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Adaptive strategies in reef-building corals

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Statement on the contribution of others

This thesis includes collaborative work with my supervisors, Prof. Andrew Baird, Morgan S. Pratchett and Terry Hughes, as well as Dr. Joshua Madin. All chapters are at different stages of preparation for submission to peer-reviewed journals. The author contributions of each chapter are outlined below.

The manuscript based on Chapter 2 will be a collaboration with Andrew H. Baird (AHB), Morgan S. Pratchett (MSP) and Joshua S. Madin (JSM). Statistical analyses were performed by CYK under the supervision of AHB, JSM and MSP. All authors will contribute to writing the manuscript.

The manuscript based on Chapter 3 will be a collaboration with AHB, Dr. Paul A. Marshall (PAM), MSP and JSM. The field survey was designed by AHB and PAM and conducted by AHB, PAM, MSP and CYK. Statistical analyses were performed by CYK under the supervision of AHB and JSM. All authors will contribute to writing the manuscript. Dr. Sally Keith (SK) was the volunteer for the fieldwork.

The manuscript based on Chapter 4 will be a collaboration with AHB and JSM. The field survey was designed by CYK and conducted by CYK and AHB. Statistical analyses were performed by CYK under the supervision of AHB and JSM. All authors will contribute to writing the manuscript.

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Contribution of authors to publications

Publication	Contribution	Author
Madin et al. 2016	Conceived the idea, compiled the preliminary data. Compiled, entered and edited trait data and jointly wrote the data descriptor	Joshua S. Madin and Andrew H. Baird
	Compiled the preliminary data	Marcela Diaz
	Compiled, entered and edited trait data and jointly wrote the data descriptor	Joshua S. Madin, Kristen D. Anderson, Magnus Heide Andreasen, Tom C.L. Bridge, Stephen D. Cairns, Sean R. Connolly, Emily S. Darling, Marcela Diaz, Daniel S. Falster, Erik C. Franklin, Ruth D. Gates, Mia O. Hoogenboom, Danwei Huang, Sally A. Keith, Matthew A. Kosnik, **Chao-Yang Kuo**, Janice M. Lough, Catherine E. Lovelock, Osmar Luiz, Julieta Martinelli. Toni Mizerek, John M. Pandolfi, Xavier Pochon, Morgan S. Pratchett, Hollie M. Putnam, T. Edward Roberts, Michael Stat, Carden C. Wallace, Elizabeth Widman, and Andrew H. Baird

*Please see Appendix C for full publication

Publication	Contribution	Author
Hughes et al. 2017	First draft	Terry Hughes
	Arial survey in 1998 and 2002	Russell C. Babcock and David R. Wachenfeld
	Arial survey in 2016	James T. Kerry, Terry Hughes, and Tristan Simpson
	Coordinated data compilation, analysis and graphics	James T. Kerry
	Underwater survey	Mariana Álvarez-Noriega, Andrew H. Baird, David R. Bellwood, Maria Byrne, Neal E. Cantin, **Chao-yang Kuo**, Guillermo Diaz-Pulido, Andrew S. Hoey, Mia O. Hoogenboom, Emma V. Kennedy, Michael J. McWilliam, Rachel J. Pears, Morgan S. Pratchett, Gergely Torda, Bette L. Willis, Tom C. Bridge, Hugo B. Harrison, Maria Byrne, Ian R. Butler, Russell C. Babcock, Steven J. Dalton, Will F. Figueira, Hamish A. Malcolm, John M. Pandolfi, Brigitte Sommer, Russell C. Babcock, Steeve Comeau, James P. Gilmour, Jean-Paul A. Hobbs, Malcolm T. McCulloch, Verena Schoepf, and Shaun K. Wilson.
	Analysis matching satellite data to the bleaching footprints on the Great Barrier Reef.	Jorge G. Álvarez-Romero, Sean R. Connolly, C. Mark Eakin, Scott F. Heron, Gang Liu, Janice M. Lough, and William J. Skirving

*Please see Appendix C for full publication

Abstract

One of the major goals of ecology is to identify metrics of assemblage structure that are easy to obtain and that enable accurate predictions of how assemblages respond to disturbance and environmental change. One recent approach, termed Universal Adaptive Strategy Theory (UAST), has been hypothesised to apply to all creatures on the tree of life. However, previous attempts to classify reef-building corals according to UAST have been inconclusive, perhaps because they have not chosen species traits according to the principles set out in the theory. In addition, the utility of the approach for predicting the response of coral assemblages to disturbance has not been effectively tested. This aims of my thesis was to test whether UAST applies to reef-building corals and whether or not adaptive strategy grouping are useful for predicting the response of taxa to disturbance. In **Chapter 2**, I first classify coral species into groups using the principles of UAST and a comprehensive database of coral traits. Next, in **Chapter 3**, I test the ability of adaptive strategy groups to predict the response of coral taxa to disturbance using a long-term dataset from inshore reefs on the Great Barrier Reef (GBR). Finally, in **Chapter 4**, I test for variation in the relative abundance of adaptive strategy groups in coral assemblages along the 1600 km latitudinal or environmental gradient that is the GBR. I found that UAST does not apply to corals and the analyses suggests only two groups of species rather than the three predicted by the theory. I also found that adaptive strategy groups do not accurately predict how a taxa will respond to disturbance nor do these groups respond in a predictable way along an environmental gradient. In conclusion, it is much more tractable and informative to explore traits directly, rather than looking for groups based on traits.

Table of Contents

List of Tables

List of Figures

CHAPTER 1

GENERAL INTRODUCTION

1.1 Adaptive strategies in ecology

Adaptive strategy theory proposes that the direction of natural selection is constrained by trade-offs in life-history traits that shape both the organism and the role it plays in ecosystem processes. Adaptive strategy theories are very appealing to tropical community ecologists because they aim to limit the number of ecological units required to describe assemblages and predict how assemblages respond to disturbance. For example, the limited number of groups typically identified by adaptive strategy approaches are likely to be much easier to work with than the 100s of species that commonly make up tropical assemblages, such as reef corals. Finally, the promise to reveal the functional role of a species in the ecosystem using the adaptive strategy approach is also very appealing, particularly in groups such as reef corals where such knowledge is limited.

The concept of adaptive strategies first emerged in MacArthur and Wilson’s classic book “The Theory of Island Biogeography” (MacArthur and Wilson 1967). The concept has since progressed through many iterations, the most recent being Grime and Pierce’s (2012) Universal Adaptive Strategy Theory (UAST) - a scheme the authors claim applies to all organisms on the tree of life. The authors summarize the scheme as follows

> *“A universal three-way trade-off constrains adaptive strategies throughout the tree of life, with extreme strategies facilitating the survival of genes via: (C) the survival of the individual using traits that maximise resource acquisition and*

> *resource control in consistently productive niches, (S) individual survival via maintenance of metabolic performance in variable and unproductive niches, or (R) rapid gene propagation via rapid completion of the life cycle and regeneration in niches where events are frequently lethal to the individual*".
>
> Grime and Pierce (2012).

The aim of my thesis is to test whether or not this scheme applies to reef-building corals as claimed by Grime and Pierce (2012) and further, whether or not the scheme offers ecological insights above and beyond alternative approaches to community ecology such as more direct trait based approaches or traditional taxonomy.

1.2 Adaptive strategies in ecology: a brief history

Numerous adaptive-strategy theories have been developed to describe the trade-offs among species traits and species interactions with their environment. Initially, r/K selection was developed to describe how selective processes work on islands where resources and space are limited. Early colonisers of an island will not experience crowding, and therefore selection should favour species that can proliferate rapidly (MacArthur and Wilson 1967). The term r refers to the maximum intrinsic rate of natural increase [r_{max}] (MacArthur and Wilson 1967). In contrast, later in the process of island colonisation, resources available for each individual are lower and selection should favour species that can maintain the population under these conditions (MacArthur and Wilson 1967). The term K refers to the carrying capacity of environment (MacArthur and Wilson 1967). Pianka (1970) further hypothesised that when the risk of mortality was high, short-lived creatures, which reproduce numerous offspring early in life, will be favoured (r-selection). In contrast, when the risk of mortality is low, selection will favour organisms that delay reproduction, have longer life-spans and a capacity to monopolize resources (*K*-selection).

While the theory of *r/K* selection initially became very popular it has gradually gone out of favour due to several perceived flaws. As Pianka (1970) pointed out "no organism is completely '*r*-selected' or completely '*K*-selected', but all must reach some compromise between the two extremes". For instance, both trees and sea turtles are long lived and delay reproduction, both characteristic of *K*-selection, but they also have *r*-selected characteristics in that both produce numerous offspring. In addition, the theory was criticised because, unlike *r*, *K* cannot be directly expressed as a function of life-history traits (Stearns 1977). In other words, there are several different strategies by which a population can approach the carrying capability of an ecosystem, such as capturing a high amount of resources or resisting unfavorable environmental conditions (Stearns 1977; Grime and Pierce 2012).

Greenslade (1972) next identified a third type of selection associated with the ability to acquire resources in unfavourable or stressful habitats that he termed "beyond *K*". These ideas were incorporated into a three-way trade-off theory, as *r, K* and *A* (Adversity) selection by Southwood (1977). *r*/*K*/*A* selection was further developed into the Southwood-Greenslade template for animals (Southwood, 1988), which shares similarities with CSR theory for plants (Grime, 1974), where by K and A selection in *r/K/A* selection is equal to C and S selection in CSR theory, separately. Other three-way trade-off schemes include the *rKL* scheme for bacteria (Golovlev 2001), *rKI* (Taylor et al. 1990), *RDV* (De Miguel et al. 2010) and the *LFG* (Enright et al. 1995) schemes for plants.

While these three-way trade-off schemes have many similarities, the UAST (Grime and Pierce 2012), developed from the CSR theory by Grime (1974, 1977), has a more detailed theoretical framework and was therefore chosen as the most appropriate scheme with which to test the utility of the adaptive strategy approach in reef-building corals. UAST identifies three adaptive strategies: **C**ompetitive species have traits that maximise resource acquisition and control in consistently productive niches where the intensity of disturbance and stress are low; **S**tress-tolerant species have traits that maintain metabolic performance in variable and unproductive niches where the intensity of disturbance is low but the intensity of stress is high; and **R**uderal species complete their life cycle or regenerate rapidly in productive niches where disturbance events are frequently lethal (Fig. 1.1, Table 1.1). The distinction between stress and disturbance is an important aspect of UAST: stress is defined as "the sum of many agents that limit the quantity of living matter created per unit of space and time by constraining its production"; and disturbance as "the sum of the great multiplicity of agents that limit biomass by partly or completely destroying it" (Grime and Pierce 2012).

1.3 Adaptive strategies and reef-building corals

A number of researchers have applied various adaptive strategy schemes to reef-building corals. Loya (1976) suggested *Stylophora pistillata* was a classic *r*-selected species on the basis of a number of traits often linked to *r*-selection: rapid colonization of primary habitats, small colony size, early reproduction and vulnerability to disturbance. Loya (1976) further suggested that most coral species could be classified along the *r-K* continuum. Similarly, Jokiel (1998) proposed that *Pocillopora damicornis* was *r*-selected because it produced numerous planula larvae every month throughout the year, in contrast to most other species in Hawaii that breed only once per year. Other *r*-selected traits include its "high success in rapidly colonizing unpredictable reef habitats, rapid development, great population turnover, early reproduction, and high rate of natural increase”.

Grime’s CSR scheme outline above has been highly influential in adaptive strategy approaches in reef-building corals. Edinger and Risk (2000) proposed a classification scheme for corals based on Grime’s CSR scheme with the aim of assisting managers with little or no taxonomic expertise to assess the conservation significance of different coral assemblages. Edinger and Risk (2000)’s scheme was based on colony morphology plus some common and easy to identify hard coral genera. Tabular colonies plus *Millepora* spp. and *Heliopora coerulea* were classified as ruderal; branching, encrusting, foliose, and mushroom corals were classified as competitive; massive and sub-massive corals were classified as stress-tolerant. Edinger and Risk (2000) suggested that the relative abundance of these three strategies in a coral assemblage was a good proxy for species richness and habitat quality (Edinger and Risk 2000). In particular, they found that coral assemblages dominated by stress-tolerant species had low coral cover and low species richness. In contrast, assemblages with a more even mix of strategies were more species rich with a more complex habitat that would better support reef-fish assemblages (Edinger and Risk 2000). Given the high correlation between morphology and the three strategies in the scheme it is difficult to understand the need to situate this work within an adaptive strategy framework. Similarly, given that the groups are defined largely on colony morphology, it is a tautology to state that assemblages with an even mix of adaptive strategy groups would have higher structural complexity. The aim of Edinger and Risk (2000) to identify habitats of conservation significance could have been achieved using colony morphology or even more simply, coral cover. Perhaps the utility of Edinger and Risk (2000)’s scheme can best be judged by the fact that it has not been used since.

Similarly, Murdoch (2007) classified coral species in the Florida Keys into five adaptive groups, based on colony morphology and the mode of larval development. The aim of Murdoch's work was to simplify the description of coral assemblages (i.e. five groups vs. 38 species in the Florida Keys) and to explore the response of each group along an environmental gradient. There are many problems with this work. In particular, the choice of traits with which to group species has no direct link to adaptive strategy theory and therefore it is difficult to predict how each group should respond to the environmental gradient, which is also very poorly defined. Furthermore, the results are difficult to judge whether or not this scheme offered any ecological insight above that gained by using morphology or taxonomy. Once again, utility of this scheme can best be judged by the fact that it has never been used since and the work has never been published outside of Murdoch's PhD thesis.

Darling et al. (2012) were the first to apply a quantitative trait based approach to identify adaptive strategy groups in reef-building reef-building corals. Darling et al. (2012) used 11 traits to classify 143 species into four groups that they named competitive, weedy, stress-tolerant and generalists. In this scheme competitive species form large colonies with branching or plating morphology that grow quickly, occur in shallow reef habitats and reproduce by broadcast spawning; weedy species are smaller and reproduce by brooding; stress-tolerant corals are mostly massive, grow slowly and reproduce by broadcast spawning; generalist are domed and plating species with a moderate growth rate and large colony size. Despite the empirical and analytical approach, there are numerous problems with this work. In particular, Darling et al. (2012) is not a legitimate test of UAST as claimed because they did not choose traits following the principals of the theory. These state that traits should reflect direct trade-offs in energy allocation towards acquisition, maintenance or regeneration (Grime and Pierce 2012). In particular, it is difficult to see how traits such as colony size, colony growth form, modularity, mode of larval development, depth range and symbiont richness compete against each other for energetic resources. For example, there are a number of different ways for a colony to reach a large size: a colony can invest in rapid growth to reach a large size quickly or it can invest in skeletal density in order to survive periods of disturbance. Thus colony size is ambiguous in terms of adaptive strategy. This poor choice of traits explains why a number of the species in Darling at al.'s groups seem out of place. For example, the slow-growing massive species *Dendrogyra cylindrus* (Hudson and Goodwin 1997) is classified as a competitor along with numerous fast-growing *Acropora* spp. possibly because both taxa can reach a large size (Veron 2000). Similarly, while the mode of larval development clearly has a strong appeal due to the apparent trade-off between a few, large offspring (brooding) versus many, small offspring (spawning) (eg Loya 1976; Jokiel 1998; Murdoch 2007), brooding and spawning do not necessarily represent differences in the amount of energy devoted to reproduction. The fact that all species in Darling at al.'s "weedy" group are brooders suggests that this trait has been given too much weight in determining the groups. In addition, Darling et al. (2012) did not specifically address how the traits of the groups relate to UAST. For example, their S-species have traits normally associated with ruderal strategies, such as high fecundity, plus traits normally associated with being good competitors for space, such as large corallite size (Lang 1973). As a test of UAST it also fails because Darling et al. (2012) identify four groups rather than the three groups predicted by the theory. Indeed, it appears that Grime's scheme was used to give the work a theoretical credibility it does not deserve.

Potential problems with the above three approaches are also revealed when they are directly compared (Table 1.2). Firstly, the same taxa are often classified into different adaptive groups. For instance, *Acropora* spp. were considered ruderals by Edinger and Risk (2000) and competitors by Murdoch (2007) and Darling et al. (2012) (Table 1.3). Similarly, *Agaricia agaricites* and *Porites astreoides* were classified as stress-tolerant by Murdoch (2007) and ruderals by Darling et al. (2012) (Table 1.3). The inconsistency of these three schemes is further evident when comparing the trait values of each strategy using data from coraltraits.org (Madin et al. 2016a). For example, all the schemes claim that C- and R-species grow quickly and S- species grow slowly (Table 1.4). However, there is no significant difference in growth between R- and S-species in either Murdoch (2007) (Fig. 1.2f, g, Table 1.5) or Darling et al. (2012) (Fig. 1.2h, Table 1.5). UAST further suggests that R-species should have a high investment in reproduction (Table 1.4). However, there was no significant difference in either fecundity or propagule size among Murdoch's three strategies (Fig. 1.2j, n, Table 1.5). Similarly, the S-species of Edinger and Risk (2000) and Darling et al. (2012) have the highest polyp fecundity in their respective schemes (Fig. 1.2i, l, Table 1.5).

It is important to note that an analytical approach to defining the groups relies on data from numerous species for numerous traits and these data are not easy to come by. For example, traits that vary greatly in time and space and among individuals, such as skeletal density and growth rate, require the destructive sampling of numerous individuals from multiple sites. Similarly, determining reproductive traits such as fecundity and sexuality requires expensive equipment and processing samples is time-consuming. Therefore, there has to be extraordinary ecological insight for the adaptive strategy approach to be worth all this effort. As I outline below, the few tests available of the utility of the adaptive strategy approach in coral reef ecology do not suggest it offers any ecological insight above more straightforward classification schemes.

Darling et al. (2013) claim in the title of their paper that “Life histories predict coral community disassembly under multiple stressors”. However, the evidence to support this statement is mixed because Darling at al.’s groups do not always respond in the way adaptive strategy theory predicts. Darling et al. (2013) investigated changes in the abundance of adaptive stratedy groups in response to fishing and a bleaching event on reefs in Kenya. On unfished reefs, all groups fluctuated in synchrony in the six years prior to the bleaching, whereas UAST predicts that competitive species should benefit in periods free of stress and disturbance. Bleaching caused all three groups to decline dramatically on unfished reefs, whereas UAST predicts that the stress-tolerant species should benefit. Similarly, all three groups on unfished reefs increased in abundance in synchrony following the bleaching, whereas the theory predicts that the competitive species should dominate. In some cases the response of the groups was context-dependent. For example, stress-tolerant species declined in response to bleaching on unfished reefs but not on fished reefs. This suggests that there is a range of different responses to bleaching among species within the stress-tolerant group. In other cases the response of groups varied through time. For example, weedy species increased on fished reefs during the six years prior to bleaching but there was no similar increase in the 12 years after the bleaching. In fact, the only finding consistent with the predictions of the theory is that competitors are more susceptible to chronic disturbance in the form of fishing than stress-tolerant and weedy species. Given that all the competitive species in Darling at al.’s scheme are branching *Acropora* and *Pocillopora* spp. the results can be summarised as branching species are more susceptible to fishing than non-branching species. Therefore, the claim for improved ecological insight using the adaptive strategies approach is not apparent. Indeed, a very simple morphological approach to classifying corals would have been equally informative (i.e. branching vs non- branching) and much less time-consuming.

Graham et al. (2014) concluded that the relative abundance of Darling at al.'s adaptive strategy groups was useful for distinguishing among reefs with a different disturbance history on the Great Barrier Reef (GBR). Specifically, the relative abundance of competitive taxa was higher on undisturbed and recovered reefs than on reefs that had not recovered from a crown-of-thorns outbreak. However, the only locally abundant species classified as competitors were *Acropora* spp. Therefore, these reefs could equally well have been distinguished by classifying taxa as *Acropora* or non-*Acropora*. In addition, the three other Darling at al.'s groups were all relatively less abundant on disturbed reefs, in contrast to the prediction of UAST that stress-tolerant or weedy species should dominate in disturbed habitats.

Sommer et al. (2014) used Darling at al.'s scheme to compare the relative abundance of species in each adaptive group among coral assemblage along a high-latitude gradient in south-eastern Australia – a gradient that included sites at the range limit of most coral species. The only clear trend in these data was a decrease in the relative abundance of stress-tolerant species in coral assemblage at higher latitudes. This is in direct contrast to UAST that predicts that stress-tolerant species should dominate in unproductive habitats, such as these marginal reefs at high latitude. Clearly, Darling at al.'s adaptive strategy groups are not behaving as the theory predicts suggesting the analyses were flawed or that the theory is not useful for corals.

Furthermore, the use of the groups does not appear to offer any ecological insight beyond that achievable with a very simple taxonomic approach.

1.4 Other potential issue in applying adaptive strategy theory to corals

The life-history traits of reef-building corals are a very different to most plants and animals, which suggest that they might be difficult to classify within existing adaptive strategy schemes. In particular, most corals are clonal with limited plasticity in many reproductive traits. While there is likely to be a large range in the longevity of corals species the clonal nature of corals makes it difficult to determine the age of individuals due to asexual reproduction, including fission and fragmentation, and the fact that multiple colonies can fuse together to form a single individual (Hughes and Jackson 1980). In addition, the vast majority of corals species have annual gametogenic cycles meaning individuals breed only once per year (Baird et al. 2009). This limits the capacity of individuals to reproduce sexually in response to stress, unlike numerous r-adapted plants and animals. Even in species that release propagules over an extended period, like most brooding species, it is unclear whether or not individual polyps within the colony breed once or repeatedly (Baird et al. 2015). However, various means of asexual reproduction, such as fission and fragmentation (Fautin 2002), means some coral populations can rapidly increase in abundance in response to stress and disturbance, such as bleaching or hurricanes (Hughes and Jackson 1985; and see Chapter 3). In addition, there is little variation in the age at first reproduction, unlike flowering plants where some species breed within weeks and others delay reproduction for many decades (Grime and Pierce 2012). While the data is limited, most corals breed within two to five years and there is no evidence of long delays in reproduction in any species (Madin et al. 2016b). The nutrition of corals is also very different to most other plants and animals. In particular, corals are both autotrophic, deriving nutrition from endosymbiotic algae, *Symbiodinium* spp., and heterotrophic, deriving nutrition from prey captured from the plankton (Goreau et al. 1971). In addition, many coral species can switch between these nutritional modes depending on the prevailing conditions (Porter 1976).

The distinction that UAST makes between stress and disturbance is not as clear in the marine environment as in the terrestrial environment. Stress as defined by UAST is rare in the marine environment. In the terrestrial realm it occurs due to a lack of water or nutrients. Coral reefs primarily occur in oligotrophic waters which are by definition nutrient poor with no shortage of water. Alternative stressors relevant to coral reefs include eutrophication and a decline in the availability of light as depth or latitude increase. While coral bleaching could potentially be regarded as a stress because it leads to lack of nutrients for affected corals, it almost always also results in a large loss of tissue. Disturbances, in particular tropical storms, however, are common. Therefore, not only do corals have life-history traits that make them difficult to place in UAST groups, the environment in which they live is also difficult to define within UAST.

1.5 Outline of the thesis

The primary aim of this thesis is to test whether the adaptive strategy approach can be applied to corals, and if so, to explore the utility of the approach by testing whether it provides improved ecological insight compared to the use of standard classification schemes based on morphology or taxonomy. In particular, I will explore how groups identified using a rigorous quantitative trait-based approach respond to stress and disturbance and whether the relative abundance of these groups varies predictably along a latitudinal gradient. The specific chapters are outlined below.

In **Chapter 2**, I test whether UAST applies to reef-building corals. I use UAST principles in combination with a recent comprehensive compilation of coral traits to explore whether or not species cluster into groups that represent different adaptive strategies.

In **Chapter 3**, I test whether the groups identified by Darling et al. (2012) are good predictors of the responses of coral taxa to environmental stasis and change. I will use a 15-year data set that documents changes in the abundance of coral genera at eight sites in the central Great Barrier Reef (GBR). This time period includes the mass bleaching of corals in 1998, a number of other stresses and disturbances, as well as periods of stasis.

In **Chapter 4**, I test whether the relative abundance of the groups identified in **Chapter 2** varies predictably along an environmental gradient: the 1800 km length of the GBR. I will use data collected in the field to describe coral assemblage structure along the length of the GBR. In particular, I use this environmental gradient to test whether coral assemblages confirm to the predictions of UAST that southern coral assemblages should have a higher relative abundance of S- adapted species.

I also include in an appendix pdfs of two publications on which I am a co-author that arose from my collaborations with colleagues at James Cook University in the course of my PhD candidature.

Table 1.1 Suggested adaptive strategies under different environmental conditions from low to high levels of either disturbances or stress. Modified from Table 1 in Grime (1977).

	Intensity of Stress	
Intensity of Disturbance	Low	High
Low	C-strategy	S-strategy
High	R-strategy	Non-available strategy

Table 1.2 A summary of previous adaptive strategy approaches in corals.

Reference	Groups	Classification scheme	Aim
Edinger and Risk (2000)	Ruderals, competitors, and stress-tolerators	Colony morphology and taxonomy but only three genera; *Acropora*, *Millepora*, and *Heliopora*	Provide an index of reef conservation significance independent of taxonomy
Murdoch (2007)	Competitive, Ruderals, Stress-tolerant, Competitive-Ruderals, and Competitive-Stress-tolerators	Colony morphology and mode of larval development	Reduce the number of groups required to categories coral assemblage structure ie an alternative to taxonomy.
Darling et al. (2012)	Competitive, weedy, stress-tolerant, and general taxa	11 traits and cluster analysis	Provide an objective and powerful tool to evaluate theories of community ecology and to predict the impact of both of natural and human stress

Table 1.3 Taxa included in each group in the various adaptive strategy schemes used previously in corals.

Asaptive strategy scheme	Adaptive strategy		
	C/K (Competitors)	S (Stress-tolerators)	r/Weedy (Ruderals)
Edinger and Risk (2000)	Branching, encrusting, foliose and mushroom corals	Massive and submassive species	*Acropora* species
Murdoch (2007)	Branching, spawning corals, such as *Acropora*	Plating, foliose and solitary, brooding corals eg *Agaricia agaricites*, *Porites astreoides*	Massive brooding corals, such as *Favia fragum* and *Siderastrea radians*
Darling et al. (2012)	*Acropora* spp.,	*Favia fragum*, *Siderastrea radians*	All brooders eg *Agaricia agaricites* and *Porites astreoides*

Table 1.4 Biological and ecological characters associated with three adaptive strategy groups of UAST.

	Adaptive-strategy		
Characteristics	C	S	R
Maximum size	Large	Wide range	Small
Longevity	Long	Long to very long	Very short
Reproductive maturity	Late	Late	Early
Frequency of reproduction	Once per year	Every few years	Numerous times per year
Reproductive effort	Small	Small	Large
Growth rate	Rapid	Slow	Rapid
Response to stress and disturbance	Sensitive	Less sensitive	Sensitive
Palatability	Variable	Low	High

* Reproduced and modified from Table 1.01 in Murdoch (2007) and Table 6 in Grime (2001).

Table 1.5 The results of Kruskal-Wallis rank tests.

Species trait	Edinger and English (2000)	Murdoch_Caribbean (2007)	Murdoch_Global (2007)	Darling et al. (2012)
Corallite width maximum	H (2) = 239.3, $p < 0.001$	H (2) = 10.62, $p = 0.004$	H (2) = 78.22, $p < 0.001$	H (2) = 68.413, $p < 0.001$
Growth rate	H (2) = 357.21, $p < 0.001$	H (2) = 21.31, $p < 0.001$	H (2) = 173.32, $p < 0.001$	H (2) = 74.06, $p < 0.001$
Polyp fecundity	H (2) = 224.84, $p < 0.001$	H (2) = 0.52, $p = 0.768$	H (2) = 38.11, $p < 0.001$	H (2) = 55.22, $p < 0.001$
Propagule size on release	H (2) = 240.97, $p < 0.001$	H (2) = 2.82, $p = 0.243$	H (2) = 50.76, $p < 0.001$	H (2) = 21.81, $p < 0.001$
Skeletal density	H (2) = 150.68, $p < 0.001$	H (2) = 7.20, $p = 0.027$	H (2) = 103.27, $p < 0.001$	H (2) = 4.75, $p = 0.093$
Colony maximum diameter	H (2) = 110.89, $p < 0.001$	H (2) = 17.65, $p < 0.001$	H (2) = 58.89, $p < 0.001$	H (2) = 17.8, $p < 0.001$

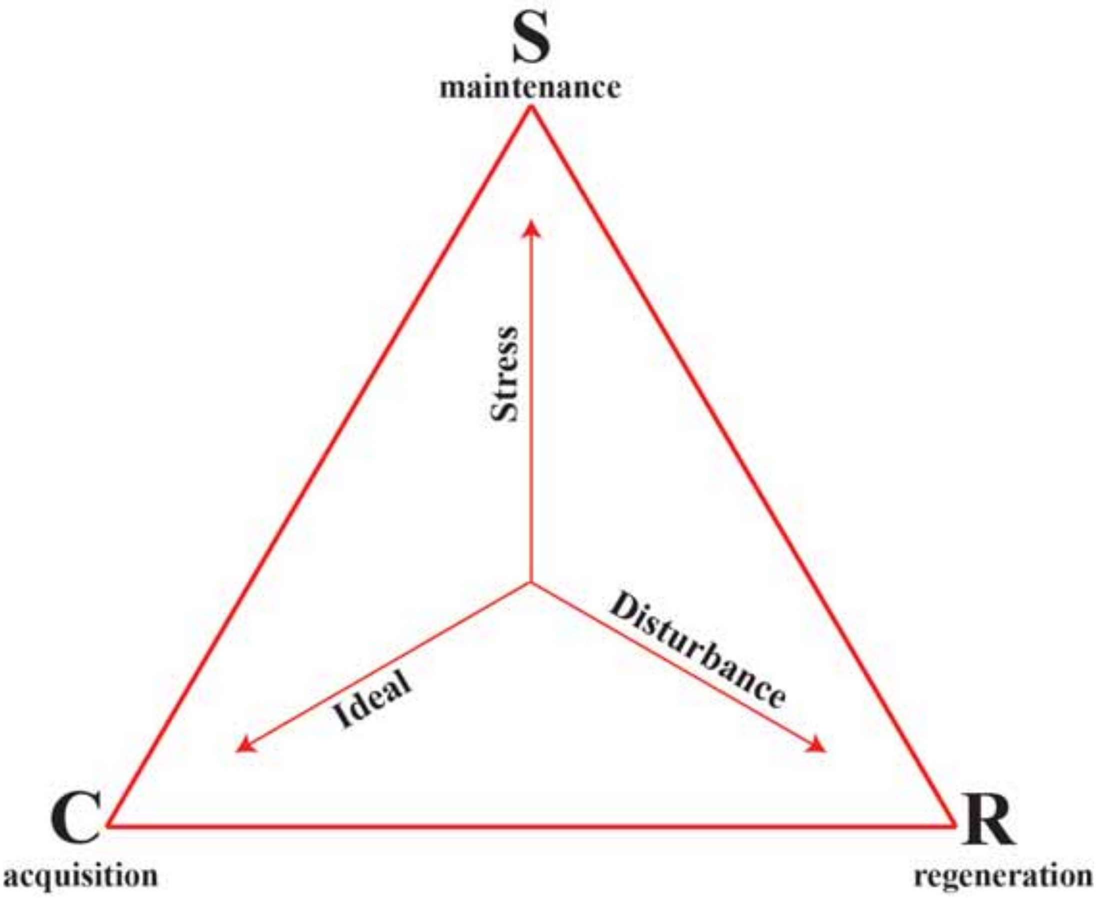
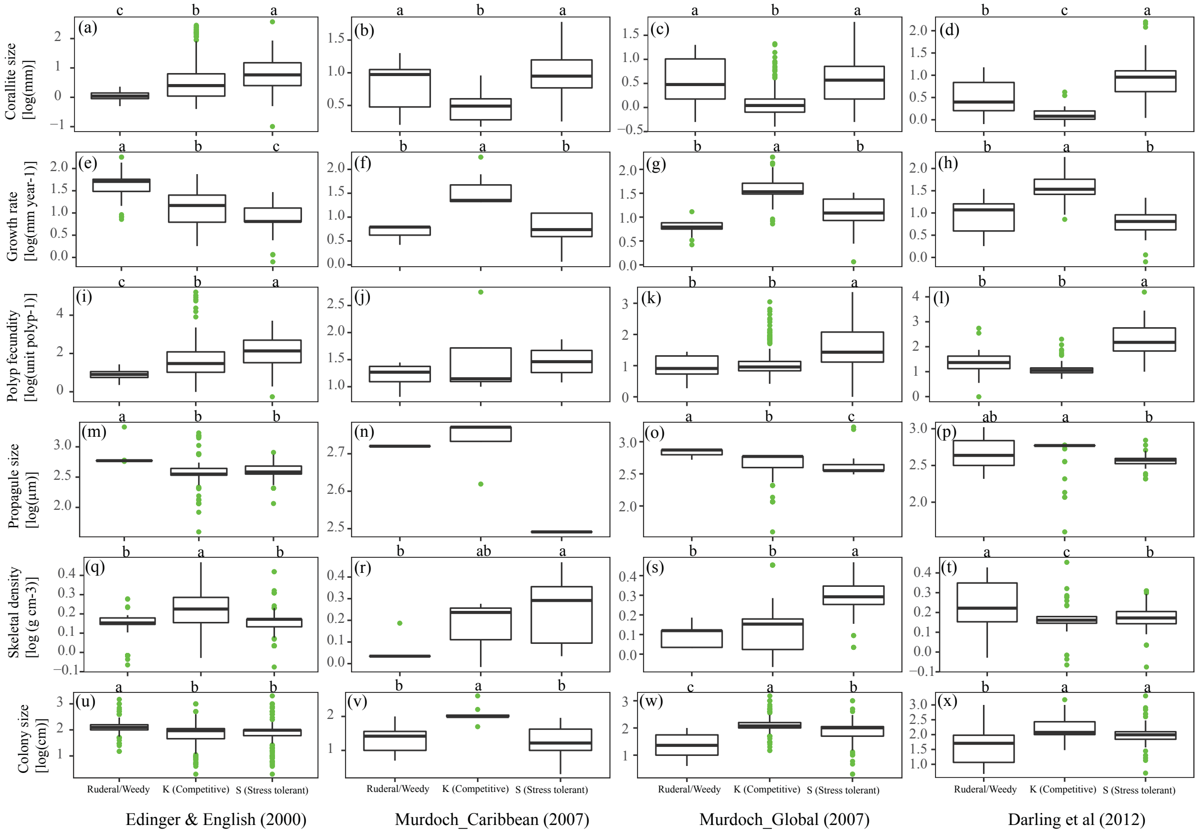


Fig. 1.1 The Universal Adaptive Strategy Theory (UAST) triangle indicating the predicted dominated strategy under different conditions.

Fig. 1.2 A comparison of corallite size (a-d), growth rate (e-h), polyp fecundity (i-l), propagule size (m-p), skeletal density (q-t), and colony size (u-x), of each adaptive strategy classified by Edinger and Risk (2000)(a, e, I, m, q, u), Murdoch_Caribbean (2007)(b, f, j, n, r, v), Murdoch_global (2007)(c, g, k, o, s, w), and Darling et al. (2012)(d, b, l, p, t, x). Murdoch_Caribbean contains only Caribbean species because Murdoch (2007) used only species from Caribbean in his adaptive strategy scheme. Murdoch_global includes Caribbean and Indo-Pacific species following the same criteria as Murdoch_Caribbean. Green points indicate outliners picked up by the analysis. The letters at the top of each plot indicates the results of a multiple comparison test after Kruskal-Wallis test. Strategies that share the same letter within a plot are not significantly different to each other for that specific trait.



CHAPTER 2

A test of universal adaptive strategy theory in reef-building corals

2.1 ABSTRACT

One of the major goals of ecology is to identify metrics of assemblage structure that are easy to obtain and that enable accurate predictions of how assemblages respond to disturbance and environmental change. One recent approach, termed Universal Adaptive Strategy Theory (UAST) (Grime and Pierce 2012), has been hypothesised to apply to all creatures on the tree of life. However, previous attempts to classify reef-building corals according to UAST have been inconclusive, because they have not chosen species traits according to the principles set out in the theory. Here, we test whether UAST applies to reef-building corals using the principles of UAST and a comprehensive database of coral traits. The analyses suggest that reef-building coral species cluster into two groups on the basis of these traits rather than the three groups predicted by UAST. Furthermore, both groups contain a mix of species with very different life history strategies. We conclude that UAST does not apply to corals because the tropical marine environment is very different to most terrestrial environments. In addition, corals are both heterotrophic and autotrophic and therefore very different to most plants and animals

2.2 INTRODUCTION

Adaptive strategy theory states that the direction of natural selection is constrained by trade-offs in life history traits that shape both the organism and the role it plays in ecosystem processes. Adaptive strategy theory is very appealing to tropical ecologists because it aims to limit the number of units required to describe assemblages. For example, the three adaptive groups proposed by the Universal Adaptive Strategy Theory (UAST) of Grime and Pierce (2012) should be more tractable than the 100s of species that commonly make up tropical assemblages such as reef corals, as long as the group that a species belongs to is easy to determine. Adaptive strategy theory is also appealing because aims to predict how taxa and assemblages respond to disturbance.

The concept of adaptive strategies was first presented by MacArthur and Wilson (1967) who suggested that species colonising islands displayed one of two broad strategies based on the parameters of Lotka and Voltera's predator-prey equations; *r*-species that proliferate rapidly in an empty landscape and *K*-species that maintain populations when resources are limited later in the colonization process. Adaptive strategy theory has since proceeded through many iterations, the most recent of which is the UAST of Grime and Pierce (2012) - a scheme the authors claim applies to all organisms on the tree of life. UAST identifies three adaptive strategies (C-, S-, R-strategy): **C**ompetitive species have traits that maximise resource **acquisition** and control in consistently productive niches where the intensity of disturbance and stress are low; **S**tress-tolerant-species have traits that **maintain** metabolic performance in variable and unproductive niches where the intensity of disturbance is low but the intensity of stress is high; and **R**uderal species complete their life cycle or **regenerate** rapidly in productive niches where disturbance events are frequently lethal (Fig. 1.1, Table 1.1). The distinction between stress and disturbance is an important aspect of UAST: stress is defined as "the sum of many agents that limit the quantity of living matter created per unit of space and time by constraining its production"; and disturbance as "the sum of the great multiplicity of agents that limit biomass by partly or completely destroying it" (Grime and Pierce 2012). However, the contrast UAST makes between stress and disturbance is less evident on coral reefs than in terrestrial environments, given that water is never limited and most reefs occur in oligotrophic waters where nutrients are by definition limited.

Adaptive strategy theory has been applied to reef-building corals in a number of studies, however the theory has generally not been applied correctly (discussed in detail in Chapter 1). Darling et al. (2012) were the first to apply a quantitative trait based approach to identify adaptive strategy groups in reef-building corals. Darling et al. (2012) used 11 traits to classify 143 species into four groups that they named competitive, weedy, stress-tolerant and generalists. Despite the quantitative approach, there are numerous problems with this work. In particular, Darling et al. (2012) is not a legitimate test of Grime's UAST as claimed because they did not choose traits following the principles of the theory i.e. traits should compete for the energy allocated towards acquisition of resources, maintenance of metabolism or regeneration (Grime and Pierce 2012). Most of the traits used by Darling et al. (2012) including colony size, colony growth form, modularity, mode of larval development, depth range and "symbiont richness" can not be expressed in a common currency to allow the trade-offs among traits for limited energetic resources to be explored. For example, there are a number of different ways for a coral to reach a large size: it can invest in rapid growth to reach a large size quickly or it can invest in skeletal density in order to survive through periods of disturbance, such as cyclones. In addition, Darling et al. (2012) did not specifically address how the traits of their groups relate to UAST. For example, their stress-tolerant species have traits normally associated with R-strategies, such as high fecundity, as well as traits normally associated with C-species, such as large corallite-size which is a proxy for competitive ability (Lang 1973). As a test of UAST it also fails because Darling et al. (2012) identified four groups rather than the three groups predicted by the theory.

Adaptive strategy theory has proved highly influential in plant and animal ecology, however attempts to apply UAST to corals have been ill-conceived or poorly executed. The first aim of my thesis was therefore to test whether or not this scheme applies to reef-building corals using appropriate traits as outlined by Grime and Pierce (2012).

2.3 MATERIAL AND METHODS

2.3.1 ***Source of trait data***

Trait data were sourced from coraltraits.org, a comprehensive database of coral life history traits (Madin et al. 2016a).

2.3.2 ***Choice of traits***

Traits for the analyses were chosen following the principles of UAST. Only traits directly related to the three primary functions of acquisition, maintenance and regeneration where used and only those traits that directly compete in a trade-off for available energy (Grime and Pierce 2012). The choice of traits was also based on what was available at coraltraits.org. For example, some measure of tissue biomass as a proxy for investment in maintenance would have been ideal, however there were insufficient data available for this trait or other similar traits.

The traits chosen for use in the analyses were 1) corallite width maximum, 2) propagule size on release, 3) polyp fecundity, 4) skeletal density and 5) growth rate (Table 2.1). For the remainder of my thesis these traits will be referred to as *corallite size, propagule size, fecundity, skeletal density* and *growth rate,* respectively. Many of these traits are often used as proxies for other traits that are more difficult to measure.

For example, species that grow rapidly are generally considered good at acquiring space (Buddemeier and Kinzie 1976; Pratchett et al. 2015), which is often the limiting resource in sessile benthic invertebrate assemblages such as coral reefs. Species with large corallites generally outcompete species with small corallites in competitive interactions involving digestion (Lang and Chornesky 1990). Species with large corallites generally rely more on heterotrophic feeding as opposed to species with small corallites that tend to rely on energy derived from photosynthesis (Goreau et al. 1971). The capacity to feed heterotrophically has been linked to a greater ability to survive periods of stress, such as those that induce coral bleaching (Grottoli et al. 2006). *Corallite size* has also been suggested as a proxy for energy stored in the polyps (van Woesik et al. 2012) and for environmental tolerance (Sommer et al. 2014). *Skeletal density* is generally seen as a proxy for investment in maintenance; species that invest heavily in a dense skeleton are more likely to survive common disturbances on the reef, like bio-erosion (Highsmith 1981) and waves generated by storms (Hughes 1987). *Fecundity* and *propagule size* are clearly related to investment in reproduction, or regeneration to use the terminology of UAST. In summary, I propose *growth rate* as a potential indicator of energy invested in acquisition (i.e. competition), *corallite size* and *skeletal density* as potential indicators of energy invested in maintenance (i.e. stress tolerance), and *fecundity* and *propagule size* as indicators of investment in regeneration (i.e. reproduction).

A number of other traits, including the *mode of larval development* (brooders vs. spawners), *sexuality* (hermaphrodites vs. gonochores), *colony morphology* (various schemes), and *colony size* (the maximum colony size observed in a species) have also been used for exploring the concept of adaptive strategies in corals and other organisms. However, I argue that these traits are not suitable for use in a test of UAST. Firstly, it is difficult to see how these traits can be converted into a common currency by which to explore trade-offs in energy allocation with other traits. Secondly, many of these traits are ambiguous with respect to the trade-offs that have shaped them. As previously discussed, there are many ways a colony can reach a large size (Chapter 1 and above). Similarly, colony growth form is best thought of as an interplay among traits and the environment. Indeed, Jackson and Hughes (1985) propose that different colony morphologies represent adaptive strategy groups. Nonetheless, given the frequent reference to these additional four non-UAST-traits (i.e. *mode of larval development*, *sexuality*, *colony morphology*, and *colony size)* in the adaptive strategy literature, I will explore how they vary among groups identified in the UAST analyses. Data for these traits was sourced from coraltraits.org.

2.3.3 ***Trait infilling***

Coraltraits.org includes almost all the empirical data from the literature (Madin et al 2016a). However, for some traits, there is a paucity of data due to a lack of research. For example, for *skeletal density* and *propagule size,* empirical data was only available for 54 and 67 species respectively. Therefore, in order to increase the number of species available for use in the analyses, a regression approach was used to fill in missing data (i.e. trait infilling) following Madin et al. (2016b).

A species × trait matrix with only one value of trait for each species was first completed using empirical data from coraltraits.org (Madin et al. 2016a). When a species had multiple empirical values for a given trait the average trait value was used as the global estimate for that species. For traits where I was interested in the maximum value, such as *corallite size*, and *colony size,* only the largest value was used. Second, I visually explored the empirical data for correlations among the traits (see Fig. 2.1) in order to help choose the variables used in each regression analysis. The decisions on which variables to use were also guided by previous work (eg Madin et al. 2016b) and expert opinion as outlined below. The variables used to infill each trait are summarised in Table 2.1 and 2.2.

The trait infilling of *growth rate* included family and morphology as predictors (Madin et al. 2016b). For colony morphology, I used the trait *growth form typical* at coraltraits.org, which includes nine morphologies modified from descriptions in Veron (2000): branching_closed, branching_open, columnar, corymbose, digitate, encrusting, laminar, massive, and tabular (Table 2.2). *Corallite size* is generally highly conserved within taxonomic family and correlated with *growth rate* (Fig. 2.1). *Skeletal density* is also likely to be phylogenetically conserved and previous work suggests that morphology is also important (Fig. 2.1, Table 2.1; Hughes 1987). *Propagule size* is generally conserved within genera and varies consistently between modes of larval development (i.e. brooded larvae are generally larger than spawned larvae) (Baird et al. 2009). Empirical data were standardized to egg/planulae number per polyp, and log transformed before the infilling process.

After infilling a species-trait matrix was available for 473 reef-building coral species. Summary statistics for the five in-filled traits are presented in Figure 2.2 and Table 2.3. Data in the matrix were standardized within each species-trait because the units varied for each combination. All analyses were performed in R using the Predict function (R Core Team 2016).

2.3.4 ***Testing UAST***

UAST predicts that each species should fall into one of three groups, C, S or R (Grime and Pierce 2012, Chapter 1). Ward’s hierarchical clustering with Euclidean dissimilarity matrix was used to group the 473 species based on the five UAST traits. I used Ward's hierarchical clustering because it tends to produce clusters of more equal size (Ward 1963). Euclidean distance matrix was used because it is the distance matrix used in Principle Component Analysis (PCA), which was used to ordinate the species in trait space.

The optimal number of groups was determined by examining how the coefficient of determination (R^2) of permutational multivariable analysis of variance (PERMANOVA) changed among the different clustering scenarios. I was looking for scenarios that minimized within-cluster dissimilarity and between-cluster homogeneity, as described in Darling et al. (2012). The optimal number of clusters of the trait dendrogram was estimated by looking at the elbow of the coefficient of determinations (R^2) across different scenarios from 2 to 100 clusters. The optimal number of clusters is the number of clusters before a significantly drop of R^2 across the 99 scenarios, the elbow. PERMANOVA was then used to test the hypothesis that there was significant variation among the number of clusters chosen. Principle component analysis (PCA) was then used to explore the relationship between the groups and the UAST traits. Multivariable analyses were performed using the "vegan" (Oksanen et al. 2017) and "FD" (Laliberté et al. 2014) packages in R (R Core Team 2016). The average value of all UAST traits as well as the continuous trait and maximum colony size, was determined for each group and differences tested using non-parametric Kruskal-Wallis rank test.

2.3.5 ***A comparison of non-UAST traits among the groups***

In addition, the relative abundance of traits with categorical values, such as colony growth form, mode of larval development and sexuality was explored among the groups to look for differences among the groups not captured by the UAST analyses.

2.4 RESULTS

The analysis suggested that a two-group scenario best captured the differences among species in trait space (PERMANOVA, $P = 0.001$, Fig. 2.3, Table 2.4). In order to 1) describe the optimal grouping (i.e. two groups) and 2) to explore whether or not the three-group scenario match the groups as predicted by UAST, I outline the characteristics of the two scenarios are below.

2.4.1 ***Principle component analysis***

Species were separated on the first principle component axis (PC1) by differences in *growth rate*, *fecundity* and *corallite size* and on PC2 by differences in *skeletal density* (Fig. 2.4). The biplot indicates that *corallite size* and *fecundity* were highly correlated and negatively correlated with *growth rate* (Fig. 2.4). *Skeletal density* was negatively correlated with *propagule size* (Fig. 2.4). The first two PCAs explained 78.42% of the variation among traits (Fig. 2.4).

2.4.2 ***Cluster analysis***

The first split separates species with high growth rates (Group 1) from those with large corallites and high fecundity (Group 2) (Fig. 2.5; Table 2.4, 2.5). The next split separates a small group of species with high skeletal density, small corallite size, and moderate fecundity from the large corallite group (Fig. 2.5; Table 2.4, 2.5).

2.4.3 ***Summary of groups in the two-and three group scenario including categorical traits and taxonomy***

Species in Group 1 are characterised by rapid growth, large propagules, small corallites, low fecundity and moderately dense skeletons (Table 2.4, 2.5). Group 1 includes 295 species from 10 genera and three families (Table 2.5). Group 1 includes all but one species of the family Acroporidae that were included in the analyses, a selection of closed-branching pocilloporids and all but one *Porites* spp. The group contains some species with each of the nine growth forms and a mix of brooders, spawners, hermaphrodites and gonochores.

Species in Group 2 are characterised by slow growth, moderate sized propagules, large corallites, high fecundity and dense skeletons (Table 2.4, 2.5). Group 2 includes 178 species from 26 genera and five families (Table 2.5). It includes all species from the family Merulinidae, all species from the genus *Goniopora* and all spawning *Pocillopora* spp. The group contains some species with seven of the nine growth forms and a mix of brooders, spawners, hermaphrodites and gonochores.

Species in Group 3 are a small subset of Group 2 above with moderate growth rate, small propagules, small corallites, moderate fecundity and very dense skeletons (Table 2.5). All species in the group are broadcast spawning *Pocillopora* spp.

2.5 DISCUSSION

The best scenario suggested by the analyss is a scenario with two groups in contrast to the three groups predicted by UAST. These two groups contain species with vastly different life histories and a mix of traits associated with different UAST groups. The three-group scenario creates two groups that are relatively homogenous, however, none of these groups fit comfortably within UAST. I conclude that UAST is not universal.

The two groups do not make good ecological sense because each group includes a mix of species with very different life-histories and traits associated with more than one UAST strategies (Table 1.4, 2.5). For example, Group 1 includes species with very small colony sizes (eg *Seriatopora* spp.) and species with some of the largest colony size recorded (eg *Porites* spp.); it includes some of the longest lived species (eg *Porites* spp.) and some of the shortest (eg *Seriatopora* spp.); it includes species that breed relatively early in life (eg *Seriatopora hystrix*) and species likely to delay maturity for many years (eg *Porites* spp.); it includes species that breed annually (*Acropora* spp. and *Montipora* spp.) and those that breed frequently each year (*S. hystrix* and *Pocillopora damicornis*); it includes some of the fastest growing species (eg *Acropora* spp.) and many slower growing species (eg *Porites* spp.); it include species that are typically among the worst affected by stress such as bleaching (eg *Pocillopora damicornis*, *Seriatopora hystrix*) and many species considered relatively immune to bleaching (some *Montipora* spp. and most *Porites* spp.); it include species that are typically among the worst affected by disturbances, in particular cyclones (eg *Acropora* spp.) and those typically regarded as relatively immune to cyclones (massive species such as many *Porites* spp.); it includes species that are palatable to a wide range of predators (eg *Acropora* spp.) and those that are not palatable, at least to crown-of-thorns starfish (eg *Porites* spp.). Group 2 is slightly more homogenous. The majority of the species are from the family Merulinidae and these share a number of traits including slow growth, delayed reproductive maturity, relative immunity to stress and disturbance. However, it also includes a number of *Pocillopora* spp. which grow relatively rapidly and breed relatively early, as well as the solitary fungiids. The three-group scenario creates two relatively homogeneous groups out of Group 2 by separating the pocilloporids from the remaining taxa; however, Group 1 is left intact with a diversity of species with very different life history strategies. Therefore, this three-group scenario does not match the groupings predicted by UAST.

There are a number of reasons why UAST might be difficult to apply to corals (Chapter 1). For example, many coral reproductive traits are not that variable. For example, the frequency of reproduction does not vary much within the order. The vast majority of reef-building species have annual gametogenetic cycles and therefore only breed once per year (Baird et al. 2009). Even in species that release brooded larvae on a monthly cycle it is not clear whether the individual polyps have multiple gametogenetic cycles or breed out of synchrony (Baird et al. 2015). Similarly, there is no evidence that individuals can reproduce sexually in response to stress. There is also very little variation in the age at first reproduction. Most corals breed within 2-5 years (Madin et al. 2016a) and there is no evidence for a long delay in any species. The clonal nature of corals also makes it very difficult to determine the age of individuals (Hughes and Jackson 1980) in addition to numerous other forms of asexual reproduction including fragmentation (Fautin 2002). Similarly as discussed previously in Chapter 1 stress and disturbance are difficult to distinguish on coral reefs.

2.6 CONCLUSIONS

The UAST approach does not appear to have produced homogenous groups that make ecological sense. Nonetheless, species within the two groups identified in the analyses might behave in a consistent and predictable way to stress and disturbance. In Chapter 3 I explore this idea by using Darling et al.’s (2012) groups at the level of genus to test whether taxa and assemblages behave in a consistent and predictable way to coral bleaching and multiple-stressors. I use a 15-year data set from sites on inshore reefs on the Great Barrier Reef (GBR). Finally, in Chapter 4, I test the utility of my two group scheme to predict how species vary in space along an 1800 km latitudinal gradient along the length of the GBR.

Table 2.1 Traits used in the analyses. The description of traits is from Madin et al. (2016b). All traits are continuous.

Trait	Abbreviation used in text	Description	Unit	Factors used when infilling
Corallite width maximum	Corallite size	The maximum typical corallite width, axial corallite width or valley size	mm	"Family", "Growth rate"
Growth rate	Growth rate	The yearly extension for branching and massive corals, or simple linear extension	mm year-1	"Family", "Growth form typical"
Polyp fecundity	Fecundity	The number of eggs (oocytes) in a polyp	units	"Corallite width maximum", "Propagule size on release"
Propagule size on release	Propagule size	The size of eggs or planula larvae on release.	µm	"Genera", "Mode of larval develop"
Skeletal density	Skeletal density	The material density of coral skeleton	g cm-3	"Family", "Growth form typical"

Table 2.2 Traits used in the data infilling process. The description of traits is from Madin et al. (2016b). All traits are categorical.

Traits	Abbreviation used in text	Description	Levels used when infilling
Mode of larval development	none	The mode of larval development classified as either a brooder, where fertilization is internal and colonies release planulae larvae, or a broadcast spawner, where gametes are release for external fertilization and the planulae develops in the plankton.	Brooder, spawner, both
Growth form typical	Growth form	The growth form (morphology) of a species as derived from text descriptions in Veron (2000). The "typical" growth form is given for each species, rather than all forms that might be observed in the field.	Branching_close, branching_open (including hispidose), columnar (including encrusting_long_uprights), corymbose, digitate, encrusting, laminar, massive (including submassive), tables/plates

Table 2.3 Summary statistics for the five continuous traits used in the analyses.

Traits	Min	Max.	Median	Mean	SE
Corallite size (mm)	0.1	284	1.3	6.5	1.2
Growth rate (mm year-1)	0.8	182	25.1	27.5	1.1
Fecundity (units)	0.5	161381.4	13.3	1214.7	485.9
Propagule size (μm)	39.4	2110	417	471	9.5
Skeletal density (g cm-3)	0.9	2.9	1.5	1.5	0.01

Table 2.4 The statistic result comparing the variations between the 2 groups. The result of (a) permutational multivariable analysis of variation (PERMANOVA) and (b) Kruskal-Wallis rank test of each species trait.

(a) PERMANOVA

	Df	Sum Sq	MeanSqs	F.Model	R^2	Pr (>F)
Group	1	10.0	10.0	183	0.28	0.001
Residuals	471	25.7	0.05		0.72	
Total	472	35.7			1	

(b) Species traits

	Chi-square	Df	Pr (>F)
Growth rate	200	1	<0.0001
Propagule size	100	1	<0.0001
Corallite size	300	1	<0.0001
Polyp fecundity	300	1	<0.0001
Skeletal density	50	1	<0.0001

Table 2.5 Summary of species traits across scenarios of 2 to 3 groups. For categorical traits (No. of family, genus, species, mode of larval development, growth form, and sexuality), abundance of each trait is presented; mean (standard deviation) is reported for continuous traits.

Group	No. of Family	No. of genera	No. of species	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Polyp fecundity (egg polyp-1)	Skeletal density (g cm-3)	Brooder	Spawner	Tables/Plates	Branching_open	Branching_closed	Corymbose	Digitate	Columnar	Massive	Laminar	Encrusting	Colony size(cm)	Gonochore	Germaphrodite	No available sexuality
(a) 2 group																							
Group 1	3	10	295	37.7 (23.1)	545.3 (216.9)	1.1 (0.4)	11.1 (9.4)	1.4 (0.3)	32	263	39	59	72	29	27	14	25	16	14	145.4 (149.7)	20	270	5
Group 2	5	26	178	10.6 (8.5)	347.7 (103.4)	15.4 (40.3)	3209.5 (17070.5)	1.6 (0.4)	7	171	0	7	16	0	8	18	97	12	20	117.6 (126.8)	39	137	2
(b) 3 group																							
Group 1	3	10	295	37.7 (23.1)	545.3 (216.9)	1.1 (0.4)	11.1 (9.4)	1.4 (0.3)	32	263	39	59	72	29	27	14	25	16	14	145.4 (149.7)	20	270	5
Group 2	5	25	161	9.1 (7.1)	372.4 (73.0)	16.9 (42.1)	3540.6 (17922.3)	1.6 (0.3)	7	154	0	0	7	0	8	17	97	12	20	120.8 (132.1)	39	120	2
Group 3	1	1	17	24.8 (8.3)	113.0 (19.5)	1.0 (0.2)	73.8 (23.2)	2.3 (0.5)	0	17	0	7	9	0	0	1	0	0	0	87.4 (45.8)	0	17	0
(d) Global	5	31	473	27.5 (23.0)	470.9 (206.2)	6.5 (25.7)	1214.7 (10568.0)	1.5 (0.3)	39	434	39	66	88	29	35	32	122	28	34	134.9 (142.0)	59	407	7

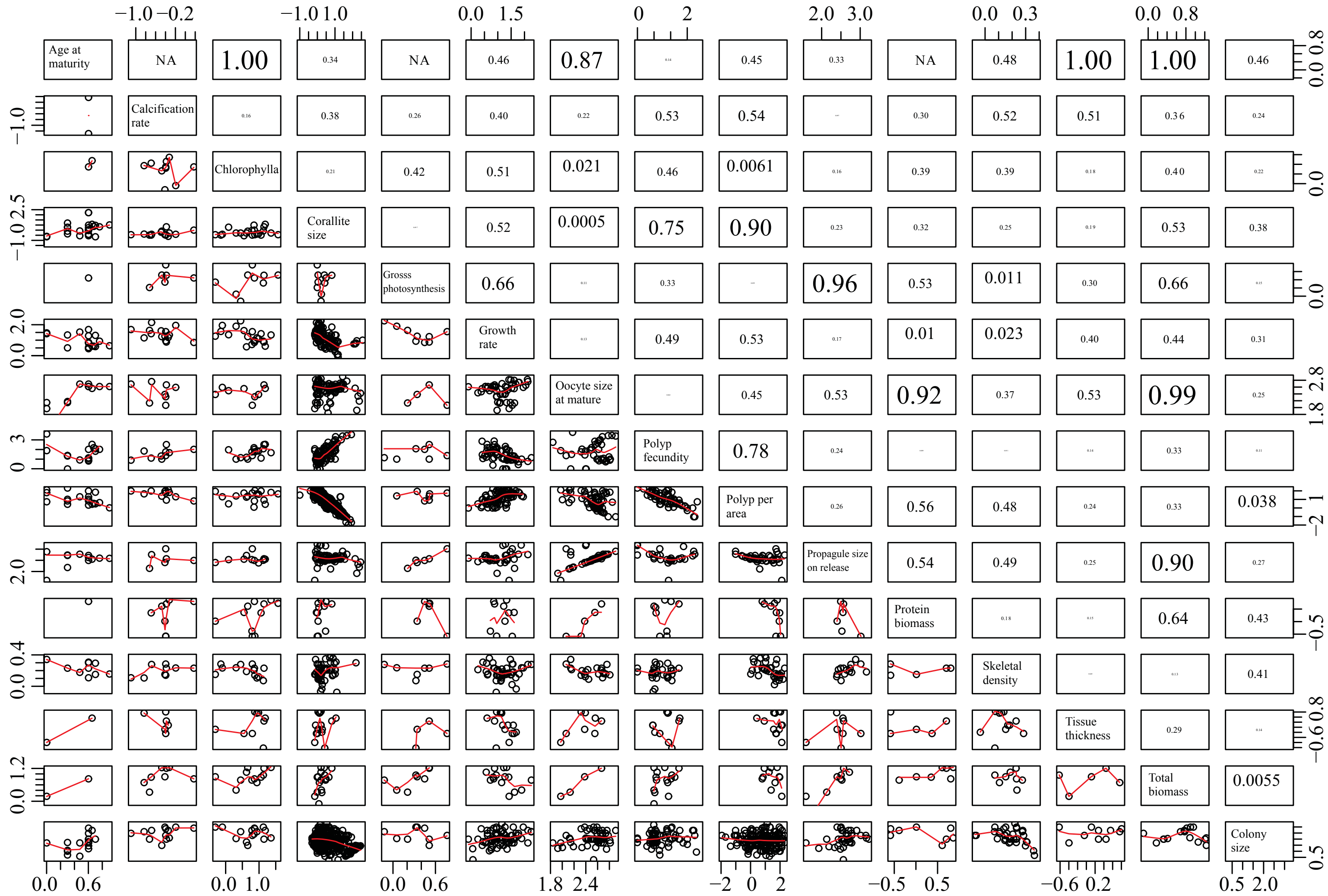


Fig. 2.1 Correlation among traits for use in determining the best model for trait infilling.

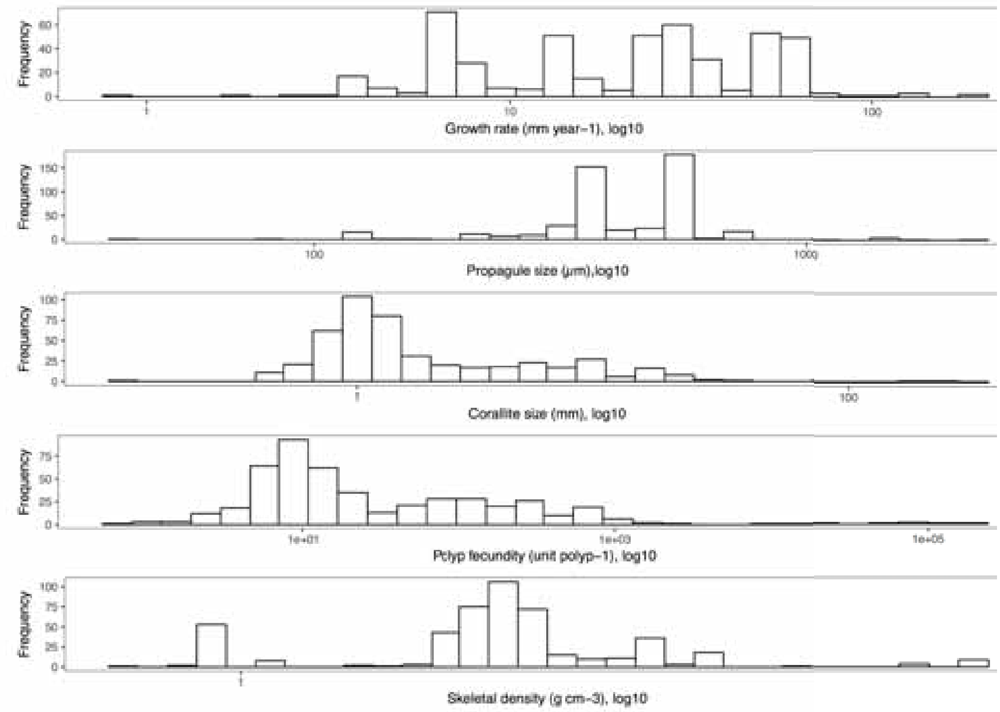


Fig. 2.2 Histogram of each of the individual traits.

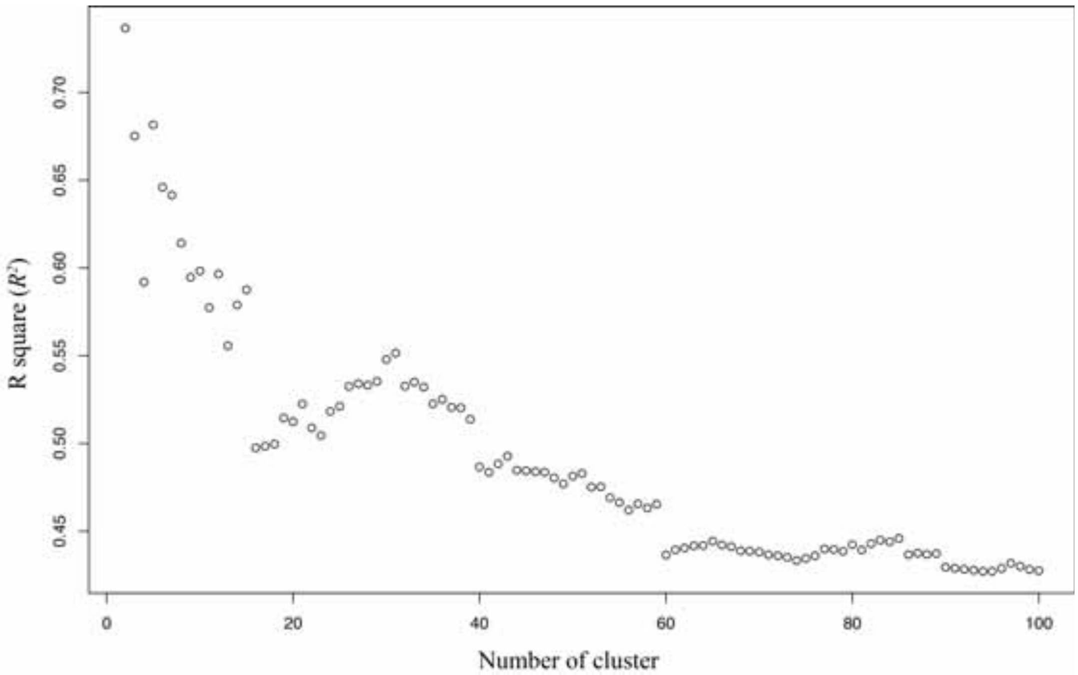


Fig. 2.3 R^2 for each of scenario of from 2 to 100 clusters from the hierarchical cluster analysis. The 2-cluster scenario is the preferred scenario with a clear drop in R^2 between 2 and 3 clusters.

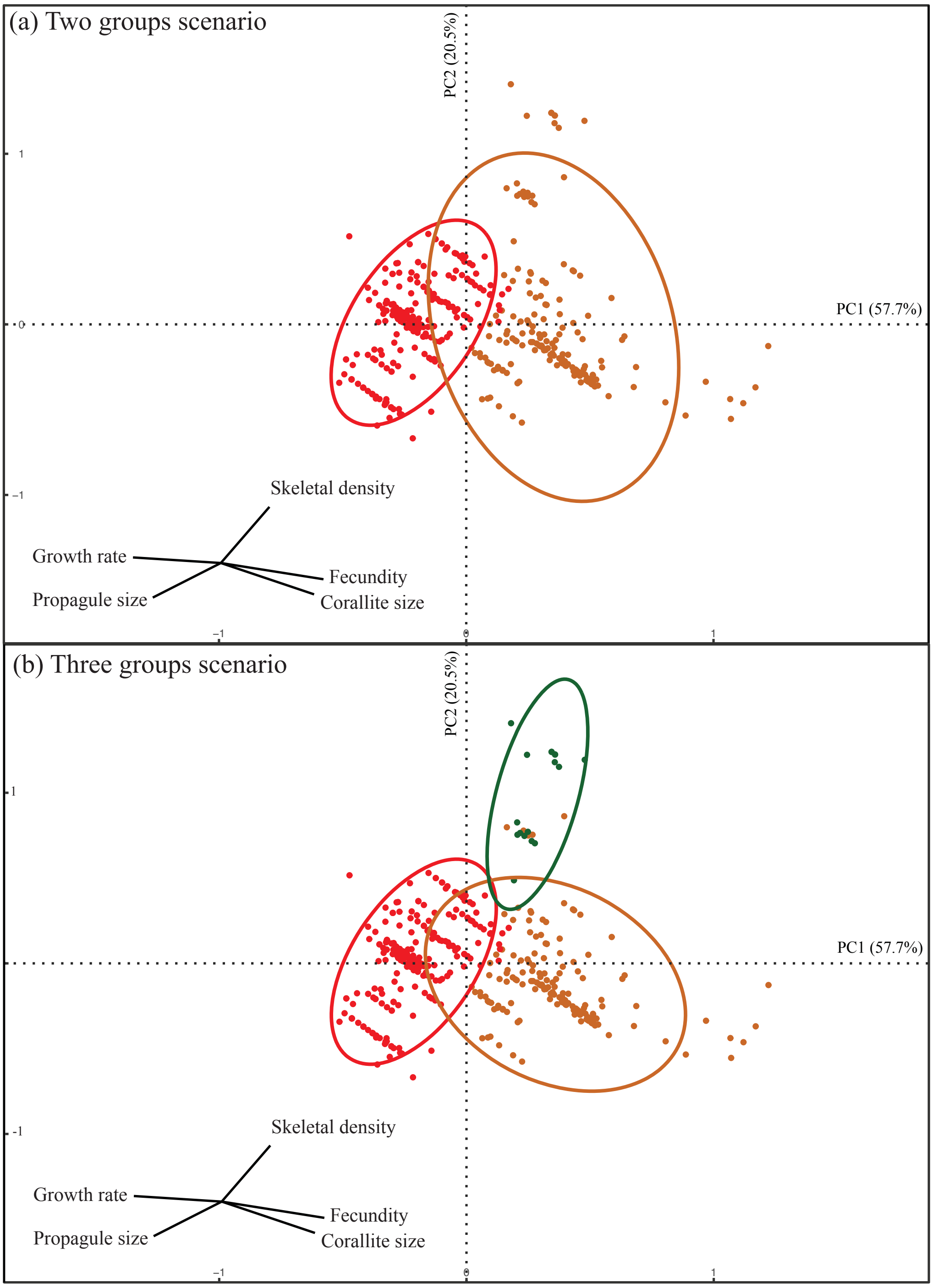


Fig. 2.4 Principle component analysis of 473 reef-building coral species and five traits with scenarios of from two to four groups. Solid lines indicate the 95% confidence ellipses (a) two groups, (b) three groups.

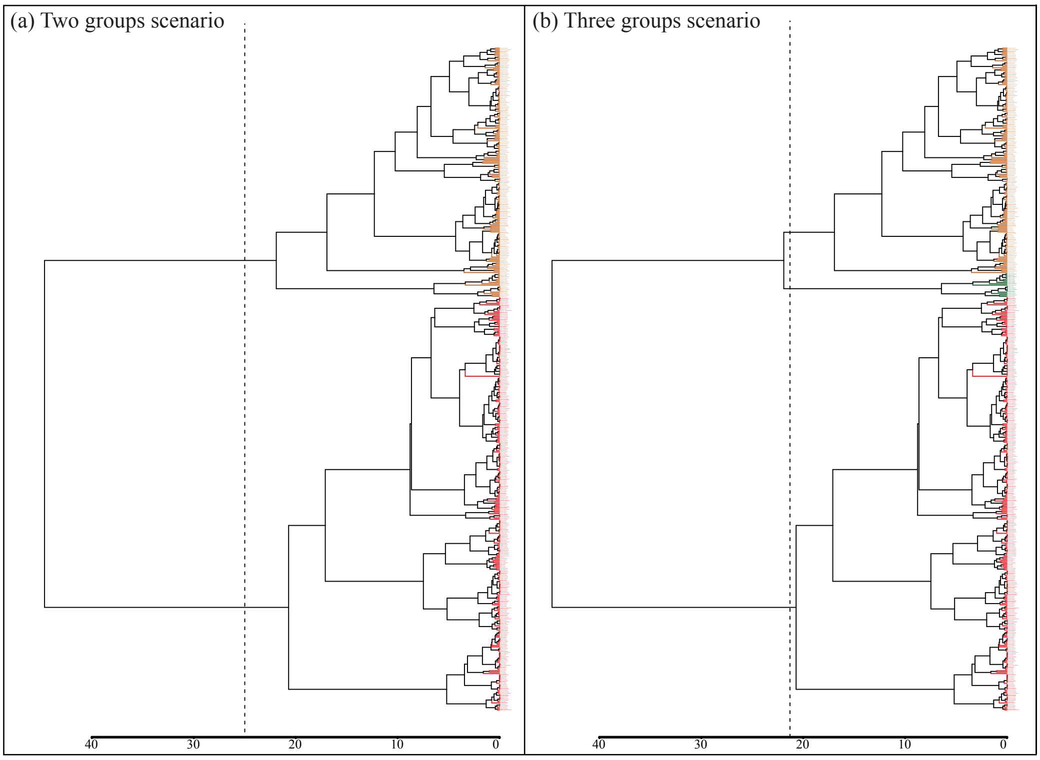


Fig. 2.5 Hierarchical cluster analysis of 473 reef-building corals species based on five species traits (a) two groups, (b) three groups.

CHAPTER 3

Fifteen years of changes in the abundance of corals on inshore reefs in the Central Great Barrier Reef: a test of adaptive strategy theory

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3.1 ABSTRACT

Universal Adaptive Strategy Theory (UAST) claims to be able to predict how taxa and assemblages respond to disturbance on the basis of adaptive strategy group membership. For example, stress tolerant species should be less affected by stress than competitive and ruderal species. Here, I tested these predictions of UAST using the recently produced adaptive strategy scheme for reef-building corals of Daring et al. (2012). I used a 15 year long dataset of coral assemblage structure from inshore reefs on the Great Barrier Reef (GBR) that included a number of stresses and disturbance events including mass bleaching and cyclones. The adaptive strategy groups did not effectively predict how a taxa respond to stress or multiple disturbance. In fact, all groups were on average equally affected by bleaching and multiple disturbances. Indeed, there were no consistent winners in response to the 1998 bleaching event. This is in contrast to much previous work suggesting clear hierarchies in susceptibility to bleaching. In conclusion, the adaptive strategy approach does not offer meaningful ecological insight over and above traditional ecological metrics and the extraordinary time involved in producing such schemes is clearly not worth the effort.

3.2 INTRODUCTION

Adaptive strategy theory aims to limit the number of units required to describe assemblages and promises to predict how taxa and assemblages respond to disturbance.

For example, the Universal Adaptive Strategy Theory (UAST) of Grime and Pierce (2012) identifies three adaptive groups and makes very specific predictions about the conditions under which each group should dominate and how each should respond to stress and disturbance.

UAST identifies three adaptive strategies and outlines the environmental conditions under which each group should benefit: **C**-species should do well when disturbance and stress are low; **S**-species should benefit when the intensity of stress is high; and **R**-species should benefit when disturbances are frequent (Fig. 1.1, Table 1.1). The distinction between stress and disturbance is an important aspect of UAST (Grime and Pierce 2012): stress is defined as “the sum of many agents that limit the quantity of living matter created per unit of space and time by constraining its production”; and disturbance as “the sum of the great multiplicity of agents that limit biomass by partly or completely destroying it”.

While the distinction between UAST stress and disturbance in terrestrial environments is clear, it is less straightforward in marine systems. In fact, stress as defined by UAST is rare in the marine environment. In the terrestrial realm it occurs due to a lack of water or nutrients while coral reefs mostly occur in nutrient-poor areas of the ocean (Muscatine and Porter 1977) and there is no shortage of water. Eutrophication can be regarded as a stress because its effects are generally sub-lethal (Koop et al. 2001). A decline the availability of light, or more specifically, photosynthetically available radiation, as depth or latitude increase could potentially be regarded as a stress. While moderate bleaching can be regarded as a stress by causing sub-lethal effects on vital rates such as growth and reproduction, severe bleaching also results in a large loss of tissue (Baird and Marshall 2002) which would classify it as a disturbance under UAST. Disturbance is very common on coral reefs, mostly in the form of wave energy generated by tropical storms (Connell 1997; Hughes and Connell 1999) and crown of thorns starfish *Acanthaster planci* outbreaks (De'ath et al. 2012). Therefore, not only do corals have life-history traits that make them difficult to place in UAST groups, the environment in which they live is also difficult to define within UAST.

A number of authors have used the adaptive strategy approach to help explain or predict the response of coral assemblage to stress and disturbance. Darling et al. (2013) claimed that the initial relative abundance of adaptive strategy groups could predict change in coral assemblage structure in response to multiple stressors including fishing, which they defined as a disturbance, and a bleaching event, defined as a stress. However, Darling et al.’s (2013) results do not support this conclusion (discussed in detail in Chapter 1). In particular, weedy species did not consistently benefit from disturbance, competitors did not benefit from periods free of disturbance and stress and the response of S-species to stress was context dependent: large declines on unfished reefs, no declines on fished reefs. In fact, the only finding consistent with the predictions of adaptive strategy theory was that competitors were more susceptible to chronic disturbance in the form of fishing than stress-tolerant and weedy species. However, all the competitive species in this study were either branching *Acropora* spp. or *Pocillopora* spp. Therefore, the only finding of significance was that branching species were more susceptible to fishing than non-branching species. Darling et al. (2013) claim for improved ecological insight using the adaptive strategies approach is false because this results would have been apparent with a very simple classification scheme i.e. branching vs non-branching corals. Similarly, Graham et al. (2014) concluded that the relative abundance of Darling et al.’s (2012) adaptive strategy groups was useful for distinguishing among reefs with a different disturbance history on the

Great Barrier Reef (GBR). Specifically, the relative abundance of competitive taxa was higher on undisturbed and recovered reefs than on reefs that had not recovered from a crown-of-thorns starfish outbreak. However, the only locally abundant species classified as competitors were *Acropora* spp. Therefore, these reefs could equally well have been distinguished by classifying taxa as *Acropora* vs non-*Acropora*. Sommer et al. (2014) also used Darling at al.'s scheme to compare the relative abundance of species in each adaptive group among coral assemblage along a high-latitude gradient in south-eastern Australia that included sites at the range limit of most coral species. The only clear trend in these data was a decrease in the relative abundance of stress-tolerant species in coral assemblage at higher latitudes in direct contrast to UAST that predicts that stress-tolerant species should dominate in unproductive habitats, such as these high latitude marginal reefs. It is clear from these examples, and despite claims made to the contrary, that Darling at al.'s groups are not behaving as predicted by adaptive strategy theory. Further, the approach does not appear to offer any particular insight. Clearly, there is a need to test the value of the adaptive strategy approach in corals with a more open mind.

In this chapter, I test whether the groups identified in Darling et al. (2012, 2013) are good predictors of the response of coral taxa to environmental stasis and change. I use a 15-year data set that documents changes in the abundance of coral genera at eight sites in the central Great Barrier Reef (GBR). This time-period includes the mass-bleaching of corals in 1998, a number of other stresses and disturbances, as well as periods without major disturbances.

3.3 MATERIAL AND METHODS

3.3.1 ***Study site***

Magnetic Island and the Palm Island group are continental islands that support extensive fringing reefs that are representative of inshore coral reefs of the central region of the Great Barrier Reef (Fig. 3.1). The reef environment is characterized by relatively shallow (<15 m), highly turbid waters, with underwater visibility rarely exceeding five metres. Reefs around these islands are relatively sheltered from oceanic conditions by the expanse of the GBR lagoon, but are exposed to the influence of nearby rivers. Reef development around inshore islands on the GBR is often patchy, giving way to soft sediments as shallow as eight metres on landward reefs. Two locations were selected in each island group: Nelly Bay (S19.167°, E146.850°) and Geoffrey Bay (S19.155° E146.861°) at Magnetic Island; and Little Pioneer Bay (S18.594° E146.485°) and Southeast Pelorus (S18.560° E146.500°) at the Palm Islands. Two depths (shallow: 2-4 m; deep: 5-8 m) were surveyed at each location to give a total of eight sites.

3.3.2 ***Survey method***

Between six and nine surveys were conducted at each site between 1998 and 2013 (Fig. 3.3). The first set of surveys was conducted in February/March 1998 during the mass bleaching event (Baird and Marshall 1998; Marshall and Baird 2000); the second set of surveys were conducted in September/October 1998 by which time the vast majority of the coral had recovered or died (Baird and Marshall 2002). Between four and six replicate 15 m x 0.5 m belt transects were used at each site on each survey. The abundance of all corals, including hard and soft corals (i.e. Scleractinia, Alcyonacea and *Millepora*), with a maximum diameter greater than 5 cm within the belt transects was recorded. All colonies were identified to genus following Veron (2000). Colonies were not identified to species because there were a number of different observers and the current poor state of taxonomy in the Scleractinia means that each observer has a different species level taxonomy. Rather, we identified colonies to Genus level to reduce differences in taxonomic opinion. I used colony abundance instead of the more commonly used metric of coral cover because it provided a much better estimate of population level mortality.

3.3.3 ***Change in coral abundance through time***

Change in the mean abundance of corals through time was tested using one-way ANOVA with Tukey post-hoc tests to identify which surveys were significantly different. Assumptions of normality of residuals and homogeneity of variances were assessed by reviewing plots of residuals against fitted values and Q-Q plots. A log-transform was applied if violations of assumptions were detected.

3.3.4 ***Disturbance regime through the course of the study***

The period of the study included a number of potential stresses and disturbances, including cyclones, bleaching, floods and low tide events. These multiple stressors affected each site to a different and often unknown level (Table 3.1). In order to test the response of the taxa and adaptive strategy groups I defined three time-intervals based on the timing of disturbances.

1. Stress - a bleaching event (March 1998 vs. October 1998)
2. Recovery - no stress or disturbance. There was a brief period free of stress and disturbance on Magnetic Island (October 1998 to April 2000) and in the Palm Islands (January 2001 to March 2005). There were no periods without disturbance at the regional scale.

3. Multiple-stressors - the total time interval of the study (March 1998 to 2012/13) during which there were multiple disturbance and stress events (Table 3.1)

3.3.5 ***The response of taxa in the different time intervals***

Changes in the abundance of the taxa during each of the three time-intervals were explored at both the site and regional scale (i.e. all sites pooled) using Cohen's *d* effect size, which is defined as the absolute value of the difference between two means of each time point, $\bar{x}_1$ and $\bar{x}_2$, divided by a pooled standard deviation, s, for the data and was estimated as follows (Cohen 1988)

$$d = \left|\frac{\bar{x}_1 - \bar{x}_2}{s}\right|$$

$$s = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}}$$

$$s_1^2 = \frac{1}{n_1 - 1}\sum_{i=1}^{n_1}(x_{1,i} - \bar{x}_1)^2$$

Cohen's *d* is regarded as a useful measure of the effect of a given event particularly when there are potential sampling issues due to low abundance. This is because it takes into account the variance in the data in addition to the difference between the means (Cohen 1988)

Losers were defined as taxa that decreased in abundance in the given time-interval and had an effect size > 0.8, which is described in the literature as a very strong effect (Cohen 1988). Winners were defined as taxa that increase in abundance in the given time interval and had an effect size > 0.8.

3.3.6 ***Bleaching mortality index vs. response as estimated by the change in effect size***

Bleaching response index, or bleaching mortality index (BMI, McClanahan 2004, McClanahan et al. 2004), was developed for predicting the mortality of coral to bleaching based on the bleaching category. I plotted the BMI index against Cohen's *d* effect size for bleaching and tested whether a linear correlation existed.

3.4 RESULTS

3.4.1 ***Changes in the abundance of coral through time***

At the regional scale, there were significant changes in coral abundance in the course of the study. The 1998 bleaching caused a 50 % reduction in the mean abundance of corals. A gradual increase until 2005 was followed by a decline in abundance towards the lowest coral abundance in the study period in 2012/13 (Fig. 3.2; Table 3.3). Seven of the eight sites had experienced significant changes at the site level, including at least one period of increase and decrease (Fig. 3.3; Table 3.3). Bleaching in 1998 caused significant declines in abundance at six of the eight sites (Fig. 3.3; Table 3.3). The only sites unaffected in terms of overall abundance of coral were the SE Pelorus sites. Increases in coral abundance were evident at all sites following the bleaching in 1998. However, recovery at Magnetic Island sites was set back by another bleaching event in 2002 followed by subsequent multiple stressors. This resulted in significantly fewer corals on Magnetic Island in 2013 compared to 1998, except for one site (GB-D) (Fig. 3.3; Table 3.3). Bleaching in 2002 did not appear to affect the sites in the Palm Island where coral abundance peaked in 2004/5. Since then, Palm Island sites have experienced multiple stressors, such as Cyclone Yasi in 2011, leading to significant declines in coral abundance. There were less corals at all sites in the Palms in 2012 compared to 1998 (Fig. 3.3; Table 3.3).

3.4.2 ***Response of taxa to bleaching in 1998***

Most taxa decreased in abundance in response to bleaching (Table 3.4). At a regional scale 37 of the 48 taxa declined in abundance (Table 3.4). Similarly, at six of the eight sites most taxa declined in abundance (Table 3.4). Based on the effect size, losers greatly out-numbered winners at all sites (Table 3.4).

The losers varied greatly among sites (Table 3.5), however, some taxa were losers at multiple sites. For example, *Montipora*, *Acropora*, *Cyphastrea*, *Turbinaria*, *Porites*, *Favia*, *Gonipora*, *Galaxea*, *Pocillopora*, *Sinularia* and *Montastrea* were always among the losers at the five most affected sites (Table 3.5). *Seriatopora* and *Stylophora* were consistent losers at the sites that did not suffer large declines in total coral abundance (i.e. SEP-S & SEP-D). At the regional scale there was no difference in the average response of the different adaptive strategy groups to stress or multiple-stressors (Fig. 3.4; Table 3.3). Losers came from all adaptive strategy groups at both the regional scale (Fig. 3.4) and at most sites (Fig. 3.5).

The winners in response to bleaching were very few (Table 3.6). At the regional scale there were no taxa that increased with an effect size of greater than 0.5 (Appendix 3.1; Fig. 3.4). At the site scale *Platygyra* was a winner at both NB-S and LPB-D and the following taxa were winners at one site: *Montipora*, *Galaxea*, *Sarcophyton*, *Alveopora* and *Leptoseris* (Table 3.6; Fig. 3.5). Winners were either stress-tolerant species or generalist taxa.

3.4.3 ***Response of taxa to multiple disturbances***

The response of taxa to multiple disturbances was very similar to the response to bleaching (Table 3.4, 3.5 & 3.6) except there were even fewer winners (Table 3.5) and more losers, particularly at the sites at SE Pelorus (Table 3.4 & 3.5). At the regional scale competitive and weedy taxa were on average more susceptible to multiple disturbances than stress-tolerant and generalist species (Fig. 3.5; Table 3.3). At the site scale, losers came from all adaptive strategy groups (Table 3.4; Fig. 3.6). At the regional scale there were no winners (Table 3.4). Winners at the site scale were either stress-tolerant species (*Porites*, Fungiidae & *Favites*) or generalists (*Mycedium* & *Pavona*; Table 3.6; Fig. 3.6).

3.4.4 ***Response of taxa to periods of no disturbance or stress***

Winners outnumbered losers in the recovery periods at most sites (Table 3.4). The losing taxa varied greatly among sites with only *Montastrea* losing at more than one site (Table 3.5). A number of taxa were consistent winners. In particular, *Montipora* and *Acropora* were winners at four sites and *Turbinaria*, *Favia*, *Favites, Sinularia, Porites* and the Fungiidae at two or more (Table 3.6). Losers were mostly stress-tolerant species and generalists (Table 3.5; Fig. 3.7) but also included weedy species and one competitor at one site (*Turbinaria* at LPB-D). Winners included taxa from all adaptive strategy groups except winning weedy species were rare (Table 3.6; Fig. 3.7).

3.4.5 ***Bleaching mortality index vs response as estimated by the change in effect size***

There was no correlation between susceptibility to bleaching as determined by the bleaching response index (BMI) and that as estimated by Cohen’s *d* effect size (Fig. 3.8).

3.5 DISCUSSION

No taxa were winners during this 15-year period of multiple stressors. At the regional scale all taxa were less abundant in 2013 than in 1998. Despite these changes and a 50% reduction in coral abundance between 1998 and 2013, there have been no extinctions at the regional scale. Therefore, multiple stressors on inshore reefs on the GBR have resulted in a lower abundance of all corals rather than caused any major shift in assemblage structure. A least one cycle of recovery in abundance has occurred at all sites, with some sites experiencing up to three periods of recovery, suggesting some level of resilience on these reefs. The current poor status of these sites is therefore most probably due to recent large-scale severe disturbance in the form of Cyclone Yasi in February 2011. Indeed, coral abundance at most sites was increasing until mass bleaching events in March 2016 and 2017 (unpublished data). Nonetheless, recent research suggests the disturbance regime on reefs has transitioned into an era where climate change and other human induced changes will predominate over natural disturbances (Hughes et al. 2017b). Furthermore, the intensity of cyclones is predicted to increase in response to ongoing climate change (Knutson et al. 2010). This 15-year period might therefore be a guide to the future status of coral reefs.

Losers greatly outnumbered winners in response to bleaching. This is not surprising because the time interval between censuses was six months and therefore the opportunity to recruit into the sampled population (i.e. greater that 5 cm maximum diameter) is mostly limited to those species susceptible to fission, such as *Platygyra* (Babcock 1991) and *Sarcophyton*. Nonetheless, these results support recent findings that very few taxa that are winners when the bleaching event is severe (Hughes et al. 2017b). In addition, traditional bleaching hierarchies based on a single census of bleaching status within populations during bleaching (eg Marshall and Baird 2000; McClanahan et al. 2004) do not reflect those based on mortality estimates from changes in abundance (Fig. 3.8). In particular, a number of taxa that rarely bleach, for example, *Cyphastrea* and *Alveopora* suffer high rates of mortality (Marshall and Baird 2000;

McClanahan 2004; Fig. 3.8). These results suggest that many taxa that are killed by the thermal anomaly that caused the bleaching do not show typical symptoms i.e. loss of symbionts and consequent paling of the colony. Accurate estimates of the effects of thermal anomalies on reefs therefore require individuals to be tagged and followed through time (eg Baird and Marshall 2002). The fact that very few taxa can cope with thermal stress is probably due to the fact that severe thermal anomalies in the ocean are a relatively recent phenomenon (Spalding and Brown 2015) and therefore corals have not had the chance to adapt to this form of stress.

Few predictions of UAST with respect to how taxa should respond to stress and disturbance are supported by these data. While the two competitive-taxa, *Acropora* and *Turbinaria*, were consistently among the winners at the site level during periods of recovery, as predicted by the theory (Table 3.6), there was no difference in the average response to stress and multiple-stressor among the adaptive groups in contrast to theoretical expectation of less effect on stress-tolerant taxa (Fig. 3.4). Indeed, there was a large range of responses among taxa within most adaptive groups. For example, the stress-tolerant taxa *Cyphastrea, Favia* and *Goniastrea* were consistently among the biggest losers at many sites in response to bleaching (Table 3.5). Winners during recovery also included taxa from all groups (Table 3.6). Similarly, the taxa responded in different ways to the same stress at different sites. For example, *Montipora* was consistently among the losers in response to bleaching, however, at SE Pelorus – D it was a winner (Table 3.5 & 3.6). This is evidence of a diversity of responses within some species-rich genera (eg *Montipora)*, suggesting that working with adaptive strategy groups at the genus level is not appropriate. Indeed, there are few traits that are similar among species with most genera, in particular species-rich genera like the *Acropora*, *Montipora* and *Porites* (Madin et al. 2016a). One prediction of UAST supported by my data is that it is not possible for organisms to adapt to a high frequency of both stress and disturbance (Grime and Pierce 2012; Table 1.1, Fig. 1.1). Indeed, there appears to be no true weedy species in the sessile coral. In other words, species capable of rapid increase in abundance in response to disturbance are rare on coral reefs, unlike the numerous species of weeds in terrestrial environments (Grime and Pierce 2012).

The relative abundance of the adaptive strategies in the initial assemblages was not a good predictor of the trajectory of the assemblage in response to stress or multiple disturbances. Indeed, seven of the eight sites were equally degraded in the 15 years of the study despite big differences in initial assemblage structure. In particular, the *Acropora* dominated assemblages at SE Pelorus were the least affected by bleaching (Fig. 3.3), at least with respect to changes in abundance. This is despite very high levels of mortality in tagged colonies of two species of *Acropora* at SE Pelorus (Baird and Marshall 2002). This again suggests that there are important differences in the response to bleaching among species within this genus and categorising adaptive strategies above species level is therefore not appropriate.

In conclusion, the adaptive strategy groups of Darling et al. (2012) rarely behaved as predicted, probably because of a diversity of response among taxon within most adaptive groups. My research in addition to that of Darling et al. (2013), Graham et al. (2014) and Sommer et al. (2014) indicate that the approach does not offer sufficient ecological insight to be worth the extraordinary effort to determine the adaptive group of a given taxa at a given site (discussed in Chapter 1). In Chapter 4 I test the utility of direct trait based approaches to offer ecological insight above and beyond the adaptive strategy approach and traditional coral reef ecological methods.

Table 3.1 History of disturbances affecting the coral assemblages on Magnetic Island and the Great Palms during study period.

Date	Incident	Nelly Bay	Geoffrey Bay	Little Pioneer Bay	SE Pelorus	References
Mar-98	Bleaching	Yes	Yes	Yes	Yes	Marshall and Baird 2000; Berkelmans et al. 2004
Mar-02	Bleaching	Yes	Yes	Unknown	Unknown	Berkelmans et al. 2004
Sep-05	Low tides	Unknown	Unknown	Yes	Unknown	Anthony and Kerswell 2007
Summer-2009	Flood - Ross River	Yes	Yes	Unknown	Unknown	Haapkylä et al. 2011
2010-2011	Flood - Burdekin River	Unknown	Unknown	Unknown	Unknown	Bainbridge et al. 2012
Jan. to early Feb.-2011	Cyclone Yasi	Unknown	Unknown	Unknown	Yes	Lukoschek et al. 2016

Table 3.2 Adaptive strategy groups.

Genus	Darling at al.'s group	Genus	Darling at al.'s group
Acanthastrea	Stress-tolerant	*Merulina*	Generalist
Acropora	Competitive	*Millepora*	Unknown
Alveopora	Stress-tolerant	*Montastrea*	Stress-tolerant
Astreopora	Stress-tolerant	*Montipora*	Generalist
Caryophyllia	Unknown	*Moseleya*	Unknown
Coeloseris	Unknown	*Mycedium*	Generalist
Coscinaraea	Unknown	*Oulophyllia*	Stress-tolerant
Cyphastrea	Stress-tolerant	*Oxypora*	Unknown
Diploastrea	Stress-tolerant	*Pachyseris*	Generalist
Echinophyllia	Stress-tolerant	*Pavona*	Generalist
Echinopora	Generalist	*Pectinia*	Unknown
Favia	Stress-tolerant	*Platygyra*	Stress-tolerant
Favites	Stress-tolerant	*Plesiastrea*	Stress-tolerant
Fungiidae	Stress-tolerant	*Pocillopora*	Weedy
Galaxea	Stress-tolerant	*Porites*	Stress-tolerant
Goniastrea	Stress-tolerant	*Psammocora*	Generalist
Goniopora	Unknown	*Sarcophyton*	Unknown
Hydnophora	Generalist	*Scolymia*	Stress-tolerant
Isopora	Unknown	*Seriatopora*	Weedy
Leptastrea	Weedy	*Sinularia*	Unknown
Leptoria	Stress-tolerant	*Stylocoeniella*	Unknown
Leptoseris	Unknown	*Stylophora*	Weedy
Lobophyllia	Stress-tolerant	*Symphyllia*	Stress-tolerant
Lobophytum	Unknown	*Turbinaria*	Competitive

Table 3.3 One-way ANOVA testing for difference in the mean coral abundance through time at eight sites in the central Great Barrier Reef region from 1998 to 2012/13.

Site (abbreviation)		Affected by 1998 bleaching?
Regional scale	F = 15.06, df = 4, 234, P < 0.001	Yes
Nelly Bay-2m (NB-S)	F= 13.16, df = 5, 28, P < 0.001	Yes
Nelly Bay-6m (NB-D)	F= 35.88, df = 5, 31, P < 0.001	Yes
Geoffrey Bay-2m (GB-S)	F = 18.28, df = 5, 28, P < 0.001	Yes
Geoffrey Bay-6m (GB-D)	F = 2.75, df = 5, 32, P = 0.036	Yes
Little Pioneer Bay-2m (LPB-S)	F= 4.97, df = 8, 46, P < 0.001	Yes
Little Pioneer Bay-6m (LPB-D)	F= 2.60, df = 8, 45, P = 0.020	No
Southeast Pelorus -4m (SEP-S)	F= 34.31, df = 6, 33, P < 0.001	No
Southeast Pelorus -6m (SEP-D)	F= 14.58, df = 6, 30, P < 0.001	No

Table 3.4 Summary of changes in the abundance of genera at each site in the three different periods.

Site	Period	Taxa	Decrease	Increase	Extinction	Coloniser	Losers	Winners
Region	Bleaching	48	37	11	0	0	13	0
Region	Multiple	48	36	12	0	5	13	0
Nelly Bay-2m	Bleaching	23	21	2	11	2	14	1
Nelly Bay-6m	Bleaching	30	27	3	13	2	12	0
Geoffrey Bay-2m	Bleaching	22	22	0	14	3	14	0
Geoffrey Bay-6m	Bleaching	33	27	6	7	5	16	0
Little Pioneer Bay-2m	Bleaching	37	31	7	10	4	15	3
Little Pioneer Bay-6m	Bleaching	38	25	13	4	5	8	5
Southeast Pelorus-4m	Bleaching	29	14	15	8	4	6	2
Southeast Pelorus-6m	Bleaching	23	10	13	4	8	4	1
Nelly Bay-2m	Multiple	23	22	1	11	1	13	0
Nelly Bay-6m	Multiple	30	25	5	14	4	12	0
Geoffrey Bay-2m	Multiple	22	18	4	13	2	11	0
Geoffrey Bay-6m	Multiple	33	24	9	7	6	11	2
Little Pioneer Bay-2m	Multiple	37	27	10	9	3	14	1
Little Pioneer Bay-6m	Multiple	38	20	18	3	3	9	1
Southeast Pelorus-4m	Multiple	29	25	4	18	1	14	0
Southeast Pelorus-6m	Multiple	23	21	2	10	6	17	1
Nelly Bay-2m	Recover	15	6	9	3	8	2	4
Nelly Bay-6m	Recover	19	7	12	4	11	2	6
Geoffrey Bay-2m	Recover	11	4	7	2	10	2	3
Geoffrey Bay-6m	Recover	32	14	18	6	6	1	3
Little Pioneer Bay-2m	Recover	25	4	21	0	8	2	10
Little Pioneer Bay-6m	Recover	38	14	24	4	6	3	6
Southeast Pelorus-4m	Recover	19	11	8	3	11	4	4
Southeast Pelorus-6m	Recover	25	15	10	3	2	1	3

Table 3.5 The losers of each of the three periods on each site and regional scale.

Site	Period	Losers
Region	Bleaching	*Cyphastrea*, *Montipora*, *Favia*, *Pocillopora*, *Stylophora*, *Acropora*, *Gonipora*, *Lobophyllia*, *Goniastrea*, *Turbinaria*, *Isopora*, *Galaxea*, *Sinularia*
Region	Multiple	*Acropora*, *Cyphastrea*, *Gonipora*, *Favia*, *Galaxea*, *Pocillopora*, *Pectinia*, *Stylophora*, *Turbinaria*, *Lobophytum*, *Oxypora*, *Millepora*, *Symphyllia*
Nelly Bay-2m	Bleaching	*Montipora*, *Acropora*, *Cyphastrea*, *Turbinaria*, *Porites*, *Favia*, *Gonipora*, *Goniastrea*, *Pavona*, *Alveopora*, *Galaxea*, *Plesiastrea*, *Leptoseris*, *Lobophyllia*, *Psammocora*
Nelly Bay-6m	Bleaching	*Cyphastrea*, *Turbinaria*, *Acropora*, *Favia*, *Montipora*, *Goniopora*, *Hydnophora*, *Galaxea*, *Porites*, *Goniastrea*, *Moseleya*, *Oxypora*
Geoffrey Bay-2m	Bleaching	*Montipora*, *Favia*, *Acropora*, *Galaxea*, *Stylophora*, *Cyphastrea*, *Turbinaria*, *Favites*, *Gonipora*, *Porites*, *Goniastrea*, *Lobophyllia*, *Pocillopora*, *Moseleya*
Geoffrey Bay-6m	Bleaching	*Lobophyllia*, *Oxypora*, *Merulina*, *Montipora*, *Favia*, *Goniastrea*, *Stylophora*, *Sarcophyton*, *Moseleya*, *Lobophytum*, *Pocillopora*, *Porites*, *Pachyseris*, *Galaxea*, *Mycedium*
Little Pioneer Bay-2m	Bleaching	*Sinularia*, *Goniopora*, *Montipora*, *Pectinia*, *Pocillopora*, *Cyphastrea*, *Millepora*, *Acropora*, *Goniastrea*, *Merulina*, *Favia*, *Montastrea*, *Favites*, *Acanthastrea*, *Echinophyllia*
Little Pioneer Bay-6m	Bleaching	*Sinularia*, *Montipora*, *Pavona*, *Lobophyllia*, *Acanthastrea*, *Echinopora*, *Favia*, *Goniastea*
Southeast Pelorus-4m	Bleaching	*Isopora*, *Leptoria*, *Pocillopora*, *Montastrea*, *Seriatopora*, *Stylophora*
Southeast Pelorus-6m	Bleaching	*Seriatpora*, *Stylophora*, *Goniastrea*, *Leptastrea*

Table 3.5 The losers of each of the three periods on each site and regional scale. (cont.)

Site	Period	Losers
Nelly Bay-2m	Multiple	*Porites*, *Acropora*, *Montipora*, *Cyphastrea*, *Goniastrea*, *Favia*, *Turbinaria*, *Favites*, *Gonipora*, *Galaxea*, *Coscinareae*, *Plesiastrea*, *Lobophyllia*
Nelly Bay-6m	Multiple	*Acropora*, *Montipora*, *Galaxea*, *Turbinaria*. *Cyphastrea*, *Gonipora*, *Favia*, *Hydnophora*, *Goniastrea*, *Montastrea*, *Pectinia*, *Oxypora*,
Geoffrey Bay-2m	Multiple	*Favia*, *Acropora*, *Galaxea*, *Stylophora*, *Turbinaria*, *Cyphastrea*, *Favites*, *Moseleya*, *Lobophyllia*, *Pocillopora*, *Porites*
Geoffrey Bay-6m	Multiple	*Sarcophyton*, *Lobophyllia*, *Lobophytum*, *Favia*, *Goniastrea*, *Symphyllia*, *Oxypora*, *Moseleya*, *Stylopora*, *Pocillopora*, *Oulophyllia*,
Little Pioneer Bay-2m	Multiple	*Gonipora*, *Montipora*, *Cyphastrea*, *Pectinia*, *Millepora*, *Favites*, *Sinularia*, *Favia*, *Merulina*, *Lobophyllia*, *Pocillopora*, *Seriatopora*, Fungidae, *Pachyseris*, *Acanthastrea*
Little Pioneer Bay-6m	Multiple	*Cyphastrea*, *Pectinia*, *Montipora*, *Symphyllia*, *Echinopora*, *Sinularia*, *Galaxea*, *Millepora*, *Astreopora*,
Southeast Pelorus-4m	Multiple	*Leptoria*, *Acropora*, *Pocillopora*, *Sinularia*, *Lobophytum*, *Favia*, *Isopora*, *Favites*, *Merulina*, *Hydnophora*, *Seriatopora*, *Stylophora*, *Goniopora*, *Porites*
Southeast Pelorus-6m	Multiple	*Sarcophyton*, *Seriatopora*, *Acropora*, *Echinopora*, *Favia*, *Pocillopora*, *Galaxea*, *Platygyra*, *Stylophora*, *Lobophytum*, *Montipora*, *Leptoria*, *Hydnophora*, *Merulina*, *Millepora*, *Sinularia*
Nelly Bay-2m	Recover	*Coscinaraea*, *Leptoseris*
Nelly Bay-6m	Recover	*Leptoria*, *Montastrea*,
Geoffrey Bay-2m	Recover	*Seriatopora*, *Leptoria*
Geoffrey Bay-6m	Recover	*Montastrea*
Little Pioneer Bay-2m	Recover	*Symphyllia*, *Platygyra*
Little Pioneer Bay-6m	Recover	*Echinophyllia*, *Montastrea*, *Turbinaria*
Southeast Pelorus-4m	Recover	*Montastrea*, *Acanthastrea*, *Astreopora*, *Goniastrea*
Southeast Pelorus-6m	Recover	*Favites*

Table 3.6 The winners of each of the three periods on each site and regional scale.

Site	Period	Winners
Region	Bleaching	none
Region	Multiple	none
Nelly Bay-2m	Bleaching	*Platygyra*
Nelly Bay-6m	Bleaching	none
Geoffrey Bay-2m	Bleaching	none
Geoffrey Bay-6m	Bleaching	none
Little Pioneer Bay-2m	Bleaching	*Leptastrea*, *Platygyra*, *Astreopora*
Little Pioneer Bay-6m	Bleaching	*Pachyseris*, *Alveopora*, *Sarcophyton*, *Oulophyllia*, *Leptoseris*
Southeast Pelorus-4m	Bleaching	*Montipora*, *Sarcophyton*
Southeast Pelorus-6m	Bleaching	*Galaxea*
Nelly Bay-2m	Multiple	none
Nelly Bay-6m	Multiple	none
Geoffrey Bay-2m	Multiple	none
Geoffrey Bay-6m	Multiple	*Porites*, Fungiidae
Little Pioneer Bay-2m	Multiple	*Pavona*
Little Pioneer Bay-6m	Multiple	*Mycedium*
Southeast Pelorus-4m	Multiple	none
Southeast Pelorus-6m	Multiple	*Favites*
Nelly Bay-2m	Recover	*Montipora*, *Acropora*, *Goniastrea*, *Turbinaria*
Nelly Bay-6m	Recover	*Favia*, Fungiidae, *Montipora*, *Galaxea*, *Turbinaria*, *Acropora*, *Favites*, *Porites*, *Cyphastrea*
Geoffrey Bay-2m	Recover	*Montipora*, *Turbinaria*, *Acropora*
Geoffrey Bay-6m	Recover	*Montipora*, *Sinularia*, Fungiidae
Little Pioneer Bay-2m	Recover	*Pectinia*, *Acropora*, *Porites*, *Lobophyllia*, *Echinophyllia*, *Favites*, *Echinopora*, *Pavona*, *Astreopora*, *Sarcophyton*
Little Pioneer Bay-6m	Recover	*Sinularia*, *Favia*, *Porites*, *Echinopora*, *Sarcophyton*, *Galaxea*
Southeast Pelorus-4m	Recover	*Acropora*, *Coeloseris*, *Favia*, *Symphyllia*
Southeast Pelorus-6m	Recover	*Pocillopora*, *Platygyra*, *Leptastrea*

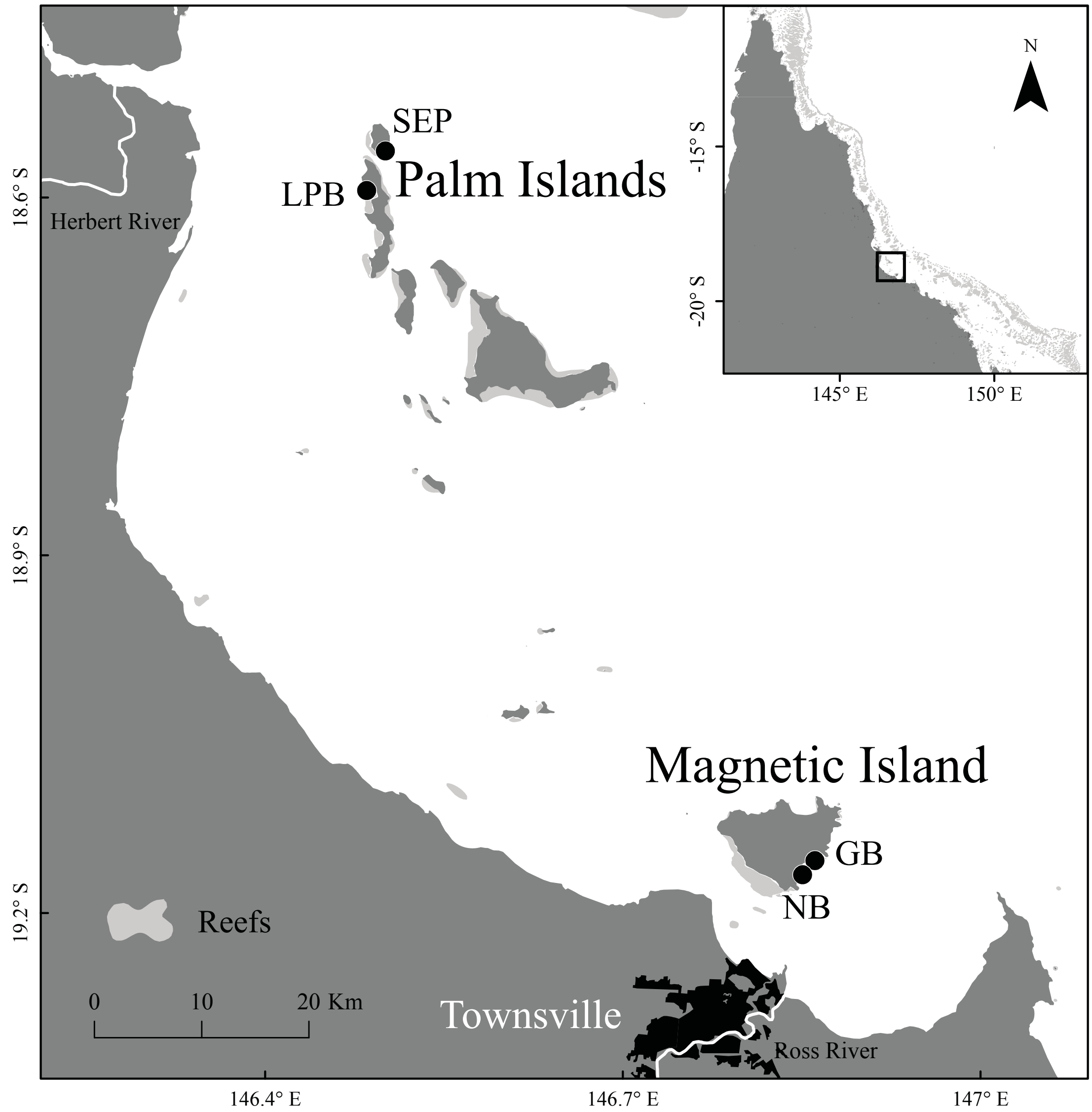

Fig. 3.1 Location of survey sites, including Nelly Bay (NB); Geoffrey Bay (GB); Little Pioneer Bay (LPB); and Southeast Pelorus (SEP).

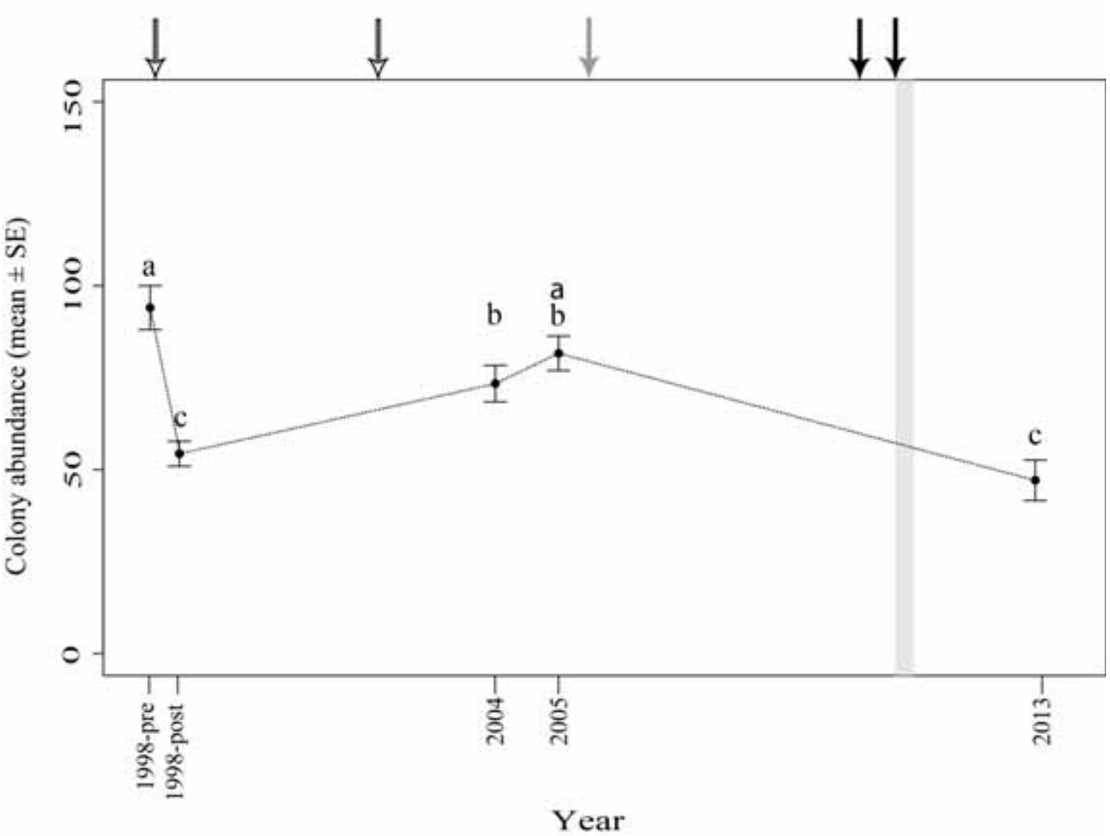

Fig. 3.2 Temporal changes in coral colony abundance at regional scale, all sites pooled together, in the central Great Barrier Reef region from 1998 to the last survey in 2013. The five time points are the surveys which were conducted at all eight sites. Arrows indicate disturbances, including two bleaching events (1998 and 2002, white), one low tide event (2005, grey), two flood events (2009, 2010-2011, black). The grey bar indicates tropical Cyclone Yasi in 2011. Letters above dots indicate significant groupings by Tukey's post hoc test at different surveys.

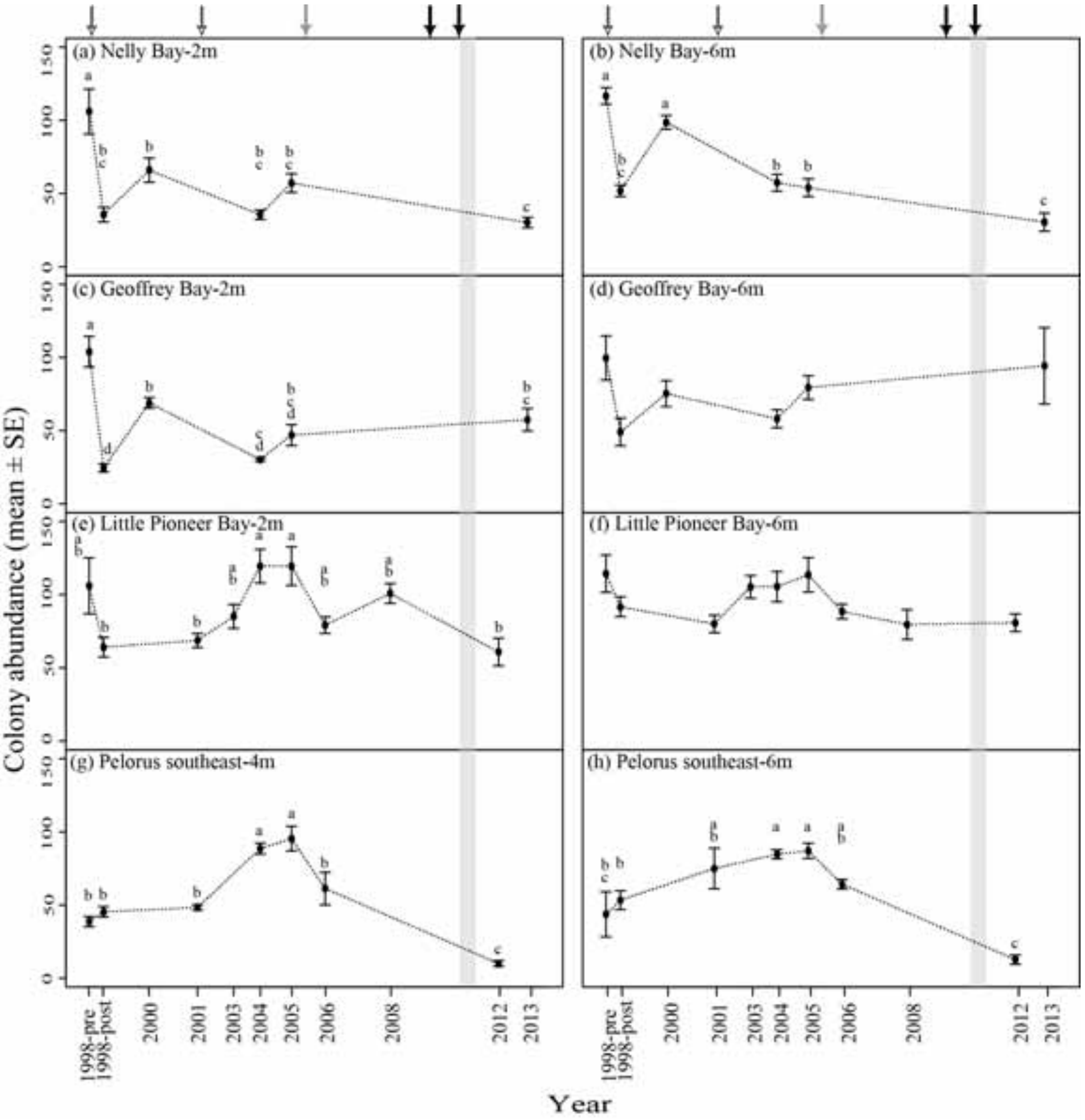

Fig. 3.3 Temporal changes in average coral colony abundance (mean ± SE) at 8 sites in the central Great Barrier Reef region from 1998 to 2013. Sites include NB 2m (a) 6m (b), GB 2m (c) 6m (d), LPB 2m (e) 6m (f), and SEP 4m (g) 6m (h). Arrows indicated disturbances including two bleaching events (1998 and 2002, white), one low tide event (2005, grey), two flood events (2009, 2010-2011, black). The grey bar indicates tropical Cyclone Yasi in 2011. Letters above dots indicate significant groupings by one-way ANOVA, Welch's F test and Tukey’s post hoc test at different surveys.

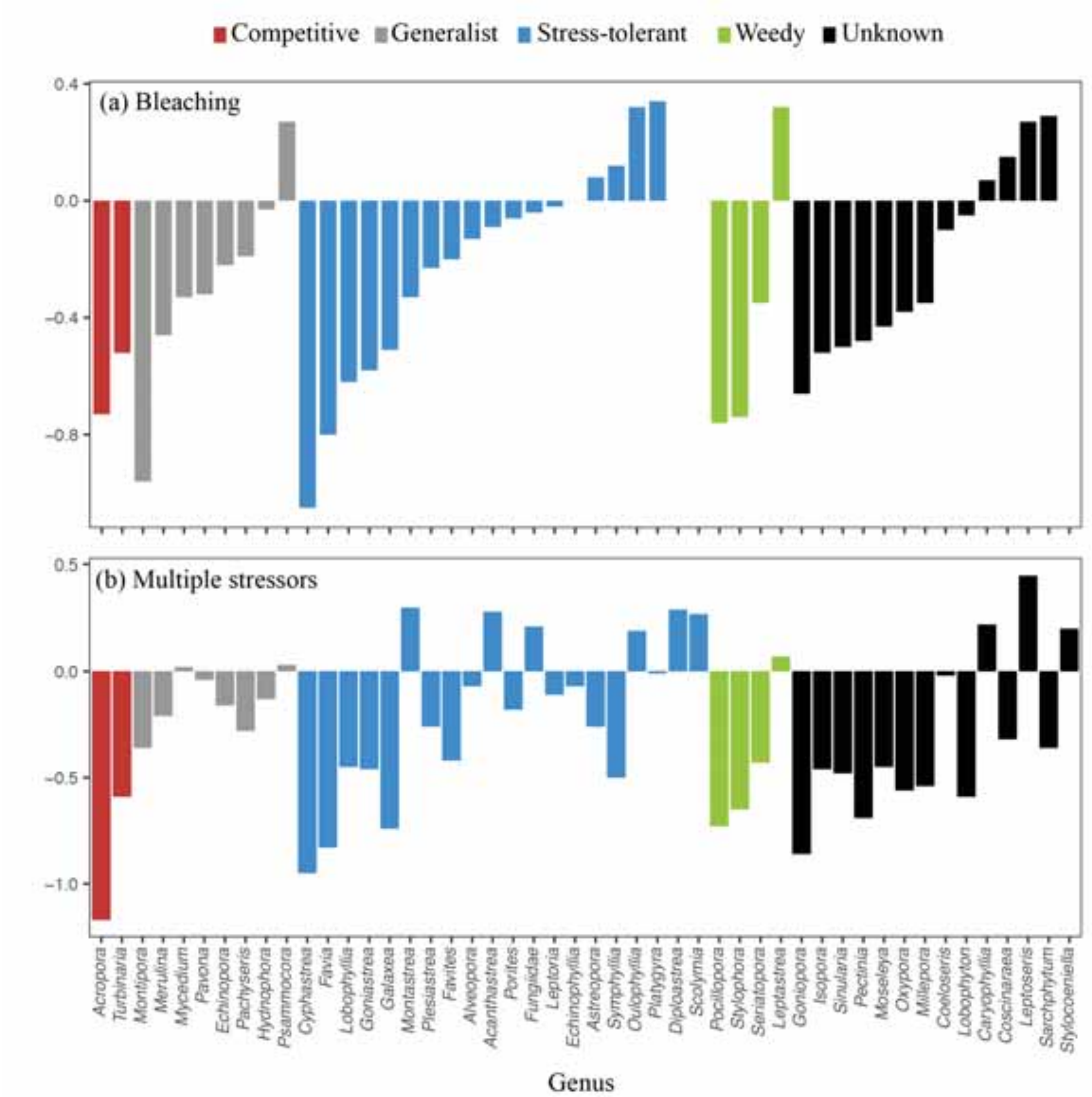

Fig. 3.4 Effect size by taxa for bleaching (a) and multiple disturbances (b) at regional scale. Colours indicate Darling at al.'s adaptive strategy scheme used, including competitive (red), generalist (gray), stress-tolerant (blue), weedy (green), and unknown (black) strategies.

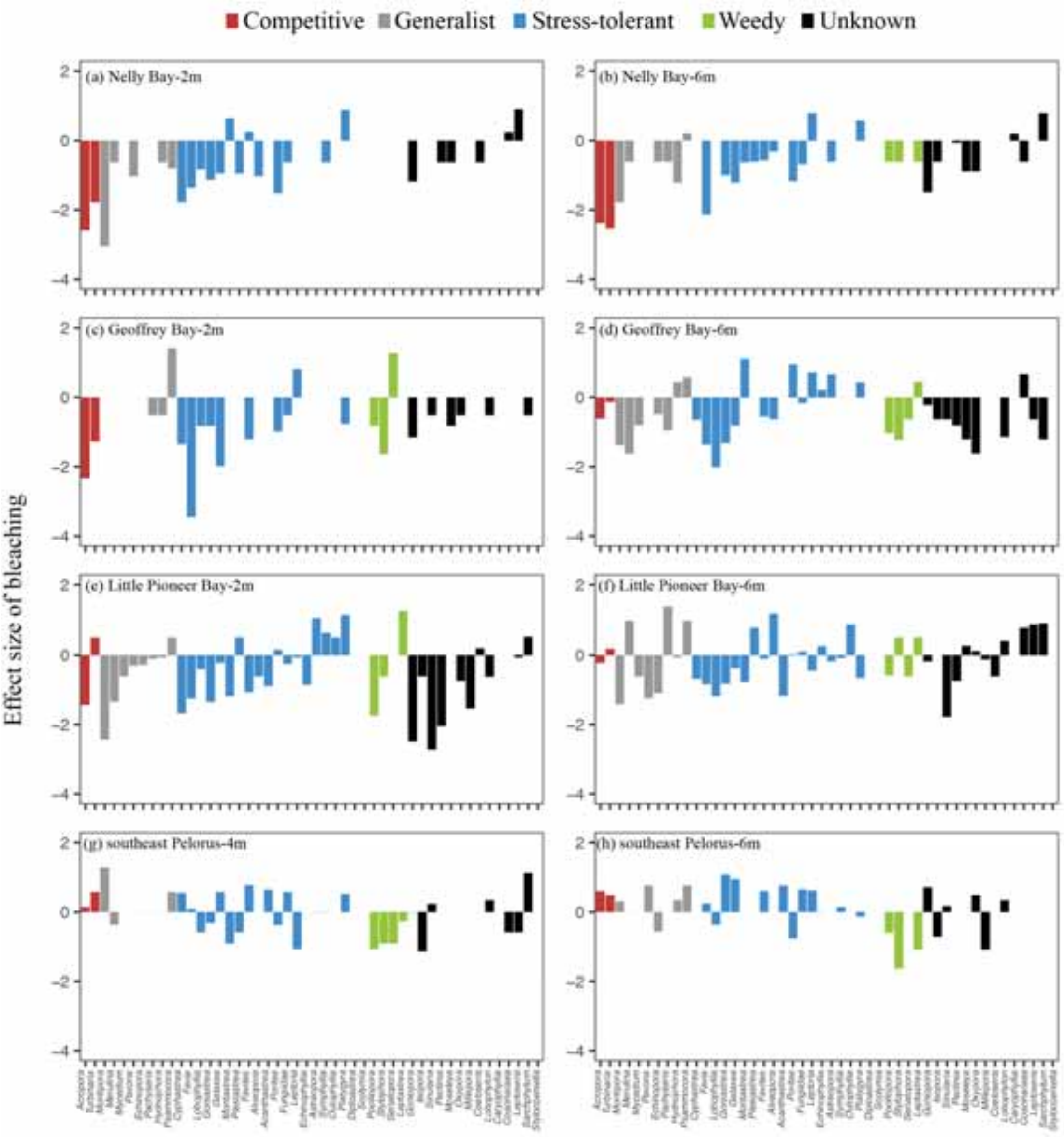

Fig. 3.5 Effect size by taxa for bleaching event. Sites include Nelly Bay 2m (a) 6m (b), Geoffrey Bay 2m (c) 6m (d), Little Pioneer Bay 2m (e) 6m (f), and Southeast Pelorus 4m (g) 6m (h). Colours indicate Darling at al.'s adaptive strategy scheme used, including Competitive (red), generalist (gray), stress-tolerant (blue), weedy (green), and unknown (black) strategies.

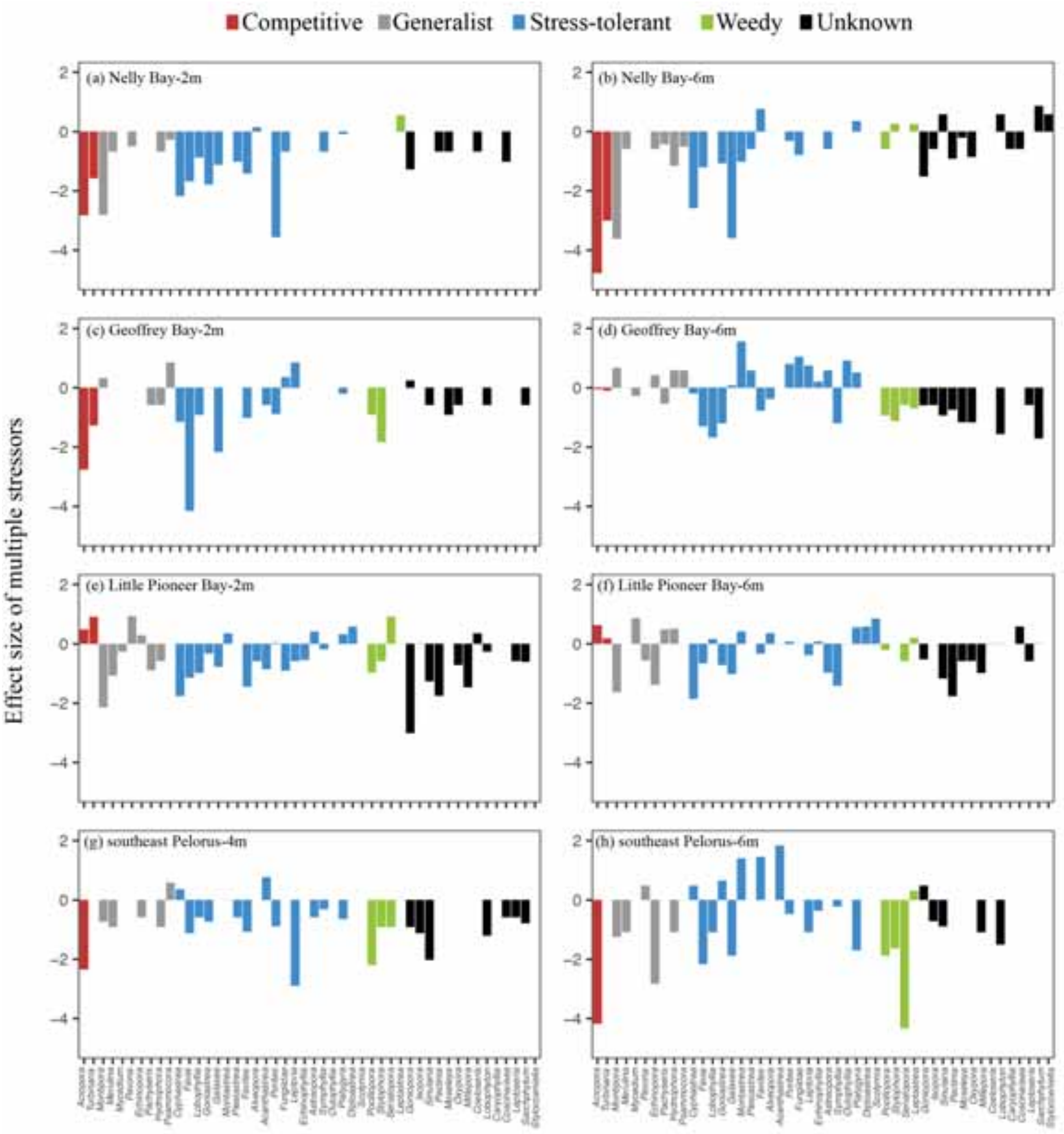

Fig. 3.6 Effect size by taxa for multiple disturbances. Sites include Nelly Bay 2m (a) 6m (b), Geoffrey Bay 2m (c) 6m (d), Little Pioneer Bay 2m (e) 6m (f), and Southeast Pelorus 4m (g) 6m (h). Colours indicate Darling at al.’s adaptive strategy scheme used, including Competitive (red), generalist (gray), stress-tolerant (blue), weedy (green), and unknown (black) strategies.

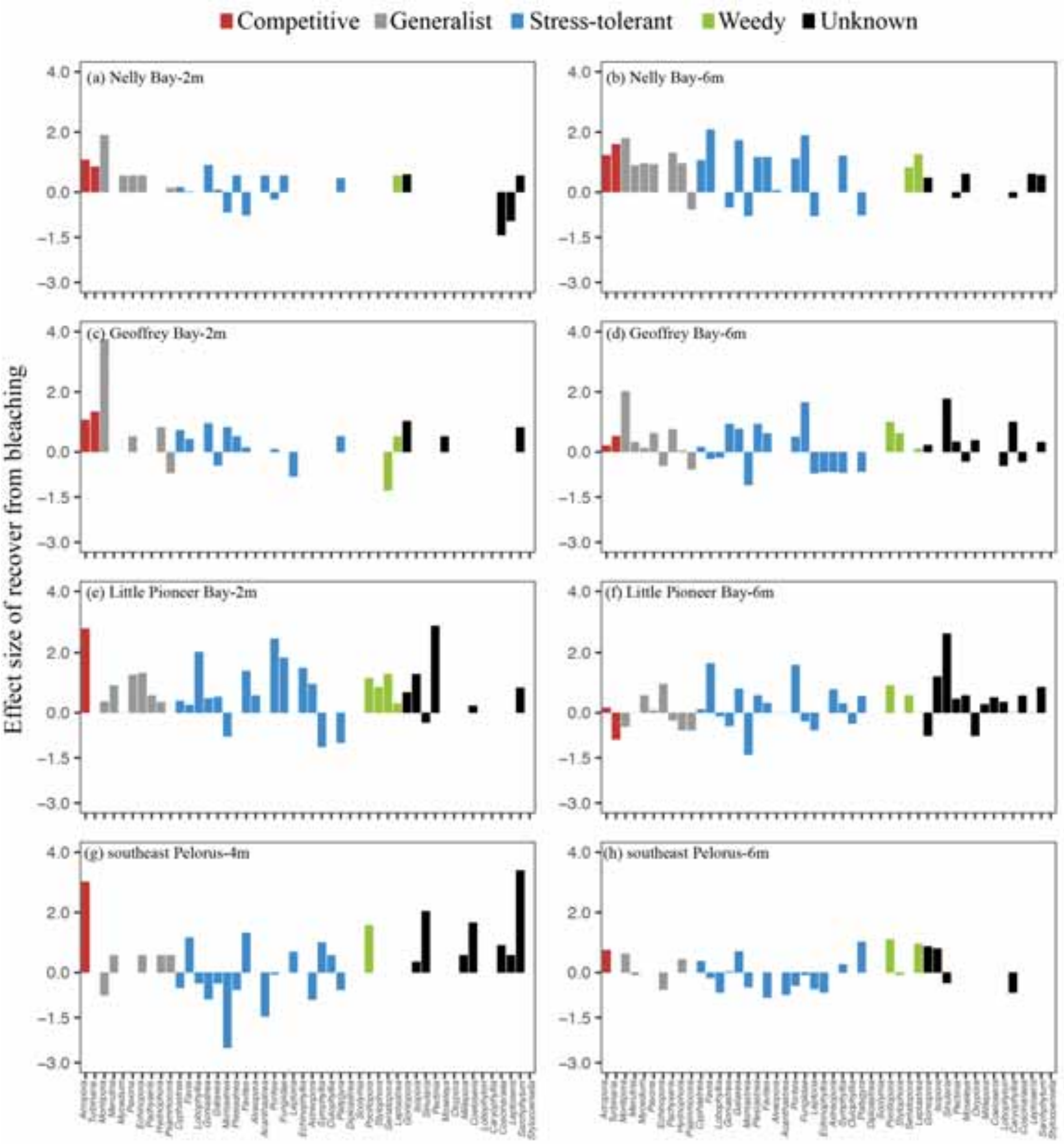

Fig. 3.7 Effect size by taxa for recover period. Sites include Nelly Bay 2m (a) 6m (b), Geoffrey Bay 2m (c) 6m (d), Little Pioneer Bay 2m (e) 6m (f), and Southeast Pelorus 4m (g) 6m (h). Colours indicate Darling at al.'s adaptive strategy scheme used, including Competitive (red), generalist (gray), stress-tolerant (blue), weedy (green), and unknown (black) strategies.

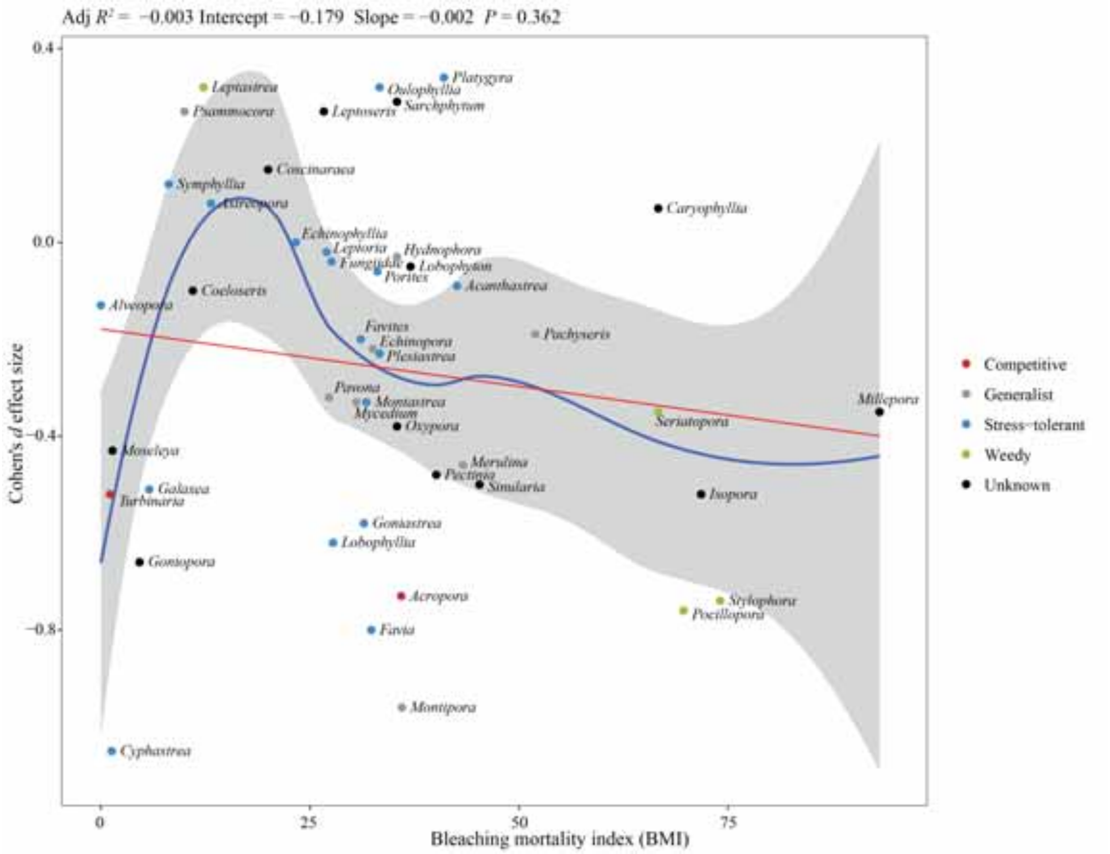

Fig. 3.8 Bleaching mortality index vs. effect size. Blue line represents the smooth line of LOESS smoother. Red line and the formula above represent the linear regression line and regression result. Colours indicate Darling at al.'s adaptive strategy scheme used, including Competitive (red), generalist (gray), stress-tolerant (blue), weedy (green), and unknown (black) strategies.

CHAPTER 4

Latitudinal variation in the relative abundance of adaptive-strategies in coral assemblages.

4.1 ABSTRACT

One of the major goals of ecology is to identify metrics of assemblage structure that enable accurate predictions of how assemblages respond to their environment. Adaptive strategy approaches promise to predict which taxa will dominate in different environments. For example, the Universal Adaptive Strategy Theory (UAST) predicts that species tolerant to stress should dominate at the latitudinal range boundaries where stresses are generally greater. The aim of this chapter was to test for variation in the relative abundance of adaptive strategy groups in coral assemblages along the 1,800 km latitudinal gradient of the Great Barrier Reef. I found that UAST groups did not respond in a predictable way along this environmental gradient. In contrast, there were significant differences in the assemblage weighted means of a number of traits that are likely to be highly correlated with fitness, including maximum colony size and growth rates. In conclusion, it is much more tractable and informative to explore traits directly, rather than looking for groups based on traits which define the adaptive strategy approach.

4.2 INTRODUCTION

The decline of species richness with increasing latitude is one of the most prominent spatial patterns in ecology (Willig et al 2003). This pattern occurs in numerous taxa (Gaston 2000; Willig et al. 2003), including reef-building corals (Wells 1955, Veron 1995, Keith et al. 2013). For example, coral species richness declines from over 300 species in northern GBR to around 250 species in the south (Veron 1995). The main driver of these patterns is believed to be temperature (Wells 1955; Veron 1995).

Adaptive strategy theory makes specific predictions about which species should be favored along environmental gradients including those correlated with latitude such as temperature. In particular, UAST predicts that as stress increases, species with traits that increase the ability of the organism to endure stress should be favoured. The GBR is approximately 1,800 km in length with a gradual decline in annual mean seawater temperatures (SST) from 28^{o}C in the north to 24 ^{o}C in the south (Lough 2008; Woolsey et al. 2015). Furthermore, variation in SST also increases predictably from north to south (Woolsey et al. 2015) suggesting that southern coral assemblages will be subject to greater stress and therefore they should have a higher relative abundance of stress tolerant species.

Sommer et al. (2014) specifically tested this hypothesis using Darling et al.'s (2012) adaptive strategy groups to compare the relative abundance of species in each adaptive group along a high-latitude gradient in south-eastern Australia. The only clear trend in these data was a decrease in the relative abundance of stress-tolerant species in coral assemblage at higher latitudes (Sommer et al. 2014). This result is the exact opposite expected from UAST that predicts that stress-tolerant species should dominate in unproductive habitats, such as these marginal reefs at high latitude. Therefore, either the theory is flawed, or the adaptive strategy scheme of Darling et al. (2012) is flawed, or both. As discussed in the general introduction and elaborated on in Chapter 3, Darling et al.'s (2012) analyses were fundamentally flawed and therefore it is worth giving the adaptive strategy approach another chance using the groups my analyses produced in Chapter 2.

Direct trait based approaches almost certainly offer a more promising way forward than the arbitrary groupings UAST produces in reef-building corals. Recently studies have used direct trait-based approaches to explore the cause and nature or latitudinal changes in assemblage structure (Sommer et al. 2014; Keith et al 2015; Mizerek et al. 2016). These studies suggest that coral species occurring at high latitudes share traits associated with greater environmental tolerance include larger depth range, more robust morphologies and greater tolerance of turbid waters (Sommer et al. 2014; Keith et al 2015; Mizerek et al. 2016).

In this chapter, I use the natural environmental gradient of the 1800 km latitudinal extent of the GBR to test the predictions of adaptive strategy theory. In addition, I compare the ability of traditional ecological metrics with an adaptive strategies approach (the two groups identified in Chapter 2) and a direct trait-based approach to provide ecological insight into latitudinal trends in coral assemblage structure along the length of the GBR.

4.3 MATERIAL AND METHODS

4.3.1 ***Study sites and survey method***

The Great Barrier Reef (GBR) extends along an approximately 1,800 km latitudinal gradient from the Torres Straight (10^{o} S) in the north to the Capricorn Bunker Group (24^{o} S) in the south. Mean annual sea surface temperatures differ by approximately 4^{o} C between the north and the south, and annual temperature variation increases predictably with increasing latitude (Woolsey et al. 2015). Consequently, the level of temperature stress increases from north to south. This makes the GBR an ideal system with which to test for changes in the relative abundance of adaptive strategy groups and traits associated with tolerance to stress. I used 47 sites on 27 mid-shelf reefs spaced at approximately 80 to 100 km intervals along the length of GBR (Table 4.1, Fig. 4.1). As much as possible, sites were chosen on the exposed south-east aspect of the reef to standardise the habitat sampled. Reefs were chosen at random within this design, except in the section between Townsville and Lizard Island where reefs with a recent history of crown-of-thorns starfish (COTs) removal were avoided. Four × 10 m line intercept transects (Loya 1972) were used at each site to quantify the reef-building coral assemblage structure. Only colonies with a maximum diameter greater than 5 cm were recorded. Colonies were identified to species level following Veron (2000). Species names were updated to the currently accepted names using the World Register of Marine Species (http://www.marinespecies.org/index.php)

4.3.2 ***Latitudinal trends in coral assemblage structure***

Linear regression was used to explore the relationship between coral cover, species richness and evenness per transect and latitude. Linear regression was performed in R (R Development Core Team 2016).

Differences among coral assemblage structure at site scale were explored using hierarchical cluster analyses, principle component analysis (PCA) and permutational multivariate analysis of variance (PERMANOVA). I pooled species data into site scale for multivariable analyses for reducing the noise on transect scale since I focus on how assemblage structures change along the latitude. The dendrogram of coral assemblage relationships was calculated using Ward’s hierarchical clustering of a Euclidean dissimilarity matrix. Species abundance data was log (x+1) transform before running analyses. Multivariate analyses were performed using the ‘vegan’ (Oksanen et al. 2017) package in R (R Core Team 2016).

4.3.3 *Assemblage-weighted mean traits values*

In addition to exploring changes in the taxonomic composition of the coral assemblages, I also explored how traits within each assemblage varied along an environmental gradient using the assemblage weighted mean (AWM).

The assemblage-weighted mean (AWM) for each trait t of each assemblage was calculated as the mean of species trait values, t_i, of the S species in each survey site, with each species, i, weighted by its relative abundance, p_i :(eg Lavorel et al. 2008; Bernard-Verdier et al. 2012):

$$AWM = \sum_{i=1}^{S} p_i \times t_i$$

I tested for linear correlations between the assemblage-weighted mean of each trait and the latitudinal gradient. The species traits used were the five traits used in the test of UAST in Chapter 2 plus colony size. A number of species that were recorded on transects were not included in the UAST analyses. For these species, trait values were assigned based on genus and morphology. Log transformations were applied before testing the linear correlations. The assemblage-weighted mean was calculated using "FD" package (Laliberté & Legendre 2010, Laliberté et al 2014) in R (R Core Team 2016). All analyses including null models testing were performed using R (R Core Team 2016).

4.3.4 *Latitudinal trends in the relative abundance of adaptive strategy groups*

Coral species were classified into one of the two groups identified in the test of UAST in Chapter 2. For the species recorded on transects but not included in the test of UAST species were placed into groups on the basis of corallite size. Species with corallite size less than 1.9 mm were classified into Group 1 and the rest were classified into Group 2. The criteria of 1.9 mm in corallite size is the mean corallite size of Group 1 plus two times the standard error (Table 2.4).

After classifying every species into the two groups, linear regression was used to explore the correlation between the relative abundance of each group per site. Linear regression was performed in R (R Core Team 2016).

4.4 RESULTS

4.4.1 ***Latitudinal trends in coral cover and species richness and evenness***

Coral cover ranged from 6.9 ± 4.0 % to 58.5 ± 9.2 %. There was no correlation between latitude and coral cover (p = 0.53, Fig. 4.2a), although there appears to be a slight dip in coral cover between latitude 16 and 21 °S, Similarly, there was no correlation between latitude and species richness, which ranged from 2 at Otter site 2 (#1808_2) to 24 at 15-043 site 1 (#1544_1), (p=0.913, Fig. 4.2b). While there was a correlation between evenness and latitude (Slope = 0.085, p= 0.011, Fig.4.2c), latitude only explained 3% of the variation in evenness (Adj R^2 = 0.028).

4.4.2 ***Latitudinal trends in assemblage structure***

Two significant groups, in terms of assemblage structure were identified in the cluster analysis (PERMANOVA $_{(1,\,45)}$ = 0.17, p = 0.001, Table 4.2, Fig. 4.3). The first group includes 23 sites from 15 reefs, 10 out of which were located between 10.52 and 14.75 S (Fig. 4.1, 4.2). This group was dominated by *Acropora muricata*, *A. intermedia*, *A. hyacinthus*, massive *Porites*, *Goniastrea pectinata*, and *P. cylindrica* (Fig.4.4). The second group includes 24 sites from 15 reefs scattered between 14.87 °S and the southern end of the GBR (Fig.4.1, 4.2). This group was dominated by *Isopora cuneata*, *A. monticulosa, A. digitifera, A. robusta, Pocillopora verrucosa,* and *G. retiformis* (Fig. 4.4).

4.4.3 ***Latitudinal trends in the assemblage-weighted mean of the traits***

Assemblage weighted mean propagule size, colony size and growth rate were correlated with latitude: propagule size increased with latitude (Adj R^2 = 0.240, Slope = 0.415, $p < 0.001$, Fig.4.5c); colony size decreased (Adj R^2 = 0.415, Slope = -1.26, $p < 0.001$, Fig.4.5f); growth rate decreased (Adj R^2 = 0.064, Slope = -0.387, $p = 0.046$, Fig.4.5b).

4.4.4 ***Latitudinal trends in the relative abundance of adaptive strategies***

There was no correlation between the relative abundance, at the site level, of the two groups identified in Chapter 2 with latitude ($p = 0.185$ and 0.373 for Group 1 and 2, separately, Fig.4.6). However, changes in the relative abundance were evident between approximately latitude 14 and 15 °S. The relative abundance of Group 1 was consistently higher than Group 2 (Fig.4.6) except the 2 sites on Switzer Reef (1434_1 and 1434_2) where the groups were more similar in abundance.

4.5 DISCUSSION

Mid-shelf reefs along the length of the GBR were homogenous in terms of coral cover, species richness and evenness. However, there were two distinct groups in terms of assemblage structure and there were also some latitudinal trends in the assemblage-weighted means in three of the six traits examined. In addition, the adaptive strategies approach indicated that some sites between latitude 14 and 15 °S differed from the rest.

Coral cover at these exposed mid-shelf sites along the length of the GBR was very similar suggesting none of the major regional differences evident in other recent work (Osborne et al. 2011, Sweatman et al. 2011, De'ath et al. 2012). In addition, coral cover was generally high with an overall mean of 30.67 ± 1.1 % suggesting that much of the GBR was in reasonable condition at the time of these surveys (Fig. 4.2). The only exceptions were some sites between 14 and 18 °S which had lower cover possibly as a result of a recent crown-of-thorns starfish outbreak (*pers. comm*. Morgan Pratchett) and cyclones, eg Cyclone Yasi in 2011. While I deliberately avoided reefs with a recent history of crown-of-thorns starfish removal because these reefs were likely to have much lower coral cover, it is still possible some of my reefs were affected. High coral cover on the length of the GBR is a result in strong contrast to other recent work (eg De'ath et al. 2012). In particular, there was no evidence in my surveys to support the suggestion that southern sections of the GBR are in poor condition (eg De'ath et al. 2012). While differences in the time of these surveys relative to recent disturbances is going to have a major influence on the results my work suggests that the sites of the AIMS long term monitoring program are not necessarily representative of the GBR. In addition, there were no latitudinal trends in species richness or evenness supporting the idea that the GBR is a relatively homogenous region despite its size (Veron 1985).

There were, however, two distinct groups in terms of assemblage structure (Fig. 4.3, 4.4). One group was dominated by species with more robust morphologies eg *Isopora cuneata* (Madin and Connolly 2006) and the other groups included species with morphologies more susceptible to disturbance eg the branching species *Acropora muricata* (Madin et al. 2014). This suggests that there were in fact slight differences in the degree of exposure to waves among these sites. The fact that there was also some geographical structure to this results i.e. most sites above Cairns were in the group with more fragile species, suggest latitudinal trends in degree of exposure, possibly related to the width of the GBR lagoon (Fig. 4.1) which is in general much wider south of Cairns that further north. A wider lagoon allows for great wind fetch and therefore larger waves. This result is also likely to be driven but the fact that reefs north of 14.5 S rarely experience cyclones (Wolff et al. 2016)

There were also some interesting latitudinal trends in the assemblage weighted means in three of the six traits examined with a shift to species with smaller maximum colony size, slower growth rates and larger propagule size and smaller colony size at increasing latitude. These trends suggest a strong role of environmental filtering in affecting assemblage structure (eg Sommer et al. 2014). The shift to species with smaller colony size is in contrast to the patterns often observed on land, where species are typically larger at higher latitude (Blackburn et al. 1999, Cushman et al. 1993, Ashton et al. 2000). Slow growth and larger propagule size also appear adaptive at high latitudes although the selective forces driving this pattern are unclear. One possibility is that the harsher environmental conditions at higher latitude favour species that invest in a few high quality offspring in contrast to numerous low quality offspring (Thorson 1950, Stearns 1992).

While there was no latitudinal trend in the relative abundance of the two groups identified in the UAST analyses some sites between latitude 14 and 15 °S had a much more even balance among the groups in contrast to the usual pattern of overwhelming dominance of Group 1 (Fig. 4.6). This difference in the relative abundance of the groups might be indicative of the recent crown of thorns outbreak mentioned above. Crown-of-thorns starfish generally prefer to eat fast growing corals, such as the tabular and branching *Acropora* (De'ath and Moran 1998, Pratchett 2007) that dominant species in Group 1. Nonetheless, this recent history of disturbance was also evident in lower coral cover, a metric much more tractable than adaptive strategy groupings.

In conclusion, there were no obvious latitudinal trends in coral cover, species richness or evenness, indicating that the GBR is relatively homogenous region with respect to these variables. There was some latitudinal structure in the corals assemblages and I hypothesize that this is driven by latitudinal differences in hydrodynamics of GBR caused in turn by differences in the width of the lagoon and the gradually increased reef matrix porosity from north to south (Gallop et al. 2014). Finally, the trait based approach indicated differences in these assemblages that were not evident in the univariate or multivariate analysis, suggesting trait-based approaches do offer ecological insight above and beyond traditional ecological metrics.

Table 4.1 Survey sites

GBR Section	Zone	Reef	Site	Latitude (S)	Longitude (E)	Site code
Cape York	Out of GBRMPA	Dugong	Dugong site 1	10.5240	143.1178	1052_1
	Out of GBRMPA	Dugong	Dugong site 2	10.5315	143.1139	1052_2
	Out of GBRMPA	Bayag	Bayag site 1	10.5685	143.2455	1056_1
	Out of GBRMPA	Bayag	Bayag site 2	10.5686	143.2536	1056_2
Lockhart River	blue	Burke	Burke site 1	12.6464	143.5608	1264_1
	blue	Zenith	Zenith site 2	12.7644	143.6064	1276_2
	blue	Zenith	Zenith site 1	12.7694	143.6023	1276_1
Cape Melville	blue	13-122	13-122 site 1	13.8989	144.0175	1389_1
	green	Corbett	Corbett site 1	14.0043	144.1402	1400_1
	green	Switzer	Switzer site 1	14.3451	144.7435	1434_1
	green	Switzer	Switzer site 2	14.3459	144.7460	1434_2
	green	Switzer	Switzer site 3	14.3700	144.7757	1434_3
	blue	Mid	Mid site 2	14.4496	144.9763	1444_2
	blue	Mid	Mid site 1	14.4564	144.9893	1444_1
Cooktown	blue	Martin	Martin site 2	14.7537	145.3584	1475_2
	blue	Martin	Martin site 1	14.7542	145.3617	1475_1
	blue	Rocky Isles B	Rocky Isles B site 1	14.8713	145.5351	1487_1
	blue	Rocky Isles B	Rocky Isles B site 2	14.8774	145.5302	1487_2
	blue	15-043	15-043 site 2	15.4499	145.5199	1544_2
	blue	15-043	15-043 site 1	15.4533	145.5087	1544_1
	green	Evening	Evening site 1	15.8996	145.6638	1589_1
	blue	Morning	Morning site 1	15.9570	145.6976	1595_1
	blue	Morning	Morning site 2	15.9608	145.6945	1595_2
Cairns	blue	Batt	Batt site 1	16.3730	145.6962	1637_1
	green	Michaelmas	Michaelmas site 1	16.5572	145.9992	1655_1
	green	Scott	Scott site 1	17.0598	146.1883	1705_1
	blue	Peart	Peart site 1	17.4679	146.4053	1746_1
	blue	Peart	Peart site 2	17.4706	146.4070	1746_2
Townsville	blue	Otter	Otter site 2	18.0804	146.5832	1808_2
	blue	Otter	Otter site 1	18.0836	146.5722	1808_1
	blue	Bramble	Bramble site 2	18.4372	146.7490	1843_2
	blue	Bramble	Bramble site 1	18.4478	146.7251	1843_1
Central and northern Great Barrier Reef	blue	Darley	Darley site 2	19.2395	148.1402	1923_2
	blue	Darley	Darley site 1	19.2401	148.1459	1923_1
	blue	Block	Block site 2	19.8007	149.4195	1980_2
	blue	Block	Block site 1	19.8075	149.4176	1980_1
	blue	Little Stevens	Little Stevens site 2	20.5897	150.0172	2058_2
	blue	Little Stevens	Little Stevens site 1	20.5948	150.0178	2058_1
	blue	Paul	Paul site 2	21.3117	150.7091	2131_2
	blue	Paul	Paul site 1	21.3498	150.7141	2131_1
Pompey and Swain Reefs, south-east Great Barrier Reef	blue	21-467	21-467 site 1	21.8876	151.9404	2188_1
	blue	21-467	21-467 site 2	21.8901	151.9014	2188_2
	blue	Hackie	Hackie site 2	22.2679	152.3941	2226_2
Capricorn bunker	yellow	North West Island	North West Island site 1	23.3131	151.7458	2331_1
	yellow	North West Island	North West Island site 2	23.3170	151.7181	2331_2
	blue	Fitzroy	Fitzroy site 2	23.6056	152.1592	2360_2
	blue	Fitzroy	Fitzroy site 1	23.6099	152.1492	2360_1

Table 4.2 Permutational multivariate analysis of variance (PERMANOVA) result of testing the two groups identified in the cluster analysis.

	Df	Sum Sq	Mean Sqs	F	R2	Pr (>F)
as.factor(group)	1	0.17	0.17	0.17	0.085	0.001
Residuals	45	1.839	0.041		0.915	
Total	46	2.008			1	

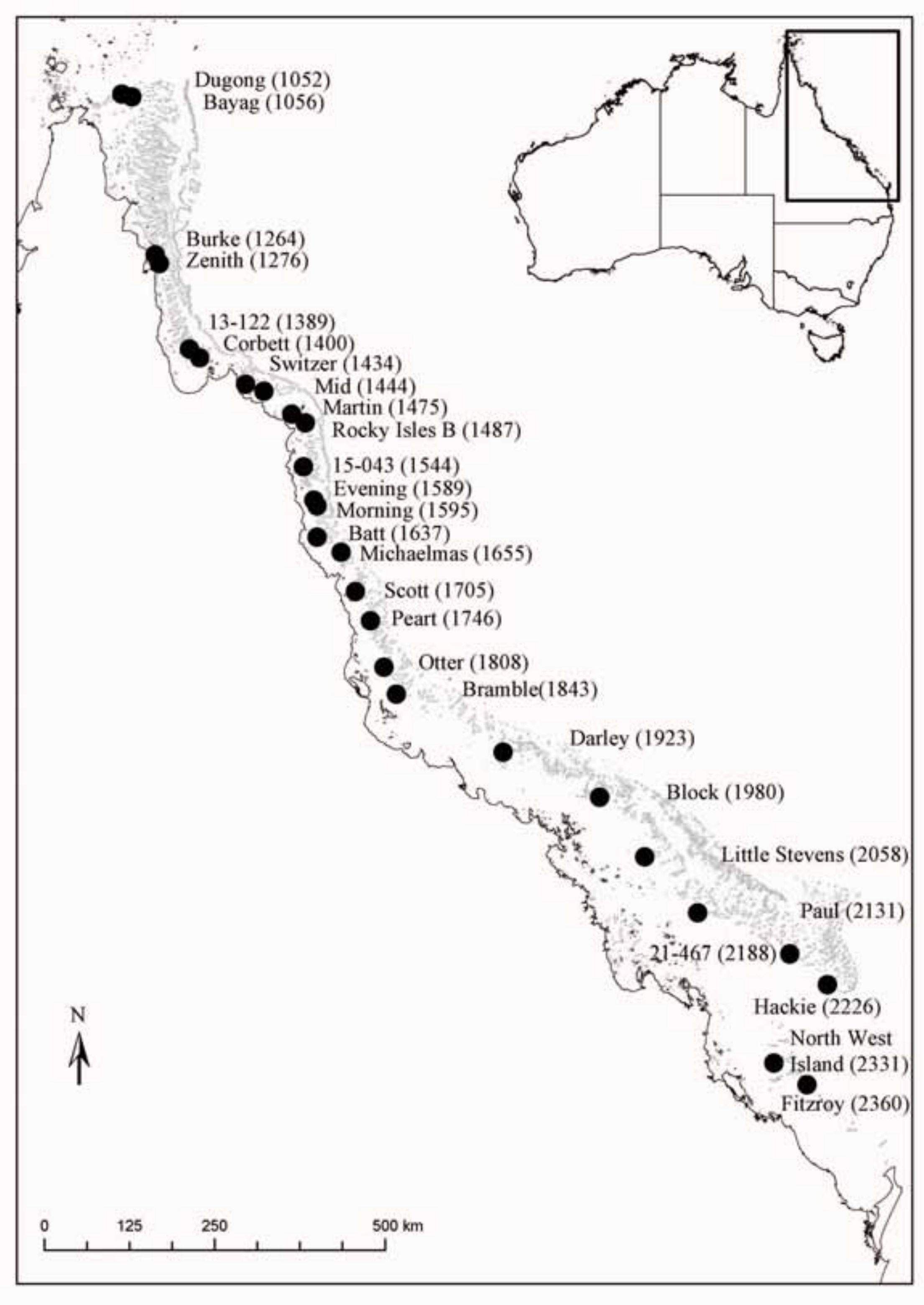

Fig. 4.1 Location of the 27 survey reefs along the Great Barrier Reef. One to three sites were surveyed per reef.

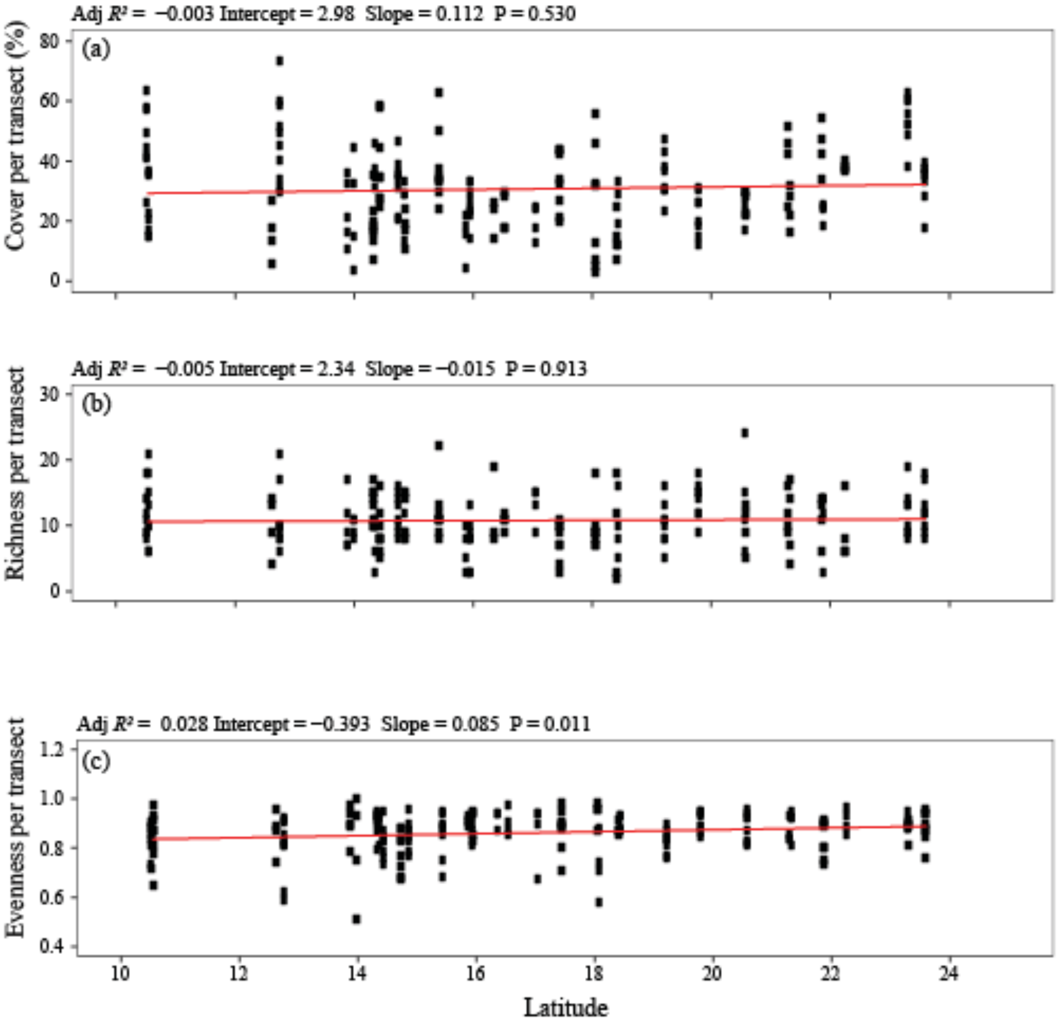

Fig. 4.2 Changes in (a) reef-building coral cover, (b) species richness, and (c) evenness along the latitude of the Great Barrier Reef. Block dots represent the value of each index recorded on each transect. Red line and the formula above each graph represent the linear regression line and regression result.

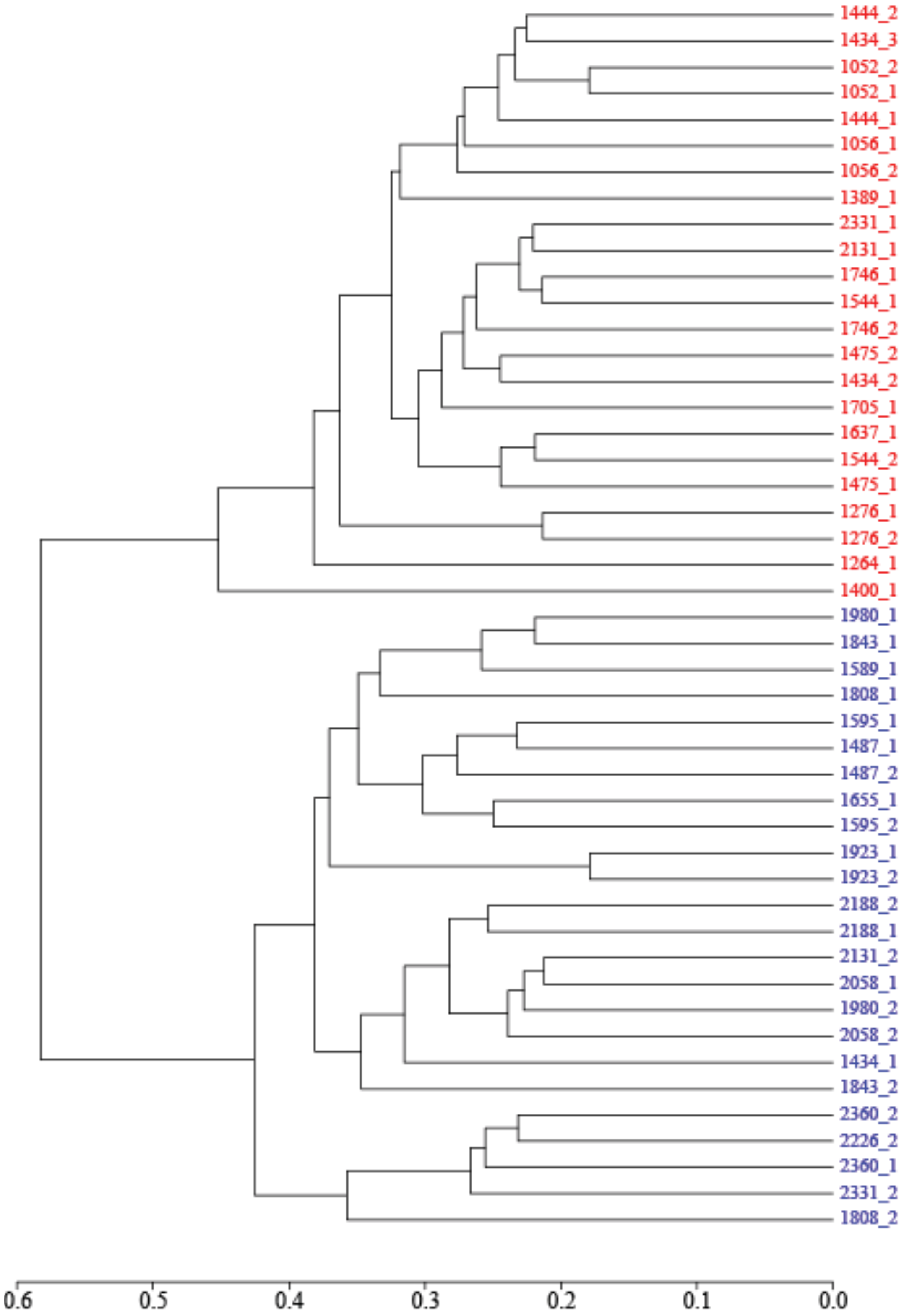

Fig. 4.3 Hierarchical cluster analyses of coral assemblage composition on 47 sites of 27 reefs. The first four digits label the reef on the map, while the last digit refers to the site on each reef. The colours show the two groups identified in the cluster analysis.

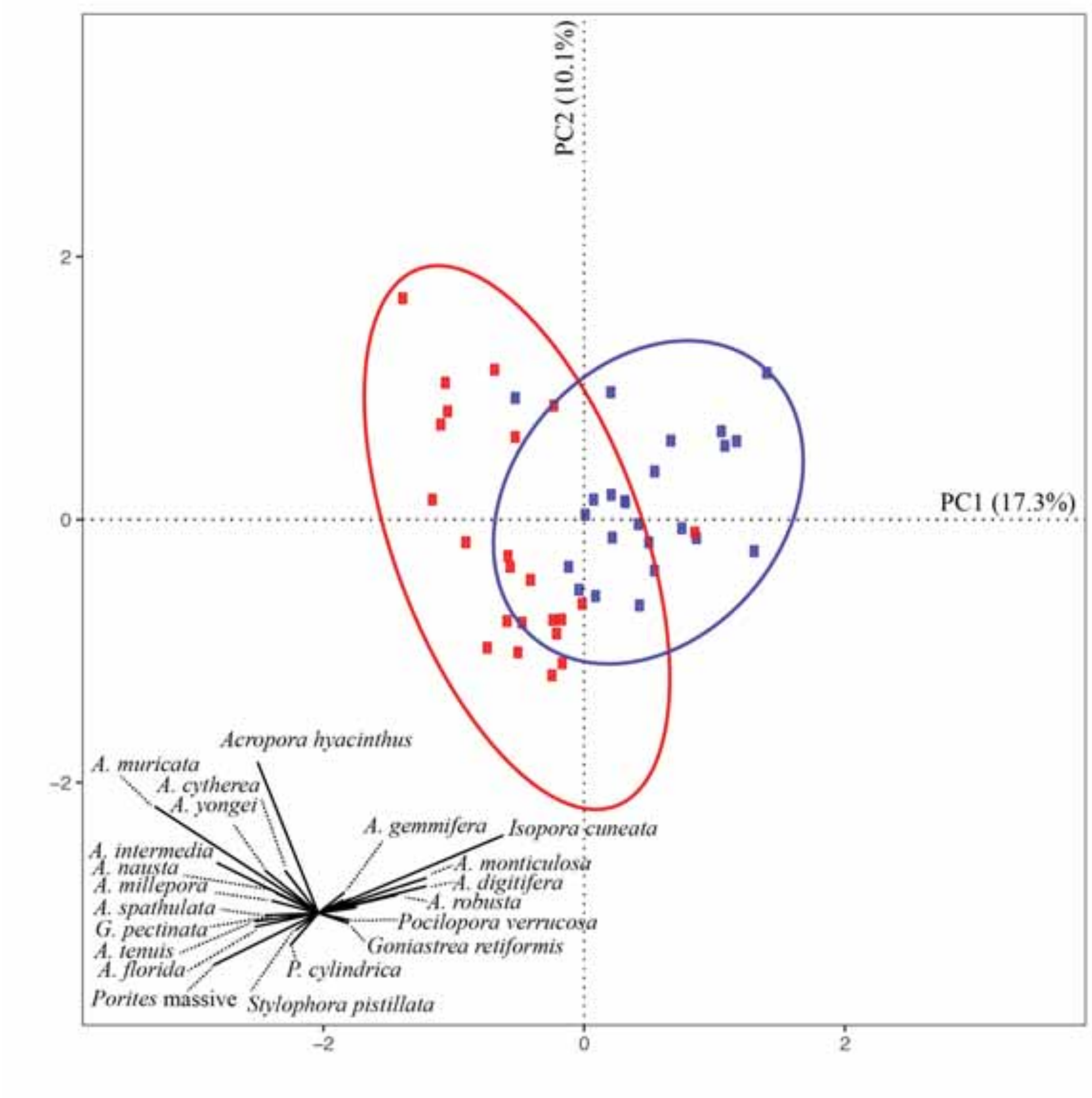

Fig. 4.4 The principle component analysis (PCA) of coral assemblage composition on 47 sites of 27 reefs. The colours show the two groups identified in the cluster analysis.

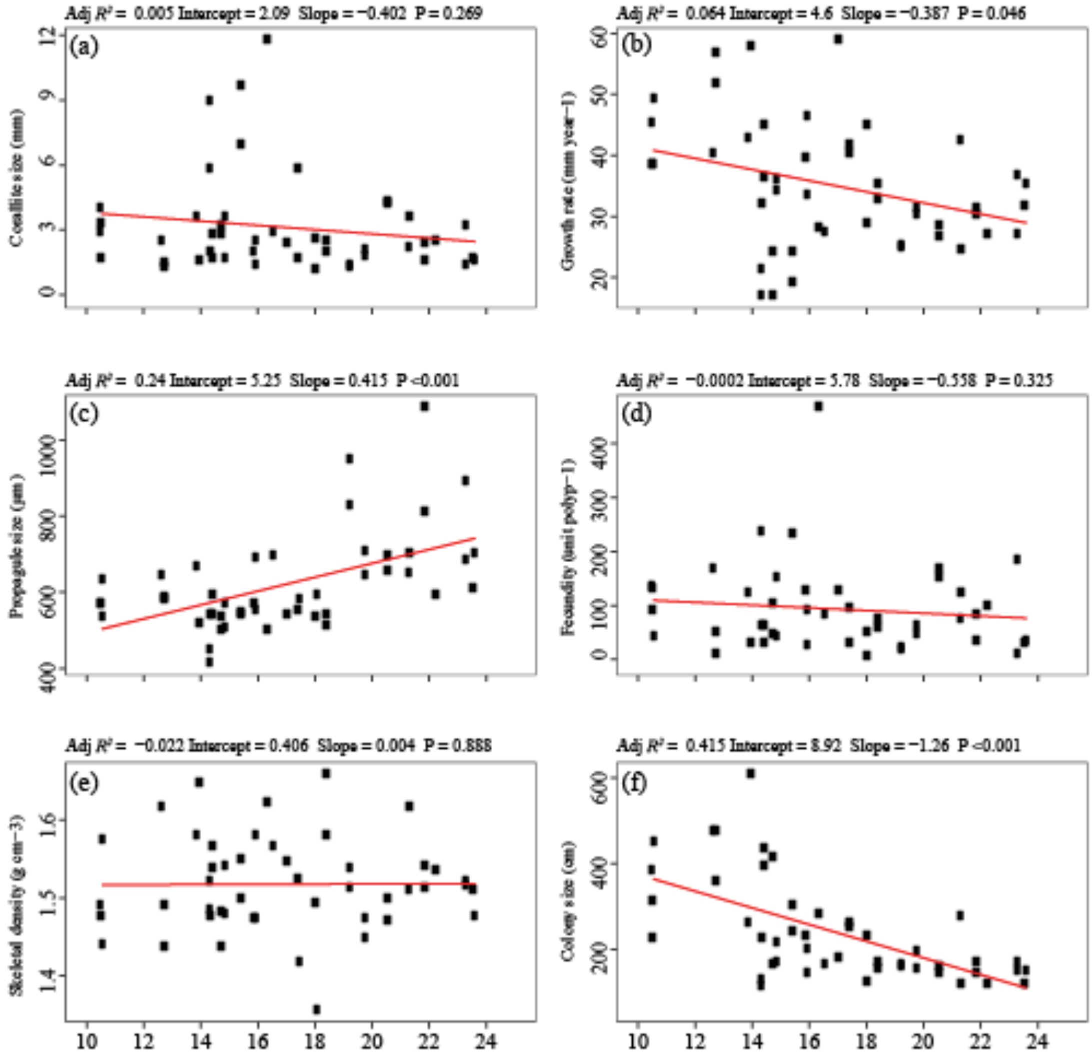

Fig. 4.5 Assemblage-weighted means (AWM), block dots, in assemblages along the latitude for six species traits, including (a) corallite size, (b) growth rate, (c) propagule size, (d) fecundity, (e) skeletal density, and (f) colony size. The red line is the linear regression line.

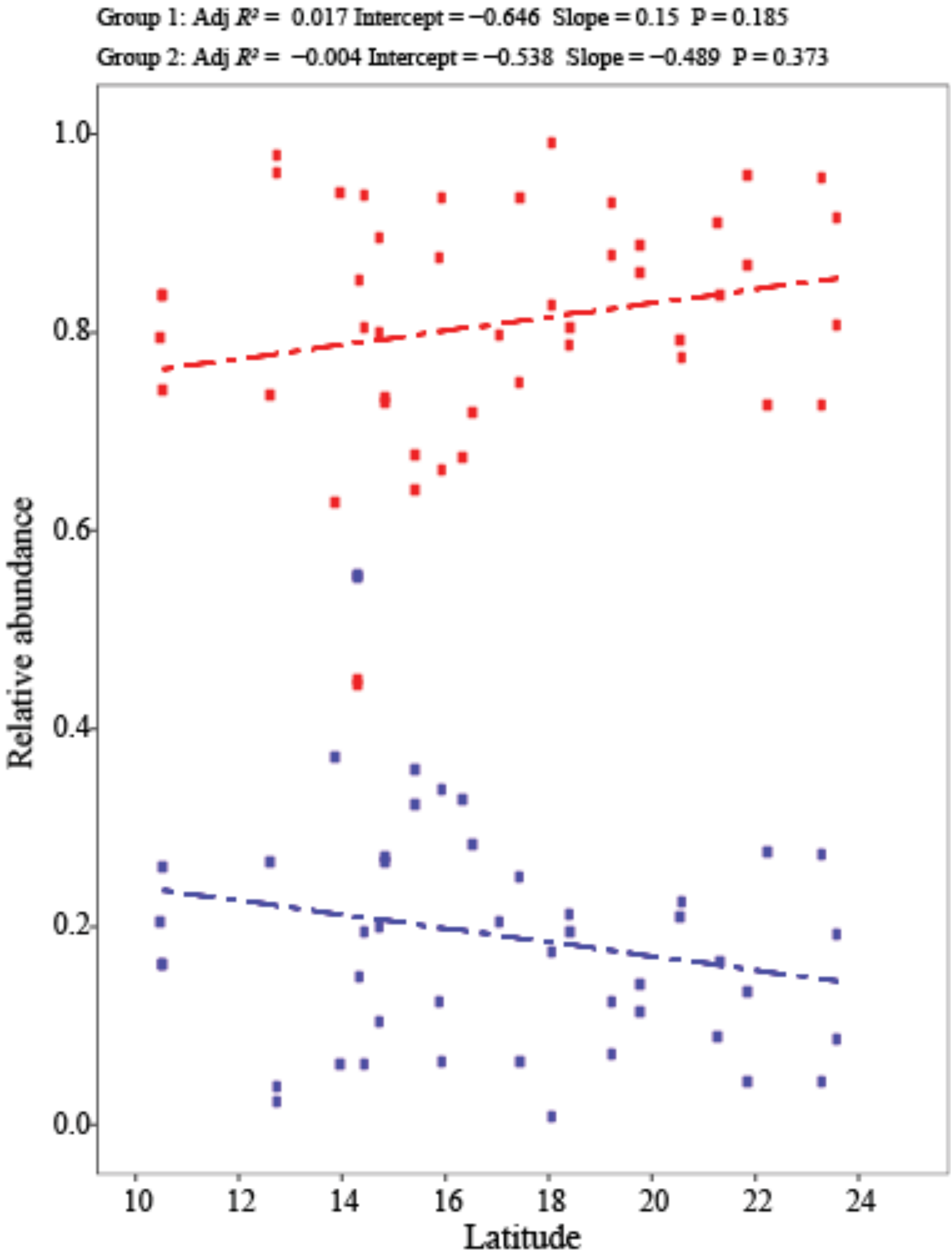

Fig. 4.6 Relative abundance of each group on each site along the latitude of the Great Barrier Reef. Two groups include red (group 1) and blue (group 2).

CHAPTER 5

GENERAL DISCUSSION

5.1 General discussion

In my thesis I tested whether Universal Adaptive Strategy Theory (UAST) applied to reef-building corals and more generally whether or not an adaptive strategy approach provided greater ecological insight than more traditional ecological metrics or direct trait based approaches. UAST does not appear to apply to corals. My analyses suggested that two groups was the optimal number for corals, in contrast to the three groups predicted by UAST. In addition, these two groups contain a mix of species with very different life history traits suggesting that it is highly unlikely they have been shaped by similar evolutionary pressures or that they will respond in a similar way to environmental stress or disturbance. My results also suggest that the adaptive strategy approach does not generally provide greater ecological insight than traditional ecological approaches. In contrast, a direct species trait approach did provide information masked by the traditional indices including coral cover and species richness (Chapter 3-4).

In Chapter 2, I found that reef-building corals can broadly be classified into two groups using five species traits relevant to energy allocation. Group 1 was dominated by species with small corallite size, high growth rate, large propagule size and low fecundity. On the other hand, Group 2 had the opposite characteristic of the four species traits listed above (Table 2.4). However, each of these two groups includes a mix of species with very different life-histories and traits associated with more than one UAST strategies (Table 1.2).

In Chapter 3, I tested the ability of the adaptive strategy scheme of Darling et al. (2012, 2013) to predict how coral taxa and assemblages respond to stress, in the form of a bleaching event in 1998 and multiple-stressors over the subsequent 15-year period that includes cyclones, floods and further bleaching events. Very few taxa behaved as predicted and there was no difference in the average response of taxa in the four adaptive strategy groups to stress, multiple stressors, or during periods of recovery.

In Chapter 4, I tested whether the groups identified in Chapter 2 respond as predicted by UAST along an environmental gradient. In contrast to the predictions of the theory, there was no trend for one group to dominate over the other along the environmental gradient represented by the GBR. Nonetheless, the relative abundance of these groups did vary which is possibly indicative of recent disturbance history. However, it is hard to justify the extraordinary time and effort required to produce this adaptive strategy scheme for such a trivial insight which was also generally evident as lower coral cover. In contrast, a direct trait based approach revealed interesting latitudinal trends in the assemblage weighted mean of these traits. In particular, there was a shift towards species with small maximum colony size, slow growth and large propagules with increasing latitude. The result suggests environmental conditions do shape coral assemblages in a predictable way and that the trait based approach can reveal differences in assemblages that are not evident using traditional ecological metrics such as coral cover and species richness.

There are a couple of reasons that UAST might not work for corals. In particular, corals have a much more complex life history than most terrestrial plants and animals, for which the theory was developed (Table 5.1). For example, the nutrition of reef-building corals is highly unusual. Corals can switch between autotrophic nutrition via photosynthesis and heterotrophic nutrition by feeding on plankton (Porter 1976).

Finally, the tropical marine environment is very different to the terrestrial environment with the marine environment dominated by disturbance and relatively free of stress, in particular lack of moisture and excess nutrients (Table 5.1). All of these fundamental differences between corals and other organism along with the fundamental difference between the marine and terrestrial environments suggest that looking for a universal theory is folly.

5.2 Future directions

Another other possible reason that my UAST analyses failed to produce the groups predicted by the theory is a lack of trait data, particularly for traits associated with energy allocated to maintenance (i.e. stress tolerant), such as tissue biomass. In addition, I only included 400 odd of the nearly 800 extant species of zooxanthellate coral in my analyses. The UAST analyses might be worth revisiting when more data are available. However, it is highly unlikely that the effort required to collect these data and classify species into adaptive groups will be worth any ecological insight gained particularly when direct trait based approaches appear to be much more promising and many traits, such as maximum corallite size are very easy to measure and already available for most scleractinian species (Madin et al. 2016a). Trait based approaches can also be used to test for more easy to measure proxies for population and ecosystem processes. For example, colony morphology is tightly linked with demographic rates such as growth (Pratchett et al. 2015, Madin et al. 2016b, Dornelas et al. 2017), mortality (Hughes and Jackson 1985; Madin and Connolly 2006; Madin et al. 2014) and fecundity (Álvarez-Noriega et al. 2016). Similarly, important ecosystem processes, such as productivity, are unlikely to be captured by metrics such as coral cover or diversity but might be captured by proxies include traits such as corallite size or colony morphology. For example, tissue biomass per unit area, one measure of productivity, is higher in assemblages dominated by branching species, eg *Acropora* and *Stylophora*, than in assemblages dominated by lower profile species, eg *Galaxea* and *Turbinaria* (Hoogenboom et al. 2015).

Another important issue not adequately addressed by current Adaptive Strategy theory in corals, despite claims to the contrary (Darling et al. 2012), is to identify the function role that species play in ecosystems. Related questions include how many functional groups are required to maintain a healthy reef and how much functional redundancy within each group is required to ensure reef persistence in the face of accelerating to stress and disturbances, as a results of climate change (Hughes et al. 2017a, b). The example of Clipperton Atoll (Glynn and Ault 2000) indicates that healthy coral reefs exist with a few as 10 coral species. Indeed, I predict that as few as five functional roles need be defined for corals: bricks and mortar to provide the reef framework, primary production as a source of carbon, secondary production and a source of other nutrients and structure to provide the habitat for other organisms fundamental to reef health, such as fish.

In common with many ideas in science, Adaptive Strategy Theory is likely to be overused and misused (Fox 2013). For example, an ASG approach is like to be used to identify reefs for conservation efforts in the flawed triage approach to saving the world’s reefs advocated by the 50 Reefs Project (https://50reefs.org/). As discussed in the General Introduction and developed in Chapter 2, claims that the relative abundance of ASGs can be used to predict how coral assemblages respond to stress are false. Indeed, as I demonstrate in Chapter 3, the UAST approach does not identify meaning ecological or biological groups. If a triage approach is adopted it would be far more meaningful to base the selection reefs on the basis of evolutionary or functional novelty (Huang 2012).

In conclusion, my thesis strongly suggests that the adaptives strategie approach in corals does not work. The two groups produced by the UAST analyses did not make ecological sense and the use of these groups to explore latitudinal patterns in assemblage structure did not provide any meaningful ecological insight. Similarly, the results of Chapter 3 suggest that previous claims for the utility of the adaptive strategy approach to predict the response of taxa to disturbance are false. Even if future analyses with much greater trait data did produce ecological meaningful groups it seems highly unlikely that the insight provided would justify the extraordinary effort to produce the groups, particularly when direct trait based approaches offer much greater insight.

Table 5.1 The comparison between coral and terrestrial plant and anima, and the environmental condition between coral reefs and terrestrial.

	Coral/Coral reefs	Plant, animal/Terrestrial
Biological aspect		
Coloniality	Most clonal	Most aclonal
Trophic	Individual can switch between autotrophic and heterotroph	Individual cannot switch
Life cycle	Complex	Simple
Type of stress on habitat		
Lack of water	Unlimited	Could be a stress
Lack of light	Could be a stress	Could be a stress
Lack of nutrients	Always lack of nutrients	Could be a stress
Eutrophication	Could be a stress	Could be a stress

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Appendix A: Supplemental information for Chapter 2

Table S1. Trait attribute of interested traits of the 473 species used in generating the scheme. (Pac: Pacific; Atl: Atlantic; spa: spawner; bro: brooder; t/p: tables/plates; br_o: branching_open; br_c: branching_close; cor: corymbose; dig: digitate; col: columnar; mas: massive; lam, laminar; enc: encrusting; her: hermaphrodite; gon: gonochore)

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (μm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Acropora abrolhosensis*	Pac	1	1	57.35	590.23	1.50	12.45	1.51	spa	br_o	1000.00	her
Acroporidae	*Acropora abrotanoides*	Pac	1	1	127.50	590.23	1.20	9.06	1.51	spa	br_o	242.96	her
Acroporidae	*Acropora aculeus*	Pac	1	1	33.95	590.23	1.00	6.99	1.45	spa	cor	40.00	her
Acroporidae	*Acropora acuminata*	Pac	1	1	57.35	590.23	1.20	9.06	1.51	spa	br_o	200.00	her
Acroporidae	*Acropora akajimensis*	Pac	1	1	51.26	590.23	1.60	13.64	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora anthocercis*	Pac	1	1	30.41	590.23	1.30	10.16	1.40	spa	t/p	100.00	her
Acroporidae	*Acropora appressa*	Pac	1	1	33.95	590.23	1.09	7.88	1.45	spa	cor	118.92	her
Acroporidae	*Acropora arabensis*	Pac	1	1	30.54	590.23	2.00	18.73	1.42	spa	dig	112.31	her
Acroporidae	*Acropora aspera*	Pac	1	1	48.52	590.23	1.80	11.35	0.92	spa	br_o	144.20	her
Acroporidae	*Acropora austera*	Pac	1	1	62.90	590.23	1.50	12.45	1.44	spa	br_o	165.89	her
Acroporidae	*Acropora awi*	Pac	1	1	57.35	590.23	1.00	6.99	1.51	spa	br_o	150.00	her
Acroporidae	*Acropora azurea*	Pac	1	1	51.26	590.23	1.40	11.28	0.96	spa	br_c	15.00	her
Acroporidae	*Acropora batunai*	Pac	1	1	30.41	590.23	0.50	2.61	1.40	spa	t/p	125.00	her
Acroporidae	*Acropora bifurcata*	Pac	1	1	30.41	590.23	0.90	6.02	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora branchi*	Pac	1	1	30.41	590.23	1.10	12.00	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora bushyensis*	Pac	1	1	30.54	590.23	1.50	3.80	1.42	spa	dig	25.00	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Acropora cardenae*	Pac	1	1	57.35	590.23	1.02	7.20	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora carduus*	Pac	1	1	57.35	590.23	0.90	6.02	1.51	spa	br_o	157.83	NA
Acroporidae	*Acropora caroliniana*	Pac	1	1	30.41	590.23	1.00	6.99	1.40	spa	t/p	50.00	her
Acroporidae	*Acropora cerealis*	Pac	1	1	26.22	590.23	0.80	9.97	1.45	spa	cor	50.00	her
Acroporidae	*Acropora cervicornis*	Atl	1	1	78.82	590.23	1.70	10.00	1.72	spa	br_o	111.00	her
Acroporidae	*Acropora chesterfieldensis*	Pac	1	1	51.26	590.23	1.00	6.99	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora clathrata*	Pac	1	1	30.41	590.23	0.90	5.15	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora convexa*	Pac	1	1	33.95	590.23	1.10	8.01	1.45	spa	cor	118.92	her
Acroporidae	*Acropora cophodactyla*	Pac	1	1	30.54	590.23	1.30	10.16	1.42	spa	dig	112.31	her
Acroporidae	*Acropora copiosa*	Pac	1	1	57.35	590.23	1.10	8.01	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora cylindrica*	Pac	1	1	57.35	2110.90	1.60	2.26	1.51	bro	br_o	100.00	her
Acroporidae	*Acropora cytherea*	Pac	1	1	59.73	600.00	1.00	5.13	1.40	spa	t/p	300.00	her
Acroporidae	*Acropora dendrum*	Pac	1	1	33.95	590.23	1.20	9.06	1.45	spa	cor	100.00	NA
Acroporidae	*Acropora derawanensis*	Pac	1	1	57.35	590.23	1.00	6.99	1.51	spa	br_o	100.00	her
Acroporidae	*Acropora desalwii*	Pac	1	1	33.95	590.23	0.80	5.09	1.45	spa	cor	30.00	her
Acroporidae	*Acropora digitifera*	Pac	1	1	37.60	590.23	1.60	8.63	1.52	spa	dig	100.00	her
Acroporidae	*Acropora divaricata*	Pac	1	1	41.50	590.23	1.10	17.35	1.40	spa	t/p	132.53	her
Acroporidae	*Acropora donei*	Pac	1	1	57.35	590.23	1.40	9.50	1.51	spa	br_o	300.00	her
Acroporidae	*Acropora downingi*	Pac	1	1	30.41	590.23	1.00	14.00	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora echinata*	Pac	1	1	57.35	590.23	1.00	6.99	1.51	spa	br_o	150.00	her
Acroporidae	*Acropora efflorescens*	Pac	1	1	30.41	590.23	0.90	6.02	1.40	spa	t/p	200.00	her
Acroporidae	*Acropora elegans*	Pac	1	1	30.41	590.23	0.80	5.09	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora elegantula*	Pac	1	1	51.26	590.23	1.10	8.01	0.96	spa	br_c	148.54	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Acropora elseyi*	Pac	1	1	135.05	590.23	0.90	5.60	1.51	spa	br_o	50.00	her
Acroporidae	*Acropora eurystoma*	Pac	1	1	40.40	590.23	2.00	21.00	1.45	spa	cor	130.62	her
Acroporidae	*Acropora exquisita*	Pac	1	1	51.26	590.23	0.80	5.09	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora fastigata*	Pac	1	1	51.26	590.23	1.70	14.87	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora fenneri*	Pac	1	1	57.35	590.23	1.30	10.16	1.51	spa	br_o	100.00	her
Acroporidae	*Acropora filiformis*	Pac	1	1	57.35	590.23	1.90	17.41	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora florida*	Pac	1	1	57.35	590.23	1.40	9.67	1.51	spa	br_o	1500.00	her
Acroporidae	*Acropora forskali*	Pac	1	1	57.35	590.23	2.00	18.73	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora gemmifera*	Pac	1	1	24.00	590.23	1.60	8.47	1.47	spa	dig	98.60	her
Acroporidae	*Acropora glauca*	Pac	1	1	30.41	590.23	1.30	11.13	1.46	spa	t/p	112.05	her
Acroporidae	*Acropora gomezi*	Pac	1	1	30.57	590.23	1.00	6.99	1.51	spa	br_o	112.36	her
Acroporidae	*Acropora grandis*	Pac	1	1	57.35	590.23	1.70	14.87	1.51	spa	br_o	700.00	her
Acroporidae	*Acropora granulosa*	Pac	1	1	7.16	590.23	0.90	13.37	1.40	spa	t/p	100.00	her
Acroporidae	*Acropora haimei*	Pac	1	1	51.26	590.23	2.00	18.73	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora halmaherae*	Pac	1	1	57.35	590.23	0.90	6.02	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora hemprichii*	Pac	1	1	9.14	590.23	1.20	27.00	1.51	spa	br_o	200.00	her
Acroporidae	*Acropora hoeksemai*	Pac	1	1	57.35	590.23	1.10	8.01	1.51	spa	br_o	400.00	her
Acroporidae	*Acropora horrida*	Pac	1	1	51.26	590.23	1.50	9.00	0.86	spa	br_c	200.00	her
Acroporidae	*Acropora humilis*	Pac	1	1	14.49	590.23	1.80	12.10	1.45	spa	dig	75.09	her
Acroporidae	*Acropora hyacinthus*	Pac	1	1	47.53	590.23	1.10	7.90	1.28	spa	t/p	300.00	her
Acroporidae	*Acropora indonesia*	Pac	1	1	57.35	590.23	1.00	6.99	1.51	spa	br_o	100.00	her
Acroporidae	*Acropora inermis*	Pac	1	1	51.26	590.23	1.40	11.28	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora insignis*	Pac	1	1	51.26	590.23	0.60	3.38	0.96	spa	br_c	148.54	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Acropora intermedia*	Pac	1	1	57.35	590.23	1.50	6.74	1.51	spa	br_o	500.00	her
Acroporidae	*Acropora irregularis*	Pac	1	1	57.35	590.23	0.80	5.09	1.51	spa	br_o	300.00	her
Acroporidae	*Acropora jacquelineae*	Pac	1	1	30.41	590.23	0.50	2.61	1.40	spa	t/p	100.00	her
Acroporidae	*Acropora japonica*	Pac	1	1	30.41	590.23	0.90	6.02	1.40	spa	t/p	112.05	NA
Acroporidae	*Acropora khayranensis*	Pac	1	1	30.41	590.23	1.10	8.04	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora kimbeensis*	Pac	1	1	51.26	590.23	0.60	3.38	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora kirstyae*	Pac	1	1	51.26	590.23	0.80	5.09	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora kosurini*	Pac	1	1	57.35	590.23	0.80	8.30	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora lamarcki*	Pac	1	1	32.40	590.23	0.80	5.09	1.41	spa	t/p	200.00	her
Acroporidae	*Acropora latistella*	Pac	1	1	33.95	590.23	0.90	5.60	1.45	spa	cor	118.92	her
Acroporidae	*Acropora lianae*	Pac	1	1	51.26	590.23	0.60	3.38	0.96	spa	br_c	50.00	her
Acroporidae	*Acropora listeri*	Pac	1	1	51.26	590.23	1.00	6.99	0.96	spa	br_c	50.00	her
Acroporidae	*Acropora loisetteae*	Pac	1	1	57.35	590.23	1.60	13.64	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora lokani*	Pac	1	1	51.26	590.23	0.90	6.02	0.96	spa	br_c	30.00	her
Acroporidae	*Acropora longicyathus*	Pac	1	1	57.35	590.23	1.30	14.10	1.27	spa	br_o	157.83	her
Acroporidae	*Acropora loripes*	Pac	1	1	33.95	590.23	1.20	12.37	1.45	spa	cor	50.00	her
Acroporidae	*Acropora loveli*	Pac	1	1	57.35	590.23	1.70	8.40	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora lutkeni*	Pac	1	1	57.35	590.23	1.20	11.83	1.51	spa	br_o	600.00	her
Acroporidae	*Acropora macrostoma*	Pac	1	1	33.95	590.23	0.60	3.38	1.45	spa	cor	100.00	her
Acroporidae	*Acropora magnifica*	Pac	1	1	30.41	590.23	1.10	8.04	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora maryae*	Pac	1	1	51.26	590.23	0.60	3.38	0.96	spa	br_c	100.00	her
Acroporidae	*Acropora meridiana*	Pac	1	1	51.26	590.23	1.40	11.28	0.96	spa	br_c	100.00	her
Acroporidae	*Acropora microclados*	Pac	1	1	33.95	590.23	1.20	9.06	1.45	spa	cor	100.00	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Acropora microphthalma*	Pac	1	1	57.35	590.23	1.00	6.99	1.51	spa	br_o	200.00	her
Acroporidae	*Acropora millepora*	Pac	1	1	33.95	590.23	1.60	5.48	1.45	spa	cor	118.92	her
Acroporidae	*Acropora minuta*	Pac	1	1	8.15	590.23	0.70	4.21	1.56	spa	enc	55.03	her
Acroporidae	*Acropora mirabilis*	Pac	1	1	33.95	590.23	1.00	6.99	1.45	spa	cor	118.92	her
Acroporidae	*Acropora monticulosa*	Pac	1	1	30.54	590.23	1.20	9.06	1.42	spa	dig	300.00	her
Acroporidae	*Acropora mossambica*	Pac	1	1	33.95	590.23	0.90	19.30	1.45	spa	cor	118.92	her
Acroporidae	*Acropora multiacuta*	Pac	1	1	51.26	590.23	2.00	18.73	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora muricata*	Pac	1	1	89.05	590.23	1.20	9.06	1.71	spa	br_o	1000.00	her
Acroporidae	*Acropora nana*	Pac	1	1	51.26	590.23	1.00	7.15	0.96	spa	br_c	15.00	her
Acroporidae	*Acropora nasuta*	Pac	1	1	30.83	590.23	1.10	7.53	1.40	spa	cor	80.00	her
Acroporidae	*Acropora natalensis*	Pac	1	1	30.41	590.23	1.50	12.45	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora navini*	Pac	1	1	57.35	590.23	1.10	8.01	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora orbicularis*	Pac	1	1	30.41	590.23	0.60	3.38	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora palmata*	Atl	1	1	181.74	590.23	1.60	14.00	1.89	spa	br_o	400.00	her
Acroporidae	*Acropora palmerae*	Pac	1	1	8.15	590.23	1.30	10.16	1.56	spa	enc	200.00	her
Acroporidae	*Acropora paniculata*	Pac	1	1	30.41	590.23	0.80	5.09	1.40	spa	t/p	200.00	her
Acroporidae	*Acropora papillare*	Pac	1	1	57.35	590.23	1.60	13.64	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora paragemmifera*	Pac	1	1	30.54	590.23	1.10	8.03	1.42	spa	dig	112.31	her
Acroporidae	*Acropora parahemprichii*	Pac	1	1	51.26	590.23	1.10	8.01	0.96	spa	br_c	400.00	her
Acroporidae	*Acropora parapharaonis*	Pac	1	1	30.41	590.23	0.80	5.09	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora parilis*	Pac	1	1	51.26	590.23	0.50	2.61	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora pectinatus*	Pac	1	1	51.26	590.23	0.70	4.21	0.96	spa	br_c	100.00	her
Acroporidae	*Acropora pharaonis*	Pac	1	1	14.44	590.23	1.50	12.45	1.40	spa	t/p	74.94	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Acropora pichoni*	Pac	1	1	30.41	590.23	0.90	6.02	1.40	spa	t/p	100.00	her
Acroporidae	*Acropora pinguis*	Pac	1	1	57.35	590.23	1.10	8.01	1.51	spa	br_o	200.00	her
Acroporidae	*Acropora plana*	Pac	1	1	30.41	590.23	0.70	4.21	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora plantaginea*	Pac	1	1	33.95	590.23	1.30	10.16	1.45	spa	cor	118.92	her
Acroporidae	*Acropora plumosa*	Pac	1	1	30.41	590.23	1.20	9.06	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora polystoma*	Pac	1	1	33.95	590.23	1.50	5.90	1.45	spa	cor	80.00	her
Acroporidae	*Acropora prolifera*	Atl	1	1	59.33	590.23	1.50	12.45	0.96	spa	br_c	160.75	her
Acroporidae	*Acropora prostrata*	Pac	1	1	33.95	590.23	0.60	3.38	1.45	spa	cor	118.92	her
Acroporidae	*Acropora proximalis*	Pac	1	1	51.26	590.23	0.60	3.38	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora pruinosa*	Pac	1	1	51.26	590.23	1.60	13.64	0.96	spa	br_c	100.00	her
Acroporidae	*Acropora pulchra*	Pac	1	1	135.92	575.00	1.20	9.40	1.90	spa	br_o	500.00	her
Acroporidae	*Acropora rambleri*	Pac	1	1	30.41	590.23	0.70	4.21	1.40	spa	t/p	100.00	her
Acroporidae	*Acropora retusa*	Pac	1	1	30.54	590.23	0.90	6.02	1.42	spa	dig	112.31	her
Acroporidae	*Acropora robusta*	Pac	1	1	22.40	590.23	1.50	7.60	1.51	spa	br_o	94.99	her
Acroporidae	*Acropora rongelapensis*	Pac	1	1	30.41	590.23	0.80	5.09	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora rosaria*	Pac	1	1	33.95	590.23	2.30	22.85	1.45	spa	cor	118.92	her
Acroporidae	*Acropora roseni*	Pac	1	1	57.35	590.23	1.60	13.64	1.51	spa	br_o	200.00	her
Acroporidae	*Acropora rudis*	Pac	1	1	57.35	590.23	1.20	9.06	1.51	spa	br_o	100.00	her
Acroporidae	*Acropora rufus*	Pac	1	1	51.26	590.23	1.10	8.01	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora russelli*	Pac	1	1	51.26	590.23	1.00	6.99	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora samoensis*	Pac	1	1	30.54	590.23	1.80	11.10	1.42	spa	dig	100.00	her
Acroporidae	*Acropora sarmentosa*	Pac	1	1	33.95	590.23	2.00	10.13	1.45	spa	cor	30.00	her
Acroporidae	*Acropora scherzeriana*	Pac	1	1	57.35	590.23	0.60	3.38	1.51	spa	br_o	157.83	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Acropora schmitti*	Pac	1	1	57.35	590.23	1.50	12.45	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora secale*	Pac	1	1	51.26	590.23	1.20	15.10	0.96	spa	br_c	100.00	her
Acroporidae	*Acropora sekiseiensis*	Pac	1	1	51.26	590.23	1.10	8.01	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora selago*	Pac	1	1	33.95	590.23	0.90	6.02	1.45	spa	cor	75.00	her
Acroporidae	*Acropora seriata*	Pac	1	1	30.41	590.23	0.60	3.38	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora simplex*	Pac	1	1	30.41	590.23	0.80	5.09	1.40	spa	t/p	100.00	her
Acroporidae	*Acropora solitaryensis*	Pac	1	1	16.70	590.23	1.10	12.60	1.45	spa	t/p	300.00	her
Acroporidae	*Acropora sordiensis*	Pac	1	1	51.26	590.23	2.00	21.50	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora spathulata*	Pac	1	1	33.95	590.23	1.50	7.50	1.45	spa	cor	118.92	her
Acroporidae	*Acropora speciosa*	Pac	1	1	40.30	590.23	0.80	5.09	1.45	spa	cor	50.00	her
Acroporidae	*Acropora spicifera*	Pac	1	1	111.00	590.23	1.10	8.01	1.40	spa	t/p	225.44	her
Acroporidae	*Acropora squarrosa*	Pac	1	1	51.26	590.23	0.80	5.09	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora stoddarti*	Pac	1	1	30.41	590.23	1.30	10.16	1.40	spa	t/p	200.00	her
Acroporidae	*Acropora striata*	Pac	1	1	51.26	590.23	1.10	8.01	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora subglabra*	Pac	1	1	57.35	590.23	0.80	5.09	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora subulata*	Pac	1	1	30.41	590.23	1.20	9.80	1.40	spa	t/p	300.00	her
Acroporidae	*Acropora suharsonoi*	Pac	1	1	33.95	590.23	0.80	5.09	1.45	spa	cor	118.92	her
Acroporidae	*Acropora sukarnoi*	Pac	1	1	30.41	590.23	1.50	12.45	1.40	spa	t/p	150.00	her
Acroporidae	*Acropora surculosa*	Pac	1	1	30.41	590.23	1.10	8.04	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora tanegashimensis*	Pac	1	1	30.41	590.23	0.80	5.09	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora tenella*	Pac	1	1	30.41	590.23	0.80	5.09	1.40	spa	t/p	112.05	her
Acroporidae	*Acropora tenuis*	Pac	1	1	33.95	590.23	1.20	12.60	1.45	spa	cor	118.92	her
Acroporidae	*Acropora teres*	Pac	1	1	57.35	590.23	1.02	7.20	1.51	spa	br_o	157.83	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Acropora tizardi*	Pac	1	1	51.26	590.23	0.60	3.38	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora torihalimeda*	Pac	1	1	51.26	590.23	0.80	5.09	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora torresiana*	Pac	1	1	51.26	590.23	1.20	9.06	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora tortuosa*	Pac	1	1	51.26	590.23	1.30	12.20	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora tumida*	Pac	1	1	8.30	590.23	1.40	11.28	0.96	spa	br_c	300.00	her
Acroporidae	*Acropora turaki*	Pac	1	1	57.35	590.23	0.80	5.09	1.51	spa	br_o	200.00	her
Acroporidae	*Acropora tutuilensis*	Pac	1	1	57.35	590.23	1.20	9.06	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora valenciennesi*	Pac	1	1	179.33	590.23	1.50	12.45	1.51	spa	br_o	400.00	her
Acroporidae	*Acropora valida*	Pac	1	1	34.30	596.00	0.90	8.14	1.50	spa	cor	50.00	her
Acroporidae	*Acropora variabilis*	Pac	1	1	51.26	590.23	0.90	23.00	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora variolosa*	Pac	1	1	57.35	590.23	1.20	9.06	1.51	spa	br_o	157.83	her
Acroporidae	*Acropora vaughani*	Pac	1	1	51.26	590.23	1.10	8.01	0.96	spa	br_c	148.54	her
Acroporidae	*Acropora vermiculata*	Pac	1	1	33.95	590.23	0.80	5.09	1.45	spa	cor	118.92	her
Acroporidae	*Acropora verweyi*	Pac	1	1	33.95	590.23	1.10	7.20	1.45	spa	cor	118.92	her
Acroporidae	*Acropora walindii*	Pac	1	1	57.35	590.23	0.50	2.61	1.51	spa	br_o	100.00	her
Acroporidae	*Acropora willisae*	Pac	1	1	33.95	590.23	1.00	6.99	1.45	spa	cor	100.00	her
Acroporidae	*Acropora yongei*	Pac	1	1	59.34	590.23	1.20	9.06	0.96	spa	br_c	200.00	her
Acroporidae	*Anacropora forbesi*	Pac	1	1	51.26	396.00	0.50	4.59	0.96	spa	br_c	148.54	her
Acroporidae	*Anacropora matthai*	Pac	1	1	51.26	396.00	0.60	5.94	0.96	spa	br_c	148.54	her
Acroporidae	*Anacropora pillai*	Pac	1	1	51.26	396.00	0.60	5.94	0.96	spa	br_c	148.54	her
Acroporidae	*Anacropora puertogalerae*	Pac	1	1	51.26	396.00	0.80	8.94	0.96	spa	br_c	148.54	her
Acroporidae	*Anacropora reticulata*	Pac	1	1	51.26	396.00	0.90	10.57	0.96	spa	br_c	148.54	her
Acroporidae	*Anacropora spinosa*	Pac	1	1	51.26	396.00	0.90	10.57	0.96	spa	br_c	148.54	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Anacropora spumosa*	Pac	1	1	51.26	396.00	0.70	7.40	0.96	spa	br_c	148.54	her
Acroporidae	*Isopora brueggemanni*	Pac	1	1	74.80	1500.00	1.60	3.66	1.51	bro	br_o	182.17	her
Acroporidae	*Isopora crateriformis*	Pac	1	1	8.15	1545.56	0.80	1.31	1.56	bro	enc	100.00	her
Acroporidae	*Isopora cuneata*	Pac	1	1	19.00	1687.00	1.00	1.00	1.56	bro	enc	100.00	her
Acroporidae	*Isopora elizabethensis*	Pac	1	1	57.35	1545.56	1.20	2.33	1.51	bro	br_o	157.83	her
Acroporidae	*Isopora palifera*	Pac	1	1	15.50	1459.00	1.40	1.00	1.52	bro	br_o	120.00	her
Acroporidae	*Isopora togianensis*	Pac	1	1	57.35	1545.56	1.20	2.33	1.51	bro	br_o	150.00	her
Acroporidae	*Montipora aequituberculata*	Pac	1	1	25.25	354.96	0.90	27.00	1.79	spa	lam	101.33	her
Acroporidae	*Montipora altasepta*	Pac	1	1	57.35	354.96	0.80	10.44	1.51	spa	br_o	157.83	her
Acroporidae	*Montipora angulata*	Pac	1	1	51.26	354.96	1.30	20.81	0.96	spa	br_c	148.54	her
Acroporidae	*Montipora aspergillus*	Pac	1	1	51.26	354.96	0.80	10.44	0.96	spa	br_c	148.54	her
Acroporidae	*Montipora australiensis*	Pac	1	1	25.10	354.96	0.10	0.54	1.39	spa	col	101.01	her
Acroporidae	*Montipora cactus*	Pac	1	1	25.10	354.96	1.20	18.57	1.39	spa	col	101.01	her
Acroporidae	*Montipora calcarea*	Pac	1	1	30.54	354.96	0.90	12.34	1.42	spa	dig	112.31	her
Acroporidae	*Montipora caliculata*	Pac	1	1	12.91	354.96	1.00	14.33	1.36	spa	mas	70.55	her
Acroporidae	*Montipora capitata*	Pac	1	1	25.81	354.96	1.00	13.05	1.39	spa	col	102.54	her
Acroporidae	*Montipora capricornis*	Pac	1	1	25.25	354.96	1.00	13.00	1.79	spa	lam	101.33	her
Acroporidae	*Montipora cebuensis*	Pac	1	1	25.25	354.96	0.80	10.44	1.79	spa	lam	101.33	her
Acroporidae	*Montipora circumvallata*	Pac	1	1	30.54	354.96	0.60	6.93	1.42	spa	dig	112.31	her
Acroporidae	*Montipora cocosensis*	Pac	1	1	12.91	354.96	1.40	23.12	1.36	spa	mas	70.55	her
Acroporidae	*Montipora confusa*	Pac	1	1	25.10	354.96	0.70	8.63	1.39	spa	col	100.00	her
Acroporidae	*Montipora corbettensis*	Pac	1	1	30.54	354.96	0.80	10.44	1.42	spa	dig	112.31	her
Acroporidae	*Montipora crassituberculata*	Pac	1	1	25.25	354.96	1.50	25.50	1.79	spa	lam	101.33	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Montipora cryptus*	Pac	1	1	8.15	354.96	0.70	8.63	1.56	spa	enc	55.03	her
Acroporidae	*Montipora danae*	Pac	1	1	25.25	354.96	1.40	23.12	1.79	spa	lam	101.33	her
Acroporidae	*Montipora delicatula*	Pac	1	1	25.25	354.96	0.60	6.93	1.79	spa	lam	101.33	her
Acroporidae	*Montipora digitata*	Pac	1	1	41.49	360.00	0.90	12.10	1.51	spa	br_o	132.52	her
Acroporidae	*Montipora dilatata*	Pac	1	1	30.54	354.96	1.20	18.57	1.42	spa	dig	30.00	her
Acroporidae	*Montipora echinata*	Pac	1	1	51.26	354.96	0.80	10.44	0.96	spa	br_c	148.54	her
Acroporidae	*Montipora edwardsi*	Pac	1	1	25.10	354.96	0.80	10.44	1.39	spa	col	101.01	her
Acroporidae	*Montipora efflorescens*	Pac	1	1	12.91	354.96	1.20	18.57	1.36	spa	mas	70.55	her
Acroporidae	*Montipora effusa*	Pac	1	1	12.91	354.96	0.80	10.44	1.36	spa	mas	70.55	her
Acroporidae	*Montipora flabellata*	Pac	1	1	25.25	354.96	0.50	5.35	1.79	spa	lam	50.00	her
Acroporidae	*Montipora florida*	Pac	1	1	25.25	354.96	0.80	10.44	1.79	spa	lam	101.33	her
Acroporidae	*Montipora floweri*	Pac	1	1	12.91	354.96	0.90	12.34	1.36	spa	mas	70.55	her
Acroporidae	*Montipora foliosa*	Pac	1	1	32.50	354.96	0.90	12.34	1.79	spa	lam	116.14	her
Acroporidae	*Montipora friabilis*	Pac	1	1	25.25	354.96	1.00	14.33	1.79	spa	lam	101.33	her
Acroporidae	*Montipora gaimardi*	Pac	1	1	25.10	354.96	0.80	10.44	1.39	spa	col	101.01	her
Acroporidae	*Montipora granulosa*	Pac	1	1	8.15	354.96	0.80	10.44	1.56	spa	enc	55.03	her
Acroporidae	*Montipora grisea*	Pac	1	1	12.91	354.96	1.20	18.57	1.36	spa	mas	70.55	her
Acroporidae	*Montipora hemispherica*	Pac	1	1	30.54	354.96	0.90	12.34	1.42	spa	dig	200.00	her
Acroporidae	*Montipora hirsuta*	Pac	1	1	57.35	354.96	0.50	5.35	1.51	spa	br_o	157.83	her
Acroporidae	*Montipora hispida*	Pac	1	1	25.10	354.96	1.40	23.12	1.39	spa	col	101.01	her
Acroporidae	*Montipora hodgsoni*	Pac	1	1	25.25	354.96	0.60	6.93	1.79	spa	lam	101.33	her
Acroporidae	*Montipora hoffmeisteri*	Pac	1	1	8.15	354.96	1.10	16.41	1.56	spa	enc	55.03	her
Acroporidae	*Montipora incrassata*	Pac	1	1	8.15	354.96	1.40	23.12	1.56	spa	enc	55.03	her

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Acroporidae	*Montipora informis*	Pac	1	1	12.91	354.96	1.30	20.81	1.36	spa	mas	70.55	her
Acroporidae	*Montipora kellyi*	Pac	1	1	51.26	354.96	0.90	12.34	0.96	spa	br_c	148.54	her
Acroporidae	*Montipora lobulata*	Pac	1	1	12.91	354.96	1.30	20.81	1.36	spa	mas	70.55	her
Acroporidae	*Montipora mactanensis*	Pac	1	1	30.54	354.96	0.90	12.34	1.42	spa	dig	112.31	her
Acroporidae	*Montipora malampaya*	Pac	1	1	30.54	354.96	0.70	8.63	1.42	spa	dig	112.31	her
Acroporidae	*Montipora meandrina*	Pac	1	1	8.15	354.96	0.90	12.34	1.56	spa	enc	20.00	her
Acroporidae	*Montipora millepora*	Pac	1	1	8.15	354.96	0.60	6.93	1.56	spa	enc	55.03	her
Acroporidae	*Montipora mollis*	Pac	1	1	12.91	354.96	0.90	12.34	1.36	spa	mas	70.55	her
Acroporidae	*Montipora monasteriata*	Pac	1	1	25.25	354.96	1.10	16.41	1.79	spa	lam	101.33	her
Acroporidae	*Montipora niugini*	Pac	1	1	30.54	354.96	0.70	8.63	1.42	spa	dig	30.00	her
Acroporidae	*Montipora nodosa*	Pac	1	1	12.91	354.96	1.30	20.81	1.36	spa	mas	70.55	her
Acroporidae	*Montipora orientalis*	Pac	1	1	25.10	354.96	1.00	14.33	1.39	spa	col	101.01	her
Acroporidae	*Montipora pachytuberculata*	Pac	1	1	51.26	354.96	0.60	6.93	0.96	spa	br_c	148.54	her
Acroporidae	*Montipora palawanensis*	Pac	1	1	25.25	354.96	0.70	8.63	1.79	spa	lam	200.00	her
Acroporidae	*Montipora patula*	Pac	1	1	25.25	354.96	0.70	8.63	1.79	spa	lam	200.00	her
Acroporidae	*Montipora peltiformis*	Pac	1	1	12.91	354.96	0.90	12.34	1.36	spa	mas	70.55	her
Acroporidae	*Montipora porites*	Pac	1	1	25.10	354.96	0.90	12.34	1.39	spa	col	101.01	her
Acroporidae	*Montipora samarensis*	Pac	1	1	57.35	354.96	0.70	8.63	1.51	spa	br_o	157.83	her
Acroporidae	*Montipora saudii*	Pac	1	1	25.10	354.96	0.80	10.44	1.39	spa	col	100.00	her
Acroporidae	*Montipora setosa*	Pac	1	1	30.54	354.96	0.80	10.44	1.42	spa	dig	112.31	her
Acroporidae	*Montipora spongiosa*	Pac	1	1	51.26	354.96	0.80	10.44	0.96	spa	br_c	148.54	her
Acroporidae	*Montipora spongodes*	Pac	1	1	8.15	354.96	1.20	18.57	1.56	spa	enc	55.03	her
Acroporidae	*Montipora spumosa*	Pac	1	1	8.15	354.96	0.90	11.00	1.56	spa	enc	55.03	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Acroporidae	*Montipora stellata*	Pac	1	1	30.54	354.96	0.90	12.34	1.42	spa	dig	112.31	her
Acroporidae	*Montipora stilosa*	Pac	1	1	12.91	354.96	0.80	10.44	1.36	spa	mas	70.55	her
Acroporidae	*Montipora taiwanensis*	Pac	1	1	12.91	354.96	0.90	12.34	1.36	spa	mas	50.00	her
Acroporidae	*Montipora tortuosa*	Pac	1	1	51.26	354.96	0.50	5.35	0.96	spa	br_c	148.54	her
Acroporidae	*Montipora tuberculosa*	Pac	1	1	12.91	350.00	1.00	14.62	1.36	spa	mas	70.55	her
Acroporidae	*Montipora turgescens*	Pac	1	1	12.91	354.96	1.00	14.33	1.36	spa	mas	70.55	her
Acroporidae	*Montipora turtlensis*	Pac	1	1	30.54	354.96	0.90	12.34	1.42	spa	dig	112.31	her
Acroporidae	*Montipora undata*	Pac	1	1	26.00	354.96	1.20	18.57	1.79	spa	lam	102.95	her
Acroporidae	*Montipora venosa*	Pac	1	1	12.91	354.96	1.80	33.04	1.36	spa	mas	70.55	her
Acroporidae	*Montipora verrilli*	Pac	1	1	17.20	354.96	0.80	10.44	1.56	spa	enc	82.37	her
Acroporidae	*Montipora verrucosa*	Pac	1	1	28.74	354.96	1.40	20.00	1.79	spa	lam	108.68	her
Acroporidae	*Montipora verruculosa*	Pac	1	1	8.15	354.96	0.80	10.44	1.56	spa	enc	200.00	her
Acroporidae	*Montipora vietnamensis*	Pac	1	1	30.54	354.96	0.70	8.63	1.42	spa	dig	112.31	her
Acroporidae	*Montipora foveolata*	Pac	2	2	12.91	354.96	2.90	65.06	1.36	spa	mas	70.55	her
Fungiidae	*Ctenactis albitentaculata*	Pac	2	2	6.20	203.05	260.00	85133.10	1.68	spa	mas	26.00	gon
Fungiidae	*Ctenactis crassa*	Pac	2	2	6.20	155.00	236.00	108578.77	1.68	spa	mas	23.60	gon
Fungiidae	*Ctenactis echinata*	Pac	2	2	6.20	266.00	284.00	65943.36	1.68	spa	mas	28.40	gon
Fungiidae	*Danafungia horrida*	Pac	2	2	6.20	215.00	204.00	55639.23	1.68	spa	mas	20.00	gon
Fungiidae	*Danafungia scruposa*	Pac	2	2	6.20	215.00	111.00	23431.58	1.68	spa	mas	24.00	gon
Fungiidae	*Heliofungia actiniformis*	Pac	2	2	5.76	369.50	142.00	15491.20	1.68	spa	mas	20.00	gon
Fungiidae	*Heliofungia fralinae*	Pac	2	2	6.20	369.50	90.00	8103.31	1.68	spa	mas	9.00	gon
Fungiidae	*Leptastrea aequalis*	Pac	2	2	3.91	273.00	2.80	89.64	1.93	spa	enc	20.00	gon
Fungiidae	*Leptastrea bewickensis*	Pac	2	2	3.91	273.00	4.20	159.49	1.93	spa	enc	100.00	gon

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Fungiidae	*Leptastrea bottae*	Pac	2	2	3.91	273.00	3.50	123.09	1.93	spa	enc	15.70	gon
Fungiidae	*Leptastrea inaequalis*	Pac	2	2	6.20	273.00	4.10	154.12	1.68	spa	mas	20.13	gon
Fungiidae	*Leptastrea pruinosa*	Pac	2	2	3.91	273.00	3.60	128.12	1.93	spa	enc	15.70	gon
Fungiidae	*Leptastrea purpurea*	Pac	2	2	1.80	273.00	10.00	547.14	1.63	spa	enc	100.00	gon
Fungiidae	*Leptastrea transversa*	Pac	2	2	3.91	273.00	9.20	486.01	1.93	spa	enc	15.70	gon
Fungiidae	*Lobactis scutaria*	Pac	2	2	9.30	83.60	169.00	161381.37	1.68	spa	mas	17.00	gon
Merulinidae	*Astrea annuligera*	Pac	2	2	4.07	352.00	6.30	198.28	1.71	spa	enc	75.95	her
Merulinidae	*Astrea curta*	Pac	2	2	2.60	352.00	9.30	723.60	1.49	spa	mas	59.66	her
Merulinidae	*Astrea devantieri*	Pac	2	2	6.44	352.00	4.50	122.92	1.49	spa	mas	150.00	her
Merulinidae	*Coelastrea aspera*	Pac	2	2	4.00	358.67	11.50	350.00	1.49	spa	mas	500.00	her
Merulinidae	*Coelastrea palauensis*	Pac	2	2	6.44	358.67	18.80	913.05	1.49	spa	mas	20.00	her
Merulinidae	*Cyphastrea agassizi*	Pac	2	2	6.44	233.19	2.20	79.47	1.49	spa	mas	97.37	her
Merulinidae	*Cyphastrea chalcidicum*	Pac	2	2	6.44	233.19	2.80	111.96	1.49	spa	mas	100.00	her
Merulinidae	*Cyphastrea decadia*	Pac	2	2	25.57	233.19	2.80	111.96	1.06	spa	br_c	205.02	her
Merulinidae	*Cyphastrea hexasepta*	Pac	2	2	6.44	233.19	1.00	25.92	1.49	spa	mas	97.37	her
Merulinidae	*Cyphastrea japonica*	Pac	2	2	6.44	233.19	1.90	64.53	1.49	spa	mas	97.37	her
Merulinidae	*Cyphastrea microphthalma*	Pac	2	2	6.44	286.00	2.70	96.13	1.49	spa	mas	97.37	her
Merulinidae	*Cyphastrea ocellina*	Pac	2	2	3.26	528.57	2.50	24.00	1.49	bro	mas	67.36	her
Merulinidae	*Cyphastrea serailia*	Pac	2	2	4.93	300.00	2.40	158.60	1.49	spa	mas	84.31	her
Merulinidae	*Dipsastraea albida*	Pac	2	2	6.44	391.00	12.10	432.20	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea amicorum*	Pac	2	2	6.44	391.00	13.20	489.08	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea danai*	Pac	2	2	6.44	391.00	9.20	292.81	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea faviaformis*	Pac	2	2	6.44	391.00	20.60	920.55	1.49	spa	mas	20.00	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Merulinidae	*Dipsastraea favus*	Pac	2	2	6.44	391.00	10.00	1000.00	1.49	spa	mas	37.00	her
Merulinidae	*Dipsastraea helianthoides*	Pac	2	2	6.44	391.00	9.00	283.81	1.49	spa	mas	97.37	NA
Merulinidae	*Dipsastraea lacuna*	Pac	2	2	6.44	391.00	9.80	320.31	1.49	spa	mas	100.00	her
Merulinidae	*Dipsastraea laddi*	Pac	2	2	6.44	391.00	6.80	190.56	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea laxa*	Pac	2	2	6.44	391.00	5.80	152.01	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea lizardensis*	Pac	2	2	6.44	391.00	16.70	683.16	1.49	spa	mas	100.00	her
Merulinidae	*Dipsastraea maritima*	Pac	2	2	6.44	391.00	18.80	808.39	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea marshae*	Pac	2	2	6.44	391.00	19.30	839.11	1.49	spa	mas	60.00	her
Merulinidae	*Dipsastraea matthaii*	Pac	2	2	6.44	391.00	13.80	520.97	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea maxima*	Pac	2	2	6.44	391.00	29.00	1496.61	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea mirabilis*	Pac	2	2	6.44	391.00	10.00	329.64	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea pallida*	Pac	2	2	4.30	391.00	10.20	339.05	1.43	spa	mas	78.28	her
Merulinidae	*Dipsastraea rosaria*	Pac	2	2	4.07	391.00	9.30	297.34	1.71	spa	enc	100.00	her
Merulinidae	*Dipsastraea rotumana*	Pac	2	2	6.44	391.00	14.20	542.56	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea speciosa*	Pac	2	2	6.25	391.00	9.90	324.97	1.49	spa	mas	75.00	her
Merulinidae	*Dipsastraea veroni*	Pac	2	2	6.44	391.00	17.50	730.13	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea vietnamensis*	Pac	2	2	6.44	391.00	14.10	537.13	1.49	spa	mas	97.37	her
Merulinidae	*Dipsastraea wisseli*	Pac	2	2	6.44	391.00	17.00	700.66	1.49	spa	mas	97.37	her
Merulinidae	*Echinopora ashmorensis*	Pac	2	2	12.52	340.00	5.10	154.21	1.52	spa	col	200.00	her
Merulinidae	*Echinopora forskaliana*	Pac	2	2	6.44	340.00	5.80	185.14	1.49	spa	mas	97.37	her
Merulinidae	*Echinopora fruticulosa*	Pac	2	2	25.57	340.00	4.80	141.48	1.06	spa	br_c	200.00	her
Merulinidae	*Echinopora gemmacea*	Pac	2	2	12.59	340.00	4.20	25.40	1.96	spa	lam	139.86	her
Merulinidae	*Echinopora hirsutissima*	Pac	2	2	6.44	340.00	4.20	117.03	1.49	spa	mas	97.37	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Merulinidae	*Echinopora horrida*	Pac	2	2	12.52	340.00	2.40	52.84	1.52	spa	col	500.00	her
Merulinidae	*Echinopora irregularis*	Pac	2	2	15.24	340.00	4.20	117.03	1.56	spa	dig	155.00	her
Merulinidae	*Echinopora lamellosa*	Pac	2	2	12.59	340.00	3.40	86.67	1.96	spa	lam	500.00	her
Merulinidae	*Echinopora mammiformis*	Pac	2	2	12.52	340.00	8.90	340.20	1.52	spa	col	500.00	her
Merulinidae	*Echinopora pacificus*	Pac	2	2	12.59	340.00	4.60	133.18	1.96	spa	lam	139.86	her
Merulinidae	*Echinopora robusta*	Pac	2	2	6.44	340.00	8.60	324.03	1.49	spa	mas	97.37	her
Merulinidae	*Echinopora taylorae*	Pac	2	2	12.59	340.00	5.00	149.93	1.96	spa	lam	139.86	her
Merulinidae	*Echinopora tiranensis*	Pac	2	2	15.24	340.00	3.50	90.32	1.56	spa	dig	155.00	her
Merulinidae	*Favites abdita*	Pac	2	2	0.80	394.00	15.00	580.21	1.49	spa	mas	100.00	her
Merulinidae	*Favites acuticollis*	Pac	2	2	6.44	378.18	9.30	311.66	1.49	spa	mas	97.37	her
Merulinidae	*Favites chinensis*	Pac	2	2	6.44	378.18	12.50	474.43	1.49	spa	mas	97.37	her
Merulinidae	*Favites colemani*	Pac	2	2	4.07	378.18	7.80	242.73	1.71	spa	enc	40.00	her
Merulinidae	*Favites complanata*	Pac	2	2	6.44	390.00	18.80	811.31	1.49	spa	mas	97.37	her
Merulinidae	*Favites flexuosa*	Pac	2	2	6.44	378.18	18.80	847.30	1.49	spa	mas	97.37	her
Merulinidae	*Favites halicora*	Pac	2	2	6.44	352.00	16.80	799.05	1.49	spa	mas	97.37	her
Merulinidae	*Favites magnistellata*	Pac	2	2	6.44	378.18	12.10	453.00	1.49	spa	mas	200.00	her
Merulinidae	*Favites melicerum*	Pac	2	2	6.44	378.18	8.10	256.10	1.49	spa	mas	97.37	her
Merulinidae	*Favites micropentagonus*	Pac	2	2	6.44	378.18	5.20	136.43	1.49	spa	mas	50.00	her
Merulinidae	*Favites paraflexuosus*	Pac	2	2	6.44	378.18	16.20	685.77	1.49	spa	mas	60.00	her
Merulinidae	*Favites pentagona*	Pac	2	2	6.44	378.18	8.50	355.00	1.49	spa	mas	100.00	her
Merulinidae	*Favites rotundata*	Pac	2	2	6.44	378.18	21.20	1005.04	1.49	spa	mas	97.37	her
Merulinidae	*Favites spinosa*	Pac	2	2	6.44	378.18	8.20	260.61	1.49	spa	mas	97.37	her
Merulinidae	*Favites stylifera*	Pac	2	2	6.44	378.18	6.80	199.74	1.49	spa	mas	97.37	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Merulinidae	*Favites valenciennesi*	Pac	2	2	6.44	378.18	10.00	345.51	1.49	spa	mas	97.37	her
Merulinidae	*Favites vasta*	Pac	2	2	6.44	378.18	17.50	765.27	1.49	spa	mas	97.37	her
Merulinidae	*Goniastrea columella*	Pac	2	2	6.44	371.00	17.50	786.25	1.49	spa	mas	97.37	her
Merulinidae	*Goniastrea edwardsi*	Pac	2	2	9.05	371.00	5.00	132.57	1.49	spa	mas	100.00	her
Merulinidae	*Goniastrea favulus*	Pac	2	2	4.05	371.00	7.50	148.00	1.49	spa	mas	75.79	her
Merulinidae	*Goniastrea minuta*	Pac	2	2	6.44	371.00	5.90	167.72	1.49	spa	mas	97.37	her
Merulinidae	*Goniastrea pectinata*	Pac	2	2	6.44	371.00	15.00	631.58	1.49	spa	mas	97.37	her
Merulinidae	*Goniastrea ramosa*	Pac	2	2	12.52	371.00	7.40	231.41	1.52	spa	col	30.00	her
Merulinidae	*Goniastrea retiformis*	Pac	2	2	7.57	371.00	6.50	322.95	1.70	spa	mas	100.00	her
Merulinidae	*Goniastrea stelligera*	Pac	2	2	10.00	371.00	5.10	136.35	1.49	spa	mas	123.48	her
Merulinidae	*Goniastrea thecata*	Pac	2	2	6.44	371.00	8.40	277.08	1.49	spa	mas	100.00	her
Merulinidae	*Hydnophora bonsai*	Pac	2	2	15.24	317.84	4.50	141.96	1.56	spa	dig	155.00	her
Merulinidae	*Hydnophora exesa*	Pac	2	2	6.44	328.00	4.50	135.79	1.49	spa	mas	100.00	her
Merulinidae	*Hydnophora grandis*	Pac	2	2	12.52	317.84	4.70	151.00	1.52	spa	col	139.41	her
Merulinidae	*Hydnophora microconos*	Pac	2	2	9.77	317.84	7.20	276.83	1.37	spa	mas	121.91	her
Merulinidae	*Hydnophora pilosa*	Pac	2	2	12.52	308.00	8.00	336.12	1.52	spa	col	139.41	her
Merulinidae	*Hydnophora rigida*	Pac	2	2	71.00	317.84	6.70	249.91	1.06	spa	br_c	355.85	her
Merulinidae	*Leptoria irregularis*	Pac	2	2	4.07	445.00	6.30	142.45	1.71	spa	enc	150.00	her
Merulinidae	*Leptoria phrygia*	Pac	2	2	6.44	445.00	3.50	10.10	1.61	spa	mas	97.37	her
Merulinidae	*Merulina ampliata*	Pac	2	2	22.49	339.00	6.20	89.90	1.96	spa	lam	191.30	her
Merulinidae	*Merulina scabricula*	Pac	2	2	12.59	344.46	3.50	88.68	1.96	spa	lam	139.86	her
Merulinidae	*Merulina scheeri*	Pac	2	2	15.24	344.46	8.20	297.31	1.56	spa	dig	30.00	her
Merulinidae	*Merulina triangularis*	Pac	2	2	25.57	350.00	8.80	321.37	1.06	spa	br_c	500.00	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Merulinidae	*Mycedium elephantotus*	Pac	2	2	12.59	430.00	10.00	288.27	1.96	spa	lam	300.00	her
Merulinidae	*Mycedium mancaoi*	Pac	2	2	12.59	430.00	7.20	180.75	1.96	spa	lam	139.86	her
Merulinidae	*Mycedium robokaki*	Pac	2	2	12.59	430.00	7.20	180.75	1.96	spa	lam	139.86	her
Merulinidae	*Mycedium steeni*	Pac	2	2	12.59	430.00	3.10	54.58	1.96	spa	lam	30.00	her
Merulinidae	*Mycedium umbra*	Pac	2	2	4.07	430.00	17.00	612.73	1.71	spa	enc	100.00	her
Merulinidae	*Orbicella annularis*	Atl	2	2	7.04	312.00	3.12	103.70	1.71	spa	mas	800.00	her
Merulinidae	*Orbicella faveolata*	Atl	2	2	8.75	319.50	2.57	120.05	1.18	spa	mas	1000.00	her
Merulinidae	*Orbicella franksi*	Atl	2	2	5.22	335.00	2.99	59.00	1.49	spa	mas	500.00	her
Merulinidae	*Paragoniastrea australensis*	Pac	2	2	3.40	417.00	10.00	301.03	1.49	spa	mas	68.96	her
Merulinidae	*Paragoniastrea deformis*	Pac	2	2	6.44	417.00	8.80	251.02	1.49	spa	mas	97.37	NA
Merulinidae	*Paragoniastrea russelli*	Pac	2	2	6.44	417.00	16.00	587.03	1.49	spa	mas	97.37	her
Merulinidae	*Pectinia africanus*	Pac	2	2	6.44	350.00	16.60	791.90	1.49	spa	mas	30.00	her
Merulinidae	*Pectinia alcicornis*	Pac	2	2	15.24	350.00	21.20	1121.04	1.56	spa	dig	155.00	her
Merulinidae	*Pectinia elongata*	Pac	2	2	25.57	350.00	11.00	441.28	1.06	spa	br_c	205.02	her
Merulinidae	*Pectinia lactuca*	Pac	2	2	4.07	350.00	30.00	1836.06	1.71	spa	enc	100.00	her
Merulinidae	*Pectinia maxima*	Pac	2	2	12.59	350.00	15.00	685.68	1.96	spa	lam	100.00	her
Merulinidae	*Pectinia paeonia*	Pac	2	2	12.59	350.00	35.00	2285.70	1.96	spa	lam	100.00	her
Merulinidae	*Pectinia pygmaeus*	Pac	2	2	25.57	350.00	4.70	131.81	1.06	spa	br_c	205.02	her
Merulinidae	*Pectinia teres*	Pac	2	2	25.57	350.00	6.20	195.38	1.06	spa	br_c	205.02	her
Merulinidae	*Platygyra acuta*	Pac	2	2	6.44	384.36	5.20	133.35	1.49	spa	mas	97.37	her
Merulinidae	*Platygyra carnosus*	Pac	2	2	6.44	384.36	5.00	126.12	1.49	spa	mas	40.00	her
Merulinidae	*Platygyra contorta*	Pac	2	2	6.44	384.36	5.60	148.15	1.49	spa	mas	97.37	her
Merulinidae	*Platygyra crosslandi*	Pac	2	2	6.44	384.36	5.90	159.56	1.49	spa	mas	97.37	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Merulinidae	*Platygyra daedalea*	Pac	2	2	22.00	374.00	10.00	10.00	1.49	spa	mas	70.00	her
Merulinidae	*Platygyra lamellina*	Pac	2	2	7.40	384.36	9.10	750.00	1.49	spa	mas	104.95	her
Merulinidae	*Platygyra pini*	Pac	2	2	6.44	384.36	7.20	211.74	1.49	spa	mas	97.37	her
Merulinidae	*Platygyra ryukyuensis*	Pac	2	2	6.44	384.36	3.30	69.88	1.49	spa	mas	97.37	her
Merulinidae	*Platygyra sinensis*	Pac	2	2	8.39	395.00	6.70	104.00	1.49	spa	mas	112.29	her
Merulinidae	*Platygyra verweyi*	Pac	2	2	6.44	384.36	4.70	115.50	1.49	spa	mas	97.37	her
Merulinidae	*Platygyra yaeyamaensis*	Pac	2	2	6.44	384.36	5.10	129.72	1.49	spa	mas	97.37	her
Pocilloporidae	*Madracis mirabilis*	Atl	1	1	22.00	310.00	1.50	30.87	1.82	bro	br_c	14.66	her
Pocilloporidae	*Palauastrea ramosa*	Pac	1	1	23.97	356.00	1.20	18.49	1.82	spa	br_c	60.51	her
Pocilloporidae	*Pocillopora damicornis*	Pac	1	1	34.80	1051.00	1.00	22.50	1.93	bro	br_c	200.00	her
Pocilloporidae	*Seriatopora aculeata*	Pac	1	1	23.97	762.50	0.50	1.82	1.82	bro	br_c	60.51	her
Pocilloporidae	*Seriatopora caliendrum*	Pac	1	1	58.00	762.50	1.10	2.75	1.82	bro	br_c	97.50	NA
Pocilloporidae	*Seriatopora dentritica*	Pac	1	1	23.97	762.50	0.60	2.36	1.82	bro	br_c	60.51	her
Pocilloporidae	*Seriatopora guttata*	Pac	1	1	23.97	762.50	0.60	2.36	1.82	bro	br_c	30.00	NA
Pocilloporidae	*Seriatopora hystrix*	Pac	1	1	29.94	762.50	0.80	3.55	2.20	bro	br_c	68.22	her
Pocilloporidae	*Seriatopora stellata*	Pac	1	1	23.97	762.50	0.60	2.36	1.82	bro	br_c	60.51	her
Pocilloporidae	*Stylophora danae*	Pac	1	1	12.00	549.00	1.10	8.87	1.82	bro	br_c	41.64	her
Pocilloporidae	*Stylophora kuehlmanni*	Pac	1	1	23.97	549.00	0.70	4.67	1.82	bro	br_c	60.51	her
Pocilloporidae	*Stylophora madagascarensis*	Pac	1	1	23.97	549.00	0.80	5.64	1.82	bro	br_c	20.00	her
Pocilloporidae	*Stylophora mordax*	Pac	1	1	23.97	549.00	1.05	8.31	1.82	bro	br_c	60.51	her
Pocilloporidae	*Stylophora pistillata*	Pac	1	1	21.34	549.00	1.40	0.98	1.70	bro	br_c	51.00	her
Pocilloporidae	*Stylophora subseriata*	Pac	1	1	23.97	549.00	0.70	4.67	1.82	bro	br_c	60.51	her
Pocilloporidae	*Stylophora wellsi*	Pac	1	1	23.97	549.00	0.70	4.67	1.82	bro	br_c	60.51	her

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Pocilloporidae	*Madracis decactis*	Atl	2	2	14.28	316.53	2.20	51.65	2.68	bro	dig	10.00	her
Pocilloporidae	*Madracis formosa*	Atl	2	2	11.74	316.53	1.60	32.85	2.62	bro	col	10.23	her
Pocilloporidae	*Madracis pharensis*	Atl	2	2	14.28	330.00	2.10	45.58	2.68	bro	dig	45.75	her
Pocilloporidae	*Madracis senaria*	Atl	2	2	3.81	310.00	1.80	39.99	2.94	bro	enc	22.42	her
Pocilloporidae	*Stylophora mamillata*	Pac	2	2	3.81	549.00	1.00	7.75	2.94	bro	enc	10.00	her
Pocilloporidae	*Pocillopora ankeli*	Pac	2	3	23.97	116.34	1.00	69.12	1.82	spa	br_c	60.51	her
Pocilloporidae	*Pocillopora brevicornis*	Pac	2	3	23.97	116.34	0.90	59.51	1.82	spa	br_c	60.51	her
Pocilloporidae	*Pocillopora capitata*	Pac	2	3	26.82	116.34	0.40	18.80	2.84	spa	br_o	64.29	her
Pocilloporidae	*Pocillopora danae*	Pac	2	3	8.20	116.34	1.20	89.56	2.84	spa	br_o	100.00	her
Pocilloporidae	*Pocillopora effusa*	Pac	2	3	26.82	116.34	1.10	79.14	2.84	spa	br_o	200.00	her
Pocilloporidae	*Pocillopora elegans*	Pac	2	3	36.90	116.34	1.00	69.12	1.93	spa	br_c	76.38	her
Pocilloporidae	*Pocillopora eydouxi*	Pac	2	3	42.60	136.00	1.00	55.46	2.84	spa	br_o	100.00	her
Pocilloporidae	*Pocillopora fungiformis*	Pac	2	3	11.74	116.34	0.80	50.34	2.62	spa	col	200.00	her
Pocilloporidae	*Pocillopora indiania*	Pac	2	3	23.97	116.34	1.20	89.56	1.82	spa	br_c	100.00	her
Pocilloporidae	*Pocillopora inflata*	Pac	2	3	31.50	116.34	1.00	69.12	1.82	spa	br_c	70.12	her
Pocilloporidae	*Pocillopora kelleheri*	Pac	2	3	26.82	116.34	1.20	89.56	2.84	spa	br_o	64.29	her
Pocilloporidae	*Pocillopora ligulata*	Pac	2	3	14.50	116.34	0.80	50.34	1.82	spa	br_c	50.00	her
Pocilloporidae	*Pocillopora meandrina*	Pac	2	3	20.48	116.34	0.70	120.00	1.42	spa	br_c	100.00	her
Pocilloporidae	*Pocillopora molokensis*	Pac	2	3	23.97	116.34	1.30	100.35	1.82	spa	br_c	60.51	her
Pocilloporidae	*Pocillopora verrucosa*	Pac	2	3	26.31	39.40	0.70	76.07	1.82	spa	br_c	50.00	her
Pocilloporidae	*Pocillopora woodjonesi*	Pac	2	3	26.82	116.34	1.10	79.14	2.84	spa	br_o	64.29	her
Pocilloporidae	*Pocillopora zelli*	Pac	2	3	26.82	116.34	1.20	89.56	2.84	spa	br_o	64.29	her
Poritidae	*Porites annae*	Pac	1	1	18.00	207.94	1.10	34.89	1.23	spa	dig	110.00	gon

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Poritidae	*Porites australiensis*	Pac	1	1	12.46	245.00	1.40	72.00	1.33	spa	mas	80.51	gon
Poritidae	*Porites branneri*	Atl	1	1	18.00	743.68	1.80	11.64	1.38	bro	dig	98.19	gon
Poritidae	*Porites brighami*	Pac	1	1	7.61	743.68	1.50	8.98	1.32	bro	mas	10.00	gon
Poritidae	*Porites compressa*	Pac	1	1	21.33	207.94	1.60	45.00	1.35	spa	col	123.00	gon
Poritidae	*Porites cylindrica*	Pac	1	1	18.36	250.00	1.10	26.91	1.42	spa	col	1000.00	gon
Poritidae	*Porites evermanni*	Pac	1	1	11.60	207.94	1.00	30.47	1.35	spa	col	120.00	gon
Poritidae	*Porites furcata*	Atl	1	1	34.60	743.68	1.90	12.57	1.05	bro	br_c	139.75	gon
Poritidae	*Porites hawaiiensis*	Pac	1	1	7.61	743.68	0.50	1.89	1.32	bro	mas	61.68	gon
Poritidae	*Porites heronensis*	Pac	1	1	10.50	743.68	1.50	8.98	1.35	bro	col	73.40	gon
Poritidae	*Porites horizontalata*	Pac	1	1	18.00	207.94	1.70	64.76	1.38	spa	dig	98.19	gon
Poritidae	*Porites lobata*	Pac	1	1	9.16	207.94	1.10	58.70	1.38	spa	mas	685.00	gon
Poritidae	*Porites lutea*	Pac	1	1	14.00	207.94	1.30	67.20	1.28	spa	mas	400.00	gon
Poritidae	*Porites murrayensis*	Pac	1	1	7.61	743.68	1.00	5.05	1.32	bro	mas	20.00	gon
Poritidae	*Porites panamensis*	Pac	1	1	6.66	743.68	0.90	2.30	1.32	bro	mas	57.40	gon
Poritidae	*Porites porites*	Atl	1	1	16.88	743.68	2.50	10.00	0.94	bro	br_c	30.00	gon
Poritidae	*Porites rus*	Pac	1	1	15.24	207.94	0.80	22.19	1.38	spa	dig	500.00	gon
Poritidae	*Porites sillimaniani*	Pac	1	1	18.00	743.68	1.90	12.57	1.38	bro	dig	98.19	gon
Poritidae	*Porites solida*	Pac	1	1	13.46	207.94	1.60	59.42	1.19	spa	mas	83.94	gon
Poritidae	*Porites stephensoni*	Pac	1	1	7.61	743.68	1.30	7.33	1.32	bro	mas	10.00	gon
Poritidae	*Goniopora albiconus*	Pac	2	2	4.80	480.62	3.20	48.80	1.51	spa	enc	100.00	gon
Poritidae	*Goniopora burgosi*	Pac	2	2	7.61	480.62	1.70	19.87	1.32	spa	mas	61.68	gon
Poritidae	*Goniopora cellulosa*	Pac	2	2	7.61	480.62	4.10	69.40	1.32	spa	mas	61.68	gon
Poritidae	*Goniopora ciliatus*	Pac	2	2	14.79	480.62	3.80	62.30	1.35	spa	col	500.00	gon

Family	Species	Ocean	2 group	3 group	Growth rate (mm year-1)	Propagule size (µm)	Corallite size (mm)	Fecundity (egg polyp-1)	Skeletal density (g cm-3)	Mode of larva development	Growth form typical	Colony size (cm)	Sexual system
Poritidae	*Goniopora columna*	Pac	2	2	14.79	480.62	3.70	59.98	1.35	spa	col	88.32	gon
Poritidae	*Goniopora djiboutiensis*	Pac	2	2	14.79	480.62	4.70	84.27	1.35	spa	col	88.32	gon
Poritidae	*Goniopora eclipsensis*	Pac	2	2	14.79	480.62	3.10	46.65	1.35	spa	col	88.32	gon
Poritidae	*Goniopora fruticosa*	Pac	2	2	4.80	480.62	3.70	59.98	1.51	spa	enc	48.11	gon
Poritidae	*Goniopora lobata*	Pac	2	2	14.79	500.00	4.60	77.30	1.35	spa	col	88.32	gon
Poritidae	*Goniopora minor*	Pac	2	2	4.80	480.62	2.50	34.36	1.51	spa	enc	48.11	gon
Poritidae	*Goniopora norfolkensis*	Pac	2	2	4.80	462.00	2.40	34.29	1.51	spa	enc	48.11	gon
Poritidae	*Goniopora palmensis*	Pac	2	2	7.61	480.62	2.40	32.43	1.32	spa	mas	61.68	gon
Poritidae	*Goniopora pandoraensis*	Pac	2	2	14.79	480.62	2.70	38.33	1.35	spa	col	88.32	gon
Poritidae	*Goniopora pearsoni*	Pac	2	2	7.61	480.62	3.30	50.98	1.32	spa	mas	200.00	gon
Poritidae	*Goniopora pendulus*	Pac	2	2	7.61	480.62	5.60	108.09	1.32	spa	mas	61.68	gon
Poritidae	*Goniopora planulata*	Pac	2	2	14.79	480.62	3.10	46.65	1.35	spa	col	88.32	gon
Poritidae	*Goniopora polyformis*	Pac	2	2	18.00	480.62	5.90	116.41	1.38	spa	dig	98.19	gon
Poritidae	*Goniopora savignyi*	Pac	2	2	14.79	480.62	2.20	75.00	1.35	spa	col	88.32	gon
Poritidae	*Goniopora somaliensis*	Pac	2	2	4.80	480.62	3.10	46.65	1.51	spa	enc	200.00	gon
Poritidae	*Goniopora stokesi*	Pac	2	2	14.79	480.62	4.70	84.27	1.35	spa	col	10.00	gon
Poritidae	*Goniopora sultani*	Pac	2	2	14.79	480.62	7.80	173.10	1.35	spa	col	88.32	gon
Poritidae	*Goniopora tenella*	Pac	2	2	4.80	480.62	2.90	42.43	1.51	spa	enc	48.11	gon
Poritidae	*Goniopora tenuidens*	Pac	2	2	7.61	480.62	3.70	59.98	1.32	spa	mas	61.68	gon
Poritidae	*Porites astreoides*	Atl	2	2	3.72	525.00	1.60	15.33	1.54	bro	mas	55.00	gon

Appendix B: Supplemental information for Chapter 3

Table S1. Abundance through time and effect size, the percent of change in abundance (%) and Cohen's *d* effect size, of for each period at regional scale. "x" indicates extinction locally.

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2012/3	Bleaching percent change	Bleaching effect size	Multiple stressors percent change	Multiple stressors effect size
Montipora	Generalist	19.50	9.00	13.25	-54	0.96	-32.05	0.36
Acropora	Competitive	14.77	7.56	3.67	-49	0.73	-75.18	1.17
Favia	Stress-tolerant	8.30	3.74	3.44	-55	0.80	-58.56	0.83
Turbinaria	Competitive	6.80	3.06	2.60	-55	0.52	-61.68	0.59
Sinularia	Unknown	5.20	2.38	2.33	-54	0.50	-55.17	0.48
Favites	Stress-tolerant	4.91	3.94	3.04	-20	0.20	-38.04	0.42
Porites	Stress-tolerant	4.86	4.50	3.85	-7	0.06	-20.76	0.18
Cyphastrea	Stress-tolerant	3.50	0.72	0.96	-79	1.05	-72.62	0.95
Galaxea	Stress-tolerant	3.18	1.92	1.19	-40	0.51	-62.68	0.74
Sarchphyton	Unknown	2.43	4.12	1.13	69	0.29	-53.74	0.36
Goniastrea	Stress-tolerant	2.16	0.96	1.08	-56	0.58	-49.82	0.46
Goniopora	Unknown	1.70	0.70	0.46	-59	0.66	-73.11	0.86
Lobophyllia	Stress-tolerant	1.43	0.48	0.69	-66	0.62	-51.98	0.45
Pectinia	Unknown	1.25	0.46	0.23	-63	0.48	-81.67	0.69
Platygyra	Stress-tolerant	1.11	1.70	1.10	53	0.34	-0.85	0.01

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2012/3	Bleaching percent change	Bleaching effect size	Multiple stressors percent change	Multiple stressors effect size
Pocillopora	Weedy	0.98	0.20	0.23	-80	0.76	-76.55	0.73
Echinopora	Generalist	0.93	0.60	0.65	-36	0.22	-30.69	0.16
Astreopora	Stress-tolerant	0.86	1.02	0.42	18	0.08	-51.75	0.26
Symphyllia	Stress-tolerant	0.82	0.98	0.31	20	0.12	-61.81	0.50
Pachyseris	Generalist	0.77	0.48	0.35	-38	0.19	-54.17	0.28
Oxypora	Unknown	0.73	0.26	0.10	-64	0.38	-85.68	0.56
Millepora	Unknown	0.70	0.22	0.06	-69	0.35	-91.13	0.54
Merulina	Generalist	0.66	0.22	0.38	-67	0.46	-43.10	0.21
Fungiidae	Stress-tolerant	0.61	0.58	1.38	-5	0.04	124.07	0.21
Lobophytum	Unknown	0.57	0.52	0.10	-8	0.05	-81.67	0.59
Moseleya	Unknown	0.55	0.12	0.08	-78	0.43	-84.72	0.45
Pavona	Generalist	0.50	0.22	0.46	-56	0.32	-8.33	0.04
Echinophyllia	Stress-tolerant	0.45	0.46	0.38	1	0.00	-17.50	0.07
Montastrea	Stress-tolerant	0.43	0.18	0.75	-58	0.33	73.68	0.30
Leptastrea	Weedy	0.43	0.84	0.50	95	0.32	15.79	0.07
Stylophora	Weedy	0.41	0.02	0.04	-95	0.74	-89.81	0.65
Hydnophora	Generalist	0.32	0.30	0.23	-6	0.03	-27.98	0.13
Leptoria	Stress-tolerant	0.32	0.30	0.23	-6	0.02	-27.98	0.11
Isopora	Unknown	0.30	0.02	0.04	-93	0.52	-85.90	0.46
Mycedium	Generalist	0.27	0.04	0.29	-85	0.33	6.94	0.02
Psammocora	Generalist	0.23	0.44	0.25	94	0.27	10.00	0.03

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2012/3	Bleaching percent change	Bleaching effect size	Multiple stressors percent change	Multiple stressors effect size
Seriatopora	Weedy	0.20	0.06	0.04	-71	0.35	-79.63	0.43
Alveopora	Stress-tolerant	0.20	0.14	0.17	-32	0.13	-18.52	0.07
Acanthastrea	Stress-tolerant	0.18	0.14	0.33	-23	0.09	83.33	0.28
Plesiastrea	Stress-tolerant	0.16	0.06	0.04	-62	0.23	-73.81	0.26
Coscinaraea	Unknown	0.11	0.18	0.02	58	0.15	-81.67	0.32
Leptoseris	Unknown	0.09	0.26	0.00	186	0.27	x	0.45
Coeloseris	Unknown	0.07	0.04	0.06	-41	0.10	-8.33	0.02
Caryophyllia	Unknown	0.02	0.04	0.00	76	0.07	x	0.22
Oulophyllia	Stress-tolerant	0.02	0.12	0.06	428	0.32	175.00	0.19
Diploastrea	Stress-tolerant	0.00	0.00	0.04			x	0.29
Scolymia	Stress-tolerant	0.00	0.00	0.06			x	0.27
Stylocoeniella	Unknown	0.00	0.00	0.02			x	0.20
Average abundance		94.02	54.30	47.10	-42		-49.90	
Generic richness		45	45	46				

Table S2. Abundance through time and effect size, the percent of change in abundance (%) and Cohen's *d* effect size, of for each period at Nelly Bay-2m. "x" indicates extinction locally.

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Montipora	Generalist	35.00	13.20	30.00	14.83	-62	3.05	127	1.90	-58	2.80
Acropora	Competitive	25.80	5.60	17.17	4.50	-78	2.59	207	1.08	-83	2.82
Turbinaria	Competitive	12.20	3.00	4.17	4.00	-75	1.78	39	0.85	-67	1.57
Cyphastrea	Stress-tolerant	7.20	1.80	2.17	1.50	-75	1.78	20	0.17	-79	2.17
Porites	Stress-tolerant	4.60	2.20	1.67	1.00	-52	1.52	-24	0.24	-78	3.56
Favia	Stress-tolerant	4.60	1.20	1.17	0.83	-74	1.36	-3	0.02	-82	1.67
Galaxea	Stress-tolerant	4.00	1.20	1.33	1.00	-70	0.95	11	0.08	-75	1.12
Goniopora	Unknown	3.00	0.20	0.50	0.17	-93	1.18	150	0.59	-94	1.27
Favites	Stress-tolerant	2.00	2.60	1.00	0.00	30	0.24	-62	0.77	-100	1.41
Goniastrea	Stress-tolerant	1.60	0.80	2.50	0.33	-50	1.13	213	0.90	-79	1.78
Psammocora	Generalist	1.40	0.40	0.50	1.00	-71	0.80	25	0.14	-29	0.27
Lobophyllia	Stress-tolerant	1.00	0.00	0.00	0.00	-100	0.82			-100	0.87
Coscinaraea	Unknown	0.60	0.80	0.00	0.00	33	0.23	-100	1.43	-100	1.01
Plesiastrea	Stress-tolerant	0.60	0.00	0.17	0.00	-100	0.95	x	0.55	-100	1.01
Pavona	Generalist	0.40	0.00	0.17	0.17	-100	1.03	x	0.55	-58	0.49
Alveopora	Stress-tolerant	0.40	0.00	0.00	0.50	-100	1.03			25	0.14
Fungiidae	Stress-tolerant	0.20	0.00	0.17	0.00	-100	0.63	x	0.55	-100	0.67
Coeloseris	Unknown	0.20	0.00	0.00	0.00	-100	0.63			-100	0.67

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Hydnophora	Generalist	0.20	0.00	0.00	0.00	-100	0.63			-100	0.67
Merulina	Generalist	0.20	0.00	0.00	0.00	-100	0.63			-100	0.67
Moseleya	Unknown	0.20	0.00	0.00	0.00	-100	0.63			-100	0.67
Pectinia	Unknown	0.20	0.00	0.00	0.00	-100	0.63			-100	0.67
Symphyllia	Stress-tolerant	0.20	0.00	0.00	0.00	-100	0.63			-100	0.67
Platygyra	Stress-tolerant	0.20	0.80	1.33	0.17	300	0.89	67	0.46	-17	0.08
Leptastrea	Weedy	0.00	0.00	0.17	0.17			x	0.55	x	0.55
Leptoseris	Unknown	0.00	1.40	0.00	0.00	x	0.90	-100	0.96		
Montastrea	Stress-tolerant	0.00	0.40	0.00	0.00	x	0.63	-100	0.67		
Sarchphytum	Unknown	0.00	0.00	0.83	0.00			x	0.55		
Acanthastrea	Stress-tolerant	0.00	0.00	0.50	0.00			x	0.55		
Echinopora	Stress-tolerant	0.00	0.00	0.33	0.00			x	0.55		
Mycedium	Generalist	0.00	0.00	0.17	0.00			x	0.55		
Generic richness		24	15	20	14		_		_		_

Table S3. Abundance through time and effect size, the percent of change in abundance (%) and Cohen's *d* effect size, of for each period at Nelly Bay-6m. "x" indicates extinction locally.

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Montipora	Generalist	32.83	19.71	29.00	3.83	-40	1.78	47	1.80	-88	3.61
Turbinaria	Competitive	24.83	11.86	21.00	8.50	-52	2.54	77	1.60	-66	3.00
Acropora	Competitive	23.33	12.43	21.00	3.50	-47	2.38	69	1.23	-85	4.77
Favia	Stress-tolerant	9.67	0.71	4.00	3.50	-93	2.14	460	2.08	-64	1.20
Cyphastrea	Stress-tolerant	8.00	0.43	3.67	2.00	-95	4.46	756	1.06	-75	2.58
Galaxea	Stress-tolerant	3.50	1.86	4.17	0.00	-47	1.21	124	1.73	-100	3.59
Goniopora	Unknown	2.50	0.43	1.00	0.67	-83	1.49	133	0.48	-73	1.51
Goniastrea	Stress-tolerant	1.50	0.14	0.00	0.00	-90	1.00	-100	0.51	-100	1.07
Favites	Stress-tolerant	1.50	0.57	2.17	3.33	-62	0.57	279	1.17	122	0.76
Porites	Stress-tolerant	1.17	0.29	1.50	0.83	-76	1.17	425	1.12	-29	0.31
Fungiidae	Stress-tolerant	1.00	0.43	2.50	0.33	-57	0.68	483	1.89	-67	0.78
Montastrea	Stress-tolerant	0.83	0.29	0.00	0.00	-66	0.63	-100	0.79	-100	1.01
Hydnophora	Generalist	0.67	0.00	0.67	0.00	-100	1.21	x	0.96	-100	1.15
Astreopora	Stress-tolerant	0.67	0.00	0.00	0.00	-100	0.61			-100	0.58
Pachyseris	Generalist	0.67	0.00	1.33	0.17	-100	0.61	x	1.31	-75	0.42
Oxypora	Unknown	0.50	0.00	0.00	0.00	-100	0.89			-100	0.85
Psammocora	Generalist	0.50	0.71	0.17	0.17	43	0.20	-77	0.57	-67	0.51
Moseleya	Unknown	0.50	0.00	0.17	0.33	-100	0.89	x	0.61	-33	0.20

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Pectinia	Unknown	0.33	0.29	0.17	0.00	-14	0.07	-42	0.19	-100	0.91
Isopora	Unknown	0.33	0.00	0.00	0.00	-100	0.61			-100	0.58
Alveopora	Stress-tolerant	0.33	0.14	0.17	0.33	-57	0.31	17	0.06	0	0.00
Plesiastrea	Stress-tolerant	0.17	0.00	1.00	0.00	-100	0.61	x	1.17	-100	0.58
Merulina	Generalist	0.17	0.00	0.50	0.00	-100	0.61	x	0.89	-100	0.58
Caryophyllia	Unknown	0.17	0.29	0.17	0.00	71	0.19	-42	0.19	-100	0.58
Coscinaraea	Unknown	0.17	0.00	0.00	0.00	-100	0.61			-100	0.58
Echinopora	Generalist	0.17	0.00	0.00	0.00	-100	0.61			-100	0.58
Pocillopora	Weedy	0.17	0.00	0.00	0.00	-100	0.61			-100	0.58
Platygyra	Stress-tolerant	0.17	0.71	0.00	0.33	329	0.57	-100	0.77	100	0.36
Leptastrea	Weedy	0.17	0.00	0.83	0.33	-100	0.61	x	1.26	100	0.26
Stylophora	Weedy	0.17	0.00	0.00	0.33	-100	0.61			100	0.26
Sarchphyton	Unknown	0.00	0.29	0.83	1.33	x	0.79	192	0.57	x	0.87
Lobophytum	Unknown	0.00	0.00	0.00	0.17					x	0.58
Sinularia	Unknown	0.00	0.00	0.00	0.33					x	0.58
Stylocoeniella	Unknown	0.00	0.00	0.00	0.17					x	0.58
Symphyllia	Stress-tolerant	0.00	0.00	0.67	0.00			x	1.21		
Mycedium	Generalist	0.00	0.00	0.33	0.00			x	0.96		
Pavona	Generalist	0.00	0.00	0.83	0.00			x	0.93		
Seriatopora	Weedy	0.00	0.00	0.67	0.00			x	0.82		
Leptoria	Stress-tolerant	0.00	0.29	0.00	0.00	x	0.79	-100	0.79		

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Leptoseris	Unknown	0.00	0.00	0.17	0.00			x	0.61		
Generic richness		30	19	26	20						

Table S4. Abundance through time and effect size, the percent of change in abundance (%) and Cohen's *d* effect size, of for each period at Geoffrey Bay-2m. "x" indicates extinction locally.

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Montipora	Generalist	37.50	10.00	38.17	41.50	-73	4.23	282	3.75	11	0.32
Acropora	Competitive	28.83	6.00	13.17	4.17	-79	2.33	119	1.07	-86	2.76
Turbinaria	Competitive	8.50	1.25	5.00	2.00	-85	1.27	300	1.34	-76	1.27
Galaxea	Stress-tolerant	6.50	2.00	1.33	1.50	-69	1.98	-33	0.45	-77	2.17
Favia	Stress-tolerant	5.33	0.75	1.17	0.67	-86	3.45	56	0.43	-88	4.15
Cyphastrea	Stress-tolerant	5.00	0.25	1.00	1.33	-95	1.35	300	0.72	-73	1.15
Porites	Stress-tolerant	4.67	2.00	2.17	2.33	-57	0.98	8	0.09	-50	0.88
Favites	Stress-tolerant	2.67	0.75	1.00	1.17	-72	1.21	33	0.15	-56	1.01
Stylophora	Weedy	0.67	0.00	0.00	0.00	-100	1.63			-100	1.83
Lobophyllia	Stress-tolerant	0.67	0.00	0.00	0.00	-100	0.82			-100	0.91
Pocillopora	Weedy	0.67	0.00	0.00	0.00	-100	0.82			-100	0.91
Goniopora	Unknown	0.50	0.00	0.67	0.67	-100	1.15	x	1.03	33	0.24
Platygyra	Stress-tolerant	0.50	0.00	0.17	0.33	-100	0.76	x	0.52	-33	0.20
Moseleya	Unknown	0.33	0.00	0.67	0.00	-100	0.82	x	0.52	-100	0.91
Sarchphyton	Unknown	0.33	0.00	0.33	0.00	-100	0.52	x	0.82	-100	0.58
Goniastrea	Stress-tolerant	0.33	0.00	2.83	0.33	-100	0.82	x	0.95	0	0.00
Hydnophora	Generalist	0.17	0.00	0.33	0.00	-100	0.52	x	0.82	-100	0.58
Lobophytum	Unknown	0.17	0.00	0.00	0.00	-100	0.52			-100	0.58

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Oxypora	Unknown	0.17	0.00	0.00	0.00	-100	0.52			-100	0.58
Pachyseris	Generalist	0.17	0.00	0.00	0.00	-100	0.52			-100	0.58
Sinularia	Unknown	0.17	0.00	0.00	0.00	-100	0.52			-100	0.58
Fungiidae	Stress-tolerant	0.17	0.00	0.00	0.33	-100	0.52			100	0.36
Leptoria	Stress-tolerant	0.00	0.25	0.00	0.50	x	0.82	-100	0.82	x	0.85
Psammocora	Generalist	0.00	0.50	0.17	0.50	x	1.41	-67	0.70	x	0.85
Acanthastrea	Stress-tolerant	0.00	0.00	0.00	0.17					-100	0.58
Seriatopora	Weedy	0.00	0.75	0.00	0.00	x	1.28	-100	1.28		
Montastrea	Stress-tolerant	0.00	0.00	0.33	0.00			x	0.82		
Leptastrea	Weedy	0.00	0.00	0.17	0.00			x	0.52		
Pavona	Generalist	0.00	0.00	0.17	0.00			x	0.52		
Plesiastrea	Stress-tolerant	0.00	0.00	0.17	0.00			x	0.52		
Generic richness		22	11	19	15						

Table S5. Abundance through time and effect size, the percent of change in abundance (%) and Cohen's *d* effect size, of for each period at Geoffrey Bay-6m. "x" indicates extinction locally.

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Favia	Stress-tolerant	15.50	6.50	5.33	7.33	-58	1.36	-18	0.23	-53	1.29
Montipora	Generalist	12.50	3.88	15.67	30.83	-69	1.37	304	2.02	147	0.67
Acropora	Competitive	10.50	5.13	5.67	9.83	-51	0.61	11	0.22	-6	0.05
Sarchphyton	Unknown	6.17	2.63	3.67	1.50	-57	1.21	40	0.33	-76	1.71
Favites	Stress-tolerant	6.00	3.75	6.00	3.00	-38	0.55	60	0.62	-50	0.77
Turbinaria	Competitive	5.67	5.13	6.83	5.17	-10	0.13	33	0.53	-9	0.10
Galaxea	Stress-tolerant	4.33	2.13	3.83	4.67	-51	0.81	80	0.77	8	0.07
Pachyseris	Generalist	3.67	0.88	2.67	2.00	-76	0.95	205	0.76	-45	0.54
Sinularia	Unknown	3.00	1.63	5.50	1.17	-46	0.63	238	1.77	-61	0.93
Oxypora	Unknown	2.83	0.25	0.50	0.67	-91	1.62	100	0.39	-76	1.17
Moseleya	Unknown	2.83	0.50	0.33	0.33	-82	1.21	-33	0.32	-88	1.16
Pectinia	Unknown	2.67	0.75	1.17	0.83	-72	0.81	56	0.34	-69	0.74
Merulina	Generalist	2.67	0.25	0.50	2.67	-91	1.62	100	0.33	0	0.00
Lobophyllia	Stress-tolerant	2.50	0.25	0.17	0.33	-90	2.01	-33	0.19	-87	1.67
Cyphastrea	Stress-tolerant	2.33	1.25	1.67	2.00	-46	0.64	33	0.17	-14	0.19
Goniopora	Unknown	2.17	1.75	2.17	1.00	-19	0.22	24	0.23	-54	0.59
Goniastrea	Stress-tolerant	1.50	0.00	0.50	0.00	-100	1.32	x	0.93	-100	1.20
Pocillopora	Weedy	1.50	0.00	0.33	0.00	-100	1.03	x	1.00	-100	0.94

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Porites	Stress-tolerant	1.50	3.50	4.67	2.33	133	0.95	33	0.51	56	0.80
Mycedium	Generalist	1.50	0.25	0.33	1.00	-83	0.80	33	0.13	-33	0.27
Lobophytum	Unknown	1.33	0.25	0.00	0.00	-81	1.14	-100	0.46	-100	1.56
Fungiidae	Stress-tolerant	1.17	1.00	3.67	9.50	-14	0.16	267	1.65	714	1.04
Symphyllia	Stress-tolerant	1.00	1.00	0.33	0.17	0	0.00	-67	0.69	-83	1.20
Stylophora	Weedy	1.00	0.00	0.17	0.00	-100	1.22	x	0.63	-100	1.12
Platygyra	Stress-tolerant	1.00	1.63	0.67	1.50	63	0.43	-59	0.66	50	0.51
Echinophyllia	Stress-tolerant	0.67	1.00	0.17	1.00	50	0.21	-83	0.67	50	0.20
Leptastrea	Weedy	0.50	0.88	1.00	0.17	75	0.45	14	0.11	-67	0.69
Alveopora	Stress-tolerant	0.50	0.00	0.00	0.17	-100	0.63			-67	0.37
Hydnophora	Generalist	0.33	0.63	0.67	1.17	88	0.44	7	0.05	250	0.59
Echinopora	Generalist	0.33	0.13	0.00	0.83	-63	0.49	-100	0.46	150	0.42
Isopora	Unknown	0.17	0.00	0.00	0.00	-100	0.63			-100	0.58
Leptoseris	Unknown	0.17	0.00	0.00	0.00	-100	0.63			-100	0.58
Seriatopora	Weedy	0.17	0.00	0.00	0.00	-100	0.63			-100	0.58
Montastrea	Stress-tolerant	0.00	0.63	0.00	1.33	x	1.10	-100	1.10	x	1.56
Oulophyllia	Stress-tolerant	0.00	0.00	0.00	0.33					x	0.91
Leptoria	Stress-tolerant	0.00	0.25	0.00	0.83	x	0.71	-100	0.71	x	0.74
Plesiastrea	Stress-tolerant	0.00	0.00	0.50	0.33			x	0.93	x	0.58
Astreopora	Stress-tolerant	0.00	0.38	0.00	0.17	x	0.66	-100	0.66	x	0.58
Psammocora	Generalist	0.00	0.63	0.00	0.17	x	0.58	-100	0.58	x	0.58

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2000	Abundance 2013	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Caryophyllia	Unknown	0.00	0.00	0.33	0.00			x	1.00		
Pavona	Generalist	0.00	0.00	0.17	0.00			x	0.63		
Coscinaraea	Unknown	0.00	0.38	0.17	0.00	x	0.66	-56	0.33		
Generic richness		33	31	31	32						

Table S6. Abundance through time and effect size, the percent of change in abundance (%) and Cohen's *d* effect size, of for each period at Little Pioneer Bay-2m. "x" indicates extinction locally.

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Sinularia	Unknown	16.83	3.14	11.33	8.83	8.33	-81	2.72	-22	0.33	-50	1.26
Porites	Stress-tolerant	12.50	14.00	5.83	27.33	12.83	12	0.15	369	2.46	3	0.03
Favites	Stress-tolerant	11.00	6.86	7.17	11.33	5.17	-38	1.06	58	1.39	-53	1.44
Montipora	Generalist	9.33	2.00	1.33	1.83	2.83	-79	2.44	38	0.37	-70	2.14
Favia	Stress-tolerant	8.50	3.57	4.17	5.17	4.00	-58	1.25	24	0.26	-53	1.14
Sarchphyton	Unknown	5.33	11.00	1.67	4.17	1.50	106	0.53	150	0.83	-72	0.60
Goniastrea	Stress-tolerant	5.00	2.00	5.67	7.67	4.00	-60	1.35	35	0.48	-20	0.32
Acropora	Competitive	3.33	0.71	4.00	16.00	4.67	-79	1.43	300	2.80	40	0.48
Millepora	Unknown	3.17	0.00	0.00	0.00	0.00	-100	1.53			-100	1.46
Goniopora	Unknown	3.00	0.43	0.83	1.83	0.17	-86	2.49	120	0.68	-94	3.01
Galaxea	Stress-tolerant	2.83	2.29	0.83	2.67	1.33	-19	0.22	220	0.53	-53	0.77
Pectinia	Unknown	2.50	0.29	0.50	3.00	0.50	-89	2.04	500	2.89	-80	1.75
Lobophyllia	Stress-tolerant	2.50	1.71	1.00	3.33	1.17	-31	0.40	233	2.02	-53	0.98
Echinopora	Generalist	2.50	1.71	0.33	3.83	3.50	-31	0.28	1050	1.32	40	0.29
Pocillopora	Weedy	2.17	0.00	0.00	0.67	0.67	-100	1.75	x	1.15	-69	0.96
Cyphastrea	Stress-tolerant	2.00	0.29	0.83	1.33	0.17	-86	1.68	60	0.39	-92	1.76
Fungiidae	Stress-tolerant	1.50	1.14	0.00	1.33	0.33	-24	0.25	x	1.83	-78	0.90
Merulina	Generalist	1.33	0.29	0.00	0.33	0.33	-79	1.34	x	0.91	-75	1.07

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Echinophyllia	Stress-tolerant	1.17	0.00	0.17	1.67	0.33	-100	0.85	900	1.49	-71	0.54
Montastrea	Stress-tolerant	1.17	0.00	5.67	2.17	1.67	-100	1.18	-62	0.79	43	0.35
Platygyra	Stress-tolerant	1.17	4.00	8.33	3.00	1.67	243	1.15	-64	1.00	43	0.32
Oxypora	Unknown	1.00	0.00	0.00	0.00	0.00	-100	0.74			-100	0.71
Symphyllia	Stress-tolerant	1.00	1.86	5.33	1.67	0.83	86	0.65	-69	1.14	-17	0.18
Pavona	Generalist	0.83	0.57	0.33	3.17	1.83	-31	0.30	850	1.26	120	0.93
Pachyseris	Generalist	0.83	0.71	0.00	0.17	0.00	-14	0.10	x	0.58	-100	0.89
Lobophytum	Unknown	0.83	0.14	0.00	0.00	0.50	-83	0.62			-40	0.26
Acanthastrea	Stress-tolerant	0.50	0.00	0.17	0.17	0.00	-100	0.89	0	0.00	-100	0.85
Astreopora	Stress-tolerant	0.33	2.00	0.50	1.50	0.67	500	1.06	200	0.95	100	0.41
Mycedium	Generalist	0.33	0.00	0.17	0.17	0.17	-100	0.61	0	0.00	-50	0.26
Leptastrea	Weedy	0.33	2.14	1.67	2.00	0.33	543	1.27	20	0.31	0	0.00
Stylophora	Weedy	0.17	0.00	0.00	0.50	0.00	-100	0.61	x	0.85	-100	0.58
Alveopora	Stress-tolerant	0.17	0.00	0.00	0.17	0.00	-100	0.61	x	0.58	-100	0.58
Hydnophora	Generalist	0.17	0.14	0.17	0.33	0.00	-14	0.06	100	0.36	-100	0.58
Leptoria	Stress-tolerant	0.17	0.14	0.00	0.00	0.00	-14	0.06			-100	0.58
Leptoseris	Unknown	0.17	0.14	0.00	0.00	0.00	-14	0.06			-100	0.58
Coeloseris	Unknown	0.17	0.29	0.67	1.17	0.33	71	0.19	75	0.23	100	0.36
Isopora	Unknown	0.17	0.00	0.00	0.50	0.17	-100	0.61	x	1.29	0	0.00
Seriatopora	Weedy	0.00	0.00	0.00	0.50	0.33			x	1.29	x	0.91
Turbinaria	Competitive	0.00	0.14	0.00	0.00	0.33	x	0.51			x	0.91

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Diploastrea	Stress-tolerant	0.00	0.00	0.00	0.00	0.17					x	0.58
Oulophyllia	Stress-tolerant	0.00	0.14	0.00	0.00	0.00	x	0.51				
Plesiastrea	Stress-tolerant	0.00	0.14	0.00	0.00	0.00	x	0.51				
Psammocora	Generalist	0.00	0.14	0.00	0.00	0.00	x	0.51				
Generic richness		37	31	25	33	31						

Table S7. Abundance through time and effect size, the percent of change in abundance (%) and Cohen's *d* effect size, of for each period at Little Pioneer Bay-6m. "x" indicates extinction locally.

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Favia	Stress-tolerant	15.17	10.29	6.00	16.83	10.67	-32	0.84	181	1.65	-30	0.65
Sinularia	Unknown	14.50	6.57	7.17	19.00	7.83	-55	1.78	165	2.63	-46	1.17
Montipora	Generalist	11.50	5.86	7.00	4.33	5.33	-49	1.41	-38	0.46	-54	1.63
Favites	Stress-tolerant	10.83	10.29	7.17	8.83	9.00	-5	0.10	23	0.32	-17	0.33
Porites	Stress-tolerant	9.50	9.57	7.50	16.00	9.67	1	0.02	113	1.59	2	0.07
Astreopora	Stress-tolerant	5.17	4.71	2.83	6.67	2.50	-9	0.18	135	0.77	-52	0.97
Goniastrea	Stress-tolerant	5.00	2.57	1.83	1.33	2.83	-49	0.82	-27	0.45	-43	0.71
Sarchphyton	Unknown	4.67	10.57	4.00	6.50	4.67	127	0.91	63	0.85	0	0.00
Lobophyllia	Stress-tolerant	3.67	1.29	3.33	2.83	4.00	-65	1.18	-15	0.12	9	0.16
Pectinia	Unknown	3.50	1.86	3.83	5.33	0.50	-47	0.74	39	0.46	-86	1.76
Platygyra	Stress-tolerant	3.50	2.43	1.67	2.67	4.33	-31	0.66	60	0.55	24	0.55
Symphyllia	Stress-tolerant	3.00	2.86	1.00	1.50	0.67	-5	0.08	50	0.31	-78	1.41
Pavona	Generalist	2.50	0.71	1.83	2.00	1.50	-71	1.24	9	0.08	-40	0.55
Echinopora	Generalist	2.33	0.86	0.83	3.33	0.67	-63	1.09	300	0.96	-71	1.38
Galaxea	Stress-tolerant	2.33	1.71	1.17	2.00	1.00	-27	0.37	71	0.80	-57	1.01
Cyphastrea	Stress-tolerant	2.17	1.00	1.00	1.17	0.17	-54	0.68	17	0.12	-92	1.85
Millepora	Unknown	1.83	1.57	0.33	0.67	0.50	-14	0.12	100	0.28	-73	0.98
Leptastrea	Weedy	1.67	2.71	1.67	1.67	2.00	63	0.52	0	0.00	20	0.20

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Goniopora	Unknown	1.50	1.29	0.67	0.17	0.83	-14	0.18	-75	0.77	-44	0.52
Acropora	Competitive	1.33	1.14	2.50	2.83	2.00	-14	0.22	13	0.17	50	0.63
Echinophyllia	Stress-tolerant	1.33	1.86	4.33	0.00	1.50	39	0.25	-100	3.12	13	0.08
Leptoria	Stress-tolerant	1.17	0.43	0.17	0.00	0.50	-63	0.44	-100	0.58	-57	0.38
Oxypora	Unknown	0.83	1.00	0.67	0.17	0.17	20	0.11	-75	0.77	-80	0.57
Montastrea	Stress-tolerant	0.83	0.00	6.00	0.83	1.50	-100	0.77	-86	1.40	80	0.41
Pocillopora	Weedy	0.67	0.29	0.00	0.33	0.50	-57	0.58	x	0.91	-25	0.20
Turbinaria	Competitive	0.67	0.86	0.83	0.17	0.83	29	0.18	-80	0.89	25	0.18
Acanthastrea	Stress-tolerant	0.67	0.14	0.17	0.17	0.67	-79	1.17	0	0.00	0	0.00
Fungiidae	Stress-tolerant	0.50	0.57	1.50	1.17	0.50	14	0.10	-22	0.28	0	0.00
Seriatopora	Weedy	0.33	0.00	0.00	0.17	0.00	-100	0.61	x	0.58	-100	0.58
Pachyseris	Generalist	0.33	1.71	1.17	0.83	0.67	414	1.40	-29	0.25	100	0.49
Mycedium	Generalist	0.17	0.00	0.00	0.17	1.17	-100	0.61	x	0.58	600	0.86
Leptoseris	Unknown	0.17	0.71	0.17	0.17	0.00	329	0.88	0	0.00	-100	0.58
Moseleya	Unknown	0.17	0.29	0.00	0.17	0.00	71	0.26	x	0.58	-100	0.58
Hydnophora	Generalist	0.17	0.14	0.17	0.00	0.50	-14	0.06	-100	0.58	200	0.51
Alveopora	Stress-tolerant	0.17	0.86	0.17	0.17	0.33	414	1.19	0	0.00	100	0.36
Oulophyllia	Stress-tolerant	0.17	0.71	0.33	0.17	0.17	329	0.88	-50	0.36	0	0.00
Coeloseris	Unknown	0.17	0.00	0.17	0.50	0.17	-100	0.61	200	0.51	0	0.00
Lobophytum	Unknown	0.17	0.43	0.17	0.33	0.17	157	0.41	100	0.36	0	0.00
Scolymia	Stress-tolerant	0.00	0.00	0.00	0.00	0.50					x	0.85

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Coscinaraea	Unknown	0.00	0.29	0.17	0.83	0.17	x	0.79	400	0.57	x	0.58
Diploastrea	Stress-tolerant	0.00	0.00	0.00	0.00	0.17					x	0.58
Psammocora	Generalist	0.00	0.57	0.17	0.00	0.00	x	0.98	-100	0.58		
Merulina	Generalist	0.00	0.57	0.17	0.17	0.00	x	0.98	0	0.00		
Plesiastrea	Stress-tolerant	0.00	0.29	0.00	0.33	0.00	x	0.79	x	0.58		
Stylophora	Weedy	0.00	0.14	0.00	0.00	0.00	x	0.51				
Isopora	Unknown	0.00	0.00	0.00	0.83	0.00			x	1.20		
Caryophyllia	Unknown	0.00	0.00	0.17	0.17	0.00			0	0.00		
Generic richness		38	39	38	40	38						

Table S8. Abundance through time and effect size, the percent of change in abundance (%) and Cohen's *d* effect size, of for each period at Southeast Pelorus -4m. "x" indicates extinction locally.

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Acropora	Competitive	12.67	13.50	6.33	30.83	0.00	7	0.14	387	3.02	-100	2.34
Montipora	Generalist	6.33	10.17	20.17	17.17	4.50	61	1.28	-15	0.76	-29	0.73
Sinularia	Unknown	2.33	2.83	0.00	9.00	0.00	21	0.23	x	2.04	-100	2.02
Favia	Stress-tolerant	2.17	2.33	0.83	2.83	0.50	8	0.09	240	1.16	-77	1.12
Favites	Stress-tolerant	2.17	3.50	2.83	5.00	0.83	62	0.77	76	1.32	-62	1.07
Porites	Stress-tolerant	1.83	1.50	5.17	5.00	1.17	-18	0.37	-3	0.06	-36	0.89
Pocillopora	Weedy	1.17	0.33	0.00	1.00	0.00	-71	1.06	x	1.58	-100	2.19
Isopora	Unknown	1.17	0.00	0.17	0.33	0.00	-100	1.12	100	0.36	-100	1.12
Goniastrea	Stress-tolerant	1.17	0.83	2.67	0.83	0.50	-29	0.31	-69	0.89	-57	0.73
Leptoria	Stress-tolerant	0.83	0.33	0.17	0.50	0.00	-60	1.07	200	0.69	-100	2.89
Lobophytum	Unknown	0.83	1.17	0.00	0.00	0.00	40	0.34			-100	1.20
Platygyra	Stress-tolerant	0.83	1.50	2.00	1.33	0.33	80	0.52	-33	0.58	-60	0.64
Sarchphyton	Unknown	0.67	3.17	0.00	14.33	0.00	375	1.12	x	3.40	-100	0.78
Plesiastrea	Stress-tolerant	0.50	0.00	0.17	0.00	0.00	-100	0.58	-100	0.58	-100	0.58
Symphyllia	Stress-tolerant	0.50	0.50	0.50	2.33	0.33	0	0.00	367	1.01	-33	0.31
Merulina	Generalist	0.33	0.17	0.00	0.17	0.00	-50	0.36	x	0.58	-100	0.91
Hydnophora	Generalist	0.33	0.33	0.00	0.17	0.00	0	0.00	x	0.58	-100	0.91
Seriatopora	Weedy	0.33	0.00	0.00	0.00	0.00	-100	0.91			-100	0.91
Stylophora	Weedy	0.33	0.00	0.00	0.00	0.00	-100	0.91			-100	0.91

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Goniopora	Unknown	0.33	0.33	0.00	0.00	0.00	0	0.00			-100	0.91
Montastrea	Stress-tolerant	0.33	0.00	3.67	0.00	0.33	-100	0.91	-100	2.51	0	0.00
Leptastrea	Weedy	0.33	0.17	0.33	0.33	0.33	-50	0.26	0	0.00	0	0.00
Acanthastrea	Stress-tolerant	0.17	0.67	1.33	0.33	0.67	300	0.64	-75	1.46	300	0.77
Coscinaraea	Unknown	0.17	0.00	0.00	0.33	0.00	-100	0.58	x	0.91	-100	0.58
Astreopora	Stress-tolerant	0.17	0.17	0.33	0.00	0.00	0	0.00	-100	0.91	-100	0.58
Leptoseris	Unknown	0.17	0.00	0.00	0.17	0.00	-100	0.58	x	0.58	-100	0.58
Echinopora	Generalist	0.17	0.17	0.00	0.17	0.00	0	0.00	x	0.58	-100	0.58
Lobophyllia	Stress-tolerant	0.17	0.00	0.33	0.17	0.00	-100	0.58	-50	0.36	-100	0.58
Cyphastrea	Stress-tolerant	0.17	0.67	0.50	0.17	0.33	300	0.55	-67	0.51	100	0.36
Psammocora	Generalist	0.00	0.17	0.00	0.17	0.17	x	0.58	x	0.58	x	0.58
Coeloseris	Unknown	0.00	0.00	0.17	1.67	0.00			900	1.66		
Millepora	Unknown	0.00	0.00	0.00	0.17	0.00			x	0.58		
Oulophyllia	Stress-tolerant	0.00	0.00	0.00	0.50	0.00			x	0.58		
Galaxea	Stress-tolerant	0.00	0.33	0.67	0.33	0.00	x	0.58	-50	0.36		
Fungiidae	Stress-tolerant	0.00	0.33	0.00	0.00	0.00	x	0.58				
Turbinaria	Competitive	0.00	0.17	0.00	0.00	0.00	x	0.58				
Generic richness		29	25	19	27	12						

Table S9. Abundance through time and effect size, the percent of change in abundance (%) and Cohen's *d* effect size, of for each period at Southeast Pelorus -6m. "x" indicates extinction locally.

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Acropora	Competitive	13.67	17.33	19.40	26.83	0.67	27	0.60	38	0.75	-95	4.17
Montipora	Generalist	7.67	9.83	24.20	31.50	2.33	28	0.30	30	0.63	-70	1.24
Echinopora	Generalist	2.67	1.67	1.60	0.83	0.17	-38	0.56	-48	0.57	-94	2.82
Sinularia	Unknown	2.67	3.50	4.20	3.00	1.00	31	0.17	-29	0.35	-63	0.89
Pocillopora	Weedy	1.67	1.00	0.40	1.33	0.67	-40	0.60	233	1.1	-60	1.87
Platygyra	Stress-tolerant	1.67	1.50	1.00	2.50	0.17	-10	0.13	150	1.02	-90	1.69
Lobophytum	Unknown	1.67	2.17	0.00	0.00	0.00	30	0.34			-100	1.50
Sarcophyton	Unknown	1.33	2.17	7.60	5.33	0.00	63	0.53	-30	0.69	-100	4.32
Seriatopora	Weedy	1.33	0.00	0.00	0.00	0.00	-100	4.32			-100	4.32
Favia	Stress-tolerant	1.33	1.67	1.40	1.17	0.00	25	0.24	-17	0.19	-100	2.16
Stylophora	Weedy	1.33	0.00	0.40	0.33	0.00	-100	1.63	-17	0.09	-100	1.63
Porites	Stress-tolerant	1.33	0.33	3.60	2.67	0.67	-75	0.76	-26	0.44	-50	0.47
Galaxea	Stress-tolerant	1.00	3.67	2.00	3.33	0.00	267	0.95	67	0.71	-100	1.87
Hydnophora	Generalist	0.67	1.00	0.80	1.50	0.17	50	0.34	88	0.44	-75	1.08
Isopora	Unknown	0.67	0.17	0.00	0.50	0.17	-75	0.71	x	0.8	-75	0.71
Symphyllia	Stress-tolerant	0.67	0.83	0.20	0.33	0.50	25	0.14	67	0.27	-25	0.22
Favites	Stress-tolerant	0.33	1.00	3.40	2.00	1.83	200	0.60	-41	0.84	450	1.45
Lobophyllia	Stress-tolerant	0.33	0.17	0.20	0.00	0.00	-50	0.36	-100	0.67	-100	1.08
Leptoria	Stress-tolerant	0.33	0.67	1.00	0.50	0.00	100	0.62	-50	0.55	-100	1.08

Genus/Family	Adaptive group	Abundance Mar-98	Abundance Oct-98	Abundance 2001	Abundance 2005	Abundance 2012	Bleaching percent change	Bleaching effect size	Recover percent change	Recover effect size	Multiple stressors percent change	Multiple stressors effect size
Merulina	Generalist	0.33	0.33	0.20	0.17	0.00	0	0.00	-17	0.08	-100	1.08
Millepora	Unknown	0.33	0.00	0.00	0.00	0.00	-100	1.08			-100	1.08
Echinophyllia	Stress-tolerant	0.33	0.33	0.20	0.00	0.17	0	0.00	-100	0.67	-50	0.36
Leptastrea	Weedy	0.33	0.00	0.20	0.67	0.67	-100	1.08	233	0.96	100	0.31
Acanthastrea	Stress-tolerant	0.00	0.33	1.00	0.33	1.17	x	0.76	-67	0.74	x	1.83
Montastrea	Stress-tolerant	0.00	0.00	0.40	0.17	1.17			-58	0.49	x	1.40
Goniastrea	Stress-tolerant	0.00	1.00	0.80	0.83	0.67	x	1.08	4	0.03	x	0.65
Goniopora	Unknown	0.00	0.50	0.00	0.33	0.17	x	0.71	x	0.87	x	0.48
Cyphastrea	Stress-tolerant	0.00	0.00	0.40	0.67	0.17			67	0.38	x	0.48
Pavona	Generalist	0.00	0.33	0.00	0.00	0.17	x	0.76			x	0.48
Caryophyllia	Unknown	0.00	0.00	0.20	0.00	0.00			-100	0.67		
Fungiidae	Stress-tolerant	0.00	0.67	0.20	0.17	0.00	x	0.65	-17	0.08		
Psammocora	Generalist	0.00	0.33	0.00	0.00	0.00	x	0.76				
Oxypora	Unknown	0.00	0.67	0.00	0.00	0.00	x	0.48				
Turbinaria	Competitive	0.00	0.17	0.00	0.00	0.00	x	0.48				
Generic richness		23	27	25	24	19						

Appendix C: Publications arising during candidature

Publications derived from thesis chapters

Madin JS, Anderson KD, Andreasen MH, Bridge TCL, Cairns SD, Connolly SR, Darling ES, Diaz M, Falster DS, Franklin EC, Gates RD, Hoogenboom MO, Huang D, Keith SA, Kosnik MA, **Kuo C-Y**, Lough JM, Lovelock CE, Luiz O, Martinelli J, Mizerek T, Pandolfi JM, Pochon X, Pratchett MS, Putnam HM, Roberts TE, Stat M, Wallace CC, Widman E, Baird AH (2016) The Coral Trait Database, a curated database of trait information for coral species from the global oceans. Scientific Data 3:160017. doi:10.1038/sdata.2017.17

Other peer-reviewed articles published during PhD candidature

Hughes TP, Kerry J, Álvarez-Noriega M, Álvarez-Romero J, Anderson K, Baird A, Babcock R, Beger M, Bellwood D, Berkelmans R, Bridge T, Butler I, Byrne M, Cantin N, Comeau S, Connolly S, Cumming G, Dalton S, Diaz-Pulido G, Eakin CM, Figueira W, Gilmour J, Harrison H, Heron S, Hoey AS, Hobbs J-P, Hoogenboom M, Kennedy E, **Kuo C-Y**, Lough J, Lowe R, Liu G, Malcolm McCulloch HM, McWilliam M, Pandolfi J, Pears R, Pratchett M, Schoepf V, Simpson T, Skirving W, Sommer B, Torda G, Wachenfeld D, Willis B, Wilson S (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373-378. doi:10.1038/nature21707

Keshavmurthy S, Tang KH, Hsu CH, Gan CH, **Kuo C-Y**, Soong K, Chou HN, Chen CA (2017) *Symbiodinium* spp. associated with scleractinian corals from Dongsha Atoll (Pratas), Taiwan, in the South China Sea. Peer J 5:e2871

Lauriane, RD, Denis V, Palmas S de, **Kuo C-Y**, Hsieh HJ, Chen CA (2016) Structure of benthic communities along the Taiwan latitudinal gradient. PloS ONE 11(8) e0160601

Kuo C-Y, Fan TY, Li HH, Lin CW, Liu LL, Kuo FW (2015) An unusual bloom of the tunicate, *Pyrosoma atlanticum*, in southern Taiwan. Bulletin of Marine Science 91(3). doi:10.5343/bms.2014.1090.

Madin JS, **Kuo C-Y**, Martinelli JC, Mizerek T, Baird AH (2015) Very high coral cover at 36°S on the east coast of Australia. Coral Reefs 34(1) doi:10.1007/s00338-014-1248-9.

Kuo FW, **Kuo C-Y**, Fan TY, Liu MC, Chen CA (2015) Hidden ecosystem function of rabbitfishes? *Siganus fuscescens* feeds on the soft coral, *Sarcophyton* sp. Coral Reefs 34(1): 57. doi:10.1007/s00338-014-1250-2

Wang JT, Hsu CM, **Kuo C-Y**, Meng PJ, Kao SJ, Chen CA (2015) Physiological outperformance at the morphologically-transformed edge of the cyanobacteriosponge *Terpios hoshinota* (Suberitidae: Hadromerida) when confronting opponent corals. PLoS ONE 10(6):e0131509. doi:10.1371/journal.pone.0131509.

Hsu CM, Palmas S. de, **Kuo C-Y**, Denis V, Chen CA (2014) Identification of scleractinian coral recruits using fluorescent censusing and DNA barcoding techniques. PLoS ONE 09/2014; 9(9):e107366. doi:10.1371/journal.pone.0107366.

Keshavmurthy S, Meng PJ, Wang JT, **Kuo C-Y**, Yang SY, Hsu CM, Gan CH, Dai CF, Chen CA (2014) Can resistant coral-symbiodinium associations enable coral communities to survive climate change? A study of a site exposed to long-term hot water input. PeerJ 04/2014; 2(7):e327. doi:10.7717/peerj.327

Denis V, Mezaki T, Tanaka K, **Kuo C-Y**, Palmas S. de, Keshavmurthy S, Chen CA (2013) Coverage, diversity, and functionality of a high-latitude coral community (Tatsukushi, Shikoku Island, Japan). PLoS ONE 8(1): e54330. doi:10.1371/journal.pone.0054330.