



Australian Government

Department of the Environment, Water, Heritage and the Arts

Marine and Tropical Sciences Research Facility Milestone Report, June 2010

Program 5(i): Climate Change: Understanding the threat, ecosystem impacts and mitigation of the Great Barrier Reef

Project 2.5i.3: Resilience to climate change

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1. Report Summary

Objective (a): Determining spatial connectivity of coral and *Symbiodinium* populations and potential for replenishment

Molecular analyses of 350 colonies of the coral *Seriatopora hystrix* from reefs in the Palm and Lizard Island regions have revealed patterns of small-scale population structuring between exposed and sheltered habitats within relatively small spatial scales. Some re-sampling is required to clarify taxonomic identification of unclear morphotypes within the species, but all other samples have been extracted for total gDNA and genotyped with six of ten microsatellite markers. The remaining four markers will be complete by the end of July. When complete, the final output will provide a comprehensive overview of the population structure and patterns of connectivity among populations of this ubiquitous coral species at sub-regional spatial scales, which will greatly enhance understanding of connectivity in this species that is currently based exclusively on broad-scale studies. Preliminary indications that there may be high rates of self-recruitment and population inbreeding in sheltered habitats within protected bays suggest that populations in these habitats are particularly vulnerable to disturbance and extinction.

Genotyping and data analyses for *Symbiodinium* strain and population-level information have been completed for seven populations of *Symbiodinium* hosted by the coral *Acropora millepora*. Results highlight stability in the symbiotic association at the strain level (potentially equivalent to species) over twelve years (1997-2009), including both the 1998 thermal and the 2009 salinity bleaching events. However, significant temporal and bleaching-associated changes in the population-level genetic composition of *Symbiodinium* were detected.

Caution in interpreting mechanisms driving population genetic shifts is required because of the lack of basic life history information available for *Symbiodinium*. The results are currently being prepared for a manuscript to be submitted for publication in 2010.

Objective (c): Identifying environmental drivers of coral disease and modelling links with thermal anomalies associated with climate change

A model to predict outbreak likelihood for the group of coral diseases known as white syndromes (WS) has been further refined to increase its utility as a predictive tool within the Great Barrier Reef Marine Park Authority (GBRMPA) disease outbreak response plan. New output formats show outbreak risk is high for sites where temperature stress is high and coral cover exceeds 26%. The incorporation of a coral cover threshold into the model has been made in response to peer-reviews of a manuscript submitted to [Global Change Biology](#) and in response to feedback from the end user managers working closely with our team. The predictions produced for 2009 were converted into an interactive Google Earth™ tool that has recently become the early warning system within a coral disease response plan currently under review at the GBRMPA. Following detection of thermal stress in northern parts of the Great Barrier Reef (GBR) in model outputs for 2009, the assessment and monitoring component of the disease response plan was implemented late last year, resulting in disease surveys at sites predicted to have high outbreak likelihood near Port Douglas and Lizard Island. Survey results increased our understanding of the threshold level of coral cover required for an outbreak of white syndromes. A new website, which will include 2010 model predictions of WS outbreak likelihood, will become publicly available in early July. In addition, links between temperature stress and outbreaks of white syndromes have now also been demonstrated for a site in NW Australia and three sites in the Pacific and Indian Oceans, further validating the veracity of our model. These results form the basis for a manuscript to be submitted shortly to [Proceedings of the Royal Society B](#). In summary, this project has identified summer warm thermal anomalies as important drivers of WS outbreaks on the GBR and also on other Indo-Pacific reefs, highlighting the increasing vulnerability of corals to disease as ocean temperatures rise.

Assessment of the appropriateness of remotely sensed measures of water quality – ocean colour variables – for exploring water quality as a driver of coral disease abundance on the Great Barrier Reef indicates that further development of satellite data processing algorithms is required. Ocean colour variables are becoming more useful for applications involving clear waters on and surrounding coral reefs as research programs at CSIRO and in other remote sensing groups advance understanding of light reflectance off coral reef substrata to enable existing systems to re-process data archives. These advances and other anticipated developments in ocean colour data processing for coral reef waters suggest strong future potential for research into links between water quality and disease dynamics. Importantly, however, advice from space agencies worldwide during the past year is that algorithms for processing *historical* data currently under development, do not yet provide data sufficiently representative of *in situ* conditions to usefully explore relationships between the relevant variables and observed patterns in the prevalence and abundance of coral diseases. Accordingly, we have compiled the datasets and connections required to develop models and analyses to explore water quality/disease links in preparation for when re-processed ocean colour datasets become available late this and early next year. Given the likelihood of increasing susceptibility of corals to disease with rising seawater temperatures, research into potential synergistic effects between thermal stress and degrading water quality is urgently needed.

Objective (d/e): Quantifying levels of herbivory and critical thresholds in macro-algal phase shifts

Data from the extensive field surveys and experimental analyses were combined with existing data to provide an overview of macroalgal removal on the GBR. Following the

development of a macro-algal bioassay to quantify browsing pressure, a full scale regional sampling programme was undertaken with over two hundred experimental assays deployed at the Low Islands, the Whitsunday and the Keppel Islands. Subsequent work has focussed on the Keppel Islands where coral-algal transitions appear to be highly unstable. In these areas herbivory is critical to constrain macroalgal growth. However, corals appear to play an important role in harbouring macroalgal populations within their branches. This provision of a safe refuge from herbivory makes these systems particularly vulnerable to algal expansion and means that the system lies close to the algal-coral threshold. Small changes in coral, algal or herbivore populations therefore would be expected to result in rapid changes to the benthic community.

Our results point strongly to a highly restricted suite of fishes capable of removing macroalgae. These species appear to play a similar role on inshore reefs along the entire length of the Great Barrier Reef. The emergent pattern is one of heterogeneity in algal removal rates with just one or two fish species filling the role in a given location. Removal rates are characterized by high among-site and among-location variation. The capacity of inshore reefs to respond to an increase in macroalgae is likely to be spatially highly variable. It appears to depend, at all scales, on the behaviour and densities of a few key fish species. Modeling coral algal phase shifts under different climate change scenarios is challenging as there appears to be multiple thresholds with extensive spatial variation in the intensity, if not the nature of, ecosystem processes.

Objective (f): Evaluating long term recovery and resilience of reef fish communities to climate change

Intensive field sampling of fish (specifically, butterflyfishes) and coral assemblages was undertaken in January 2010, including extending the sampling design to include Trunk Reef, Rib Reef and Bramble Reef. This represents the third and final annual survey to assess recovery and resilience of coral communities and butterfly fish assemblages in the aftermath of the 2001-02 bleaching event. Since 2005, there has been a moderate increase in coral cover to 12.3% in January 2010, mostly due to increases in coral cover of *Acropora*. There has not however, been any apparent increase in the abundance of butterflyfishes over the last three years. Rather abundance of butterflyfishes (especially non-corallivores) declined between 2009 and 2010. These results reveal limited resilience among fish and coral assemblages in the central Great Barrier Reef, and show coral reef assemblages may be significantly altered as climate related disturbances become more frequent.

To identify appropriate scales and likely sources of larval supply, especially among reef fishes, a comprehensive microsatellite library has been developed (and now published) based on collections of genetic material for *Chaetodon lunulatus* and *Chaetodon trifascialis* from Trunk Reef. The next step is to collect genetic material from newly settled butterflyfishes in recovering populations, combined with hierarchical sampling of butterfly fish populations within and around the study sites to identify source populations. However, this study has not progressed due to the limited recruitment of butterflyfishes at any of the study sites, including sites where coral cover has exhibited dramatic recovery.

To explore the relative importance of pre- versus post-settlement processes in limiting recovery and resilience of coral reef communities, densities of coral recruits (defined as juvenile corals that had settled on natural substrates and visible with the naked eye) were quantified in January 2009 and 2010 at nine study sites across three reefs in the central Great Barrier Reef, as well as annual surveys of adult corals. Spatial variation in rates of replenishment was then compared to patterns of adult abundance to test whether limited settlement of corals was limiting recovery and resilience of local coral populations. While there was marked variation in densities of coral recruits within and among reefs, this did not relate to variation in current coral cover (measured in January 2010).

2. Science Summary

Objective (a): Determining spatial connectivity of coral and *Symbiodinium* populations and potential for replenishment

Identifying the genotypes of colonies of the brooding coral *Seriatopora hystrix* within the Palm and Lizard Island regions has provided insights into how populations are related between exposed and sheltered habitats at small spatial scales. Surprisingly, populations at exposed reefs in the two regions, which are approximately five hundred kilometres apart, were found to be more closely related than those of sheltered and exposed populations within a region (1-10 km apart). Current understanding of connectivity in this species is limited to GBR-wide studies that lack sufficient detail to detect small-scale processes governing broad-scale patterns. When complete, results will provide a comprehensive overview of patterns of connectivity among populations of this ubiquitous coral species at sub-regional spatial scales. Preliminary indications, that there may be high rates of self-recruitment and population inbreeding in sheltered habitats within protected bays, suggest that populations in these habitats are particularly vulnerable to disturbance and extinction.

The *Symbiodinium* strain hosted by the common scleractinian coral *Acropora millepora* was found to be constant through space and time within the Palm Island group. More than 99% of coral colonies sampled ($n = >400$) hosted exclusively *Symbiodinium* strain C2 (sensu van Oppen) regardless of whether they were healthy or bleached. However the population-level genetic composition of *Symbiodinium* C2 at seven reef sites was significantly different between sampling years and between healthy and bleached sub-populations. These population genetic shifts could potentially be attributed to genetic drift in asexually maintained populations, sexual recombination, acquisition of new *Symbiodinium* genotypes from the external environment, and/or natural selection. Elucidating the relevant mechanism(s) requires further research into the basic life history characteristics of *Symbiodinium* such as the timing and location of sexual reproduction.

Objective (c): Identifying environmental drivers of coral disease and modelling links with thermal anomalies associated with climate change

Understanding links between thermal stress and coral disease is critical for the development of disease outbreak response plans for the Great Barrier Reef. A modelling framework for predicting outbreaks of the group of coral diseases known as white syndromes, developed as part of this MTSRF-funded project, has been refined to include a coral cover overlay from the Australian Institute of Marine Science Long Term Monitoring Program (AIMS LTMP), which greatly increases interpretability of the model outputs and resultant tools. A paper submitted to Global Change Biology has been revised in light of reviewers' comments and discussions with end users, and will be resubmitted in the coming month. The website, which resides in the ReefTemp area of the CSIRO Marine and Atmospheric homepage, will be updated to include predictions of outbreak likelihood for 2010 in the coming month and then will be made publicly available. A coral disease response plan was co-drafted with the end user managers and the modelling tools developed in this project form the early warning system within the response plan. The assessment and monitoring component of this response plan were implemented in late 2009. Ground-truthing surveys increased our knowledge of coral cover threshold requirements and provided critical input to the Global Change Biology submission. The links between temperature stress and temporal variability in the abundance of white syndromes shown in the southern Great Barrier Reef have now been demonstrated for a site in NW Australia, as well as sites in the Indian and Pacific Oceans. These results form the basis of a manuscript to be submitted to Proceedings of the Royal Society of Biological Sciences in July. We continue to collaborate with end user managers regarding the application of the models and tools developed in this project to management decision-making and will work with managers to refine the response plan in preparation for the 2010/2011 summer. Overall, our results highlight the increasing vulnerability of corals to

disease as oceans warm and the need for further research into potentially interactive links between water quality, thermal stress and disease outbreak risk.

Objective (d/e): Quantifying levels of herbivory and critical thresholds in macro-algal phase shifts

Inshore reefs are increasingly showing their susceptibility to human induced changes. The vulnerability of marginal systems has been highlighted by one algal species *Lobophora* (a brown leathery alga) which appears to be highly resistant to grazing. This species may have the capacity to dominate inshore reefs regardless of herbivore presence. It is this species that drove algal outbreaks in the Keppels and elsewhere on inshore reefs. This is one algal species that herbivores may struggle to control (details in Bennett *et al.*, [Coral Reefs](#) 2010). Furthermore, we find extensive spatial variation in the magnitude of algal removal. We have found documented huge variation in the capacity of reef herbivores to remove algae on inshore reefs. In the north (Cairns Low Isles region) algal removal was strong with good prospects for continued coral development. In contrast the Keppel Islands had just five percent of the effective herbivore activity, due to low herbivore numbers and low feeding rates. Thresholds are going to depend on both fish abundance and behaviour. This suggests that southern reefs and the Keppels in particular, are more likely to be dominated by macro algae and once in place the algae are likely to remain. Some northern reefs have healthy herbivore communities where browsing surgeonfish and rudderfish can help keep areas clear of algae. The Keppels, however, are more vulnerable to prolonged domination by algae. Protection of herbivorous fishes is a clear logical management priority. But this may not be enough. The ongoing challenge is to understand the environmental factors that moderate herbivore activity on inshore reefs.

Objective (f): Evaluating long term recovery and resilience of reef fish communities to climate change

Climate change poses a major threat to the Great Barrier Reef, and the most immediate threat comes from sustained and ongoing increases in sea surface temperatures. The future of coral reef ecosystems is heavily dependent upon the rate at which populations and communities can recover from successive disturbances associated with periodic temperature extremes. Ongoing monitoring of fishes and corals has been conducted in the central GBR following significant coral bleaching and associated habitat degradation, which was caused by a localised warm pool in 2001-02. Significant bleaching and subsequent coral mortality reduced coral cover to <5% across several reefs in the central Great Barrier Reef, which has remained low for up to eight years. Even where there has been spectacular recovery of coral cover, the structure of coral assemblages has markedly changed in the aftermath of the 2001-02 bleaching event. Further, changes in cover and composition of reef-building corals have had significant effects on fish communities. Most notably, coral-feeding butterflyfishes all but disappeared following extensive coral loss, and recovery has been very slow and highly variable among species. Directional shifts in the structure of butterflyfish assemblages have been strongly influenced by changes in the structure of coral assemblages. These results suggest that there is limited resilience among fish and coral assemblages in the central Great Barrier Reef, and that further increases in the frequency and/or severity of warm water bleaching will cause major (potentially catastrophic) changes in the structure of local reef assemblages. Even if reef assemblages are resilient and just take more than 8 years to become re-established, it seems unlikely that contemporary reef assemblages could be sustained in the face of future global warming. Further research is urgently required to assess what factors are limiting the resilience of reef assemblages in the central Great Barrier Reef.

Milestones extracted from Project 2.5i.3 Schedule

Delivery Date: June 2010

Description

- A report describing the small-scale population genetic structure of Lizard Island and Palm Island *S. hystrix* populations, a comparison of habitats (i.e. exposed vs. sheltered) and regions [(a) AIMS/JCU]
- A report describing: (a) the genotypes of *Symbiodinium* C2 within healthy and stressed (=bleached) colonies of *Acropora millepora* from different reefs using *Symbiodinium* microsatellites developed under this project; (b) the temporal variation in the genetic composition of *Symbiodinium* assemblages hosted by corals; and (c) the impacts of coral bleaching on genetic variation in *Symbiodinium*. [(a) AIMS/JCU]
- Submission of paper (with appropriate attribution of MTSRF funding and with copies delivered to the RRRC) on testing the temperature-disease model in relation to white syndrome outbreaks on the GBR and throughout the Indo-Pacific and assessment of the vulnerability of corals to disease in relation to ocean warming. [(c) JCU]
- A final report on the capacity of remotely sensed measures of water quality to predict spatial patterns in the prevalence and abundance of diseases like black band disease on the inshore Great Barrier Reef. [(c) JCU]
- Completed field and experimental evaluation of algal ecosystem thresholds, modelling of coral algal phase shifts under different climate change scenarios; submit paper (s) for publication (with appropriate attribution of MTSRF funding and with copies delivered to the RRRC). Outputs of models delivered to the e-Atlas. [(d,e) JCU]
- A final report on vulnerability of GBR to climate change induced shifts in macroalgae distribution and abundance in relation to fish herbivory and present options for alternate management options. Spatial components of the report delivered to the e-Atlas. [(d,e) AIMS/JCU]
- A report on the relative roles of pre- versus post-settlement processes in limiting recovery of coral reef assemblages. [(f) JCU]
- Paper submitted (with appropriate attribution of MTSRF funding and copy delivered to the RRRC) discussing patterns and processes of extreme spatial variation in recovery and resilience of fish and coral assemblages. [(f) JCU]
- Meta-data describing all data generated by MTSRF Project 2.5i.3 lodged on the e-Atlas.

3. Project Results

3.1 Resilience of coral assemblages to climate change

- A report describing the small-scale population genetic structure of Lizard Island and Palm Island *S. hystrix* populations, a comparison of habitats (i.e. exposed vs. sheltered) and regions [(a) AIMS/JCU]

Background

Connectivity among populations of coral species has been inferred from large-scale studies of population genetic structure along large sections of the GBR (Ayre and Dufty, 1994; Ayre and Hughes, 2000; Ayer and Hughes, 2004; van Oppen *et al.* 2008), but few studies have investigated small-scale patterns of connectivity among local habitats and populations. Identification of these smaller scale population patterns and processes is essential to understand broader scale species structures. Therefore, this study has evaluated local-scale population genetic structure of a ubiquitous brooding coral species, *Seriatopora hystrix*, within and between two GBR regions (i.e. Palm Islands in the Central region and Lizard Island in the Northern region) and habitats (i.e. sheltered (s) vs exposed (e) habitats). In addition, these data will be integrated with those of a comprehensive broad scale study conducted by van Oppen *et al.* (2008; *in prep*) to evaluate processes driving population genetic structures of this species along the entire GBR.

Methodology

Overall, nine hundred *S. hystrix* samples were collected between December 2008 and November 2009 within the two regions, which are separated by approximately 450 km. In the Palm Islands, samples have been collected from fifty individuals at two sites from four locations (n = 400; PB(s), CB(s), SWP(s), SEP(e)). Distances between colonies sampled varied from within-reef scales (<500m to 1km) to between-reef scales and encompassed colonies in both the same and different habitat (sheltered/ exposed). To date, three locations at the sheltered margin of the Palm Islands (n = 300) and one location at the exposed margin (n = 100) have been completely sampled. The ultimate design will be more equal, as one additional exposed location is planned to be re-sampled in July 2010. Previously collected samples for this fifth Palm Islands site required additional taxonomic discrimination with genetic tools to target the desired species. The Lizard Island collection is complete and comprises a similar design with two sheltered (n = 200; L, WB) and two exposed (n = 200; WM, BI) locations. All samples have been extracted for genomic DNA and are currently undergoing further processing to determine individual genotypes with ten microsatellite markers previously developed by Underwood *et al.* (2006).

Results and Discussion

Currently, a subset of genotypic results have been generated with six of ten markers for 350 individuals, comprising three populations from the Palm Islands (CB(s), SWP(s), SEP(e)) and four populations from Lizard Island (L(s), WB(s), WM(e), BI(e)). These data indicate that populations of this species are highly structured even at small scales. Analysis of Molecular Variance (AMOVA) indicates that 28% of the total molecular variance is attributable to differences among populations. Furthermore, pairwise F_{ST} comparisons indicate significant differentiation for all possible population combinations. Interestingly, there is more separation between populations from different habitats within regions (<10km apart), than between populations from the same habitat (e.g. sheltered) in different regions. For example, within the Palm Islands region, the F_{ST} comparing CB(s) with SEP(e) is 0.336, whereas the pairwise comparison between CB(s; PI) and L(s; LI) is approximately half this value ($F_{ST} = 0.183$), although these sites are separated by almost 50 times the distance. Moreover, there appears to be slightly less isolation among populations on exposed reefs,

even between regions (mean $F_{ST}=0.091\pm 0.023$ SD), than between sheltered reefs within regions (mean $F_{ST}=0.162\pm 0.030$ SD). Interestingly, the greatest population differentiation ($F_{ST} = 0.401$) occurred within the Lizard Island region between the lagoonal site L(e) and exposed BI(e), which are less than 5 km apart and lack convincing physical barriers (i.e. a submerged reef flat with large channel connects the exposed and lagoonal habitats).

These preliminary data suggest intriguing patterns of population structuring between habitats within relatively small spatial scales for *S. hystrix*. The clearest difference between sheltered and exposed habitats sampled is the depth at which the populations are found. At sheltered sites, collection depths typically range from <1-7 m, whereas *S. hystrix* at exposed sites are generally found deeper. However, even this is not consistent between the regions, as colonies occur between 8 m and 18 m in the exposed Palm Island sites, but shallower (<12 m) in the Lizard Island region. Other than some degree of habitat specialization within the species, there is no obvious reason why populations between these two regions would be relatively highly connected on exposed margins, while remaining significantly more isolated within sheltered habitats. Previous suggestions have cited the relatively weak cross-shelf flow of water (van Oppen *et al.* 2008), however the applicability of this explanation to sites connected by hundreds of kilometres latitudinally and isolated by a few kilometres longitudinally seems unconvincing. On the other hand, the physical structure of sites on sheltered margins and their locations within relatively protected bays may cause the seemingly small distinctions between moderately connected and more isolated populations.

Following re-sampling of the fifth PI location in July 2010, final data analysis is expected to be completed by September and a manuscript will be prepared for submission late this year. Completion of the remaining markers and samples will strengthen results presented above and incorporate an additional level of potential subdivision (i.e. within location/ reef). The within reef comparisons may indicate the ultimate scale at which these sheltered bay populations are isolated from one another, and suggest further directions for future studies. Fine-scale analysis of within reef/ sheltered bay hydrodynamics would assist in estimating the extent to which particles, such as coral larvae, would be trapped within these habitats, leading to high rates of self-recruitment and population inbreeding. *S. hystrix* is often densely populated in these sheltered habitats; however, its apparent success may be threatened by limited genetic diversity, thus making these populations particularly vulnerable to disturbance and extinction.

- A report describing: (a) the genotypes of *Symbiodinium* C2 within healthy and stressed (=bleached) colonies of *Acropora millepora* from different reefs using *Symbiodinium* microsatellites developed under this project; (b) the temporal variation in the genetic composition of *Symbiodinium* assemblages hosted by corals; and (c) the impacts of coral bleaching on genetic variation in *Symbiodinium*. [(a) AIMS/JCU]

Introduction

Due to their small size and lack of morphological identification, very little is known about the dynamics of *Symbiodinium* populations. In this study, genetic methods were used to follow changes in the genetic composition of *Symbiodinium* on reefs between sampling years and during coral bleaching.

Methods

Sampling design

Samples from colonies of the scleractinian coral *Acropora millepora* were collected from a total of seven inshore reef sites within the Palm Island group, in the central section of the Great Barrier Reef Marine Park (Figure 1). For part (b) of the study, samples (n = 10-50) were

collected from sites 1-3, in 1997, 2004 and 2009 (site 3 only). For parts (a) and (c), samples were collected from sites 3-7 during a bleaching event induced by low salinity in March-April 2009. At each site, healthy ($n = 14-24$), pale ($n = 5-12$), and bleached ($n = 12-30$) colonies were sampled across a uniform depth range. At Fantome Island (site 3) only healthy colonies were sampled as no bleaching was observed. At each sampling point, a branch was collected from the centre of each individual coral colony and preserved in 100% ethanol.

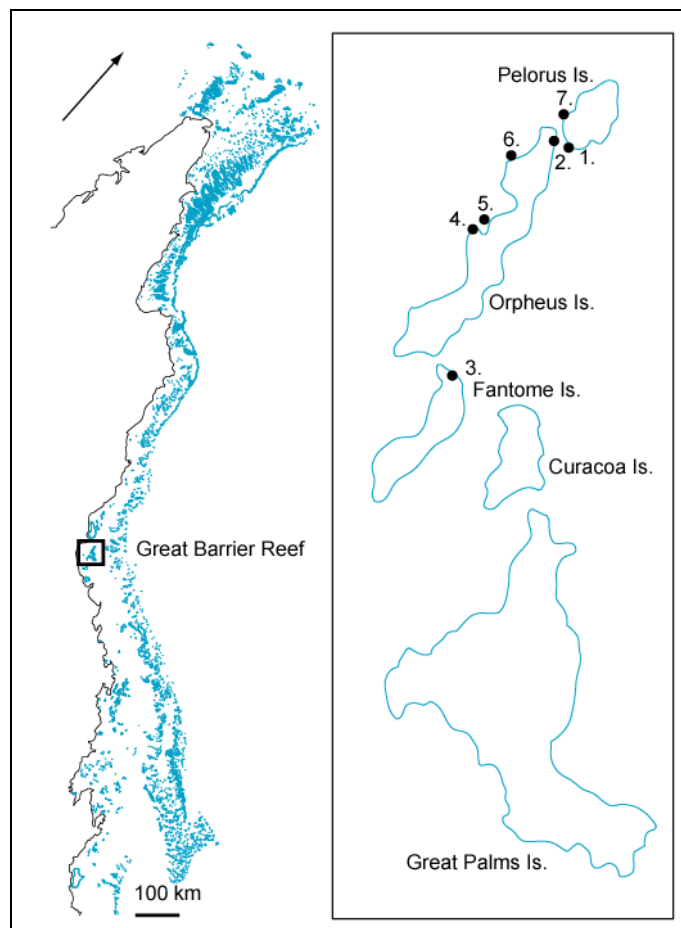


Figure 1. Location of seven investigated reef populations of *Symbiodinium* hosted by *Acropora millepora* on the Great Barrier Reef between 1997 and 2009.

Genotyping

Genetic variation of *Symbiodinium* hosted by *A. millepora* at each reef site was investigated at the strain-level (putative species-level) using the internal transcribed spacer 1 (ITS1) rDNA marker, and at the population-level using microsatellite markers. ITS1 rDNA genotyping was conducted using polymerase chain reaction (PCR) amplification and single stranded conformation polymorphism (SSCP) as per van Oppen *et al.* (2005). Microsatellite genotyping was conducted with 8 polymorphic microsatellite loci: *SymC_3-02*, *SymC_3-04* (Howells *et al.* 2009); *C1.01*, *C1.02*, *C1.05*, *C1.07*, *C1.15*, *C2.08* (Bay *et al.* 2009). Microsatellite loci were amplified using PCR and purified products were genotyped by capillary electrophoresis (*MegaBACE 1000*) at the Genetic Analysis Facility at James Cook University (Bay *et al.* 2009). Fluorescence peaks at each locus were scored using *MegaBACE Fragment Profiler version 1.2* (Amersham Biosciences). Observed peaks were scored as alleles if they were within the expected size range, in phase with the locus repeat motif, and at a minimum intensity of 10% of the most intense peak within a sample. As *Symbiodinium* samples represent the DNA content of $\sim 10^5$ cells, samples could potentially contain multiple alleles at each locus,

representing genetically distinct individuals belonging to the same *Symbiodinium* strain. The presence/absence of alleles within samples was scored and population genetic differentiation was evaluated using analysis of molecular variance (AMOVA; performed in GENALEX v6, Peakall and Smouse 2006)

Results and Discussion

The following points are in the process of being written up for publication:

- Genotypes of *Symbiodinium* C2 within healthy and stressed (=bleached) colonies of *Acropora millepora* from different reefs using *Symbiodinium* microsatellites developed under this project
- Temporal variation in the genetic composition of *Symbiodinium* assemblages hosted by corals
- Impacts of coral bleaching on genetic variation in *Symbiodinium*

Conclusions

Preliminary results highlight significant temporal and bleaching associated changes in the population-level genetic composition of *Symbiodinium*. However, cautious interpretation of the mechanisms driving population genetic shifts is required due to a lack of basic life history information for *Symbiodinium*. Future research needs to be directed at improving understanding the life cycle of *Symbiodinium*, particularly the timing and location (within-host or free-living) of sexual reproduction.

Acknowledgements

M van Oppen and B Willis contributed to the collection of coral samples analysed in this project. A Muirhead and L Peplow extracted the DNA for samples from 1997 and 2004.

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- Submission of paper (with appropriate attribution of MTSRF funding and with copies delivered to the RRRC) on testing the temperature-disease model in relation to white syndrome outbreaks on the GBR and throughout the Indo-Pacific and assessment of the vulnerability of corals to disease in relation to ocean warming. [(c) JCU]

A paper entitled 'Forecasting climate-driven coral disease outbreaks', which included appropriate attribution of MTSRF funding, was submitted to Global Change Biology in March 2010. Peer reviews and comments from the subject editor of Global Change Biology recommended resubmission following refinement of model output formats. Recommendations to incorporate coral cover as an additional layer in the model significantly improve the utility of model outputs for key end-user groups and are in accord with recommendations from managers at GBRMPA, with whom we have been closely collaborating. Accordingly, the model has been expanded to include a coral cover overlay from the AIMS LTMP and now displays outbreak risk as a combination of outbreak likelihood (based on temperature) *and* consequence (based on coral cover), rather than *just* outbreak likelihood. Outputs from the first version of the model highlighted all ~1km pixels that experienced temperature stress above thresholds defined by the model (i.e. minimum thermal stress experienced at sites where outbreaks of white syndromes (WS) occurred in 2002), including reefs from Lord Howe Island to the Torres Strait on the east coast of Australia and a similar range on the west coast. In the revised model, outbreak risk is only assessed as being high at sites where summertime temperature stress is above the 2002 threshold *and* where coral cover is moderate to high. Whereas outputs of the first model required users to interpret temperature-based images of outbreak likelihood in light of their knowledge of coral cover at sites of interest, the revised model has coral cover incorporated as a layer. Consequently, the revised model obviates the risk that users might misinterpret outputs, for example concluding that a coral disease outbreak was imminent at sites of high thermal stress where corals either do not exist (e.g. inter-reefal or oceanic waters) or coral abundance is too low for an outbreak to occur.

The relationship between temperature stress, coral cover, and disease abundance in our model is strong ($R^2 > 0.90$), but there is a paucity of data on coral cover in the 26 to 50% range (see Figure 2). Given that the threshold values of coral cover required for an outbreak of white syndromes is currently unknown, we have set the coral cover level at 26% as a conservative threshold. This threshold increases the likelihood that tools developed to target research and monitoring in response to outbreaks will be applied in a timely manner, thereby enabling appropriate responses and ensuring that our understanding of the threshold levels of coral cover required to cause an outbreak improves in the future. Figure 3 showcases the difference between the original and new model output formats for 2009. Until feedback from targeted research and monitoring provides further insights into coral cover thresholds, the model output will be as seen in Figure 3b. Thus outbreak likelihood will be assessed as high at sites experiencing high thermal stress where coral cover exceeds 26%. The new model output format, customised for use in the Great Barrier Reef, has been included in the Global Change Biology re-submission and a revised manuscript will be submitted by mid-June (see revised Abstract below).

Revised abstract for manuscript submitted to Global Change Biology

Coral reefs are already highly endangered by warming events associated with climate change. Links between anomalously high temperatures and outbreaks of coral diseases known as white syndromes (WS) in the Indo-Pacific represent an additional threat, but further advances in understanding aetiologies of disease and in developing management actions to mitigate their impacts are hampered by not knowing where or when outbreaks will occur. Before 2009, the only known outbreaks of WS on the Great Barrier Reef (GBR) were documented in 2002. Outbreak sites experienced high values of temperature stress, as measured by a mean positive summer anomaly (MPSA), and had high cover of

corals within the genus *Acropora*, the primary hosts. Here, we use an empirical regression model based on the MPSA and *Acropora* abundance at outbreak sites to hindcast the likelihood of WS outbreaks on Australian reefs for 2002 and subsequent summers. Data from 45 sites surveyed from 2003 to 2008 confirmed that the model never predicted outbreaks when there were none. The model identified reefs with high MPSA values in 2009 and forecast high outbreak likelihood in both the north-central and southern GBR. Targeted surveys to validate the model detected greatest WS abundance at a site in the north-central GBR with a high MPSA value but only medium host cover. Although a severe outbreak was not documented, WS abundance approached outbreak thresholds, which increases our understanding of the threshold host density required for an outbreak. Forecasting disease outbreaks in an era of changing climate requires integration of biological and physical data, and can be accomplished for selected disease syndromes. The approach and forecasting model for coral disease outbreaks developed here, now an early warning system within a disease response plan, can be widely adapted for use in other ecosystems.

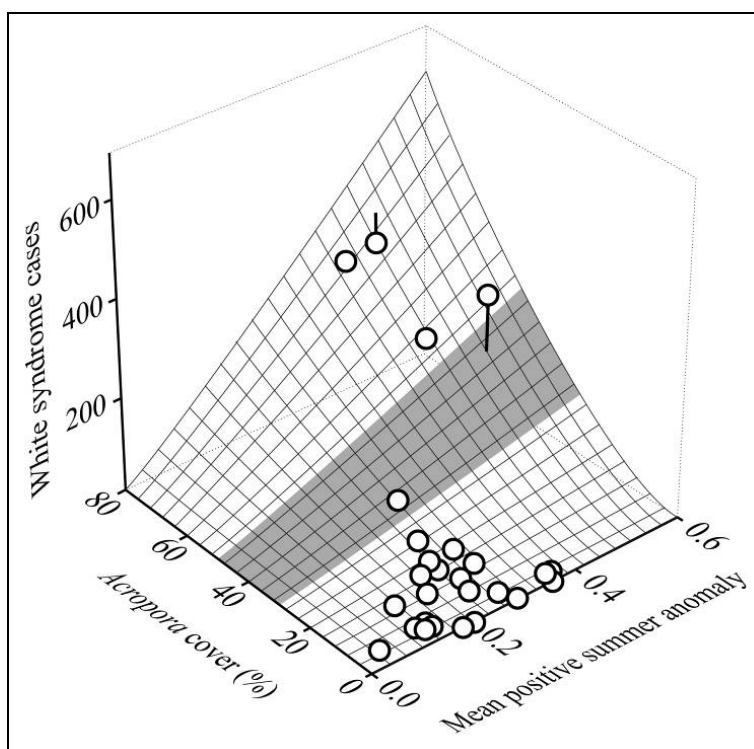


Figure 2. Regression model relating host cover, a measure of temperature stress, and the abundance of white syndromes observed at sites surveyed during the white syndrome outbreak year of 2002. The grey portion of the plane shows the paucity of data between 25-50% coral cover, which highlights that the threshold coral cover required for an outbreak is unknown but likely to exceed 25%.

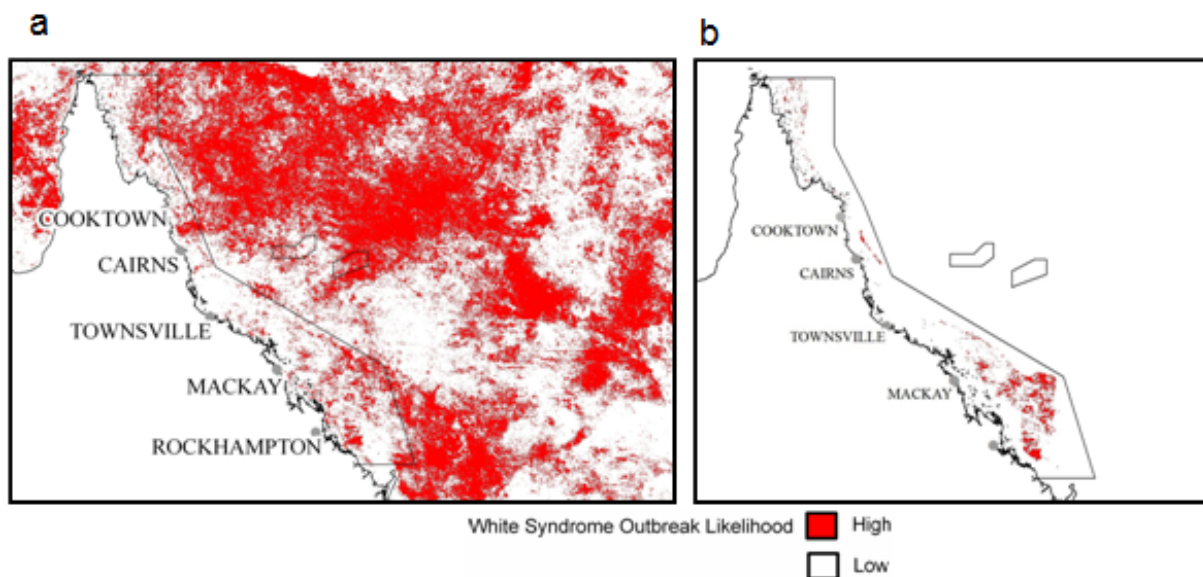


Figure 3. Model outputs comparing white syndrome outbreak likelihood for 2009 based on: (a) temperature stress alone (original version of model), and (b) temperature stress combined with coral cover of at least 26% (revised version).

Evaluation of model predications of outbreak likelihood in 2009

Following forecasts of high WS outbreak likelihood for late 2009, based on outputs of the original version of the model, we developed a rapid survey method to monitor and compare WS abundance on reefs predicted to have either high or low outbreak likelihood. In collaboration with managers from the GBRMPA and the Queensland Parks and Wildlife Service (QPWS), we completed disease surveys at more than thirty sites northeast of Cairns, comprising approximately equivalent numbers of reefs predicted to have high versus low outbreak likelihood. At each of the sites surveyed (east of Port Douglas and in the area of Lizard Island), three surveyors swam transects two metres apart (6 m transect width) along the reef crest for 3 x 10 minute intervals (~500 m²/transect) recording cases of WS on corals, which were identified to the genus/morphology level. These snorkel surveys resulted in a measure of WS abundance / 1,500 m², making the data comparable to those collected by the AIMS LTMP team.

Overall, WS abundance was similar at sites predicted to have high outbreak likelihood, based on temperature stress alone (see text above for comparison of original versus revised model outputs), and at sites predicted to have low outbreak likelihood (Figure 4). Although all sites had medium (30-40%) coral cover, we detected highest WS abundance (~30 cases per 1,500 m²) on the reef with highest average coral cover, providing corroborative support for our regression modelling, which shows that WS abundance requires both high temperature stress and high host cover. Notably, cases of white syndromes were observed at all of the sites surveyed (Figure 5), which was not the case during all of the other years that disease surveys were conducted.

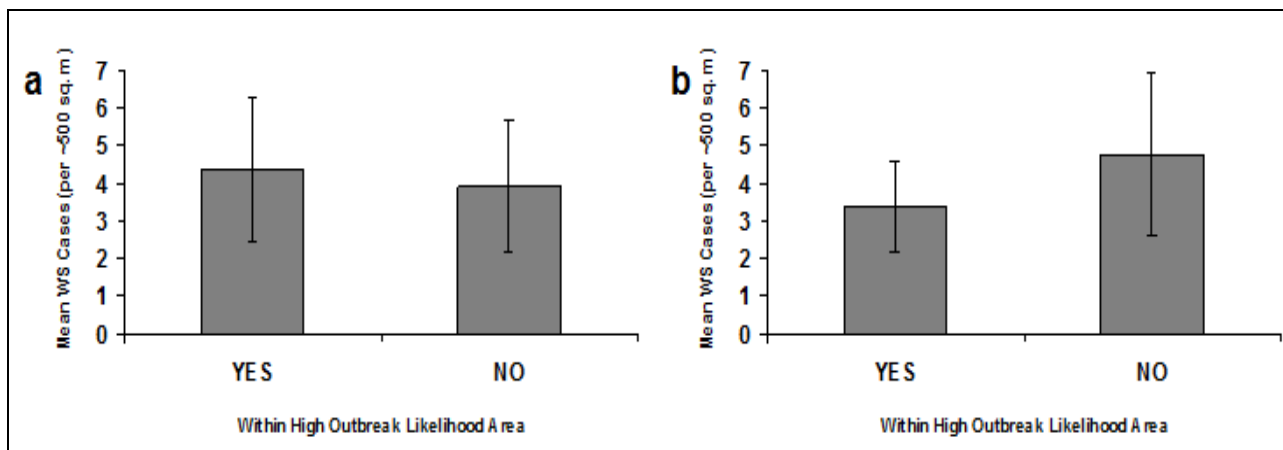


Figure 4. Comparison of mean (\pm SE) WS abundance between sites predicted to have high outbreak likelihood (YES) versus low outbreak likelihood (NO), based on temperature stress along, in the vicinity of: (a) Port Douglas, and (b) Lizard Island. All sites had medium (30-40%) coral cover, thus lack of significant difference in WS abundance highlights, in accordance with our model, that both high heating rates and high coral cover are required for WS outbreaks.

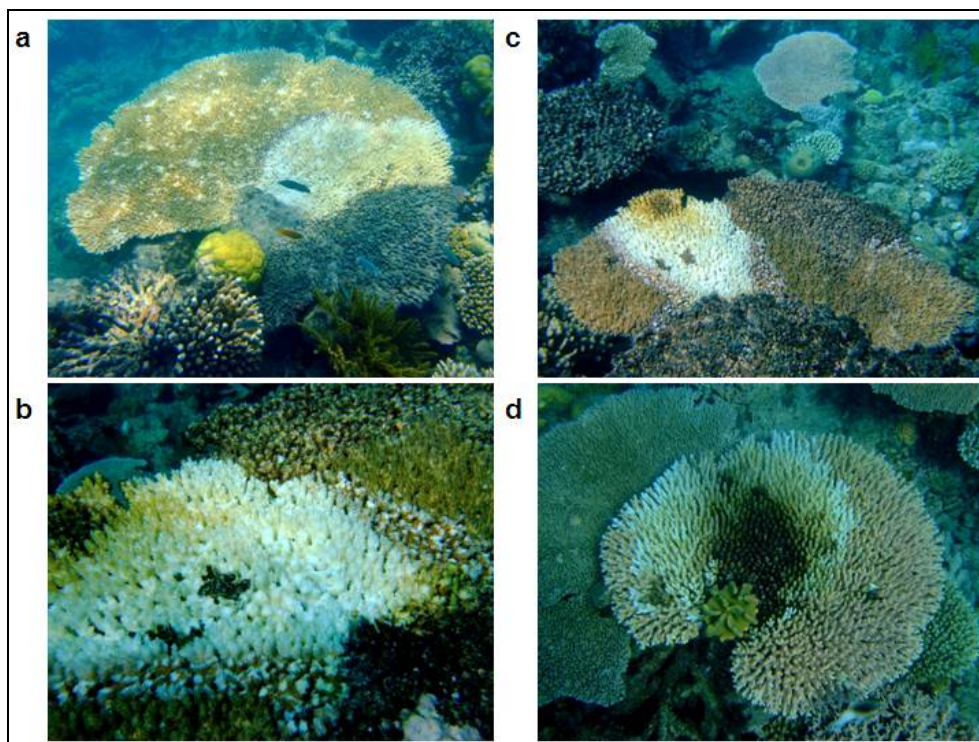


Figure 5. Images of white syndromes affecting tabular species of *Acropora* observed during surveys to evaluate WS outbreak likelihood forecasts in November 2009 on reefs near Port Douglas: (a-c) Rudder Reef, and (d) Mackay Reef.

Rapid surveys of WS abundance on reefs predicted to have high outbreak likelihood in 2009 comprised the assessment and monitoring component of the 2009 implementation of a 'coral disease response plan' that has been co-written by members of our team and representatives of the GBRMPA. Modelling tools developed to predict disease outbreaks as part of this project form the early warning system within the coral disease response plan, in combination with a volunteer monitoring network. Volunteers participating in the monitoring network ground-truth model predictions and, even when an outbreak has not been predicted, alerts managers when disease abundances reach levels higher than the observers are accustomed to seeing at sites that they regularly visit.

Importantly, as we prepare this report, the GBRMPA is working to finalise sign-off on a contract for services that will enable our team to produce the predictions of outbreak risk for 2010 and update the website developed last year. All indications are that the updated website will become publicly available in July at the same link that the tools originally developed by our group can be accessed:

http://www.cmar.csiro.au/remotesensing/reeftemp/web/ReefTemp_Disease.htm

Further testing of the model for reefs throughout the Indo-Pacific

A number of reports of white syndrome outbreaks on Indo-Pacific reefs outside of the GBR suggest links with temperature stress, but there have been no studies formally analysing these links. In collaboration with the GBRMPA and the CSIRO Marine and Atmospheric Research, our group has collated a nearly twenty-year time series of daily temperature data for sites in coastal northeast and northwest Australia (southern GBR and Rowley Shoals, respectively) and at three sites in the Indian and Pacific Oceans (Christmas Island, Marshall Islands, and Nikko Bay in Palau). At all sites included in the analysis, outbreaks of white syndromes have been observed in the last decade and coral cover prior to the outbreaks was high (>50%). For four of the five sites, the highest temperatures occurred in the months to year that preceded the observed outbreaks (Figure 6). These results strongly suggest that correlative relationships between coral cover, temperature stress, and the abundance of white syndromes are not unique to the Great Barrier Reef.

In contrast to patterns of disease outbreaks closely following highest recorded summer temperatures at four of the sites, the highest temperatures on record occurred two years prior to the first detection of the white syndrome outbreak at Christmas Island. We speculate that, either earlier potential outbreaks were not detected, or pathogens suspected to cause WS were not present until 2007, when the first cases of the disease were documented at this site. Use of modelling to explore the links between thermal stress, coral cover and disease outbreaks has been a productive research area arising from this project and further papers, the first of which we aim to target at Proceedings of the Royal Society of Biological Sciences, will acknowledge MTSRF funding.

Conclusions

The links between thermal stress, coral cover and outbreaks of white syndromes demonstrated in this project, on reefs both within the GBRMP and throughout the Indo-Pacific, highlight the seriousness of the coral disease threat to the GBR. Increases in the frequency and severity of coral disease outbreaks are expected to accompany changes in climate that are projected for tropical Australia and the Coral Triangle. We intend to continue to advance this work in the coming months and years to include improving our understanding of links between temperature stress and the abundance and prevalence of other coral diseases, as well as to explore links between *in situ* measures of water quality and coral disease prevalence on inshore reefs of the GBR.

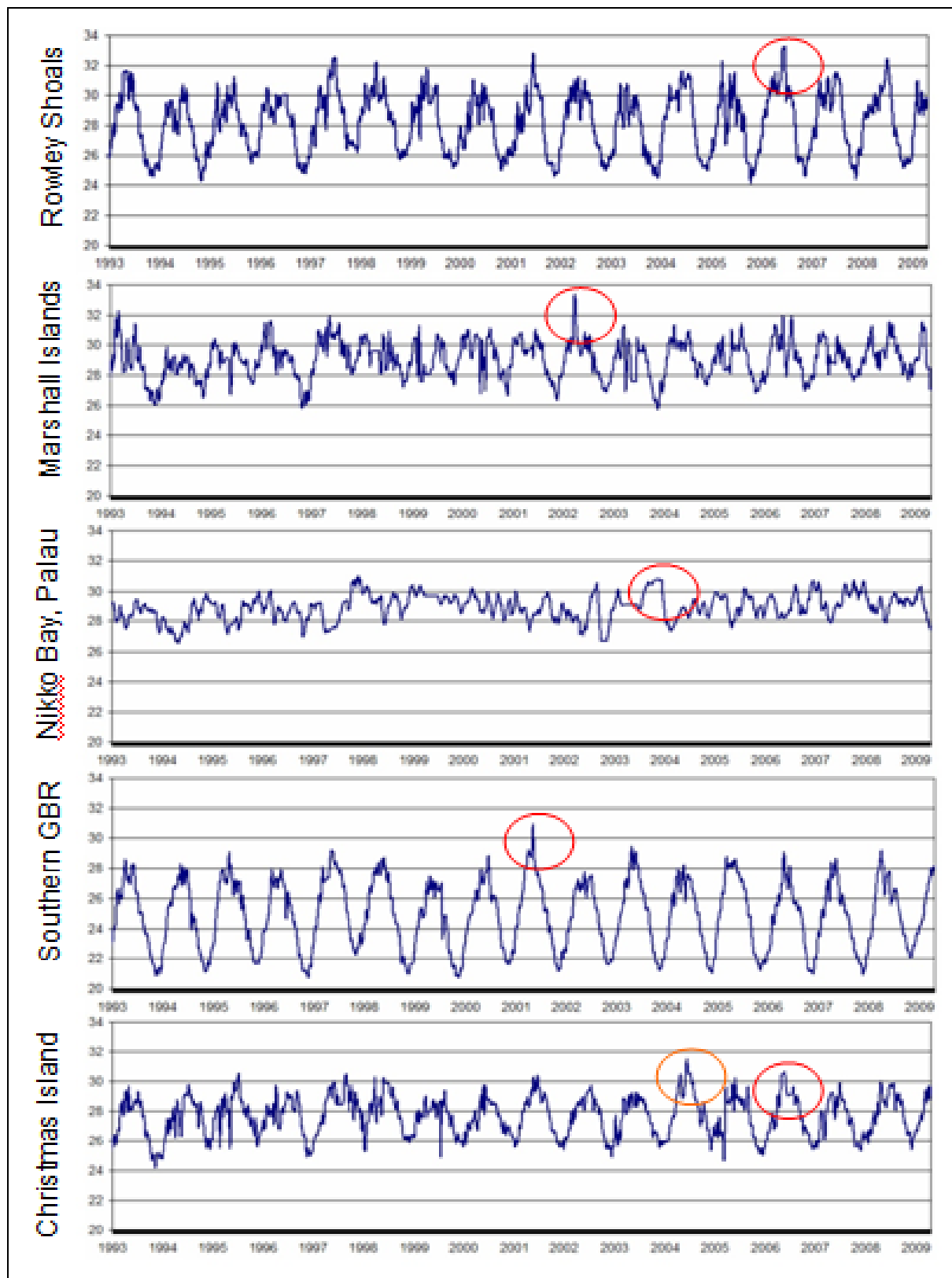


Figure 6. Daily temperatures from 1993 to 2010 at five Indo-Pacific sites where white syndrome outbreaks have been documented. Red circles denote the year of documented outbreaks, which occurred in the months to year that followed the warmest temperatures on record at four of the five sites. The orange circle highlights the timing of the warmest temperature on Christmas Island (see text for further explanation of this exception to the pattern).

- A final report on the capacity of remotely sensed measures of water quality to predict spatial patterns in the prevalence and abundance of diseases like black band disease on the inshore Great Barrier Reef. [(c) JCU]

Background

In addition to higher temperatures and resultant bleaching events, pressures on reefs associated with a changing climate are predicted to include increases in the frequency of severe storms, which typically both decrease local water quality and increase injuries to corals. In combination with deteriorating water quality from anthropogenic activities, storm-related stressors will further increase the likelihood that coral diseases will be more common in the future and that outbreaks will occur more frequently. Given the compounding nature of climate-related and anthropogenic stressors, research into potential links between water quality and coral disease dynamics is critical.

Methods and Results

To explore links between water quality and disease abundance, we have collated data on water quality from twenty sites where disease surveys have been conducted over the last five to ten years. The source of water quality data available to us at all of our survey sites is the remote sensing community within Australia and abroad. We corresponded with the major space agencies around the world this last year and found that reliable data on ocean colour variables most closely linked to water quality cannot yet be obtained for the sites for which we have disease prevalence and abundance data. The two key ocean colour variables – ‘chl_a’ and ‘kd’ – are proxies for algal biomass/nutrient levels and a descriptor of the penetration of sunlight in water, respectively. Researchers are working towards fully resolving these issues to produce reliable estimates of chl_a and kd for the clear waters on and surrounding coral reefs. The primary challenge arises from the satellite being able to see – the satellite’s ‘optical depth’ – to a depth that exceeds the physical depth, requiring the development of algorithms to calculate ocean colour variables that take into account the nature of light reflectance off a highly variable substrate.

Overcoming challenges and moving forward

Various groups have been working consistently towards understanding the nature of light reflectance from various reef substrata. Once these values are known, it will be possible to produce reliable estimates of the relevant ocean colour variables from remotely sensed data. The challenge, however, lies in there being at least several dozen (if not several hundred) different combinations of bare space, hard coral, soft coral, sponges, algae, other invertebrates, rubble and sand on reefs, all of which have a different reflectance value. Therefore, algorithms developed can be used in locations where the extant community is known or can be reliably estimated, allowing for the monitoring of the relevant ocean colour variables through time. However, spatially disparate sites, even sites only kilometres apart, would require a different algorithm. New contacts our team has made suggest that research into ocean colour over reefs will be sufficiently advanced in the coming years for our group to use remotely sensed data to predict spatial patterns in the prevalence and abundance of diseases like black band disease, as we had hoped to do this last year. Until advances in this area enable the reprocessing of archival ocean colour datasets, we are unable to advance research into potential links between water quality and disease. Accordingly, our team has focused on improving current understanding of the links between temperature and disease, and on interacting with the end user managers to produce strategic and effective coral disease response plans (as discussed in the above sections). In the coming months and years, our team aims to re-visit this research objective by using remotely sensed data on water quality as it becomes available and by using *in situ* data on key water quality parameters. The number of sites for which data on both *in situ* water quality and patterns in

disease prevalence and/or abundance are available is limited, so we will be looking to combine our modelling and statistical-based work with an increase in monitoring. In light of the increasing susceptibility of corals to disease predicted with rising ocean temperatures, it is paramount that we also understand the links between potentially synergistic effects between temperature and deteriorating water quality on coral health.

3.2 Resilience of reef fish assemblages to climate change

- Completed field and experimental evaluation of algal ecosystem thresholds, modelling of coral algal phase shifts under different climate change scenarios; submit paper (s) for publication (with appropriate attribution of MTSRF funding and with copies delivered to the RRRC). Outputs of models delivered to the e-Atlas. [(d,e) JCU]

One of the greatest challenges facing coral reefs is the threat of phase-shifts, particularly an increase in macroalgae. Today on the GBR, inner shelf reefs are often dominated by macroalgae. The primary goal of this study was to evaluate the extent to which herbivorous fishes are able to respond to an increase in macroalgae that may arise as a result of human activity or climate change. An initial status and trend report (Cvitanovic *et al.* 2007) identified the limits of our knowledge and the spatial limits of current research (Figure 7).

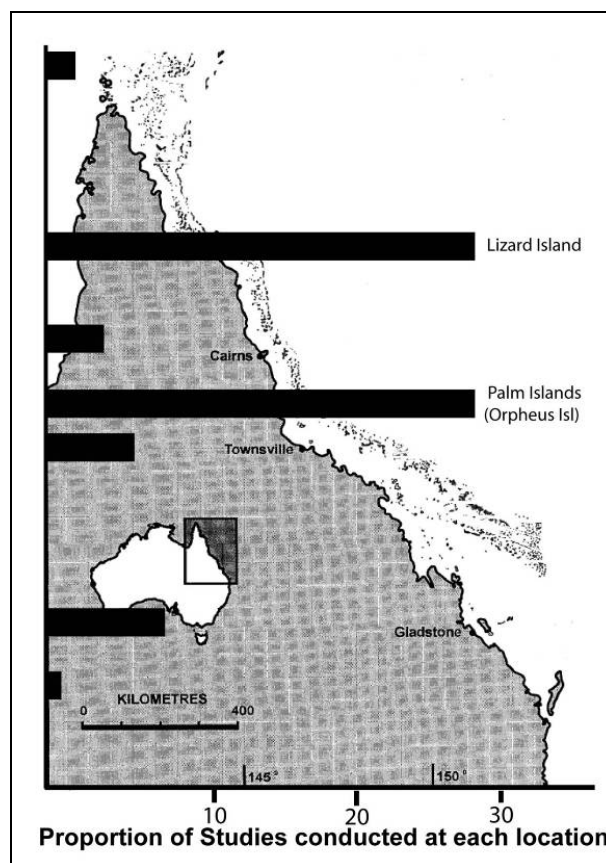


Figure 7. The distribution of studies on herbivory on the GBR. The number of studies conducted at particular latitudes and locations are shown as a percentage of the total number of herbivory publications from the GBR (after Cvitanovic *et al.* 2007).

Following the development of a macro-algal bioassay to quantify browsing pressure (Cvitanovic *et al.* 2009), a full scale regional sampling programme was undertaken with over 200 experimental assays deployed at the Low Islands, the Whitsunday and the Keppel Islands. Initial results point strongly to a highly restricted suite of fishes capable of removing macroalgae. These species appear to play a similar role on inshore reefs along the entire length of the Great Barrier Reef. The emergent pattern appears to be supporting earlier findings of high local heterogeneity in algal removal rates with just one or two species filling the role in a given location. Removal rates are characterized by high among-site and among-location variation (Cvitanovic & Bellwood 2008, Cvitanovic & Hoey, in press). The capacity of inshore reefs to respond to an increase in macroalgae is likely to be spatially highly variable. It appears to depend, at all scales, on the behaviour and densities of a few key fish species. Modelling coral algal phase shifts under different climate change scenarios is challenging as there appears to be multiple thresholds with extensive spatial variation in the intensity, if not the nature of, ecosystem processes (Bennett & Bellwood in review).

To date this work has resulted in a review of herbivory on the GBR (MTSRF internal report), Seven publications have arisen from this work to-date: a conference paper (Cvitanovic *et al.* 2009 MTSRF Conference Proceedings) and three in international journals *Coral Reefs* (Cvitanovic & Bellwood, 2008 *Coral Reefs* 28:127-133; Bennett *et al.* *Coral Reefs* 2010; Cvitanovic & Hoey in press). Another is in review and two more publications are in prep. The results have been presented at the Cairns MTSRF meeting, at the 11th International Coral Reef Symposium in Florida and at several meetings in Townsville. In terms of outcomes, this work, and meetings with end users, has laid the foundations for further development of coral reef management in order to ensure protection of critical functional groups. Specific herbivorous fishes have been identified as a key ecological feature in the East Marine Region and are likely to be considered a priority for protection when planning conservation policies.

References cited (all publications with appropriate attribution to MTSRF funding):

C. Cvitanovic, R.J. Fox and D.R. Bellwood (2007) Herbivory by fishes on the Great Barrier Reef: A review of knowledge and understanding. MTSRF Project Report.

Cvitanovic, C., A.S. Hoey and Bellwood, D.R. (2009) Developing a technique to quantify spatial variation in herbivory on the Great Barrier Reef. In: Long, S. and Taylor, R. (eds). *Proceedings of the 2008 Marine and Tropical Sciences Research Facility Annual Conference, 28 April to 1 May*. Reef & Rainforest Research Centre Ltd, Cairns.

Cvitanovic, C. and D.R. Bellwood (2009) Local variation in herbivore feeding activity on an inshore reef of the Great Barrier Reef. *Coral Reefs* 28:127-133.

Bennett, S., A. Vergés and D.R. Bellwood (2010) Branching coral as a macroalgal refuge in a marginal coral reef system. *Coral Reefs* 29: 471-480.

Cvitanovic, C. and Hoey, A.S. (In press) Benthic community composition influences within-habitat variation in macroalgal browsing on the Great Barrier Reef. *Marine and Freshwater Research*.

Bennett S and DR Bellwood Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Marine Ecology Progress Series* (In review).

To date:

1. All field work, video and statistical analyses completed with just two of the seven identified manuscripts remaining to be completed.
2. All data and preliminary analyses have now been formatted and delivered to the e-Atlas.

- A final report on vulnerability of GBR to climate change induced shifts in macroalgae distribution and abundance in relation to fish herbivory and present options for alternate management options. Spatial components of the report delivered to the e-Atlas. [(d,e) AIMS/JCU]

Our results have provided a new view of herbivory and susceptibility of coral reefs to algal expansion on the GBR. To date most approaches have assumed that visual censuses can give an indication of herbivore activity. Unfortunately visual counts do not equate to fish presence and presence does not reflect removal rates. There is marked regional variation in ecosystem processes, with multiple thresholds based on herbivore presence and realised effect. Based on direct assays and video-based censuses of fish activity some southern reefs (Keppels Islands) recorded only five percent of the browsing activity of reefs in the northern GBR. Southern reefs have fewer fishes that are less likely to eat macroalgae. These reefs are highly vulnerable to algal overgrowth.

The vulnerability of marginal systems: One algal species *Lobophora* (a brown leathery alga) appears to be highly resistant to grazing. This species may have the capacity to dominate inshore reefs regardless of herbivore presence. It is this species that drove algal outbreaks in the Keppels and elsewhere on inshore reefs. This is one algal species that herbivores may struggle to control (details in Bennett *et al.* Coral Reefs 2010).

Marginal coral reef systems may provide valuable insights into the nature of ecosystem processes in systems on the trajectory toward a phase-shift to an alternate ecosystem state. Our study investigated the process of herbivory in a marginal coral reef system in the Keppel Islands at the southern end of the Great Barrier Reef (GBR). Branching *Acropora* coral and the brown macroalga *Lobophora variegata* occupied up to 95% of the reef substratum at the three reefs surveyed in the Keppel Islands. Feeding rates of herbivorous fishes and removal rates of *Lobophora* were directly quantified within and surrounding areas of branching *Acropora*. Feeding rates by herbivorous fishes on *Lobophora* were extremely low in both flat surfaces and branching habitats, whilst feeding on the epilithic algal matrix (EAM) was two orders of magnitude higher and highly habitat-dependent, with the highest bite rates being found in flat habitats. The overall low rates of *Lobophora* removal and significant suppression of herbivory on EAM in branching habitats were consistent with the high biomass of this brown alga throughout the Keppel Islands and with its distribution on reef crests, where *Lobophora* biomass was 20 times greater in branching than in flat habitats. This suppression of feeding by herbivorous fishes within branching coral habitats in the Keppel Islands contrasts with the typical role of coral and topographic complexity on herbivores on coral reefs and highlights the potential for complex interactions between algae, corals and fishes on coral reefs. On marginal systems herbivory may modify algal distributions but may be unable to contain the proliferation of algae such as *Lobophora*.

Management options

1. The logical first step is to protect coral reef herbivores. This includes those species that prevent algal growth (parrotfishes primarily) and those that browse on foliose macroalgae. However, it appears that there will be no simple single threshold and no single preferred management option. Various locations can vary dramatically in the rates of potential and effective herbivory. Some marginal reefs appear to be particularly vulnerable. In the north, protection of existing herbivore stocks appears to be warranted, while on southern reefs herbivore populations are limited and measures to enhance their populations may be necessary.
2. Current fishing practices do not appear to significantly impact herbivorous fish populations across much of the GBR, yet in many areas these unfished populations are unable to control macroalgae. Southern and inshore reefs are particularly vulnerable to

macroalgal dominance and the brown alga *Lobophora* appears to be particularly resistant to herbivore control.

In these locations the lack of adequate herbivore populations would suggest that the ability of reefs to reverse a phase shift to macroalgae is limited and here, measures to limit algal growth may be paramount. In these areas, particular attention to non-herbivore factors including water quality (inc. nutrients and sedimentation) would appear to be most critical with the goal of preventing rather than reversing a phase-shift to macroalgae.

Management via protection therefore appears to be a logical first step. This action will increase the probability of maintaining low algal cover on reefs. However, it is far from a guarantee. For many reefs protection of herbivores will not be enough and improved water quality, algal suppression and action to enhanced herbivore populations or herbivore activity will probably be required to help create and /or maintain low macroalgal cover on these reefs. High macroalgal cover may be a natural phenomenon on inshore reefs but an increase in algal cover will be a difficult trend to reverse, especially on marginal reef systems.

- A report on the relative roles of pre- versus post-settlement processes in limiting recovery of coral reef assemblages. [(f) JCU]

Introduction

Coral reefs are highly vulnerable to sustained and ongoing climate change owing to the temperature sensitivities of reef-building corals (Jokiel & Coles 1990), which are the primary habitat-forming species (foundation species; Dayton 1972). Severe climate-induced coral bleaching causes widespread mortality among reef-building corals (Wilkinson 2000) and is predicted to become more frequent and more severe in coming decades (Sheppard 2003, Donner *et al.* 2005). However, susceptibility to bleaching, and particularly proportional mortality due to bleaching, varies greatly within and among coral genera (Brown & Suharsono 1990, Marshall & Baird 2000, Loya *et al.* 2001, McClanahan *et al.* 2004, 2007). Therefore, increased incidence of climate-induced coral bleaching is more likely to cause marked changes in the structure of coral assemblages, rather than killing all corals over similar time frames (Hughes *et al.* 2003).

The increasing incidence of climate-induced coral bleaching will not necessarily favour those corals that are resistant to bleaching (Baker *et al.* 2008). Given projected increases in the frequency and/or severity of coral bleaching episodes (Donner *et al.* 2005), the long-term persistence of different corals may depend largely upon their capacity for recovery following recurrent bleaching (Baker *et al.* 2008). Accordingly, highly susceptible corals (e.g. *Acropora*) have become even more dominant in the aftermath of severe bleaching at some locations (Sheppard *et al.* 2002). Elsewhere, however, coral bleaching (often in combination with other disturbances) have caused declines in the abundance of highly susceptible coral species (Table 1).

There is a well-established hierarchy of bleaching susceptibility among different coral genera (Loya *et al.* 2001, McClanahan *et al.* 2007). *Acropora*, for example, is the first and worst affected genera, whereas *Porites* is resistant to all but the most severe episodes of coral bleaching (Riegl 1999, Loya *et al.* 2001, Baird & Marshall 2002). Increasing frequency of coral bleaching and differential mortality between these two genera have led to predictions of increasing dominance of *Porites* at the cost of *Acropora* (Riegl and Purkis 2009). Replacement of erect branching corals (e.g., *Acropora*) with encrusting and/or massive corals (e.g., *Porites*), greatly reduces habitat availability and topographical complexity of coral reef environments, thereby reducing biodiversity and productivity. While *Acropora* species are fast-growing and structurally complex corals, *Porites* tend to be massive, slow-

growing species, which provide little shelter to reef-associated organisms, such as fishes (Pratchett *et al.* 2009a).

The abundance and composition of fish communities are strongly influenced by the physical and biological structure of benthic reef environments (e.g. Ault & Johnson 1998). Reefs with low habitat complexity and topographic relief support far fewer fishes (e.g., Sano *et al.* 1987, Graham *et al.* 2006) owing to the critical role of topographic complexity in moderating recruitment, competition and predation (Coker *et al.* 2009). Thus, the interplay between *Acropora* and *Porites* (and other major coral genera) is of key importance for contemporary and future ecology of tropical coral reefs. However, conventional monitoring of coral reef habitats is invariably based on estimates of total coral cover (reviewed by Bruno and Selig 2007), which does not account for potential shifts in community structure. Similarly, predicted effects of coral reef degradation on coral reef fishes focus on consequences arising from extensive coral loss (Munday *et al.* 2008, Pratchett *et al.* 2008a), rather than changes in the community structure of coral assemblages.

The purpose of this study was to assess changes in the structure of coral assemblages in the aftermath of the 2001-02 mass-bleaching in the central Great Barrier Reef, as well as assessing effects of coral recovery (or lack thereof) on local fish assemblages. Long-term monitoring of fish and coral assemblages (up to 8 years post-bleaching) was undertaken to assess the resilience of fish and coral assemblages, and to identify what factors potentially limit resilience of coral reef assemblages. Two critical components of resilience are; i) resistance, which is generally assessed based on the ability to survive during major bleaching events, and ii) recovery, which is the rate at which different corals recruit and grow to colonise available space in the aftermath of mass-bleaching and widespread coral mortality. Only a few previous studies have explored differential recovery of coral assemblages (Table 1 and references therein), but this is fundamental to assessing if, and how, reef assemblages will change due to climate change.

Methodology

Sampling design

This study was conducted at Trunk Reef (18°17'S, 146°53'E), in the central section of the Great Barrier Reef (GBR), Australia. Trunk reef is a large (ca. 125km²) submerged reef, located ~120km north of Townsville. This reef, like many throughout the GBR, was subject to extensive and wide-spread coral bleaching during the summer (November to March) of 2001-02 (Berkelmans *et al.* 2004). In order to assess impacts of coral bleaching, local assemblages of both scleractinian corals and butterflyfishes were examined at Trunk Reef in May 2000 (eighteen months before bleaching), in March 2002 (towards the end of the bleaching event), in March 2005 (three years after bleaching), and most recently, in January each year from 2008 to 2010. Sampling was conducted on the shallow reef crest (two to three metres' water depth), at three randomly selected sites along the exposed (south-east) side of Trunk Reef. All sites were non-overlapping and independent, but were very similar in their physical structure, aspect, and exposure to prevailing south-east trade winds.

In 2008-2010, coral cover and composition was quantified using photographic records of the benthos taken at one-metre intervals along the length of fifty-metre transects that were deployed to survey butterflyfishes. Within each photograph we recorded the substrate type or benthic organisms immediately beneath the transect line corresponding with one-metre markings (e.g. 1.0, 2.0, etc.).

Densities of butterflyfishes on the reef crest at Trunk reef were quantified using underwater visual census (UVC) along fifty-metre transects. Adult butterflyfishes observed within two metres either side of the transect line were counted and recorded to species. All transects were positioned within ten metres of the edge of the reef crest, following the natural contours of the

reef. Five replicate transects were conducted at each site. To test for differences in responses of butterflyfishes according to their specific trophic requirements (Graham, 2007), all species were categorised as either, i) obligate corallivores (OC), ii) facultative corallivores (FC), or iii) non-coral feeders (NC). Species were assigned to feeding guilds following Pratchett (2005).

Coral recruitment

Densities of coral recruits, defined as juvenile corals that had settled on natural substrates and visible with the naked eye were quantified in January 2009 and 2010, to test for differential rates of replenishment among study sites. Only corals that were <5cm diameter were counted, following Rylaarsdam (1983), representing the several distinct year classes of coral recruits. Densities of coral recruits were quantified within a one-metre wide belt along the first ten metres of transects deployed to quantify benthic composition.

Results and Discussion

a) Changes in coral cover and composition

Coral cover on the reef crest at Trunk reef declined significantly between May 2000 and March 2005, to a low of 3.2% (± 0.8 SE) in March 2005 (Figure 8, Table 1). Since 2005, there has been a moderate increase in coral cover to 12.3% (± 1.4 SE) in January 2010 (Figure 8). Recent increases in coral cover are mainly due to increased cover of *Acropora* species (Figure 9).

The rapid recovery and increasing dominance of *Acropora* spp. in the aftermath of extensive coral bleaching suggests that climate forcing of coral communities may initially favour coral species with rapid recovery potential, rather than slow-growing corals that might otherwise have greater resistance to bleaching, as suggested previously (e.g. McClanahan *et al.* 2007). Fortunately, faster growing corals (especially *Acropora*) contribute most to topographic complexity of reef habitats and are also the major corals used by corallivorous and coral-dwelling fishes (Pratchett, *et al.* 2008). However, persistence of *Acropora* populations will depend on sufficient time between successive bleaching events to allow for recovery. Recovery was mostly very limited (but occasionally spectacular) in the five years since extensive bleaching in the central GBR. Donner *et al.* (2005) project that bleaching is likely to occur at least every two years on most coral reefs around the world by 2040, meaning that there would be insufficient time for recovery of *Acropora* spp., let alone other slower growing species (e.g. *Porites*). Sustained and ongoing climate change will undoubtedly change the community structure of coral assemblages (Hughes *et al.* 2003; McClanahan *et al.* 2007); yet specific effects will depend on the severity, extent and recurrence of future bleaching events.

b) Effects of coral loss on butterflyfishes

Climate-induced coral bleaching represents one of the most significant and increasingly prevalent disturbances to coral reef ecosystems, which not only causes extensive coral mortality, but also reduces the abundance of many other coral reef organisms that are reliant on corals for food, shelter or recruitment (e.g. Wilson *et al.* 2006; Pratchett *et al.* 2008a).

At Trunk Reef, extensive coral depletion was accompanied by a five-fold reduction in the abundance of butterflyfishes. Declines in abundance of butterflyfishes were most rapid and most severe for obligate corallivores, which is to be expected given their obligate dependence on coral for food. Corallivorous fishes have the most apparent and direct reliance on live corals and are consistently among the worst affected fishes following extensive coral loss (Wilson *et al.* 2006).

The extent to which corallivorous fishes feed on corals (versus other non-coral prey) is highly variable (e.g. Pratchett 2005) and obligate coral-feeders are much more affected by coral loss than facultative coral-feeders (e.g. Graham 2007). Accordingly, facultative corallivores

were relatively unaffected by initial declines in abundance of corals at Trunk Reef, but did experience declines over the longer-term. The only species that was seemingly unaffected by the coral loss and associated habitat-degradation was *C. citrinellus* (Figure 10), which is one of the few butterflyfishes reported to feed on algae.

Protracted declines in the abundance of butterflyfishes may be attributable to the loss of habitat structure or habitat diversity associated with extensive coral loss (Pratchett *et al.* 2008a), and this may also be the reason why non-coral feeding butterflyfishes have ultimately declined in abundance more than five years after the initial coral loss. It is also possible that coral depletion has reduced settlement success by butterflyfishes (e.g. Jones *et al.* 2004), which might explain protracted declines in population size. However, butterflyfishes with low coral content in their diet as adults tend not to recruit to live corals (Pratchett *et al.* 2008b), but overall declines in habitat complexity may have reduced post-settlement survivorship of all species (Graham *et al.* 2007).

Topographic complexity of coral reef habitats has an important influence on biotic interactions, such as predation and competition, and has a major influence on the local abundance of coral-reef fishes, especially during early life stages (Almany, 2004). Climate-induced coral bleaching kills corals, but leaves the underlying skeleton completely intact (Hoegh-Guldberg, 1999). Exposed coral skeletons are then subject to a whole suite of bio-eroding organisms that undermine the structural integrity of these carbonate structures (Hutchings, 1986). Reef habitats with reduced topographic complexity typically support lower fish abundance, fewer species, and increased evenness (Gratwicke & Speight, 2005; Graham *et al.* 2006).

c) Spatial variation in coral recovery and coral recruitment

This study focused on specific study locations along the exposed reef crest at Trunk reef as baseline data on coral and butterflyfish assemblages were recorded prior to the bleaching in 2000 (Pratchett *et al.* 2004, 2006). However, the extent of coral depletion and declines in abundance of butterflyfishes (especially corallivorous species) reported for Trunk Reef are similar across the full range of locations (reef crest and reef slope habitat at three different reefs; Trunk Reef, Bramble Reef and Rib Reef) surveyed since 2008. Interestingly however, coral recovery has been highly variable within and among reefs. At Bramble reef, for example, there are two sites where coral cover has increased to ninety percent within the five years since the bleaching (Figure 11). Even so, there has been no apparent recovery of butterflyfishes at any of these sites. These findings contradict previous studies that suggested recovery of fishes would closely follow coral recovery (Halford *et al.* 2004). Recovery of fish populations at these sites appears to be currently limited by a lack of new recruits. Recruitment rates by butterflyfishes are generally low (Pratchett *et al.* 2008b) and may have been further constrained by limited coral cover at potential settlement sites, as well as widespread depression of breeding populations.

Spatial variation in coral recovery (within and among reefs) could not be explained on the basis of differential coral recruitment. Densities of coral recruits (small corals <5cm diameter) varied greatly within and among reefs, ranging from 3.1 (\pm 0.03) recruits per m² at site 1 at Rib reef, to 6.5 (\pm 0.33) recruits per m² at site 2 at Rib reef. In all, mean rates of recruitment were fairly similar among reefs, but varied greatly among sites within each reef (especially at Rib and Trunk). At Bramble reef, rates of recruitment were very consistent among sites, despite a fourfold difference in adult coral cover (Figure 12).

Conclusion

These results suggest that there is limited resilience among fish and coral assemblages in the central Great Barrier Reef, and that further increases in the frequency and/or severity of warm water bleaching will cause major (potentially catastrophic) changes in the structure of

local reef assemblages. Even if reef assemblages are resilient and just take more than 8 years to become re-established, it seems unlikely that contemporary reef assemblages could not be sustained in the face of future global warming, where climate-induced coral bleaching is expected to become more frequent and/ or more severe (Sheppard 2003). The only corals that did expect significant resilience and may persist in face of increasingly frequent coral bleaching were the *Acropora*, as was also shown in the central Indian Ocean (Table 1). Ongoing research is required to establish what factors are limiting the resilience of non-*Acropora* corals in the central Great Barrier Reef, but this probably relates to slow growth rates of post-settlement colonies given that there was seemingly high levels of coral recruitment across all study sites.

Acknowledgements

Field sampling was conducted by Andrew Baird, Andrew Cole, Darren Coker, Nick Graham, Dominique McCowan, and Shaun Wilson.

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Table 1. Contrasting shifts in the structure of coral assemblages associated with major disturbances, mostly the 1998 global mass-bleaching event.

Location	Increasing dominance	Decreasing dominance	Major disturbance(s)	Reference(s)
Arabian Gulf	<i>Porites</i>	<i>Acropora</i>	Recurrent Bleaching	Riegl & Purkis 2009, Sheppard <i>et al.</i> 2010
Western Indian Ocean	<i>Porites</i> and <i>Pocillopora</i>	<i>Acropora</i>	Bleaching (1998 & 2005)	McClanahan <i>et al.</i> 2007
Chagos	<i>Acropora</i>	-	Bleaching (1998)	Sheppard <i>et al.</i> 2002
Southern Japan	<i>Porites</i> and <i>Montipora</i>	<i>Acropora</i>	Bleaching (1998)	Kayanne <i>et al.</i> 2002
French Polynesia	<i>Porites</i> and <i>Pocillopora</i>	<i>Acropora</i>	Multiple disturbances	Berumen & Pratchett 2006, Adjeroud <i>et al.</i> 2009

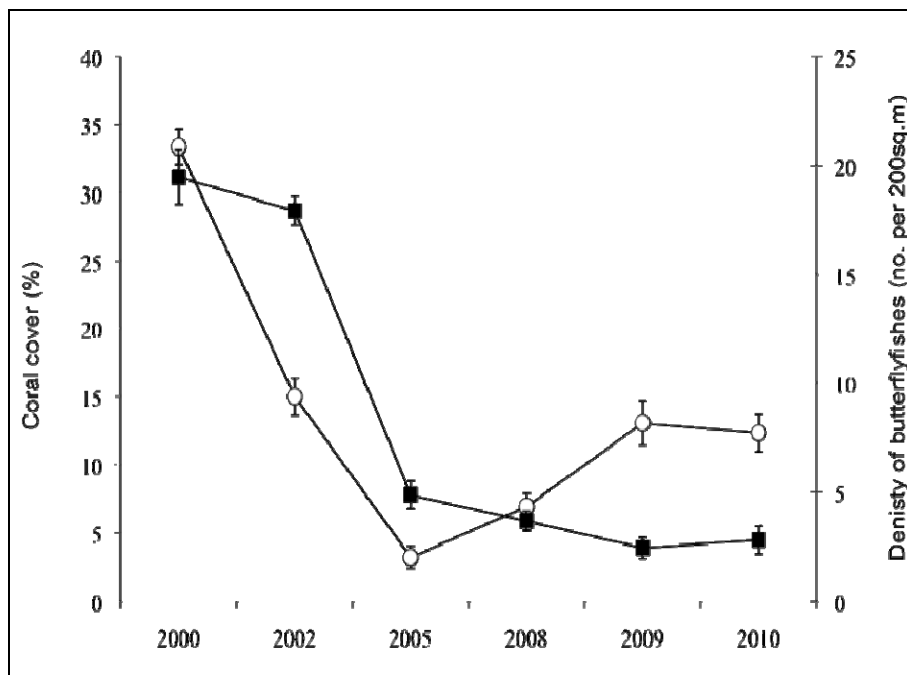


Figure 8. Mean (\pm SE) coral cover (open circles) and local densities of butterflyfishes (closed circles) on the reef crest at Trunk Reef, central Great Barrier Reef. Local abundance of fish and corals declined following climate-induced coral bleaching in 2001-02, and while there is some evidence of coral recovery five years post-bleaching, there is yet to be an increase in local abundance of butterflyfishes.

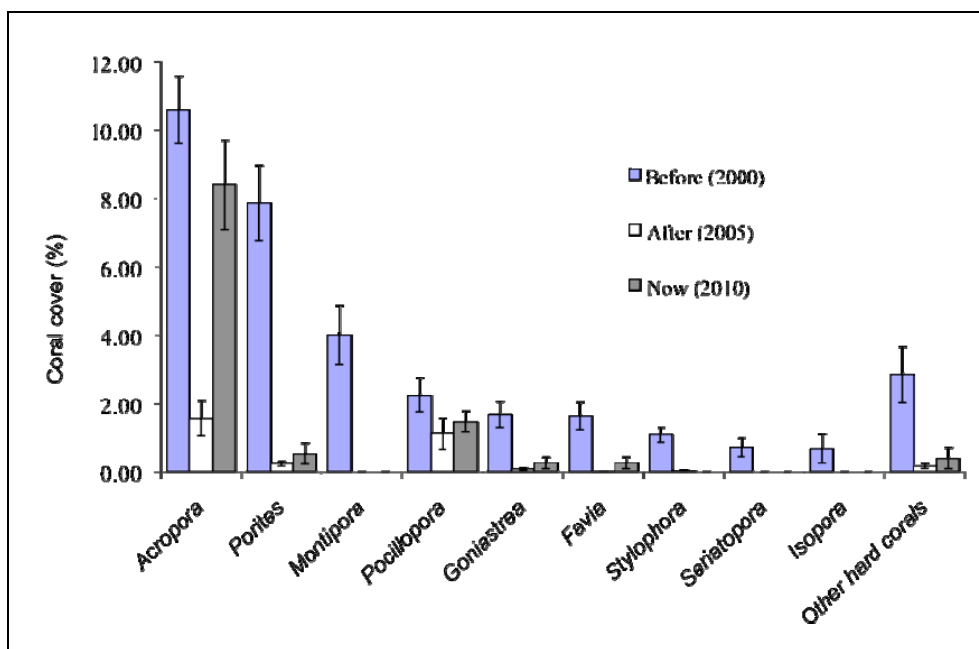


Figure 9. Temporal changes in mean (\pm SE) coral cover (%) of major coral genera on the reef crest at Trunk Reef, central Great Barrier Reef. Live cover of virtually all coral taxa (except *Pocillopora*) declined significantly between 2000 and 2005 (mostly due to mass bleaching in 2001-02), and only *Acropora* has shown substantial recover since that time.

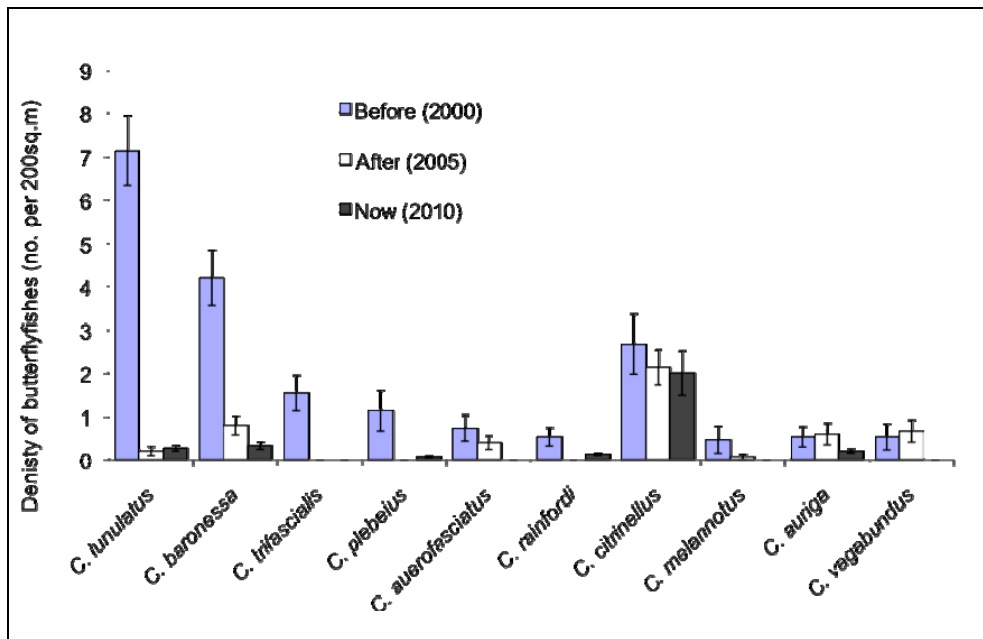


Figure 10. Temporal changes in mean (\pm SE) abundance of butterflyfishes at Trunk Reef, central Great Barrier Reef. Species are ordered according to their initial abundances within broad trophic groups (Obligate corallivores: *C. lunulatus* – *C. rainfordi*; Facultative corallivores: *C. citrinellus* and *C. melannottus*; Non-coralivores: *C. auriga* and *C. vagabundus*)



Figure 11. Extensive cover of *Acropora* (mostly *A. hyacinthus*) at Bramble Reef in January 2008.

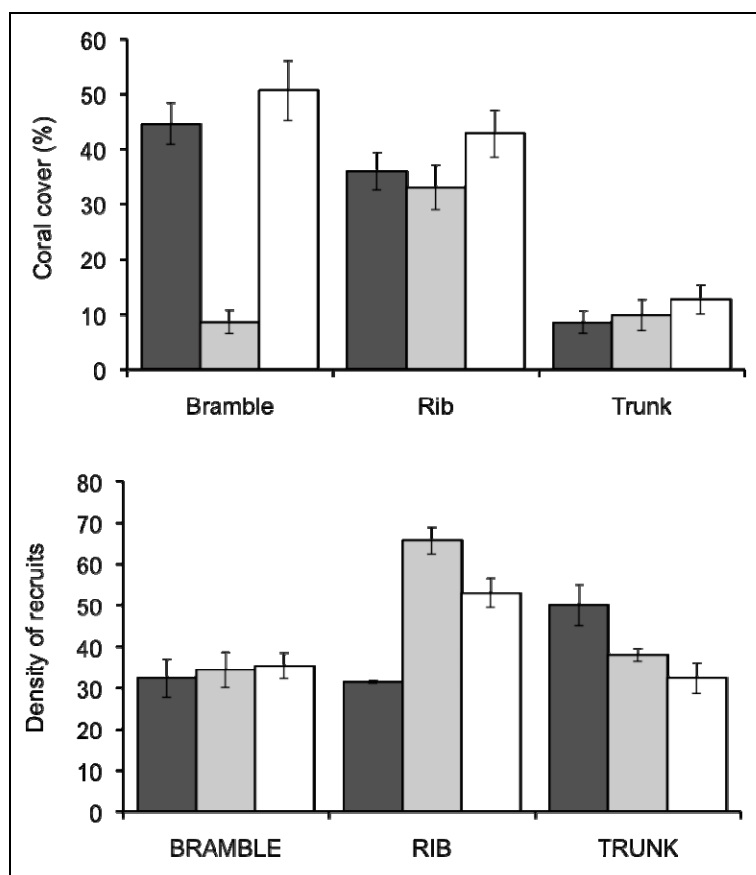


Figure 12. Spatial variation in A) adult cover (%) of scleractinian corals and B) average densities of coral recruits (no. per 10m²) for three sites at each of three reefs in the central Great Barrier Reef in January 2010.

- Paper submitted (with appropriate attribution of MTSRF funding and copy delivered to the RRRC) discussing patterns and processes of extreme spatial variation in recovery and resilience of fish and coral assemblages. [(f) JCU]

Two papers have been published, arising from the abovementioned research on recovery and resilience of fish and coral assemblages at Trunk Reef, central Great Barrier Reef:

1. Pratchett MS, Baird AH, McCowan DM, Coker DJ, Cole AJ, Wilson SK (2009) Protracted declines in coral cover and fish abundance following climate-induced coral bleaching on the Great Barrier Reef. *Proceedings of the 11th International Coral Reef Symposium*, Ft. Lauderdale, Florida 1: 1042-1046.
2. Lawton RJ, Bay LK, Pratchett MS (2010) Isolation and characterization of 29 microsatellite loci for studies of population connectivity in the butterflyfishes *Chaetodon trifascialis* and *Chaetodon lunulatus*. *Conservation Genetics Resources* [doi 10.1007/s12686-009-9138-0]

The first of these papers outlines the results of surveys conducted at Trunk Reef up until 2008, highlighting mostly protracted, but highly variable recovery among fish and coral assemblages. The second manuscript relates to ambitious extension of the original research, where we hoped to establish source populations for newly recruiting butterflyfishes, to assess the scale of dispersal relative to the scale of major disturbances, such as mass-bleaching events. A first step in completing this project was to develop the necessary toolkit to quantify population connectivity among butterflyfishes, and thus, we have prepared an extensive microsatellite library, based on genetic samples of two common and widespread butterflyfishes, *Chaetodon trifascialis* and *Chaetodon lunulatus*.

A further manuscript, outlining the comprehensive findings from recent and ongoing field surveys is currently in preparation, and will be submitted to the Journal of Fish Biology within coming months. The purpose of this paper is to explore the differential rates of population declines among butterflyfishes from different trophic groups and show the lack of recovery despite local increases in coral cover.

3.3 Lodgement of meta-data

- Meta-data describing all data generated by MTSRF Project 2.5i.3 lodged on the e-Atlas.

Meta-data, in the form of predictive maps of outbreak likelihood for the group of coral diseases known as white syndromes in relation to thermal stress, have been submitted to the RRRC for lodgement on the e-Atlas. [(c) JCU]

All data and preliminary analyses have now been formatted and delivered to the e-Atlas. [(d/e) JCU]

4. Communications, major activities and events

During 2009-10 combined milestone reporting period:

- Emily Howells (PhD candidate) presented her results on the effects of coral bleaching on *Symbiodinium* populations at the Australian Coral Reef Society Conference (Darwin, 2009) and was awarded the Vicki Harriott Memorial Prize for best student presentation. [(a) AIMS/JCU]
- A media release has been drafted through the ARC Centre of Excellence for Coral Reef Studies and will be submitted to the RRRC and GBRMPA to review in the coming weeks to coincide with the public release of the modelling tool for predicting the likelihood of white syndrome outbreaks on the Great Barrier Reef. Release of the tool suite has been delayed waiting for final sign-off by the GBRMPA on a contract for services that will enable our team to produce the predictions of outbreak risk for 2010 and update the website. It is envisaged that final sign-off will occur in the next few weeks, thus release of the tool suite is planned for early July and will coincide with the updating of the website with this year's predictions. [(c) JCU]
- The model for predicting WS outbreak likelihood developed in this project was presented by Professor Bette Willis in a talk entitled *Predicting white syndrome outbreaks on the Great Barrier Reef: enabling targeted research and informing management* (authors: JA Maynard and BL Willis) at a NOAA workshop on *Environmental monitoring of coral disease and bleaching in the Hawaiian Islands* in Honolulu in August 2009. The primary objective for the workshop was to develop similar tools for predicting disease outbreak likelihood for Hawaiian reefs. [(c) JCU]
- Final results and conclusions were presented at the *Impacts and Achievements of the MTSRF Conference* held 18-20 May in Cairns by Morgan Pratchett in a paper entitled *Where is our resilience? Changes in the structure of reef assemblages following warm water bleaching on the Great Barrier Reef in 2001-02*. [(f) JCU]