four bleaching events revealed that bleaching susceptibility of corals was significantly different among years (Freidman test = 10.6, df=3, p<0.05), since bleaching susceptibility depends very much on stress intensity (DHW). To focus on bleaching tolerance increasing (or not), and regardless of the effect of different degrees of DHWs, BMI therefore was considered between taxa for each year. The more bleaching tolerant corals in 2016 with relatively low BMI were *Acropora*, *D. heliopora, Echinopora*, *Goniopora, Montipora*, and *Pocillopora damicornis*. Most of them displayed moderate or low bleaching tolerance in the past (Table 3.3.2), except *Diploastrea heliopora*, which has had high bleaching tolerance over the years. Moreover, *P. damicornis* appeared to be bleaching resistant across all sizes from juveniles (<5cm) to adults (>30cm) (n=386), with 92-99% of assigned size classes exhibiting no bleaching. No significant differences were found in BMI among colony size categories of *P. damicornis* (Kruskal-Wallis test, df = 3, p>0.05). Corals that exhibited moderate bleaching tolerance in 2016 included *Coeloseris*, *Ctenactis*, *Favites*, *Leptastrea*, *Pachyseris*, *Pavona*, massive *Porites*, *Psammocora*, and *Symphyllia.* Other thirteen taxa had low tolerance to bleaching, namely *Cyphastrea*, *Dipsastraea* (formerly known as *Favia*), *Fungia*, *Galaxea*, *Goniastrea*, *Herpolitha*, *Hydnophora*, *Merulina*, *Pectinia*, *Platygyra*, *Podabacia*, *Porites rus*, and *Turbinaria*. Some of these moderate and low bleaching tolerant corals showed higher bleaching tolerance in the past.

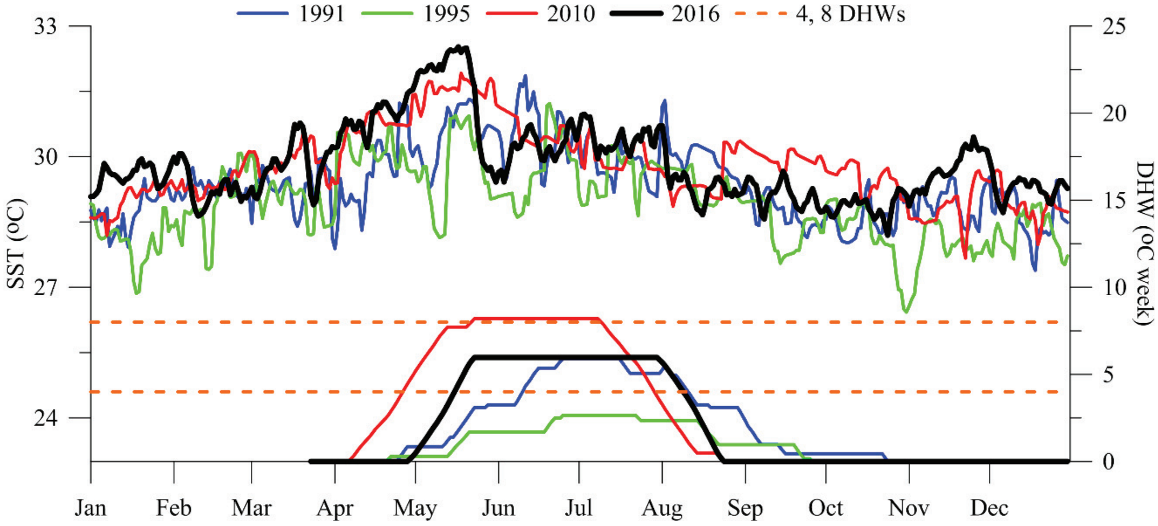
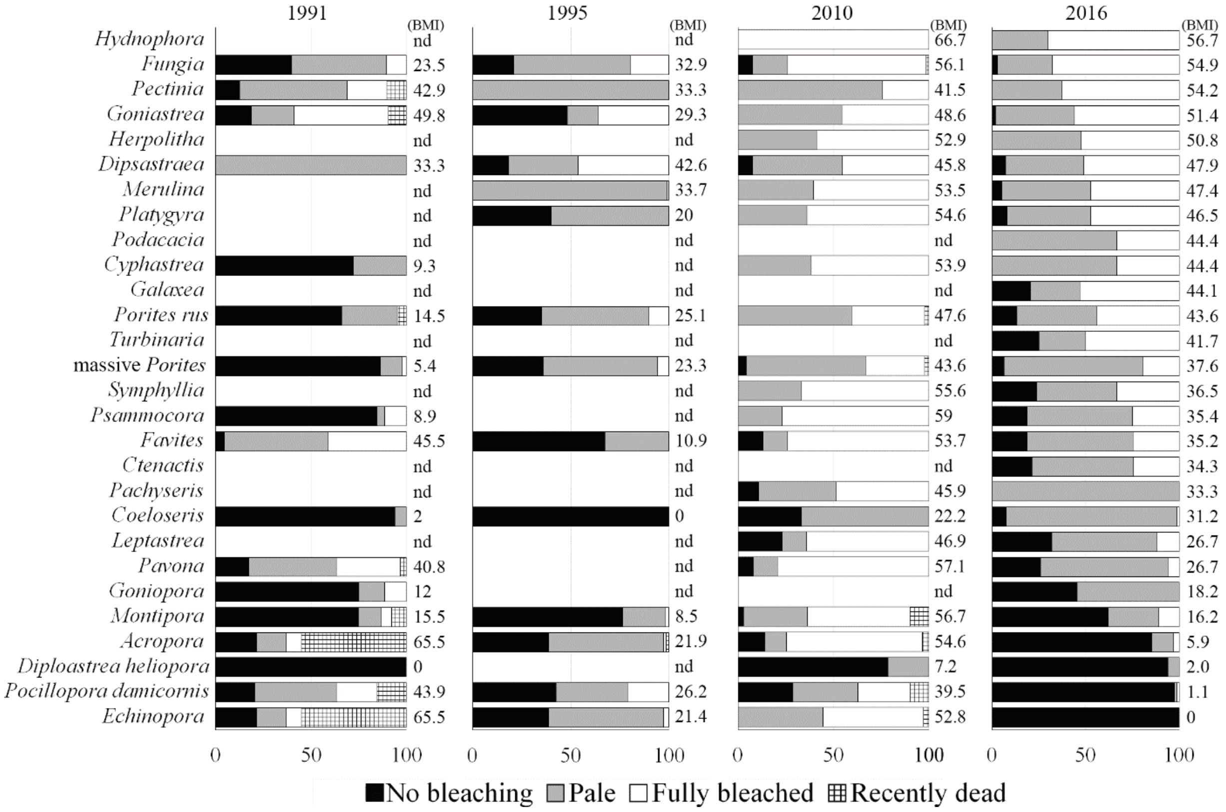


Figure 3.3.2 Daily sea surface temperature and degree heating week (DHW) at Panwa, southern Phuket in bleaching years 1991 (blue), 1995 (green), 2010 (red), and 2016 (black). Orange hatched lines indicate where DHW is 4 and 8°C-weeks which results in widespread bleaching and subsequent mortality, respectively.

Some coral displayed a decrease in bleaching tolerance, for example, *Coeloseris, Cyphastrea*, massive *Porites*, *Pectinia* and *Porites rus*. A reason behind increasing bleaching susceptibility may involve colony size as is the case with *Coelastrea aspera* (formerly known as *Goniastrea aspera*), *Pocillopora* spp., *Colpophyllia natans*, *Montastraea faveolata*, *and Siderastrea siderea* (Brandt, 2009; Pratchett et al., 2013; Brown et al., 2014). On the other hand, it appears that the severity of bleaching in other coral species was more pronounced in smaller colonies such as *Porites* (Bena and van Woesik, 2004; Pratchett et al., 2013), or independent of colony size as in *Platygyra daedalea*, *Acropora*, *Pocillopora damicornis*, and *Porites* (Baird and Marshall, 2002; Ortiz et al., 2009; Pratchett et al., 2013). Moreover, those patterns can differ between places (Vargas-Ángel et al., 2011; Pratchett et al., 2013; this study). For example, *Acropora* populations from the neighboring coral islets of the US Phoenix Islands exhibited different bleaching responses; with bleaching extent greater in smaller colonies of *Acropora* at Baker, while the opposite was observed at Howland (Vargas-Ángel et al., 2011). These various patterns may indicate that demographic change in term of colony size–frequency distributions alone may not able to fully explain the change in bleaching susceptibility of corals.

Some corals, in contrast, showed an increase in bleaching tolerance, namely *Acropora*, *Echinopora*, *Montipora*, *and P. damicornis*. They are commonly considered to be some of the most bleaching sensitive taxa (Marshall and Baird, 2000; McClanahan, 2004; Furby et al., 2013), and suffered extensive mortality at the study sites after the 2010 bleaching event (Fig. 3.3.2). Results suggest that these coral taxa were more resistant to bleaching in 2016 than other taxa ordinarily considered more bleaching-resistant (Fig. 3.3.4). 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., 2008a). 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 changes in the symbiotic associations with coral hosts (Baker, 2003; Baird et al., 2007), 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., 2012b) and previous environmental experience (Brown et al., 2002a).

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 and Chansang, 2012). Lower bleaching susceptibility in some taxa may have been the result of acclimatization as reported by Maynard et al. (2008a), 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 and 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.



Taxon	1991 (BMI)	1995 (BMI)	2010 (BMI)	2016 (BMI)
Hydnophora	nd	nd	66.7	56.7
Fungia	23.5	32.9	56.1	54.9
Pectinia	42.9	33.3	41.5	54.2
Goniastrea	49.8	29.3	48.6	51.4
Herpolitha	nd	nd	52.9	50.8
Dipsastraea	33.3	42.6	45.8	47.9
Merulina	nd	33.7	53.5	47.4
Platygyra	nd	20	54.6	46.5
Podacacia	nd	nd	nd	44.4
Cyphastrea	9.3	nd	53.9	44.4
Galaxea	nd	nd	nd	44.1
Porites rus	14.5	25.1	47.6	43.6
Turbinaria	nd	nd	nd	41.7
massive Porites	5.4	23.3	43.6	37.6
Symphyllia	nd	nd	55.6	36.5
Psammocora	8.9	nd	59	35.4
Favites	45.5	10.9	53.7	35.2
Ctenactis	nd	nd	nd	34.3
Pachyseris	nd	nd	45.9	33.3
Coeloseris	2	0	22.2	31.2
Leptastrea	nd	nd	46.9	26.7
Pavona	40.8	nd	57.1	26.7
Goniopora	12	nd	nd	18.2
Montipora	15.5	8.5	56.7	16.2
Acropora	65.5	21.9	54.6	5.9
Diploastrea heliopora	0	nd	7.2	2.0
Pocillopora damicornis	43.9	26.2	39.5	1.1
Echinopora	65.5	21.4	52.8	0

Figure 3.3.3 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 (hatched). 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.

Table 3.3.2 Bleaching susceptibility level: low, moderate, and high, classified by relative bleaching and mortality index (BMI) for each bleaching years separately.

Susceptibility Level	1991	1995	2010	2016
Low	*Coeloseris* *Cyphastrea* *D. heliopora* *Goniopora* *Montipora* massive *Porites* *P. rus* *Psammocora*	*Coeloseris* *Favites* *Montipora*	*Coeloseris* *D. heliopora*	*Acropora* *D. heliopora* *Echinopora* *Goniopora* *Montipora* *P. damicornis*
Moderate	*Dipsastraea* *Fungia* *Pavona* *Pectinia*	*Acropora* *Echinopora* *Platygyra* *P. damicornis* massive *Porites* *P. rus*	*Pectinia* *P. damicornis* massive *Porites*	*Coeloseris* *Ctenactis* *Favites* *Leptastrea* *Pachyseris* *Pavona* massive *Porites* *Psammocora* *Symphyllia*
High	*Acropora* *Echinopora* *Favites* *Goniastrea* *P. damicornis*	*Dipsastraea* *Fungia* *Goniastrea* *Merulina* *Pectinia*	*Acropora* *Cyphastrea* *Echinopora* *Dipsastraea* *Favites* *Fungia* *Goniastrea* *Herpolitha* *Hydnophora* *Leptastrea* *Merulina* *Montipora* *Pachyseris* *Pavona* *Platygyra* *Porites rus* *Psammocora* *Symphyllia*	*Cyphastrea* *Dipsastraea* *Fungia* *Galaxea* *Goniastrea* *Herpolitha* *Hydnophora* *Merulina* *Pectinia* *Platygyra* *Podabacia* *P. rus* *Turbinaria*

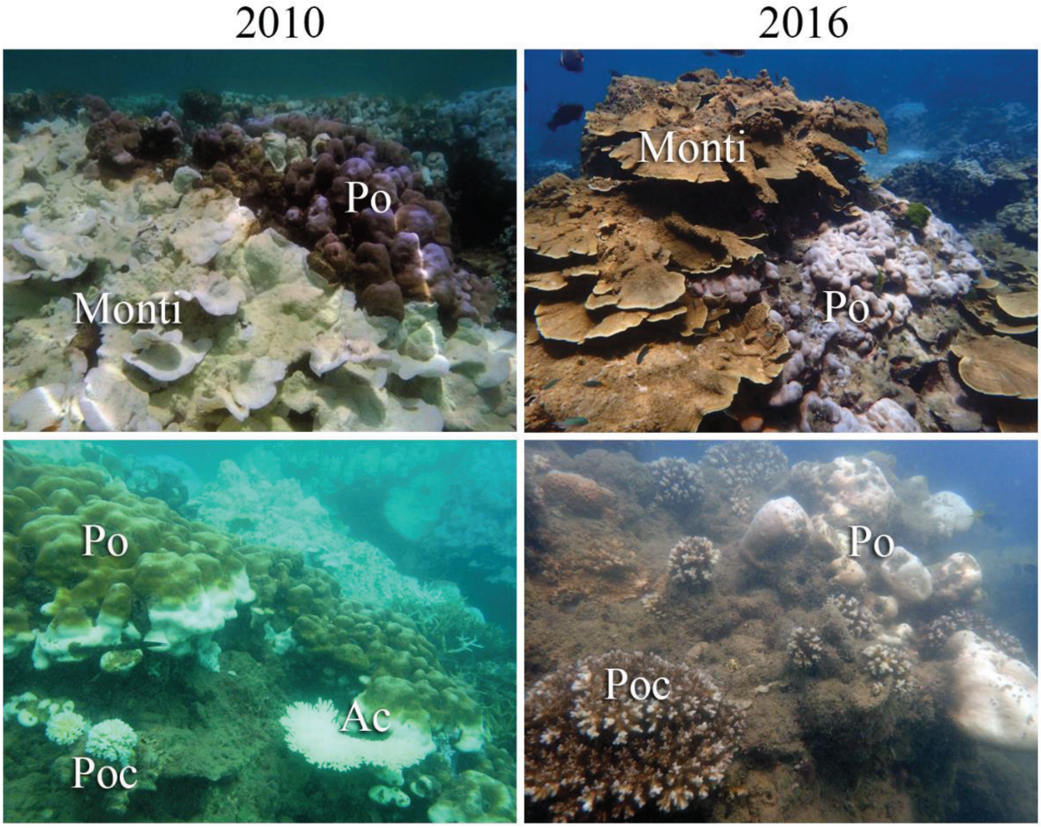


Figure 3.3.4 Coral bleaching responses to increased temperature. In 2010 (right panel), highly bleached *Montipora* (Monti), *P. damicornis* (Poc), and *Acropora* (Ac) adjacent to pale and partial bleached colonies of *Porites*. The opposite was observed in 2016 (left panel): *Porites* (Po) were bleached, while *Montipora* (Monti) and *P. damicornis* (Poc) appear unaffected.

Observed changes in bleaching susceptibility may relate to coral life history traits and evolutionary potential (Darling et al., 2012; Madin et al., 2016). Species with 'competitive' life history traits such as *Acropora* and *Montipora* 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 (Richmond, 1987; Jerker, 2002; 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., 2010a). *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., 2010a). The eroding tolerance 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. This can highlight the role of other resistance factors in determining the improving the thermal tolerance.

Besides hosting tolerant symbionts, change in symbiont community composition (symbiont shuffling) is also a possible function increasing bleaching tolerance in corals. *Acropora millepora*, for example, changed the dominant symbiont from sensitive symbiont (type C) to tolerant (type D) during the 2006 bleaching event in the southern Great Barrier Reef (Jones et al., 2008). Symbiont communities were also found to fluctuate seasonally, which related to temperature conditions, and also shift from a single type to multi types (Chen et al., 2005). However, symbiont shuffling may occur in only some cases. Several corals species resist to environmental stress without changes in symbiont composition (Stat et al., 2009a; Bellantuono et al., 2012b). Recently the study on *Symbiodinium* diversity in *P. damicornis* and *Acropora* spp. distributing over large spatial scales (15° of latitude) in western Australia found that the composition of symbionts is quite stable and commonly dominated by a single type of *Symbiodinium* (McGinley et al., 2012; Thomas et al., 2014). Thus, symbiont shuffling may be limited by host-symbiont specificity.

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

Acknowledgements

We thank Prof. Barbara Brown and Dr. James Guest for helpful comments on the manuscript. We would like to thank reviewers for the insightful comments on the paper, as these comments led us to an improvement of the work.

Supplementary data is given in Appendix 3

3.4 Manuscript IV

The reef coral *Goniastrea aspera*: a 'winner' becomes a 'loser' during a severe bleaching event in Thailand.

BE Brown[1], RP Dunne[2], N Phongsuwan[3], **L Putchim[3]** & JM Hawkridge[4]

[1] School of Biology, University of Newcastle
Newcastle upon Tyne NE1 7RU, UK

[2] West Briscoe, Baldersdale, Barnard Castle, Co. Durham DL12 9UP, UK

[3] Phuket Marine Biological Center, Phuket, Thailand
51 Sakdidet Road, 83000 Phuket, Thailand

[4] Joint Nature Conservation Committee
Monkstone House, City Road, Peterborough PE1 1JY, UK

Brown BE, Dunne RP, Phongsuwan N, **Putchim L**, and Hawkridge JM. 2014. The reef coral *Goniastreaaspera*: a 'winner' becomes a 'loser' during a severe bleaching event in Thailand. Coral Reefs 33:395-401. Doi:10.1007/s00338-013-1120-3

Abstract

The reef coral *Goniastreaaspera* is regarded as one of the most environmentally tolerant species on Indo-Pacific reefs. Its demise, following a severe bleaching event in the Andaman Sea in the north-eastern Indian Ocean in 2010, was surprising in view of the rapid recovery of co-existing species such as *Porites lutea*. Demographic studies of *G. aspera* at this site showed the population was mainly composed of large individuals, which recruited in the early 1990s. These results, and size-specific mortality observed in *G. aspera*, post-bleaching, suggest that factors, related to size and age, may have contributed to the coral's marked decline.

Introduction

The reef coral, *Goniastrea aspera*, is known to be a physiologically robust species living in intertidal, marginal conditions (Kai and Sakai, 2008; Hennige et al., 2010). Veron (1986) describes the genus as being ‘encountered frequently in places where no coral might be expected to live’. In shallow intertidal settings, such as those at the study site at Phuket, Thailand, *Goniastrea* colonies are subject to aerial exposure, dessication, intense solar radiation (Brown et al. 1994) and sedimentation (Scoffin et al., 1997). Not surprisingly, this species is well endowed with behavioural and physiological defences such as tissue retraction (Brown et al. 1991), considerable tissue depth (Loya et al., 2001) and up-regulation of stress protein and antioxidant production (Brown et al., 2002c). *Goniastrea aspera* is also one of several massive corals described as ‘winners’ following extreme bleaching at Sesoko Island, Japan in 1998 (Loya et al., 2001). Here, *G. aspera* increased in abundance by almost threefold between 1997 and 1999 as a result of reduced susceptibility to bleaching-induced mortality and proved itself a ‘long term winner’ with continued high cover 10 yrs later (van Woesik et al., 2011). Colonies of *G. aspera* at Sesoko Island and Phuket are aerially exposed on low spring tides throughout the year with corals at Sesoko above water around noon on spring tides in spring and summer and midnight in autumn and winter (Sakai, pers. comm.). Colonies at Phuket are exposed before or just after dawn and from late afternoon onwards but never at midday. At Phuket, *G. aspera* is abundant on intertidal reefs (Brown et al., 1994), but following severe regional bleaching in 2010, which affected Sumatra and Singapore (Guest et al., 2012); Western Australia (Depczynski et al., 2013); Andaman Sea (Phongsuwan and Chansang, 2012); and the Gulf of Thailand (Sutthacheep et al., 2012), it followed a very different fate to counterparts in Japan (Phongsuwan and Chansang, 2012). Thus, at Phuket there was a major mortality with all colonies tagged during early stages of bleaching showing 100 % mortality 11 months later (Phongsuwan and Chansang, 2012). The species was also more seriously affected by bleaching than co-existing *Porites* spp., *Platygyra* spp. and *Goniastrea favulus* raising questions about its recognised environmental tolerances. In this paper, we investigate the coral’s abundance and demography and the relative susceptibility of juveniles and adults to bleaching-induced mortality.

Materials and Methods

(a) Study site

Study sites are situated in the Andaman Sea around the south-east of Phuket, Thailand (Fig. 3.4.1). They have been described in detail in previous publications (Scoffin et al., 1992; Brown et al., 2011), and in the present study, the focus of attention was the inner reef flat dominated by *G. aspera* and *Porites lutea*.

During the 1980s, a tin ore washing plant operated at site A and the resultant concentrated effluent, rich in heavy metals, was allowed to flow onto the reef during aerial exposure at low tide. Run-off to the sea occurred across the inner reef flat and few corals occupied this area. In the late eighties, the ore washing operation became intermittent and ceased in 1990. By 1994, young *G. aspera* colonies were abundant in this area, averaging ~10 colonies per m^2 in 1997 (Fig. 3.4.2a). This species subsequently became an important coloniser of the inner reef flat (Fig. 3.4.2b–d), together with *P. lutea*.

(b) Coral abundance

Reef flats at three sites (A, B and C) have been monitored either annually or every 2 yrs since 2000. At all sites, 10-m-long transects have been run parallel to the shore and spaced at 10 m distance from each other along a line perpendicular to the shoreline, from the inner shore to the outer reef. At site A, five permanently marked belt transects (10 m X 2 m) have also been photographed 1–3 times a year over time (Brown et al., 2011). In the present study, only the first four 10 m transects at each site were monitored for live coral cover of *G. aspera* and *Porites lutea* between 2000 and 2012 because beyond this distance from the shore abundance of *G. aspera* declines sharply.

(c) Coral colony demography

In 1996, following successful settlement of larvae and subsequent juvenile survival in the early 1990s, size-frequency measurements were made on all colonies of *G. aspera* in seventeen 5 X 5 m quadrats on the inner reef flat at site A (Hawkridge, 1998). The position of these quadrats was recorded for subsequent relocation. In 2010, one of these quadrats, where colonies were previously particularly abundant (n = 237 in 1996), was located and colony size measurements repeated (n = 312 in 2010). Colonies of *G. aspera* are nearly hemispherical so a range of sizes were measured using a mean radius from the maximum colony diameter and the corresponding diameter at right angles to this dimension.

(d) Size-specific responses of G. aspera colonies to bleaching

Following the 2010 bleaching, the fate of *G. aspera* was monitored by visually recording the percentage of colonies in different size classes that showed no partial mortality; <30 % partial mortality; 30–49 % partial mortality; 50–99 % partial mortality and 100 % mortality within three randomly placed 5 × 5 m quadrats on the inner reef flat at site A (total number of colonies = 237). Colony size was again recorded using the mean radius measure as for colony demography. These estimates were carried out 24 months after initial bleaching since massive corals showed considerable delayed bleaching-induced mortality post-2010 (Brown and Phongsuwan, 2012). During this period tagged, *Goniastrea* colonies were monitored for disease and other factors that could have caused subsequent mortality, and it was concluded that the extended bleaching state (>6 months) led to partial or total colony mortality.

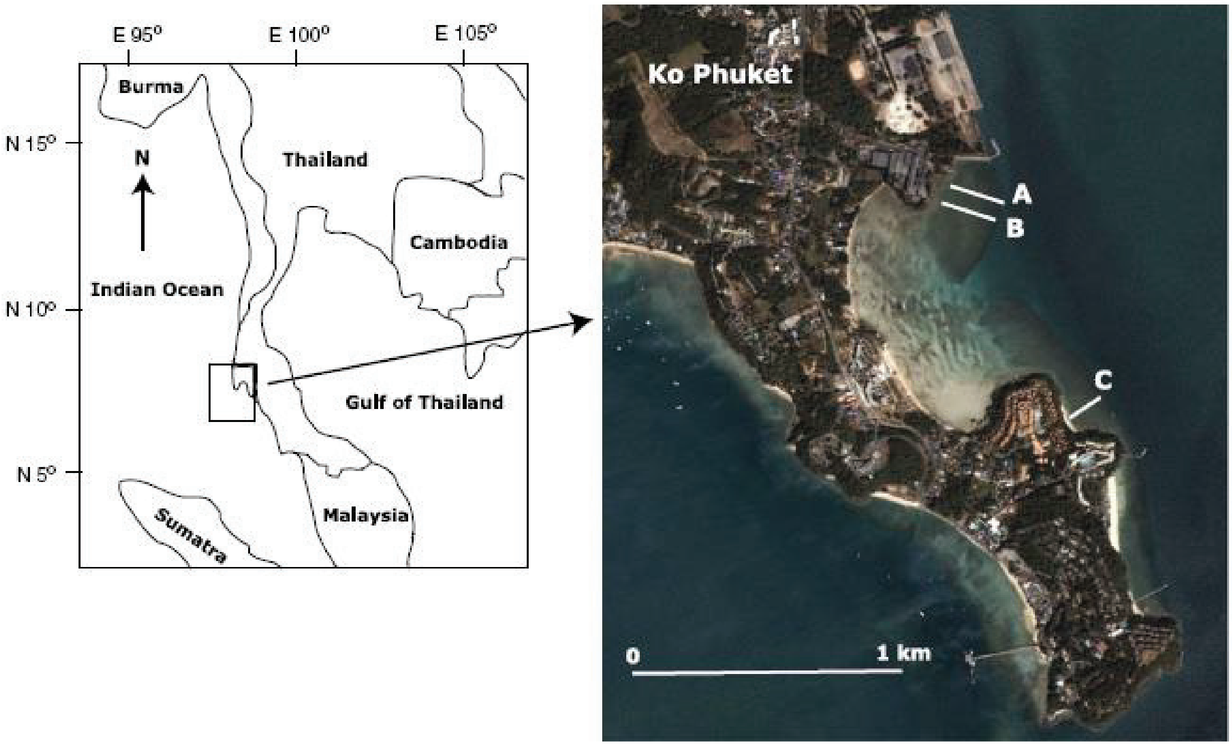


Figure 3.4.1 Map showing location of Phuket Island on the Thai/Malaysia peninsula and satellite image showing location of sites A, B and C on SE tip of island

Figure 3.4.2 Temporal changes in appearance of *G. aspera* colonies at site A. **a** 1997 **b** 2005 **c** 2010 during bleaching **d** 2011 showing bleaching-induced mortality of colonies now covered in sediment

Results and discussion

Measurement of *G. aspera* and *P. lutea* cover from 2000 to 2012 showed that both species co-existed on the inner reef flat at sites A, B and C until 2011 when *G. aspera* was no longer recorded (Fig. 3.4.3). A very limited recovery of this species was noted in 2012 at sites A and B but not at site C, whereas cover of *P. lutea*, showed marked recovery. Inspection of photo-transects at site A between May 2010 and November 2011 revealed the fate of a typical *G. aspera* colony at the same height on the reef flat as *P. lutea* (Fig. 3.4.4). In this section of the photo-transect, both species had paled by early May 2010; by June 2010 both species were stark white though some *P. lutea* colonies retained colour; by August 2010 *G. aspera* remained white though *P. lutea* regained normal colouration. By March 2011, *G. aspera* was dead whilst surrounding *P. lutea* colonies, now normally coloured, were either alive or showing limited partial mortality. This sequence of events was representative of the fate of these two species across the inner reef flat as confirmed by examination of other photo-transects (data not shown) and percentage cover data (Fig. 3.4.3). The greater overall recovery post-bleaching of *P. lutea* compared with *G. aspera* is likely associated with the lower relief of colonies of the former on the reef flat (Scoffin et al., 1997) and resultant mitigation of stresses associated with aerial exposure.

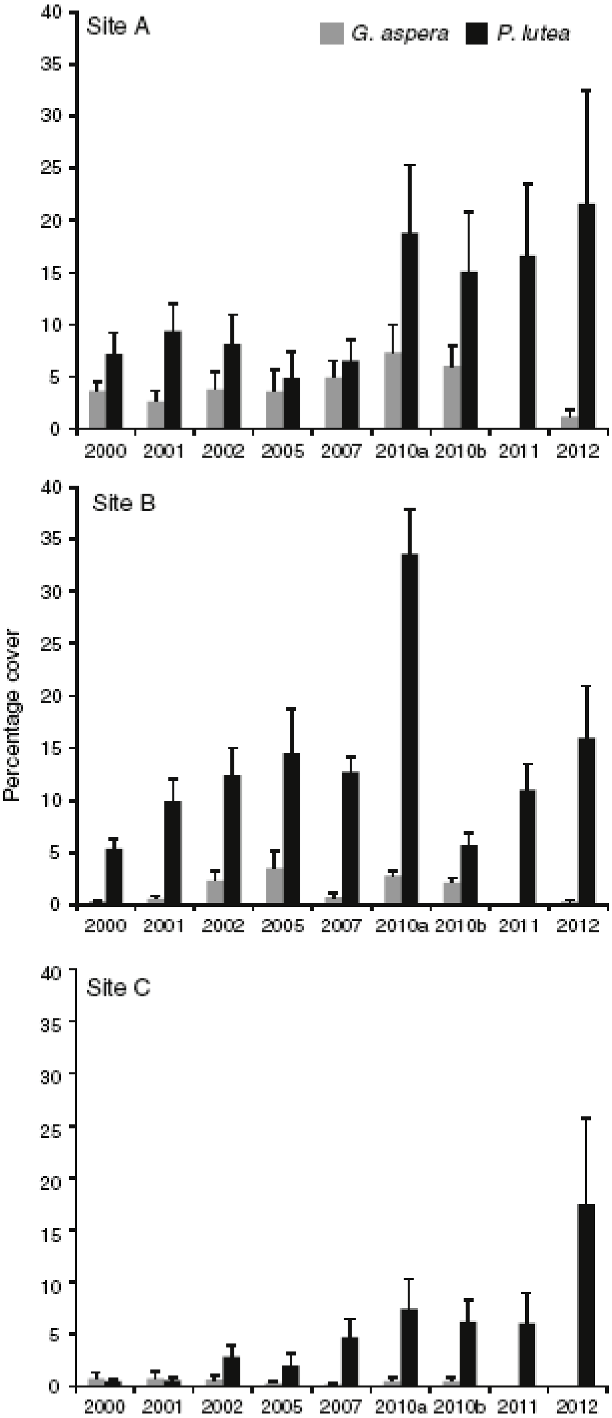


Figure 3.4.3 Mean percentage cover (±SE) of *G. aspera* and *P. lutea* on monitored transects from 2000 to 2012. 2010a = April pre-bleaching and 2010b = June post-bleaching

The size-frequency distribution of *G. aspera* colonies at site A in 2010, prior to bleaching, was very different from that in 1996 (Fig. 3.4.5), being composed mainly of large and old individuals. In 1996, the mean radius of colonies was 34.4 mm compared with 97.1 mm in 2010. The 1996 *G. aspera* population, which was dominated by young colonies, had grown into larger individuals which dominated the population in 2010. The majority of these large colonies had a micro-atoll like form (Fig. 3.4.2c). Successful recruitment of juveniles was limited and not on the scale of that noted in the early 1990s.

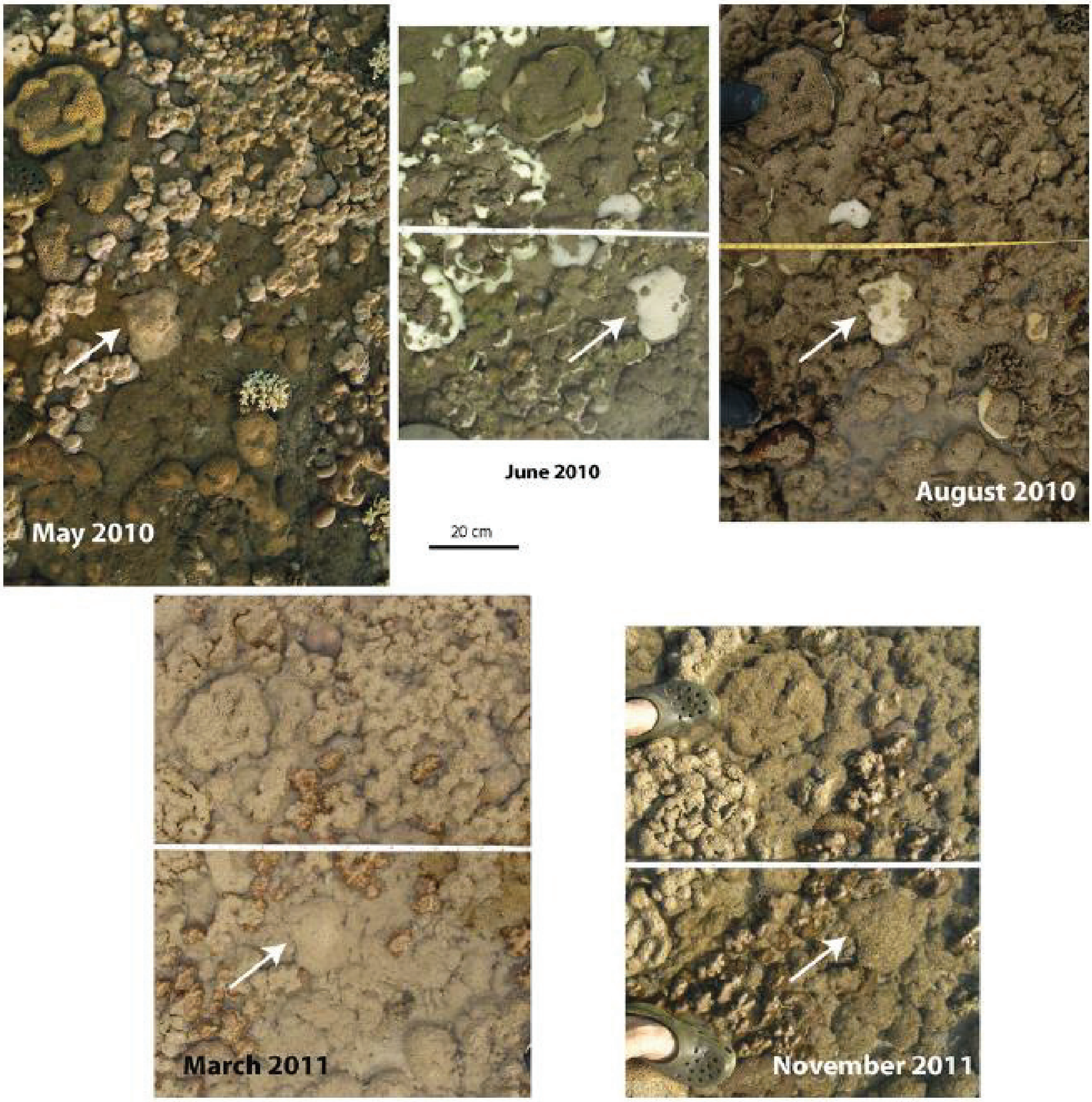


Figure 3.4.4 Sequence of photographs from permanent photo-transects at site A showing demise of *G. aspera* and recovery of *P. lutea* post bleaching by following *G. aspera* colony (arrowed) and surrounding nodular *P. lutea* colonies to the lower left and upper right of *G. aspera* colony, from May 2010 to November 2011

Mortality in *G. aspera*, following bleaching, was size specific (Fig. 3.4.6) with the majority of colonies less than 40 mm in radius showing no mortality whilst all colonies with a radius of between 60 and 100 mm showed partial mortality. In many cases, colonies in this size range displayed 50–99 % mortality. The majority of colonies between 101 and 140 mm radius displayed 50–99 % mortality, whereas over 25 % of the largest colonies (121–140 mm radius) were completely dead.

Interpretation of size-related mortality (Fig. 3.4.6) should, however, take account of partial mortality caused by factors other than thermally induced bleaching. When hemispherical *G. aspera* colonies reach a size of ~40 mm radius, they become susceptible to solar lesions and subsequent partial mortality (Brown et al., 1994; Scoffin et al., 1997). As colonies continue to grow upwards, they suffer further mortality from desiccation on aerial exposure and also sedimentation (Scoffin et al., 1997). Such effects are evident in Fig. 3.4.2c where larger colonies display a microatoll like form. It is estimated that colonies within the largest size classes (100–160 mm radius) are subject to 30–50 % partial mortality from these effects alone (Brown et al., 1994; Scoffin et al., 1997); such colonies being estimated to be ~15–20 yr old based on alizarin staining and X-radiography of skeletons (Hawkridge, 1998). However, regardless of prior partial mortality, the effects of colony size on bleaching-induced mortality were clear with the survival of the smallest colonies, and the complete or almost complete mortality of the largest size classes examined.

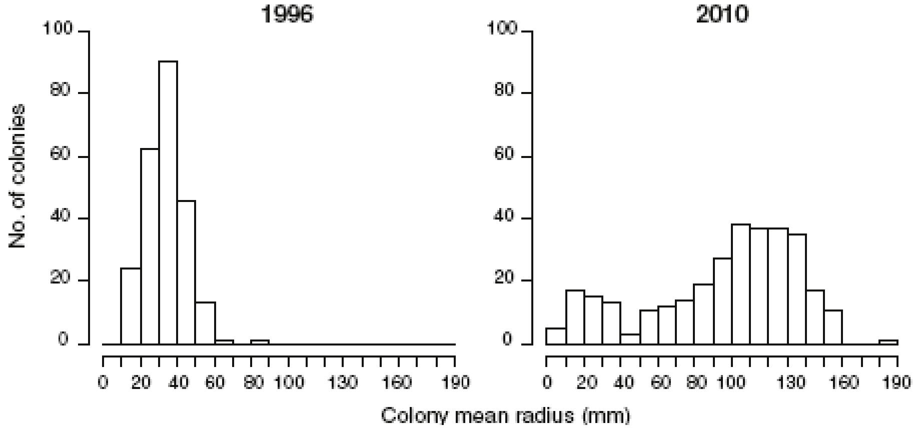


Figure 3.4.5 Size distribution plots for *G. aspera* colonies at site A in 1996 and 2010

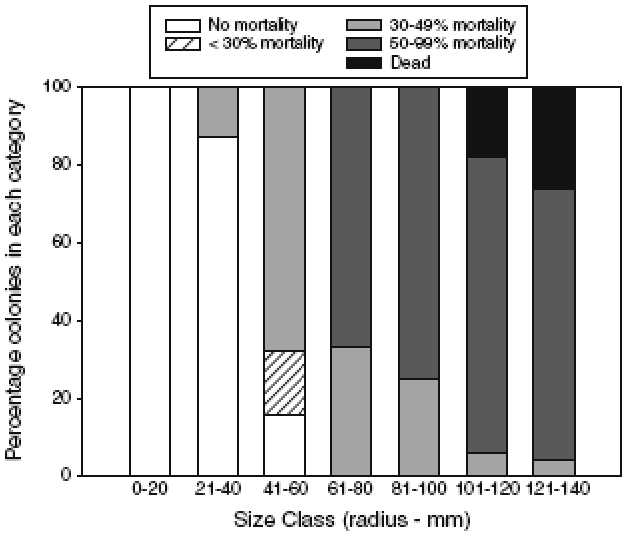


Figure 3.4.6 Size-specific mortality of *G. aspera* following bleaching in 2010

Greater susceptibility of large, adult corals to bleaching induced mortality, compared with juveniles, has been widely reported in the literature (Hoeksema, 1991; Edwards et al., 2001; Loya et al., 2001; Brandt, 2009; Phongsuwan and Chansang, 2012; Depczynski et al., 2013). Explanations for superior survival of branching juvenile corals and fungiids have included shading effects in cryptic habitats occupied by recently settled corals (Hoeksema, 1991; Mumby, 1999). However, *G. aspera* colonies surviving at site A measured up to ~40 mm radius and were not found in shaded habitats but on open reef surfaces.

Improved water flow rates (Nakamura and van Woesik, 2001) have also been invoked as an explanation for superior survival of small branching corals. In terms of water flow, the smooth contours of hemispherical massive corals such as *G. aspera* would not increase frictional drag and mass transfer potential in the same way as that described for branching corals (Nakamura and van Woesik, 2001) with massive corals having a higher mass transfer rate than branching species (van Woesik et al., 2012). In the field, spatial flow patterns at the colony level on a shallow reef flat, composed of hemispherical colonies, are extremely complex and where colonies are densely spaced, as at site A, inertial forces can significantly reduce the amplitude variations between colonies with higher water flows around larger colonies cf. smaller ones (Hench and Rosman, 2013; Hench, per. comm.).

Given that the population of *G. aspera* at site A was dominated by large (and old) individuals prior to 2010, which were the result of very successful recruitment in the early 1990s, it is pertinent to ask what role senescence might have played in their decline. Theoretically colonial animals, such as most corals, are non-ageing and potentially immortal at the level of the asexual lineage (Hughes and Jackson, 1980). Other studies, however, suggest that corals may not escape ageing as reflected in decreased reproduction (Rinkevich and Loya, 1986), reduced regeneration potential (Meesters and Bak, 1995) and reduced growth rate (Rinkevich and Loya, 1986; Elahi and Edmunds, 2007) whilst more recently Sköld et al. (2011) provided the first evidence of long-term senescence in asexual lineages in a colonial metazoan, the ascidian *Diplosoma listerianum*.

In this comprehensive paper on coral demography (Babcock, 1991) recognised that environmental constraints on large colonies of *G. aspera* may be equivalent in their demographic consequences to a period of 'senescence', there being little evidence at the time of any physiological senescence in corals. With recent evidence of the latter, it is possible that senescence and energetic constraints in large colonies of *G. aspera* both played a role in its marked decline at site A following the bleaching. Whether a coral is a 'winner' or a 'loser' after bleaching may well depend on the demography of the species at any particular site, and it is interesting to note that *G. aspera* colonies at Sesoko Island, Japan, were relatively small with a 40–50 mm radius (van Woesik, pers. Comm.). Clearly, more work is needed to address possible senescence in these corals and the effect it may have on the outcomes of bleaching events.

Acknowledgments

We would like to thank the Director and staff of the Phuket Marine Biological Center for their continued support of our work. We are also grateful to the Percy Sladen Fund of the Linnean Society for funding our monitoring of the 2010 bleaching event and the Leverhulme Trust for supporting work on coral senescence.

3.5 Manuscript V

Preliminary studies on the genetic diversity of the coral symbiont *Symbiodinium* spp. in the Thai Andaman Sea and Gulf of Thailand

Lalita Putchim[1], Wirulda Pootakham[2], Thippawan Yoocha[2], and Nalinee Thongtham[1]

[1] *Phuket Marine Biological Center, Phuket, Thailand*
51 Sakdidet Road, 83000 Phuket, Thailand

[2] *National Center for Genetic Engineering and Biotechnology (BIOTEC), National Science and Technology Development Agency, Pathum Thani, Thailand.*

In preparation

Abstract

Thailand has been facing a dramatic decrease in its coral population due to repeated bleaching events. The dinoflagellate genus *Symbiodinium* living in close endosymbiosis within the coral has often been found to play a crucial role in determining the response of the coral holobiont to thermal stress. *Symbiodinium* appears in molecularly highly diverse and various lineages in the coral symbiosis. In the present study we assessed the genetic diversity of the algal symbionts in the massive coral *Porites lutea* at several sites from the Andaman Sea and the Gulf of Thailand, based on the ITS1 and ITS2 sequences analysed using single molecule real-time PacBio sequencing technology. Preliminary results show that the *Symbiodinium* clade composition was similar between different populations with an overall number of 4 clades. The proportions of the symbionts were as follows: C15 (78%), C1 (20%), C17 (2%), and D1a (<1%). These *Symbiodinium* types have been reported to exhibit different heat tolerances. Future studies are needed to confirm the genetic determination of the symbionts in these corals and the effect this may have on the corals´ bleaching response.

Introduction

As a consequence of global climate change, sea surface temperatures (SST) have risen and subsequently coral bleaching is more frequent and severe (Baker et al., 2008; van Hooidonk et al., 2013). Bleaching is a major threat to coral health and more attention has been given to understanding if corals can adapt quickly enough to rapid climate change (Hughes et al., 2017). Physiological acclimatization of zooxanthellae living in the coral host can play a fundamental role in adaptation. The recently proposed Adaptive Bleaching Hypothesis (ABH) is gaining attention from scientists (Buddemeier and Fautin, 1993). A basic explaination of the ABH is that one strategy for corals to adapt to different environmental stress is to change their associated *Symbiodinium* composition. The diversity and flexibility of coral-algae symbiosis occurs over small areas after environmental change (Berkelmans and van Oppen, 2006; Bay et al., 2016). The molecular genetic classification of *Symbiodinium* has divided this genus into eight clades (A-H). All of these clades have different documented tolerances to temperature ranges and other factors of the coral's environment. Hosting different symbiont types can subsequently influence the environmental tolerance of the holobiont (Baker et al., 2004; LaJeunesse et al., 2010a). Indeed, it is clear that even closely related *Symbiodinium* types can differ widely in their physiological responses to environmental conditions or host specificity (Sampayo et al., 2008). For example, Clade D *Symbiodinium* is a diverse group and occurs frequently in coral hosts from the Andaman Sea. It has been observed to occur where temperatures are warmer and water column turbidity is high. One of the critical factors that influence coral response is genetic variation in zooxanthellae clades (Rowan et al. 1997). *Symbiodinium* Clade D appears to be particularly resistant to the precursor conditions for coral bleaching and thus enables the coral host to avoid bleaching stress (LaJeunesse et al., 2007; LaJeunesse et al., 2010b).

Hosting tolerant symbiont types can increase the environmental tolerance of corals (Baker et al., 2004; LaJeunesse et al., 2010a). On the other hand, some coral species have been observed to harbour a single specific type of symbiont and show various environemtal tolerances (Brown et al., 2002a; Zhanga et al., 2011; Wicks et al., 2012; Thomas et al., 2014; Thomas et al., 2017). Moreover, Howells et al. (2012) also showed that the same Symbiodinium type display different heat responses if they have different thermal experiences, i.e. *Symbiodinium* derived from corals that came from warm reefs exhibited higher heat tolerance than those from corals living in lower temperature environments. This highlights the role of other resistance factors and the role of acclimatization in determining the coral's bleaching response.

Survey data suggests that oceanic processes like internal waves may play a role in mitigating bleaching, as bleaching frequency appeared to be lower in areas affected by internal waves (Wall et al., 2015). Another interesting observation from the bleaching surveys was that not all colonies of a given species of coral at a given site bleached, especially the massive coral *Porites lutea*. The recovery of this coral was also remarkable (Putchim et al., in review). Bleching tolerance of *Porites* to elevated sea temperature can can temporally vary. This is likely to relate to genetic adaptation and physiological acclimatization, which are poorly understood in this region. Understanding the genetic distribution of zooxanthellae and their adaptation to a changing marine environment will be an important contribution to predicting the impact of climate change on coral communities in the Andaman Sea

Materials and methods

(a) Coral tissue sampling and processing

Tissue of *Porites lutea* were collected in February 2016 at about 7–12 m depth from 13 sites in the Gulf of Thailand and Andaman Sea (Fig. 3.5.1). The number of sampling colonies is shown in Table 3.5.1. Sampling tissues were collected underwater from visually healthy colonies (dark brown colour) by using scalpel blades and placed in sterile disposable 2-mL screw-capped tubes. Seawater was then removed from each tube and coral tissue samples were preserved in absolute ethanol and stored at −20 °C prior to DNA extraction.

Coral tissue samples were pulverized in liquid nitrogen with sterile mortars and pestles, and genomic DNA was extracted using the High Pure Template PCR Preparation Kit (Roche Life Science, Indianapolis, IN, USA) according to the manufacturer's instruction. DNA was eluted in 50 µL of elution buffer and its quality was assessed on 0.8% agarose gel to ensure that there was no degradation. DNA samples were subsequently quantified using the NanoDrop ND-1000 Spectrophotometer (Termo Fisher Scientific, Waltham, MA, USA) and diluted to 50 ng/µL for PCR amplification. For steps in PCR amplification, please see material and methods in Pootakham et al. (2017).

(b) ITS1 and ITS2 DNA gene amplification, sample barcoding and PacBio sequencing.

The diversity of symbiont with corals from various habitats was analysed using single molecule real-time PacBio sequencing technology (Pacific Biosciences, Menlo Park, CA, USA). ITS 1 and 2 regions were amplified from 50 ng of genomic DNA using the primer 5′ GGG ATC CGT TTC CGT AGG TGA ACC TGC 3′ and 5′ GGG ATC CAT ATG CTT AAG TTC AGC GGG T 3′ (LaJeunesse, 2001). All primers were synthesized and HPLC-purified (according to PacBio's SMRTsequencing recommendation) by Integrated DNA Technology (San Jose, CA, USA).

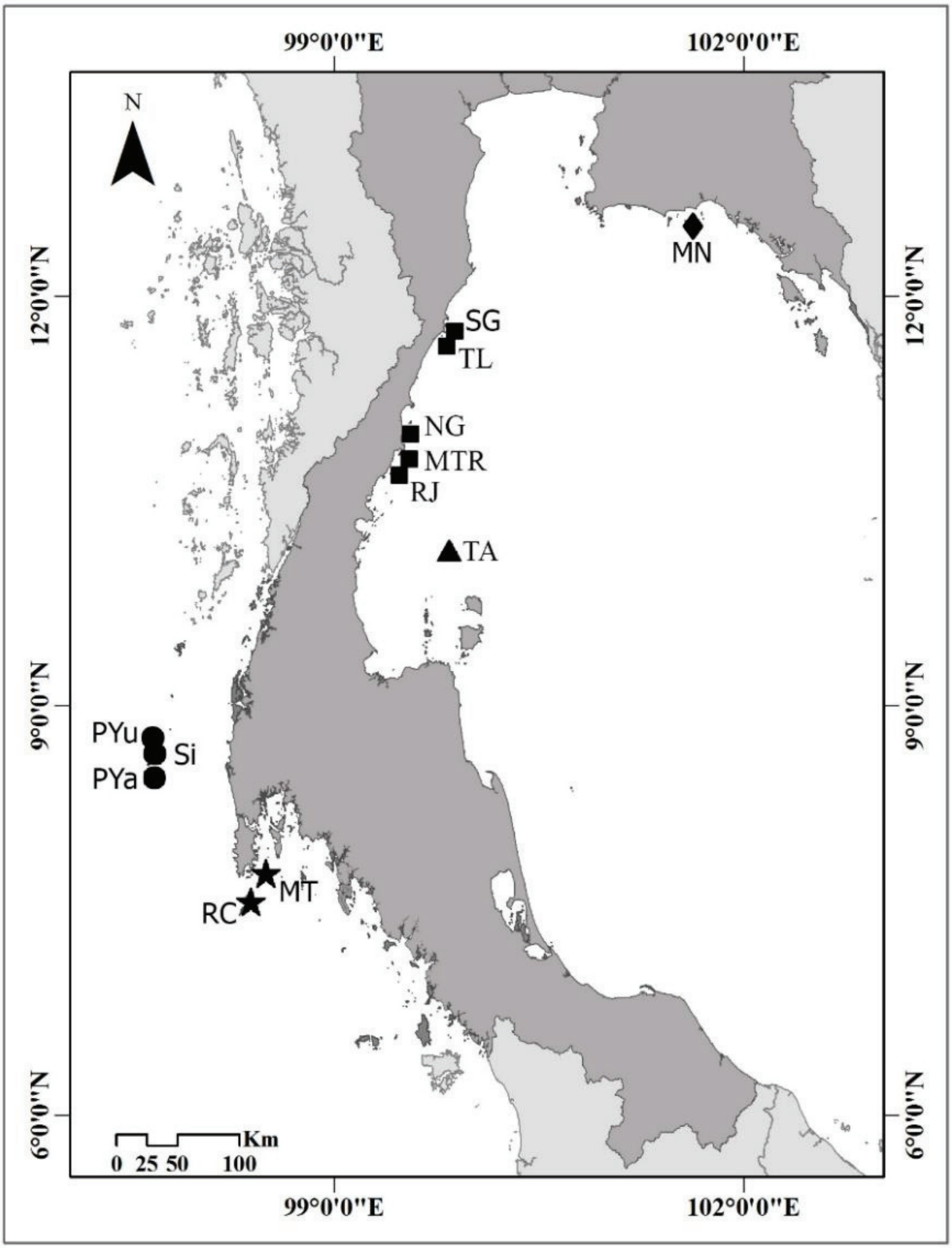


Figure. 3.5.1 Location of sampling sites. The symbols indicate sites in the Phang-Nga province (circles), Phuket (stars), Chumphon province (squares), Suratthani province (Triangle), and Rayong province (diamond). Site names and codes are as shown in Table 3.5.1.

Table 3.5.1 The locations of studied sites, site codes used in this paper, and total number of sampling colonies.

Location	Province	Site	Site code	number of samples
the Andaman Sea	Pang-nga	Similan Island_East	SiE	9
	Pang-nga	Similan Island_West	SiW	10
	Pang-nga	Miang Island	MN	6
	Pang-nga	Payang Island	PYa	10
	Pang-nga	Payu Island	PYu	10
	Pang-nga	Tachai Island	TS	9
	Phuket	Maiton Island	MT	13
	Phuket	Racha Yai Island	RC	27
the Golf of Thailand	Chumphon	Matra Island	MTR	13
	Chumphon	Ngamyai Island	NG	10
	Chumphon	Rangajew Island	RG	12
	Chumphon	Singh Island	SG	9
	Chumphon	Talu Island	TL	10
	Rayoung	Mannai Island	MN	17
	Suratthani	Tao Island	TA	11

Results and discussion detect

Our investigation of 176 healthy *Porites lutea* colonies demonstrated the existence of four *Symbiodinium* types in the samples. These included *Symbiodinium* C15 with approximately 78%, followed by C1 with approximately 20%, and very low percent of C17 (2%) and D1a (<1%). The pattern was similar across 6 study sites from the Andaman Sea and the Gulf of Thailand (Fig. 3.5.2). The predominance of clade C in corals from this region is consistent with previous studies on several different sites in the Indian Ocean, Pacific Ocean, and Arabian Peninsula (Howells et al., 2009; LaJeunesse et al., 2010a; Ziegler et al., 2017a). For *Porites*, it was similar to previous studies which indicated that the Andaman *Porites* are associated mainly with *Symbiodinium* type C15 (LaJeunesse et al., 2010a; Buerger et al., 2015). Four *Symbiodinium* types found in this study are suggested with different heat tolerances (Baker et al., 2004; Deschaseaux et al., 2014; Keshavmurthy et al., 2014). Although *Symbiodinium* type D has been described as relatively more stress tolerant than type C (LaJeunesse et al., 2010b; Yuyama and Higuchi, 2014; Ziegler et al., 2015; Yuyama et al., 2016), *Porites* harbouring D has been found in very limited instances (LaJeunesse et al., 2010a; Yuyama et al., 2016). The thermal resistance of zooxanthellae can also vary among subcladal types (Sampayo et al., 2008). Within *Symbiodinium* type C, for example, type C78 and C8/a were found to be more tolerant to bleaching when compared to types C79 and C35/a (Sampayo et al., 2008), and *Symbiodinium* type C15 is likely to be more resilient to stress conditions compared to other clade C types (LaJeunesse et al., 2003; Fisher et al., 2012). On the other hand, *Porites* is often found to have relatively high resistance to a variety of stressors, although the association is more specific with a *Symbiodinium* type (LaJeunesse et al., 2010a;

Putnam et al., 2012; Buerger et al., 2015). Finer scale studies, therefore, are necessary to understand the variation in bleaching responses of coral species under a given condition.

Since our samples were collected after a serious bleaching event in 2010, it may be tempting to conclude that the presence of clade D1 in these samples rendered them more heat tolerant than other colonies and allowed them to survive elevated water temperatures. However, it is necessary to bear in mind that the methods used to detect *Symbiodinium* clades associated with *P. lutea* in previous studies were based mostly on denaturing gradient gel electrophoresis technique (Stat et al., 2009b; LaJeunesse et al., 2010a; Yang et al., 2012; Keshavmurthy et al., 2017), which had much less sensitivity and resolution in differentiating *Symbiodinium* clades/subclades compared to the PacBio sequencing technology. Studies that examined *Symbiodinium* types using Sanger sequencing also lacked the coverage offered by the PacBio sequencing technique. As the cost of Sanger sequencing was very expensive, the number of sequences investigated in previous work were often in the order of 100-200 per sample, if not fewer. The chances of detecting ITS sequences from clade D members were extremely small since they represented less than 1% of the population. The high resolution output of PacBio sequencing technology allowed us to examine tens of thousands of sequence reads per sample, giving us an opportunity to detect rare members of the dinoflagellate community. Our discovery of clades C1, C17, and D1 members in *P. lutea* samples here should not lead to a conclusion that this particular clade is associated with heat tolerance of the coral holobiont. A well-designed experiment in which the same technique is employed for detection of *Symbiodinium* type is required to demonstrate the association of clade D1 with thermal tolerance in *P. lutea.*

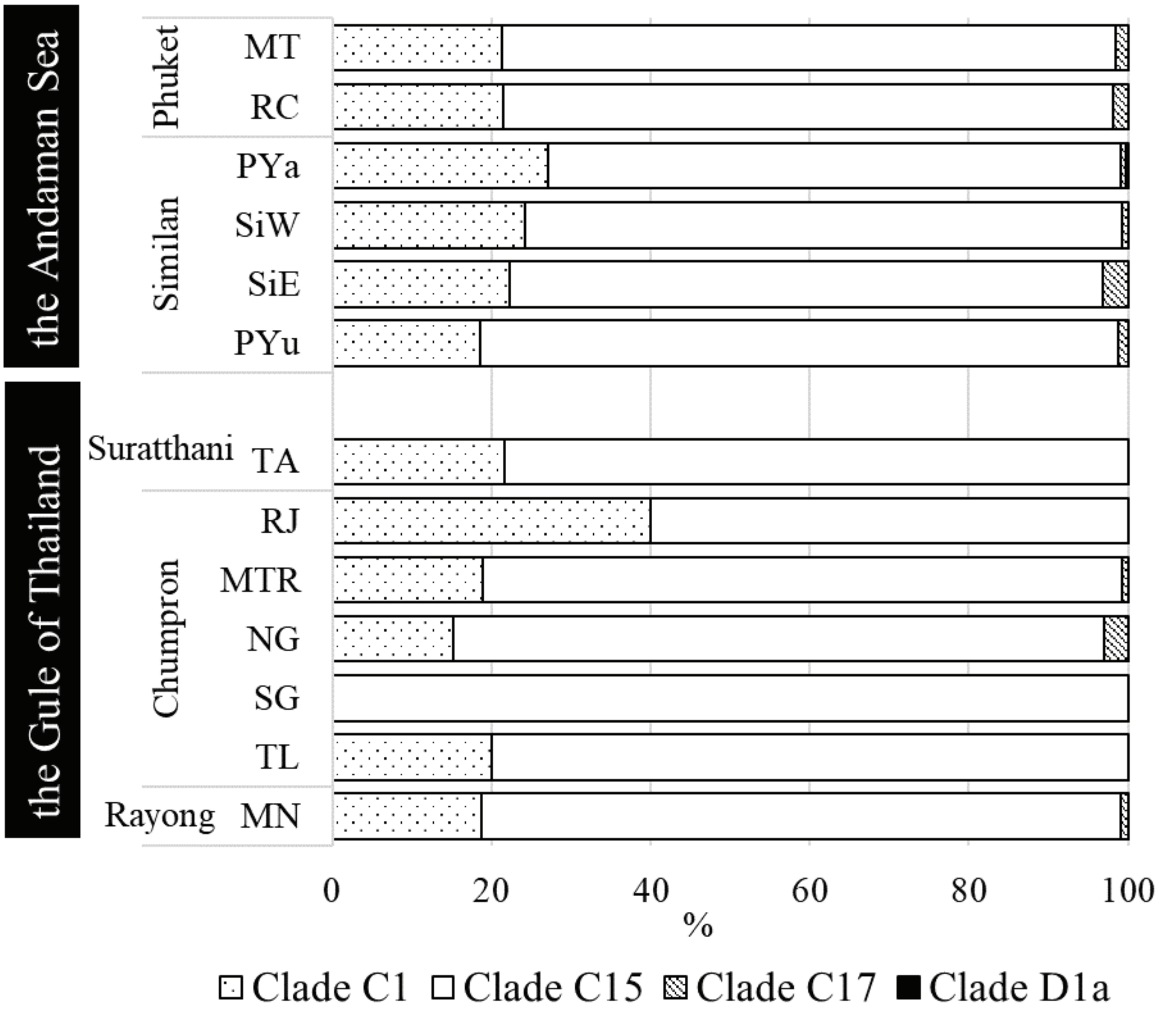


Figure 3.5.2 Relative abundance (%) of *Symbiodinium* in the massive coral *Porites lutea* at the 13 study sites in the Andaman Sea and the Gulf of Thailand.

3.6 Manuscript VI

Taxon-specific differences in re-pigmentation of fully bleached corals after the 2010 mass bleaching event in the Andaman Sea

Putchim L[1,2], Wall M[3], Schmidt GM[1], Phongsuwan N[2] and Richter C[1]

[1] *Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Science, Bentho-Pelagic Processes, Bremerhaven, Germany*

[2] *Phuket Marine Biological Center, Phuket, Thailand*
51 Sakdidet Road, 83000 Phuket, Thailand

[3]*GEOMAR, Helmholtz Center for Ocean Research, Marine Geosystems,*
Wischhofstraße 1-3, 24148 Kiel, Germany

In preparation

Abstract

The bleaching susceptibility and mortality of corals has been thoroughly studied over the last three decades. However, coral recovery patterns are still not well understood and limited to a few species. In May 2010, at the peak of the Andaman Sea coral mass bleaching event, surveys were conducted around the southern Phuket archipelago, Thailand, to (1) assess the bleaching and mortality of corals to elevated sea temperature and (2) monitor the recovery of fully bleached colonies over time. A total of 392 fully bleached corals belonging to 25 taxa were tagged and re-visited in July and September of the same year to record the levels of recovery over a period of five months. Colonies and individuals from 19 taxa survived full bleaching, with various levels of re-pigmentation ranging from <1% to 97% of colony surface area. Massive corals like *Diploastrea heliopora* and three genera of the fungiid family of solitary corals showed the highest re-pigmentation. Six branching and plating coral taxa suffered total mortality after 5 months: *Hydnophora rigida, Pectinia alcicornis, Pocillopora damicornis, Echinopora echinata, Montipora aequituberculata*, and *Porites nigrescens*. Re-pigmentation appeared to be independent of bleaching susceptibility (n=15, r=-0.447, p=0.095) and colony size, but showed a significant correlation with tissue biomass (n=14, r=0.8, p<0.001). Our results suggest recovery from bleaching depends primarily on the availability of energy stores.

Introduction

Climate models predict that the world's oceans could warm by 1-3°C by the end of the 21st century (Collins et al., 2013). The resulting increase in coral bleaching frequency and severity are considered a major threat to coral reefs (Baker et al., 2008; van Hooidonk et al., 2013). Various environmental stressors may account for coral bleaching, and the major impacts throughout the last 30 years were due to elevated seawater temperature and light. Bleaching occurs when water temperatures exceed thermal thresholds for prolonged periods, causing corals to expel their *Symbiodinium* microalgal symbionts. As a result, corals pale and may eventually turn 100% white. While there has been intense research on the bleaching susceptibilities of different coral species (Marshall and Baird, 2000; Bruno et al., 2001; Brandt, 2009; Williams et al., 2010; Guest et al., 2012; Furby et al., 2013; Pratchett et al., 2013), only a few observations are available regarding the fate of bleached coral colonies in the aftermath of a bleaching event.

Since *Symbiodinium* are vital to corals' energy supply, extended bleaching following severe thermal stress may lead to coral mortality. A positive correlation between bleaching and mortality has never been observed (McClanahan, 2004). There are many field observations documenting recovery after bleaching events on the coral reef community scale (Kayanne et al., 2002; Golbuu et al., 2007; Gilmour et al., 2013; Pandolfi, 2015), suggesting that recovery is often related to extrinsic factors such as habitat and location. For example, relatively high coral recovery was found in deeper (Golbuu et al., 2007) and remote reef areas (Ceccarelli et al., 2011; Gilmour et al., 2013; Johns et al., 2014).

Studies found that some highly bleached corals were able to recover after a return to normal sea temperatures (Obura, 2005). Different recovery capacities are often linked to intrinsic factors such as colony morphology (Marshall and Baird, 2000; McClanahan, 2004) and colony size (Shenkar et al., 2005; Brandt, 2009; Pratchett et al., 2013; Brown et al., 2014), while recovery is also dependent on bleaching intensity (Baird and Marshall, 2002). These factors are related to the amount of energy stores, which play an important role in their survival (Grottoli et al., 2006; Rodrigues and Grottoli, 2007; Anthony et al., 2009). Photosynthesis, which is typically the principal energy source for many coral species, is very limited under bleaching conditions when their symbionts are significantly decreased. Therefore the survival of corals is dependent on the size of energy stores (Loya et al., 2001; Grottoli et al., 2006), which in turn is related to the amount of tissue biomass (Fitt et al., 1993).

In the Andaman Sea, bleaching events have been recorded many times over the last 30 years with various intensities. The 2010 bleaching event was the most severe bleaching event ever recorded in Thailand (Phongsuwan and Chansang, 2012). Most of the corals were 100% bleached. We took this opportunity to monitor the individual trajectories of fully bleached coral colonies to assess the taxon-specific differences in mortality and recovery. We measured tissue biomass and hypothesized that it is related to the corals' ability to recover. Conservation efforts often target the most common or presumptive "key" species – but not generally the species showing the highest resistance against bleaching. We suggest to target those species (even if they are not common) that show the fastest recovery from severe bleaching as these may be the ones which show the best promise for survival in a warming ocean.

Materials and methods

(a) Response to elevated sea temperature

At the height of the bleaching event in May 2010, bleaching surveys were carried out at 5 reef islands located around southeast Phuket: Panwa peninsula (PW), Aeo Island (AO), Loan Island (LN), Hae Island (HE), and Racha Island (RC) (Fig. 1). In this study, we classified coral to the species level and recorded colony morphology and colony size. A 100 m transect at each site was placed at about 5 m depth. The colony's bleaching status was classified to one of four different categories and their percentage of all colonies assessed: (c_1) fully pigmented or no bleaching, (c_2) pale (loss of colour), (c_3) fully bleached, and (c_4) recently dead as a result of bleaching-induced mortality. A bleaching and mortality index (BMI) was used to assess the response of each coral species to elevated sea temperature. BMI was calculated (McClanahan et al., 2004) according to the weighted average percentage of colonies in the above categories as follows:

$$\mathrm{BMI} = \frac{(0 \times c_1 + 1 \times c_2 + 2 \times c_3 + 3 \times c_4)}{3}$$

(b) Re-pigmentation

All fully bleached coral colonies (> 5 cm diameter) within the first 10m and 1m to each side of each transect (20m^2) were tagged. The tags used were numbered plastic markers that were fixed on the substrate with stainless steel nails next to each colony. A total of 392 fully bleached colonies belonging to 25 taxa were marked (Table 3.6.1). Recovery was estimated by measuring the percentage of re-pigmented colony surface areas. Tagged colonies were re-visited after 2 months (July 17th) and 5 months (September 30th), respectively. Surface area of the above four bleaching categories was estimated *in situ* and documented by scaled photographs.

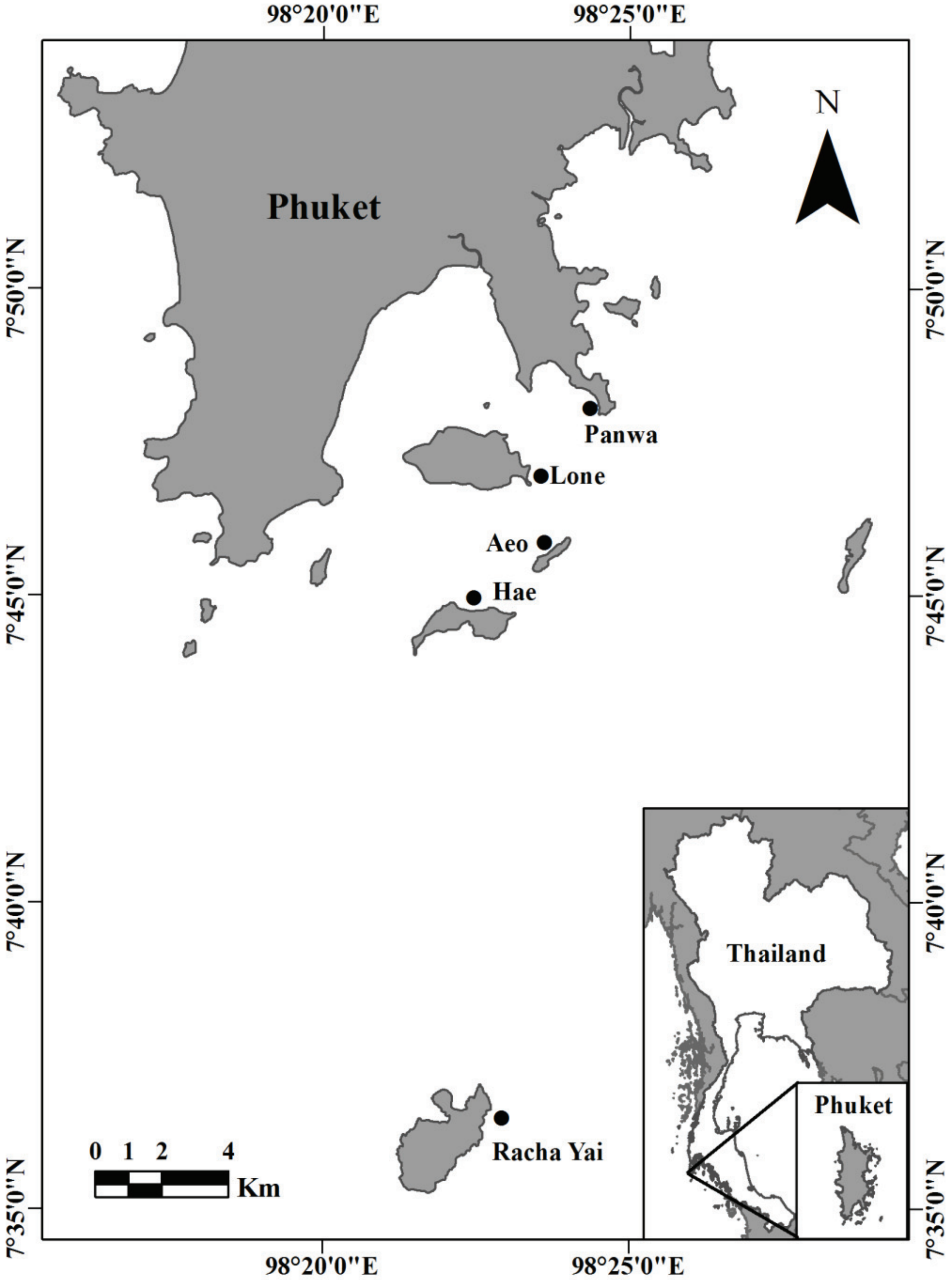


Figure 3.6.1. The location of Phuket Island in the Andaman Sea, Thailand (insert), and positions of five study sites: Panwa peninsula, Lone Island, Aeo Island, Hae Island, and Racha Island.

Table 3.6.1. List of tagged coral species and genera, their morphologies, total number and distribution at the study sites. (PW=Panwa, LN=Loan Island, AO=Aeo Island, HE=Hae Island, RC=Racha Island.)

Taxa	Growth from	Number of colonies					
		Total	PW	LN	AO	HE	RC
Acropora spp.	Branching	67	9	15	26	8	9
Pocillopora damicornis	Branching	38	8	8	10	6	6
Porites nigrescens	Branching	4	-	-	4	-	-
Hydnophora rigida	Branching	13	2	1	8	-	2
Porites rus	Encrusting	15	-	2	5	-	8
Pavona varians	Encrusting	4	-	-	-	4	-
Merulina ampliata	Plating	6	3	-	-	-	3
Echinophyllia echinata	Plating	6	-	-	6	-	-
Montipora aequituberculata	Plating	8	-	2	-	2	4
Pectinia alcicornis	Plating	6	3	3	-	-	-
Symphyllia radians	Massive	8	-	-	5	3	-
Porites lutea	Massive	60	9	10	22	8	11
Platygyra daedalea	Massive	2	-		-	2	-
Physogyra lichtensteini	Massive	5	-	-	-	-	5
Lobophyllia hemprichii	Massive	11	3	-	-	8	-
Galaxea fascicularis	Massive	5	-	2	-	1	2
Goniastrea spp.	Massive	8	2	3	2	1	-
Favites spp.	Massive	12	-	2	2	1	7
Dipsastraea spp.	Massive	10	2	4	2	-	2
Leptoria phrygia	Massive	5	-	-	-	-	5
Astreopora myriophthalma	Massive	9	-	-	-	2	7
Diploastrea heliopora	Massive	10	3	3	-	3	1
Psammocora digitata	Columnar	3	-	1	2	-	-
Ctenactis spp.	Solitary	31	2	6	4	9	13
Fungia spp.	Solitary	35	5	2	6	8	14
Herpolitha spp.	Solitary	11	-	2	1	3	5

(c) Determination of coral tissue biomass

Fragments of five healthy and fully pigmented colonies or individuals of each of the 25 coral taxa were collected from Hae Island in 2017 to determine tissue biomass, following a modified protocol based on Johannesand Wiebe (1970) and (Schoepf et al., 2015). Coral tissue was removed from the skeleton with an air gun and placed into porcelain crucibles, and then dried for 48 hours in the oven at 60°C to constant dry weight. After determining the dry mass, the porcelain crucibles were burned at 500°C for 4 hours and re-weighed for ash-free dry mass determination (AFDW). Surface area was determined using the single wax dipping technique (Veal et al., 2010). Forty wooden cylinders and cubes with different known surface areas ranging from 1 to 100 cm^2 were used as calibration standards. Calibration objects were measured using digital calipers (Senator®), accurate to 0.01 mm to determine geometric surface area. Wax dipping was conducted using paraffin wax heated to 65°C in a water bath. Dipped skeletons and calibration objects were maintained at room temperature (25°C) for about 15 minutes before being reweighed. The regression relationship between wax weight and surface area of calibration objects ($y = 0.0326x - 0.078$, $r^2 = 0.9911$) was used to determine the surface area of all assessed coral fragments. Dry mass and ash-free dry mass were standardized to surface area.

(d) Data analysis

Statistical analyses were performed with the program SPSS 15.00 for Windows. Non-parametric tests were used when the requirements for parametric analyses were not met even after transforming the data (Levene's test for homogeneity of variances, $p < 0.05$). To test for significant differences in the percentage of re-pigmented colony surface areas between July and September 2010, paired Wilcoxon t-tests were used. The effect of colony morphology and colony size on re-pigmented was tested with Kruskal-Wallis tests followed by multiple comparisons of mean ranks using Mann-Whitney U tests for pairwise comparisons. Colony size covered a wide range. Only abundant coral taxa were assigned to 5 different size classes (Table 3.6.2).

Table 3.6.2. Size classes (coral colony diameters) and their frequency distribution of the 5 most abundant coral species and genera, respectively. Numbers in brackets give total number of tagged colonies.

Taxa	Size classes (cm)				
	A	B	C	D	E
Acropora spp.	≤30 (17)	31-50 (16)	51-70 (11)	71-90 (13)	91-130 (10)
Pocillopora damicornis	≤10 (10)	11-15 (17)	16-20 (7)	21-26 (6)	
Ctenactis spp.	≤10 (5)	11-20 (10)	21-26 (10)	27-37 (6)	
Fungia spp.	≤10 (9)	11-15 (14)	16-20 (7)	21-28 (5)	
Porites lutea	≤30 (14)	31-50 (9)	51-70 (14)	71-90 (9)	91-200 (14)

Results

Bleaching response

There were considerable differences in bleaching response across 43 coral species during the 2010 bleaching event (Fig. 3.6.2). *Diploastrea heliopora* was the most bleaching-tolerant species with no fully bleached colonies on transects (BMI = 7.2), followed by *Astreopora myriophthalma,* and

Isopora palifera (BMI = 12.2 and 12.3, respectively). The most bleaching-susceptible species were *Hydnophora rigida* and *Pavona clavus* (BMI = 66.7).

Re-pigmentation after full bleaching

Two months after the bleaching event in July, the bulk of the tagged bleached colonies remained bleached (46%) or died (40%) while only 14% showed re-pigmentation. In September, re-pigmentation continued to increase (35%), but so did mortality, showing a 59% of dead colonies at the end of our 5-month observation period with only few bleached remnants (6%). Solitary corals showed the highest re-pigmentation (83.5% of colony area) by the end of the observation period, followed by massive and encrusting corals with about 44% and 20% (Fig. 3.6.3). In general, branching and plating corals showed the lowest re-pigmentation potential with less than 2% re-pigmentation. In general, branching and plating corals showed the lowest re-pigmentation potential with less than 2% re-pigmentation (Fig.3.6.4.).

By the end of the observations, coral re-pigmentation varied widely between 0 and 97% of colony surface area (Fig. 3.6.3). A few taxa did not show clear trajectories to re-pigmentation or mortality, displaying bleaching over more than 30% of the colony surface area (e.g. *Physogyra lichtensteini*, *Leptoria phrygia, Lobophyllia hemprichii,* and *Symphyllia radians,* Fig. 3.6.3A). Nineteen of 25 taxa (76%) were able to recover, showing various levels of re-pigmented colony surface area (Fig. 3.6.3B). *Diploastrea heliopora, Ctenactis, Herpolithas* spp.*, Fungia* spp.*,* and *Psammocora digitata* showed the highest re-pigmentation with more than 60% of colony surface area re-pigmented between May and July. The very low re-pigmentation was found in *Merulina, P. rus*, and *Acropora* with less than 2%. Re-pigmentation rates were higher in the period of July-September compared to the first period (May - July), except for *D. heliopora, P. lichtensteini* and *Galaxea fascicularis* (Wilcoxon, $p<0.05$, Fig. 3.6.3B). The remaining six taxa that showed no sign of re-pigmentation were *H. rigida*, *Pectinia alcicornis*, *Pocillopora damicornis*, *Echinopora echinata*, *Montipora aequituberculata*, and *Porites nigrescens* (Fig. 3.6.3C).

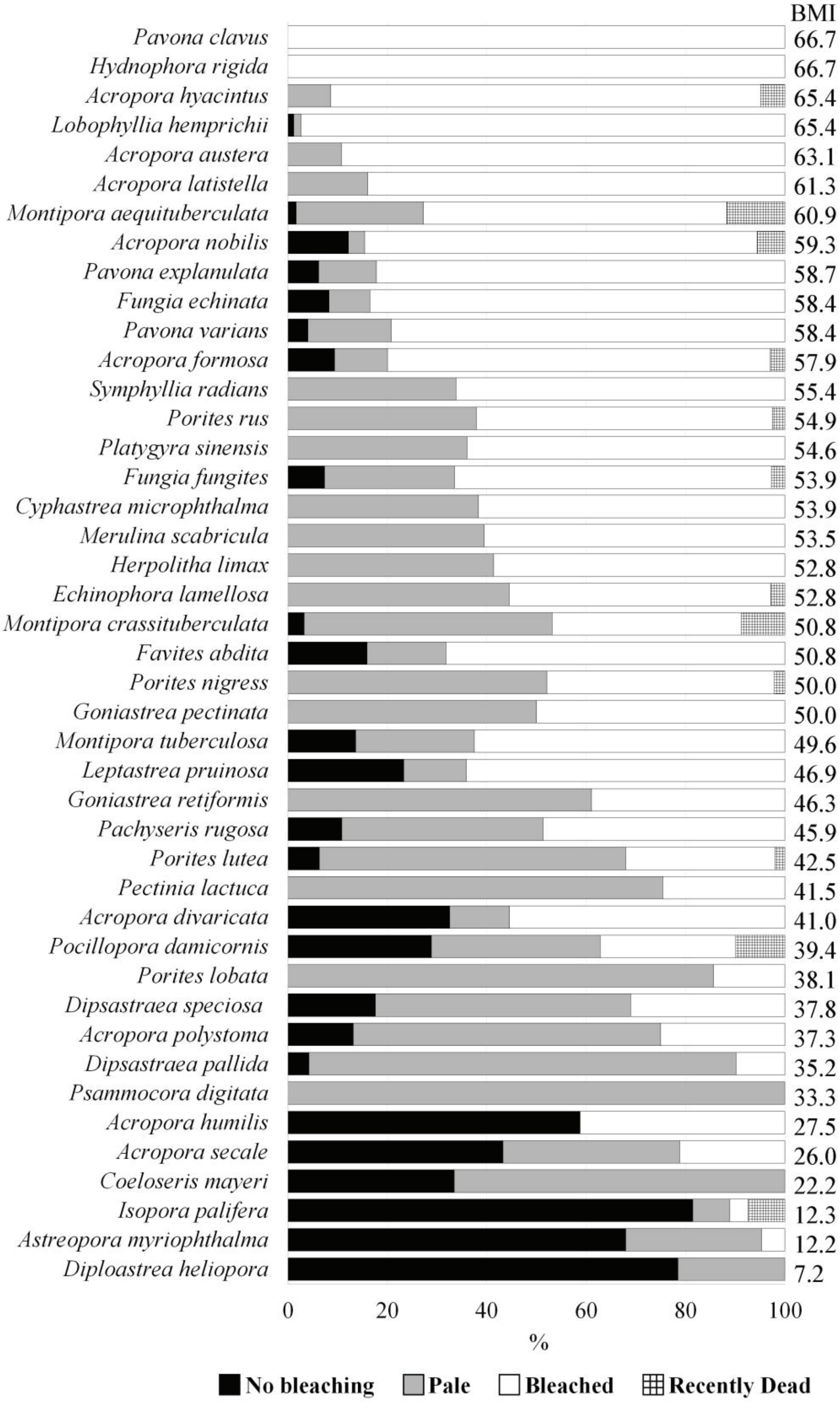


Figure 3.6.2. Bleaching susceptibility of 43 coral species during the height of the bleaching event in May 2010. Data are displayed as the percent cover of 4 recorded bleaching categories: no bleaching (black), pale (light gray), bleached (white), and recent dead (black stripe). Number right after bars indicate bleaching mortality indices (BMI). Data present only species represented by 5 or more replicates.

The pattern of re-pigmentation was different among coral species (Fig. 3.6.5, Table 3.6.S1). For example, branching *Acropora* whole colony died (Fig. 3.6.5A). In *Porites lutea* re-pigmentation started from the edge of the colonies (Fig. 3.6.5B) whereas in *Diploastrea heliopora* and fungiids the re-pigmentation occurred randomly across the colonies (Fig. 3.6.5E). Re-pigmentation and subsequent mortality in *Pavona variance* both initially started from the exterior region of the colony (Fig. 3.6.5C). *Physogyra lichtensteini* were fully bleached throughout the studied period (Fig. 3.6.5D). We found no correlation between the re-pigmentation of the fully bleached corals and the bleaching and mortality response (BMI) of the respective taxon to thermal stress (Fig. 3.6.S1, n= 16, *r*=-0.447, *p*=0.098).

The effect of colony size on re-pigmentation was examined for the five coral species that were present across all size classes (*Acropora* spp., *P. damicornis*, *P. lutea*, *Ctenactis* spp., and *Fungia* spp.). No significant differences were found in re-pigmentation among colony size classes (Kruskal-Wallis test, *p*>0.05; Table 3.6.S2) for all tested coral species. Colonies of *Acropora* and *Pocillopora* died independent of colony size. Other genera (*Ctenactis, Fungia,* and *Porites*) regained full pigmentation independent of colony size.

Full tissue removal was achieved in 14 of 25 taxa (Fig. 3.6.6), but for the 9 remaining coral taxa it was not possible to remove the entire tissue. The ash free dry weight (AFDW) varied between taxa and colony morphologies (df=4, p<0.01). The highest mean AFDW was found in solitary corals with about 5.2 mg tissue / cm^2, followed by massive and encrusting corals with about 4.3 and 3.7 mg tissue / cm^2, respectively. The lowest mean AFDW was found in branching and plating corals as *Acropora, Pocillopora damicornis*, and *Montipora* with about 1.7-2.2 mg tissue / cm^2. There was a strong correlation between percent re-pigmentation and the ash free dry weight (*r*=0.761 and 0.8, for July and September, n=14, *p*<0.01) (Fig. 3.6.7).

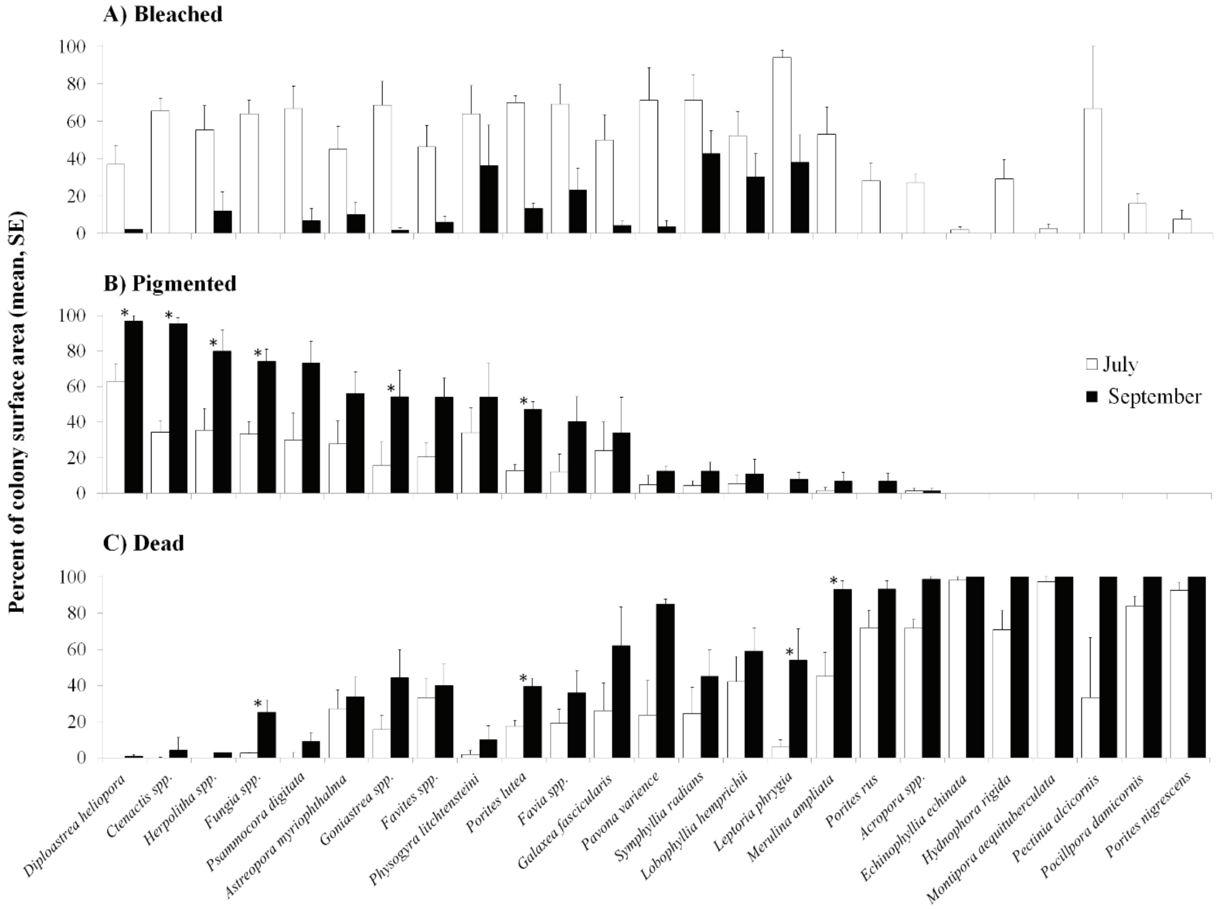


Fig 3.6.3. Dynamics of coral colonies after fully bleaching: mean percent of bleached colony surface area (A), mean percent of re-pigmented colony surface area (B) and mean percent of dead colony surface area (B). White bars represent data in July and black bars represent data in September. Illustrations showed the various levels of tolerance ranging from high to low and susceptible with 100% mortality. An asterisk indicates significant difference in colony area between those two sampling times detected at p<0.05.

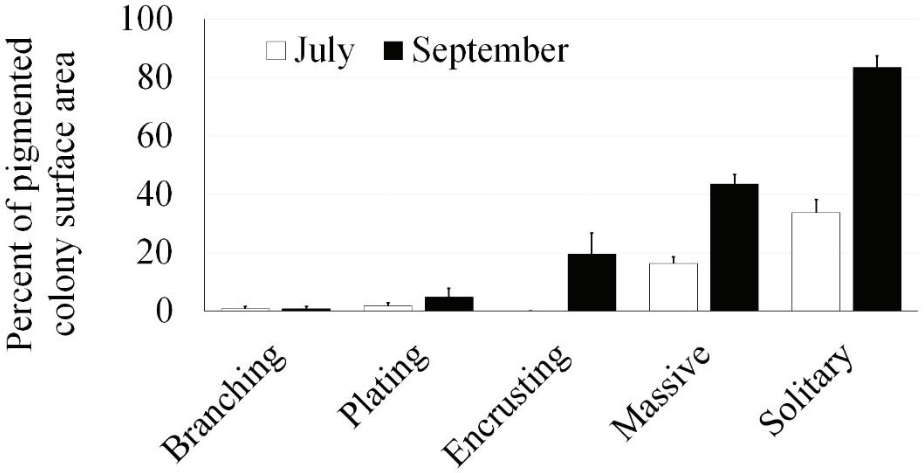


Figure 3.6.4. Colony surface area (%, mean (±SE)) of pigmented tissue ordered by colony morphology in July and September 2010.

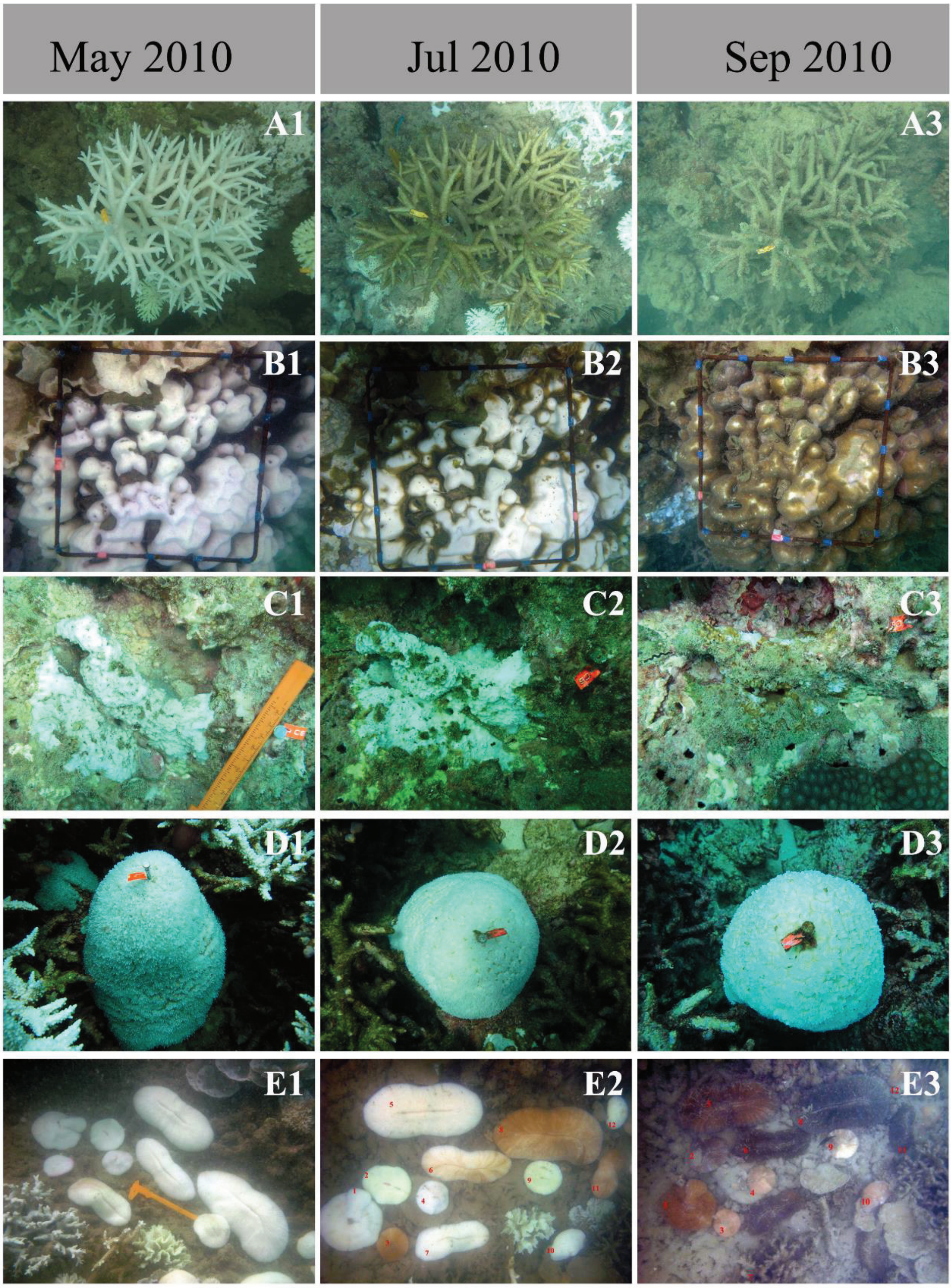


Figure 3.6.5. Examples of coral colonies from different species marked in May (left panel) and re-monitored in June (middle panel) and September 2010 (right panel), showing different subsequences after whole-colony bleaching in *Acropora Formosa* (A1-3), massive *Porites lutea* (B1-3), *Pavona variance* (C1-3), *Physogyra lichtensteini* (D1-3)*,* solitary fungiid corals (E1-3).

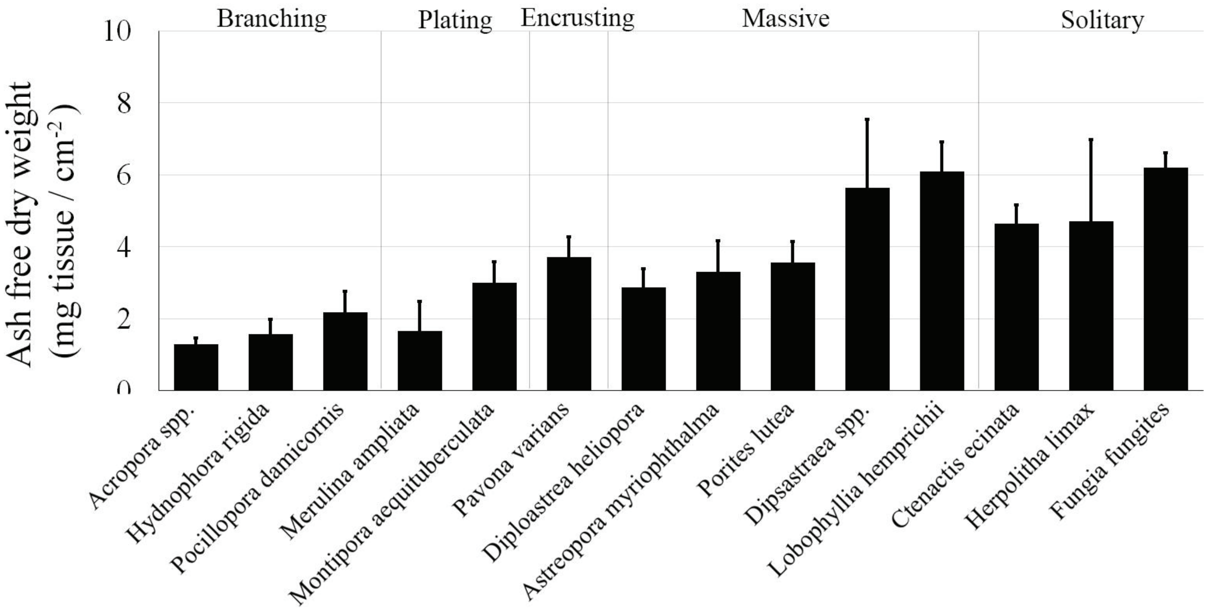


Figure 3.6.6. Tissue biomass of 14 different coral taxa, grouping by morphology (n=5). Biomass was measured by ash-free dry weight in mg tissue/cm^{-2}.

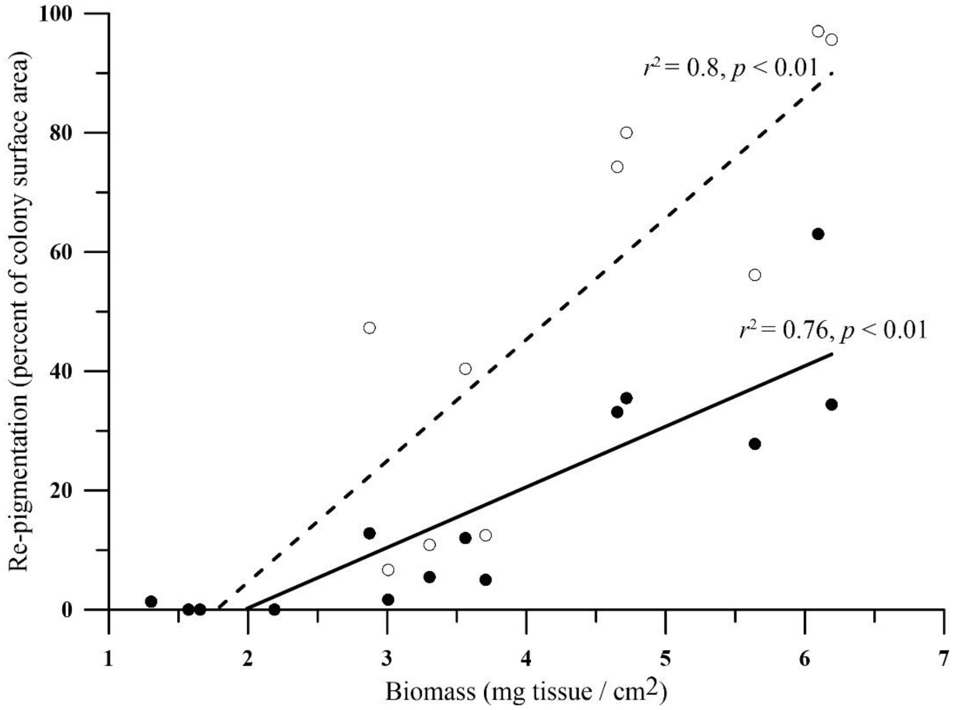


Figure 3.6.7. Correlation between re-pigmentation rate and the ash free dry weight of fifteen coral taxa in July (black dots) and September (circles). Black solid and dashed lines refer to the best-fit in July and September, respectively.

Discussion

Re-pigmentation of fully bleached corals

This is the first study in the Andaman Sea that simultaneously investigates the effects of bleaching on the coral community level and the ability of fully bleached coral colonies of various species to recover in the aftermath of a severe bleaching event. Re-pigmentation rates of corals were not related to the level of their bleaching susceptibility. Fully bleached colonies of tolerant coral species may recover as much as fully bleached colonies of non-tolerant coral species.

In a bleached coral, the concomitant loss of photosynthesis leaves the coral host dependent on its own stored energy reserves and/or supply of food and its survival depends on its ability to balance the energetic expenditures (e.g. respiration, growth). For long-term recovery, heterotrophy may be the main source of energy covering the metabolic demand of the corals (Grottoli and Rodrigues, 2011). Tissue layer thickness and tissue biomass as bio-indicators of the size of energy is often related to colony morphology (Loya et al., 2001; Thornhill et al., 2011), which is likely to explain the majority recovery patterns in this study. Re-pigmentation was affected by colony morphology and strongly related to tissue biomass. This clearly explains the low recovery ability of branching and plating corals as *Acropora, Pocillopora,* and *Montipora*, which had relatively low tissue biomass and low rate of energy gain through feeding mode (reviewed in Ferrier-Pagès et al., 2011). Massive corals, which displayed high bleaching susceptibility, also turned out to be most bleaching tolerant with the highest amount of stored energy (or with the greatest energy store). This should mean that bleaching susceptible corals might be able to recover if they have available energy resources. Our field observations are supported by laboratory experiments where bleaching caused higher mortality in branching corals compared to massive species (Hueerkamp et al., 2001). Massive species of *Porites* and Faviidae are frequently among the survivors with partial colony mortality (Marshall and Baird, 2000; Baird and Marshall, 2002) .

Colony size determines bleaching patterns in some other species such as *Pocillopora damicornis*, *Oculina patagonica*, *Colpophyllia natans*, *C. natans*, *Montastraea faveolata*, and *Siderastrea siderea* (Shenkar et al., 2005; Brandt, 2009; Pratchett et al., 2013). Larger colonies were often found to have greater bleaching susceptibility; however, the colony size effect on coral recovery is not well understood. To examine the fate of corals after bleaching, individual colonies must be tagged. Our results showed that *Acropora* and *Pocillopora* died, while massive *Porites* and fungiids fully recovered after being 100% bleached, regardless of colony size. This was consistent with the finding of Bairdand Marshall (2002), who showed no correlation between mortality rate and colony size. They indicated that mortality rate increased with severity of bleaching (percent of colony surface area). Since all studied colonies were totally bleached, they were presumed to bleach at the same intensity. This could explain that the recovery rate and mortality rate in this study was independent of colony size. However, recent field evidence indicated that the bleaching-induced mortality was more pronounced in larger colonies (i.e. 8 to 14 cm diameter) (Brown et al., 2014). Small colonies may initially have bleached less than large colonies, leading to higher bleaching-induced mortality in larger colonies. In this case, the recovery of bleached corals depends on energy reserves but not colony size, while mortality rate of coral after bleaching is dependent on bleaching intensity, which could be related to colony size.

Patchy and irregular colony recovery after bleaching has been reported (Hayes and Bush, 1990). Our study observed some patterns of re-pigmentation such as re-pigmentation of bleached massive colonies often started from the exterior region of the colony and continued towards the colony center. This may involve different parts of the colony experiencing different micro-environments, such as conditions of light and sedimentation. High light intensity and increased sediment settling around the top of the colony may interfere with coral tissue recovery (Dunne and Brown, 2001; Brown et al., 2002b; Rotmann and Thomas, 2012), leading to initial re-pigmentation occurring from the side of massive *Porites* colonies. However, this was not the case for all other massive corals. The effects of dimensions would explain why we found no particular pattern in flat corals like fungiids. In addition, those differing physical conditions within an individual colony may also lead to preference conditions to symbiont genotype. Rowan et al. (1997) found that colony tops mainly harbour *Symbiodinium* clade C, while *Symbiodinium* clade A and B are predominant in colony sides. Association with multiple clades of zooxanthellae within a colony may then interact with the top-side or random recovery pattern. This partial surviving tissue can account for potential recovery to re-gain coral cover (Phongsuwan, 1991; Gilmour et al., 2013).

Implication for coral rehabilitation

Coral rehabilitation contributes to reef conservation and management by regaining coral populations in degraded coral reef ecosystems (Edwards and Gomez, 2007). Various rehabilitation techniques have been applied in Thailand (Thongtham, 2010). These include coral fragment transplantation, coral transplantation by using sexual reproduction, coral floating nurseries, and introducing artificial substrate for coral recruitment. The most commonly applied method is coral fragment transplantation. To minimize disturbances to the mother colony, small broken fragments are nursed until a proper colony size is reached before transplanting them back to degraded reefs (Rinkevich, 1995). Many studies investigated crucial issues concerning the task of finding an appropriate nursery and transplantation technique for the respective area. These include survival and growth rates of fragments on the nurseries and after transplantation (Putchim et al., 2008a; Putchim et al., 2008b; Yucharoen et al., 2008; Yucharoen et al., 2011; Sujirachato et al., 2013). The success of such approaches relies on coral species, the initial fragment size and water quality. The coral species typically used for this technique are mainly branching corals, i.e. *Acropora*, *Hydnophora, Montipora,* and *Pocillopora*, because they grow fast and there is minimal disturbance to the mother colony (Putchim et al., 2008b; Thongtham, 2010). Massive corals such as *Porites* are applied to increase the survival rate of transplanting (Thongtham and Chansang, 2008). Rehabilitated corals (transplanted corals, nursed corals) bleached as much as naturally grown corals during the severe 2010 bleaching event. Yet, until recently, there was no colony/species selection for rehabilitation activities. As a result, most of transplanted corals and nursed corals were also affected by bleaching in 2016 (L. Putchim, unpublished data), whereas there is variation on bleaching response in the reefs. The knowledge gained from this study, including better understanding the bleaching response of particular species, can support principles for the selection of appropriate locations and target coral species used for rehabilitation techniques.

Acknowledgements

This study was funded by the Deutscher Akademischer Austauschdienst (DAAD) with additional support by the German Federal Ministry for Education and Research (BMBF, Grant number: 03F0608B, Bioacid 3.2.3, Coral calcification in marginal reefs) and Alfred-Wegener-Institute. The Phuket Marine Biological Center (PMBC) and its staff supported logistics and field work.

Supplementary data is given in Appendix 3

3.7 Manuscript VII

Observation of coral disease in *Porites lutea* in the Andaman Sea following the 2010 bleaching

L Putchim, C Yamarunpattana, & N Phongsuwan

Phuket Marine Biological Center, Phuket, Thailand
51 Sakdidet Road, 83000 Phuket, Thailand

Putchim L, Yamarunpattana C, and Phongsuwan N. 2012. Observations of coral disease in *Porites lutea* in the Andaman Sea following the 2010 bleaching. Phuket Marine Biological Center Research Bulletin 71: 57-62 ISSN 0858-1088

Abstract

During 2008 - 2009 preliminary surveys on coral disease were conducted at 40 stations from 18 islands throughout the Andaman Sea along the coast of Thailand. The belt transect method was employed to quantify the occurrence of coral diseases. The data indicated that 90% of the surveyed reefs showed 5 categories of disease, i.e., White Syndrome (WS), Ulcerative White Spot (UWS), Focal Bleaching (FB), Non-Focal Bleaching (NFB) and Pink Spot (PS). The PS was the most prevalent syndrome, i.e., it occurred in about 95% of sites visited. Other categories were rare. After the bleaching event in 2010, especially in some areas of Similan Islands and Surin Islands, the UWS syndrome on *Porites lutea* appeared to have increased. In addition, the PS was still the most prevalent disease.

Introduction

Coral disease has become a phenomenon that has been widely reported from coral reefs around the world within the last 30 years (Green and Bruckner, 2000; Weil et al., 2000; Porter et al., 2001; Sutherland et al., 2004). In areas such as the Caribbean, where coral disease outbreaks were noted as early as 1980, important coral genera such as the Acropora suffered significant damage, particularly from White Band Disease (Aronson and Precht, 2000). Damage to these major reef building corals has the potential to change an ecosystem from one dominated by corals to one dominated by macro-algae(Hughes, 1994; Aronson and Precht, 2000; Porter et al., 2001; Gardner et al., 2003; Sutherland et al., 2004). Both White Band Disease and Black Band Disease have been reported in the Caribbean, and the Indo-Pacific(Rützler and Santavy, 1983; Antonius, 1985; Edmunds, 1991; Kuta and Richardson, 2002). The first study of coral diseases in the Andaman Sea was published in 2008. Three categories of diseases were identified, namely: White Syndrome, Pink Line Syndrome and Black Band Disease (Kenkel, 2008). However, our understanding of the incidence and spread of coral disease on reefs in Thailand is still very limited. In 2010 corals in the Andaman Sea suffered the most severe bleaching event so far reported in Thai waters. This preliminary study focuses on the occurrence of disease in the major reef building coral in the region, *Porites lutea*, following the 2010 bleaching event.

Material and Methods

In this study, belt transects measuring 2m by 20m were laid on surveyed reefs. Three transects per site were deployed. The number of colonies of *Porites lutea* – categorized into normal colonies and diseased colonies - were recorded. Diseases were identified based on the Indo-Pacific Underwater ID Card (Beeden et al., 2008). Percent of disease was calculated as follows:

$$\frac{\text{number of diseased colonies}}{\text{number of total surveyed colonies}} \times 100$$

Two offshore locations were selected in Thai waters in the Andaman Sea – the Surin Islands and the Similan Islands (Fig. 3.7.1). An initial study was carried out in 2008 in the Similan Islands and a further study after the bleaching in 2010. In the Surin Islands an initial study was carried out in 2009 with a follow up study in 2010. In addition, in the Similan Islands 100 diseased colonies affected by Ulcerative White Spot (UWS), were tagged in November 2010. Then 50 colonies at Ba-Ngu Island and western Similan Island were monitored 2 months later.

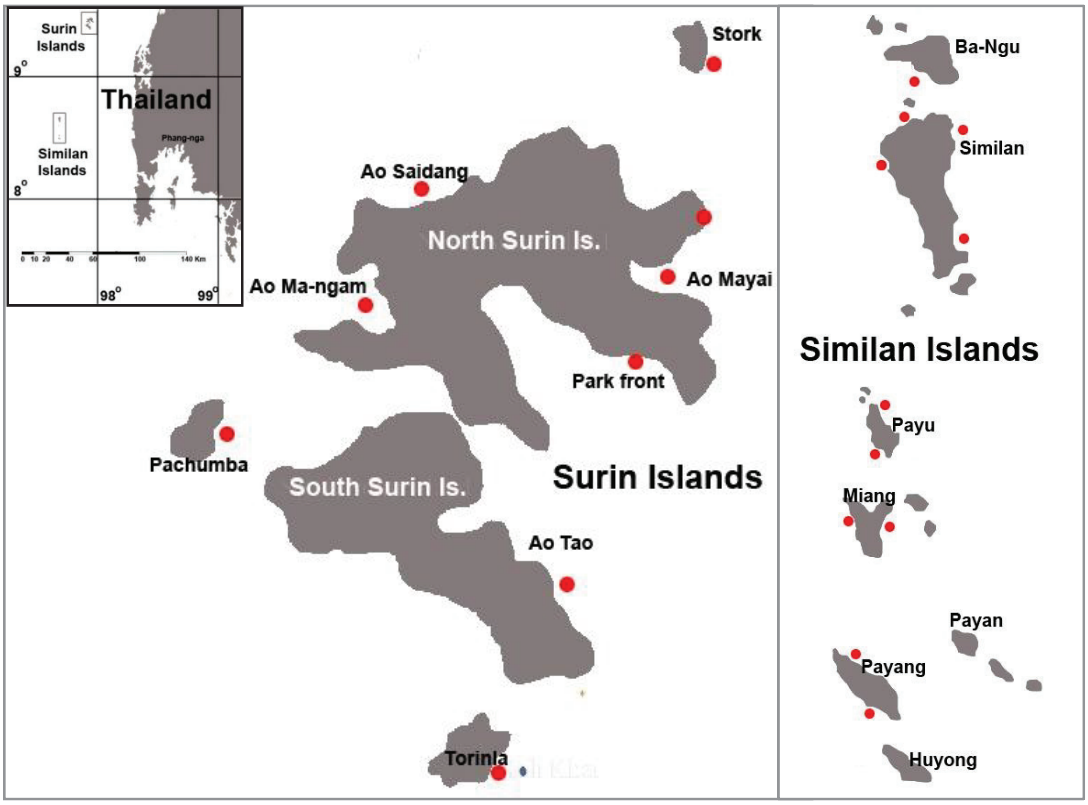


Figure 3.7.1 Map of the study sites in Surin and Similan Islands**.**

Results and Conclusions

During 2008-2009 disease occurred at 16 stations out of 17 surveyed, with 5 categories i.e. White Syndrome (WS), Ulcerative White Spot (UWS), Focal Bleaching (FB), Non-Focal Bleaching (NFB) and Pink Spot (PS) (Fig. 3.7.2). The PS exhibited the greatest prevalence both in the Similan Islands and Surin Islands. There was about 16.4% and 8.5%, respectively at these locations. While for UWS, values of 3.6% in the Similan Islands and 0.8% in the Surin Islands were recorded. After the 2012 beaching event, values for UWS were higher in both areas with 4.8% recorded in the Similan Islands and 22.3% in the Surin Islands (Fig. 3.7.3). Other diseases were still categorized as rare. In addition, post-bleaching, the PS was still the most prevalent disease. Preliminary results of monitoring of individual colonies show that there was little visual change in the colonies with all remaining alive and intact.

There are many factors that contribute to disease including temperature, water pollution, overfishing, water depth, coral diversity, concentrations of orthophosphate and nitrite(Jackson et al., 2001; Kuta and Richardson, 2002; Szmant, 2002). Elevated temperature is a likely significant factor in causing an increase in disease in many areas (Kushmaro et al., 1998; Rosenberg and Ben-Haim, 2002; Jones et al., 2004; Bruno et al., 2007; Selig et al., 2013). Several reviews speculate that there has been an increase in many categories of coral disease since the 1990s (Green and

Bruckner, 2000; Porter et al., 2001; Jones et al., 2004; Sutherland et al., 2004; Willis et al., 2004). Although there have been few reports on UWS it does appear it results in coral tissue loss (Raymundo et al., 2003). The present study was carried out over a limited time period; nevertheless, it does provide a valuable base-line. Continued monitoring is planned to follow the tagged colonies and other corals on the belt transects in order to understand more about the impacts of the various diseases described above.

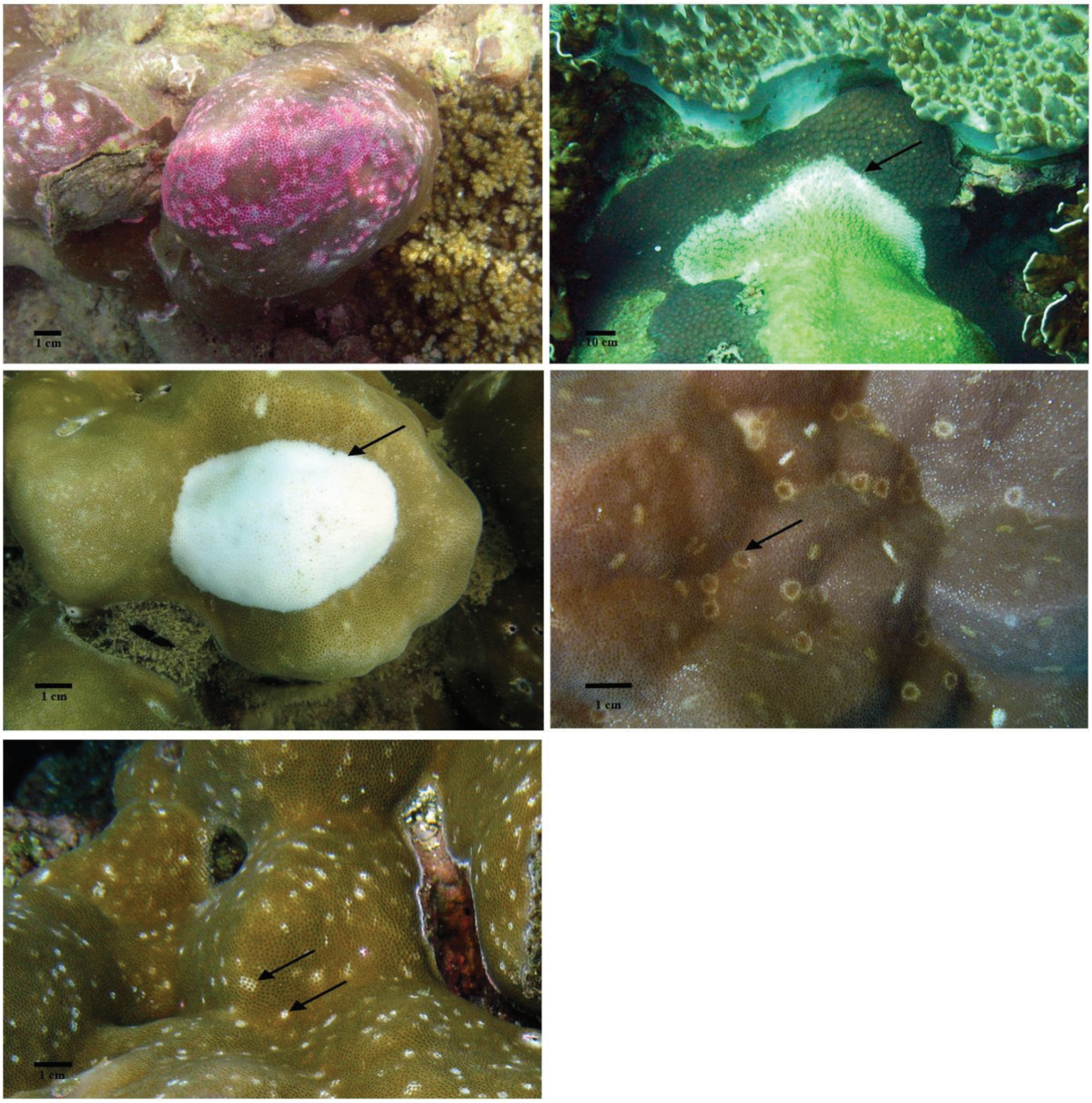
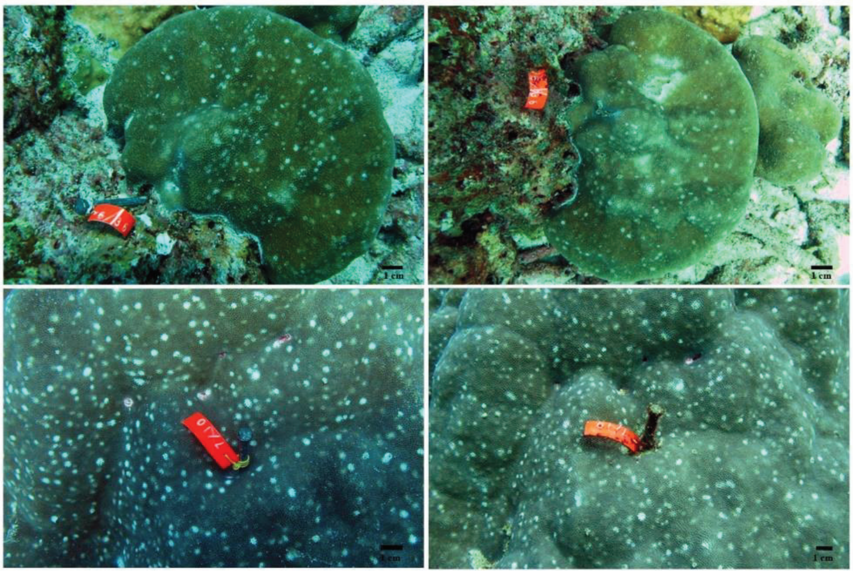


Figure 3.7.2 Five categories of coral diseases found in the Andaman Sea: a) Pink Spot (PS): Pink coloured lesion may be swollen or thickened: Pigmentation may form lines, bumps, spots, patches or irregular shapes. **b)** White Syndromes (WS): Irregular white lesion shape, with a sharp demarcation between normal tissue and bare skeleton. **c)** Non-Focal Bleaching (FB): Irregular shape lesion and border between bleached stripes and tissue with typical colouration are often discrete. **d)** Focal Bleaching (FB): Circular white lesion, or annular margins <3cm diameter **e)** Ulcerative White Spot (UWS): Circular white spot <1cm diameter. Disease description developed from the Indo-Pacific Underwater ID Card (Roger et al., 2008).



Decamber 2010 February 2011

Figure 3.7.3 Monitoring Ulcerative White Spot on *Porites lutea*

Table 3.6.1 The percent of diseases in 2008-2009 and in November 2010

	#surveyed station	#total colony	*Porites lutea* (%)					
			normal	UWS	WS	NFB	FB	PS
Similan Is 2008	10	1030	77.4	3.6	2.1	0.1	0.4	16.4
Similan Is 2010*	5	312	86.9	4.8	0.6	0	0	8
Surin Is 2009	7	247	90.7	0.8	0	0	0	8.5
Surin Is 2010*	6	292	68.2	22.3	0.3	0	0	9.2

.* after bleaching event

CHAPTER 4 THESIS DISCUSSION

Responses to climate change can be detected at different scales, from the cellular to the regional scale. The present thesis shows the diversity in thermal stress response across this entire spectrum. It highlights the genotypic diversity of unicellular *Symbiodinium* populating the coral *Porites lutea*, analyses the patterns of re-pigmentation and recovery at the organismal and colony level, looks at coral community responses in bleaching and mortality across space and time, and investigates how bleaching and disease vary between sites, across the continental shelf and between regions (Andaman Sea and Gulf of Thailand). It explores the factors influencing the observed differences in bleaching susceptibility (Fig. 4.1) and traces the fate of corals and corals reefs in the aftermath of bleaching. Both extrinsic and intrinsic parameters causing coral bleaching can be prioritized to elucidate the main factors responsible for the bleaching event. The combined effect of these factors can be used to predict bleaching impacts on corals and coral recovery, as well as to identify potential refuge areas for corals in a warming ocean. The following discussion addresses the listed research questions as follows:

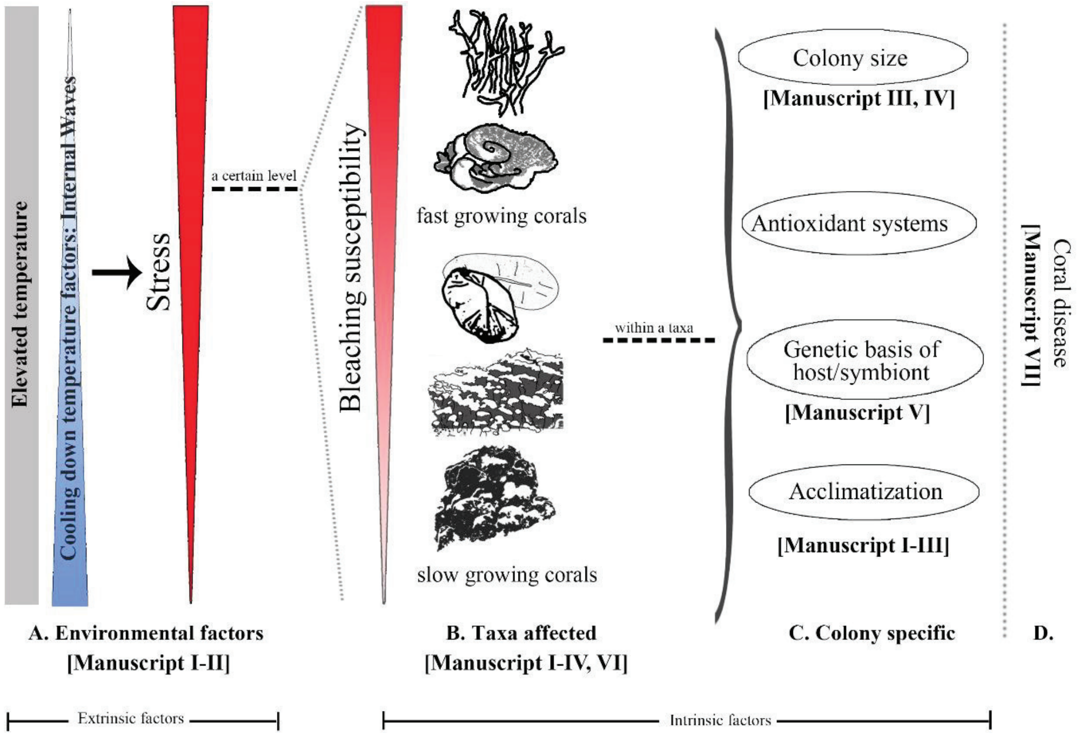


Figure 4.1 Schematic illustration showing factors affecting coral bleaching susceptibility at different scales with links to corresponding manuscripts in this thesis. Section A displays extrinsic factors can trigger coral bleaching: this study focused only on elevated temperature, the primary stress factor causing coral bleaching, and stress-relieving factors are examined (manuscript I, II). Section B shows that different coral taxa respond differentially under the same stress level (manuscript I-IV, VI). Section C shows the finer-scale intrinsic factors, which are important to control the bleaching susceptibility at the colony scale, e.g. colony size (manuscript III-IV) and acclimatization (manuscript I-III). Section D shows indirect effects of bleaching on coral disease (Manuscript VII).

➢ *What are the reasons for the observed spatial variability in bleaching, mortality and recovery between colonies and reefs?*

Sea surface temperature (SST) is the most important parameter used in predicting the probability and timing of mass bleaching events. Satellite remote sensing techniques have been widely used to measure the ocean's SST in space and time. Whereas most studies of thermal stress on reefs have relied on SST data, our results showed that SSTs retrieved from remote sensing failed to predict the observed spatial variability in bleaching between coral reefs (Manuscript I). The discrepancy could be resolved by relating the observed bleaching to sub-surface in situ data in the immediate vicinity of the corals during an unprecedented bleaching event. Our *in situ* temperature loggers at 15 m were able to detect large (several °C) and recurring (several per day) but short-lived (half-hour to hour) drops in ambient temperatures invisible to the surface-sensing satellites. We identified the source of the temperature oscillations as large amplitude internal waves (LAIW) and were the first to demonstrate that the observed variability in bleaching was due to the degree of exposure to LAIW. The *in situ* temperature data, along with data on the coral community composition (Manuscript II), significantly improved the hindcasting of the bleaching observations and determination of site-specific bleaching temperature thresholds. Our results show that where satellite remote sensing predictions fail at local scales, a detailed understanding of the oceanographic environment is needed to assess spatial variability in bleaching. Our finding that LAIW benefit corals during thermal stress (Manuscript I) and fluctuating environments enhance coral thermal tolerance (Manuscript II), was recently validated by Buerger et al. (2015), who simulated LAIW in the laboratory and examined the thermal tolerance of corals by measuring photosynthetic efficiency, protein energy reserve, and observing bleaching response. They found that LAIW reduced heat stress responses in all corals, but that the most stress-resistant corals originally came from LAIW-exposed areas. This finding was consistent with previous studies showing that natural variations in upwelling intensity, current flow conferred thermal stress relief and bleaching mitigation. While Barshis et al. (2013) investigating tide-pool corals showed that high-temperature extremes may 'front-load' corals to resist thermal stress, to the best of our knowledge, our results on LAIW are the first to show that also low-temperature variations appear to effectively pre-dispose corals to high-temperature stress.

At the small scale within reefs, we observed variation in bleaching among colonies of the same species and explored potential factors that may be responsible for such a variation, e.g. genetic diversity of coral's symbiont (*Symbiodinium*) (Manuscript V). Whereas *Porites lutea* has originally been thought *to* contain a single dominant *Symbiodinium* ITS2 type, C15 (LaJeunesse et al., 2004), it has subsequently been found to engage in flexible associations with diverse *Symbiodinium* types (Apprill and Gates, 2007; Ziegler et al., 2015), depending on season and depth. In the Andaman Sea, *Porites lutea* has been reported to associate only with *Symbiodinium* types C15 (LaJeunesse et al., 2010a). Here, we report for the first time the detection of types C1, C17, and D1a in Andaman

Sea *Porites lutea*. The 'new' *Symbiodinium* ITS2 types were found before the 2016 bleaching event, but nearly six years after the severe 2010 mass bleaching event, inviting speculation of possible causes for the observed increase in *Symbiodinium* diversity: The small fraction (<1%) of D1 type, belonging to a symbiont clade considered heat-tolerant, may be a remainder of the 2010 mass bleaching in line with the Adaptive Bleaching Hypothesis (Buddemeier and Fautin, 1993). While C1 has been described as less heat-tolerant symbiont type in *Stylophora* (Wang et al., 2012), different host-symbiont combinations may yield very different susceptibilities to thermal stress (Abrego et al., 2008), so that it may be possible that the high proportion (up to 20%) of the 'new' C1 type may indicate the transition to a new 'stable state' of *Porites lutea* associated *Symbiodinium* community in the Andaman Sea. Spatial variability in bleaching at the small scale (within the reef) was demonstrated between depths (Penin et al., 2007), which may be explained by the interactive effects of environmental factors such as hydrodynamic conditions, and by intrinsic factors such as differential adaptation and/or acclimation of the coral/algal association (Bongaerts et al., 2013; Bongaerts et al., 2015; Ziegler et al., 2015). In the case of the contrasting thermal responses between adjacent colonies, however, it is likely that intrinsic factors are dominating (LaJeunesse et al., 2007). Following this primary study of *Symbiodinium* diversity in *Porites lutea*, additional studies are needed, to understand to what extent the diversity of *Symbiodinium* may explain the remarkable co-occurrence of healthy and bleached colonies in the same area.

When heat stress persists for a long time, such as during the 2010 event, almost all corals may end up bleached. Under severe thermal stress it is thus often difficult to identify which corals/colonies are more bleaching resistant. However, variability in bleaching between colonies can be well recognized at the beginning of increasing SST or during mild bleaching (L. Putchim, personal observation). We were able to mark different types of bleaching response during the recent 2016 moderate bleaching event. Historical bleaching data of individual colonies would be sufficient material that could be used to study the effects of intrinsic factors and its dynamics on spatial variability in bleaching between colonies in the future.

In addition to the response of bleaching susceptible and bleaching resistant corals to thermal stress, we were interested in the tolerance of the corals to this major disturbance, i.e. if and to what extent bleached corals were able to return to a healthy pigmented state. We were also curious to explore the role of the corals' energy stores in explaining the corals trajectories to death versus survival. Manuscript VI is the first study in this region showing that fast growing taxa possess less stored energy (biomass) than slower growing taxa. This is crucial since this energy storage plays a fundamental role in recovery after a bleaching event. Our findings suggest that fully bleached corals are able to recover if they have enough available energy resources prior to the bleaching event. Since we do not know if and to what extent corals were able to acquire additional energy from heterotrophic feeding (Grottoli et al., 2006), it is difficult to make predictions on the recovery rate of corals for future bleaching events. For example, if feeding provides enough energy to meet metabolic demands during thermal stress, this would extend the initial energy stores and, hence, survival. We indeed found that some coral species exhibited bleaching for extended periods. This means that they can meet their energetic demands in the absence of photoautotrophic sources by feeding (Grottoli et al., 2006) and/or high initial energy stores (Anthony et al., 2009). Conversely, bleached corals with only limited energy stores and/or supplies will have fewer chances for survival, let alone tissue growth and/or reproduction (Anthony et al., 2002), and render the reef more vulnerable to other anthropogenic stressors.

➢ *What are the reasons for the observed temporal variability in coral bleaching between recent and earlier stress events?*

Long-term monitoring data have revealed the dynamics of coral communities to various disturbances, both natural (e.g. storms and outbreaks of *Acanthaster planci*) and anthropogenic (e.g. recreational use and blast fishing) (Phongsuwan and Chansang, 2012). We showed that some corals in the Andaman Sea have already shown an ability to acclimate (or adapt) to the heat stress during the 2016 heat event (Manuscript III), which may allow them to survive a future, warming climate. Putatively stressful experiences from natural causes, such as large short-term temperature variations due to internal waves (Manuscript I) or reduced water exchange in tide pools may play an important role in promoting phenotypic plasticity and, hence, physiological ‘frontloading’ against future change (Barshis et al., 2013). However, the results from this thesis challenge the hope that the acclimatization (or adaptation) will be fast enough to catch up with rapid climate change. *Pocillopora damicornis* and *Acropora*, for example, displayed a high increase in bleaching resistance over time (Manuscript III), but following the severe 2010 mass bleaching and mortality their populations were strongly reduced in terms of percent cover, e.g. <1% of *Acropora* at Aeo Island, Phuket compared to 25% in 2009 (N. Phongsuwan, unpublished data). Moreover, this increased bleaching resistance in 2016 was detected in a year with only moderate thermal stress in the Andaman Sea. The causes of improved thermal stress resistance and upper limits of thermal tolerance are still unknown.

However, not all corals showed improved stress resistance over time. Our long-term monitoring data also showed a decrease in bleaching resistance in *Goniastrea aspera* (Manuscript IV), which coincided with demographic changes: as the colonies grew older and larger, their bleaching susceptibility increased. This somewhat counterintuitive finding (large massive colonies may be considered more ‘robust’ than small colonies, (Johnson et al., 1995)) also appeared to contradict other results in this thesis showing that the bleaching resistance in *P. damicornis* (Manuscript III) and recovery (re-pigmentation) of *Porites lutea* and fungiid corals (Manuscript V) were independent of colony size. To explore if these conflicting results can be reconciled with life history characteristics of the respective corals, we consider species-specific differences in habitat, morphology, physiology, and reproduction. All 3 species are common in shallow waters, but *G. aspera* appears to be especially successful in reef-top environments enduring periods of desiccation during extreme tides. *G. aspera* and *P. lutea* are massive and slow-growing corals (Babcock, 1991; Tanzil et al., 2009), while *P. damicornis* is a branching fast-growing form (Martin and Le Tissier, 1988). *G. aspera* is a hermaphroditic spawner, *P. lutea* is a gonochoric spawner, and *P. damicornis* is a hermaphroditic brooder (Madin et al., 2016). The differences in growth partly reflect different energy allocations that have to be invested by the massive corals to survive in shallow water, i.e. into photoprotection and mucus production to cope with high radiation, high sedimentation and occasional desiccation. In shallow water, growth is lateral (not upwards), with the effect that mounding corals become increasingly flat. As both the photon flux and sedimentation rate reaches its maximum on a flat surface, the growth-related change in shape exacerbates the negative effect of radiation and sedimentation, leading to the observed partial mortalities in *G. aspera* in older colonies, and the formation of micro-atolls. This may explain the observed demographic effects in Manuscript IV, where bleaching-related mortality was most severe in large colonies – i.e. the colonies that due to their flattened shape had to cope most with radiation and sedimentation stress. This does not explain, however, the success of *P. lutea*, which was able to take advantage of *G. aspera*' s demise in spite of a weakened bleaching resistance (Manuscript III). Differential senescence may also have played a role, where the larger corals may have lost part of their bleaching resistance through such mechanisms as weakening photoprotection (Titlyanov, 1991). The different reproductive modes may also have affected energy allocation in the corals. Edingerand Risk (1995) showed that survivorship following large-scale disturbances appears to be correlated with the reproductive mode of the corals: brooders survived in greater proportions than spawners. They suggested that this survival preference resulted from the enhanced recruitment success of individual brooded coral planulae. Recently, Williams et al. (2015) have found differences in bacterial assemblages between different colony size classes of *Coelastrea aspera* (formerly known as *Goniastrea aspera*). A difference in microbial community may result in different successes under different environmental conditions and different thermal tolerances of holobionts (Lee et al., 2012; Ziegler et al., 2017b). Bacterial communities associated with corals, however, are found with a high species specificity regardless of location and season (Hong et al., 2009; Carlos et al., 2013). Moreover, a shift in a bacterial community under thermal stress was observed and enhanced the bleaching tolerance in some corals depending on their habitat (Ziegler et al., 2017b). This may explain why the variation of thermal tolerance in respect to colony size was not consistent in our findings.

Overall, the different and often conflicting results show the complexity of interacting environmental and biological factors contributing to the coral community responses under thermal stress, where former winners (*G. aspera*) may become losers, and former losers (*P. damicornis*) may perhaps be able to adapt as long as the rates of environmental change do not outpace the rates of biological acclimation (or adaptation).

➢ *How does bleaching affect the fitness of corals?*

Exposure to temperature stress is considered to reduce coral fitness and make corals more vulnerable to disease (Muller et al., 2008). However, with a few exceptions the causes of coral diseases are not well understood (Haapkylä et al., 2009; Miller et al., 2015). An outbreak of White Syndrome Disease were shown following thermal stress or bleaching event in the Florida, the Great Barrier Reef, and the Caribbean (Bruno et al., 2007; Miller et al., 2009; Selig et al., 2013; Precht et al., 2016). Coral disease is caused not only by high water temperatures, but many other physical causes such as light. It has been suggested that annual outbreaks in Black Band Disease on the Great Barrier Reef are driven by light intensity, whilst high temperatures were not found to have a significant effect on disease progression (Sato et al., 2011).

Available baseline data from the Andaman Sea showed cases of Ulcerative White Spot (UWS) disease in the aftermath of the 2010 mass coral bleaching event (Manuscript VII). But overall, only 22% of the corals were affected, representing no increase relative to the frequency before the bleaching event (20%), where Pink Spot (PS) disease was dominant (11% of colonies). The figures show that coral disease was not a major cause for coral reef degradation in this region after the severe 2010 mass bleaching event. UWS exhibited much lower rates of tissue loss than white syndrome. Raymundo et al. (2003) indicated that healthy colonies developed white lesions within 5 weeks after contact to diseased colonies, suggesting that infection could come from a neighbouring colony and may not be spreading from a particular source. This could mean that high temperature alone may not cause the outbreak of disease. Increased SST associated with anthropogenic factors can increase frequency of opportunistic diseases (Harvell et al., 1999). Our study, however, was carried out in remote areas where anthropogenic effects due to land run-off were limited. We thus do not know if and to what extent thermal stress and anthropogenic impacts may have weakened coral health in coastal areas and render them more vulnerable to disease.

CHAPTER 5 REFERENCES

Abrego D, Ulstrup KE, Willis BL, van Oppen MJH. 2008. Species–specific interactions between algal endosymbionts and coral hosts define their bleaching response to heat and light stress. Proc. R. Soc. B. 275: 2273-82

Abrego D, Willis BL, van Oppen MJH. 2012. Impact of light and temperature on the uptake of algal symbionts by coral juveniles. PLoS ONE 7(11): e50311

Ailsa PK, Ross JJ. 2003. Effects of hypo-osmosis on the coral *Stylophora pistillata*: nature and cause of 'low-salinity bleaching'. Mar. Ecol. Prog. Ser. 253: 145-54

Alemu JB, Clement Y. 2014. Mass coral bleaching in 2010 in the southern Caribbean. PLoS ONE 9(1): e83829

Anthony KRN, Connolly SR, Willis BL. 2002. Comparative analysis of energy allocation to tissue and skeletal growth in corals. Limnol. Oceanogr. 47: 1417-29

Anthony KRN, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R. 2009. Energetics approach to predicting mortality risk from environmental stress: A case study of coral bleaching. Funct. Ecol. 23: 539-50

Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O. 2008. Ocean acidification causes bleaching and productivity loss in coral reef builders. Proc. Natl. Acad. Sci. U.S.A. 105: 17442-46

Antonius A. 1985. Coral Diseases in the Indo-Pacific: A First Record. Mar. Ecol. 6: 197-218

Apprill AM, Gates RD. 2007. Recognizing diversity in coral symbiotic dinoflagellate communities. Mol. Ecol. 16: 1127-34

Aronson RB, Precht WF. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. Limnol. Oceanogr. 45: 251-55

Babcock RC. 1991. Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. Ecol. Monogr. 61: 225-44

Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Wilson SK, Willis BL. 2003. Identification of scleractinian coral recruits from Indo-Pacific reefs. Zool. Stud. 42

Bagnato S, Linsley BK, Howe SS. 2004. Evaluating the use of the massive coral *Diploastrea heliopora* for paleoclimate reconstruction. Plaleoceanogrphy 19: PA1032

Baird AH, Bhagooli R, Ralph PJ, Takahashi S. 2009. Coral bleaching: The role of the host. Trends Ecol. Evol. 24: 16-20

Baird AH, Cumbo VR, Leggat W, Rodriguez-Lanetty M. 2007. Fidelity and flexibility in coral symbioses. Mar. Ecol. Prog. Ser. 347: 307-09

Baird AH, Marshall PA. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar. Ecol. Prog. Ser. 237: 133-41

Baker AC. 2003. Flexibility and specificity in coral-algal symbiosis: diversity, ecology, and biogeography of *Symbiodinium*. Annu. Rev. Ecol. Evol. Syst. 34: 661-89

Baker AC, Glynna PW, c BR. 2008. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuar. Coast. Shelf. Sci. 80: 435–71

Baker AC, Starger CJ, McClanahan TR, Glynn PW. 2004. Coral reefs: Corals' adaptive response to climate change. Nature 430: 741-41

Ban NC, Pressey RL, Weeks S. 2012. Conservation Objectives and Sea-Surface Temperature Anomalies in the Great Barrier Reef. Conserv. Biol. 26: 799-809

Barkley HC, Cohen AL, Golbuu Y, Starczak VR, DeCarlo TM, Shamberger KEF. 2015. Changes in coral reef communities across a natural gradient in seawater pH. Sci. Adv. 1: e1500328

Barshis DJ, Ladner JT, Oliver TA, Seneca FO, Traylor-Knowles N, Palumbi SR. 2013. Genomic basis for coral resilience to climate change. Proc. Natl. Acad. Sci. U.S.A. 110: 1387-92

Bay LK, Doyle J, Logan M, Berkelmans R. 2016. Recovery from bleaching is mediated by threshold densities of background thermo-tolerant symbiont types in a reef-building coral. R. Soc. open sci. 3: 160322

Bay Rachael A, Palumbi Stephen R. 2014. Multilocus adaptation associated with heat resistance in reef-building corals. Curr. Biol. 24: 2952-56

Bayraktarov E, Pizarro V, Eidens C, Wilke T, Wild C. 2013. Bleaching susceptibility and recovery of colombian Caribbean corals in response to water current exposure and seasonal upwelling. PLoS ONE 8(11): e80536

Beeden R, Willis B, Raymundo LJ, Page CA, Weil E. 2008. Underwater cards for assessing coral health on Indo-Pacific reefs. Melbourne: Global environment fund coral reef targeted research (GEF-CRTR) program, Currie Commission.

Bellantuono AJ, Granados-Cifuentes C, Miller DJ, Hoegh-Guldberg O, Rodriguez-Lanetty M. 2012a. Coral thermal tolerance: Tuning gene expression to resist thermal stress. PLoS ONE 7(11): e50685

Bellantuono AJ, Hoegh-Guldberg O, Rodriguez-Lanetty M. 2012b. Resistance to thermal stress in corals without changes in symbiont composition. Proc. R. Soc. B. 279: 1100-07

Bellwood DR, Hughes TP, Folke C, Nystrom M. 2004. Confronting the coral reef crisis. Nature 429: 827-33

Bena C, van Woesik R. 2004. The impact of two bleaching events on the survival of small coral colonies (Okinawa, Japan). Bull. Mar. Sci. 75: 115-25

Berkelmans R, Jones AM, Schaffelke B. 2012. Salinity thresholds of *Acropora* spp. on the Great Barrier Reef. Coral Reefs 31: 1103-10

Berkelmans R, Oliver JK. 1999. Large-scale bleaching of corals on the Great Barrier Reef. Coral Reefs 18: 55-60

Berkelmans R, van Oppen MJH. 2006. The role of zooxanthellae in the thermal tolerance of corals: a ‘nugget of hope’ for coral reefs in an era of climate change. Proc. R. Soc. B. 273: 2305-12

Birrell CL, Mccook LJ, Willis BL, Diaz-Pulido GA. 2008. Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceangr. Mar. Biol. Annu Rev. 46: 26-63

Blakeway DR. 2005. Pattern of mortality from nature and anthropogeneic influences in Dampier corals: 2004 cyclone dredging impacts. In: Stoddart, J.A., Stoddart, S.E. (Eds.), Corals of the Dampier harbour: Their survival and reproduction during the dredging programs of 2004: 65–76

Bongaerts P, Carmichael M, Hay KB, Tonk L, Frade PR, Hoegh-Guldberg O. 2015. Prevalent endosymbiont zonation shapes the depth distributions of scleractinian coral species. R. Soc. open sci. 2

Bongaerts P, Frade PR, Ogier JJ, Hay KB, van Bleijswijk J, et al. 2013. Sharing the slope: depth partitioning of agariciid corals and associated *Symbiodinium* across shallow and mesophotic habitats (2-60 m) on a Caribbean reef. BMC Evo.l Biol. 13: 205-05

Boulotte NM, Dalton SJ, Carroll AG, Harrison PL, Putnam HM, et al. 2016. Exploring the *Symbiodinium* rare biosphere provides evidence for symbiont switching in reef-building corals. ISME. J. 10: 2693-701

Brandt ME. 2009. The effect of species and colony size on the bleaching response. Coral Reefs 28: 911–24

Bridge TCL, Hoey AS, Campbell SJ, Muttaqin E, Rudi4 E, Nur Fadli4 AHB. 2013a. Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. F1000Res. 2: 187

Bridge TCL, Hoey AS, Campbell SJ, Muttaqin E, Rudi E, et al. 2013b. Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. F1000Res. 2: 187

Brown B, Dunne R, Goodson M, Douglas A. 2002a. Experience shapes the susceptibility of a reef coral to bleaching. Coral Reefs 21: 119-26

Brown BE. 1997a. Adaptations of reef corals to physical environmental stress. In Advances in marine biology, ed. JHS Blaxter, AJ Southward, pp. 221-99: Academic Press

Brown BE. 1997b. Coral bleaching: causes and consequences. Coral Reefs 16: S129-S38

Brown BE. 2007. Coral reefs of the Andaman Sea — An integrated perspective. Oceanogr. Mar. Biol. Annu. Rev. 45: 173-94

Brown BE, Clarke KR, Warwick RM. 2002b. Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. Mar. Biol. 141: 21-29

Brown BE, Downs CA, Dunne RP, Gibb SW. 2002c. Exploring the basis of thermotolerance in the reef coral *Goniastrea aspera*. Mar. Ecol. Prog. Ser. 242: 119-29

Brown BE, Dunne R, Scoffin TP, Tissier MDAL. 1994. Solar damage in intertidal corals. Mar. Ecol. Prog. Ser. 105: 219-30

Brown BE, Dunne RP, Chansang H. 1996. Coral bleaching relative to elevated seawater temperature in the Andaman Sea (Indian Ocean) over the last 50 years. Coral Reefs 15: 151-52

Brown BE, Dunne RP, Phongsuwan N, Putchim L, Hawkridge JM. 2014. The reef coral *Goniastrea aspera*: a 'winner' becomes a 'loser' during a severe bleaching event in Thailand. Coral Reefs 33: 395-401

Brown BE, Dunne RP, Phongsuwan N, Somerfield PJ. 2011. Increased sea level promotes coral cover on shallow reef flats in the Andaman Sea, eastern Indian Ocean. Coral Reefs 30: 867-78

Brown BE, Phongsuwan N. 2012. Delayed mortality in bleached massive corals on intertidal reef flats around Phuket, Andaman Sea, Thailand. Phuket Mar. Biol. Cent. Res. Bull. 71: 43-48

Bruno J, Siddon C, Witman J, Colin P, Toscano M. 2001. El Niño related coral bleaching in Palau, Western Caroline Islands. Coral Reefs 20: 127-36

Bruno JF, Selig ER. 2007. Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. PLoS ONE 2(8): e711

Bruno JF, Selig ER, Casey KS, Page CA, Willis BL, et al. 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. PLOS Biology 5(6): e124

Buddemeier R, Fautin D. 1993. Coral bleaching as an adaptive mechanism. BioScience. 43: 320-26

Buerger P, G.M.Schmidt, M.Wall, Held C, Richter a b. 2015. Temperature tolerance of the coral *Porites lutea* exposed to simulated large amplitude internal waves (LAIW). J. Exp. Mar. Biol. Ecol. 47: 232-39

Burke L, Reytar K, Spalding M, PEerry A. 2011. Reefs at risk revisited. Washington DC: World Resources Institute.

Carilli JE, Norris RD, Black B, Walsh SM, McField M. 2010. Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. Glob. Chang. Biol. 16: 1247-57

Carlos C, Torres TT, Ottoboni LMM. 2013. Bacterial communities and species-specific associations with the mucus of Brazilian coral species. Sci. Rep. 3: 1624

Carrigan AD, Puotinen M. 2014. Tropical cyclone cooling combats region-wide coral bleaching. Glob. Chang. Biol. 20: 1604-13

Castillo K, Helmuth B. 2005. Influence of thermal history on the response of Montastrea annularis to short-term temperature exposure. Mar Biol 148: 261-70

Ceccarelli DM, Richards ZT, Pratchett MS, Cvitanovic C. 2011. Rapid increase in coral cover on an isolated coral reef, the Ashmore Reef National Nature Reserve, north-western Australia. Mar. Freshwater Res. 62: 1214-20

Cesar H, Burke L, Pet-Soede L. 2003. The economics of worldwide coral reef degradation. pp. 23. Zeist, The Netherlands: Environmental Economics Consulting, Arnhem, and WWF-Netherlands

Cesar HSJ. 2000. Coral reefs: Their functions, threats and economic value. In Collected Essays on the Economics of Coral Reefs, ed. HSJ CESAR, pp. 14-39. University of Kalmar, Sweden: CORDIO

Chabanet P, Adjeroud M, Andréfouët S, Bozec Y-M, Ferraris J, et al. 2005. Human-induced physical disturbances and their indicators on coral reef habitats: A multi-scale approach. Aquat. Living Resour. 18: 215-30

Changsang H. 1999. Coral reef maps of Thailand 2: Andaman Sea. Phuket: Coral reef management programme, department of fisheries, Thailand. 198 pp.

Chen CA, Jih-Terng W, Lee-Shing F, Ya-Wen Y. 2005. Fluctuating algal symbiont communities in *Acropora palifera* (Scleractinia: Acroporidae) from Taiwan. Mar. Ecol. Prog. Ser. 295: 113-21

Chollett I, Mumby PJ. 2013. Reefs of last resort: Locating and assessing thermal refugia in the wider Caribbean. Biol. Conserv. 167: 179-86

Coles SL. 2003. Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: a comparison to the Indo-Pacific Region. Atoll Res. Bull. 507

Coles SL, Jokiel PL. 1978. Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. Mar. Biol. 49: 187-95

Collins M, Knutti R, Arblaster J, Dufresne J-L, Fichefet T, et al. 2013. Long-term climate change: Projections, commitments and irreversibility. In Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change ed. TF Stocker, D Qin, G-K Plattner, M Tignor, SK Allen, et al, pp. 1031-106. United Kingdom and New York, USA: Cambridge University Press, Cambridge

Connell JH, Hughes TP, Wallace CC. 1997. A 30-year study of coral abundance, recruitment, and disturbance at the several scale in the space and time. Ecol. Monogr. 67: 461-88

Costanza R, d'Arge R, Groot Rd, Farber S, Grasso M, et al. 1997. The value of the world's ecosystem services and natural capital. Nature 387: 253-60

Côté IM, Darling ES. 2010. Rethinking ecosystem resilience in the face of climate change. PLoS Biology 8(7): e1000438

Császár NBM, Ralph PJ, Frankham R, Berkelmans R, van Oppen MJH. 2010. Estimating the potential for adaptation of corals to climate warming. PLoS ONE 5(3): e9751

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, te´ IMC. 2012. Evaluating life-history strategies of reef corals from species traits Ecol. Lett.

Darling ES, McClanahan TR, Côté IM. 2013. Life histories predict coral community disassembly under multiple stressors. Glob. Chang. Biol. 19: 1930-40

Davies PS. 1991. Effect of daylight variations on the energy budgets effect of daylight variations on the energy budgets of shallow-water coralsof shallow-water corals. Mar. Biol. 108: 137-44

Day T, Laura Nagel, van Oppen MJH, M. Julian Caley. 2008. Factors affecting the evolution of bleaching resistance in corals. Am. Nat. 171: E72-E88

De'ath G, Fabricius KE, Sweatman H, Puotinen M. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc. Natl. Acad. Sci. U.S.A. 109: 17995-99

Depczynski M, Gilmour JP, Ridgway T, Barnes H, Heyward AJ, et al. 2013. Bleaching, coral mortality and subsequent survivorship on a West Australian fringing reef. Coral Reefs 32: 233-38

Deschaseaux ESM, Beltran VH, Jones GB, Deseo MA, Swan HB, et al. 2014. Comparative response of DMS and DMSP concentrations in *Symbiodinium* clades C1 and D1 under thermal stress. J. Eep. Mar. Biol. Ecol. 459: 181-89

Dixon GB, Davies SW, Aglyamova GV, Meyer E, Bay LK, Matz MV. 2015. Genomic determinants of coral heat tolerance across latitudes. Science 348: 1460-62

DMCR. 2013. Corals in Thailand (in Thai). 2017: http://marinegiscenter.dmcr.go.th/km/coral_doc3/#.WXDxGYiLTIU

Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg OVE. 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. Glob. Chang. Biol. 11: 2251-65

Dunn S, Thomason J, Tissier ML, Bythell J. 2004. Heat stress induces different forms of cell death in sea anemones and their endosymbiotic algae depending on temperature and duration. Cell death and differentiation 11: 1213-22

Dunne R, Brown B. 2001. The influence of solar radiation on bleaching of shallow water reef corals in the Andaman Sea, 1993-1998. Coral Reefs 20: 201-10

Dunne RP. 2012. The record of sea temperature during the 2010 coral bleaching at Phuket, Thailand -different datasets, different perspectives -unexplained errors in hadisst 1.1. Phuket Mar. Biol. Cent. Res. Bull. 71: 11-18

Eakin CM, Morgan JA, Heron SF, Smith TB, Liu G, et al. 2010. Caribbean corals in crisis: Record thermal Stress, bleaching, and mortality in 2005. PLoS ONE 5(11): e13969

Edinger EN, Risk MJ. 1995. Preferential survivorship of brooding corals in a regional extinction. Paleobiology 21: 200-19

Edmunds PJ. 1991. Extent and effect of Black Band Disease on a Caribbean reef. Coral Reefs 10: 161-65

Edwards A, Gomez E. 2007. Reef restoration concepts and guidelines. St Lucia, Australia: The coral reef targeted research & capacity building for management program. 38 pp.

Edwards AJ, Clark S, Zahir H, Rajasuriya A, Naseer A, Rubens J. 2001. Coral bleaching and mortality on artificial and natural reefs in Maldives in 1998, sea surface temperature anomalies and initial recovery. Mar. Pollut. Bull. 42: 7-15

Elahi R, Edmunds PJ. 2007. Tissue age affects calcification in the scleractinian coral *Madracis mirabilis*. Biol. Bull. 212: 20-28

Erftemeijer PLA, Riegl B, Hoeksema BW, Todd PA. 2012. Environmental impacts of dredging and other sediment disturbances on corals: A review. Mar. Pollut. Bull. 64: 1737–65

Falter JL, Atkinson MJ, Lowe RJ, Monismith SG, Koseff JR. 2007. Effects of nonlocal turbulence on the mass transfer of dissolved species to reef corals. Limnol. Oceanogr. 52: 274-85

Fang L-s, Huang S-p, Lin K-l. 1997. High temperature induces the synthesis of heat-shock proteins and the elevation of intracellular calcium in the coral *Acropora grandis*. Coral Reefs 16: 127-31

Faraway J. 2005. Linear models with R. London, UK: Chapman & Hall.

Ferrier-Pagès C, Hoogenboom M, Houlbrèque F. 2011. The role of plankton in coral trophodynamics.

Finelli CM, Helmuth BST, Pentcheff ND, Wethey DS. 2006. Water flow influences oxygen transport and photosynthetic efficiency in corals. Coral Reefs 25: 47-57

Fisher PL, Malme MK, Dove S. 2012. The effect of temperature stress on coral-*Symbiodinium* associations containing distinct symbiont types. Coral Reefs 31: 473-85

Fitt WK, Brown BE, Warner ME, Dunne RP. 2001 Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. Coral Reefs 20: 51-56

Fitt WK, Spero HJ, Halas J, White MW, Porter JW. 1993. Recovery of the coral *Montastrea annularis* in the Florida Keys after the 1987 Caribbean “bleaching event”. Coral Reefs 12: 57-64

Foster R, Hagan A, Perera N, Gunawan CA, Silaban I, et al. 2006. Tsunami and earthquake damage to coral reefs of Aceh, Indonesia, Reef check foundation, coral restoration, California, USA

Fournier A. 2013. The story of symbiosis with zooxanthellae, or how they enable their host to thrive in a nutrient poor environment. BioSciences Master Reviews

Frieler K, Meinshausen M, Golly A, Mengel M, Lebek K, et al. 2012. Limiting global warming to 2 °C is unlikely to save most coral reefs. Nat. Clim. Chang 3: 165-70

Furby KA, Bouwmeester J, Berumen ML. 2013. Susceptibility of central Red Sea corals during a major bleaching event. Coral Reefs 32: 505-13

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide declines in Caribbean corals. Science 301: 958-60

Gates RD, Edmunds PJ. 1999. The physiological mechanisms of acclimatization in tropical reef corals. Amer. zool. 39: 30-43

GDRMN. 2010. Status of coral reefs in East Asian seas region: 2010. Japan: Ministry of the Environment.

Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS. 2013. Recovery of an Isolated coral reef system following severe disturbance. Science 340: 69-71

Glynn PW. 1991. Coral reef bleaching in the 1980s and possible connections with global warming. Trends Ecol. Evol. 6: 175-79

Glynn PW. 1996. Coral reef bleaching: facts, hypotheses and implications. Glob. Chang. Biol. 2: 495-509

Glynn PW, D'Croz L. 1990. Experimental evidence for high temperature stress as the cause of El Nifio-coincident coral mortality. Coral Reefs 8: 181-91

Golbuu Y, Victor S, Penland L, Jr DI, Emaurois C, et al. 2007. Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. Coral Reefs 26: 319–32

Gorbunov MY, Kolber ZS, Lesser MP, Falkowski PG. 2001. Photosynthesis and photoprotection in symbiotic corals. Limnol. Oceanogr. 46(1): 75-85

Goreau TF, Goreau NI, Yonge CM. 1971. Reef corals: autotrophs or heterotrophs? Biol. Bull. 141: 247-60

Goreau TJ, Cervino J, Goreau M. 1998. Rapid spread of diseases in Caribbean coral reefs. Rev. Biol. Trop. 49: 157-71

Goulet TL. 2006. Most corals may not change their symbionts. Mar. Ecol. Prog. Ser. 321: 1-7

Gove JM, Williams GJ, McManus MA, Heron SF, Sandin SA, et al. 2013. Quantifying climatological ranges and anomalies for Pacific coral reef ecosystems. PLoS ONE 8(4): e61974

Graham EM, Baird AH, Connolly SR. 2008. Survival dynamics of scleractinian coral larvae and implications for dispersal. Coral Reefs 27: 529-39

Green EP, Bruckner AW. 2000. The significance of coral disease epizootiology for coral reef conservation. Biol. Conser. 96: 347-61

Grottoli AaG, Rodrigues LJ. 2011. Bleached *Porites* compressa and *Montipora capitata* corals catabolize d13C-enriched lipids. Coral Reefs 30: 687-92

Grottoli AaG, Rodrigues LJ, Palardy JE. 2006. Heterotrophic plasticity and resilience in bleached corals. Nature 440: 1186-89

Guan Y, Hohn S, Merico A. 2015. Suitable Environmental Ranges for Potential Coral Reef Habitats in the Tropical Ocean. PLoS ONE 10(6): e0128831

Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, et al. 2012. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS ONE 7(3): e33353

Guest JR, Low J, Tun K, Wilson B, Ng C, et al. 2016. Coral community response to bleaching on a highly disturbed reef. Sci. Rep. 6: 20717

Haapkylä J, Unsworth RKF, Seymour AS, Melbourne-Thomas J, Flavell M, et al. 2009. Spatio-temporal coral disease dynamics in the Wakatobi Marine National Park, South-East Sulawesi, Indonesia. Dis. Aquat. Org. 87: 105-15

Harriott cJ, Banks SA. 1995. Recruitment of scleractinian corals in the Solitary Islands Marine Reserve, a high latitude coral-dominated community in Eastern Australia. Mar. Ecol. Prog. Ser. 123: 155-61

Harrison P, Wallace C. 1990. Reproduction, dispersal and recruitment of scleractinian corals. In Ecosystems of the World, ed. Z Dubinsky, pp. 133–207. Coral Reefs: Elsevier

Harvell C, Jordan-Dahlgren E, Merkel S, Rosenberg E, Raymundo L, et al. 2007. Coral disease, environmental drivers, and the balance between coral and microbial associates. Oceanogr. Mar. Biol. Annu. Rev. 20 (1): 172-95

Harvell CD, Kim K, Burkholder JM, Colwell RR, Epstein PR, et al. 1999. Emerging marine diseases--climate links and anthropogenic factors. Science 285: 1505-10

Hawkridge JM. 1998. Physiological and biochemical defences against environmental stressors in Cnidarians. University of Newcastle upon Tyne

Hayes RL, Bush PG. 1990. Microscopic observations of recovery in the reef-building scleractinian coral, *Montastrea annularis*, after bleaching on a Cayman reef. Coral Reefs 8: 203-09

Hench JL, Rosman JH. 2013. Observations of spatial flow patterns at the coral colony scale on a shallow reef flat. J. Geophys. Res. Oceans. 118: 1142-56

Hennige SJ, Smith DJ, Walsh S-J, McGinley MP, Warner ME, Suggett DJ. 2010. Acclimation and adaptation of scleractinian coral communities along environmental gradients within an Indonesian reef system. J. Exp. Mar. Biol. Ecol. 391: 143-52

Heron SF, Maynard JA, van Hooidonk R, Eakin CM. 2016. Warming trends and bleaching stress of the World's coral reefs 1985–2012. Sci. Rep. 6: 38402

Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, et al. 2010. Theme section on "Mesophotic Coral Ecosystems: Characterization, Ecology, and Management". Coral Reefs 29: 247-51

Hirose M, III RAK, HIDAKA M. 2000. Early development of zooxanthella-containing eggs of the corals *Pocillopora verrucosa* and *P. eydouxi* with special reference to the distribution of zooxanthellae. Biol. Bull. 199: 668-75

Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshwater Res. 50: 839-66

Hoegh-Guldberg O, Fine M, Skirving W, Johnstone R, Dove S, Strong A. 2005. Coral bleaching following wintry weather. Limnol. Oceanogr. 50(1): 265-71

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, et al. 2007. Coral reefs under rapid climate change and ocean acidification. Science 318: 1737-42

Hoegh-Guldberg O, Ross JJ. 1999. Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. Mar. Ecol. Prog. Ser. 183: 73-86

Hoeksema BW. 1991. Control of bleaching in mushroom coral populations (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life history strategy. Mar. Ecol. Prog. Ser. 4: 225-37

Hong M-J, Yu Y-T, Chen CA, Chiang P-W, Tang S-L. 2009. Influence of Species Specificity and Other Factors on Bacteria Associated with the Coral Stylophora pistillata in Taiwan. Applied and Environmental Microbiology 75: 7797-806

Hongo C, Yamano H. 2013. Species-specific responses of corals to bleaching events on anthropogenically turbid reefs on Okinawa island, Japan, over a 15-year period (1995–2009). PLoS ONE 8(4): e60952

Howells EJ, Beltran VH, Larsen NW, Bay LK, Willis BL, van Oppen MJH. 2012. Coral thermal tolerance shaped by local adaptation of photosymbionts. Nat. Clim. Chang 2: 116-20

Howells EJ, van Oppen MJH, Willis BL. 2009. High genetic differentiation and cross-shelf patterns of genetic diversity among Great Barrier Reef populations of *Symbiodinium*. Coral Reefs 28: 215-55

Hueerkamp C, Glynn PW, D'Croz L, Maté JL, Colley SB. 2001. Bleaching and recovery of five eastern Pacific corals in an El Niño-related temperature experiment. Bull. Mar. Sci. 69: 215-36

Hughes TP. 1994. Catastrophes, ohase shift, and large-scale degradation of a Caribbean coral reef. Science 265: 1547-51

Hughes TP, Connell JH. 1987. Population dynamics based on size or age? A reef-coral analysis. Am. Nat. 129: 818-29

Hughes TP, Jackson JBC. 1980. Do corals Lie about their age? Some demographic consequences of partial mortality, fission, and fusion. Science 209: 713-15

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, et al. 2017. Global warming and recurrent mass bleaching of corals. Nature 543: 373-77

Ineke W, AndrÃƒÂ© JU, Porfirio MAo, Therese A, Jan EV. 1999. Damage and recovery of four Philippine corals from short-term sediment burial. Mar. Ecol. Prog. Ser. 176: 11-15

Jackson C. 2007. Internal wave detection using the moderate resolution imaging spectroradiometer (MODIS). J. Geophys. Res. Oceans. 112

Jackson J, Donovan M, Cramer K, Lam V. 2014. Status and Trends of Caribbean Coral Reefs: 1970-2012. Gland, Switzerland: Global Coral Reef Monitoring Network, IUCN. 306 pp.

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629-37

Jan AP. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. Mar. Ecol. Prog. Ser. 177: 269-97

Jerker T. 2002. Coral recruitment following a mass mortality event. Ambio 31: 551-57

Johannes R, Wiebe W. 1970. Method for determination of coral tissue biomass and composition. Limnol. Oceanogr. 21: 540-47

Johns KA, Osborne KO, Logan M. 2014. Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef. Coral Reefs 33: 553-63

Johnson KG, Budd AF, Stemann TA. 1995. Extinction selectivity and ecology of Neogene Caribbean reef corals. Paleobiology 21: 52-73

Jokiel PL. 2004. Temperature stress and coral bleaching. In Coral health and disease, ed. E Rosenberg, Y Loya, pp. 401-25. Berlin, Heidelberg: Springer Berlin Heidelberg

Jokiel PL, Rodgers KS, Brown EK, Kenyon JC, Aeby G, et al. 2015. Comparison of methods used to estimate coral cover in the Hawaiian Islands. PeerJ 3: e954

Jones AM, Berkelmans R, van Oppen MJH, Mieog JC, Sinclair W. 2008. A community change in the algal endosymbionts of a Scleractinian coral following a natural bleaching event: field evidence of acclimatization. Proc. R. Soc. B. 275: 1359-65

Jones RJ, Bowyer J, Hoegh-Guldberg O, Blackall LL. 2004. Dynamics of a temperature-related coral disease outbreak. Mar. Ecol. Prog. Ser. 281: 63-77

Kai S, Sakai K. 2008. Effect of colony size and age on resource allocation between growth and reproduction in the corals *Goniastrea aspera* and *Favites chinensis*. Mar. Ecol. Prog. Ser. 354: 133-39

Kayanne H, Harii S, Ide Y, Akimoto F. 2002. Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. Mar. Ecol. Prog. Ser. 239: 93–103

Kenkel CD. 2008. Coral disease: baseline surveys in the Andaman Sea and Gulf of Thailand. Phuket Mar. Biol. Cent. Res. Bull. 69: 43-53

Kenkel CD, Goodbody-Gringley G, Caillaud D, Davies SW, Bartels E, Matz MV. 2013. Evidence for a host role in thermotolerance divergence between populations of the mustard hill coral (*Porites astreoides*) from different reef environments. Mol. Ecol. 22: 4335-48

Keshavmurthy S, Meng P-J, Jih-TerngWang, Kuo C-Y, Dai C-F, et al. 2014. Can resistant coral-*Symbiodinium* associations enable coral communities to survive climate change? A study of a site exposed to long-termhot water input. PeerJ 327: e327

Keshavmurthy S, Tang K-H, Hsu C-M, Gan C-H, Kuo C-Y, et al. 2017. Symbiodinium spp. associated with scleractinian corals from Dongsha Atoll (Pratas), Taiwan, in the South China Sea. PeerJ 5: e2871

Khokiattiwong S, Yu W. 2012. Note on the occurrence of high sea surface temperature in the Andaman Sea, in 2010. Phuket Mar. Biol. Cent. Res. Bull. 71: 1-9

Kinzie RA, Takayama M, Santos SR, Coffroth MA. 2001. The adaptive bleaching hypothesis: experimental tests of critical assumptions. Biol. Bull.Biol. Bull. 200: 51-58

Kirkland JB. 1991. Lipid peroxidation, protein thiol oxidation and DNA damage in hydrogen peroxide-induced injury to endothelial cells: role of activation of poly(ADP-ribose)polymerase. Biochim. Biophys. Acta 1092: 319-25

Klymak JM, Moum JN. 2003. Internal solitary waves of elevation advancing on a shoaling shelf. Geophys. Res. Lett. 30

Kohler KE, Gill SM. 2006. Coral Point Count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. Comput. Geosci. 32: 1259-69

Kuguru BL, Mgaya YD, Öhman MC, Wagner GM. 2004. The reef environment and competitive success in the Corallimorpharia. Mar. Biol. 145: 875-84

Kuo C-Y, Yuen YS, Meng P-J, Ho P-H, Wang J-T, et al. 2012. Recurrent disturbances and the degradation of hard coral communities in Taiwan. PLoS ONE 7 (8): e44364

Kushmaro A, Rosenberg E, Fine M, Haim YB, Loya Y. 1998. Effect of temperature on bleaching of the coral Oculina patagonica by Vibrio AK-1. Mar. Ecol. Prog. Ser. 171: 131-37

Kuta K, Richardson L. 2002. Ecological aspects of black band disease of corals: relationships between disease incidence and environmental factors. Coral Reefs 21: 393-98

LaJeunesse TC, Loh WKW, van Woesik R, Hoegh-Guldberg O, Schmidt GW, Fitt WK. 2003. Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean. Limnol. Oceanogr. 48: 2046-54

LaJeunesse TC, Pettay DT, Sampayo EM, Phongsuwan N, Brown B, et al. 2010a. Long-standing environmental conditions, geographic isolation and host–symbiont specificity influence the relative ecological dominance and genetic diversification of coral endosymbionts in the genus *Symbiodinium*. J. Biogeogr. 37: 785-800

LaJeunesse TC, Reyes-Bonilla H, Warner ME. 2007. Spring "bleaching" among *Pocillopora* in the Sea of Cortez, Eastern Pacific. Coral Reefs 26: 265-70

LaJeunesse TC, Smith R, Walther M, Pinzo´n J, Pettay DT, et al. 2010b. Host–symbiont recombination versus natural selection in the response of coral–dinoflagellate symbioses to environmental disturbance. Proc. R. Soc. B. 227: 2925–34

LaJeunesse TC, Thornhill DJ, Cox EF, Stanton FG, Fitt WK, Schmidt GW. 2004. High diversity and host specificity observed among symbiotic dinoflagellates in reef coral communities from Hawaii. Coral Reefs 23: 596-603

Lee OO, Yang J, Bougouffa S, Wang Y, Batang Z, et al. 2012. Spatial and species variations in bacterial communities associated with corals from the Red Sea as revealed by pyrosequencing. Appl. Environ. Microbiol. 78: 7173-84

Leggat W, Seneca F, Wasmund K, Ukani L, Yellowlees D, Ainsworth TD. 2011. Differential responses of the coral host and their algal symbiont to thermal stress. PLoS ONE 6(10): e26687

Leichter JJ, Deane GB, Stokes MD. 2005. Spatial and temporal variability of internal wave forcing on a coral Reef. J. Phys. Oceanogr. 35: 1945-62

Leichter JJ, Helmuth B, Fischer AM. 2006. Variation beneath the surface: Quantifying complex thermal environments on coral reefs in the Caribbean, Bahamas and Florida. J. Mar. Res. 64: 563-88

Leichter JJ, Stokes MD, Hench JL, Witting J, Washburn L. 2012. The island-scale internal wave climate of Moorea, French Polynesia. J. Geophys. Res. Oceans. 117

Leichter JJr, Salvatore JG. 2006. Intermittent upwelling and subsidized growth of the Scleractinian coral *Madracis mirabilis* on the deep fore-reef slope of Discovery Bay, Jamaica. Mar. Ecol. Prog. Ser. 316: 95-103

Leletkin VA. 2000. The energy budget of coral polyps. Russian J. Mar. Biol. 26: 389-298

Lesser MP. 1996. Elevated temperatures and ultraviolet radiation cause oxidative stress and inhibit photosynthesis in symbiotic dinoflagellates. Limnol. Oceanogr. 41: 271-83

Lesser MP. 1997. Oxidative stress causes coral bleaching during exposure to elevated temperatures. Coral Reefs 16: 187-92

Lesser MP. 2004. Experimental biology of coral reef ecosystems. J. Exp. Mar. Biol. Ecol. 300 217–52

Lesser MP. 2006. Oxidative stress in marine environments: Biochemistry and physiological ecology: Biochemistry and physiological ecology. Annu. Rev. Physiol. 68: 253-78

Leuzinger S, Willis BL, Anthony KRN. 2012. Energy allocation in a reef coral under varying resource availability. Mar. Biol. 159: 177-86

Lirman D, Schopmeyer S, Manzello D, Gramer LJ, Precht WF, et al. 2011. Severe 2010 cold-water event caused unprecedented mortality to corals of the florida reef tract and reversed previous survivorship patterns. PLoS ONE 6(8): e23047

Liu G, Strong AE, Skirving W. 2003. Remote sensing of sea surface temperatures during 2002 Barrier Reef coral bleaching. Eos 84: 197-44

Liu G, Strong AE, Skirving W, Arzayus LF. 2006. Overview of NOAA Coral Reef Watch program's near-real-time satellite global coral bleaching monitoring activities. Proc. 10th Int Coral Reef Symp, Okinawa, Japan: 1783-93.

Logan CA, Dunne JP, Eakin CM, Donner SD. 2014. Incorporating adaptive responses into future projections of coral bleaching. Glob. Chang. Biol. 20: 125-39

Lopez-Maury L, Marguerat S, Bahler J. 2008. Tuning gene expression to changing environments: from rapid responses to evolutionary adaptation. Nat. Rev. Genet.

Loya Y. 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. Mar. Biol. 13: 100-23

Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R. 2001. Coral bleaching: the winners and the losers. Ecol. Lett. 4: 122-31

Madin JS, Anderson KD, Andreasen MH, Bridge TCL, Cairns SD, et al. 2016. The coral trait database, a curated database of trait information for coral species from the global oceans. Sci. Data 3: 160017

Manzello DP, Brandt M, Smith TB, Lirman D, Hendee JC, Nemeth RS. 2007. Hurricanes benefit bleached corals. Proc. Natl. Acad. Sci. U.S.A. 104: 12035-39

Marshall P, Schuttenberg H. 2006. A reef manager's guide to coral bleaching. Australia: Great Barrier Reef Marine Park Authority,Townsville.

Marshall PA, Baird AH. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19: 155-63

Martin DA, Le Tissier A. 1988. The growth and formation of branch tips of *Pocillopora damicornis* (Linnaeus). J. Eep. Mar. Biol. Ecol. 124: 115-31

Martins EA, Meneghini R. 1994. Cellular DNA damage by hydrogen peroxide is attenuated by hypotonicity. Biochem. J. 299: 137-40

Maynard JA, Anthony KRN, Marshall PA, Masiri I. 2008a. Major bleaching events can lead to increased thermal tolerance in corals. Mar. Biol. 155: 173-82

Maynard JA, Turner PJ, Anthony KRN, Baird AH, Berkelmans R, et al. 2008b. ReefTemp: An interactive monitoring system for coral bleaching using high-resolution SST and improved stress predictors. Geophys. Res. Lett. 35

McClanahan TR. 2004. The relationship between bleaching and mortality of common corals. Mar. Biol. 144: 1239-45

McClanahan TR, Ateweberhan M, Ruiz Sebastián C, Graham NAJ, Wilson SK, et al. 2007. Predictability of coral bleaching from synoptic satellite and in situ temperature observations. Coral Reefs 26: 695-701

McClanahan TR, Baird AH, Marshall PA, Toscano MA. 2004. Comparing bleaching and mortality responses of hard corals between southern Kenya and the Great Barrier Reef, Australia. Mar. Pollut. Bull. 48: 327-35

McClanahan TR, Cinner JE, Graham NAJ, Daw TM, Maina J, et al. 2009. Identifying reefs of hope and hopeful actions: contextualizing environmental, ecological, and socialpParameters to respond effectively to climate change. Conserv. Biol. 23: 662-71

McGinley MP, Aschaffenburg MD, Pettay DT, Smith RT, LaJeunesse TC, Warner1 ME. 2012. *Symbiodinium* spp. in colonies of eastern Pacific *Pocillopora* spp. are highly stable despite the prevalence of low-abundance background populations. Mar. Ecol. Prog. Ser. 462: 1-7

Meesters EH, Bak RPM. 1995. Age-related deterioration of a physiological function in the branching coral *Acropora palmata*. Mar. Ecol. Prog. Ser. 121: 203-09

Middlebrook R, Hoegh-Guldberg O, Leggat W. 2008. The effect of thermal history on the susceptibility of reef-building corals to thermal stress. J. Exp. Biol. 211: 1050-56

Miller J, Muller E, Rogers C, Waara R, Atkinson A, et al. 2009. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. Coral Reefs 28: 925

Miller J, Sweet MJ, ElizabethWood, Bythell J. 2015. Baseline coral disease surveyswithin three marine parks in Sabah, Borneo. PeerJ

Miller K, Mundy C. 2003. Rapid settlement in broadcast spawning corals: implications for larval dispersal. Coral Reefs 22: 99-106

Moberg F, Folke C. 1999. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29: 215-33

Muller EM, Rogers CS, Spitzack AS, van Woesik R. 2008. Bleaching increases likelihood of disease on *Acropora palmata* (Lamarck) in Hawksnest Bay, St John, US Virgin Islands. Coral Reefs 27: 191-95

Mumby PJ. 1999. Bleaching and hurricane disturbances to populations of coral recruits in Belize. Mar. Ecol. Prog. Ser. 190: 27-35

Mumby PJ, Chisholm JRM, Edwards AJ, Andrefouet S, Jaubert J. 2001. Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. Mar. Ecol. Prog. Ser. 222: 209-16

Muscatine L, Pool RR. 1979. Regulation of numbers of intracellular algae. Proc. R. Soc. B. 204: 131-39

Nadon M-O, Stirling G. 2006. Field and simulation analyses of visual methods for sampling coral cover. Coral Reefs 25: 177-85

Nakamura T, van Woesik R. 2001. Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar. Ecol. Prog. Ser. 212: 301-04

Nozawa Y, Harrison PL. 2005. Temporal settlement patterns of larvae of the broadcast spawning reef coral *Favites chinensis* and the broadcast spawning and brooding reef coral *Goniastrea aspera* from Okinawa, Japan. Coral Reefs 24: 274-82

Obura DO. 2005. Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. Estuar. Coast. Shelf. Sci. 63: 353-72

Oliver J, Setiasih N, Marshall P, Hansen L. 2004. A global protocol for monitoring of coral bleaching. pp. 49-53. Jakarta: Penang, Malaysia and WWF Indonesia

Oliver JK, Berkelmans R, Eakin CM. 2009. Coral bleaching in space and time. In Coral bleaching, ed. MJH van Oppen, JM Lough, pp. 21-39: Springer Berlin Heidelberg

Oliver TA, Palumbi SR. 2011a. Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs 30: 429-40

Oliver TA, Palumbi SR. 2011b. Many corals host thermally resistant symbionts in high-temperature habitat. Coral Reefs 30: 241-50

Ortiz JC, Gomez-Cabrera MdC, Hoegh-Guldberg O. 2009. Effect of colony size and surrounding substrate on corals experiencing a mild bleaching event on Heron Island reef flat (southern Great Barrier Reef, Australia). Coral Reefs 28: 999

Osborne AR, Burch TL. 1980. Internal Solitons in the Andaman Sea. Science 208: 457-60

Pacherres CO, Schmidt GM, Richter C. 2013. Autotrophic and heterotrophic responses of the coral *Porites lutea* to large amplitude internal waves. J. Exp. Biol. 216: 4365-74

Pandolfi JM. 2015. Ecology: Deep and complex ways to survive bleaching. Nature 518: 43-44

Penin L, Adjeroud M, Schrimm M, Lenihan HS. 2007. High spatial variability in coral bleaching around Moorea (French Polynesia): patterns across locations and water depths. C. R. Biol. 330: 171-81

Perry RB, Schimke GR. 1965. Large-amplitude internal waves observed off the northwest coast of Sumatra. J. Geophys. Res. 70: 2319-24

Philipp E, Fabricius K. 2003. Photophysiological stress in scleractinian corals in response to short-term sedimentation. J. Eep. Mar. Biol. Ecol. 287: 57-78

Phillips WN. 2014. Tourism threats to coral reef resilience at Koh Sak, Pattaya. Proc. 1st ENRIC.: 215-30

Phongsuwan N. 1991. Recolonization of a coral reef damageed by a strom on Phuket Island. Phuket Mar. Biol. Cent. Res. Bull. 56: 75-83

Phongsuwan N, Chansang C. 1992. Assessment of coral communities in the Andaman Sea (Thailand). Proc. 7th Int. Coral Reef Sym.

Phongsuwan N, Chansang H. 2012. Repeated coral bleaching in the Andaman Sea, Thailand, during the last two decades. Phuket Mar. Biol. Cent. Res. Bull. 71: 19-41

Phongsuwan N, Yamarunpattana C, Paokanta S, Areechon P. 2008. Status of coral reefs in the Surin and Similan archipelagos, Thailand. In Ten years after bleaching - facing the consequences of climate change in the Indian Ocean.CORDIO Status report 2008, ed. DO Obura, J Tamelander, O Linden. Mombasa

Pinzón JH, Kamel B, Burge CA, Harvell CD, Medina M, et al. 2015. Whole transcriptome analysis reveals changes in expression of immune-related genes during and after bleaching in a reef-building coral. R. Soc. Open Sci. 2: 140214

PMBC. 2015. Monitoring and evaluation report of marine and coastal resources: coral and seagrass 2015 (in Thai). Nonthaburi, Thailand: Department of Marine and Coastal Resources. 156 pp.

Pomar L, Morsilli M, Hallock P, Bádenas B. 2012. Internal waves, an under-explored source of turbulence events in the sedimentary record. Earth-Sci. Rev. 111: 56-81

Pootakham W, Mhuantong W, Yoocha T, Putchim L, Sonthirod C, et al. 2017. High resolution profiling of coral-associated bacterial communities using full-length 16S rRNA sequence data from PacBio SMRT sequencing system. Sci. Rep. 7: 2774

Porter JW, Dustan P, Jaap WC, Patterson KL, Kosmynin V, et al. 2001. Patterns of spread of coral disease in the Florida Keys. Hydrobiologia 460: 1-24

Potts DC, Done TJ, Isdale PJ, Fisk DA. 1985. Dominance of a coral community by the genus *Porites* (Scleractinia). Mar. Ecol. Prog. Ser. 23: 79-84

Pratchett MS, McCowan D, Maynard JA, Heron SF. 2013. Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. PLoS ONE 8 (7): e70443

Precht WF, Gintert BE, Robbart ML, Fura R, van Woesik R. 2016. Unprecedented disease-related voral mortality in Southeastern Florida. Sci. Rep. 6: 31374

Putchim L, Thoangtham N, Yucharoen M. 2008a. Preliminary study on survival and growth of coral fragmentation on mid-water rope nursery (Thai). The 1st marine science conference, Phuket, Thailand.

Putchim L, Thongtham N, Hewett A, Chansang H. 2008b. Survival and growth of *Acropora* spp. in mid-water nursery and after transplantation at Phi Phi Islands, Andaman Sea, Thailand. Proc. 11th. Int. Coral Reef Symp., Lauderdale, Florida.

Putchim L, Yamarunpattana C, Phongsuwan N. 2012. Observations of coral disease in *Porites lutea* in the Andaman Sea following the 2010 bleaching. Phuket Mar. Biol. Cent. Res. Bull. 71: 57–62

Putnam HM, Edmunds PJ. 2011. The physiological response of reef corals to diel fluctuations in seawater temperature. J. Eep. Mar. Biol. Ecol. 396: 216-23

Putnam HM, Stat M, Pochon X, Gates RD. 2012. Endosymbiotic flexibility associates with environmental sensitivity in scleractinian corals. Proc. R. Soc. B. 279: 4352-61

Raymundo LJ, Couch CS, Harvell CD. 2008. Coral Disease Handbook: Guidelines for Assessment, Monitoring & Management. Melbourne, Australia: Coral Reef Targeted Research and Capacity Building for Management Program,.

Raymundo LJH, Harvell CD, Reynolds TL. 2003. *Porites* ulcerative white spot disease: description, prevalence, and host range of a new coral disease affecting Indo-Pacific reefs. Dis. Aquat. Org. 56: 95-104

Reaka-Kudla ML. 1997. The global biodiversity of coral reefs: A comparison with rain forests: In biodiversity II: Understanding and protecting our biological resources pp. 83-109. The National Academy of Sciences.

Reidenbach MA, Koseff JR, Monismith SG, Steinbuck JV. 2006. The effects of waves and morphology on mass transfer within branched reef corals. Limnol. Oceanogr. 51: 1134-41

Reshef L, Koren O, Loya Y, Zilber-Rosenberg I, Rosenberg E. 2006. The Coral Probiotic Hypothesis. Environmental Microbiology 8: 2068-73

Richardson LL, Goldberg WM, Carlton RG, Halas JC. 1998. Coral disease outbreak in the Florida Keys: Plague Type II. Rev. Biol. Trop. 46: 187-98

Richmond RH. 1987. Energetic relationships and biogeographical differences among fecundity, growth and reproduction in the reef coral *Pocillopora damicornis*. Bull. Mar. Sci. 41: 594-604

Riegl B. 2003. Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa). Coral Reefs 22: 433-46

Riegl B, Brancha GM. 1995. Effects of sediment on the energy budgets of four scleractinian (Bourne 1900) and five alcyonacean (Lamouroux 1816) corals. J. Exp. Mar. Biol. Ecol. 186: 259-75

Riegl B, Heine C, Branch GM. 1996. Function of funnel-shaped coral growth in a high-sedimentation environment. Mar. Ecol. Prog. Ser. 145: 87-93

Riegl B, Purkis SJ, Keck J, Rowlands GP. 2009. Monitored and modeled coral population dynamics and the refuge concept. Mar. Pollut. Bull. 58: 24-38

Rinkevich B. 1995. Restoration strategies for coral Reefs damaged by recreational activities: The Use of sexual and asexual recruits. Restor. Ecol. 3: 241-51

Rinkevich B, Loya Y. 1986. Senescence and dying signals in a reef building coral. Experientia 42: 320-22

Roder C, Fillinger L, Jantzen C, Schmidt GM, Khokiattiwong S, Richter C. 2010. Trophic response of corals to large amplitude internal waves. Mar. Ecol. Prog. Ser. 412: 113-28

Roder C, Kattner G, Jantzen C, Phongsuwan N, Schmidt GM, Richter C. 2011. Metabolic plasticity of the corals *Porites lutea* and *Diploastrea heliopora* exposed to large amplitude internal waves. Coral Reefs 30: 57–69

Rodrigues LJ, Grottoli AaG. 2007. Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnol. Oceanogr. 52: 1874-82

Rodríguez-Troncoso AP, Carpizo-Ituarte E, Pettay DT, Warner ME, Cupul-Magaña AL. 2014. The effects of an abnormal decrease in temperature on the Eastern Pacific reef-building coral *Pocillopora verrucosa*. Mar. Biol. 161: 131-39

Rosenberg E, Ben-Haim Y. 2002. Microbial diseases of corals and global warming. Environmental Microbiology 4: 318-26

Roth MS, Goericke R, Deheyn DD. 2012. Cold induces acute stress but heat is ultimately more deleterious for the reef-building coral *Acropora yongei*. Sci. Rep. 2 : 240

Rotmann S, Thomas SRI. 2012. Coral tissue thickness as a bio-indicator of mine-related turbidity stress on coral reefs at Lihir Island, Papua New Guinea. Oceanogr. 25(4): 52-63

Rowan R. 2004. Thermal adaptation in reef coral symbionts. Nature 430

Rowan R, Knowlton N, Baker A, Jara J. 1997. Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. Nature 388: 265-69

Rützler K, Santavy DL. 1983. The Black Band Disease of Atlantic Reef Corals. Mar. Ecol. 4: 301-19

Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O. 2008. Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proc. Natl. Acad. Sci. U.S.A. 105: 10444-49

Sato Y, Bourne DG, Willis BL. 2011. Effects of temperature and light on the progression of black band disease on the reef coral, *Montipora hispida*. Coral Reefs 30: 753

Saxby T, Dennison WC, Hoegh-Guldberg O. 2003. Photosynthetic responses of the coral *Montipora digitata* to cold temperature stress. Mar. Ecol. Prog. Ser. 248: 85-97

Schmidt GM, Phongsuwan N, Jantzen C, Roder C, Khokiattiwong S, Richter C. 2012. Coral community composition and reef development at the Similan Islands, Andaman Sea, in response to strong environmental variations. Mar. Ecol. Prog. Ser. 113: 113-26

Schmidt GM, Richter C. 2013. Coral growth and bioerosion of *Porites lutea* in response to large amplitude internal waves. PLoS ONE 8(12): e73236

Schmidt GM, Wall M, Taylor M, Jantzen C, Richter C. 2016. Large-amplitude internal waves sustain coral health during thermal stress. Coral Reefs 35: 869–81

Schoepf V, Stat M, Falter JL, McCulloch MT. 2015. Limits to the thermal tolerance of corals adapted to a highly fluctuating, naturally extreme temperature environment. Sci. Rep. 5: 17639

Scoffin T, Brown B, Dunne R, Le Tissier M. 1997. The controls on growth form of intertidal massive corals, Phuket, South Thailand. PALAIOS 12: 237–48

Scoffin TP, Tudhope AW, Brown BE, Chansang H, Cheeney RF. 1992. Patterns and possible environmental controls of skeletogenesis of *Porites lutea*, South Thailand Coral Reefs 11: 1-11

Scott A, Harrison PL, Brooks LO. 2013. Reduced salinity decreases the fertilization success and larval survival of two scleractinian coral species. Mar. Environ. Res. 92: 10-14

Selig ER, Drew Harvell C, Bruno JF, Willis BL, Page CA, et al. 2013. Analyzing the relationship between ocean temperature anomalies and coral disease outbreaks at broad spatial scales. In Coral reefs and climate change: Science and management, pp. 111-28: American Geophysical Union

Shashar N, Kinane S, Jokiel PL, Patterson MR. 1996. Hydromechanical boundary layers over a coral reef. J. Eep. Mar. Biol. Ecol. 199: 17-28

Shenkar N, Fine M, Loya Y. 2005. Size matters: bleaching dynamics of the coral *Oculina patagonica*. Mar. Ecol. Prog. Ser. 294: 181-88

Sheppard C. 2009. Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: comparison with satellite data and relevance to coral refuges. Coral Reefs 28: 399-403

Shlesinger Y, Loya Y. 1991. Larval development and survivorship in the corals *Favia favus* and *Platygyra lamellina*. Hydrobiologia 216/217: 101-08

Sköld HN, Asplund ME, Wood CA, Bishop JDD. 2011. Telomerase deficiency in a colonial ascidian after prolonged asexual propagation. J. Exp. Zool. (Mol. Dev. Evol.) 316B: 276-83

Smith DJ, Walsh S-J, McGinley MP. 2005. Is photoinhibition of zooxanthellae photosynthesis the primary cause of thermal bleaching in corals? Glob. Chang. Biol. 11: 1-11

Smith EG, Vaughan GO, Ketchum RN, McParland D, Burt JA. 2017. Symbiont community stability through severe coral bleaching in a thermally extreme lagoon. Sci. Rep. 7: 2428

Smith WHF, Sandwell DT. 1997. Global sea floor topography from satellite altimetry and ship depth soundings. Science 277: 1956-62

Spalding MD, Ravilious C, Green EP. 2001. World atlas of coral reefs. Berkeley, USA: University of California.

Stafford-Smith MG. 1993. Sediment-rejection efficiency of 22 species of Australian scleractinian corals. Mar. Biol. 115: 229-43

Stat M, Loh WKW, LaJeunesse TC, Hoegh-Guldberg O, Carter DA. 2009a. Stability of coral–endosymbiont associations during and after a thermal stress event in the southern Great Barrier Reef. Coral Reefs 28: 709–13

Stat M, Pochon X, Cowie ROM, Gates RD. 2009b. Specificity in communities of *Symbiodinium* in corals from Johnston Atoll. Mar. Ecol. Prog. Ser. 386: 83-96

Storlazzi CD, Field ME, Cheriton OM, Presto MK, Logan JB. 2013. Rapid fluctuations in flow and water-column properties in Asan Bay, Guam: implications for selective resilience of coral reefs in warming seas. Coral Reefs 32: 949-61

Sujirachato P, Thamrongnawasawat T, Jantrarotai P, Thongtham N, Worachananant S. 2013. Survival rate of coral fragments transplanted by different methods. Galaxea, Journal of coral reef studies Special Issue: 351-58

Sutherland KP, Porter JW, Torres C. 2004. Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. Mar. Ecol. Prog. Ser. 273: 273-302

Sutthacheep M, Yucharoen M, Klinthong W, Pengsakun S, Sangmanee K, Yeemin T. 2012. Coral mortality following the 2010 mass bleaching event at Kut Island, Thailand. Phuket Mar. Biol. Cent. Res. Bull. 71: 83–92

Szmant AM. 1986. Reproductive ecology of Caribbean reef corals. Coral Reefs 5: 43-53

Szmant AM. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? Estuaries 25: 743-66

Tanzil JTI, Brown BE, Dunne RP, Lee JN, Kaandorp JA, Todd PA. 2013. Regional decline in growth rates of massive *Porites* corals in Southeast Asia. Glob. Chang. Biol. 19: 3011-23

Tanzil JTI, Brown BE, Tudhope AW, Dunne RP. 2009. Decline in skeletal growth of the coral *Porites lutea* from the Andaman Sea, South Thailand between 1984 and 2005. Coral Reefs 28: 519-28

Thomas FIM, Atkinson MJ. 1997. Ammonium uptake by coral reefs: Effects of water velocity and surface roughness on mass transfer. Limnol. Oceanogr. 42: 81-88

Thomas L, Kendrick GA, Kennington WJ, Richards ZT, Stat M. 2014. Exploring *Symbiodinium* diversity and host specificity in *Acropora* corals from geographical extremes of Western Australia with 454 amplicon pyrosequencing. Mol. Ecol. 23: 3113-26

Thomas L, Kennington WJ, Evans RD, Kendrick GA, Stat M. 2017. Restricted gene flow and local adaptation highlight the vulnerability of high-latitude reefs to rapid environmental change. Glob. Chang. Biol. 23: 2197-205

Thongtham N. 2010. Coral reef rehabilitation in Thailand. Phuket: Department of Marine Coastal Resources Press. 49 pp.

Thongtham N, Chansang H. 2008. Transplantation of *Porites lutea* to rehabilitate degraded coral reef at Maiton Island, Phuket, Thailand. In Proc. 12th Int. Coral Reef Symp., ed. D Yellowlees, T Hughes. Cairns, Australia: James Cook University

Thongtham N, Phongsuwan N. 2012. Thailand's response plan on the 2010 coral bleaching. Phuket Mar. Biol. Cent. Res. Bull. 70: 111-16

Thornhill DJ, Rotjan RD, Todd BD, Chilcoat GC, Iglesias-Prieto R, et al. 2011. A connection between colony biomass and death in Caribbean reef-building corals. PLoS ONE 6(12): e29535

Trapon ML, Pratchett MS, Adjeroud M, Hoey AS, Baird AH. 2013. Post-settlement growth and mortality rates of juvenile scleractinian corals in Moorea, French Polynesia versus Trunk Reef, Australia. Mar. Ecol. Prog. Ser. 488: 157-70

Ulstrup KE, Ray B, Peter JR, Madeleine JHvO. 2006. Variation in bleaching sensitivity of two coral species across a latitudinal gradient on the Great Barrier Reef: the role of zooxanthellae. Mar. Ecol. Prog. Ser. 314: 135-48

UNEP-WCMC, WorldFish Centre, WRI T. 2010. Global distribution of coral reefs, compiled from multiple sources including the Millennium coral reef mapping project Version 1.3. ed. IMaRS-USF, I (2005), I-U (2005), Sea (2001). Cambridge (UK): UNEP world conservation monitoring Centre

van Hooidonk R, Maynard A, Planes S. 2013. Temporary refugia for coral reefs in a warming world. Nat. Clim. Chang 3: 508-11

van Hooidonk RJ, Manzello DP, Moye J, Brandt ME, Hendee JC, et al. 2012. Coral bleaching at Little Cayman, Cayman Islands 2009. Estuar. Coast. Shelf. Sci. 106: 80-84

van Woesik R, Irikawa A, Anzai R, Nakamura T. 2012. Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. Coral Reefs 31: 633-39

van Woesik R, Sakai K, A. Ganase1 YL. 2011. Revisiting the winners and the losers a decade after coral bleaching. Mar. Ecol. Prog. Ser. 434: 67-76

Vargas-Ángel B, Looney EE, Vetter OJ, Coccagna EF. 2011. Severe, widespread El Nino-associated coral bleaching in the US Phoenix islands. Bull. Mar. Sci. 87: 623-38

Veal CJ, Carmi M, Fine M, Hoegh-Guldberg O. 2010. Increasing the accuracy of surface area estimation using single wax dipping of coral fragments. Coral Reefs 29: 893-97

Veron J, Pichon M. 1976. Scleractinia of Eastern Australia. Townsville, Australia: Australian Institute of Marine Science.

Veron JEN. 1986. Corals of Australia and the Indo-Pacific. London: Angus & Robertson Publishers.

Veron JEN. 2000. Corals of the World, vols. 1–3. pp. 1410. Townsville, Australia: Australian Institute of Marine Science.

Vlasenko V, Hutter K. 2002. Numerical experiments on the breaking of solitary internal waves over a slope–shelf topography. J. Phys. Oceanogr. 32: 1779-93

Vlasenko V, Stashchuk N. 2007. Three-dimensional shoaling of large-amplitude internal waves. J. Geophys. Res. Oceans. 112

Wagner DE, Kramer P, van Woesik R. 2010. Species composition, habitat, and water quality influence coral bleaching in southern Florida Mar. Ecol. Prog. Ser. 408: 65–78,

Wall M, Putchim L, Schmidt GM, Jantzen C, Khokiattiwong S, Richter C. 2015. Large-amplitude internal waves benefit corals during thermal stress. Proc. R. Soc. B. 282

Wall M, Schmidt GM, Janjang P, Khokiattiwong S, Richter C. 2012. Differential impact of monsoon and large amplitude internal waves on coral reef development in the Andaman Sea. PLoS ONE 7(11): e50207

Wang J-T, Meng P-J, Chen Y-Y, Chen CA. 2012. Determination of the thermal tolerance of *Symbiodinium* using the activation energy for inhibiting photosystem II activity. Zool. Stud. 51: 137-42

Wang Y-H, Dai C-F, Chen Y-Y. 2007. Physical and ecological processes of internal waves on an isolated reef ecosystem in the South China Sea. Geophys. Res. Lett. 34

Webster PJ, Moore AM, Loschnigg JP, Leben RR. 1999. Coupled ocean-atmosphere dynamics in the Indian Ocean during 1997-98. Nature 401: 356-60

Weil E, Urreiztieta, Garzón-Ferreira J. 2000. Geographic variability in the incidence of coral and octocoral diseases in the wider Caribbean. Proc 9th Int Coral Reef Symp, Bali.

Weis VM. 2010. The susceptibility and resilience of corals to thermal stress: adaptation, acclimatization or both? Mol. Ecol. 19: 1515-17

Wessel P, Smith WHF. 1996. A global, self-consistent, hierarchical, high-resolution shoreline database. J. Geophys. Res. Solid Earth 101: 8741-43

West JM, Salm RV. 2003. Resistance and resilience to coral bleaching: Implications for coral reef conservation and management. Conserv. Biol. 17: 956–67

Wicks LC, Gardner JPA, Davy SK. 2012. Host tolerance, not symbiont tolerance, determines the distribution of coral species in relation to their environment at a Central Pacific atoll. Coral Reefs 31: 389-98

Wilkinson C. 2008. Status of coral reefs of the world: 2008. pp. 296. Townsville, Australia: Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre.

Williams AD, Brown BE, Putchim L, Sweet MJ. 2015. Age-related shifts in bacterial diversity in a reef coral. PLoS ONE 10(12): e0144902

Williams GJ. 2011. Outbreak of *Acropora* white syndrome following a mild bleaching event at Palmyra Atoll, Northern Line Islands, Central Pacific. Coral Reefs 30: 621

Williams GJ, Knapp IS, Maragos JE, Davy SK. 2010. Modeling patterns of coral bleaching at a remote Central Pacific atoll. Mar. Pollut. Bull. 60: 1467-76

Willis BL, Page CA, Dinsdale EA. 2004. Coral Disease on the Great Barrier Reef. In Coral Health and Disease, ed. E Rosenberg, Y Loya, pp. 69-104. Berlin, Heidelberg: Springer Berlin Heidelberg

WMO. 2010. Climate, carbon and coral reefs.

Wolanski E, Delesalle B. 1995. Upwelling by internal waves, Tahiti, French Polynesia. Cont. Shelf. Res. 15: 357-68

Wolanski E, Pickard G. 1983. Upwelling by internal tides and kelvin waves at the continental shelf break on the Great Barrier Reef. Mar. Freshw. Res. 34: 65-80

Wooldridge SA. 2013. Breakdown of the coral-algae symbiosis: towards formalising a linkage between warm-water bleaching thresholds and the growth rate of the intracellular zooxanthellae. Biogeosciences 10: 1647-58

XiuBao L, Hui H, JianSheng L, JianHui Y, Cheng Y, et al. 2013. Coral community changes in response to a high sedimentation event: A case study in southern Hainan Island. Chin. Sci. Bull. Mar. Sci. 58: 1028-37

Yang S-Y, Keshavmurthy S, Obura D, Sheppard CRC, Visram S, Chen CA. 2012. Diversity and distribution of *Symbiodinium* associated with seven common coral species in the Chagos Archipelago, central Indian Ocean. PLoS ONE 7(5): e35836

Yee SH, Santavy DL, Barron MG. 2008. Comparing environmental influences on coral bleaching across and within species using clustered binomial regression. Ecol. Model. 218: 162–74

Yeemin T, Saenghaisuk C, Yucharoen M, Klinthong W, Sutthacheep M. 2012. Impact of the 2010 coral bleaching event on survival of juvenile coral colonies in the Similan Islands, on the Andaman Sea coast of Thailand. Phuket Mar. Biol. Cent. Res. Bull. 70: 93–102

Yeemin T, Sutthacheep M, Pettongma R. 2006. Coral reef restoration projects in Thailand. Ocean Coast Manag. 49: 562-75

Yucharoen M, Putchim L, Thoangtham N. 2008. Survival and growth of corals after transplantation at Cape Panwa, Phuket (in Thai). The 1st marine science conference, Phuket, Thailand. Department of marine and coastal resources.

Yucharoen M, Putchim L, Thongtham N, Charoenphol A, Laemkha S. 2011. Coral transplantation at Hae Island, Phuket (Thai abstract). The 2nd marine science conference, Phuket, Thailand. Ramkhamhaeng University.

Yuyama I, Higuchi T. 2014. Comparing the effects of symbiotic algae (*Symbiodinium*) clades C1 and D on early growth stages of *Acropora tenuis*. PLoS ONE 9(6): e98999

Yuyama I, Nakamura T, Higuchi T, Hidaka M. 2016. Different stress tolerances of juveniles of the coral *Acropora tenuis* associated with clades C1 and D *Symbiodinium*. Zool. Stud. 55

Zhanga Z, Lowea R, Falter J, Ivey G. 2011. A numerical model of wave- and current-driven nutrient uptake by coral reef communities. Ecol. Modell. 222: 1456–70

Ziegler M, Arif C, Burt JA, Dobretsov S, Roder C, et al. 2017a. Biogeography and molecular diversity of coral symbionts in the genus Symbiodinium around the Arabian Peninsula. J. Biogeogr. 44: 674-86

Ziegler M, Roder C, Büchel C, Voolstra CR. 2015. Niche acclimatization in Red Sea corals is dependent on flexibility of host-symbiont association. Mar. Environ. Res. 533: 149-61

Ziegler M, Seneca FO, Yum LK, Palumbi SR, Voolstra CR. 2017b. Bacterial community dynamics are linked to patterns of coral heat tolerance. Nat. Commun. 8: 14213

CHAPTER 6 APPENDICES

APPENDIX 1: Supplements to Manuscript I*:*

Large-amplitude internal waves benefit corals during thermal stress

Sublementary Matrials and Methods:

1. *(*d*)* Data analysis*:*

*(*i*)* Temperature analysis – site specific temperature indices*:*

Satellite degree heating weeks (DHW_s) were derived from the ReefGIS data base (http://reefgis.reefbase.org/ default.aspx? wms=RGWDHW provided by ReefBase) by using the maximum DHW value determined for May 2010 (the time of the thermal stress period and bleaching monitoring) for each location. Where data were unavailable (e.g. Tachai and Bon were located too close to land with no valid SST estimate), the nearest pixels were used.

In situ temperature data were decomposed into weekly means and residuals to the long-term climatological maximum monthly mean SST *(*MMM*)* to calculate temperature anomalies as DHW_f (Liu et al., 2003). DHW_f were derived for the time of bleaching monitoring in May 2010 by considering the weakly residuals of the 12 weeks prior to that time point; residuals were only summed if they were ≥ 1°C (i.e. temperature above the NOAA bleaching threshold of 30.62°C). To calculate MMM long-term temperature data were derived from remotely sensed SST using Advanced Very High Resolution Radiometer *(*http*:*//ncdc.noaa.gov/thredds/dodsC/oisst*/*NetCDF/AVHRR*/*, OISST-V2-AVHRR_agg, Long*:* 97.4E, Lat*:* 8.4N*)* for the time period 1985 to 2009 (MMM = 29.62°C).

In order to receive a measure of the intensity of LAIW cooling the temperature anomalies were calculated as cumulative degree days *(*DDC in *[*°C d*])* according to Leichter and Genovese (Leichter and Genovese*,* 2006). Here we only considered temperature drops as cooling during the heat anomaly period if they fell below the NOAA bleaching threshold *(*30.62°C*)*. Each single temperature value was subtracted from the bleaching threshold. The negative temperature anomalies were integrated over time.

Supplementary tables:

Table 3.1.S1. Cover of corallimorpharian at each site during thermal stress and recovery period. Percentage of corallimorpharian cover for the different exposed west (W) and sheltered east (E) sites (Tachai W (TW), Payang W (PW), Miang W (MW), Similan W (SiW), Racha W (RW), Surin W (SuW), Bon W (BW), Racha E (RE), Payang E (PE), Miang E (ME), Similan E (SiE) and Surin E (SuE)) observed during the bleaching monitoring in May and recovery period in December 2010 in 15 m water depth.

% cover corallimorpharian		
sites/time	**May 2010**	**December 2010**
TW	41.85	33.81
PW	0.00	0.00
MW	0.00	0.00
SiW	0.00	0.00
RW	0.92	0.00
SuW	0.00	0.00
BW	0.00	0.00
RE	0.00	0.00
PE	0.00	0.00
ME	0.00	0.00
SiE	0.00	0.00
SuE	0.00	0.00

Supplemental figures:

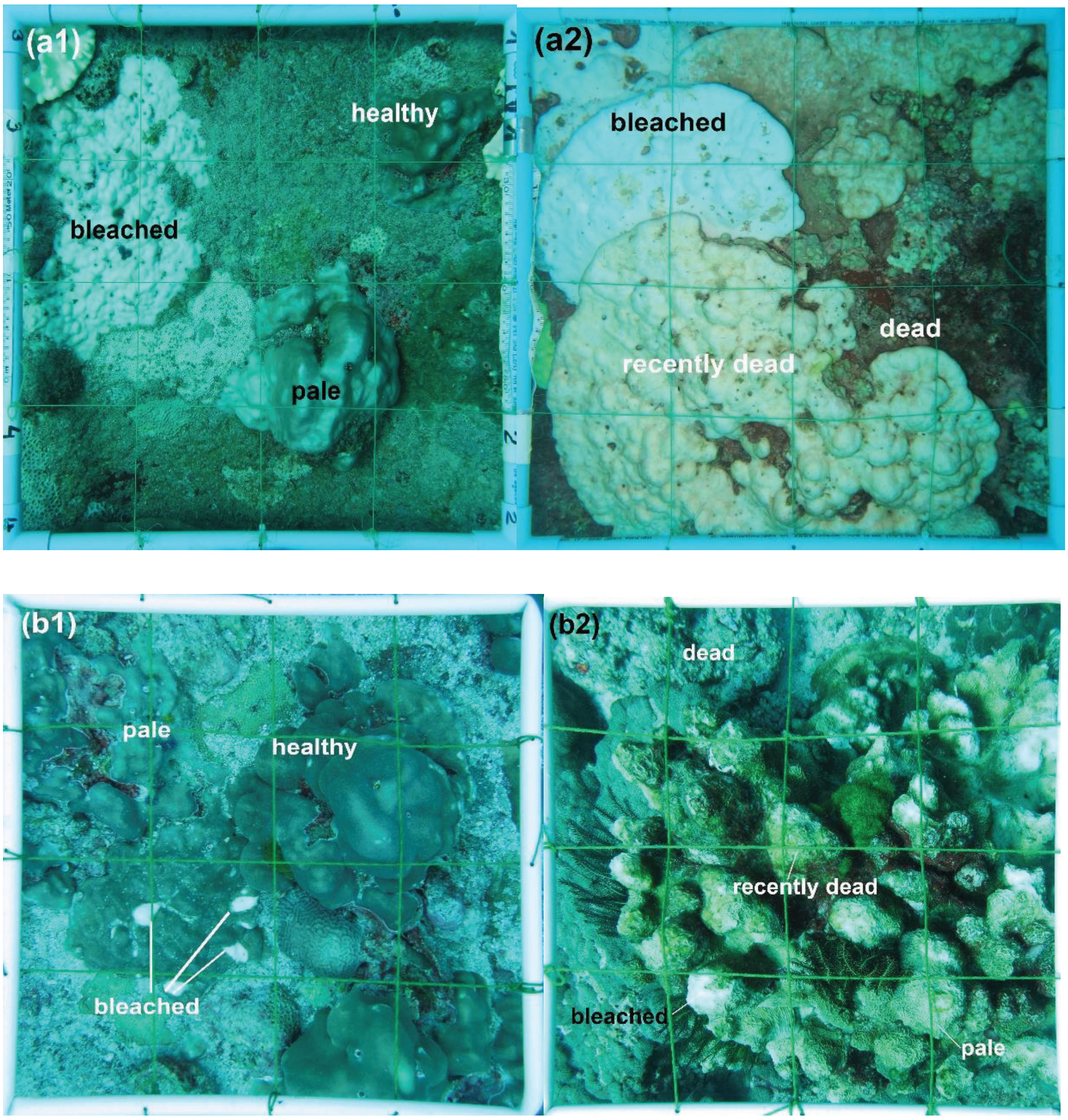


Figure 3.1.S1. Photoquadrats taken in May (a1,2) and December (b1,2) that illustrate the different bleaching categories (‘healthy’, ‘pale’, ‘bleached’, ‘recently dead’ and ‘dead’).

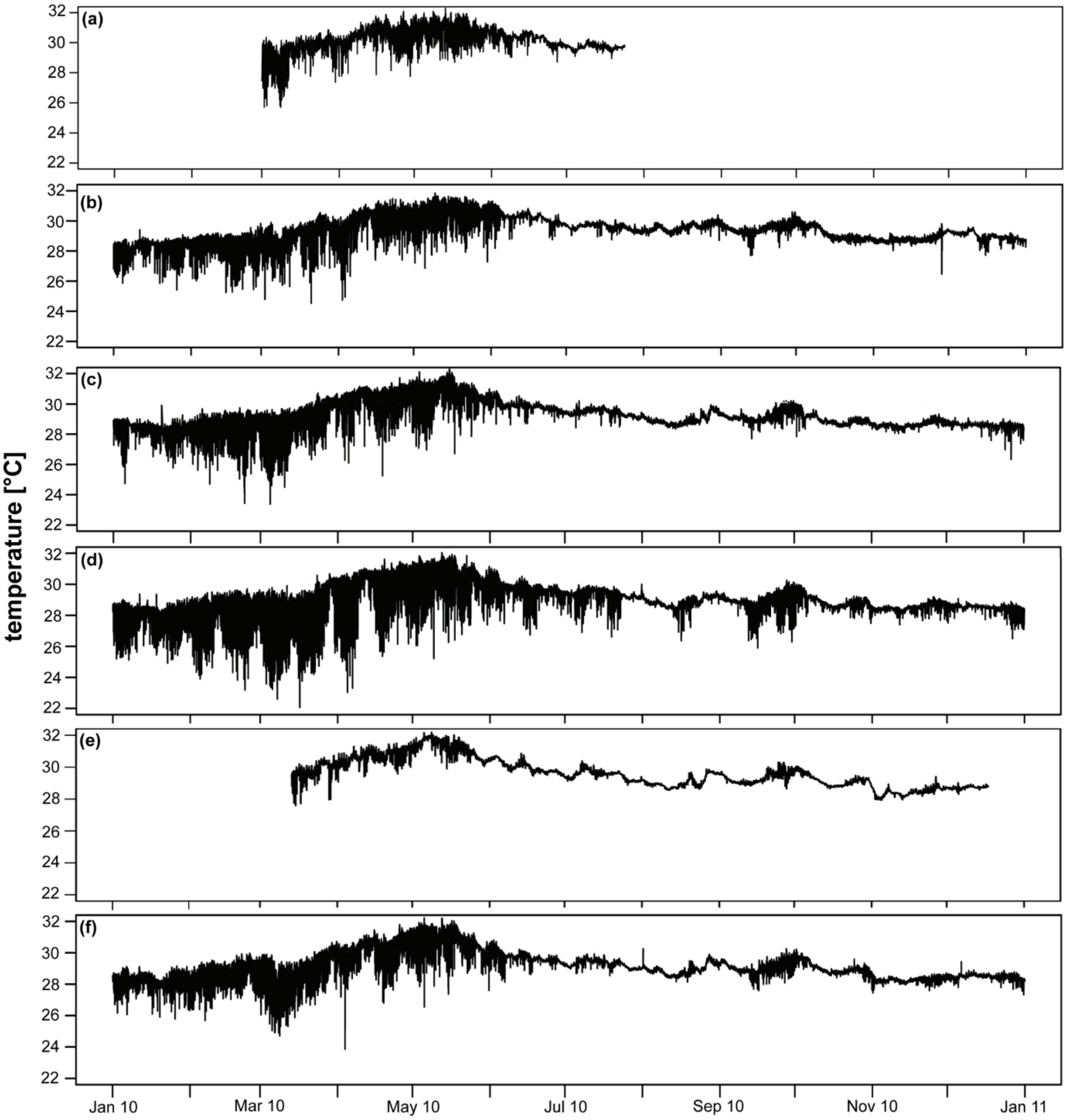


Figure 3.1.S2. Temperature record from additional sites for the period logger data were available. Temperature record during the bleaching year 2010 derived for exposed west (W) and sheltered east (E) sites ((a) Racha E, (b) Racha W, (c) Bon W, (d) Tachai W, (e) Surin E and (f) Surin W) measured at 15 m water depth expect Racha East temperature record derived from 20 m water depth.

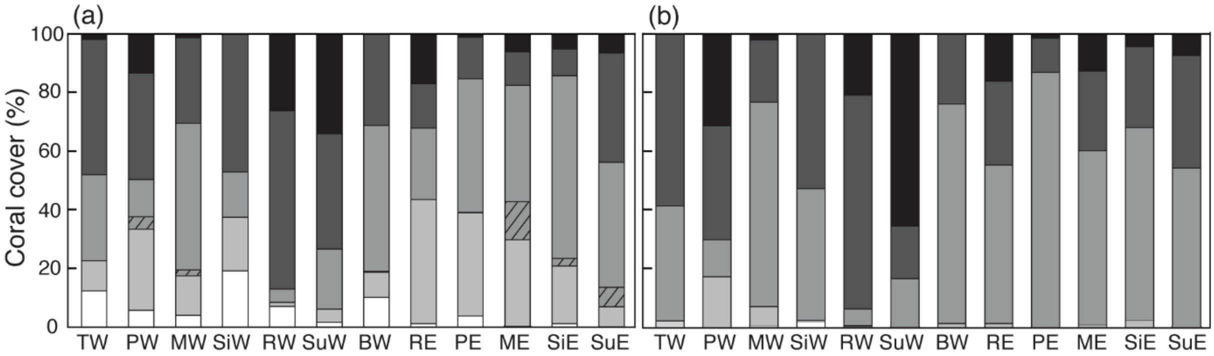


Figure 3.1.S3. Coral community composition. Coral community composition (Pocilloporidae (white), *Acropora* (light grey), *Porites* branching (grey-stripped), *Porites* massive (grey), other (dark grey) and *Diploastrea* (black) arranged from bottom to the top from the most bleaching susceptible to least susceptible taxa) as a fraction of coral cover during the bleaching event in May (a) and recovery phase in December 2010 (b). All data are displayed for all exposed west (W) and sheltered east (E) sites (Tachai W (TW), Payang W (PW), Miang W (MW), Similan W (SiW), Racha W (RW), Surin W (SuW), Bon W (BW), Racha E (RE), Payang E (PE), Miang E (ME), Similan E (SiE) and Surin E (SuE)). Sites are arranged from highest to lowest cooling left to right.

Figure 3.1.S4. Corallimorpharian space competitors. Corallimorpharian space invaders impact the reef in Tachai west covering 42% of the available substrate. Image was taken during the bleaching monitoring in May 2010.

APPENDIX 2: Supplements to Manuscript II*:*

Living in a highly fluctuating environment: how does it shape thermal tolerance across coral taxa?

1. Sea Temperature conditions

There were notable differences of temperature pattern between east and west of Meang Island between January to December 2010 (Fig. 3.2.S1). West site were exposed to frequent and strong cold water pulses, which were were less intense on the east: minimum temperature was 22°C and 25.2°C at the west and east, respectively. Daily mean sea temperature at east site was increasing and reached bleaching threshold on 23 March, 4 days before west sites. Total day with mean daily temperature exceeded threshold temperature (heat day) was 51 and 84 days at west and east site, respectively. Moreover, heat day at east site was continuing since it began, while west site was interrupted by cooling days (mean daily temperature < 30.1).

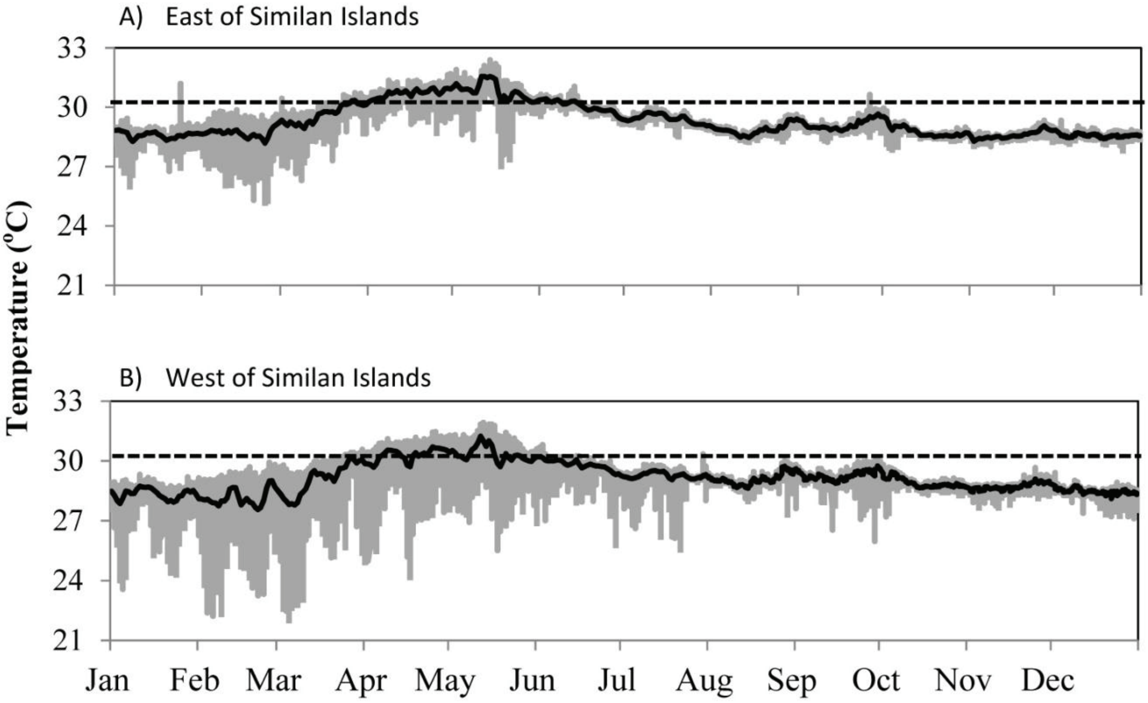


Figure 3.2.S1. Record of temperature during the study period between January and December 2010. Gray line is displaying the difference between protected (A) and exposed (B), data were measured at 15 m water depth at east and west of Miang Island, respectively. Solid black line represents mean daily temperature and dotted reference line shows the bleaching threshold temperature for coral reefs in this region (30.1°C, cf. Brown *et al.,* 1996).

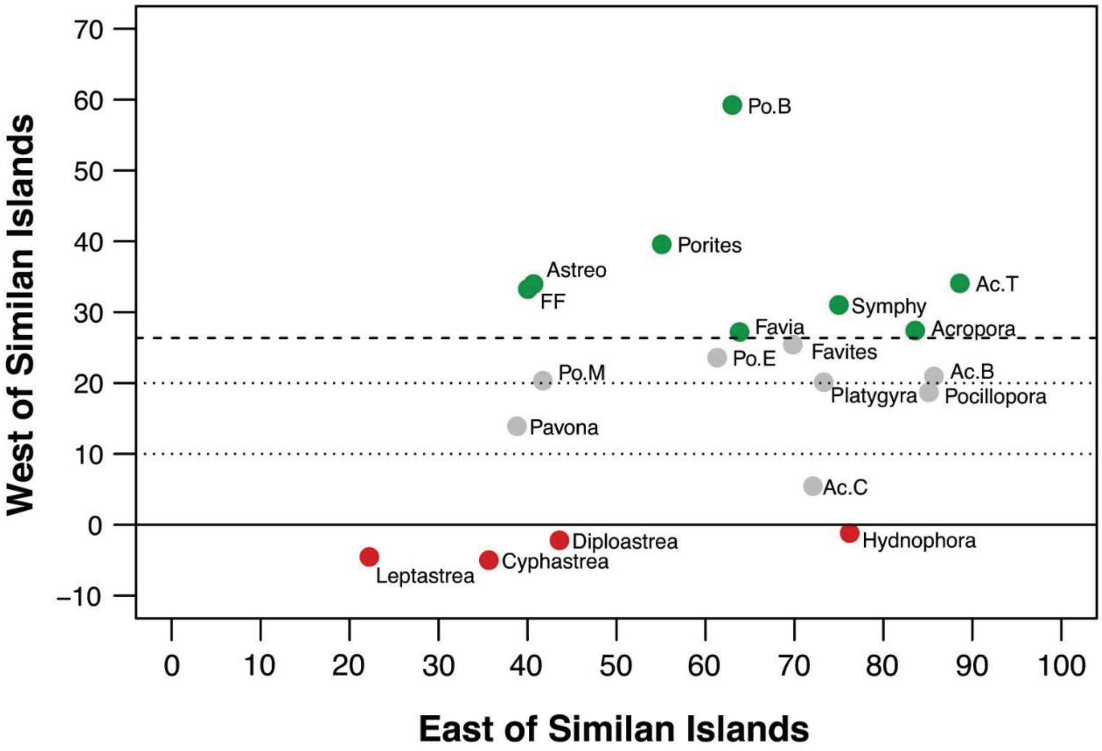


Figure 3.2.S2*:* Resdidual plot. Resudiuals were calculated from a 1:1 rel ationship between bleaching response of east and west Similan Island coral genera. Red dots are below the 1:1 relationship indicating a stronger bleaching response on the west compared to the east.

APPENDIX 3: Supplements to Manuscript III:

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

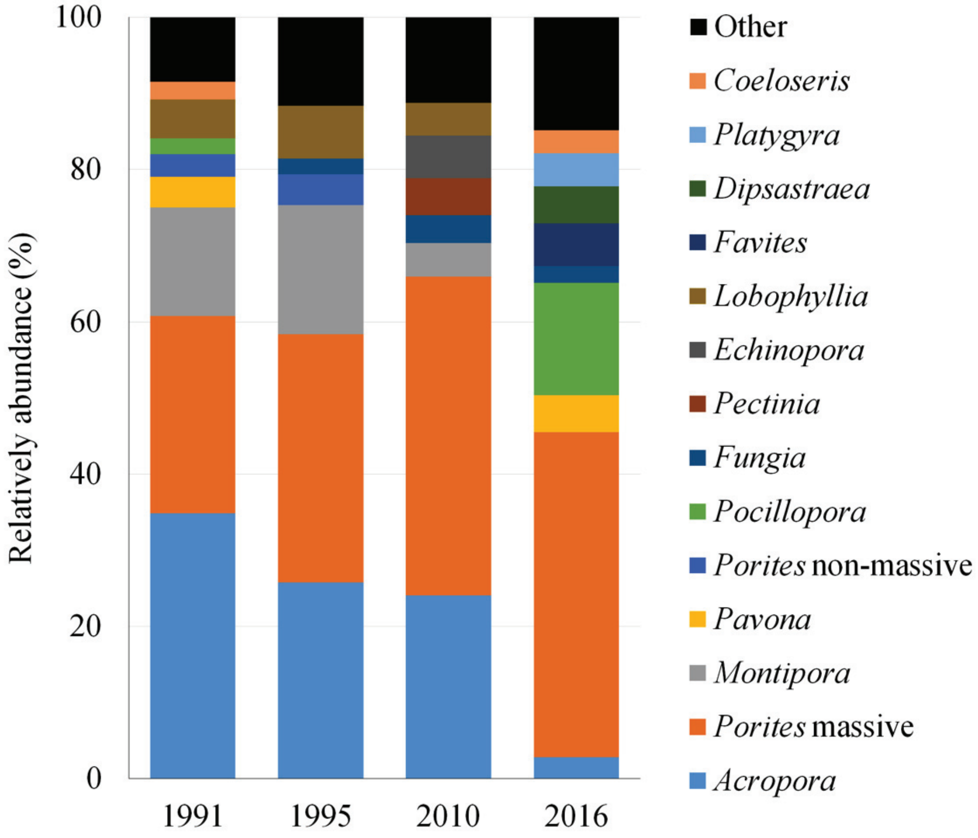


Fig 3.3.S1. Coral composition (by genus) at sites around the southern Phuket sea region regardless of bleaching status in the bleaching years 1991, 1995, 2010, and 2016. Differential mortality led to the near disappearance of branching species (e.g. *Acropora*), and increased dominance of massive *Porites* over this 25y period.

Table 3.3.S1: ANOVA results for coral bleaching susceptibility (BMI) difference during the 2016 bleaching event of 8 individual taxa as a function of site. Statistical analyses were performed with the program SPSS 15.00 for Windows. The preliminary assumption was the existence of normal distribution (Levene's test for homogeneity of variances, p>0.05).

Acropora					
	SS	df	MS	F	Sig.
Between Groups	87.747	4	21.937	0.694	0.613
Within Groups	315.987	10	31.599		
Total	403.733	14			
Considered sites: Panwa, Lone, Hae, Maiton, Tang-khen					
Dipsastraea					
	SS	df	MS	F	Sig.
Between Groups	571.076	4	142.769	1.38	0.315
Within Groups	930.94	9	103.438		
Total	1502.016	13			
Considered sites: Panwa, Lone, Hae, Racha, Tang-khen					
Favites					
	SS	df	MS	F	Sig.
Between Groups	1012.275	4	253.069	1.847	0.197
Within Groups	1369.941	10	136.994		
Total	2382.216	14			
Considered sites: Panwa, Lone, Hae, Racha, Tang-khen					
Goniastrea					
	SS	df	MS	F	Sig.
Between Groups	896.0291	3	298.6764	3.255327	0.080803
Within Groups	734.0002	8	91.75003		
Total	1630.029	11			
Considered sites: Panwa, Lone, Racha, Tang-khen					
Montipora					
	SS	df	MS	F	Sig.
Between Groups	1358.009	4	339.502	3.361	0.068
Within Groups	808.108	8	101.013		
Total	2166.117	12			
Considered sites: Panwa, Lone, Aeo, Hae, Tang-khen					
Pavona					
	SS	df	MS	F	Sig.
Between Groups	941.641	4	235.41	2.975	0.074
Within Groups	791.243	10	79.124		
Total	1732.883	14			
Considered sites: Panwa, Lone, Hae, Maiton, Racha					
Pocillopora damicornis					
	SS	df	MS	F	Sig.
Between Groups	183.8721	2	91.93607	4.393462	0.066807
Within Groups	125.5539	6	20.92566		
Total	309.4261	8			
Considered sites: Panwa, Lone, Tang-khen					
Porites					
	SS	df	MS	F	Sig.
Between Groups	297.659	6	49.61	1.577	0.226
Within Groups	440.413	14	31.458		
Total	738.072	20			
Considered sites: Panwa, Lone, Aeo, Hae, Maiton, Racha, Tang-khen					

APPENDIX 4: Supplements to Manuscript V:

Taxon-specific differences in re-pigmentation of fully bleached corals after the 2010 mass bleaching event in the Andaman Sea

Table 3.6.S1. Pattern of recovery or dying of tagged colonies of various species from qualitative observation data combined from 5 sites in southern Phuket.

Taxa	Patterns
Acropora, *Echinopora echinata,* *Hydnophora rigida,* *Montipora aequituberculata,* *Pectinia alcicornis,* *Pavona varians* *Pocillopora damicornis,* *Porites nigrescens,* and *Porites rus*	Whole colony mortality spread rapidly 2 months after bleaching (in July). For survivors, dying occurred randomly across the colonies and continued to complete in September, except only one colony *Acropora* survived with fully repigmented. Fully bleached colonies (i.e. in *Acropora, Pectinia*) could be found in July before dying in September anyway.
Astreopora myriophthalma, Dipsastraea, Favites, Goniastrea, Galaxea fascicularis, and *Merulina ampliata,*	All survivors presented both pigmented and dead tissue with no particularly pattern of colony changing to recovery and/or dying.
Physogyra lichtensteini, *Leptoria phrygia,* *Lobophyllia hemprichii,* and *Symphyllia radians*	Most of colony surface of all survivors still bleached in September. Particularly, unlike other massive corals species, a colony of *L. hemprichii* consists of separately numerous large polyps. Re-pigmentation or mortality was found randomly across the colonies by completely each polyp. Bleached, recovering, and dying polyps could be next to each other's (Fig. 5.E1-3).
Diploastrea heliopora	Non-uniform patterns of re-pigmentation: some re-pigmented randomly across the colonies, some began from colony tops, and some began from colony sides.
Porites lutea	Most of survivors (76%) presented both pigmented and dead tissue with or without remaining bleached tissue; some (24%) fully changed to either dying or recover. Percent mortality in September was positively correlated with the mortality rate in July.
Psammocora digitata	Random re-pigmentation occurred for all colonies and most dead tissue restricted on the tops of each columns.
Ctenactis, Fungia, Herpolitha	Almost all polyps showed whole polyps changing to either recovery or dying after bleaching (Fig. 5.G1-3).

Table 3.6.S2 Kruskal Wallis results for re-pigmentation (% colony surface area) difference among assigned colony size classes of each coral taxon. Statistical analyses were performed with the program SPSS 15.00 for Windows.

Acropora			*Ctenactis*		
	Jul	Sep		Jul	Sep
Chi-Square	2	2	Chi-Square	2.877	2.594
df	4	4	df	3	3
Asymp. Sig.	0.736	0.736	Asymp. Sig.	0.411	0.459
Pocillopora damicornis			*Fungia*		
	Jul	Sep		July	sep
Chi-Square	0	0	Chi-Square	2.807	1.89
df	3	3	df	4	4
Asymp. Sig.	1	1	Asymp. Sig.	0.591	0.756
Porites					
	Jul	Sep			
Chi-Square	5.96	1.13			
df	4	4			
Asymp. Sig.	0.202	0.890			

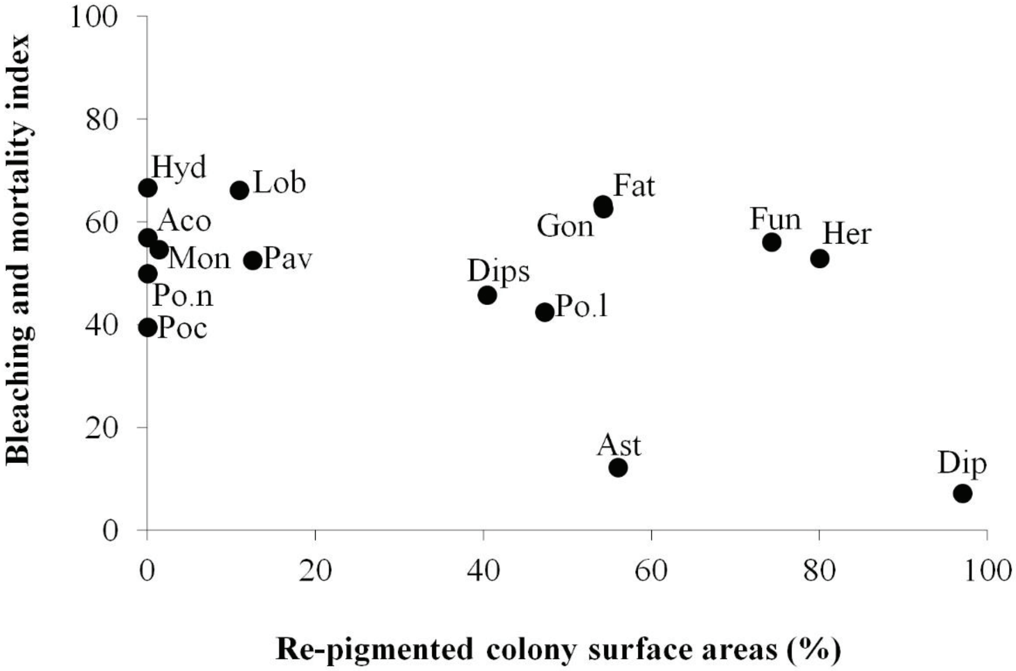


Figure 3.6.S1. Scatter plot of the relationship between Bleaching and mortality indices at the height of the bleaching event and percent re-pigmentation 5 months after bleaching (n=15). Species Abbreviation: Dip=Diploastrea heliopora, Her=*Herpolitha,* Fun=*Fungia,* Ast=*Astreopora myriophthalma,* Fat=*Favites,* Gon=*Goniastrea,* Po.l=*Porites lutea,* Dips=*Dipsastraea,* Pav=*Pavona variance,* Lob=*Lobophyllia hemprichii,* Acr=*Acropora,* Poc=*Pocillopora damicornis,* Po.n=*Porites nigrescens,* Mon=*Montipora aequituberculata,* Hyd=*Hydnophora rigida.*