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Multiple stressor effects on coral reefs

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Abstract

Coral reef ecosystems around the world face a number of threats, including ocean acidification, increased ocean temperatures due to anthropogenic global warming (AGW), increased disease outbreaks, crown-of-thorns starfish outbreaks, terrestrial sedimentation, eutrophication, pollution, and fishing pressure. At the same time, coral reef ecosystems provide valuable direct and indirect economic and social benefits to millions of people worldwide. However, the intensity and spatial distribution of threats are likely to change with increasing human population and economic development, and thus understanding how multiple stressors may interact and affect coral reefs – particularly in the face of incomplete knowledge about these stressors – is an issue of pressing importance.

This thesis aims to explore and advance the understanding of interactions between multiple stressors and their effects as they pertain to coral reefs generally and the Great Barrier Reef specifically. I review several of the components that are integral to this issue, including: stressors and stress ecology, research to date on the issue of multiple stressors and coral reefs, the multiple threats from climate change to coral reefs, and approaches to modelling and managing multiple stressors.

The overall aim of this thesis is to quantitatively evaluate the importance of multiple stressor interactions to coral reef ecosystems and to assess alternative management approaches to mitigating the effects of potentially increased prevalence and severity of these stressors. I do this through both assessing the state of existing knowledge as well as by using new approaches to model stressors and stressor effects within the context of the GBR. In addition, I seek to provide an example of how these effects can be conceptualized and managed more effectively in the face of uncertain knowledge and incomplete data.

The specific research objectives of my thesis are as follows:

1. To synthesize the available knowledge of multiple stressors on coral reefs;
2. To use the occurrence of bleaching and disease in the GBR as a case study to determine the spatial and temporal overlap of these stressors;

3. To use expert knowledge to identify key uncertainties and knowledge gap(s) regarding multiple stressor interactions on coral reef systems;
4. To apply expert-elicited knowledge about stressors and stressor interactions on the GBR to map potential threats to reefs under a variety of different climate change and management scenarios.

Chapter 2 addresses research objective 1 by using a formal literature search to provide the foundation for a qualitative and selected quantitative meta-analysis of multiple-stressors as they pertains to coral reef ecosystems, and by examining the evidence for the prevalence of synergistic, antagonistic, and additive interactions between stressors. Here I investigate stressor interactions in two ways: first by examining stressor interactions with other stressors, and secondly by looking at potentially synergistic effects between two or more stressors on a response variable (where stressors interact to produce an effect that is greater than purely additive). For stressor-stressor interactions, I found 176 studies that examined interactions between at least two stressors. Applying network analysis to analyse relationships between stressors, I found that pathogens were exacerbated by more co-stressors than any other stressor, while sedimentation, storms, and water temperature directly affected the largest number of other stressors. Pathogens, nutrients, and crown-of-thorns starfish were the most-influenced stressors. In terms of responses to multiple stressors, I found 187 studies that examined the effects of two or more stressors on a third dependent variable. The interaction of irradiance and temperature on corals has been the subject of more research than any other combination of stressors, with many studies reporting a synergistic effect on coral symbiont photosynthetic performance. Second, I performed a quantitative meta-analysis of existing literature on the interaction between temperature and irradiance. Although the sample size was small, I found that the mean effect size of combined treatments was statistically indistinguishable from a purely additive interaction. This chapter provides evidence that considerable gaps remain in our knowledge regarding numerous stressor interactions and effects, and that the available evidence is inconclusive on whether synergistic effects are widespread in coral reef systems.

Chapter 3 addresses research objective 2 by using data from the AIMS Long-term Monitoring Program (LTMP) to examine the spatial and temporal overlap of bleaching and disease in the

GBR. Coral bleaching and disease have often been hypothesized to be mutually reinforcing or co-occurring, but much of the research supporting this has only drawn an implicit connection through common environmental predictors. I examine whether an explicit relationship between white syndrome and bleaching exists using assemblage-level monitoring data from up to 112 sites on the reef slopes spread throughout the GBR over 11 years of monitoring. None of the temperature metrics commonly used to predict mass bleaching performed strongly when applied to these data, and the inclusion of bleaching as a predictor did not improve model in predicting white syndrome outbreaks. Conversely, the inclusion of white syndrome as a predictor did not improve models of bleaching. Evidence for spatial co-occurrence of bleaching and white syndrome at the assemblage level in this dataset was also very weak. These results suggest the hypothesized relationship between bleaching and disease events may be weaker than previously thought, and more likely to be driven by common responses to environmental stressors, rather than directly facilitating one another.

Chapter 4 addresses research objective 3 by exploring the use of Bayesian Belief Networks (hereafter BBNs) in conjunction with expert elicitation to determine the degree of expert consensus about the greatest threats to the GBR, and assessing the degree of confidence that experts have about the effects of various stressors both alone and in combination. BBNs are finding increasing application in adaptive ecosystem management where data are limited and uncertainty is high. I used a formal expert-elicitation process to obtain estimates of outcomes associated with a variety of scenarios in the GBR that combined stressors both within and outside the control of local managers. Among consulted experts, there was much stronger consensus about certain stressor effects - such as between temperature anomalies and bleaching – than others, such as the relationship between water quality and coral health. In general, models generated from the mean responses from experts predicted that climate change effects could potentially overshadow the mitigating effects of management actions to reduce local stressors.

Chapter 5 addresses research objective 4 by implementing the model developed in Chapter 4 in a spatial way through the use of several scenarios. Coral reefs are one example of an ecosystem where management of local stressors may be a way of mitigating or delaying the effects of climate change. In this chapter, I use a combination of an expert-elicited BBN and empirical, spatial environmental data to examine how hypothetical scenarios of climate change and local management would result in different outcomes for coral reefs on the GBR. I also assess whether reefs within the existing protected area network differ in their predicted probability of decline from reefs outside the protected area network. Parameterizing the BBN using the mean responses from my expert pool resulted in predictions of limited efficacy of local management in combating the effects of climate change; however, there was considerable variability in expert responses; thus, I also examine the effect that using optimistic versus pessimistic expert responses has on the model predictions of coral cover decline on the GBR. Many reefs within the central GBR appear to be at risk of further decline, but further parameterization of the model as data and knowledge become available will improve predictive power. This approach serves as a proof of concept for subsequent work that can fine-tune parameters and explore uncertainties in predictions of responses to management.

My thesis thus addresses two critical elements that are often missing from studies examining the conservation implications of multiple stressors (especially on coral reefs): interactions between stressor/stressor effects and assessing the effect of different management options on these interactions.

Publications associated with this thesis

Publications

Evidence for multiple stressor interactions and effects on coral reefs. **Ban, S.S.**, Graham, N.A.J., Connolly, S.R. Global Change Biology 20(3): 681-697. (Chapter 2)

Relationships between temperature, bleaching and white syndrome on the Great Barrier Reef. **Ban, S.S.**, Graham, N.A.J., Connolly, S.R. 2013. Coral Reefs 32: 1-12. (Chapter 3)

Assessing interactions of multiple stressors when data are limited: A Bayesian belief network applied to coral reefs. **Ban, S.S.**, Pressey, R.L., Graham, N.A.J. Global Environmental Change 20(3): 681-697. (Chapter 4)

Conference Presentations

- **Ban, S.** Expert elicitation of a Bayesian Belief Network for climate change effects on the Great Barrier Reef. Oral presentation, 2013. North Pacific Marine Science Organization Annual Meeting. Nanaimo, British Columbia. October 11-20, 2013.
- **Ban, S.**, Pressey, R.L. Expert elicitation of a Bayesian Belief Network for the Great Barrier Reef. Oral presentation, 2012. Society for Conservation Biology Oceania. Darwin, Northern Territory. September 21-23, 2012.
- **Ban, S.,** Connolly, S.R.C., Graham, N.A.J. Interactions between bleaching and white syndrome on the Great Barrier Reef. Oral presentation, 2012. International Coral Reef Society. Cairns, Queensland. July 9-13, 2012.
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- **Ban, S.**, Pressey, R.L. An Integrated Bayesian Model of Coral Bleaching and Disease. Oral presentation, International Marine Conservation Congress. Victoria, BC. May 14-18, 2011.
- **Ban, S.,** Pressey, R.L. Modelling resilience and spatial responses of coral reef ecosystems to climate change and associated stressors. Oral presentation, 2010 International Congress of Conservation Biology, Edmonton, AB. July 3-7, 2010.

Other publications produced during my candidature

Publications

Designing, implementing and managing marine protected areas: emerging trends and opportunities for coral reef nations. Ban, N.C., Adams, V.M., Almany, G.R., **Ban, S.**, Cinner, J., McCook, L.J., Mills, M., Pressey, R.L., White, A. 2011. Journal of Experimental Marine Biology and Ecology 408(1):21-31.

Recasting shortfalls of marine protected areas as opportunities through adaptive management. 2012. Ban, N.C., Cinner, J.E., Adams, V.M., Mills, M., Almany, G.R., **Ban, S.S.**, McCook, L.J., White, A. Aquatic Conservation: Marine and Freshwater Ecosystems 22(2):262-271.

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Chapter 1 General Introduction

Thesis rationale

This thesis aims to quantitatively evaluate the importance of multiple stressor interactions in coral reef systems generally and the Great Barrier Reef (hereafter GBR) specifically, and to assess management options for potentially mitigating the effects associated with increased prevalence and severity of these stressors. In this introduction, I briefly review several of the components that are integral to this set of issues, including: stressors and stress ecology, research to date on the issue of multiple stressors and coral reefs, the multiple threats from climate change to coral reefs, and approaches to modeling and managing multiple stressors. A more comprehensive review of the literature on multiple stressors and coral reefs is provided in Chapter 2.

Stress ecology and multiple stressors

The question of how ecosystems respond to stress has become one of the cornerstones of ecological research, and thus defining stress and stressors is paramount. The term "stress" and "stressor" were first defined in the field of physiology (Mason 1975). In the physiological literature, the distinction was made quite early between stress and stressor (Selye 1950), with the former being defined as "[a condition] within the organism in response to evocative agents" and the latter referring to these evocative agents. In the ecology literature, there was much debate over the definition of what a stress was, how it could be measured, and whether a stress and stressor were distinct concepts. For example, Barrett et al (1976) defined a stress as "a perturbation (stressor) applied to a system (a) which is foreign to the system, or (b) which is natural to that system but applied at an excessive level". Odum (1979) distinguished between a stress and a subsidy, the latter of which he defined as "favourable deflections in which the performance is in some manner improved." Stress has also been described as an effect rather than as a cause: "stress acts as a dependent variable, internal to the organism, being a response or output which is caused by some known factor that is usually identified as the stressor." (Franz 1981). A more general definition of stress was provided by Underwood (1989): "any environmental change in a factor that causes some response by a population of interest".

Furthermore, within the ecological literature, the terms "disturbance", "stress", and "perturbation" have been used almost interchangeably (Borics et al. 2013). However, with increasing human pressure on global ecosystems, it is the deleterious effect(s) of stress that have received the most research attention, and thus are the focus of this thesis. Additionally, I use Selye's (1950) and Franz's (1981) convention where a stressor is the cause and stress (or stress response) is the effect.

Ecosystems have always been subject to disturbances, whether from within or from external influences, but with rapid human population growth and the extent of human activity on the planet, many ecosystems are exposed to multiple stressors of anthropogenic origin (Breitburg et al. 1998). Anthropogenic stressors are likely to co-occur, since many human activities produce more than one type of potential stressor. Thus most ecosystems are likely exposed to multiple anthropogenic stressors, possibly in addition to natural stressors.

Although the importance of stressor interactions on ecological systems was identified over a decade ago (Breitburg et al. 1999), only recently have such interactions been quantified, especially from an ecosystem management perspective (Halpern et al. 2008a; Halpern et al. 2008b). Much of what we know about disturbance effects on ecosystems comes from single-stressor experiments, due largely to the number of permutations of experimental treatments required as the number of stressors increases beyond two. This infeasibility of performing multiple-stressor experiments at the ecosystem level has led to a search for alternate ways of studying their effects, such as the use of mesocosms and novel statistical analyses of ecological data across environmental gradients (Breitburg et al. 1998).

Multiple stressors interact in different ways. In the simplest case – which is often the default assumption when modeling their effects – the effect of two or more stressors is simply additive, *i.e.* the effect of two stressors in combination is the sum of their individual effects. Furthermore, stressors are often assumed to be independent – at the ecosystem level, different stressors will affect different members of an ecological community (Vinebrooke et al. 2004); or, at the organismal level, different stressors will affect different physiological processes (e.g., Sanders 1979). However, stressors can also be antagonistic (inhibiting the adverse effects of one or more of the other stressors), or synergistic (exacerbating the adverse effects of one or more of the others). Because multiple stressors can interact in non-additive ways (i.e., antagonistically or synergistically) their effects on ecosystems is often non-linear, possibly resulting in phenomena such as phase shifts (Hughes 1994; Beisner et al. 2003; Mangel & Levin 2005) and ecological surprises - where the behaviour of a natural system may radically deviate from expectations or historic conditions (Lindenmayer et al. 2010). Although phase shifts can also occur in response to single stressors, there is some evidence that synergistic effects between disparate stressors have resulted in ecological surprises (Hecky et al. 2010). For example, even though temperature, dissolved organic carbon, and pH individually had the effect of reducing consumer biomass in temperate lakes, when applied together they had the effect of increasing consumer biomass (Christensen et al. 2006). In another example, the combined effects of eutrophication, acidification, and salinization led to regime shifts between macrophyte-dominated and phytoplankton-dominated lentic systems (Davis et al. 2010). Despite this evidence that multiple stressors often act in non-additive ways, both theoretical and applied research still commonly uses an additive model for cumulative impacts (Crain et al. 2008). While there is likely no single reason for the near-ubiquity of the additive assumption, part of it may be due to ANOVAs typically being the first type of statistical model that many scientists are exposed to in their statistical training and thus are most comfortable using. Furthermore, the use of additive models is likely self-perpetuating, with their commonality justifying their further use. Thus, understanding how multiple stressors interact is a key part of practically managing human impacts on ecosystems.

Multiple stressors can also have higher-order effects through their interactions (Billick & Case 1994; Crain et al. 2008); these can be thought of as proximate vs. ultimate effects or direct vs. indirect effects. For example, in a coral reef context, a first-order (direct, proximate) interaction would be a reduction of irradiance by increased sediment loading. A second order (indirect, ultimate) interaction would be a decrease in bleaching due to the reduction in irradiance. Outside of a laboratory setting, few studies have quantified or even considered such higher-order effects.

Two recent reviews have quantitatively examined interaction of multiple stressors in marine systems, highlighting the relative paucity of knowledge regarding the real-world consequences of these stressor interactions, especially in coral reef ecosystems. Crain et al (2008) reviewed multiple stressor studies in marine systems across all types of response variable and found a total of 202 studies, excluding those that looked at indirect impacts (such as trophic cascades due to fishing pressure); this study found that cumulative effects were additive in 26% of studies, antagonistic in 38%, and synergistic in 36%. Darling & Cote (2008) found only 23 studies in the entire ecological literature from 1965-2007 (none of which were specific to coral reefs) that featured controlled factorial experiments concerning two stressors and with mortality as the response variable. Both of these reviews observed that the majority of studies investigating stressor interactions found non-additive (*i.e.*, either synergistic or antagonistic) effects. These reviews underscore the need to better understand the nature of stressor interactions in a coral reef context.

Multiple stressor implications for coral reefs

Interactions of multiple stressors, and the resulting cumulative impacts, have been identified as a research priority for coral reefs (GBRMPA 2009b). Coral reef ecosystems around the world face a multitude of threats, most of which are ultimately – if not proximately – anthropogenic. These threats include, but are not limited to: ocean acidification, increased ocean temperatures due to anthropogenic global warming (AGW), increased disease outbreaks (Willis et al. 2004), crown-of-thorns starfish outbreaks (Brodie et al. 2005), terrestrial sedimentation (Fabricius 2005), eutrophication (Bell 1992), pollution (Lewis et al. 2009), and fishing pressure (Jackson et al. 2001). In addition, increasing human population, economic development, and coastal development may affect the future spatial distribution and severity of these stressors.

Different disturbances and stressors have varying effects on components of coral reef ecosystems. For example, the main effect of cyclones is physical damage to coral structures, and fragile, branching corals tend to be disproportionately affected by this damage. Similarly, there are species-specific and size-specific differences in coral susceptibility to bleaching and disease with corresponding differences in mortality rates (Marshall & Baird 2000; Willis et al. 2004; Roff et al. 2011). Other disturbances such as outbreaks of crown-of-thorns (*Acanthaster planci*) starfish also differentially affect mortality, recovery and diversity of coral species (Glynn 1974; Endean et al. 1988; Cameron et al. 1991b, a).

Most organism-specific research on the response of coral reefs to stress has focused on coral organisms. Coral organisms exhibit several different kinds of stress responses. One indicator of environmental stress in corals is bleaching, where the primary trigger is thought to be the combination of high irradiance with high water temperatures (Hoegh-Guldberg 1999). However, bleaching is also known to occur in response to cold water stress, salinity stress, and sedimentation stress (Fitt et al. 2001). Other types of physical and biological stress may be manifested by responses up to, and including, mortality – including increased susceptibility to disease, reduced growth and calcification, decreased photosynthetic efficiency, and reduced heterotrophic feeding efficiency. Adding to the complexity, the response of coral organisms to changes in basic physical conditions such as salinity, temperature, pH, and irradiance is highly variable and likely both species- and context-specific (Abrego et al. 2008).

Although coral reefs play host to a suite of other taxa besides corals, reef fish have also attracted a great deal of research interest (Halford et al. 2004; Feary 2007; Feary et al. 2007; Holbrook et al. 2008; Feary et al. 2010; Emslie et al. 2011; Graham et al. 2011). Given that fishing is the largest human use of coral reefs (Jennings & Polunin 1996) and that marine reserves or no-take areas are a commonly-used management tool, this research interest is not surprising. As with corals, this research occurs both at the physiological/organismal level (e.g., Munday et al. 2009; Rummer et al. 2013) and the community/ecosystem level (Spalding & Jarvis 2002; Wilson et al. 2009).

The most straightforward and widely-used indicator of a reef system under stress is a decline in overall coral cover, but changes in the structure and function of the ecosystem may occur even while coral cover remains relatively stable (Graham et al. 2006; Wilson et al. 2008). However, many other stress indicators have been used or proposed, including fish abundance (Hourigan et al. 1988), structural complexity (Rogers et al. 1982), and colony size (Loya 1972; Fishelson 1977), and no single indicator is likely to capture an overall degree of stress (Hill & Wilkinson 2004). In addition, recently there have been proposals to use a suite of ecosystem indicators to measure reef systems' ability to cope with climate change (Pelletier et al. 2005; McClanahan et al. 2012). On the whole, however, there is a paucity of research concerning interactive effects of multiple stressors on reefs at the ecosystem level.

Climate change and coral reef management

Coral reefs have persisted over evolutionary time despite five major extinction events, at least some of which have been associated with high atmospheric carbon dioxide concentrations and/or greenhouse conditions (Veron 2008). However, carbon dioxide levels are on a trajectory to values not seen since the mid-Eocene epoch, and increasing at a rate that is faster than any seen in at least the past 420,000 years (Hoegh-Guldberg et al. 2007). Furthermore, the slow exchange of CO_2 between the atmosphere and the oceans means that further acidification and warming is inevitable, even with an immediate reduction in CO_2 emissions.

Climate-change stressors will likely include increased ocean temperatures (Reaser et al. 2000; Graham et al. 2008) and possibly increased ocean acidification (Feely et al. 2004). Different climate change and management scenarios may entail changes in aragonite saturation state, sea surface temperature, severity or frequency of severe cyclone events (and correspondingly, flood severity), seasonal rainfall patterns, nutrient loading, and sedimentation.

A key concern for scientists and managers is to forestall and/or reduce climate change impacts on coral reefs. Identifying potential management actions that aim to mitigate the effects of climate change and acidification requires understanding factors that are either contributing to, or mitigating against, the inevitable adverse effects of warming and acidification. For example, Obura (2005) identified some management interventions that can mitigate coral bleaching, including promoting recovery through enhancing water quality, and protecting reef areas that had shown a historical ability to acclimate to thermal stress. Indeed, these two management options are commonly suggested (e.g., Hughes et al. 2003; Wooldridge & Done 2009; Baskett et al. 2010; Negri et al. 2011).

Some of these mitigating factors, such as intrinsic resistance and reducing exposure to certain deleterious conditions, are difficult to directly address through management actions. However, knowledge about reef resistance and resilience can contribute to more effective policy decisions in other areas, such as protected area design. For example, there is a potential linkage between thermal bleaching thresholds and nutrient enrichment (DIN loading) in the GBR (Wooldridge et al. 2006; Wooldridge 2009; Wooldridge & Done 2009), and decreased bleaching resilience has been linked to chronic stress in Mesoamerican reefs (Carilli et al. 2009; Carilli et al. 2010), although the optimal protection strategies associated with these findings are not yet clear (Game et al. 2008). Specifically, the selection of protected areas can represent prevailing currents (*e.g.*, areas that tend to entrain cooler waters) and consider local stressors to ensure the protection of more resilient areas as sources of larval replenishment. For the GBR, the first governance steps towards the management of stressors of terrestrial origin were taken with the Reef Water Quality Protection Plan initiated in 2003, and further improvements are underway in the form of planning reform initiatives (GBRMPA 2009b). The logical next step is to consider how changes in protected area design can incorporate these types of stressor management plans.

Discerning the interactions and consequences of multiple stressors also has numerous other management implications. For example, regulatory limits for pollutants are almost always set for individual, isolated contaminants, and at the organismal, not ecosystem, level (Adams 2005; Munns Jr 2006). It is possible, though, that interactions between pollutants result in adverse effects at lower concentrations than expected (Negri et al. 2011). Another example where knowledge of interactions provides a useful management tool is the relationship between fishing pressure and crown-of-thorns starfish outbreaks, where evidence suggests that the frequency of *Acanthaster* outbreaks on reefs open to fishing was much higher than on reefs closed to fishing (Sweatman 2008). Thus, identification of potential synergistic effects may also allow for more efficient mitigation by focusing on stressors that have the greatest potential for enhancing the effects of others (Folke et al. 2004).

Research gaps

A key gap in our knowledge about coral reef systems is how interactions between multiple stressors may affect the community composition and overall trajectories in coral cover. The effects of multiple stressors on bleaching likelihood or susceptibility are only just being explored (e.g., Wooldridge 2007; Wooldridge & Done 2009), but no studies to date have quantitatively examined the effects of more than two interacting stressors on coral reef ecosystems. Increasing attention is being paid to single stressors and two-stressor interactions, but the literature regarding synergism between stressors has also been marked by a lack of rigorous definition for the term, as well as confusion over how to detect it (Dunne 2010).

Some of my thesis chapters are GBR-specific because the co-occurrence of multiple stressors and ecosystem responses has received little research attention in this area compared to other regions. Multiple stressors have received much attention in the Caribbean (e.g., Hughes 1994; Hughes & Connell 1999) but there are few studies of similar scope in the GBR that have explicitly examined multiple stressor interactions in an ecological context (but see Osborne et al. 2011; De'ath et al. 2012). One reason for this is that the historical drivers of ecosystem change are very different between Caribbean reefs and Indo-Pacific reefs (Rotjan & Lewis 2008; Bruno et al. 2009; Hughes et al. 2010b), For example, Caribbean reefs have been heavily fished and depleted of top predators for much longer than Indo-Pacific reefs (Jackson 1997), and Caribbean reef fish may be less dependent on coral for habitat than Indo-Pacific species (Paddack et al. 2009). On the GBR, one study that took account of multiple stressor interactions was that of Wooldridge and Done (2009) who used a Bayesian belief network (hereafter BBN) to predict coral bleaching likelihood based on the combination of water quality (as measured by dissolved inorganic nitrogen), thermal history, and short-term heat stress.

The phenomenon of bleaching poses an interesting research problem, because it can be construed as both (or either) a stressor in itself and a response to stress. For example, because bleaching results in the expulsion of photosynthetic zooxanthellae, their prolonged absence results in an energetic deficiency in the coral host that ultimately leads to mortality. On the other hand, bleaching generally occurs in response to specific stressors, such as anomalous temperatures. Bleaching has been extensively studied and modeled: the spatial pattern of major bleaching events in 1998 and 2002 was well-fit at large spatial scales by a simple model of maximum 3-day sea surface temperature (SST) (Berkelmans et al. 2004). At smaller spatial scales, though, the bleaching patterns between the two events were quite different. However, the degree and extent to which bleaching and disease facilitate one another is still the subject of some debate. Thus, improving models of coral bleaching and disease together should also improve the ability to predict coral mortality and hence changes in ecosystem condition.

Another research gap is the development of quantitative models that identify, prioritize and predict which stressors can be mitigated to have most effect in managing and mitigating climate change impacts on ecosystems, especially when climate-related stressors themselves are unlikely to be controllable by managers. However, understanding climate-change stressors is important to anticipate potential impacts and their interacting effects with controllable stressors. Thus modelling of climate change effects on coral reef ecosystems has been identified as a specific knowledge gap (Wilson et al. 2010). Furthermore, current models of coral responses to anthropogenic stress (including models of bleaching) seldom include prescriptions for management actions to mitigate these effects. From a management perspective, it is important to identify which (controllable) stressors on coral reefs may play a role in minimizing and/or mitigating deleterious anthropogenic effects on coral reefs, and more specifically within the GBR system.

As with many complex ecological problems, data concerning the effects of multiple stressor interactions are frequently deficient. Because the number of possible interactions increases exponentially with the number of stressors, gathering data on all of the interactions and their strengths is fraught with difficulty (Wootton & Emmerson 2005). Thus, any attempt to model multiple stressor interactions realistically must contend with the scarcity of data typically available to parameterize the model, as well as which model components are stochastic vs. deterministic (Clark 2005). A number of qualitative approaches have been used to sidestep this quantification problem, such as ranking of ecosystem stressors by experts (Halpern et al. 2008b), relative risk models (Landis & Wiegers 1997; Landis et al. 2013), qualitative loop models (Levins 1974; Dambacher et al. 2003), and Fuzzy Cognitive Maps (FCM) (Kosko 1988; Özesmi & Özesmi 2004; Kok 2009).

Each of these techniques has their advantages and drawbacks. While relative risk models have the advantage of being simple and requiring few assumptions, the disadvantages include the fact that the outputs cannot be used for quantitative analysis (such as in a regression), and the limited ability to empirically test the projected risks (Landis & Wiegers 1997). Qualitative loop models have the advantage of being easily generalizable while still being realistic (specificity-idealization), at the cost of only being applicable to systems close to equilibrium, and being unable to predict system responses to perturbations. Qualitative loop models are also unable to determine the magnitude of response for variables within the model, only their sign. The information required to determine these responses also grows factorially with the number of variables (Justus 2006). Fuzzy cognitive maps share many of the same advantages and disadvantages of qualitative loop models, although they have much more flexibility regarding variable or uncertain interaction strengths between model components because they are able to use numbers instead of signs to represent these relationships. More generally, qualitative models of all types are useful in a number of contexts, but often are unable to provide the kind of outputs that are required by managers and regulatory bodies in formalized monitoring and enforcement frameworks. For example, quantitative fisheries stock assessment models can provide managers with a specific total catch that should not be exceeded, with an associated uncertainty regarding the probability that exceeding that catch will drive a stock to extinction. Additionally, most qualitative techniques lack a formalized treatment of uncertainty, which is often required by managers and decision makers in order to effectively evaluate and appropriately weight the information provided by models.

One way of bridging the gap between empirically-collected data and strictly qualitative descriptions involves the use of expert elicitation. Data obtained by expert elicitation – either as a complement to, or as a substitute for empirical data - is rapidly gaining prominence in conservation biology as a means of obtaining information that would otherwise be impractical or too time-consuming to collect (Martin et al. 2012). Informally, expert elicitation has long been used to guide policy in the form of think tanks, special commissions, and consultations, but the formalization of this process to reduce biases and groupthink expert elicitation is generally credited to the development of the Delphi technique (Brown 1968). The Delphi technique uses structured questionnaires and constant feedback to and from experts in an attempt to minimize heuristic biases. Over time, the structure and format of the questions used to obtain reliable knowledge from experts have been refined to ensure that the data collected are as unbiased and consistent as possible (Aspinall 2010; Speirs-Bridge et al. 2010). Fortunately, the development and improvement of formalized expert elicitation techniques has demonstrated the utility and validity of expert knowledge for ecological research (Drescher et al. 2013), and these techniques are now commonplace in the model development and parameterization process (Choy et al. 2009; Krueger et al. 2012).

Bayesian Belief Networks (BBNs) also straddle the qualitative-quantitative model gap, as they can accommodate both empirical and subjective (often, expert-elicited) data. BBNs are superficially similar to qualitative loop networks and fuzzy cognitive maps in terms of using directed acyclic graphs to visualize and link processes and variables in a semi-quantitative fashion. However, because they are probability based, they are considerably more useful in complex situations with high uncertainty, taking into account the unreliability of some data sources (Phillips 2005). In the context of BBNs, structured expert elicitation allows experts to contribute to the development of model structure as well as contributing informative priors to parameterize the model. The process of developing the BBN model structure can be as useful an exercise in conceptualizing a system as the model output(s) (Marcot et al. 2006). The expert elicitation process also meshes with the Bayesian ability to accommodate subjective opinions and impressions about costs, benefits, and uncertainties while using empirical data (where available) (Walton & Meidinger 2006). BBN's focus on probabilistic ways of thinking is particularly well-suited for use in adaptive management through the exploration of alternate management scenarios and incorporating new data into existing management and monitoring frameworks.

Relevance and Importance

Increasing attention is being paid to single stressors and two-stressor interactions, but the literature regarding synergism between stressors has also been marked by considerable confusion (Dunne 2010). The scarcity of practical approaches to the multiple-stressor problem is largely due to the limited amount of data available; in part, this is a consequence of the number of interactions increasing exponentially with the number of stressors, and in part due to the general lack of ecological data from formal monitoring and assessment surveys that are sufficiently comprehensive to statistically examine these interactions. My thesis is seeking to explore and identify ways around some of these problems.

Identification and characterization of multiple stressors is not merely an academic exercise; this knowledge can be meaningfully applied in a management context to identify ripple effects of otherwise seemingly disconnected components in an ecosystem (*e.g.*, by quantifying the effects of riparian area management on reef health), as well as conversely to maximize the long-term benefit of short-term management decisions. The results of my review and meta-analysis will help to identify key research gaps as well as important stressor interactions that may deserve further management attention. Analysis of the interactions between bleaching and disease in corals will help determine whether protecting areas of persistently cooler ocean temperatures (thermal refugia) will address both problems, or whether disease needs to be managed as a separate issue from bleaching. Outputs from Chapters 4 and 5 will also be directly relevant to conservation planners and environmental managers by providing a means to visualize and compare the effects of different management strategies under various climate change scenarios. Furthermore, modeling of climate change effects on coral reef ecosystems has recently been identified as a specific knowledge gap (Wilson et al. 2010).

Aims and objectives of the thesis

The overall aim of this thesis is: 1) to quantitatively evaluate the importance of multiple stressor interactions to coral reef ecosystems; and 2) to assess alternative management approaches to mitigating the effects of potentially increased prevalence and severity of these stressors. I do this through both assessing the state of existing knowledge as well as by using new approaches (i.e., network analysis of stressor interactions) to model stressors and stressor effects within the context of the GBR. In addition, I seek to provide an example of how various modelling techniques can be used to conceptualize multiple-stressor problems and identify possible management solutions in the face of uncertain knowledge and incomplete data.

I explore how different climate change and management response scenarios might interact with altered stressor regimes to affect the short- to medium-term resilience and persistence of the GBR. My thesis addresses two critical elements that are often missing from studies examining the conservation implications of multiple stressors (especially on coral reefs): interactions between stressor/stressor effects and assessing the effects of different management options on these interactions.

The specific research objectives of my thesis are as follows:

1. To synthesize the available knowledge of multiple stressors on coral reefs, specifically investigating the evidence for non-additive and non-independent interactions between stressors on coral reefs.
2. To determine the spatial and temporal overlap of two key stressors/stress responses (bleaching and disease) on the GBR, and to determine whether the combined effects of bleaching and disease are affecting coral growth, recovery, and mortality.
3. To identify experts' perceptions and uncertainties about knowledge gap(s) regarding multiple stressor interactions, and to use expert knowledge to help fill these gaps.
4. To integrate quantitative data with expert-elicited knowledge about stressors on the GBR to examine the consequences of interactions between stressors, and use the resulting models to determine the implications of multiple stressor interactions for coral reef conservation in the GBR.

Chapter 2 addresses research objective 1 by using a formal literature search to provide the foundation for a qualitative and selected quantitative meta-analysis of multiple stressors as they pertain to coral reef ecosystems, and by examining the evidence for the prevalence of synergistic, antagonistic, and additive interactions between stressors. In the qualitative component, I map out the relationship between stressors themselves, and between pairs of interacting stressors and responses at both the organismal and ecosystem level. In the quantitative component, unlike previous meta-analyses that aggregated across ecosystems and response variables, I look for evidence of deviations from additive behavior by calculating the effect sizes of specific variables in response to consistent stressors. This chapter identifies some of the crucial research gaps concerning multiple stressors and coral reefs, and also identifies some shortcomings of previous reviews in this area. This chapter has been published in *Global Change Biology*.

Chapter 3 addresses research objective 2 by using data from the Australian Institute of Marine Science (AIMS) Long-term Monitoring Program (LTMP) as a case study of two stressors (coral bleaching and white syndrome disease) to examine the spatial and temporal overlap of these stressors in the GBR, and whether co-occurrence of these stressors can be explained by a common environmental variable. I use statistical models to detect spatial and temporal patterns of correlation between bleaching and disease in response to ocean temperature anomalies, to identify any spatial clustering and determine whether these are different responses to a common stress, or whether they directly facilitate one another. I also test the utility of existing thermal stress metrics for predicting bleaching and white syndrome on reef slope habitats. Finally, I apply an underutilized metric, the Peirce Skill Score, to test the ability of various thermal anomaly metrics to predict bleaching on reef shelf habitats. This chapter has been published in *Coral Reefs*.

Chapters 4 and 5 seek to understand and model multiple stressor interactions on the GBR in the absence of complete data about interaction effects using a combination of two techniques: Bayesian belief networks (BBNs) and expert elicitation. Bayesian belief networks have an advantage over strictly qualitative models due to their ability to integrate quantitative data with qualitative data, and to use either (or both) to form informative priors (McCann et al. 2006; Uusitalo 2007; Kuhnert 2011). BBNs are increasingly being applied as a decision support tool in adaptive management (e.g., Marcot et al. 2006; Smith et al. 2007; Thomas 2008) where predictive utility is paramount but data are limited and uncertainty is high (Cain 2001). They have also been used for complex social-ecological problems, such as the management of the multi-jurisdictional Murray-Darling Basin (Hart & Pollino 2009).

Chapter 4 addresses research objective 3 by exploring the use of Bayesian belief networks (BBNs) in conjunction with expert elicitation to determine the degree of expert consensus about the greatest threats to the GBR, and assessing the degree of confidence that experts have about the effects of various stressors both alone and in combination. This chapter lays the groundwork for my final chapter by establishing the methodology for constructing the model and evaluating the consistency and uncertainty of experts' responses.

Chapter 5 addresses research objective 4 by implementing spatially the model developed in Chapter 4 through the use of several scenarios. Here, I assess whether local management interventions in the form of reductions in fishing pressure and catchment management could be effective in reducing the impact on coral cover of climate change as manifested by an increase in average sea surface temperature. I also assess whether reefs within the existing protected area network differ in their predicted probability of decline from reefs outside the protected area network. Finally, I look at the effect of using optimistic versus pessimistic expert responses on the model predictions of coral cover decline on the GBR.

Chapter 6 summarizes the findings of this thesis, reviews some of the limitations and assumptions of the research, and suggests future research directions. I also discuss the broader implications of my thesis in terms of other ecosystems and areas of research.

Chapter 2 Evidence for multiple stressor interactions and effects on coral reefs[1]

[1]Evidence for multiple stressor interactions and effects on coral reefs. **Ban, S.S.**, Graham, N.A.J., Connolly, S.R. Global Change Biology 20(3): 681-697.

Abstract

Concern is growing about the potential effects of interacting multiple stressors, especially as the global climate changes. Here, I provide a comprehensive review of multiple stressor interactions in coral reef ecosystems, which are widely considered to be one of the most sensitive ecosystems to global change. First, I synthesized coral reef studies that examined interactions of two or more stressors, highlighting stressor interactions (where one stressor directly influences another) and potentially synergistic effects on response variables (where two stressors interact to produce an effect that is greater than purely additive). For stressor-stressor interactions, I found 176 studies that examined at least 2 of the 13 stressors of interest. Applying network analysis to analyze relationships between stressors, I found that pathogens were exacerbated by more co-stressors than any other stressor, with ~78% of studies reporting an enhancing effect by another stressor. Sedimentation, storms, and water temperature directly affected the largest number of other stressors. Pathogens, nutrients, and crown-of-thorns starfish were the most-influenced stressors. I found 187 studies that examined the effects of two or more stressors on a third dependent variable. The interaction of irradiance and temperature on corals has been the subject of more research (62 studies, 33% of the total) than any other combination of stressors, with many studies reporting a synergistic effect on coral symbiont photosynthetic performance (n=19). Second, I performed a quantitative meta-analysis of existing literature on this most-studied interaction (irradiance and temperature). I found that the mean effect size of combined treatments was statistically indistinguishable from a purely additive interaction, although it should be noted that the sample size was relatively small (n=26). Overall, although in aggregate a large body of literature examines stressor effects on coral reefs and coral organisms, considerable gaps remain for numerous stressor interactions and effects, and insufficient quantitative evidence exists to suggest that the prevailing type of stressor interaction is synergistic.

Introduction

Globally, biodiversity and ecosystem services are under threat from a suite of human activities (Dawson et al. 2011), with climate change likely exacerbating existing stressors (Halpern et al. 2008b). The increased sense of urgency associated with these global threats adds to a long-standing call for a better understanding of the effect of multiple stressors on biodiversity and ecosystem function (Breitburg et al. 1999). A stressor has been defined as any environmental change in a factor that causes some response by a population of interest (whether beneficial or deleterious) (Underwood 1989); here I focus on deleterious effects at the community, population or individual (including physiological) level, whether natural or anthropogenic in origin. However, despite the additional attention multiple stressors have received (Sutherland et al. 2009; Blackwood et al. 2011; Melbourne-Thomas et al. 2011b), our knowledge about their interactions remains nascent (Halpern et al. 2008b).

Much of the concern over multiple stressors stems from the potential for their combined effects to exceed their individual effects – often referred to as synergism (Folt et al. 1999). If the combined effect of stressors is less than the sum of their individual effects, this is considered antagonistic. Additive effects occur when the combined effects are equal to the sum of the individual effects. Reviewing evidence for synergistic and antagonistic effects, Crain et al (2008) found 202 experiments assessing direct impacts of multiple stressors in marine systems (33 of which applied to coral reefs), while Darling & Côté (2008) found 23 studies (112 experiments) across the terrestrial, marine, and freshwater ecological literature (although none pertained to coral reefs) that featured controlled factorial experiments with two stressors and mortality as the response variable. Both of these reviews concluded that the majority of studies investigating stressor interactions found non-additive (*i.e.*, either synergistic or antagonistic) effects. Crain et al (2008) found synergistic effects in 36% of studies and antagonistic effects in 38%, with 26% additive. By contrast, Darling & Côté (2008) found synergistic effects in 35% of their sample and antagonistic effects in 23%, with 42% being additive. Furthermore, evidence for the existence of ecological surprises – where the behaviour of a natural system sometimes drastically deviates from expectations or historic conditions – continues to mount (Lindenmayer et al. 2010). In many cases, synergistic effects may have played a role in these ecological surprises (Hecky et al. 2010). For example, Christensen et al (2006) found that the interaction between temperature, dissolved organic carbon, and pH in temperate lakes had a positive, synergistic effect on consumer biomass, even though individually each variable exerted negative effects. In another example, Davis et al (2010) found the combined effects of eutrophication, acidification, and salinisation led to regime shifts between macrophyte-dominated and phytoplankton-dominated lentic (standing-water) systems.

Effective management responses to growing anthropogenic impacts on ecosystems requires an understanding of how stressors interact, and coral reefs are a particularly good example of the interplay between global and local stressors. Coral reefs are widely believed to be one of the world's most stressed ecosystems (Walther et al. 2002; Hughes et al. 2003; Carpenter et al. 2008; Hoegh-Guldberg & Bruno 2010), and hence understanding – and managing – multiple stressor interactions is particularly urgent. Coral reefs are also among the most biologically diverse and socioeconomically valuable biomes (Moberg & Folke 1999), and face many natural, anthropogenic, and anthropogenically-enhanced natural stresses. Specifically, Harriott and Banks (Harriott & Banks 2002) identify a number of physical factors - including light, nutrients, aragonite saturation state, and temperature - that interact to affect coral species diversity and coral reef accretion. Identifying synergisms between stressors would allow prioritization of management to mitigate the most severe interactions, such as reducing sedimentation or fishing pressure in order to potentially enhance recovery from bleaching (e.g., Carilli et al. 2009; Graham et al. 2011), or improving water quality to enhance resistance to thermal bleaching (Wooldridge 2009; Carilli et al. 2010). Similarly, if signs or precursors of ecological surprises can be reliably detected, managers may be able to take early preventative action such as reducing fisheries catches (McClanahan et al. 2011) or prohibiting fertilizer application in upstream watersheds (Brodie et al. 2012). Thus, interactions of multiple stressors, and the resulting cumulative impacts, have been identified as a research priority or necessity by management and regulatory bodies (Council on Environmental Quality 2005; Office of Research and Development 2005; Fisheries and Oceans Canada 2008; Great Barrier Reef Marine Park Authority 2009; NOAA 2012; PICES (North Pacific Marine Science Association) 2012) and researchers (Paine et al. 1998; Vinebrooke et al. 2004; Salbu et al. 2005) alike. While the phenomenon of multiple stressors in coral reef ecosystems has been studied previously (Coles & Jokiel 1978; Lesser et al. 1990; Shick et al. 1996; Darling et al. 2010), to date little agreement exists about which stressors are likely to act synergistically, or how they should be managed where they do occur (Folt et al. 1999; Dunne 2010). Thus far, no reviews have specifically focused on the coral reef literature to assess the prevalence of synergistic effects.

The purpose of this study is to review the research on multiple stressor interactions in coral reef ecosystems, and I use two approaches to examine the problem of multiple stressors. First, I synthesize coral reef studies that examined interactions of two or more stressors and differentiate between stressor interactions (where one stressor directly influences another) and the effects of multiple stressors on another response variable. My qualitative overview provides the state of current knowledge of multiple stressor interactions on coral reefs, allows for identification of research gaps, and highlights areas where sufficient data may exist for future meta-analyses. I apply a network-analysis approach to analyzing stressor interactions (Wenger et al. 1999) to identify the most influential or most-influenced stressors. This approach may allow managers to focus on reducing those stressors whose interactions with other stressors are likely to have the most deleterious effects. Second, I perform a quantitative meta-analysis on one of the most-studied stressor interaction effects on coral organisms - irradiance and temperature - and assess whether sufficient evidence exists to draw general conclusions about this interaction. In this analysis, I consider three of the most commonly and consistently measured stress response variables from the coral reef literature: coral symbiont (zooxanthellae) density, photosynthetic efficiency (Fv/Fm), and chlorophyll *a* concentration.

Study Selection

To categorize research on stressor interactions, I identified thirteen stressor categories through key review papers in the coral reef and multiple-stressor literature (Hoegh-Guldberg 1999; Halpern et al. 2007; Keller et al. 2009) (Table 2.2.1). Some potential stressor categories (e.g., ocean mining, ecotourism, coastal development: (Halpern et al. 2007)) manifest their effects indirectly through other stressors (e.g., nutrient loading, sedimentation), and hence I excluded these indirect stressor categories in favour of the specific types of stressor they produce. In the case of disease, in order to avoid conflating the stressor (i.e., pathogens) with the response of the host to the stressor (infection and associated symptoms) I differentiated studies that directly measured changes in pathogen abundance or virulence factors from those that observed disease symptoms or host mortality that were presumed to be disease-related. I searched each combination of stressors (using a combination of the Booleans *and* with *or* for synonymous terms – see Appendix A, Table A.1) using the Topic search feature on ISI Web of Knowledge using the Science Citation Index (SCI-Expanded, 1972-Present) and the Conference Proceedings Citation Index (CPCI-S, 1990-Present).

Table 2.2.1 List of stressor categories used to examine potential interactions between stressors.

Stressor	Selected references
Ocean acidification	(Kleypas et al. 1999; Anthony et al. 2008)
Crown-of-thorns starfish outbreaks	(Moran 1986; Done 1992)
Eutrophication	(Bell 1992; Szmant 2002)
Fishing pressure	(Jackson et al. 2001; Valentine & Heck Jr 2005)
Increased ocean temperatures	(Goreau & Hayes 1994; Carpenter et al. 2008)
Irradiance	(Brown et al. 1994)
Pathogen-induced disease	(Willis et al. 2004)
Pollution	(Lewis et al. 2009)
Reduced salinity	(Brown 1997; Kerswell & Jones 2003)
Storms	(van Woesik et al. 1991; Cheal et al. 2002)
Terrestrial sedimentation	(Dubinsky & Stambler 1996; Fabricius 2005)
Ultraviolet radiation	(Dunne & Brown 1996; Lesser 1997)
Sea level rise	(Przeslawski et al. 2008; Selkoe et al. 2009)

I used the Topic search because it is more comprehensive than using title or keyword searches. All studies up to September 2013 were included.

The studies returned from the searches were examined for their applicability, and entered into a database. If more than 150 results were returned from the topic search, I imported the search results into Endnote X4 (Thomson Reuters 1988-2010) and then filtered the results by searching only the keyword field. I manually screened this subset of results, and discarded studies that were outside the purview of my analysis (e.g., studies concerning "sediment" in a geological context). If 150 or fewer results were returned, I manually screened each abstract to produce a subset of studies that explicitly examined (i.e., either manipulated or controlled for) the stressors of interest. In order to keep the number of search term permutations tractable, I confined my search to studies that pertained in some way to tropical or temperate hermatypic coral reefs or scleractinian coral organisms. Thus, studies on deep water and cold-water corals were excluded, as were organisms such as macroalgae, foraminifera, etc. Because marine reserves and no-take areas are a common management mechanism in coral reefs, I also included the effects of reef fisheries and stressors affecting reef-associated fish. I also disregarded studies that did not measure at least two stressors of interest. Both field and laboratory studies (including mesocosm studies) were included. Reviews and modelling studies without an experimental component were excluded. In this paper, all of the response variables I discuss pertain to corals unless otherwise specified.

Meta-analysis approach

Qualitative Meta-analysis

Studies were divided into two groups: those that reported the effect of one stressor on another, and those that reported the effect of two (or more) stressors on a response variable. In the first group, for each stressor combination, I first created a table where the number of studies examining a specific interaction were tallied according to the direction of effect one stressor had on another. I did not evaluate synergistic or antagonistic effects in these interactions, merely whether one stressor increases (reinforces) or reduces (mitigates) the level or incidence of another. These interactions were considered asymmetrically (e.g., sediment loading is typically associated with increased nutrients, but the converse cannot be assumed). To examine the relative stressor influences, I imported an unweighted (i.e., relationships were not weighted by the number of studies) version of the table into the software UCINet (Borgatti et al. 2002) and NetDraw (Borgatti 2002) for analysis and network diagram creation. Using this stressor "network" of interactions, I calculated both in-degree centrality, out-degree, and betweenness to determine stressors with either the most influence on other stressors or that were affected by the highest number of stressors. In-degree centrality calculated the number of stressors that have a direct influence on each stressor; out-degree is the number of stressors influenced by a particular stressor, and betweenness is an indicator of how central a stressor is in terms of relationships to other stressors via indirect pathways (Freeman 1979).

For the studies that examined the effect of multiple stressors on a response variable, I identified the response variable for each stressor combination and the net direction of the response variable when stressor effects were combined. I also noted whether or not the experimental design (statistically and/or methodologically) allowed synergistic or antagonistic interactions to be detected quantitatively.

Quantitative meta-analysis

Using the database of multiple stressor studies, I tabulated the number of studies by dependent variable type to identify candidates for quantitative meta-analysis. I segregated studies by response variable to keep analysis subgroups as homogenous as possible. I also recorded the genus and species of organism used in the experiment, as well as geographical region and biographical information for each study. I then picked one of the most numerous response types (n=31) to carry out a quantitative meta-analysis: the effect of temperature and irradiance on coral symbiont photosynthesis. Within this category, photosynthetic performance was most commonly measured by three different parameters. These parameters were (1) dark-adapted maximal chlorophyll fluorescence (F_v/F_m) (n = 20), (2) symbiotic zooxanthellae density (n = 6), and (3) chlorophyll *a* concentration (n = 16). I extracted data from electronic (PDF) versions of manuscripts using either Adobe Acrobat's on-screen measuring tools or directly from reported results. For studies reporting time series data, I took two measures to avoid pseudoreplication. First, I used the last point in the experimental time series except in cases where complete mortality occurred before the end of the experiment, in which case I used the last non-zero point. Second, if an experiment was long-term, I only used results from the acute stress phase of the experiment (i.e., I did not use values from a recovery phase). If multiple treatment levels (e.g., high and moderate temperature treatments) were applied, I only used the largest treatment differential to calculate effect size. However, in studies that included multiple species, I treated each species as a separate experiment. I discarded studies that were missing information about sample error, sample size, or did not manipulate each stressor both jointly and independently.

After these screening steps, 17 studies for F_v/F_m, 6 studies for zooxanthellae density, and 3 studies for chlorophyll *a* concentration remained that were suitable for meta-analysis.

Ideally, meta-analysis of synergistic effects would analyze, from each study, an estimate of the interaction term from a statistical model (e.g., ANOVA or other linear model), and its associated standard error. Unfortunately, most studies do not report this statistic. Consequently, previous meta-analyses have tended to use a “two-interval” approach: inferring synergistic effects when the confidence intervals on the meta-analysis estimate of the combined treatment effect does not overlap with the confidence intervals on the estimate of the additive effect (Crain et al. 2008; Darling & Côté 2008). However, this approach is subject to potentially large Type II error—failure to detect a synergistic effect when one is, in fact, present (Schenker & Gentleman 2001; Payton et al. 2003)(see Appendix A and Table A.2 for an illustration).

As an alternative to the two-interval approach, I instead use a Monte Carlo method, the parametric bootstrap (Efron & Tibshirani 1994), to approximate the standard error of the interaction term from each study, and I use those as my test statistics in the meta-analysis. The approach is similar to the better-known non-parametric bootstrap, but values are drawn from a probability distribution, rather than being resampled from actual observations. Specifically, I randomly draw a mean value for each treatment (control, irradiance only, temperature only, irradiance & temperature), from a normal distribution with a mean equal to the observed treatment mean, and a standard deviation equal to the standard deviation of the mean (i.e., the standard error). I then calculate temperature, irradiance, and combined effects by taking the difference between the relevant Monte Carlo-sampled treatment mean value and the sampled mean of the control. The interaction term is then the difference between the combined treatment effect and the additive effect (temperature effect + irradiance effect). If the combined effect is larger than the additive effect (i.e., the interaction term is positive), this indicates synergy; if it is smaller than the additive effect, then antagonism is indicated. Finally, I convert this to an estimate of Hedges’ *g* (Hedges 1981), a measure of effect size, by dividing this interaction term by the pooled standard deviation. I repeat this procedure 1000 times for each study, producing a frequency distribution of interaction term values. The standard deviation of this statistic is the standard error that I use in my meta-analysis for that study.

I calculated these bootstrap estimates of interaction terms for each response variable (i.e., maximal chlorophyll fluorescence (F_v/F_m), zooxanthellae density, chlorophyll *a* concentration), and evaluated subgroup heterogeneity using the I^2 index (Higgins & Thompson 2002) in R (R Core Team 2012) with the "metafor" package (Viechtbauer 2010). Heterogeneity measures provide an indication of whether the variation in effect size between studies is entirely due to measurement error around a single true effect size, or whether the true effect sizes being measured in each study actually vary around an overall mean (e.g., due to difference in how treatments were administered or to choice of study organism). As species and treatment conditions varied from study to study, I used a random-effects model (see Chan & Connolly 2012 for more details) to estimate the combined effect size for each group of response variables and treatments. I also explored possible explanations for any heterogeneity by performing a meta-regression on the study characteristics of region of origin, genus of study species, and magnitude of temperature and irradiance treatments (absolute difference between treatment condition and control condition). Finally, I assessed whether a publication bias may exist (i.e., whether studies reporting large or significant effect sizes may be overrepresented relative to studies reporting no effect), by plotting reported effect sizes against the standard error of each study to produce a funnel plot (Møller & Jennions 2001). If no publication bias is present, this plot should show a larger variation in effect size as the standard error increases (Figure A1.1).

Multiple stressors on coral reefs: Much interest, few quantitatively comparable findings

Taken as a whole, there is an extensive body of literature concerning single and multiple stressor effects on coral reef ecosystems. However, I found that the number of studies that quantitatively examined combined stressor effects in a way that clearly demonstrates the presence or absence of synergistic effects was quite low (e.g., in the case of photosynthesis, only three studies examining temperature and nutrient interactions, and only one examining temperature and salinity interactions – see Table A1.3). Further complicating attempts to synthesize the literature is the diversity of response variables measured and the lack of consensus on what indicators or metrics best represent the state of coral reef health (e.g., coral cover, mortality, fecundity; Hughes et al. 2010b). Here I describe some of the interactions between stressors themselves and between stressors and response variables in terms of their support (or

lack thereof) in the literature. I also propose some ways in which managers could use these findings to assist in quantifying stressor interactions and help to identify those stressors with the most wide-reaching potential effects.

Qualitative Meta-analysis: Stressor-Stressor Interactions

Using my search criteria, I found 176 studies that examined the interaction of at least 2 of the 13 stressors (Table A1.4). The most frequently-studied stressors were nutrient loading (37 studies, 21% of all studies), pathogen growth and virulence (32 studies, 18%), sedimentation (29 studies, 17%) and fishing pressure (29 studies, 17%). Some of the notable data gaps regarding stress-stressor interactions concern irradiance (other than interactions with sedimentation), salinity (other than interactions with nutrients), pollution, and ultraviolet radiation. Converting the table into a network diagram (Figure 1) and calculating the in-degree centrality (i.e, the number of other stressors directly affecting each stressor) and betweenness (i.e., number of other stressors that are directly or indirectly mediated by that node) of each node showed that pathogen loading had the highest in-degree and the highest betweenness measure. Nutrients also had a high in-degree, but a relatively low betweenness measure. Stressors with a high outdegree measure (i.e., those influencing the highest number of other stressors) were sedimentation, storms, and temperature. Weighting the network by the number of studies would reflect a bias in the topics that attract the most research interest, rather than the weight of evidence for (or against) a particular stressor interaction. In a weighted network, the degree centrality and betweenness metrics would be biased towards nodes that had a larger number of studies contributing to the linkages between nodes. Thus, in an unweighted network, both degree centrality and betweenness provide an unbiased way of quantifying the degree to which a stressor mediates or influences other stressors. However, betweenness reflects both direct and indirect linkages to other stressors, whereas indegree and outdegree only measure direct linkages. The limitation of all these metrics is that additional interactions may exist that have not been reported in the literature. For example, increased irradiance is physically linked with increased water temperature, but this fundamental linkage is unlikely to be reported in the biological literature as a key finding. Additionally, other linkages may exist that have not been reported simply because the studies have not been performed to test or verify their existence.

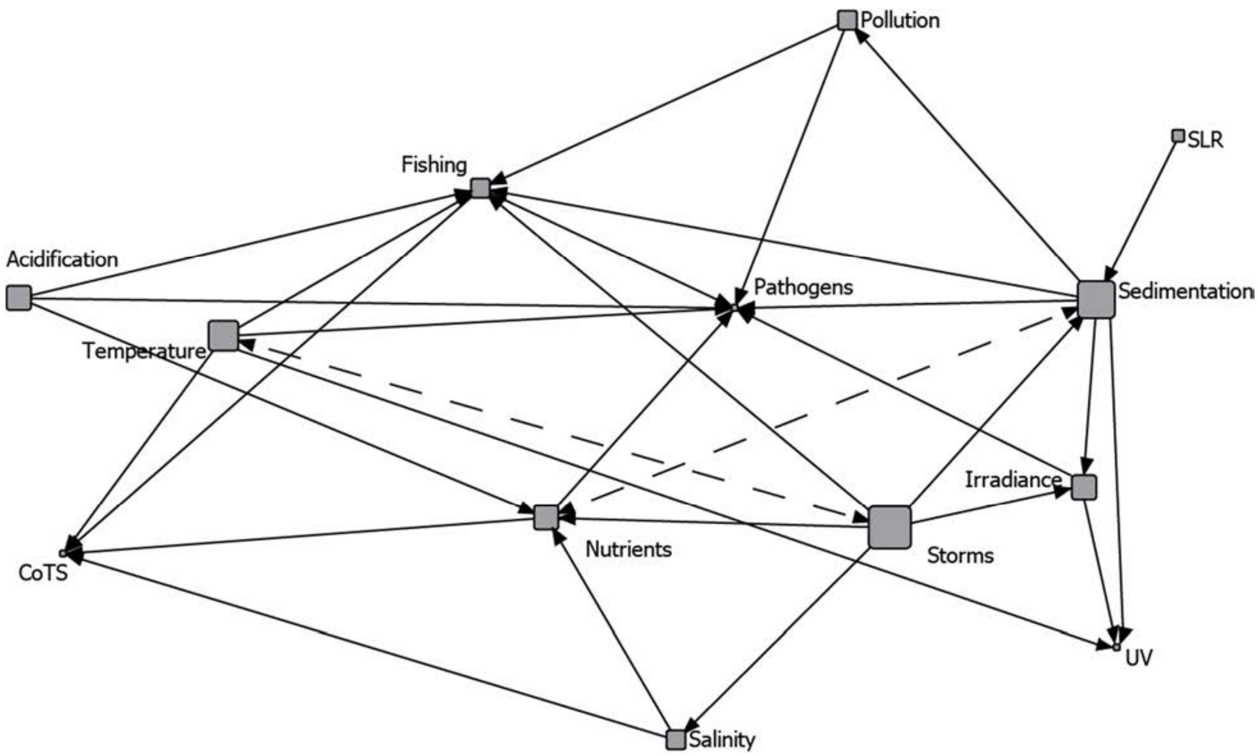


Figure 2.1 Network diagram of stressor-stressor relationships. Node size reflects betweenness measure for that node, i.e. the number of other stressors that are directly or indirectly mediated by that node. Unidirectional relationships are depicted with solid lines; bidirectional relationships are depicted with dashed lines. SLR = Sea level rise.

Most influential stressors: Sedimentation, storms, temperature

According to my network analysis of stressor relationships as reported in published studies, the stressors that were most influential on other stressors were sedimentation, storms and temperature (Figure 2.1). Sedimentation directly affected fishing (by affecting catches), irradiance, nutrient loading, pathogen loading, pollution, and ultraviolet exposure. Sedimentation correlates with or reinforces the effects of nutrients, pathogens, and pollution, but mitigates irradiance and UV exposure. Sedimentation effects on reef-associated fish and fisheries vary depending on the habitat association and prey composition of fish species. Storms (variously called cyclones, hurricanes, and typhoons, depending on the ocean basin in which they occur) directly influenced three of the same stressors as sedimentation (nutrients, ultraviolet exposure, and fishing) and three others (salinity, temperature, sedimentation). Storms, while causing direct and indirect damage to reefs, also potentially mitigate some stressors: they can reduce water temperatures (Manzello et al. 2007; Carrigan & Puotinen 2011), decrease irradiance (van Woesik et al. 1995), and potentially reduce sediment burial (Manzello et al. 2007; Carrigan & Puotinen 2011).

Temperature was the most-studied influencing stressor, with ~23% of studies considering temperature and 57% of those reporting a reinforcing effect on another stressor. These reinforcing effects were seen with ultraviolet radiation (Anderson et al. 2001) and pathogen growth (Bally & Garrabou 2007) and virulence (Banin et al. 2003) as well as fishing (by causing shifts in community structure or abundance; however, the aggregate response of reef fish populations to temperature increases appears to be complex and variable, resulting in changes in physiology, behavior, and recruitment (Feary et al. 2010; Gardiner et al. 2010; Lo-Yat et al. 2011)). Potentially reinforcing effects were seen between increased temperature and cyclone and hurricane frequency (Pielke 2005; Anthes et al. 2006), and for low-salinity stress (Faxneld et al. 2010), although the former is controversial (Hayne & Chappell 2001; Hetzinger et al. 2008; Kumar et al. 2009) and there is conflicting evidence of the latter (Porter et al. 1999). Potentially mitigating stressor interactions were seen for crown-of-thorns starfish, which appear to have a relatively narrow temperature tolerance during their larval stage (Johnson & Babcock 1994), with adult mortality occurring at temperatures of 33-34°C (Yamaguchi 1974). In short, increasing water temperatures have a suite of effects on other stressors affecting coral reefs; on balance, most of these effects appear to be deleterious.

Most-influenced stressors: nutrients, crown-of-thorns starfish, pathogens

The stressors that were influenced by the greatest number of other stressors were nutrients, crown-of-thorns starfish, and pathogens (Figure 2.1). Most of the stressors influencing nutrient loading were associated either directly or indirectly with flood events due to terrestrial runoff, and also sediment resuspension by storms (Delesalle et al. 1993). Nutrient loading has been hypothesized to contribute to crown-of-thorns outbreaks (also known as the "terrestrial runoff hypothesis" or "larval survival hypothesis") (Birkeland 1982), but evidence to date is mainly correlative (Brodie et al. 2005; Fabricius 2005). Pathogen growth and virulence can be enhanced by increased temperature (Ward et al. 2007) and increased nutrient availability (Richardson & Ragoonath 2008), while host susceptibility to infection can also be affected by stress due to increased irradiance (Griffin 1998), acidification (Thurber et al. 2008), pollution (Arboleda & Reichardt 2009), and sedimentation (Vargas-Angel et al. 2007) in addition to temperature stress (Ward et al. 2007).

Although the network analysis is unweighted, it nonetheless will reflect any bias in research effort and subsequent publication. Thus, the stressors that this analysis identified as most-influential or most-influenced may not necessarily indicate the strength or ubiquity of these interactions. Furthermore, some stressors are difficult to quantify and measure due to their multi-faceted and complex nature (such as crown-of-thorns outbreaks or fishing pressure), whereas others are more straightforward to measure and manipulate – at least in a laboratory setting (such as temperature and salinity). Thus, there is likely to be a bias in the literature towards stressors that lend themselves to experimental manipulation. This division between complex and simple stressors may partially explain why two of the most-influenced stressors are complex biological phenomena (crown-of-thorns and pathogens), whereas two of the most-influential stressors are relatively simple physical factors (sedimentation and temperature).

Qualitative Meta-analysis: Coral reef responses to multiple stressors

I found 187 experiments (some studies contained multiple experiments and thus contributed to more than one category) that examined the effects of two or more stressors on a third dependent variable (Table 2.2.2, Table A1.5). Coral calcification, coral bleaching/symbiont photosynthesis, coral cover, observations of coral disease symptoms, and coral mortality were among the most commonly studied response variables (Figure 2.2) in multiple-stressor studies. Of the 187 experiments, 111 were assessed quantitatively in the original studies. Nearly all of the studies used an ANOVA to detect interaction effects, with some using techniques such as boosted regression trees (Cervino et al. 2003), discriminant function analysis (Mumby et al. 2001), or multi-model selection (Yee et al. 2008; Yee & Barron 2010). Of these 111 experiments with a quantitative basis, 60 reported a synergistic effect, 17 reported an antagonistic effect, and 33 reported an additive effect or no significant interaction (and 1 did not report either way regarding an interaction despite being designed to do so).

Table 2.2.2 Effect of interacting stressors on response variables. Bold text denotes a deleterious effect on individual corals or the overall amount of coral cover; unbolded entries are either neutral or potentially beneficial. The first number reflects how many studies were found reporting the corresponding effect, whether qualitatively or quantitatively. The number that follows in parentheses is the number of studies that quantitatively tested for an interaction. Arrows denotes the direction of the change in response variable associated with an increase in both of the stressor variables; sideways arrows indicate that the response is either complex (e.g., U-shaped) or dependent on some other factor. Columns and rows containing no studies were removed: for columns, sea level rise, storms and UV; for rows, acidification, crown of thorns outbreaks, and disease. Direction of effect is in relation to the associated stressor increasing (except for salinity). The same response variable may appear more than once within a row if there are conflicting findings regarding direction of effect.

Stressor	Acidification	CoTS	Disease	Fishing	Irradiance	Nutrients	Pollution	Salinity	Sedimentation	Temperature
Fishing			**1↑Algal cover (0)**							
Irradiance	**1↑ Bleaching (1)** 3↔Calcification (3) **1↓Calcification (1)** **1↓Zoox. Photosynthesis (1)** ↑Photosynthesis (1)[2]									
Nutrients	**3↓Calcification (0)** 1↔Calcification (1) **2↑Pathogen growth (1)** **1↔Zoox. Photosynthesis (0)**			**1↑Algal cover (1)** 1↑Corallimorphs (0) **1↓Herbivory (0)** 1↑Sea urchin grazing (0)	1↑Microalgal production (0) **1↓Calcification (0)** 2↔ Zoox. Photosynthesis (2) 1↑ Zoox. density (1) 1↔Pigmentation (1) 1↓Photosystem damage (1)					

[2] This experiment compared sub-saturating irradiance with saturating irradiance; the effects of higher irradiances were not tested

Stressor	**Acidification**	**CoTS**	**Disease**	**Fishing**	**Irradiance**	**Nutrients**	**Pollution**	**Salinity**	**Sedimentation**	**Temperature**
Pollution				**1↓Reef condition(1)**	**2↑Bleaching (0)** **1↓ Zoox. Photosynthesis (1)**					
(Reduced) Salinity					1↑ Zoox. Photosynthesis (1)	**1↓Fertilization (1)** **1↑Mortality (0)**	**1↓Zoox primary production (1)**			
Sediment.				**1↓ Coral cover (0)** **1↔ Disease prevalence (0)** 1↔ Coral cover[3] (1)	1↓Coral mortality (1) **1↑UV penetration**	**2↓Coral cover (0)** **1↓Fert. (1)** **1↓Growth rate (0)** **1↑Macroalgal growth (0)** **2↑Mortality (0)** 1↔Mortality (1) **1↓ Photosynthesis (0)**		**1↓ Coral cover (0)** **1↓ Fertilization (1)** 1↔ Growth rate (0) **1↑Mortality (1)** **1↓Photosynthesis (1)**		**1↑Mortality (1)**
Sea Level Rise					1↔ Photosynthesis (0)			**1↓Growth rate (0)**		
Storms		**1↓Recovery (0)** 1↑Larval settlement (0)		**1↑Physical damage (0)**		1↓ Algal cover (0) 1↑Fish abundance (0)				**1↑Disease (0)**

[3] Possibly confounded by poaching in ostensibly protected areas

Stressor	Acidification	CoTS	Disease	Fishing	Irradiance	Nutrients	Pollution	Salinity	Sedimentation	Temperature
Temp.	**3↓Calcification (2)** 4↔ Calcification (4) **2↑Pathogenesis (2)** **1↓Nutrient uptake (1)** 1↓Aerobic scope of fish (1) 2↔ Photosynthesis (2) 1↔ Zoox density (1) **1↑Bioerosion (0)** 1↓Fertilization (1) 1↔Fertilization (1) 1↔Photosynthesis (1) 1↔Coral mortality (1) **1↑Coral mortality (1)**		**1↓Zoox density (1)**	1↔Zoox growth rate	1↔ Antioxidant enzyme activity (1) 1↔Bleaching (1) **7↑Bleaching(1)** 1↑ Calcification (1) 1↔ Calcification (0) **3↑Coral mortality (2)** **4↑ Disease (4)** 1↔ Disease (1) 1↓ [Polyunsaturated FAs] (1) 2↑ [MAA] (0) **35↓ Photosynthesis (25)** 1↑ Photosynthesis (1) 5↔ Photosynthesis (4) 1↔ Symbiont clade (0)	**1↑Bleaching (0)** 1↔ Calcification (0) **1↑Disease (0)** 1↔ Disease (0) 3↔ Photosynthesis (3) **1↓ Photosynthesis (1)**	**1↓Larval metamorphosis (1)** **2↓ Photosynthesis (2)**	**1↑Bleaching (0)** **1↓Photosynthesis (1)**	**1↑Bleaching (0)** 1↓Mortality (1) 1**↓Coral cover (0)** 1 **↔** Photosynthesis[4] (0)	

[4] This study was not unable to disentangle the effects of sedimentation from the effects of nutrient loading.

Stressor	**Acidification**	**CoTS**	**Disease**	**Fishing**	**Irradiance**	**Nutrients**	**Pollution**	**Salinity**	**Sedimentation**	**Temperature**
UV	**1↓ Calcification (1)** **1↓ Photosynthesis (1)**				**1↓Community productivity (0)** 1↔ Photosynthesis (0)		**1↑ Coral mortality (1)** **1↓ Photosynthesis (1)**			**1↑Bleaching (0)** **2↑ Coral mortality (2)** **1↓ Growth rate (0)** **7↓Photosynthesis (6)** 1↔Photosynthesis (1)

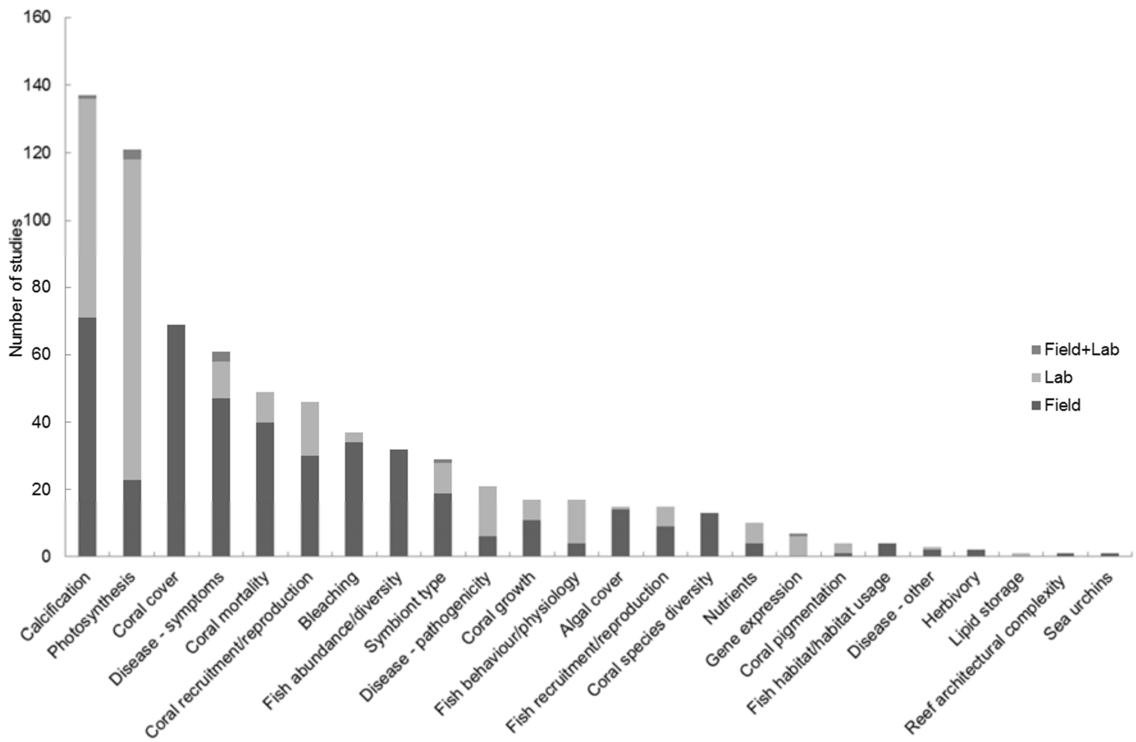


Figure 2.2 Category of response variable of studies that fit two or more of the stressor search criteria listed in Table 2.1. Studies conducted in the field, lab or both are depicted by the different shading in the bars. Note that studies with response variables that I considered to be stressors in themselves (e.g., temperature, irradiance), are excluded. Search results are from ISI Web of Science from 1965 to September 2013. Note that if a study included more than one response variable category, it will contribute to the frequency distribution in all relevant categories.

Examples of reported synergistic effects included nutrients and acidification enhancing the growth of the white plague pathogen *Aurantimonas coralicida* (Remily & Richardson 2006), and increased sediment interacting with hyposaline conditions to depress fertilization and development of *Acropora millepora* (Humphrey et al. 2008). Examples of antagonistic effects included increased nutrients offsetting the effects of acidification on coral calcification (Langdon & Atkinson 2005; Holcomb et al. 2010; Chauvin et al. 2011), although the opposite effect has been more commonly reported (see Suggett et al. 2013 for a list of all such studies). Similarly, sedimentation can reduce the effects of increased temperature and irradiance, either by augmenting heterotrophy or reducing light penetration (Anthony et al. 2007). The relatively low proportion of studies reporting either a strictly additive effect or no significant interaction at all may be due at least in part to publication bias, where studies that do not find deviations from additivity may be less likely to be submitted or published (although, as I note in the following section, I did not find evidence for such a bias in the case of temperature-irradiance-photosynthesis studies). Crain *et al.*

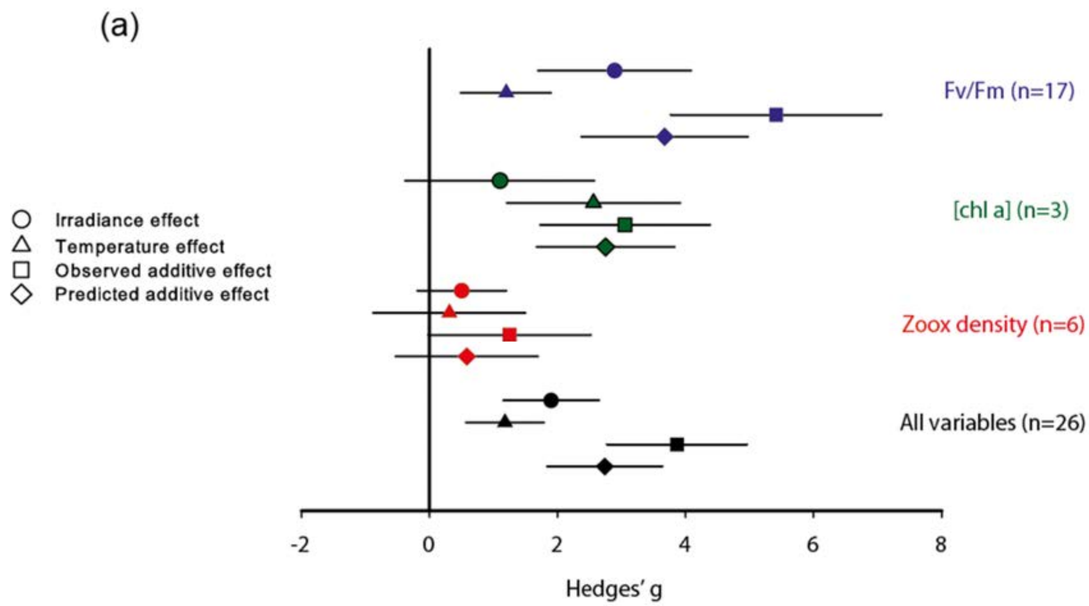
(2008) also suggest that the literature in general is likely to be biased towards stressors that are amenable to factorial experiments (e.g., temperature is easier to manipulate than fishing pressure), and that stressors that are known or suspected to be synergistic (e.g., ultraviolet light and toxins) are more likely to attract research attention than those that are not.

The interaction of irradiance and temperature has been the subject of more research (62 studies, 33% of the total number of experiments) than any other combination of stressors. Including studies that examined the combination of ultraviolet radiation and temperature (n = 12), there are more than 10 times as many studies on the combined effects of irradiance and temperature than the next highest stressor combination of nutrients and sedimentation (n = 6 studies). Of these 62 irradiance-temperature studies, 47 used either qualitative bleaching or quantitative measures of photosynthesis as a response variable, and 27 of these 47 employed a fully-factorial design. Most of the quantitative studies in the irradiance and temperature category reported a synergistic effect on photosynthetic performance (n = 19). Two studies found an antagonistic effect associated with conditioning or pre-exposure to stressful conditions (Dunne & Brown 2001; Brown et al. 2002a) and two (Venn et al. 2006; Yee et al. 2008) found that the response varied with either species or experimental conditions. Certain coral species such as *Porites astreoides* (Venn et al. 2006), *Porites porites* (Venn et al. 2006), *Pachyseris rugosa* (Yakovleva & Hidaka 2004b) and *Pavona divaricata* (Yakovleva & Hidaka 2004b) were resistant to bleaching even under the combination of high light and temperature. A similar variability in responses was found for ultraviolet radiation and temperature, with five studies finding synergistic increases in bleaching and mortality, but some finding no effect of UV on bleaching (Fitt & Warner 1995) or even a mitigating effect (Fine et al. 2002). Again, conditioning or acclimation to stressful conditions appears to play a role in subsequent responses to these stressors (Rogers et al. 2010).

Bleaching was the most commonly-reported response variable, with 52 studies reporting either a qualitative or quantitative bleaching metric. Many other studies measured other parameters that are either direct or indirect proxies for bleaching, such as mycosporine amino acid (MAA) composition, photosynthetic performance, or oxidative stress. While bleaching clearly has deleterious effects on individual coral organisms, even when it does not cause mortality, disagreement still exists about whether non-lethal bleaching may also play a role as an adaptive response to environmental stress (Fautin & Buddemeier 2004; Jones 2008).

The complex interactions between bleaching and disease are unusual in that they could be considered an example of an interaction between stressor responses. Some have hypothesized that bleaching is actually a result of infection by a pathogen that is facilitated by corals' response to environmental stress (Ben-Haim et al. 2003; Rosenberg et al. 2009), but reports of such a relationship are confined mainly to the Mediterranean region. In addition, there is some evidence – primarily from the Caribbean – that bleaching episodes may facilitate disease outbreaks, and vice-versa (Miller et al. 2006; Brandt & McManus 2009; Mydlarz et al. 2009), or that sequential bleaching and disease outbreaks could have a synergistic effect on coral mortality (Harvell et al. 2001; Miller et al. 2006). However, it is unclear whether bleaching and disease are as tightly coupled in other regions, such as the Indo-Pacific (Maynard et al. 2011; Ban et al. 2013). I found few studies that examined the effect on any response variable of interactions of any other stressor with pathogens (n = 1), crown-of-thorns (n = 2), sea level rise (n = 2), storms (n = 4) or pollution (n = 6). Thus, these areas may represent a potential research gap in terms of coral responses to multiple stressors. Additionally, as with my stressor-stressor analysis, there are categories where it is reasonable to assume that interactions occur based on physical principles. For example, increased irradiance will increase temperatures, and sea-level rise will decrease irradiance for photosynthetic organisms with accretion rates slower than the rate of rise – as has occurred in the geologic past (Kendall & Schlager 1981; Blanchon & Shaw 1995; Zhao et al. 2008) and may again in the future (Pittock 1999; Knowlton 2001; Grigg et al. 2002). Indeed, Table 2.2.2 makes it clear that conspicuous gaps exist in the literature with respect to numerous interaction pairs.

Some of these gaps include the interaction between nutrients and irradiance including UV radiation), and between nutrients and pollution. The broad categories also belie the shortage of studies that examine interactions between stressors of the same type, e.g., between different herbicides, or between heavy metals and pesticides. One exceptional study (Negri et al. 2011) not only examined the interaction between temperature and three different herbicides (diuron, atrazine, and hexazinone) independently, but also investigated the interaction between temperature and the simultaneous application of all three herbicides. Nonetheless, all of the herbicides in this study used the same mechanism of action, namely



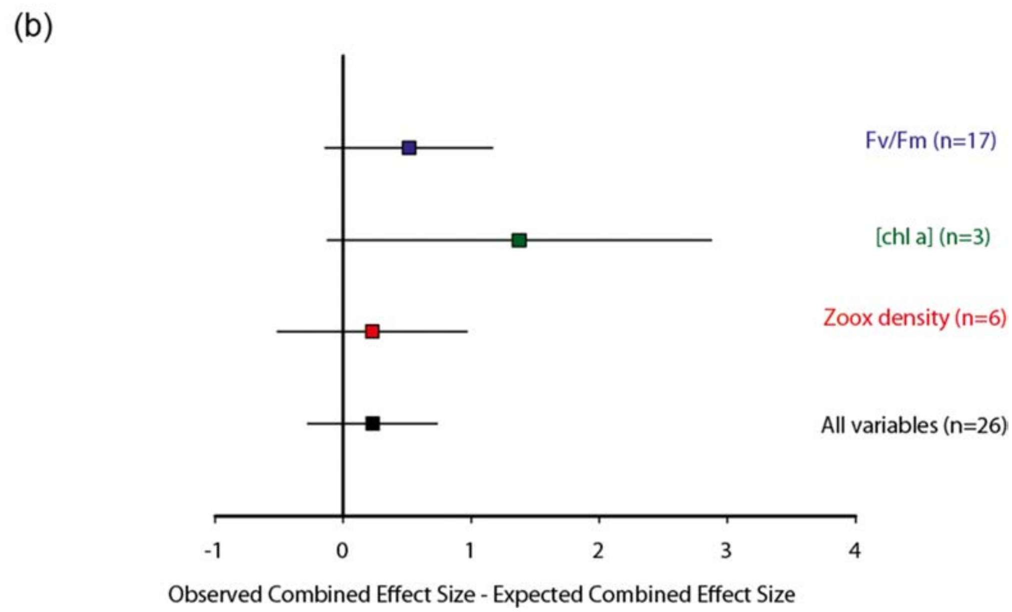


Figure 2.3. a) Mean effect sizes by response variable and stressor type, as predicted by a random effect model. Error bars represent 95% confidence interval. Fv/Fm is a measure of Photosystem II photosynthetic efficiency; [chl a] is chlorophyll a concentration; Zooxanthellae density is the density of symbiotic zooxanthellae contained within coral tissue. b) Effect-size difference between observed and predicted (i.e., additive) combined effect using Monte Carlo simulation. Differences greater than zero indicate synergistic effect; differences less than zero indicate antagonistic effect.

photosystem II inhibitors. Thus, as is the case with toxicology in general, much work remains to be done investigating interaction effects between specific compounds and even entire classes of compounds (Thompson 1996). Given the paucity of studies on most interactions, relative to those concerning irradiance, temperature, and bleaching, there is a clear need to further explore many of these less well-understood stressors and responses.

Quantitative meta-analysis: Combined effect of irradiance and temperature on photosynthesis in corals

Of the 114 studies that measured one or more photosynthetic parameters of scleractinian corals as the response variable, 72 controlled or manipulated at least two factors and 45 examined the interaction between temperature and irradiance. Of these 45 studies, 26 used a fully factorial design that made them suitable for meta-analysis (see Table A1.3). From this quantitative meta-analysis, I found that although the mean of combined stressor effects predicted from the random-effect models tended to be larger than the predicted mean additive effect for each of the three response variables (F_v/F_m, [chl a], zooxanthellae density, Figure 2.3a), the Monte Carlo estimate of the difference between these effect sizes was not significantly different from a purely additive effect for any of the response variables (Figure 2.3b). Pooling all of the response variables (n = 26) also showed that the combined effect of temperature and irradiance stresses were not significantly different from the effect that would be predicted from the sum of the individual effects. Within this pooled group, there was a significant degree of heterogeneity (I^2 = 89.2%); however, this heterogeneity was not well explained by the magnitude of the temperature treatment, irradiance treatment, region of origin, nor genus of the study organism (Table A1.6). Given the relatively small sample size, though, the lack of statistical significance of the region and genus-level analyses should be interpreted with caution.

It is surprising to find a lack of statistical evidence for a synergistic effect between irradiance and temperature for the three photosynthetic variables I examined, given that photosystems that are already damaged or impaired by high temperatures are known to be more susceptible to photoinhibition at lower temperatures (Fitt et al. 2001). However, there is considerable variety in species-specific responses (e.g., Abramovitch-Gottlib et al. 2003; Zhu et al. 2004; Abrego et al. 2008; Yee et al. 2008), as well as evidence for a possible mitigating effect of pre-exposure to irradiance on subsequent temperature exposure (Brown et al. 2002a; Brown & Dunne 2008), and acclimation to both temperature and irradiance (Robison & Warner 2006; Visram & Douglas 2007; Armoza-Zvuloni et al. 2011). Factors such as heating rate (Middlebrook et al. 2010) and pre-conditioning (Bellantuono et al. 2012) also introduce additional variation into the stress response. Outside of a laboratory setting, temperature and particularly irradiance can be difficult to control (Brown 1997). Thus, drawing broad conclusions about the irradiance-temperature-photosynthesis relationship poses a considerable challenge. Furthermore, given that few studies use more than one treatment temperature and/or irradiance level, determining the shape of an almost certainly nonlinear dose-response curve between these two factors will require more sophisticated experimental designs.

Lack of evidence for a synergistic effect at an aggregate level does not mean that synergistic effects were not present in individual studies or that synergistic effects do not exist. For example, in Darling and Côté's (2008) meta-analysis, the overall effect of multiple stressors was not synergistic despite more than a third of the individual experiments finding synergistic effects. In contrast, Crain *et al*. (2008) found evidence for an overall synergistic effect between stressors, despite the majority of individual stressor pairs having an additive effect. Both Crain *et al*. (2008) and Darling and Côté (2008) used the two-interval method, which increases the risk of type II error; hence, both may actually have underestimated the strength of evidence for an overall tendency towards synergistic effects. Here I find that of the 45 studies that examined combined temperature and irradiance effects, 14 (31%) reported a synergistic effect on at least one of the response variables; 7 reported no synergistic effect, and 4 reported a combination of synergistic and additive effects (Table A1.3). A further 18 studies had experimental designs that did not allow for the detection of potentially synergistic effects – generally because the stressors were not independently manipulated or controlled.

Conclusions

In general, the majority of stressor-stressor interactions – whether through reinforcing the incidence of another stressor or resulting in a synergistic effect on a response variable – have deleterious consequences for corals at both the organismal and ecosystem level, but considerable gaps in our understanding remain for numerous stressor interactions and interaction effects. There is some evidence of interactions between chemical pollutants (e.g., herbicides, pesticides, and heavy metals) and physical stressors such as increased temperature and irradiance, and between pathogen virulence and these physical environmental factors. I did not find any studies that quantitatively examined interactions between different kinds of the same type of pollutant (e.g., interactions between two herbicides). By contrast, irradiance and temperature effects are well-studied for a variety of response variables (e.g., bleaching, photosynthesis). However, differences in experimental design, protocols, and lack of consistency in choice of specific measures of response variables makes synthesizing the results of even well-studied interactions difficult. For example, I found only three studies that studied the effect of irradiance and temperature on chlorophyll a concentration using a fully factorial design.

Despite my study being one of the most comprehensive reviews on multiple-stressor effects in coral reef ecosystems to date, I found little data for many types of stressor interactions, particularly of the quality needed to perform quantitative meta-analyses. Thus, while the impacts of some stressor interactions have been well-described in the literature, many others remain unstudied and considerable knowledge-gaps remain, with particularly few studies examining interactions between crown-of-thorns starfish, disease, pollution, low-salinity events and other stressors. Additionally, interactions between (and within types of) nutrients and pollutants, and between both of these stressors and irradiance remain largely unstudied.

Despite more than a decade of research interest in multiple stressors across a variety of ecosystems and in both field and laboratory settings, it remains difficult to predict when and where synergistic effects may occur (Breitburg et al. 1999; Folt et al. 1999; Crain et al. 2008; Darling & Côté 2008; Dunne 2010). Since my review was deliberately focused on stressors that affect corals and coral reefs, it likely under-sampled the body of literature concerning other reef-associated organisms (such as other invertebrate taxa and algae) that may have as-yet unknown interactions and effects on coral reef ecosystems. Furthermore, although I did include papers concerning reef-associated fish and fisheries where they met my search criteria, I did not extensively sample the considerable body of physiological, ethological and fisheries science literature specific to coral reef fishes. It would thus be instructive to conduct reviews of multiple-stressor interactions for other specific coral reef-associated taxa to extend both my stressor-stressor and stressor-response matrices.

Relying on published literature to determine the relative importance of stressors is constrained by the existence of publication bias; although I attempted to minimize this by using an unweighted network analysis, there may be stressor interactions that exist that are not reflected in my network if no studies exist (or could be found) documenting these interactions. A lack of literature documenting a specific interaction could be due either to the difficulty or complexity associated with studying it, or due to the apparent self-evident nature of an interaction – such as between irradiance and temperature. Examples of gaps that deserve further investigation are whether changes in salinity, ultraviolet exposure, crown-of-thorns abundance, and fish abundance or diversity affect either disease pathogenicity or susceptibility. Salinity changes could affect the growth rate of pathogens or make corals more susceptible to disease through stress. Similarly, ultraviolet exposure could reduce pathogenicity by either causing DNA damage or inhibiting pathogen growth and/or increase host susceptibility. Finally, changes in fish community diversity and abundance (particularly corallivores) - as well as crown-of-thorns abundance - could affect the transmission of coral diseases if either fish or *A. planci* serve as carriers.

Additional attention also needs to be given to the question of whether the types of responses observed are sensitive to the choice of variables measured, and if so, whether the ways these variables are measured should be standardized. For example, Chan and Connolly (2012) demonstrated that the apparent response of calcification to acidification varied between studies depending on whether calcification was measured using the alkalinity anomaly or buoyant weighting technique, a difference they attributed to the time frame over which such measurements are typically taken.

Even though global climate change is an urgent issue, coral reef managers are mainly able to carry out local-scale management actions, and thus have to rely on local interventions to maximize coral reef resilience to climate change (Hughes et al. 2007a; Carilli et al. 2009; Brown et al. 2013; Graham et al. 2013b). Using local management actions to increase the potential resilience of an ecosystem is not limited just to coral reefs, however; others have recognized the utility of such an approach in rocky subtidal habitats (e.g., Przeslawski et al. 2005; Russell et al. 2009). Treating stressors as components of a network that is interconnected by reinforcing and mitigating relationships may help to identify the most influential components, and the topology of this network of stressor relationships may aid in identification of tipping points and critical thresholds within the system. By focusing management efforts on stressors that have a leverage effect on other stressors (e.g., sedimentation) and those that exert the largest or most frequent synergistic effects, it may be possible to maximize the effectiveness of those actions. Such efforts should include management of coral reef fisheries that considers effects beyond only target species' abundance (Mumby & Steneck 2008). This will require broader implementation of ecosystem-based management and possibly management across multiple spatial scales (Hughes et al. 2005). Future research should not only attempt to fill the gaps with regard to under-studied stressors, but also investigate community-level responses to multiple stressors and whether synergistic effects are evident (e.g., Graham et al. 2011; Darling et al. 2013).

Identifying the most-influenced or most influential stressors at either an organismal or ecosystem level may be a useful monitoring and management tool. For example, my finding that disease is linked with so many other stressors means that disease outbreaks may serve as an early indicator of non-specific ecosystem stress when it is otherwise difficult to determine when an individual stressor or combination of stressors are at harmful levels (e.g., Harvell et al. 1999; Knowlton 2001). This approach of identifying indirect stressor effects has been used in both lacustrine and estuarine systems, where the recognition that eutrophication was directly or indirectly linked with issues of high turbidity, harmful algal blooms, anoxia, and loss of seagrasses allowed for rapid and effective ecosystem recovery following reductions in both phosphorus and nitrogen loading (Cloern 2001). This recognition was partly a consequence of a shift in conceptual and management models that were based on single, direct responses to those that accommodated multiple, indirect responses (Cloern 2001). A similar approach could be useful in coral reef systems. For example, nutrient loading and sedimentation could be managed to reduce susceptibility to bleaching (Wooldridge 2009; Carilli et al. 2010). I am not the first to propose such an approach: a graph-theoretic analysis of ecosystem stressors was first proposed over a decade ago (Wenger et al. 1999), but it has seen little uptake thus far in management applications.

While my findings underscore both the lack of consensus about interacting stressor effects and the need for more consistency and structure in experimental design, they may also point a way forward by highlighting key research gaps on specific stressor interactions pertaining to coral reefs as well as the general need for study designs and protocols that allow for the identification of synergistic and antagonistic effects in all types of ecosystems. I believe that both the qualitative and quantitative approaches I have used are also readily applicable to the general problem of identifying and quantifying multiple stressor interactions.

Chapter 3 Relationships between temperature, bleaching and white syndrome on the Great Barrier Reef [5]

[5] **Ban, S.S.**, Graham, N.A.J., Connolly, S.R. Relationships between temperature, bleaching and white syndrome on the Great Barrier Reef. 2013. Coral Reefs 32: 1-12.

Abstract

Coral bleaching and disease have often been hypothesized to be mutually reinforcing or co-occurring, but much of the research supporting this has only drawn an implicit connection through common environmental predictors. In this study, I examine whether an explicit relationship between white syndrome and bleaching exists using assemblage-level monitoring data from up to 112 sites on the reef slopes spread throughout the Great Barrier Reef (GBR) over 11 years of monitoring. None of the temperature metrics commonly used to predict mass bleaching performed strongly when applied to these data. Furthermore, the inclusion of bleaching as a predictor did not improve model skill over baseline models for predicting white syndrome. Similarly, the inclusion of white syndrome as a predictor did not improve models of bleaching. Evidence for spatial co-occurrence of bleaching and white syndrome at the assemblage level in this dataset was also very weak. These results suggest the hypothesized relationship between bleaching and disease events may be weaker than previously thought, and more likely to be driven by common responses to environmental stressors, rather than directly facilitating one another.

Introduction

Many studies have posited a relationship between two of the most prevalent causes of large, episodic declines in coral cover: coral bleaching and coral diseases (e.g., Brandt & McManus 2009; Croquer & Weil 2009). Understanding the strength and causal direction of any such relationship is important because increasing ocean temperatures are expected to lead to more frequent and extensive coral bleaching episodes (Nicholls et al. 2007), and possibly also to increased frequency and intensity of coral disease outbreaks through factors such as increased pathogen growth rates with warmer ocean temperatures and increased host susceptibility due to environmental stress (Mydlarz et al. 2009; Sokolow 2009). Thus, if the two kinds of events are self-reinforcing, any projections of the effects of coral cover that do not account for such synergies may underestimate likely declines in coral cover. However, there are few comprehensive assessments of interactions between bleaching and disease on regional scales, in comparable habitats and over long time periods.

Bleaching and disease events may co-occur because they are responses to common environmental stresses, such as temperature. However, several mechanisms for a direct causal relationship between bleaching and disease have been suggested. For example, according to the microbial hypothesis of coral bleaching (Ben-Haim et al. 2003; Rosenberg et al. 2009), bleaching is pathogenically-induced, and reduces the coral host's ability to defend against other infections. Alternatively, according to the coral probiotic hypothesis (Reshef et al. 2006), the symbiotic bacterial community associated with corals is disrupted during bleaching, or portions of the symbiotic bacterial community normally residing in the gastrodermis penetrate the coral epithelial layer (Ainsworth & Hoegh-Guldberg 2009), increasing the host's vulnerability to infection by reducing the competitive exclusion of pathogens. Finally, bleaching has been proposed to compromise immune competence (Banin et al. 2003; Mydlarz et al. 2009), by reducing protective enzyme (e.g., prophenoloxidase (PPO)) activity.

All of the above hypotheses suggest that disease may be more likely to occur coincident with, or in the aftermath of, bleaching events, but there are few instances where the possibility of a direct causal link has been tested explicitly. Indeed, the pattern of co-occurrence of coral bleaching and disease outbreaks, although frequently hypothesized to exist, is poorly documented. Much of the evidence for a link between bleaching and disease has been qualitative or anecdotal, and the lag at which disease outbreaks have been proposed to follow bleaching events has ranged from several months (Miller et al. 2006; Brandt & McManus 2009) to over a year (Mydlarz et al. 2009). Some studies have noted increased mortality relative to bleaching-only episodes when bleaching and disease co-occur (Harvell et al. 2001; Miller et al. 2006), but few to date have explicitly tested the hypothesis that the occurrence of disease is affected by bleaching (or vice-versa). For instance, previous work (Bruno et al. 2007; Heron et al. 2010; Maynard et al. 2011) on the relationship between bleaching and white syndrome disease outbreaks has used common environmental predictors of bleaching and disease (specifically, temperature anomalies), rather than explicitly testing whether, under a given set of environmental conditions, disease outbreaks were more likely when bleaching had previously occurred. Thus, the available evidence does not allow us to distinguish between the possibility that bleaching and disease events share common physical environmental drivers, and the possibility that the occurrence of bleaching events makes disease outbreaks more likely (or vice versa), as has been hypothesized.

Of the environmental variables that have been used to predict both bleaching and disease, temperature appears to be the strongest and most common. However, other potential common environmental predictors include nutrient loading and pollution (Hayes & Goreau 1998; Wooldridge 2007), high irradiance (Boyett et al. 2007; Richier et al. 2008; Muller & van Woesik 2009), and sedimentation (Anthony et al. 2007; Harvell et al. 2007). Predictive models for mass bleaching are well-established for shallow reef flat habitats (Goreau & Hayes 1994; Gleeson & Strong 1995; Lough 2000; McClanahan et al. 2007; Maina et al. 2008; Donner 2011), but reef slope bleaching models are far less common (Glynn 1996). This is important because even during mass-bleaching events, incidence and severity vary widely between inshore and offshore areas, and between different reef zones (Berkelmans & Oliver 1999) and depths. Because most coral species that occupy reef flats also occupy other habitats, and because bleaching may vary with both depth (Spencer et al. 2000; Richier et al. 2008) and aspect (Spencer et al. 2000; McClanahan et al. 2005), the extent to which coral assemblages in habitats such as the shallow reef slope respond similarly to environmental stressors like temperature has important implications for the likely capacity for heavily bleached habitats to recover.

To date, the most successful models for predicting bleaching use multiple temperature metrics, including duration, rate, and magnitude of temperature anomalies (Maynard et al.

2008). In contrast, predictive models for disease are relatively recent and still being refined. Although several coral diseases have been hypothesized to have a link with temperature stress, White Syndrome (WS) has been the focus of most research in this regard. In the Indo-Pacific context, WS describes a variety of conditions (including white pox, white band, and white plague) with similar symptoms, the cause(s) of which are still unknown (Willis et al. 2004). Models used to predict WS have incorporated at least one temperature metric, such as weekly sea surface temperature anomaly (WSSTA) (Bruno et al. 2007), Mean Positive Summer Anomaly (MPSA) (Maynard et al. 2011), and Hot Snap (Heron et al. 2010), in addition to a measure of coral cover. All of these temperature metrics measure short-term (intra-annual) deviations from a climatological mean value, but differ in how the magnitude and duration of those deviations are integrated to generate a cumulative predictor of risk. These models have shown remarkable ability to hindcast the occurrence of white syndrome outbreaks, but the definition of an outbreak has varied in each study (e.g., Heron et al. (2010) – 50 cases per $1500m^2$; Maynard et al. (2011) – 60 cases per $1500m^2$ with a "severe" outbreak constituting 100 cases per $1500m^2$).

In this paper, I provide a comprehensive, regional-scale assessment of whether observations of coral bleaching and disease confer any additional mutual predictability over and above common environmental drivers, using a long-term monitoring dataset of the reef slope in the GBR region, Australia. This dataset assesses both bleaching and disease occurrence at the assemblage level using a consistent depth, reef aspect, and methodology. Specifically, I 1) examine whether traditional physical environmental predictors of mass bleaching in shallow water reef flat habitats are also useful for predicting bleaching events on the reef slope; 2) test the utility of established predictors of white syndrome for these coral assemblages; 3) determine whether, once common physical drivers are accounted for, the occurrence of bleaching is an informative predictor of white syndrome (and vice-versa) at the assemblage level; and 4) examine the spatial patterns of white syndrome and bleaching events at the assemblage level for evidence of overlap or spatial clustering. I focus on white syndrome specifically to facilitate comparison with previous studies (e.g., Bruno et al. 2007; Heron et al. 2010; Maynard et al. 2011), and because it is the most commonly reported disease.

Methods

Bleaching and disease surveys

I used observations of bleaching and disease from the Australian Institute of Marine Science (AIMS) Long Term Monitoring Program (LTMP) and Representative Areas Program (RAP). The total number of reefs visited in a given year ranged from a minimum of 27 in 2003 to a maximum of 112 in 2006. At each reef, five 2-metre wide, 50-metre long fixed transects were surveyed at each of three sites by trained observers using SCUBA along a depth contour of 6-9 metres, providing a total of 1500m^2 area surveyed per location. Benthic cover estimates were obtained using point sampling from video recordings of transects. Sites were visited annually or biennially; for full survey protocols see Sweatman et al. (2008). I also included data from 39 sites in the AIMS inshore monitoring program. Since the inshore survey design differs, disease counts were segregated by depth (2m or 5m) and normalized for area (inshore monitoring transects are 40 m^2 each; LTMP transects are 100 m^2 each) to be comparable with the LTMP and RAP counts. The mean values for white syndrome counts and average bleaching across all transects on each reef were compared between the inshore and LTMP datasets using an independent-samples t-test and not found to be significantly different for either bleaching or disease; thus, the two datasets were combined and analysed together. Although both bleaching and disease observations were collected simultaneously, bleaching data were only collected starting in 1999; thus in both the inshore and LTMP surveys, complete disease and bleaching data existed from 1998 and 1999 onwards, respectively. Between the inshore and LTMP data, there were a total of 93 locations spanning latitudes from 23.91°S to 12.23°S that were visited a minimum of twice and a maximum of 14 times in the 1998-2010 period, giving a total of 961 reef-year replicates. In all surveys, disease observations were recorded as number of diseased colonies per transect, whereas bleaching observations were recorded as percent area of the transect bleached. The genus and species of bleached or diseased colonies were not recorded; thus all data for these conditions were at the transect level only. Although genus and species information were not recorded for either bleaching or disease observations, the proportion of coral cover represented by each genus each transect was recorded. This allowed me to use taxonomic composition as a statistical predictor for transect level bleaching or disease responses.

Table 3.3.1. Summary of temperature metrics used in this study and how they are calculated.

Index	Accumulation Period (prior to survey date)	Formula
Weekly Sea Surface Temperature Anomaly (WSSTA)*	52 weeks	$WSSTA, week\ i+51 = \sum_{i}^{i+51} \begin{cases} 1, Week_i\ SST > Climatological\ Week_i\ SST\ Mean + 1℃ \\ 0, Week_i\ SST \leq Climatological\ Week_i\ SST\ Mean + 1℃ \end{cases}$
Degree-Heating Week (DHW)**Error! Bookmark not defined.**	12 weeks	$DHW, week\ i+11 = \sum_{i}^{i+11} \begin{cases} Week_i\ SST - (Clim.Max\ SST\ + 1℃), Week_i\ SST \geq Clim.Max\ SST + 1℃ \\ 0, Week_i SST < Clim.Max\ SST\ + 1℃ \end{cases}$ Climatology maximum is highest monthly SST value from the climatology period.
Hot Snap†	Variable length; from start-of-preceding spring	$Hot\ Snap = \sum \begin{cases} SST - (Clim.Summer\ Mean\ SST + 1\sigma), SST > (Clim.Summer\ Mean\ SST + 1\sigma) \\ 0, SST \leq (Clim.Summer\ Mean\ SST + 1\sigma) \end{cases}$
Cold Snap†	39 week period prior to most recent summer	$Cold\ Snap = \sum_{i}^{i+39} \begin{cases} SSTweek_i - (Clim.Winter\ Mean\ SST - 1\sigma), SSTweek_i < (Clim.Winter\ Mean\ SST - 1\sigma) \\ 0, SSTweek_i \geq (Clim.Winter\ Mean\ SST - 1\sigma) \end{cases}$
Winter Condition†	39 week period prior to most recent summer	$Winter\ Condition = \sum \begin{cases} Weekly\ SST - (Clim.Winter\ Mean\ SST), winter\ weeks \\ Weekly\ SST - (Clim.Winter\ Mean\ SST), nonwinter\ week\ and\ SST \leq (Clim.Winter\ Mean\ SST + 1\sigma) \end{cases}$
Mean Positive Summer Anomaly (MPSA)‡	Up to 12 weeks, summer months only	$MPSA, week_i = \sum_{First\ summer\ week}^{i} \frac{DHW\ week_i}{\#\ of\ weeks\ where\ DHW > 0}$ where $DHW\ week_i = \sum \begin{cases} (SSTweek_i - (Clim.\ month\ SST), SSTweek_i > Clim.\ month\ SST \\ 0, SSTweek_i < Clim.month\ SST \end{cases}$

* Selig et al, 2010; † Heron et al, 2010; ‡ Maynard et al, 2008

Environmental variables

I used or calculated six temperature metrics for subsequent inclusion in analyses of bleaching and disease (Table 3.1). In previous studies, these metrics have been found to be useful predictors of either bleaching or disease (or both) (e.g., Bruno et al. 2007; Heron et al. 2010; Maynard et al. 2011). I obtained the first two metrics, weekly sea surface temperature anomaly (WSSTA) and degree-heating-weeks (DHW) from version 3 of the global CoRTAD dataset (Selig et al. 2010), which contains data until the end of calendar year 2009; thus I constrained the analyses that used environmental data to this time period, even though the bleaching and disease data extend to November 2010. WSSTA counts the frequency of warm anomalies greater than 1°C from the climatological mean (1985-2004) during the 52-weeks prior to the survey date. A degree-heating week is the sum of the previous 12 weeks where the temperature exceeded the climatological maximum temperature by at least 1°C.I calculated the next three metrics - Hot Snap, Cold Snap, and Winter Condition - for each survey location according to Heron et al. (2010) using the CoRTAD gap-filled temperature data. The Hot Snap metric accumulates when temperatures exceed the climatological (1998-2005) summer mean plus one standard deviation, for a period of accumulation that begins three months prior to the summer preceding the survey date and ends at the survey date. The Cold Snap index accumulates when temperatures are more than one standard deviation below the climatological winter mean over a period of accumulation for the nine months preceeding the most recent summer. Finally, the Winter Condition index records unusually cold periods (more than one standard deviation below the climatological mean) outside of the winter months, as well as unusually mild (more than one standard deviation above the climatological mean) winters, thus accumulating both positive and negative values. The Winter Condition index thus records both unusually mild winters as well as unusually cold periods during other times of the year. A difference of note is that the CoRTAD database uses daytime-nighttime averages, whereas Heron et al. (Heron et al. 2010) used nighttime temperature data only. The spatial (4 km) and temporal (weekly) resolution of the data were otherwise identical.

The final temperature metric was mean positive summer anomaly (MPSA). I calculated the MPSA values as per Maynard et al. (2008) using 4km Pathfinder SST data, but using weekly instead of daily values so as to maintain a consistent temporal resolution for all of the temperature predictors.

Data analyses

I performed several steps in analyzing the data. First, because bleaching data were encoded using an eight-category system (absent; individual colonies; 1-5%; 6-10%; 11-30%; 31-50%; 51-75%; 76-100%) that recorded percentage of bleached hard coral cover for each transect, I used the midpoint of each area category as a weighting factor when determining the average bleaching severity for a given reef (i.e., 0 for absent, 1 for individual colonies, 3 for 1-5%, 8 for 6-10%, 20.5 for 11-30%, 40.5 for 31-50%, 63 for 51-75%, and 88 for 76-100%). I aggregated transect data to the reef level (15 transects per reef); any reefs that were surveyed only once were excluded from the temporal analysis but not the spatial analysis. For each reef, I summed white syndrome counts, and calculated an average % bleaching using the weighting described above. White syndrome counts were normalized for area in the rare instances where the total area surveyed was less than 1500 m^2 due to missed transects. I also considered normalizing white syndrome counts by the amount of coral cover in each transect, but found the normalized diseased count to be highly correlated ($r = 0.725$) with the raw counts, and thus conducted all analyses using the raw count data. Because the transect-level data contained no additional spatial information (i.e., there was no information on the position of transects relative to each other), these reef-level data were also used for the spatial analyses.

Second, I examined all of the potential predictor variables for simple correlations using Pearson's *r* and the variance inflation factor (VIF). VIF provides an estimate of how much of the increase in variance of a regression coefficient for a particular variable is due to collinearity with another variable; VIF values above 5 are generally considered to indicate a problem with multicollinearity (Menard 1995). Neither metric indicated collinearity at a high enough level to require exclusion of variables from the baseline models. Potential predictor variables were standardized using z-scores prior to inclusion in the statistical models, to facilitate comparison of effect magnitudes within and between models.

Third, I used logistic models for both bleaching and white syndrome because both appear to exhibit a threshold-type response (Fitt et al. 2001; Bruno et al. 2007; Jones 2008). Since logistic models require a binary dependent variable, both bleaching and white syndrome data needed to be recoded as presence/absence, and thus I needed to set a threshold for counts (in the case of WS) or area (in the case of bleaching) to identify bleaching and disease "events".

For bleaching, all non-zero observations were considered to be bleaching events. For disease, rather than defining a single threshold *a priori*, I evaluated model performance using thresholds that varied from 0 to 50 counts per reef for WS. For the spatial analysis, the raw count/area data was used rather than thresholds.

For each model, I report the hit rate (% of cases in which the model predicts presence where presence is observed), false positive (% of cases in which the model predicts presence where absence is observed), false negative (% of cases in which the model predicts absence where presence is observed), and overall % classification (total # of correct classifications divided by the total number of cases). Overall % classification can be a misleading metric of model utility in cases where, for example, a "constant" model predicting that events never occur may have high apparent predictive power when events are rare. Thus, I used the Peirce Skill Score (PSS) (Peirce 1884; van Hooidonk & Huber 2009) as the primary indicator of model performance; standard errors for the scores were calculated according to Stephenson (2000). The PSS ranges from -1 (for a model where the predicted state is exactly the opposite of the observed state) to 1 (for a model where all cases are predicted correctly), with random or constant models standardized to a score of 0. I present only results of the disease threshold that resulted in the highest Peirce skill scores (a threshold of 5 observed cases per reef).

To examine the utility of each of the six temperature metrics in predicting bleaching or disease, I first used each of the metrics in isolation in a logistic regression model. Then, to examine the effect of incorporating multiple abiotic predictors, I constructed baseline models for both bleaching and white syndrome using a backwards stepwise removal process based on the likelihood-ratio statistic for variable removal, with initial models containing all uncorrelated temperature predictors. For models predicting white syndrome, % acroporid cover (i.e., the proportion of each transect composed of acroporids) and interaction terms between abundance and each of the temperature metrics were also included, as per Bruno et al. (2007) and Heron et al. (2010). I did not include interactions between temperature metrics due to the lack of a plausible mechanism and corresponding meaningful physical interpretation of such effects. Bleaching was not used in any interaction terms so as to facilitate direct comparison with the baseline models without bleaching as a predictor. Acroporid cover was used from the year previous to the surveys where white syndrome was reported, as the correlation with white syndrome abundance was higher. This takes into account the possibility that acroporid cover may have already declined between the point of initial infection and when the survey detecting disease was carried out. Three alternate models for predicting bleaching were evaluated against the baseline model: one incorporating white syndrome from the same survey year, one incorporating white syndrome from the previous year, and one that used just white syndrome as a predictor without using any temperature variables. Similarly, for predicting white syndrome, I considered models that included bleaching. I evaluated models with and without an AR(1) covariance structure for white syndrome counts to account for the possibility of temporal autocorrelation. Furthermore, I also ran the models using transect-level data to verify whether the parameter estimates were sensitive to data aggregation. For the transect-level logistic models, a threshold value of 1 white syndrome case per transect was used due to the relative rarity of high counts. I also compared the results of models considering only presence/absence of white syndrome with those using the raw counts using a negative binomial error distribution with fits obtained through generalized estimating equations in SPSS.

Finally, a spatial analysis of the reef-level bleaching and disease count data (i.e., using actual counts rather than threshold values) was conducted using Moran's I (Moran 1950), Ripley's K (Ripley 1976, 1977), and semivariograms to check for potential spatial autocorrelation in either bleaching or white syndrome cases at broad scales. Moran's I was run at several distance bands ranging from <1 km to ~40 km to examine trends in spatial autocorrelation and to verify that non-spatially explicit statistical models were appropriate to use. Local non-random clustering of high or low values was quantified using the Getis-Ord Gi* (Ord & Getis 1995) and Anselin Local Moran's I statistic (Anselin 1995). To verify that temporal aggregation was not obscuring patterns of spatial clustering, a year-by-year analysis of bleaching and white syndrome events was also conducted using the Getis-Ord Gi* statistic (see Appendix B). These analyses were conducted using ArcGIS 10.

Results

Between 1999 and 2010, a total of 914 surveys were conducted (i.e., 129 reefs visited an average of 6 times over the 11-year period). The actual amount of data available for each analysis varied slightly due to data being missing for certain variables (see table legends for sample sizes for each analysis). A total of 8,792 white syndrome-affected colonies were observed during that time, with the mean bleaching category ranging between 0.02 and 1.43 (meaning that the maximum amount of observed bleaching when averaged across all reefs surveyed in a year was less than 5% per transect). Within these reefs, there was a pronounced spike in white syndrome cases in 2002 which coincided with increased bleaching (Figure 3.); however, a much larger increase in bleaching in 2006 was not matched by an accompanying increase in white syndrome cases. Aside from the large outbreak in 2002, the number of white syndrome cases since 1999 has been relatively constant.

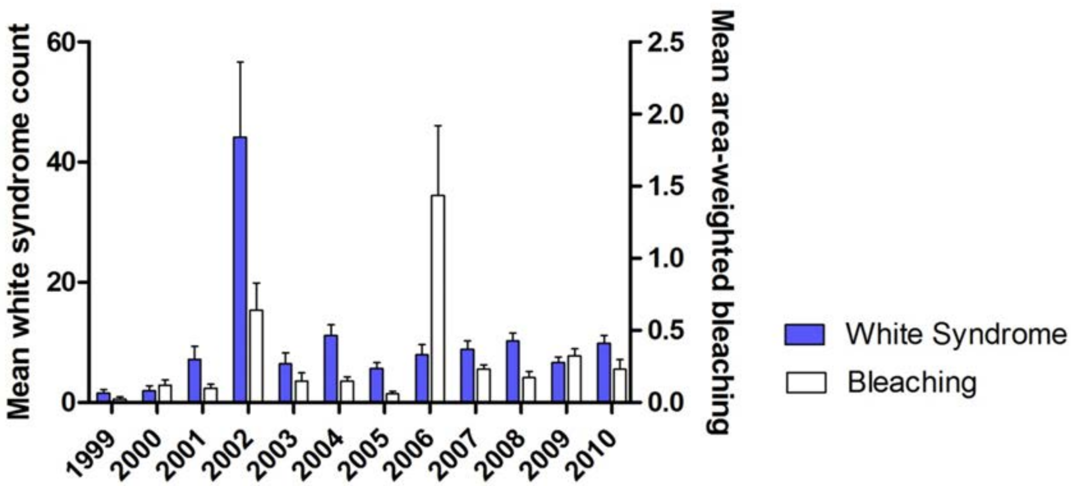


Figure 3.2 Observations of average white syndrome and area-weighted (extent category reweighted by area) bleaching counts over time (1999-2010) across all surveyed reefs (normalized to 15 transects/1500 m2 survey area per reef). Error bars represent one standard error. Numbers above bars represent sample size (# of reefs surveyed) for each year.

The baseline model for white syndrome included Cold Snap index, % acroporid cover, and an interaction term of the Hot Snap index and % acroporid cover (Table 3.2). Overall model classification success was 74%, with a PSS of 0.329. The addition of bleaching as a predictor did not improve model performance (Figure 3.2a), and the bleaching term was non-significant (Table 3.2). Consistent with this, the model using only bleaching and % acroporid cover had higher false positive and false negative rates than the baseline model, as well as a lower PSS score. The bleaching term itself was not significant in this model either, indicating that acroporid cover alone provided most of the predictive utility. Finally, the model that included observations of bleaching from the previous survey year had an only marginally higher PSS score than the baseline model, and, again, the bleaching term of the model was

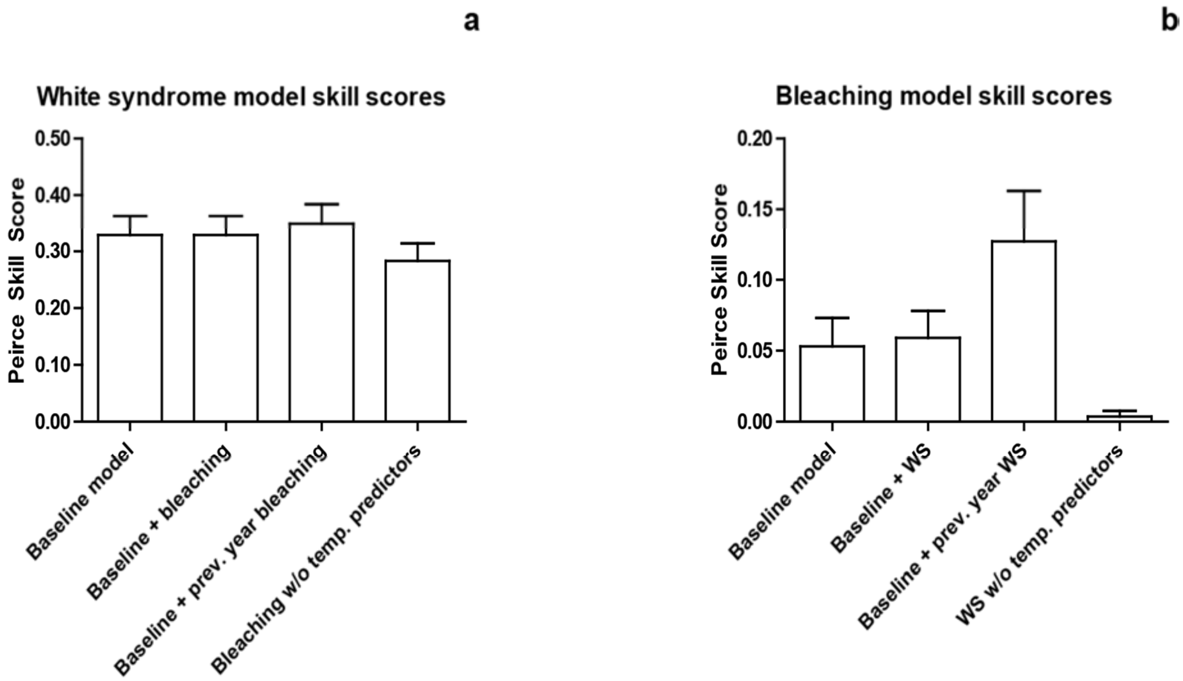


Figure 3.3. Peirce skill scores for models predicting a) bleaching and b) white syndrome. Error bars represent 1 standard error.

non-significant with and without bleaching in the same/previous year as a predictor. (Absence: 0-5/Presence: >5). The baseline model (first column) was derived by backwards-stepwise selection starting with all potential predictor variables. For all effects, the effect size and standard errors are shown.

Since the PSS is dependent on the presence/absence threshold percentage, I verified that my conclusions were not sensitive to my choice of PSS as my model diagnostic by examining two other diagnostics (ROC AUC score, and Nagelkerke R-square value), both of which also indicated that the baseline model without bleaching was the best model.

Hierarchical logistic models that used disaggregated (transect-level) data yielded parameter estimates with the same sign and very similar magnitude as the logistic models that used the aggregated (reef-level) data, but performed no better than chance according to their ROC scores (Table B.1); additionally, bleaching was not a significant predictor in any of these models. The inclusion of an AR(1) covariance structure for white syndrome also did not improve model fits, indicating that there was no temporal autocorrelation of white syndrome. Hierarchical models of white syndrome counts produced similar results in terms of predictors and relative model performance as the reef-level logistic models. In particular, bleaching in the same or previous year was not a significant predictor of white syndrome count (Table B.2).

The baseline model for bleaching included three temperature indices: Hot Snap, Cold Snap, and Winter Condition (Table 3.3, Figure 3.2b). However, this model had a relatively low PSS of 0.053. Adding white syndrome counts from the same year to the baseline model decreased the false positive rate with no change to the false negative rate, although the PSS was largely unchanged from the baseline model and the WS term was non-significant. Using white syndrome counts from the previous survey year rather than the same year led to a substantial increase in the PSS, but, again, the WS term was non-significant. Finally, the model that used only white syndrome to predict bleaching predicted virtually no bleaching: it had the highest false negative rate of all the models (99.5%), the lowest false positive rate (0.5%), and had a very low PSS. Again, in this model, the WS term itself was non-significant. Bleaching models based on transect-level data were uninformative, producing uniform predictions and Peirce skill scores of 0 in all cases (Table B.3).

Overall, bleaching occurrence and white syndrome prevalence do not appear to be correlated (Figure 3.) at the regional scale based on the assemblage-level data available to my study. Pooling across all years, no spatial autocorrelation of either bleaching or disease was detected with semivariograms or Moran's *I* statistic; i.e., the occurrence of bleaching or disease does not decay as a predictable function of distance from a given point (Figure B.1). However, the results of the Getis-Ord Gi* statistic calculated on the average prevalence of bleaching and white syndrome across all years (Figure 3.4a, b) did suggest that white syndrome cases tended to be clustered at the latitudinal extremes of the GBR (Figure 3.5a). Bleaching was also patchy, but significant clustering of high values occurred in different regions than disease, specifically between Townsville and Cairns, and near Heron Island in the south (Figure 3.5b). No clustering of unusually low (but non-zero) values was detected for either bleaching or white syndrome. The results of the Anselin Local Moran's I analysis showed the same patterns as the Getis-Ord Gi* statistic and thus are not shown. The year-by-year Getis-Ord Gi* analysis also did not show any overlap of bleaching and white syndrome clusters for any year (Figure B.2a,b). Clustering of the two events thus does not appear to be spatially congruent.

Table 3.3.2. Comparison of logistic models for presence of white syndrome.

	Model without bleaching		Model with bleaching		Model with bleaching, w/o temperature predictors		Model with previous year bleaching	
Parameter (standardized)	Estimate	Significance	Estimate	Significance	Estimate	Significance	Estimate	Significance
Hot Snap	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Winter Condition	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Cold Snap	0.553 ±0.124	**0.000**	0.558 ±0.125	**0.000**	n/a	n/a	0.576 ±0.127	**0.000**
Hot Snap*Acroporid cover	-0.260 ±0.072	**0.000**	-0.262 ±0.072	**0.000**	n/a	n/a	-0.255 ±0.073	**0.000**
Cold Snap*Acroporid cover	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Winter Condition*Acroporid cover	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
% Acroporid cover	1.146 ±0.113	**0.000**	1.152 ±0.114	**0.000**	0.958 ±0.094	**0.000**	1.131 ±0.115	**0.000**
Proportion bleached	n/a	n/a	0.078 ±0.085	0.359	0.051 ±0.082	0.535	0.097 ±0.080	0.228
Constant	-0.647 ±0.091	0.091	-0.650 ±0.091	**0.000**	-0.587 ±0.080	**0.000**	-0.609 ±0.092	**0.000**
Hit Rate (H)	41.4%		41.4%		38.4%		43.4%	
False Positive % (F)	8.6%		8.6%		10.1%		8.4%	
False Negative % (1-H)	58.6%		58.6%		61.6%		57.6%	
Overall %	74.0%		74.0%		71.2%		74.2%	
PSS (H-F) ±SE	0.329 ±0.034		0.329 ±0.034		0.283 ±0.031		0.350 ±0.034	

Table 3.3.3. Comparison of logistic models for presence/absence of bleaching with and without white syndrome in the same/previous year as a predictor. The baseline model (first column) was derived by backwards-stepwise selection starting with all temperature variables.

	Model w/o WS disease		Model with WS disease		Model with WS disease (previous year)		Model with WS disease, w/o temperature variables	
Variable (standardized)	Estimate ±SE	Significance	Estimate ±SE	Significance	Estimate ±SE	Significance	Estimate ±SE	Significance
Hot Snap	0.237 ±0.071	**0.000**	0.234 ±0.071	**0.001**	0.181 ±0.077	**0.018**	n/a	n/a
Cold Snap	0.172 ±0.077	**0.002**	0.170 ±0.078	**0.028**	0.306 ±0.084	**0.000**	n/a	n/a
Winter Condition	-0.183 ±0.073	**0.013**	-0.184 ±0.073	**0.012**	-0.253 ±0.082	**0.002**	n/a	n/a
WS Count	n/a	n/a	0.024 ±0.067	0.726	-0.141 ±0.099	0.154	0.044 ±0.065	0.501
Constant	-0.444 ±0.070	**0.000**	-0.444 ±0.070	**0.000**	-0.146 ±0.078	0.061	-0.416 ±0.066	**0.000**
Hit Rate (H)	10.8%		10.8%		42.4%		0.5%	
False Positive % (F)	5.5%		4.9%		29.7%		0.2%	
False Negative % (1-H)	89.2%		89.2%		57.6%		99.5%	
Overall %	61.6%		62.0%		57.4%		60.4%	
PSS (H-F) ±SE	0.0533 ±0.020		0.0589 ±0.019		0.127 ±0.036		0.00351 ±0.0041	

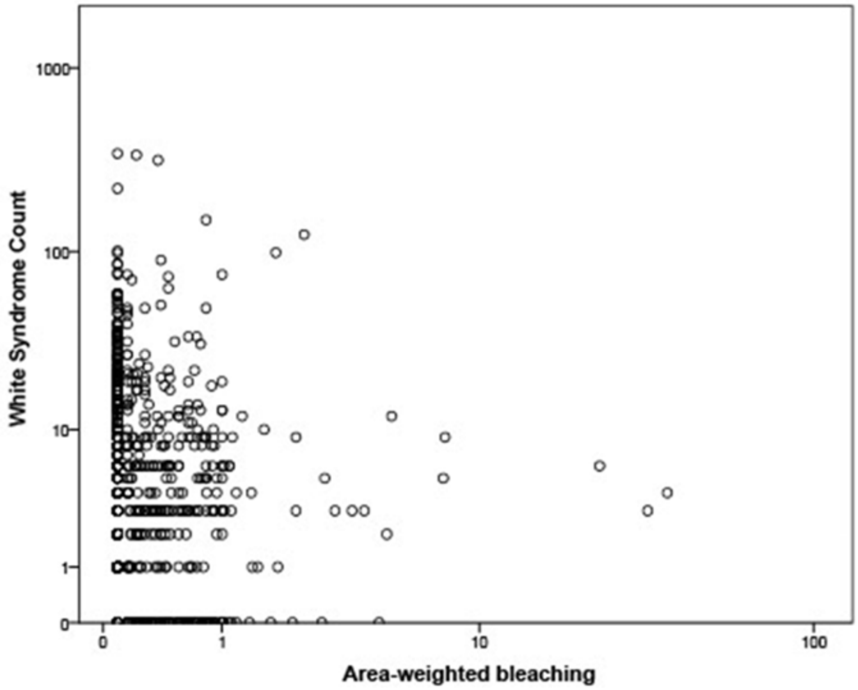


Figure 3.4. White syndrome counts vs. Bleaching severity (area-weighted) across all years and reefs. Axes are log (x+1).

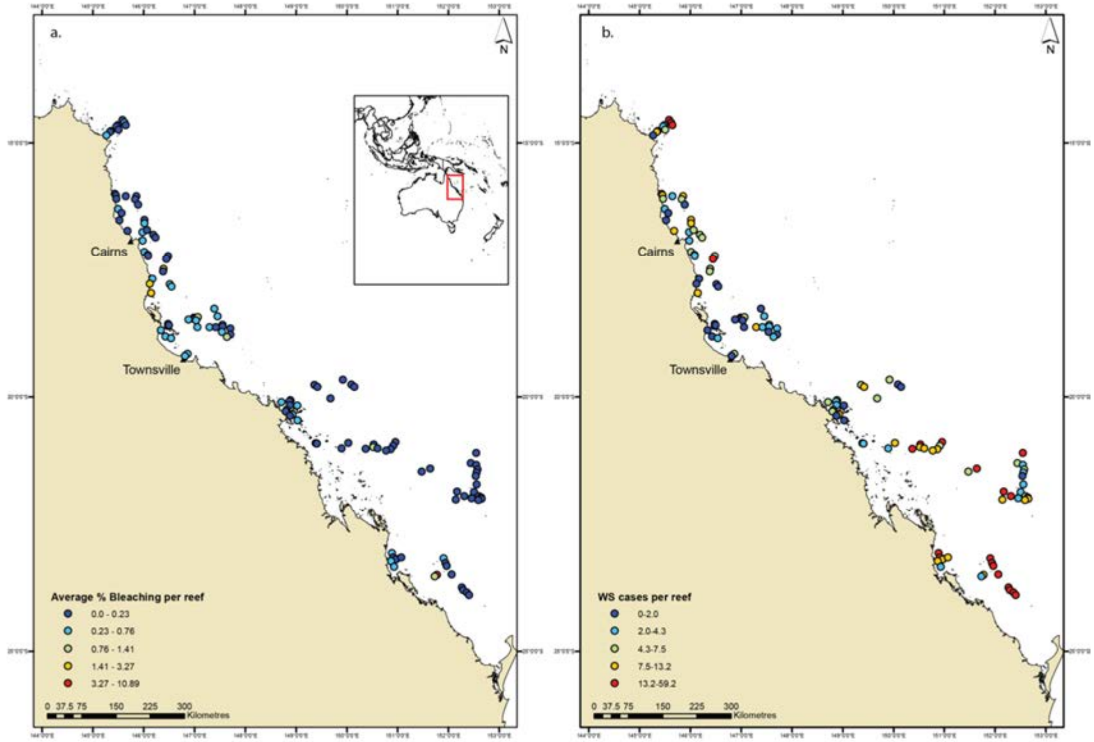


Figure 3.5. Cumulative area-weighted bleaching and white syndrome frequencies across all years (1999-2010) for the 129 reefs surveyed at least once during the study. Blue represents lowest numbers; red represents highest numbers. Each point represents a sampled reef. Categories are quantiles (i.e., bins with an equal numbr of records in each). A) Average % bleaching. In this dataset, recorded instances of bleaching is generally low apart from some sites between Cairns and Townsville and in the far south of the GBR. B) Average number of white syndrome cases per reef; the main areas of high white syndrome occurrence are in the far north and the far south of the GBR.

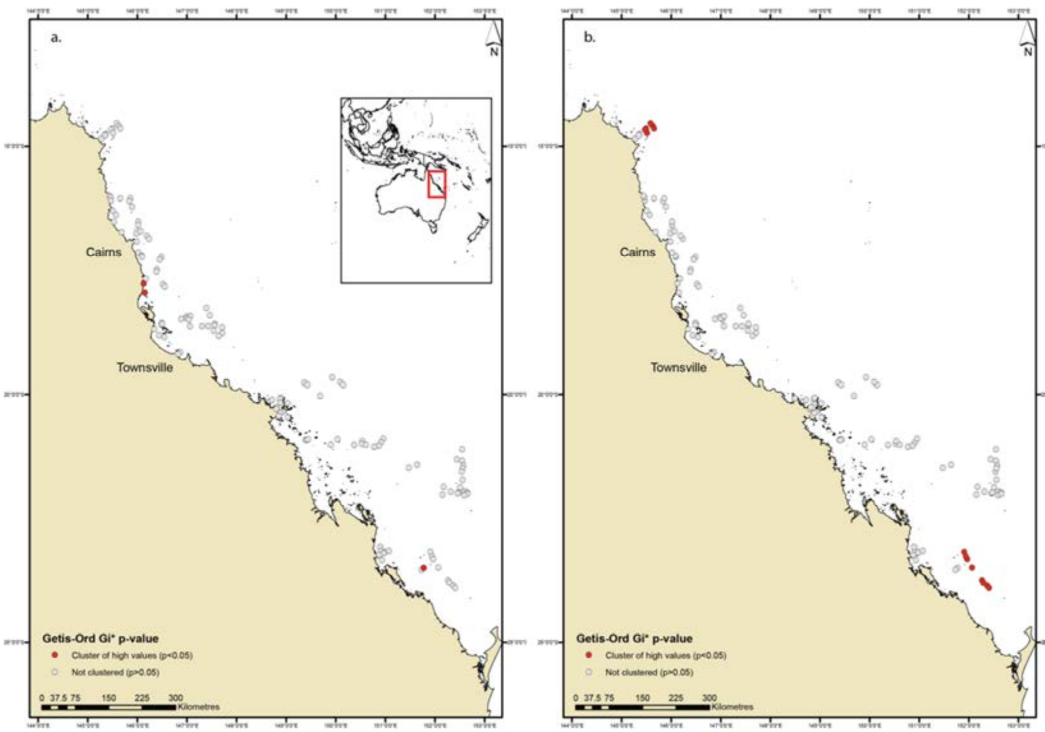


Figure 3.6. Getis-Ord Gi* p-values for average number of white syndrome and bleaching cases across all years (1999-2010) for the 129 reefs surveyed at least once during the study. Significant p-values (p <0.05) in red indicate non-random clustering of high values. Non-significant p-values in grey indicate no clusters of high or low values. A) Bleaching. Statistically significant clusters of high bleaching observations occurred at two inshore sites between Cairns and Townsville, and around Heron Island in the southern GBR. B) White syndrome cases. Statistically significant clustering of high values occurred in the far north and far south of the GBR. No clusters of low values were detected.

Discussion

While many studies have suggested a direct causal relationship between coral bleaching and disease (Jones et al. 2004; Muller et al. 2008; Croquer & Weil 2009), I found no evidence of a correlation between observations of white syndrome and observations of bleaching, at the assemblage level. Moreover, over the past decade, the spatial patterns of bleaching and white syndrome on the GBR have not generally coincided. This is consistent with recent findings by Roff et al. (2011), who suggest that bleaching and white syndrome occurrence could be negatively correlated, possibly due to density-dependence of white syndrome. Given that including the occurrence of bleaching – whether in the same year or the previous year – did not significantly improve model performance, bleaching does not appear to be a useful predictor of white syndrome prevalence when using assemblage-level data, except perhaps insofar as it may indirectly capture the presence of physical environmental stresses that may cause bleaching. Even then, however, the large-scale environmental variables themselves were better predictors of WS.

My results indicate that there have been localized hotspots of white syndrome outbreaks, which is consistent with white syndrome resulting from a spreading pathogen or another multiple-point-source or clustered risk factor exposure in addition to – or instead of – being a purely environmentally-driven phenomenon (e.g., Ainsworth et al. 2007; Kvennefors et al. 2010). This contrasts with Roff et al.'s (2011) findings, who concluded that the pathogenicity of white syndrome was low in both aquaria and field settings, and found a lack of spatial aggregation of white syndrome cases at the colony level. However, I do find that bleaching and disease share some temperature-related environmental predictors, although these variables were relatively weak predictors of bleaching risk in these data, even though these temperature indicators were at extreme values in some years, such as during the 2002 mass bleaching event on the GBR (Liu et al. 2003).

In all models, an increasing Cold Snap index was associated with an increasing probability of white syndrome occurrence, but an increasing Winter Condition was associated with a decrease in white syndrome occurrence. This contrasts with Heron et al. (2010), who found that an increasing Winter Condition correlated with increasing white syndrome counts. However, while the Hot Snap term by itself was not significant, the interaction of Hot Snap and % acroporid cover was significant in all three of the models where it was included, indicating that the Hot Snap index has a greater influence on white syndrome occurrence when acroporid cover is low than when it is high. While my results differ from Heron et al’s (2010), a key difference between the approaches is that I was predicting presence/absence of white syndrome rather than linear severity above an outbreak threshold. Additionally, my analysis included an additional four years of environmental data and five additional years of disease/bleaching data compared to Heron et al. (2010). These findings may indicate that the temperature-white syndrome relationship is more complicated than previously suspected; for example, Roff et al. (2011) found that initiation and progression of white syndrome occurred under both summer and winter conditions and that there was only a weak relationship between white syndrome lesion progression and thermal stress.

Using multiple temperature indices to predict bleaching improved Peirce Skill Scores, although all of the skill scores were low compared with the DHW-based models assessed by van Hooidonk and Huber (2009), which had an average PSS of 0.55. Although, in my analysis, the model that incorporated white syndrome occurrence from the previous year had the highest PSS score of all models, the bleaching term itself was non-significant. Given the large change in the coefficient of the Cold Snap term when WS is added as a predictor (from 0.172 to 0.306), this could indicate that an interaction exists between white syndrome and another unknown variable that the model does not include. Interestingly, all three of the temperature indices developed by Heron et al. (2010) for predicting white syndrome remained as significant predictors, with unusually cold winters (as measured by Cold Snap) and hot summers (as measured by Hot Snap) increasing, and unusually mild winters (as measured by Winter Condition) decreasing the likelihood of bleaching. The direction of the bleaching relationship with the Cold Snap and Winter Condition indices is opposite to that found by Heron et al. (2010) for white syndrome. This provides further support that the bleaching in my data set was predominantly environmentally stress-linked rather than causally linked with white-syndrome occurrence. Furthermore, my findings support the hypothesis that unusually cold winters (i.e., temperatures below the lower limit of corals’ thermal optimum range) may result in a physiological stress that persists long enough to affect susceptibility to later heat stress, while a mild winter may pre-condition corals to an ensuing warm summer – similar to a concept first suggested by Berkelmans and Willis (1999).

None of the commonly-used temperature metrics on their own proved to be good predictors of bleaching in the LTMP survey data. While this result was unexpected, Berkelmans and Oliver (Berkelmans & Oliver 1999) reported that, even during the 1998 mass bleaching event on the GBR, bleaching was most severe on the reef flat and at depths shallower than 4m, although bleaching was observed to as much as 20m depth on some mid- and outer-shelf reefs. Since the LTMP transects are on the reef slope at depths of 6-9m, they may not bleach substantially even if mass bleaching is occurring at shallower depths and/or on the reef flat. While the LTMP bleaching data do not encompass the 1998 mass bleaching event, there was a second mass bleaching event on the GBR in 2002, in which a greater proportion of offshore reefs bleached (41%) (Berkelmans et al. 2004). This event is also not reflected in the LTMP data (Figure 3.), although there was a pronounced spike in white syndrome cases that year. Bruno et al. (2007) also proposed there was little or no spatial overlap between the 2001/2002 mass bleaching event and white syndrome severity during the same period. However, Bruno et al. (2007) were only able to compare bleaching observations from aerial surveys conducted by Berkelmans et al. (2004) (and thus likely dominated by reef flat habitats) with disease data from in situ observations of the reef slope. My study confirms the conjecture of Bruno et al. (2007), at least for reef slope habitats, by direct comparison of bleaching and disease outbreaks observed on the same transects.

The apparent lack of co-occurrence of bleaching and white syndrome in my study could have been influenced by the survey design. As others (e.g., Jones 2008) have pointed out, sampling frequency should ideally be matched to the temporal scale of the events being monitored, and thus annual surveys may be missing episodes that are too temporally fleeting or localized to be detectable weeks or months after the event. Although lags of as long as a year between a bleaching episode and disease onset have been reported (Mydlarz et al. 2009), the annual or biennial frequency of sampling means that short-term lags that leave no lasting visible effects may be missed between survey visits. Studies that have used longitudinal monitoring of individual coral colonies (e.g., Brandt & McManus 2009; Bruckner & Hill 2009; Croquer & Weil 2009) have generally found stronger correlations between bleaching and disease. Thus, patterns of bleaching and disease that are readily apparent at the colony level scales may not be manifest at the assemblage level, highlighting the need for long-term, regional monitoring studies that track the progression of bleaching and disease at the level of individual colonies (similar to Roff et al (2011), but replicated across a larger area and over a longer time period)

Whether or not bleaching and disease have a direct causal link at the level of individual colonies, information about one could still, in principle, be useful for predicting the other indirectly. In particular, where environmental data are lacking, or coarse in scale, bleaching and disease may serve as useful surrogate measures of localized environmental stress. Indeed, it is in this context that the lack of a strong relationship between these two variables in my analysis was most surprising. The temperature data I used are remotely-sensed, and thus are more reflective of conditions prevailing near the ocean surface. Temperatures on the reef slope are likely to be partially decoupled from surface temperatures due to such influences as tidal bores, mixing, and bottom topography (Wolanski & Hamner 1988; Jiménez 2001). I expected that bleaching and disease would be particularly useful co-predictors under these circumstances. Instead, I found that my measurements of the physical variables themselves were much more reliable, and, moreover, they worked well for predicting disease. This tends to suggest that the remotely sensed temperature data actually provided a reasonably good index of the thermal conditions on the reef slope, but that bleaching susceptibility is simply much lower in those habitats, perhaps due to lower irradiance or higher flow.

Disease and bleaching are just two of the many stressors at work in coral reef ecosystems that pose a complex problem for ecologists and resource managers. The response of an ecological community to these stressors is at least partially dependent on whether the community has a positive or negative co-tolerance (Vinebrooke et al. 2004), and thus regions or habitats in which disease and bleaching are not strongly associated or cannot be used as reliable co-predictors are likely to pose a more difficult management problem than those areas in which they are tightly coupled. It remains to be seen whether the findings of this study are indicative of biogeographical (e.g., Caribbean vs Indo-Pacific) or habitat-specific (e.g., reef-flat vs. reef-slope) difference in bleaching-disease susceptibility and responses, or whether these relationships may have been obscured through the temporal and spatial aggregation necessary with my dataset. Effect sizes that are readily apparent at the colony level may become more difficult to detect when scaled up to the assemblage and community level. While I did not find any spatial or temporal correlations at this regional scale, I cannot rule out the existence of a bleaching-white syndrome connection at fine spatial scales or in different reef habitats.

Chapter 4 Assessing interactions of multiple stressors when data are limited: A Bayesian belief network applied to coral reefs[6]

[6] Assessing interactions of multiple stressors when data are limited: A Bayesian belief network applied to coral reefs. **Ban, S.S.**, Pressey, R.L., Graham, N.A.J. Global Environmental Change (in press).

Abstract

Bayesian belief networks useful for conceptualizing systems and evaluating probable outcomes of scenarios in situations where data are limited and uncertainty is high. The combined effect of multiple stressors is one area where considerable uncertainty exists. My study area, the Great Barrier Reef is simultaneously data-rich – concerning the physical and biological environment - and data-poor – concerning the effects of interacting stressors. I used a formal expert-elicitation process to obtain estimates of outcomes associated with a variety of scenarios that combined stressors both within and outside the control of local managers. There was much stronger consensus about certain stressor effects - such as between temperature anomalies and bleaching – than others, such as the relationship between water quality and coral cover. In general, the expert outlook for the Great Barrier Reef is pessimistic, and local management actions may not be sufficient to forestall the ongoing decline in coral cover.

Introduction

Coral reefs face multiple stressors at both local and global scales. At the local scale, coral reef managers can do little to directly affect the pace of climate change, but management of local and regional-level stressors can also increase the resilience of coral reefs to climate-related stressors (Mumby & Steneck 2008; Carilli et al. 2009; Graham et al. 2011). The impact of multiple stressors, and potential management actions to address them, have thus been identified as a key research need (GBRMPA 2009a; NOAA 2012).

Bayesian belief networks have seen increasing use in terrestrial wildlife and aquatic management contexts. For example, Nyberg et al (2006) used a Bayesian belief network to evaluate forest management options for woodland caribou in British Columbia, Canada. Using a workshop-based expert elicitation process, they produced a model that could be used by forest managers to evaluate the costs and benefits of various harvesting strategies on the availability of lichen for caribou. Marcot et al (2001) developed a series of Bayesian belief networks at different spatial scales to evaluate the effects of different planning alternatives on key species of concern such as bats. These models identified key habitat features which could affect population responses.

In a coral reef context, while some relationships between stressors and their impacts are reasonably well-characterized (e.g., temperature and irradiance effects on coral bleaching), many are not, and much uncertainty remains around the interacting effects of multiple stressors on coral reefs and other ecosystems (Darling & Côté 2008; Ban et al. 2014). Furthermore, it remains uncertain whether the combined effect of individual stressors is greater or less than the sum of their individual effects. Managers are usually required to act in the absence of complete information, so estimates of the individual and interacting effects of stressors will be necessary. However, explicit acknowledgement of uncertainty during the planning process is important to avoid poor conservation outcomes – mainly because the higher the expected utility of a decision, the more vulnerable it is to uncertainty (Regan et al. 2005). Consequently, one of the challenges that scientists and managers face is to synthesize the best available scientific information for use in policy decisions, while recognizing gaps and uncertainties - not only in data about the system being managed, but also in conceptualizing the system (Kinzig et al. 2003).

Bayesian belief networks are decision-support tools that facilitate rapid conceptualisation of a system to be managed, and allow the effects of uncertainty on management decisions to be explored (Kuikka et al. 1999; Barton et al. 2008; Henriksen & Barlebo 2008). Bayesian belief networks accommodate qualitative opinions about costs, benefits, and uncertainties (Phillips 2005). These data can then be combined with empirical data (where available) and incorporated into a formal evaluation of likely outcomes given specific actions. Bayesian belief networks have been increasingly applied in adaptive management contexts (Nyberg et al. 2006) and to complex social-ecological problems, such as the management of the multi-jurisdictional Murray-Darling Basin (Hart & Pollino 2009), and. However, as a form of directed acyclic graph (Cooper & Herskovits 1992; Tulupyev & Nikolenko 2005), one of the key limitations of Bayesian belief networks is that they do not allow the existence of feedback functions (such as between predators and prey), and temporal dynamics are difficult to implement. Nonetheless, used in concert with other decision support and modelling tools, Bayesian belief networks can be a useful part of the adaptive management process by providing a formalized overview of system structure and potential responses to management actions.

This study used expert elicitation to parameterize a Bayesian belief network to better understand the interaction of multiple stressors and related management options (such as reducing terrestrial inputs or reducing fishing catches) where data about the effects of these interactions were incomplete. I used the Great Barrier Reef as a case study because: a) multiple stressors are affecting the reef (Haynes et al. 2007; De'ath et al. 2012); b) understanding stressor interactions has been identified as a priority by park managers (GBRMPA (Great Barrier Reef Marine Park Authority) 2009); and, c) the system presents a combination of a data-rich and data-limited situation, for which Bayesian belief networks are well-suited. Data-rich areas include extensive climatological data and long-term monitoring of selected reefs. Data-limited areas concern the understanding of the effects of certain combinations of stressors, and the relative scarcity of data regarding combinations of conditions that could arise more frequently in the future. For example, it is unknown how the combination of disease outbreaks and bleaching may affect coral mortality rates (Ban et al. 2013), or how nutrient loading may affect coral susceptibility to bleaching (Wooldridge & Done 2009). This elicitation and modelling approach could help to identify which management actions, if any, would be most effective in forestalling or mitigating the effects of climate change on the Great Barrier Reef.

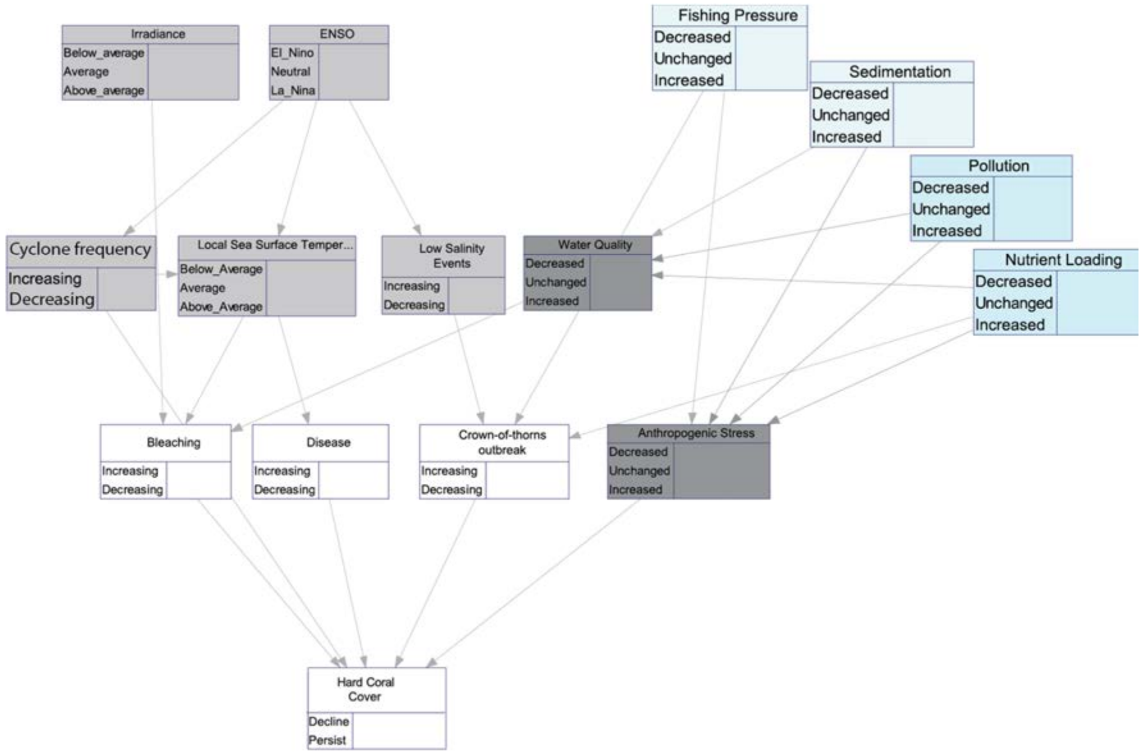


Figure 4.1. Conceptual model of interacting stressors in the Great Barrier Reef. Light grey nodes were informed by data; dark grey nodes are composite nodes formed by assigning weights to each of their inputs; white nodes were my response variables (outcomes) of interest. Blue nodes represent activities or processes amenable to alteration by management.

Methods

Expert elicitation

I identified potential experts based on a literature search of the most-published authors on the topic of coral reef ecology in the Great Barrier Reef, and subsequently used a snowball approach (Klovdahl et al. 1977; Frank 1979) to identify experts that may not have been identified through the literature search approach alone (n=21 total respondents; see suppl. methods for additional details). This falls in the middle of the suggested size of pools for expert elicitation, which range from as few as three (Ferrell 1985; Clemen & Winkler 1999) to as many as 60 (de França Doria et al. 2009). Experts were first contacted in June 2012 and the last interview was conducted in November 2012. Interviews generally took less than hour, ranging from approximately 30 minutes to two hours.

In a BBN, variables are depicted as nodes in the network; relationships between nodes are shown as links or arcs (Figure 4.1). If node A has an influence on the state of node B, node A is said to be a parent node of node B; conversely, node B is said to be a child of node A. Each node contains a conditional probability table (CPT – see example in Figure 4.1), which describes the probability of that node taking on a certain value for each of the possible states of its parent nodes; for example, it may be more likely that a flood (low salinity event) will occur in an El Nino year than in a La Nina year, so the CPT for the low salinity node would have a flood probability of 82% in an El Nino year, 64% in a La Nina year, and 66% in a neutral year. In the absence of short-term predictions regarding these events, we assumed that future probabilities would continue to reflect historical frequencies.

I developed an initial BBN conceptual model of stressor interactions (Figure 4.1) to be assessed by interviewees, the structure of which was based on existing literature about stressors on the GBR (Done 1992; Wooldridge & Done 2009; Ban et al. 2014). At the beginning of interviews with experts, I provided a standard statement that described the model's scope and limitations (see Appendix C for details), and that the model was intended to apply only to mid-shelf reefs with approximately 30% coral cover. This choice to focus on mid-shelf reefs was twofold: first, that the composition of inner, mid, and outer shelf reefs is markedly different with inshore reefs generally being degraded from chronic siltation and mid-shelf reefs showing the greatest species and community diversity (Done 1982). Second, midshelf reefs are generally situated at such a distance from shore that they could be expected to encounter the effects of terrigenous activities in only years with exceptional flood activity (King et al. 2001).

In my model, the probabilities linking stressors and their effects related to the chance that an event could occur in any given year over the next 10 years. This timeframe applied to all aspects of the model, so that the probability of the variable of interest (coral cover) translates into the probability that coral cover in ten years' time will be higher or lower than at present. This timeframe is sufficiently long to average out interannual variations, but sufficiently short for experts to be able to provide a more confident estimate of probabilities than would be the case for a model with a longer time horizon. Furthermore, the first Reef Water Quality Protection Plan in 2003 (Queensland Government 2003) set a 10-year goal to achieve its water quality objectives, with a subsequent plan (Queensland Government 2013) revising the target year to 2020. Current conditions were used as the baseline, so all changes to the severity and/or frequency of stressors were assumed to be relative to their present state. The initial conceptual model also identified nodes and links for which empirical data exist.

There were five physical and climatological nodes in my model for which I had sufficient data to empirically determine the CPTs for some or all of their child nodes: El Niño Southern Oscillation (ENSO), incident solar irradiance, sea surface temperature (SST) anomalies, cyclone frequency (for cyclones greater than category II), and flood event frequency (for flood events described by the BoM as "moderate" or worse in catchments draining to the GBR, light grey in Figure 4.1). I obtained data for historic frequencies of El Niño events, cyclones, and floods from the Australian Bureau of Meteorology website (Australian Government Bureau of Meteorology 2012b, c, a). The frequency of SST anomalies was calculated using monthly gap-filled Pathfinder 4km day-night data for the entire GBR from 1985-2009. Similarly, irradiance anomalies were calculated from NASA SeaWIFs photosynthetically active radiation (PAR) monthly 9km data from 1997-2010. For each node based on empirical data, I derived the conditional probability table based on the historical frequency of these events (e.g., the number of times a flood event has occurred in an El Niño vs. a La Niña year).

I presented the initial BBN conceptual model to participants individually, and asked them to parameterize the model. I also asked for feedback on the model to identify areas of disagreement with the model structure (Figure C.1). Respondents were then asked to assess the conditional probabilities associated with the stressors and outcomes depicted by the initial model, using a scale of two or three categories (e.g., for two categories - present/absent; increasing/decreasing; for three categories - below average/average/above average). Because a CPT must contain a value for each combination of states of the parent nodes, it is recommended to use as few discrete states as possible so that the resulting probability tables are kept tractable (Marcot et al. 2006). I used three categories for nodes relating to manageable stressors (blue nodes in Figure 4.1). I used two categories for non-manageable stressors (light grey nodes in Figure 4.1) except for temperature and irradiance, for which I wished to capture the effects of both increases and decreases from average. Furthermore, although I had data on ENSO event frequencies, I also had empirical data for all of the child nodes, so the values in this node did not influence the rest of the model. The elicitation of probabilities focused only on nodes where data were not available to empirically calculate the probabilities (below).

Single stressor effects

I asked respondents about uncertainty in individual stressor effects (i.e. the range of possible values within a CPT) using a four-question elicitation technique: the interviewee was asked for the lowest possible estimate, the highest possible estimate, the most likely estimate, and their level of confidence in their answer (Speirs-Bridge et al. 2010). To avoid respondent fatigue, I used this technique only for stressors directly related to a subset of nodes in the model: mass bleaching, disease outbreaks, and overall probability of coral decline. I chose bleaching and disease for their strong linkages with temperature and thus climate change, and probability of coral decline because it is the ultimate endpoint of my model. For both bleaching and disease, I asked respondents whether such events would occur at random in the absence of unusual environmental conditions.

Multiple stressor weighting

The idea of using composite nodes in a Bayesian belief network is not new (Pearl 1991; Krieg 2003, 2006), but in the absence of quantitative data about the relative effect of stressors, in constructing these nodes I used an approach similar to Teck et al (2010). Unlike Teck et al (2010), however, instead of having experts rank the stressors, I directly elicited a weighting score of the individual stressors. For water quality - where chemical pollution, nutrients, and sediments occur together in flood plumes - and anthropogenic stress, where all of the stressors are at least theoretically manageable - I asked participants to assign a weight to each stressor to form a single composite node (dark grey in Figure 4.1). Respondents were then asked to allocate a total stressor weight of 1 among the stressors for each composite index. This weighting was used to weight the state of each composite node according to the state of the individual stressors that contributed to it; for example, if four stressors were weighted equally and three of the four were increasing while one was unchanged, the conditional probability table of the composite node had a 75% probability of increasing and a 25% probability of being unchanged. In short, I used these composite node to reduce the complexity of the CPTs in the child nodes, as well as to capture variations in coral cover that were not explained by other, more explicit nodes and links in the model.

In my model, the composite index for water quality consisted of sedimentation, chemical pollution, and nutrient loading, and the anthropogenic stress index contained all of the water quality parameters plus the effect of fishing pressure. Although this means that the parent water quality nodes were effectively used twice in the model, I wanted to separate the direct effects of anthropogenic stressors on coral reef health from the indirect effects of water quality on other outcomes such as bleaching and disease outbreak probability. Combining the use of linear interpolation with composite nodes, I was able to limit the total number of stressor combinations (i.e., scenarios) that interviewees were asked to assess to six for disease, eight for bleaching, seven for crown-of-thorns outbreaks, and eight for coral decline (Table C.1).

Multiple stressor effects

I directly elicited probabilities for the states of response variables ("outcomes") given different combinations of stressors (parent node states). I presented four response variables for evaluation under multiple-stressor scenarios: probability of a mass bleaching event; probability of a coral disease outbreak; probability of a crown-of-thorns outbreak; and the probability of hard coral cover on a hypothetical reef maintaining its present level (or increasing) versus declining. The number of scenarios varied depending upon the number of parent nodes and the number of states for each parent (Tables C.2-C.5), ranging from 9 scenarios for the disease outbreak node to 48 scenarios for the coral cover decline node. I presented the interviewee with a scenario (i.e., a combination of parent node states from the model) and asked for their best estimate of the probability of the outcome associated with each scenario. To keep the number of scenarios tractable for the purposes of elicitation, I only elicited probabilities for the most extreme conditions (Table C.1) and then used linear interpolation to infer probabilities for intermediate conditions (Bashari et al. 2008; Wisse et al. 2008). For the largest conditional probability table, this allowed me to reduce the number of directly elicited probabilities from 48 to 8.

Sensitivity analysis

I conducted a sensitivity analysis on the model to determine which nodes had the most influence on the probability of coral cover persisting. In a BBN, sensitivity analysis quantifies the reduction in uncertainty at a given node due to the finding of evidence at another node. This entropy reduction measure thus calculates the change in variance for an outcome variable (node) attributable to each input variable (Marcot 2012). Thus, a larger value for entropy reduction or mutual information at a node represents a greater influence on the probability of coral cover declining. I conducted this analysis using Netica (Norsys Software Corporation 1992-2010), which quantifies how much variation in a particular expected outcome can be attributed to changes in state in other parts of the model (Pearl 1991).

Results

Single-stressor effects

Based on expert opinion, temperature increase (95% Bayesian credible interval (BCI): 19.6 - 39.2) and decreased water quality (95% BCI: 16.4 - 39.5) have the most influence on disease outbreaks (i.e., the mean best-estimate probability was above background, 95% BCI: 3.7 - 12.1) (Figure 4.2a). The experts also believed that only increased temperature (defined as at least 1°C above the long-term climatological mean for a minimum of 4 weeks) and irradiance (defined as one standard deviation above normal) affected the probability of bleaching (mean best estimates of 54% and 18%, respectively; 95% BCI: 44.0 – 64.9 and 8.6 – 27.4) (Figure 4.2b).

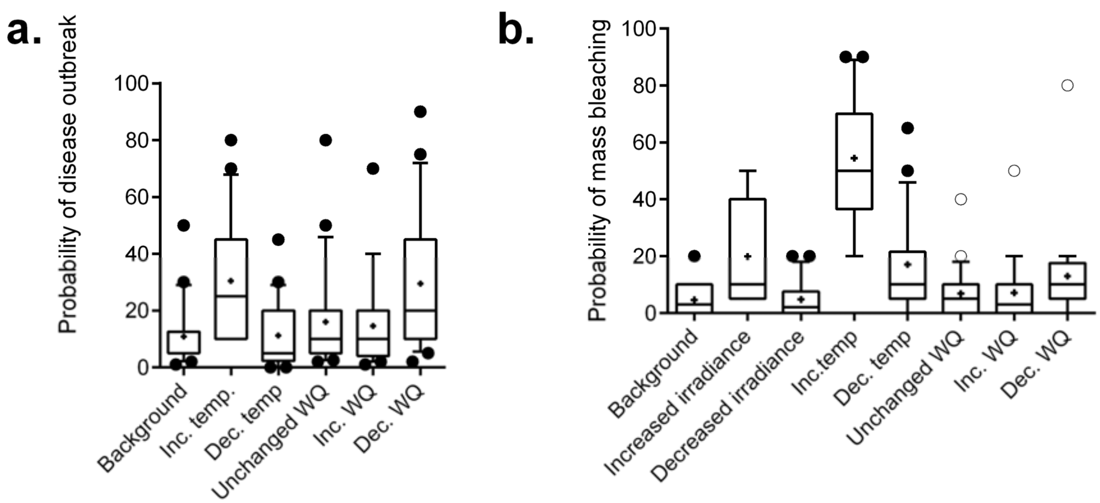


Figure 4.2. Probability of outcomes associated with changes in single stressors for: a) disease, and; b) bleaching. WQ = water quality. Lines within boxes are medians of expert responses. Crosses within boxes are means. Ends of boxes represent 25th to 75th percentiles. Whiskers represent 10th and 90th percentiles. Points represent outliers. Except for temperature (for which increases or decreases indicate a +2°C or -2°C deviation, respectively, from the climatological mean is indicated), changes refer to a +/- 1-standard deviation from current stressor levels.

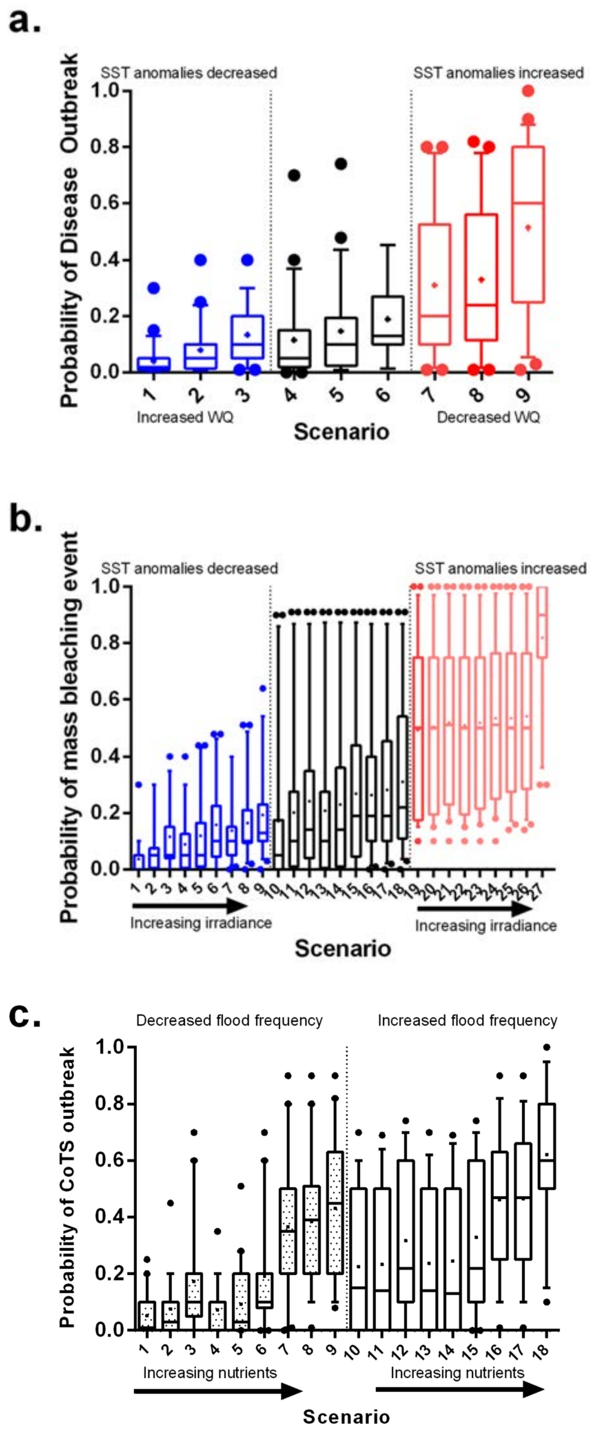


Figure 4.3. Expert-elicited probabilities for multiple-stressor interactions for: a) coral disease outbreaks (temperature + water quality); b) mass bleaching events (temperature + irradiance); and c) crown-of-thorns starfish outbreaks (nutrients + flood frequency). Lines within boxes are medians of expert responses. Crosses within boxes are means. Ends of boxes represent 25th to 75th percentiles. Whiskers represent 10th and 90th percentiles. Points represent outliers. Scenarios are ordered from best-case (all stressors minimal) to worst-case (all stressors maximized). Complete descriptions of scenarios for each outcome are provided in Appendix C.

Comparing the effects of stressors, the only differences where the 95% Bayesian credible intervals of the self-rated mean confidence estimates did not overlap were between the very highest (background bleaching, effect of lower irradiance on bleaching; mean confidence 81% and 79%, respectively) and the very lowest (water quality effect on disease, mean confidence 63-66%). Overall, the mean confidence for estimates of single-stressor effects was 71%. For bleaching there was no difference in the mean confidence between stressor influences (temperature, irradiance, water quality), as all of the 95% BCIs overlapped. There was also no difference in the mean confidence between stressor influences (temperature, water quality) on disease based on the 95% BCIs (Figure C.2).

The number of self-described years of experience of our respondents did not have any effect on the degree of confidence in their responses ($F = 1.15$, $p > 0.05$), and neither was there any correlation between years of experience and any of the probability estimates, i.e., respondents with more time in the field were neither more optimistic nor pessimistic about certain outcomes than less experienced respondents.

Multiple-stressor weighting

Respondents assigned weights for four stressors to form an anthropogenic index and three stressors to produce a composite water quality index. For anthropogenic stress, the mean weighting was equally distributed among all factors except chemical pollution (95% BCI), which was given a lower mean weight of 0.16 (Figure C.3a). For water quality, chemical pollution was also weighted lower than sedimentation or nutrient loading (95% BCIs overlapped for all weights), with a mean respondent weighting of 0.22 (Figure C.3b). However, there were several outliers for each of the stressors, with weightings ranging from as low as 0% to as high as 90% for the same stressor. An increase in the combined anthropogenic stress index increased the mean probability of hard coral cover declining from the baseline figure of 38% to 70% (Figure C.4).

Multiple stressor effects

The mean probability estimate of coral disease outbreaks ranged from 4% in the best-case scenario (#1) of reduced temperatures and improved water quality to 51% in the worst-case scenario (#9) of increased temperature anomalies and decreased water quality (Figure 4.3a). The mean estimate under the worst-case scenario was significantly higher than all scenarios except for scenario 8, which had increased temperature anomalies and unchanged (status quo) water quality (non-overlap of 95% BCIs)..

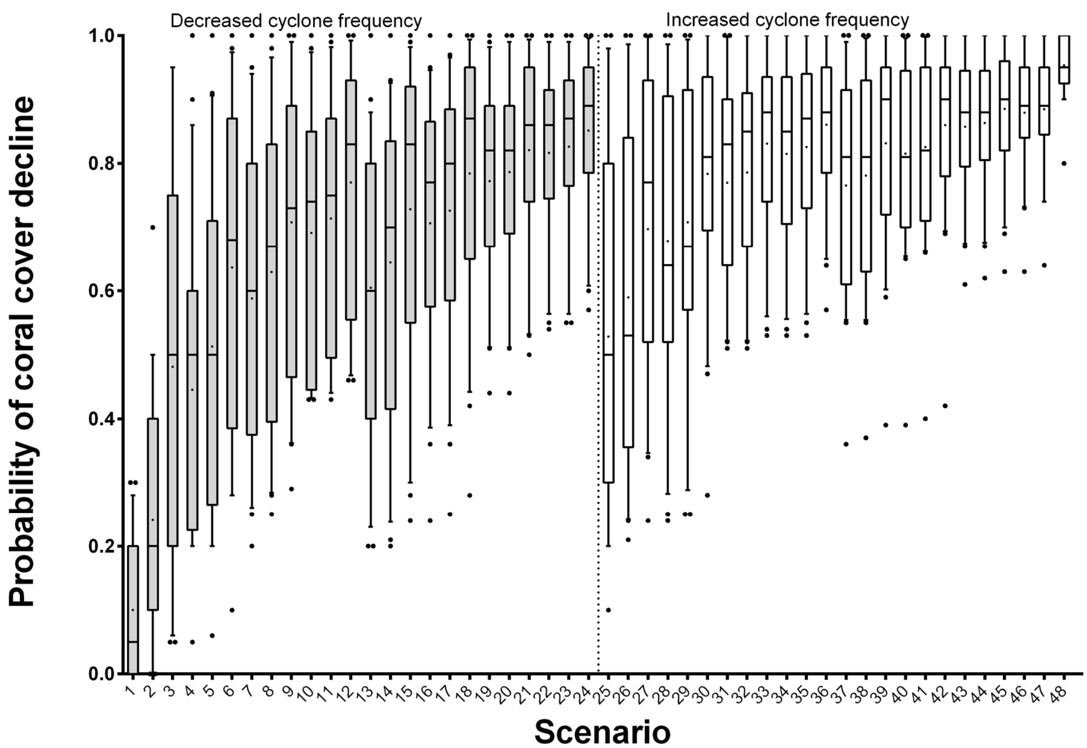


Figure 4.4. Expert-elicited probability of hard coral cover decline under various scenarios. Lines within boxes are medians of expert responses. Crosses within boxes are means. Ends of boxes represent 25th to 75th percentiles. Whiskers represent 10th and 90th percentiles. Points represent outliers. Scenarios are ordered from best-case (all stressors minimal) to worst-case (all stressors maximized). Dotted line separates reduced-cyclone frequency scenarios (left side) from increased-cyclone frequency scenarios (right side). Other stressors (bleaching, disease, CoTS outbreaks, anthropogenic stress) also vary between scenarios; see C.5 for full description of stressor combinations within each scenario.

Mean estimates for the probability of a mass bleaching event ranged from a low of 4% under the best-case scenario (#1, reduced temperature anomalies, reduced irradiance, and improved water quality) to 82% under the worst-case scenario (#27, increased temperature anomalies, increased irradiance, and decreased water quality) (Figure 4.3b). All mass-bleaching scenarios with elevated temperature (Table C.3, scenarios 19-27) had a mean bleaching risk higher than all of the reduced-temperature scenarios (1-9) and two of the status-quo temperature scenarios (10, 11) (95% BCI). The mean estimate for the worst-case scenario also did not overlap the 95% Bayesian credible interval of any other scenarios.

The mean estimate for increasing crown-of-thorns outbreaks (relative to present) ranged from a low of 5% with decreased flood frequency, fishing pressure, and nutrients to a high of 62% with all three of these factors increasing (Figure 4.3c). Flood frequency alone did not change the mean probability of outbreaks (scenarios 10, 11, 13, 14), whereas all six scenarios with increased nutrient loading (7, 8, 9, 16, 17, 18) were significantly higher than all other scenarios (95% BCI).

The mean estimate of the probability of hard coral cover declining ranged from 0.1 under the best-case scenario (#1) to 0.95 under the worst-case scenario (#48), in which bleaching, disease, cyclones, crown-of-thorns outbreaks, and anthropogenic stress (fishing, pollution, nutrient loading, and sedimentation) all become worse than at present (Figure 4.4). All scenarios other than scenario 2 had a significantly higher mean estimate of decline than the best-case scenario (#1) in which all stressors decreased (95% BCI).

Table 4.1. Sensitivity of probability of coral cover decline to state of other nodes in the network.

Node	Mutual Information	Percent	Variance of Beliefs
Coral cover decline	0.86961	100	0.2061893
CoTS	0.04022	4.62	0.0122382
Bleaching	0.01848	2.13	0.0049828
Stress	0.01626	1.87	0.0047391
Cyclones	0.01485	1.71	0.0040347
Nutrients	0.00887	1.02	0.0025145
WQ	0.00520	0.598	0.0014945
Disease	0.00497	0.571	0.0013880
Flooding	0.00421	0.484	0.0011568
Temperature	0.00257	0.296	0.0007193
Fishing	0.00227	0.261	0.0006484
Sedimentation	0.00117	0.135	0.0003337
ENSO	0.00097	0.111	0.0002747
Pollution	0.00029	0.0332	0.0000822
Irradiance	0.00011	0.0131	0.0000324

Sensitivity Analysis

Evaluating the sensitivity of the bottom node in the network (probability of hard coral cover declining) to changes in the state of other nodes revealed that crown-of-thorns outbreaks have the highest degree of influence (Table 4.1). This is followed by aggregate anthropogenic stress (as a direct stressor), cyclones, and nutrients alone as an indirect stressor. The remaining nodes represent less than 1% each of the mutual information measure in the network.

Discussion

In many natural systems, there is only scarce or incomplete data about interactions between ecosystem components (whether those be species, functional groups, communities, or other assemblages) and even less data regarding how human interactions with the system may affect the individual and collective functioning of those components. Bayesian belief networks offer a way of integrating expert subjective knowledge with data to obtain both qualitative and quantitative predictions about system behaviour (Uusitalo 2007). At the same time, there are some limitations of BBNs: the need to discretize continuous variables for the purposes of generating conditional probability tables, the inability to model feedbacks (unless constructed as a dynamic or discrete time-step model), and the complexity associated with gathering and interpreting expert knowledge (Uusitalo 2007).

In general my findings indicate that even the perceived short-term outlook for the Great Barrier Reef is not particularly optimistic. Even with a reduction in all local stressors, if the frequency and/or severity of largely uncontrollable factors such as cyclones and high water temperature anomalies increase, the mean probability of hard coral cover on mid-shelf reefs stabilizing or increasing is little better than 50% in a ten-year timeframe based on expert opinion. Given the decline of coral cover on the GBR over the past 20 years, a continuation of this trend would not be surprising (De'ath et al. 2012). However, there was considerable variation in the responses from interviewees, with some respondents estimating a virtually certain decline in coral cover with only modest increases in stress, while others estimating a probability of decline of "only" 80% even under the worst-case scenario. Interestingly, temperature did not emerge as a strong influence in my sensitivity analysis even though mass bleaching did. This is partly an artefact of model structure because, generally, the more intervening steps there are between a stressor and a variable of interest (in this case coral cover), the lower the sensitivity (Henrion 1987). However, the fact that my model indicated a low sensitivity of coral cover to temperature could reflect the opinions of experts regarding mitigating factors to this sensitivity, such as the potential influence of water quality (particularly nutrients) on bleaching susceptibility (Wooldridge 2009; Wooldridge & Done 2009; Wooldridge et al. 2012).

I found that most experts associated increased temperatures and decreased water quality with a significantly increased risk of coral disease outbreaks. Some experts emphasized the effect of temperature much more than water quality. Much recent literature has posited a link between temperature and disease outbreaks (Jones et al. 2004; Bruno et al. 2007; Ward et al. 2007; Heron et al. 2010; Maynard et al. 2011), but water quality has also been linked with disease severity (Bruno et al. 2003; Haapkylä et al. 2011). There was also a strong consensus that a sustained (minimum 4 week duration) temperature anomaly of at least 1°C above the climatological mean is sufficient to significantly increase the probability of a mass bleaching event, although there was not unanimous agreement that this temperature was the appropriate threshold. Agreement on a single threshold for bleaching is also complicated by the possibility that bleaching thresholds vary by species (Middlebrook et al. 2010), location (Berkelmans & Willis 1999), and rate of heating (Berkelmans 2002). Increased irradiance alone only modestly increased the probability of bleaching, whereas the combination of increased irradiance and increased temperature was deemed likely to result in bleaching. This is also supported by the literature (e.g., Dunne & Brown 2001; Dove 2004), although instances of bleaching have also been linked to increased irradiance alone (Anthony & Kerswell 2007).

There was little consensus that water quality plays a strong role in bleaching, although one respondent put the bleaching risk as high as 80% due to water quality alone. I cannot be sure whether this diversity of opinions represents opposing schools of thought or merely uncertainty in the literature, because the role of water quality in bleaching susceptibility remains an area of active research (Wooldridge & Done 2009; Wooldridge et al. 2012). The complex and multi-faceted nature of water quality – which we chose to represent as a composite node in the model – could also play a role in the diversity of responses we received.

The estimated probability of coral cover decreasing showed no significant difference between the status quo and the scenario involving a 30% decrease in anthropogenic stress, but there was a significant (and large) decrease in coral cover with a hypothetical 30% increase in anthropogenic stress. The consensus therefore appears to be that current levels of human impact on the GBR are already near a critical threshold.

Limitations

Some limitations are associated with my scenario elicitation approach. One limitation is that constraining the survey length required us to linearly interpolate between extreme endpoints (e.g., the worst-case and best-case scenarios) rather than eliciting probabilities for all of the levels of each stressor. This would tend to obscure thresholds and non-linear behaviour that might otherwise be apparent at intermediate stressor levels, although this problem is minimized in cases where there are only two states for a node (since both states are always elicited). This is a general limitation of any expert-elicitation exercise, where the choice of elicitation method is often constrained by the amount of time experts are able to offer; however, rapid elicitation techniques are a useful way of obtaining initial estimates that can then be refined using a stepwise procedure (Renooij 2001). In this context, we emphasize that our modelling approach was intended to be high-level, conceptual, and preliminary.

Furthermore, since my model is a descriptive rather than process-based model of stressor interactions, it may not fully capture the level of detail required for use in an adaptive management capacity where changes in monitored quantities may be slower or smaller than the relatively coarse categories I used to describe changes in stressor values. However, more sophisticated mechanistic models typically require a greater time commitment from both experts and their elicitors, thus trading off the number of experts consulted with the amount of time spent with each. For example, the Bayesian belief network developed by Thomas (2008) had an expert pool of three, with each expert being interviewed for up to 8 hours following a two-week period in which background material was provided. We viewed our abbreviated process of eliciting probability estimates as an acceptable trade-off given the broad scope of our model design. Thus, future work could focus on establishing more precise values to serve as potential tipping points within the model, as well as exploring a more mechanistic way of describing stressor interactions. Furthermore, it would be instructive to devote further elicitation exercises to exploring the full parameter space of large conditional probability tables to capture expert opinions about threshold behaviour.

Another limitation of individual interviews is that interpretations of each question might vary. In a group workshop setting, these variations are minimized by having an open discussion between participants to ensure that a common understanding is reached about the questions. I attempted to minimize the limitations of individual interviews by using a scripted introduction and highly structured question format for the survey, and by providing standardized definitions for potentially ambiguous terms. Nonetheless, there remains room for individual biases and error inherent in making subjective probabilistic estimates.

Finally, I constrained the timeframe of my model to only ten years - partly to make estimating probabilities easier for the experts, and partly to coincide with the planning timeframes for water quality goals on the GBR. It would be instructive to construct models or obtain estimates for longer timeframes as well, to determine whether some stressors may have greater long-term importance than others.

Applications for management and implications

One of the benefits of Bayesian methods is that objective data can be combined with informative priors in the form of expert opinions to produce better estimates of effect sizes than data alone. I suggest that my model could serve as a useful starting point for further development, especially as more data become available regarding multiple stressor effects. While considerably more complex models have been constructed for seagrass ecosystems on the GBR (e.g., Thomas 2008), such models require either extensive data to parameterize them and/or elicited knowledge from numerous experts across multiple disciplines. The use of expert-elicitation instead of, or in addition to, collection of field data to inform models could also be a way for managers to rapidly and cost-effectively evaluate possible consequences of management actions (Martin et al. 2005). Further, models that identify key data gaps, identify novel threats, and highlight uncertainties are often useful for managers and policymakers (Kinzig et al. 2003; Pressey et al. 2007). However, given that empirical data is not uncertainty-free, scenarios should be used to explore the full parameter space of models, including those scenarios which may be deemed unlikely.

In the judgment of most of the experts I consulted with, the stressors most amenable to management action were perceived to have very little influence on the probability of coral cover persisting – at least for the case of mid-shelf reefs. This comports with a recent study that found that the three largest contributors to coral cover decline on the Great Barrier Reef were bleaching, crown-of-thorns starfish, and cyclones (De'ath et al. 2012). While reductions in nutrient loading (De'ath et al. 2012), fishing pressure (McCook et al. 2010), or even the use of direct culling (Rivera-Posada & Pratchett 2012) could be used to reduce crown-of-thorns outbreaks, there is little that can be done about cyclones and temperature-induced mass bleaching events unless radical geoengineering solutions are implemented (Rau et al. 2012) Even limiting global warming to 2°C may not be sufficient to prevent widespread and common mass bleaching events (Frieler et al. 2013). If my model structure and associated probabilities are an accurate reflection of the system, this implies that coral reef managers have less control over the fate of local systems than previously believed. However, my model is only intended as a generic, broad-scale assessment of the vulnerability of coral cover on the Great Barrier Reef. Given the unique nature of the Great Barrier Reef compared to other reef ecosystems in terms of its size and proximity to a developed nation with a relatively small population, we would also caution against making direct inferences from this model to other coral-reef contexts. We would, however, encourage application of this technique to develop similar models for other reef settings.

The vulnerability of specific reefs to particular disturbances is likely to vary widely depending on community composition and disturbance history, and coral cover is potentially a poor measure of the health and overall resilience of coral reef systems (Hughes et al. 2010b). The effects of shifts in community composition following massive reef mortality events are also largely unknown (Riegl & Purkis 2012). Additionally, interactions between climate change effects and local stressors are likely to vary considerably depending on the location and composition of a reef system, and management options need to be considered in this context. For example, local stressors play much more of a role in affecting reef condition in southeast Asia versus reefs in the south Pacific (Ateweberhan et al. 2013). Furthermore, small-scale management actions may not provide much protection against large-scale climate-related disturbances (McClanahan et al. 2001; Graham et al. 2008). It is unlikely that there will be any management action panacea that will apply to all reefs in all areas. Indeed, the effectiveness and feasibility of any given management action is likely to be site-specific, and multiple approaches across the seascape will likely be most effective (Hughes et al. 2010a; Graham et al. 2013a).

In this chapter, I constructed a relatively simple BBN in an attempt to capture the implications of interactions between natural and anthropogenic stressors on mid-shelf reefs of the GBR. According to the consensus opinion of my experts, the outlook for the GBR is not optimistic, even with effective local and regional management action. The probability of maintaining coral cover is likely to hinge on how severe future climate change effects will be, as well as whether coral reefs are likely to become more or less susceptible to repeated and ongoing stressors.

Chapter 5 Comparison of local management effectiveness using a spatial Bayesian modeling approach of multiple stressor effects

Abstract

Multiple stressors are an increasing concern in the management and conservation of ecosystems, and have been identified as a key gap in research. Coral reefs are one example of an ecosystem where management of local stressors may be a way of mitigating or delaying the effects of climate change. Predicting how multiple stressors interact, particularly in a spatially explicit fashion, is a difficult challenge. Here I use a combination of an expert-elicited Bayesian Belief Network (BBN) and spatial environmental data to examine how hypothetical scenarios of climate change and local management would result in different outcomes for coral reefs on the Great Barrier Reef (GBR). Parameterizing my BBN using the mean responses from my expert pool resulted in predictions of limited efficacy of local management in combating the effects of climate change; however, there was considerable variability in expert responses. Many reefs within the central GBR appear to be at risk of further decline, but further parameterization of the model as data and knowledge become available will improve predictive power. My approach serves as a proof of concept for subsequent work that can fine-tune parameters and explore uncertainties in predictions of responses to management.

Introduction

Multiple stressors are an increasing concern in the management and conservation of ecosystems because interactions between stressors can potentially exacerbate biodiversity declines (Folt et al. 1999; Vinebrooke et al. 2004; Przeslawski et al. 2005; Salbu et al. 2005; Hecky et al. 2010). Interactions between stressors can result in "ecological surprises" (Lindenmayer et al. 2010), as have been observed in freshwater (Hecky et al. 2010), marine (Russell et al. 2009), and terrestrial (Bansal et al. 2013) ecosystems. Multiple stressors do not affect ecosystems uniformly. Instead, they can exhibit spatial heterogeneity (and kelp beds Marcot 2006; e.g., salt marshes Kujala et al. 2013) that can affect the probability of regime shifts at particular sites (van Nes & Scheffer 2005).

Models of the effects of multiple stressors that provide spatially explicit outputs would be useful for informing management, yet few such models exist to date. Spatially explicit models would be particularly helpful in marine ecosystems, where ocean zoning has been proposed as one way of addressing cumulative impacts (Halpern et al. 2008a). Interactions may occur at multiple spatial scales, ranging from local to global, with some stressors manageable, others not. Ecosystem managers may be able to influence anthropogenic stressors to build resistance or resilience to non-manageable stressors such as storms and disease (Wooldridge 2007; Page et al. 2009). With the increasing threat of climate change, assessing management options at the local and regional scales at which managers operate will be increasingly important (Carilli et al. 2009; NOAA 2012) as one way to delay or mitigate climate-change effects (Russell et al. 2009; MacNeil & Graham 2010; Brown et al. 2013). However, few practical approaches assess, model, or guide management of multiple stressors, particularly in marine ecosystems, largely due to data limitations. Data are limited partly by the number of interactions increasing exponentially with the number of stressors, and by the general lack of ecological data from monitoring and assessment surveys that are sufficiently comprehensive to statistically examine the interactions between stressors. Additionally, estimating the strength of interactions between stressors is difficult for several reasons. One is the non-linear behaviour of ecosystem responses; another is mis-matches in timescale between discretely-measured empirical data and the instantaneous changes predicted by theory (Wootton & Emmerson 2005).

There are several modeling approaches for working in data-limited situations. Holmes and Johnstone (2010), for example, used a dynamic systems model that was not spatially explicit but was parameterized at least partly with expert judgment and input. However, the predictive ability of models using classical inference is limited by scale-dependent effects, constraints on model dimension and parameterization, and uncertainty about which model components are stochastic or deterministic (Clark 2005). Some techniques that have been applied to multiple-stressor management have included qualitative ranking of ecosystem stressors by experts (Halpern et al. 2008b) and relative risk models (Landis et al. 2013). Bayesian belief networks (BBNs) have also found increasing application as a decision support tool in ecology and adaptive management (e.g., Marcot et al. 2006; Smith et al. 2007; Thomas 2008) where predictive utility is paramount but data are limited and uncertainty is high (Cain 2001). Furthermore, the expert elicitation process commonly used in the development of Bayesian belief networks allows experts to contribute to the development of model structure as well as informing model parameters, thereby conceptualizing interactions between stressors as well as understanding their effects (Marcot et al. 2006).

Despite the increasing acceptance of BBNs in ecology and management, spatial implementations of these models in marine settings remains relatively rare; searching Web of Science using the keywords “Bayesian belief”, “spatial”, and “marine”, for example, finds only six papers (Grech & Coles 2010; Kininmonth et al. 2010; Stelzenmuller et al. 2010; Palmer et al. 2011; Stelzenmuller et al. 2011; Payo et al. 2013). In a marine-planning context, a recent paper (Stelzenmüller et al. 2010) did use a BBN in conjunction with a GIS to evaluate cumulative human impacts on the coastal waters of England and Wales; however, the model output in their study was a generic vulnerability score across ecosystem and habitat types that is difficult to interpret in terms of biological consequence, and was unable to account for ecosystem-specific effects of each human activity component. Furthermore, the cumulative impact score in Stelzenmüller et al’s (2010) study was simply the sum of the qualitative scores for each of three human activities given equal weighting.

In terms of evaluating ecosystem effects of climate change, many climate-change models and scenarios focus on slow-changing variables such as average temperature and acidification. Such models may not take into account interactions with variables that change on much shorter (annual or seasonal) timescales, and thus may underestimate the ecosystem effects of climate change. Thus few models are readily applicable to the short- and medium-term timeframes most useful for ecosystem managers (but see Meesters et al. 1998; Melbourne-Thomas et al. 2011a), and fewer still attempt to incorporate interaction effects between multiple stressors.

Multiple stressors have been identified as a key problem facing managers in coral reef ecosystems (GBRMPA 2009a; NOAA 2012) because reefs face threats on both global and local scales (Riegl et al. 2009). However, these threats vary over both time and space, and effective conservation planning for dynamic threats requires a spatially explicit prediction of those threats (Pressey et al. 2007). Furthermore, spatial heterogeneity becomes increasingly important for reserve system design as the scale of management diverges from the scale of underlying ecosystem processes (Possingham et al. 2005). Thus, in this paper, I spatially implement an expert-elicited Bayesian belief network (BBN) in a coral reef ecosystem: the Great Barrier Reef (GBR) in Queensland, Australia. I chose the GBR as a case study because the key stressors have been identified (De'ath et al. 2012; Schroeder et al. 2012), and because good spatial data exist for many of these stressors. Stressors that may be locally manageable include nutrient loading, sedimentation, pollution, and fishing pressure, whereas stressors that are difficult or infeasible to manage directly or at all include coral disease, coral bleaching, outbreaks of crown-of-thorns (CoTS) starfish, and cyclones. Furthermore, the existence of an extensive protected-area network means that many reefs suffer little or no extractive pressures, allowing us to examine the potential effectiveness of these managed areas in reducing multiple-stressor effects, where coral cover is used as a proxy for reef condition.

Scenario planning is a way of considering possible futures for systems that contain high levels of uncertainty where direct experimental manipulations of the system are impractical (Peterson et al. 2003). Scenarios are one way to frame complex and uncertain issues that define the boundaries of a problem, but are neither forecasts nor predictions (Huss 1988; Swart et al. 2004). In this study, I use scenarios in the form of possible combinations of stressor levels to model the effects of potential stressor interactions. I then use these model outputs to identify which management actions might most affect the future trajectory of coral cover. I present this study, not as a policy prescription, but as a proof of concept that can be built upon and fine-tuned to guide management of multiple stressors.

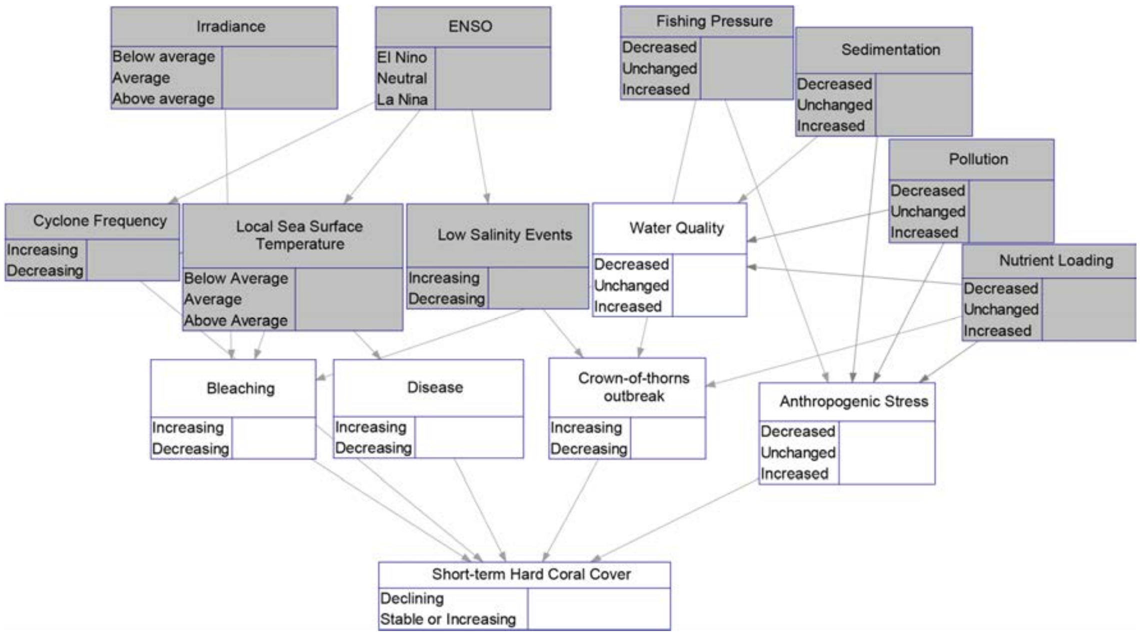


Figure 5.1. Schematic of the Bayesian belief network structure. Nodes in grey are informed by empirical data; nodes in white are elicited from experts. The nodes for water quality and anthropogenic stress are composite nodes that assign a weight to each of their parent nodes to create an overall index.

Methods

I implemented a Bayesian belief network model using two types of data: empirical data and expert opinion (Figure 5.1). All of the spatial environmental data input to the model were empirical; the consequences of various combinations of these environmental conditions were generated from the BBN model using expert opinion. Within my model, I devised a set of four scenarios, each one describing a different qualitative combination of possible future conditions (Table 5.1). In these scenarios, changes in stressors (except for temperature) were described in terms of a one standard deviation change from the long-term mean either from the frequency for discrete events (cyclones, floods, crown-of-thorns outbreaks, mass bleaching events, disease outbreaks) or in intensity for fishing pressure, sedimentation, pollution, and nutrient loading. The choice of one standard deviation was arbitrary, but was chosen to be readily interpretable by the experts, consistent across variables, and represented a significant enough change to lie outside the bounds of normal variations without being extreme enough to be unlikely. In the case of temperature, an increase of 1°C above the climatological mean was used as a conservative threshold value for coral bleaching (Goreau & Hayes 1994). It should be clarified that in the survey, experts were asked how a temperature anomaly above this threshold would affect the chances of a mass bleaching event occurring, not the probability that these anomalies would occur. The scenarios were as follows:

1) Baseline: all variables unchanged from present conditions
2) Climate change without local management: assume that temperature anomalies increase 0.2 degrees (based on 1°C of mean ocean warming by 2050) above those observed to date, with a concomitant increase in cyclone frequency, disease outbreaks, and mass bleaching events, without any reductions in fishing pressure or terrestrial inputs (nutrients, sediments, pollution)
3) Climate change with local management: as in the previous scenario, only with management actions to reduce fishing pressure and terrestrial inputs by 30%.
4) Local management without further climate change: implementation of management actions as in the previous scenario, but without any change in climate-related variables beyond present conditions.

Table 5.1. Climate change and management scenarios with associated changes to input layers. n.c. = no change from baseline (current conditions); plus sign = 1 standard deviation increase above baseline; minus sign = 1 standard deviation decrease below baseline condition, except for temperature (0.2 degree above/below climatological mean). CoTS = Crown-of-thorns-starfish.

Scenario number (see text for description)	Temperature	Cyclones	Disease	Bleaching	Irradiance	CoTS	Nutrients	Sediment	Pollution	Fishing
1	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.
2	+	+	+	+	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.
3	+	+	+	+	n.c.	n.c	-	-	-	-
4	n.c.	n.c.	n.c.	n.c.	n.c.	n.c.	-	-	-	-

The empirical data for the model came from several sources (Table D.1, grey nodes in Figure 5.1). Historical cyclone tracks were obtained from IBTRACS (Knapp et al. 2010). Only Category II and higher cyclones were included, and the tracks were buffered asymmetrically as per Fabricius et al. (2008). The average and maximum extent of flood plumes from 2007-2011 were obtained from Alvarez-Romero et al (2013), as were data on loadings of nutrients (dissolved inorganic nitrogen) and sediment. Sea surface temperature anomalies were identified from satellite climatology data (1985-2007) as per the methods described in Ban et al (2012). Mean solar irradiance was obtained from NASA SeaWiFS satellite data (1997-2010). Data on fishing catch and effort for line fisheries were obtained from the Queensland Department of Agriculture, Fisheries and Forestry. Some data on commercial catch and effort were only available at a resolution of 30 nautical miles due to confidentiality rules, whereas others had a resolution of 6 nautical miles. I downscaled the lower-resolution data by assuming that the relative effort distribution of the data at resolution of 30 nautical miles was similar to the 6 nautical mile data, and reapportioned the 30-nautical mile effort data accordingly. Reefs within no-take areas were assumed to have no fishing effort or catch. Except for temperature, all input data layers were re-coded into three categories to be consistent with the survey questions, which specified 3 possible states or conditions for each variable: 1 standard deviation or more above average; within 1 standard deviation of average; and 1 standard deviation or more below average. For temperature, anomalies were coded as being greater than/less than/within 1°C from the climatological mean. All of the input layers, consisting of spatially explicit values for individual reefs, were then placed in different combinations for each of my scenarios (Table 5.1).

The second type of data used in the model was based on expert opinions about the degree of influence each empirical variable had on the probability of a certain event (white nodes, Figure 5.1). The expert pool consisted of 21 coral reef ecologists with extensive experience with the GBR specifically. These experts were asked to consider the probability of various events occurring within a ten-year timeframe for a hypothetical mid-shelf, mid-latitude reef with approximately 30% hard coral cover. The complete methodology of this expert elicitation process is described in the previous chapter. In my model, the events considered by the experts were: probability of a mass bleaching event, probability of a coral disease outbreak, and probability of a crown-of-thorns starfish (CoTS) outbreak. The ultimate endpoint of the model was the probability of hard coral cover declining below present levels over a ten-year timeframe, which was also estimated by my experts. This probability was contingent upon the various events (bleaching, disease, CoTS) increasing or decreasing in frequency. I used three sets of probabilities of events from the expert elicitation process as inputs (parameterizations) to the model: the group mean, the 25th percentile (pessimistic), and the 75th percentile (optimistic). The pessimistic parameterization corresponded to higher probabilities of adverse events; the optimistic parameterization corresponded to lower probabilities of adverse events.

Both the empirical data and the expert-elicited probabilities were entered in the form of conditional probability tables into Netica (Norsys Software Corporation 1992-2010), where each unique combination of event states (e.g, high/average/low temperature, presence/absence of a flood plume) is associated with a discrete probability of an outcome (e.g., mass bleaching). All data layers were plotted onto a common 500 metre geographic grid, which was the finest resolution of the input layers. Model predictions for the probability of coral cover declining below current levels was then calculated for each mid-shelf reef by supplying the model with input values from that location. These overall probabilities of decline were also the result of expert opinions regarding various combinations of events (e.g., a mass bleaching event and a disease outbreak event occurring in close succession on the same reef). Additionally, due to the decade-scale time frame, these probabilities of recovery were intended to capture the net result of both mortality events and subsequent recovery (i.e., whether a reef would be able to recover its pre-disturbance coral cover following a certain combination of events).

I limited the extent of the study area for two reasons: first, to match the availability of my input spatial data layers, and second to avoid over-generalizing the applicability of a scenario given the very different characteristics of inshore, mid-shelf, and offshore reefs. My study area was thus confined to the central GBR (inset, Figure 5.2). I constrained the model inputs and outputs only to those areas designated as “mid-shelf” under GBRMPA’s bioregional classification system (Day et al. 2002; Fernandes et al. 2005); this encompassed 775 individual reefs in a latitudinal range extending between 15.77°S and 22.31°S, corresponding with the minimum extent of the data input layers.

The four scenarios compared model predictions using four different combinations of conditions: with and without management action, and with and without additional climate change effects (Table 5.1; Appendix D, Table D.2). These four scenarios were: Baseline, Climate Change without Local Management, Climate Change with Local Management, and a best-case scenario of Management without (further) Climate Change. The Baseline scenario represented the mean of the available environmental data for each grid cell. Under the climate-change scenarios, I increased the risk category uniformly for cyclones so that the chance of any given reef being hit by a cyclone increased by 30%, added 0.2°C to historical temperature anomalies (based on the IPCC A1B scenario of ~2.2°C average SST rise by 2100; (IPCC 2007)), and increased the extent/severity of flood plumes, sedimentation, and nutrient loading by one standard deviation (~30%). Incident irradiance and frequency of CoTS outbreaks remained unchanged across all scenarios. In the improved management scenarios, fishing pressure, sedimentation, and nutrient loading were reduced by one standard deviation.

I used the centroid (geographic centre) of each reef within the study area to determine the values of the input layers, and mapped the corresponding model-predicted probability of coral decline for each scenario at that location. The output vales of the model thus correspond to the input values for the centroid of each reef. I then compared the average probability of predicted decline of hard coral cover for reefs both within highly protected (no-take) zones (green, orange, and pink zones: Great Barrier Reef Marine Park Authority 2013) and outside these zones. Finally, I produced a series of change maps by taking the difference in predicted probability of decline between two scenarios and calculating the relative change by dividing this difference by the first scenario's predicted value. The change maps compared the following pairs of scenarios:

1. Climate change with local management vs. baseline
2. Climate change with local management vs. climate change without local management
3. Local management without further climate change (best-case scenario) vs. baseline

Results

Under the baseline scenario, my model predicted probabilities of decline for mid-shelf reefs ranging from about 35% to 75% (Figure 5.2a), with a median value of 57.6% and a mean of 58.6% with respect to the number of reefs. Under the climate change without local management scenario, few reefs had a probability of decline of less than 70%, with some having probabilities of more than 85% and most falling into the 70-80% range (Figure 5.2b). The mean probability of decline in this scenario was 77.2%, with a median of 76.5%. Under the climate change with local management scenario, in which fishing pressure, sedimentation, and nutrient loading were reduced by at least 30% (Figure 5.2c), most reefs showed a very similar probability of decline to the climate change without local management scenario, with a mean decline probability of 77.0% and a median decline probability of 76.5%. Finally, under the best-case scenario (reduced fishing, sediment and nutrient loading without further climate change), the mean predicted probability of decline was 58.1% with a median of 57.6% (Figure 5.2d).

The climate change without local management scenario increased the mean probability of decline 32% relative to baseline (Figure 5.3). For the other scenario pairs, although the means differed very little, the distributions of decline probabilities did differ (Figure 5.4). Local management without further climate change reduced the probability of decline by a mean of 0.7% relative to baseline (Figure 5.4a). Climate change with local management resulted in a mean 0.3% reduction of probability of decline relative to climate change without local management (Figure 5.4b).

Reefs outside no-take zones had marginally higher mean probabilities of decline than reefs inside no-take zones in each of my scenarios (Figure 5.5). The mean difference in probability of decline between no-take and other zones ranged from just under 1% in the climate change with local management scenario (Figure 5.5c) to just over 5% in the baseline scenario (Figure 5.5a).

Using the 25^{th} (pessimistic) and 75^{th} (optimistic) percentile model parameterizations with the same input data scenarios shifted the distribution of probabilities of decline accordingly (Figures D.1, D.2). There was less variability between reefs in both the 25^{th} and 75^{th} parameterizations compared to the mean parameterization, particularly in the case of the 25^{th} percentile under both climate change scenarios (Figure D.2), for which the mean predicted probability of decline was more than 90%.

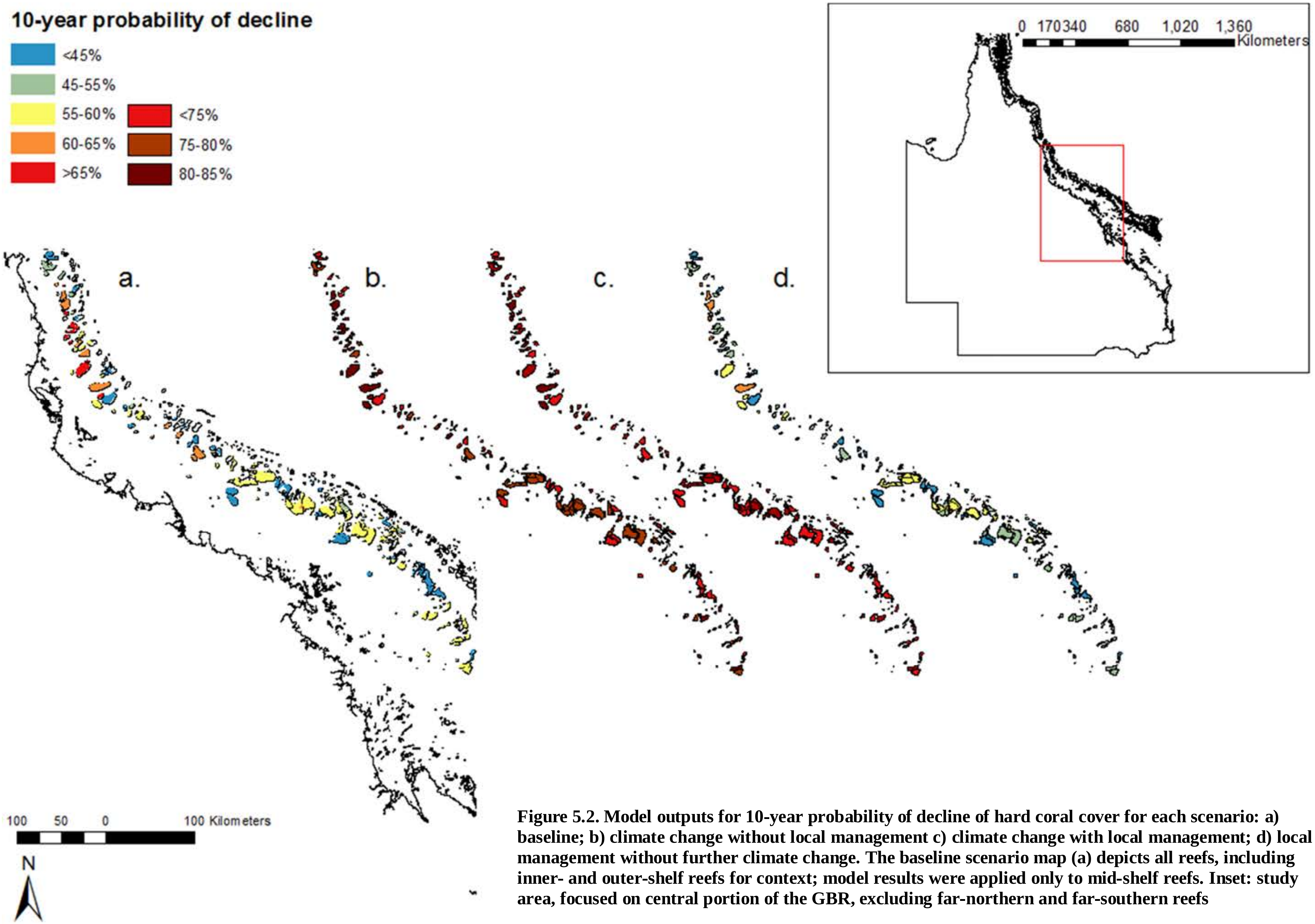


Figure 5.2. Model outputs for 10-year probability of decline of hard coral cover for each scenario: a) baseline; b) climate change without local management c) climate change with local management; d) local management without further climate change. The baseline scenario map (a) depicts all reefs, including inner- and outer-shelf reefs for context; model results were applied only to mid-shelf reefs. Inset: study area, focused on central portion of the GBR, excluding far-northern and far-southern reefs

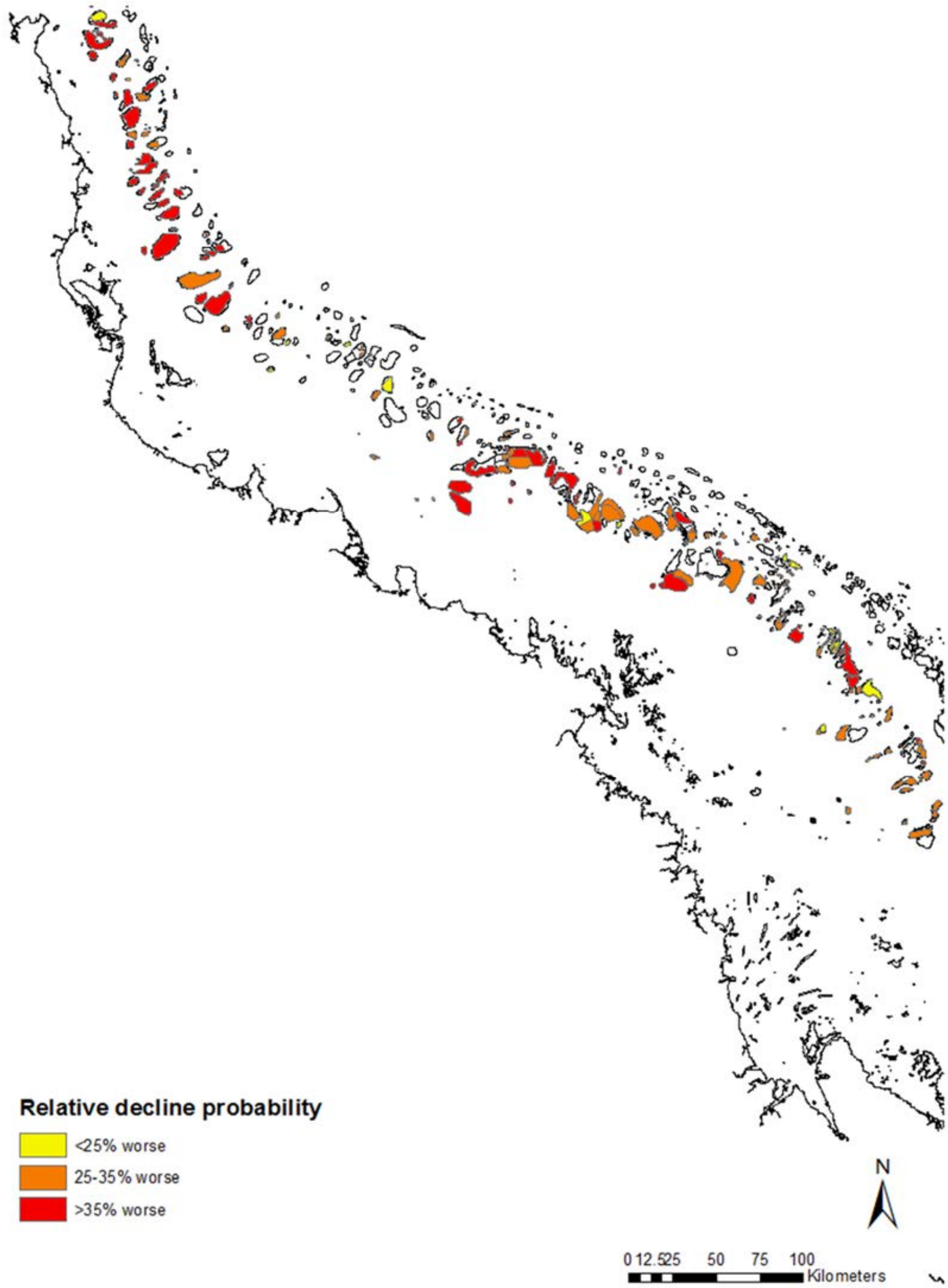


Figure 5.3. Relative change in probability of decline in hard coral cover between two scenarios: climate change without local management and the baseline scenario. Differences between other scenarios not shown because they were minimal.

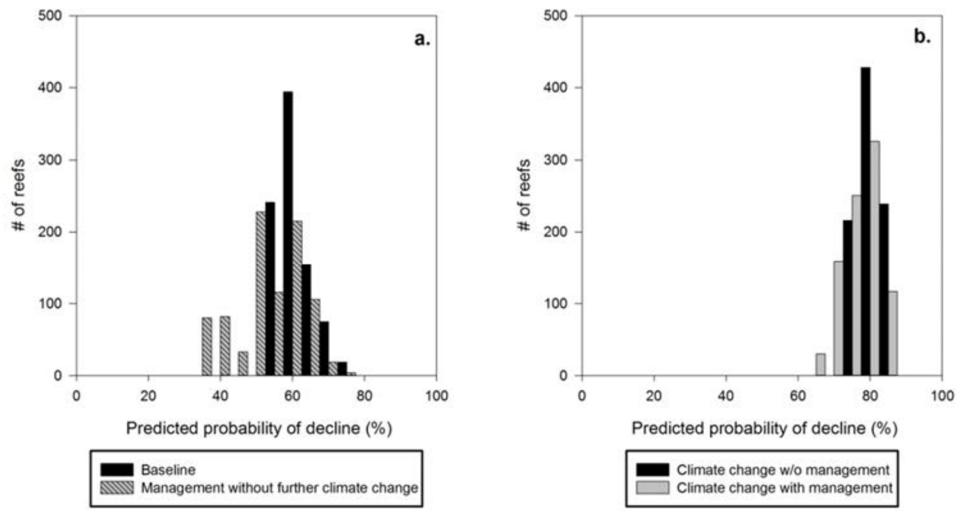


Figure 5.5. Comparison of predicted 10-year decline probabilities between all four scenarios: a) baseline vs management with no further climate change; b) climate change with management action vs climate change without management action.

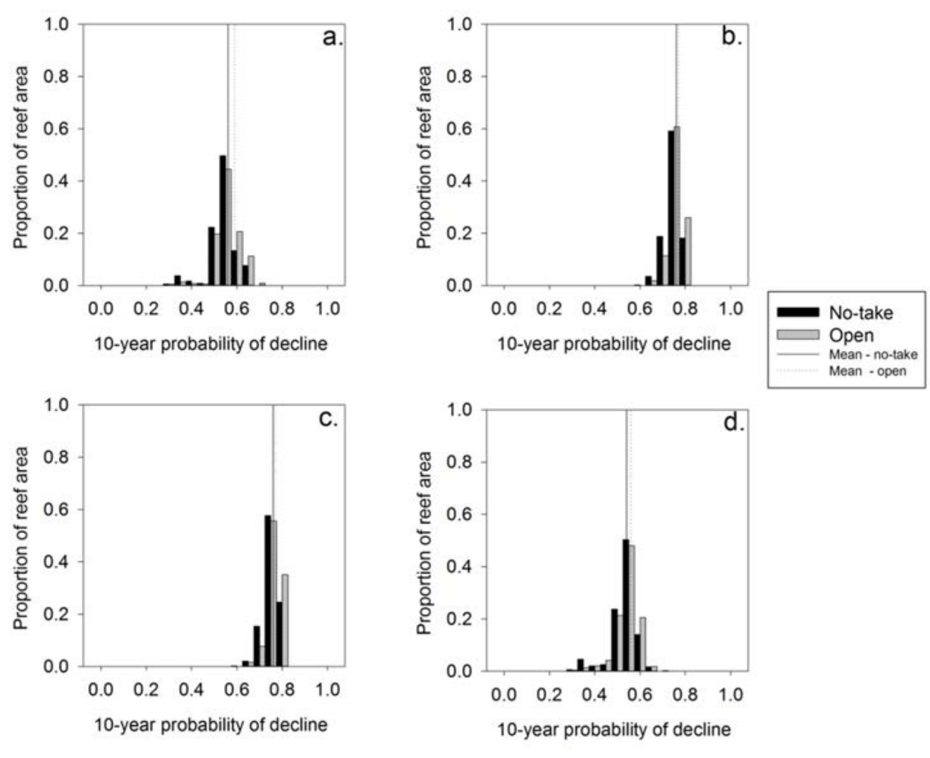


Figure 5.4. 10-year predicted probability of decline in hard coral cover in relation to proportion of total reef area. Black bars indicate reefs inside existing no-take zones ("no-take"). Grey bars indicate reefs outside existing no-take zones ("open"). a) baseline scenario b) climate change without local management c) climate change with local management d) local management without further climate change.

Discussion

I used an expert-elicited BBN to explore possible differences in vulnerability to multiple stressors on mid-shelf reefs within the GBR, and found a moderate probability of continued decline in coral cover, even in the best-case scenario of no further climate change combined with reductions in local stressors. My intent was to construct a model that could be used to generate spatially explicit outputs using only basic and readily-available input data and to compare hypothetical outcomes of different management and stressor scenarios over a relatively short (10-year) time frame. However, given the preliminary nature of my models and their parameterization, I believe this should only be the first step in constructing more sophisticated models that are tailored specifically to different types of reefs.

My results highlight experts' opinions of the dire situation of coral reefs in the GBR, as well as the uncertainty or lack of consensus between experts about many stressor effects. Even under my baseline scenario, in which I assumed that all stressors remained unchanged, my model predicted a moderate probability that coral cover on mid-shelf reefs would decline. This result is consistent with recent findings that coral cover on the Great Barrier Reef as a whole has been declining at an average rate of 0.5% per year since surveys began in 1985, with a steepening rate of decline since 2006 (De'ath et al. 2012). Perhaps more surprising is how little the best-case scenario (reduction of all locally manageable stressors without further climate change) differed from the baseline scenario. There are several possible explanations for this lack of change. One is that many mid-shelf reefs rarely experience the effects of terrigenous flood plumes and their associated chemicals, sediment, and nutrients (Brodie et al. 2012), so reductions in any or all of these factors would be unlikely to have a significant effect on the trajectory of coral cover on these reefs. Secondly, the effects of stressors that are not under direct management control (such as outbreaks of CoTS, mass bleaching and cyclones) are likely to have a much stronger immediate influence on coral mortality and subsequent declines in cover than many of the manageable stressors. This also comports with the findings of De'ath et al (2012), who concluded that CoTS outbreaks and cyclones, along with bleaching, were key drivers of coral decline in the GBR.

Based on expert opinion, my model predicted a slight but consistent difference in the predicted probability of decline between reefs within and outside the existing protected area network on the GBR. Since fishing pressure is one of the stressors in the model, and I assumed that fishing pressure inside protected areas was zero, this result is not surprising. Research on the GBR has shown higher coral cover on reefs inside versus outside no-take areas - partly due to protection from direct damage from fishing gear and anchors and partly from indirect effects possibly associated with trophic interactions (McCook et al. 2010). Although fishing pressure has been linked to changes in coral cover through a trophic cascade process (Mumby et al. 2006; Hughes et al. 2007b), fishing pressure was only weakly associated with the probability of declining coral cover in my model. However, the difference between no-take and fished reefs remained even in all of the improved management scenarios where the 30% reduction in fishing pressure would occur outside reserves. While commercial fishing pressure within the GBR is thought to be sustainable (DPI&F (Department of Primary Industries and Fisheries) 2012), insufficient data exist for many species, and increased shark landings are a particular concern (Chin et al. 2012); thus, a 30% across-the-board reduction in fishing may be less effective than larger catch reductions in selected keystone or apex species (Goeden 1982; Roberts 1995). Since my model did not incorporate patterns of larval dispersal or connectivity between reefs, it does not capture the benefits of a protected area network as a recruitment source, nor some of the other benefits of marine reserves beyond direct fishing impacts, such as trophic cascade effects that may reduce outbreaks of crown-of-thorns starfish and sea urchins and so result in increases in coral cover (Mumby & Steneck 2008; Page et al. 2009; McCook et al. 2010).

These findings should not be interpreted to mean that local management actions to mitigate or reverse declines in coral cover are futile or unimportant. Recent studies have demonstrated possible effects of local management on enhancing resistance and resilience of coral reefs to other stresses (Carilli et al. 2009; Page et al. 2009; Brown et al. 2013; Graham et al. 2013b). One example is where rebuilding fish biomass and diversity may increase the resistance of reefs to other disturbances (Graham et al. 2013b). The effectiveness of local management actions may also depend on the nature of the interaction between stressors, as reducing a stressor that is interacting in an antagonistic or mitigative fashion with another may actually make the net result worse (Brown et al. 2013). Other local management actions include reductions in sediment and pollutant loading, as well as decreased fishing pressure. One possible implication of my model is that the current level of anthropogenic stress is such that even a 30% reduction in all local impacts may be insufficient to stop or reverse the trend of declining coral cover, and thus that more drastic management interventions are required.

For example, Wooldridge et al (2006) reported that a 50-80% reduction in dissolved inorganic nitrogen inputs would be necessary to return the GBR to pre-European conditions.

There are some limitations to the model I have developed. First, it was parameterized for only one type of reef (mid-shelf and mid-latitude) within the GBR, and it assumes uniform susceptibilities to threats like disease and bleaching, regardless of community composition. I also deliberately confined the model to have a limited number of input states. This was mainly a limitation of the expert-elicitation approach and the need to have a tractable number of stressor permutations within scenarios (see previous chapter for more details). These limited input states then required using linear interpolation between inputs, a clear assumption and area that requires refinement. It is also important to recognize the limitations of expert judgment (Camerer & Johnson 1997), and that my model was intended as a form of hypothesis generation and testing rather than as a prescriptive guide. Furthermore, conclusions about the effectiveness of management action are dependent upon the structure of the model; different model structures would likely result in quite different qualitative (and quantitative) predictions.

My study is one of the few examples of expert-elicited Bayesian networks that have been applied spatially in a marine environment (Grech & Coles 2010; Kininmonth et al. 2010; Stelzenmuller et al. 2010; Palmer et al. 2011; Stelzenmuller et al. 2011; Payo et al. 2013). Expert elicitation has seen increasing application in ecological contexts where empirical data are absent, incomplete, or uncertain, and is especially useful in combination with Bayesian methods (Drescher et al. 2013). While the model I developed and applied here was somewhat simplified, it is also one of the few that has attempted to capture the effects of simultaneous multiple stressor effects. Despite their relatively crude nature, coarse or approximate models can still be useful as a decision-support tools (Burgman & Yemshanov 2013). Further development of this model - such as by developing more sophisticated sub-models and incorporating specific elements affecting recovery and resilience factors, and, if possible, ground-truthing the results – will likely be necessary before it can be used in a real-world management context. However, ultimately spatially explicit models informed by expert-opinion are likely to be a useful tool to assess and prioritize areas of conservation concern in many data-limited and/or time-sensitive systems beyond coral reefs.

Chapter 6 General Discussion

In this chapter I summarise the key findings of my thesis and consider how I addressed the objectives of my thesis, first identified in the introduction and reiterated below. I also discuss how my thesis contributes to a broader understanding of multiple stressors and how they interact on coral reefs.

Achievement of thesis goal and objectives

The overall goal of my thesis was to explore and advance the understanding of multiple stressor interactions in terms of their effects on coral reef ecosystems generally and on the Great Barrier Reef (GBR) specifically. I achieved this goal through four research objectives:

1. Synthesizing the available knowledge of multiple stressors on coral reefs (Chapter 2)
2. Determining the spatial and temporal overlap of bleaching and disease on the GBR, and determining how bleaching and disease events have affected coral growth, recovery, and mortality (Chapter 3).
3. Identifying experts' perceptions and uncertainty about knowledge gap(s) regarding multiple stressor interactions, and using expert knowledge to help fill these gaps (Chapter 4).
4. Integrating quantitative data with expert-elicited knowledge about stressors on the GBR to examine the consequences of interactions between stressors, and using this information to explore the implications of multiple-stressor interactions for coral reef conservation in the GBR (Chapters 4 & 5).

Objective 1: Synthesizing the available knowledge of multiple stressors on coral reefs

In Chapter 2, I provided a comprehensive literature review of multiple-stressor interactions in coral reef ecosystems. I identified numerous gaps in our understanding of multiple-stressor interactions and the prevalence of departures from additive behavior in the context of coral reef ecosystems, and used some novel analysis techniques to assess the nature of these interactions. Although others have reviewed and conducted meta-analyses using the general ecology literature (Crain et al. 2008; Darling & Côté 2008), I used a unique approach by drawing on ecosystem-specific literature and by quantitatively analyzing only those studies that used a common response variable. Furthermore, instead of using an overlapping-confidence-interval approach, I used a Monte Carlo simulation of the interaction effect size to assess potential synergistic or antagonistic effects. Overall, in this chapter I found that, although in aggregate a large body of literature examines stressor effects on coral reefs and coral organisms, considerable gaps remain for numerous stressor interactions and effects, and insufficient quantitative evidence exists to indicate that the prevailing type of stressor interaction is synergistic.

Objective 2: Determining the spatial and temporal overlap of bleaching and disease on the GBR

In Chapter 3, I selected two stressors that are potentially linked to rising ocean temperatures from climate change, and that drive many mass coral-mortality events: bleaching and disease. Thus, this chapter addresses objective 2 by determining whether there is a linkage between these two stressors (or stress responses), which have often been hypothesized to be mutually reinforcing or co-occurring. Much of the research supporting this linkage has drawn only an implicit connection through common environmental predictors (Harvell et al. 2001; Miller et al. 2006; Harvell et al. 2007). By using assemblage-level monitoring data from reef slope sites throughout the GBR, I showed that there was neither temporal nor spatial overlap between white syndrome outbreaks and bleaching events. Furthermore, none of the temperature metrics commonly used to predict mass bleaching performed well when applied to these data, which implies that bleaching at deeper depths and in areas other than the reef crest may be more difficult to predict from remotely sensed data. This is consistent with other studies that have found that bleaching on the reef slope does not necessarily coincide with shallow-water bleaching. My results suggest the hypothesized relationship between bleaching and disease events may be weaker than previously thought (at least in the GBR region), and that overlap between the two is more likely to be driven by common responses to environmental stressors, rather than by mutual facilitation.

Objective 3: Identifying experts' perceptions and uncertainty about knowledge gap(s) regarding multiple stressor interactions, and using expert knowledge to help fill these gaps

Having shown in Chapter 2 that considerable knowledge gaps exist about multiple-stressor interactions, my third research objective was to determine whether expert knowledge could be used to help fill gaps in empirical data. Thus, in Chapter 4, I consulted with experts regarding their knowledge about a specific study area (the GBR) that is simultaneously data-rich – concerning the physical and biological environment - and data-poor – concerning the effects of interacting stressors. I used a formal expert-elicitation process to obtain estimates of outcomes associated with a variety of scenarios that combined stressors both within and outside the control of local managers. There was much stronger consensus about certain stressor effects - such as between temperature anomalies and bleaching – than others, such as the relationship between water quality and coral health. In general, the experts' mean outlook for the GBR was pessimistic, with climate-change effects potentially overshadowing the mitigating effects of local management actions. Finally, quantitative data were used in the model to determine the relationships between physical variables such as temperature anomalies, cyclone and flood frequency, and irradiance anomalies. Outputs from the model indicated that stressors amenable to management – such as fishing pressure and nutrient loading – made little overall difference to the probability of coral cover continuing to decline. Thus, in the view of the experts I interviewed, many of the stressors on the GBR are already at an unsustainably high level and may be difficult to manage.

Objective 4: Integrating quantitative data with expert-elicited knowledge about stressors on the GBR to examine the consequences of interactions between stressors, and use this to explore the implications of multiple stressor interactions for coral reef conservation in the GBR

Research objective 4 concerns the implications of multiple-stressor interactions for conservation practice, which was the focus of Chapter 5. As with many other ecosystems, coral reefs face threats at both global and local scales, and it has been proposed that management of local stressors could play a significant role in minimizing or mitigating the effects of climate change. However, neither stressors nor ecosystem responses to stressors are spatially homogeneous, so management strategies to contend with these threats must also account for this spatial heterogeneity. In this chapter, I used the expert-elicitation results from Chapter 4 to inform a Bayesian belief network (BBN) model of multiple stressors on the Great Barrier Reef (GBR) over a timeframe of 10 years. I then implemented this model using a set of hypothetical scenarios with different climate-change and stressor-management combinations to map the potential vulnerability of midshelf reefs to the combined effects of local and climate-related stressors using optimistic, pessimistic, and mean responses of the expert pool. As with the previous chapter, I combined the use of quantitative data for many of the physical variables such as temperature and water quality with expert opinion about possible responses to these stressors to inform the model outputs. Additionally, I examined whether the modeled vulnerability of reefs differs within and outside the existing network of marine reserves. Even under my baseline scenario in which none of the stressors are worse than at present, my model predicted a moderate-to-high probability (mean: 59%) of continued coral cover decline. In summary, local management may prevent or offset some effects of climate change, but may require more drastic interventions than those envisioned in my scenarios to be fully effective.

Original contributions

My thesis has contributed to the understanding of multiple-stressor interactions in several ways. While there have been literature reviews concerning the issue of multiple stressors (e.g., Crain et al. 2008; Darling & Côté 2008), to my knowledge Chapter 2 is the first analysis that has taken an ecosystem-specific approach. The method I used to combine a qualitative and quantitative meta-analysis of stressors was successful in illuminating areas of research strength and identifying information gaps. In addition, the approach of using network theory to look at interactions between stressors is also novel in this context. Highlighting this distinction between stressor-stressor interactions and stressor-response interactions – and drawing on network analysis techniques to conceptualize them - is a novel contribution to the broader field of stressor ecology.

Furthermore, instead of using overlapping confidence intervals, used in previous meta-analyses, to infer the presence of synergistic effects, I used a Monte Carlo estimation of the interaction term between variables. This is also novel in its application, and is a general approach that can be used for other analyses in other ecosystems.

Although many studies have tested the validity of temperature-anomaly metrics in predicting shallow water (reef flat) bleaching (McClanahan et al. 2007; Maynard et al. 2008; van Hooidonk & Huber 2009), very few have attempted to test these metrics' ability to predict deeper, reef-slope bleaching. In Chapter 3, I tested a suite of metrics and found that they had only limited predictive ability, both for mass-bleaching events and white-syndrome outbreaks. Furthermore, I also demonstrated a lack of correspondence between bleaching episodes and white syndrome outbreaks, which contradicts many previous findings, primarily from the Caribbean (Harvell et al. 2001; Miller et al. 2006; Brandt & McManus 2009; Croquer & Weil 2009).

Although Bayesian belief models are seeing increasing acceptance for modeling ecological systems (Varis 1995; Taylor 2003; Nyberg et al. 2006; Smith et al. 2007; Thomas 2008), their use remains relatively rare for the purposes of applied management. Both

Chapter 4 and Chapter 5 were novel in using a combination of expert elicitation with a BBN to elucidate the possible effects of stressor interactions and identifying key uncertainties as well as areas of consensus about threats to the GBR. Furthermore, spatializing the model outputs using a scenario based-approach, as was done in Chapter 5, also represents a novel application of the BBN-expert elicitation framework.

In short, my thesis demonstrates the utility of approaching the problem of multiple stressors from multiple angles: qualitatively and quantitatively; using long-term ecological datasets as well as laboratory experiments; using information from expert opinion to complement existing data; and incorporating both types of data into a Bayesian belief network model.

Potential practical applications

By comprehensively reviewing the literature on multiple stressors of coral reefs and highlighting key areas of uncertainty and incomplete data, my thesis may help to guide both researchers and managers to better prioritize research investments and more realistically account for uncertain knowledge when proposing management actions. Additionally, some of these research and knowledge gaps may be filled using expert elicitation – if only as a stopgap until appropriate data can be obtained.

Furthermore, I have demonstrated the practical utility of using expert knowledge in conjunction with readily available spatial data sets to allow mapping of current and future threats and vulnerabilities. When combined with scenarios of different management options and potential changes in the threat landscape, this type of mapping has broad applicability for adaptive ecosystem management.

Limitations, opportunities for improvement and further research

Given the exploratory nature of much of the work presented in this thesis, some limitations and caveats should be mentioned.

In Chapter 2, although I sought to compile as comprehensive a review as possible of the multiple-stressor literature, there were practical constraints on how wide-reaching the literature search could be. For example, I only used Web of Science for the initial literature search, although other databases are available (e.g., Scopus). Secondly, I only included

English-language publications, since including other languages would have required resources well beyond the scope of a single Ph.D. chapter. Nevertheless, I am not aware of any other published work within the coral reef literature that has attempted such an analysis. It would be valuable to conduct another such analysis in a few years' time to determine whether any of the research gaps have been filled, and whether the evidence concerning the prevalence of synergistic effects has changed. One of the main challenges in this area concerns the generalizability of findings across species and between different reef systems. To this end, a larger quantitative meta-analysis could be performed using a different set of response variables to perform a meta-regression that could identify what characteristics differentiate susceptible reef systems from resilient ones.

The approach I used in Chapter 2 that examined evidence for synergistic effects by focusing on specific response variables could be applied not only to other types of response variables, but also to other ecosystems. Additionally, further research should be done to test the empirical and practical validity of using network analysis to identify key stressors. While some of these stressors would be difficult to manipulate in an experimental context, it may still be possible to empirically test whether the stressors predicted by network diagrams to be the most influential do in fact exert cascading or follow-on effects. One potentially important source of uncertainty and variability concerns the weight or strength of interactions between stressors in the network, and whether these interaction strengths need to be modified to reflect their biological or ecological importance.

Analysis of the data in Chapter 3 was constrained by the design of the Long-Term Monitoring Program (LTMP) and the way in which data were collected for both bleaching and white syndrome, as the LTMP was not originally intended to track either of these phenomena specifically. Thus, the timing of the surveys is such that they could have missed the maximum extent or severity of both these events. Furthermore, since the revisit frequency is annual at best, intervening events may also have been missed.

The expert elicitation process used in Chapter 4 was limited by logistic constraints associated with the interview process, which was also the primary reason for using one-on-one interviews rather than the more commonly-used group workshop setting. Although I attempted to minimize variation due to individual differences in interpretation of survey questions, it is not possible to remove all subjectivity and other forms of bias from the elicitation process. Furthermore, the general nature of the model means that the result is only an approximation of the type of reefs I set out to describe – namely, mid-latitude, mid-shelf reefs. In contrast to the usual workshop-type approach, I also did not have the opportunity to have the experts update or revise their estimates after having seen the contributions of others. Going through another iteration of the elicitation process likely would have removed or reduced some of the outlying estimates, since individual estimates tend to converge somewhat after this process (Martin et al. 2012). Thus, the method I used may somewhat overestimate the uncertainty around some of the estimates.

Finally, in Chapter 5, the main constraint was the availability and quality of spatially explicit data that were used as model inputs. There is considerable uncertainty regarding the spatial heterogeneity of climate change and its effects, particularly at the scales relevant to individual reefs. Thus, while we can be reasonably certain that surface ocean temperatures will generally continue to rise and sea surface temperature anomalies are likely to become more frequent (Parry 2007), variations in community composition and the existence of small-scale temperature refugia mean that climate change impacts may be highly variable from reef to reef. While the timeframe I chose for the model predictions was much shorter than that of any existing regional climate models, continued advances in these models may make it possible to use finer temporal and spatial resolution data in future BBN models as well as allowing the use of iterative or dynamic BBNs to predict longer-term climate-related changes in ecosystems.

Determining whether bleaching and disease are related phenomena in terms of incidence and/or susceptibility is an area of ongoing research. Ideally, demonstrating such a relationship would be performed in a laboratory setting under controlled conditions; however, field-based studies that tracked disease and bleaching incidence at the colony level would also enhance understanding of this relationship. More research also needs to be done to test how well various thermal-anomaly metrics perform in predicting mass bleaching events in deeper habitats; nearly all work to date on this subject has focused on shallow, reef-crest areas.

The model developed and applied in Chapters 4 and 5 should be seen as largely exploratory in nature; with further consultation, different expert pools, and alternate model structures, it should be feasible both to develop highly specialized models for specific types of reefs or to develop even more generalized models that would apply to other reef systems beyond the GBR.

Conclusion

Globally, coral reefs face an uncertain future, and the Great Barrier Reef in particular is at a crossroads concerning greatly expanded coastal development. Hopefully, this thesis has helped to identify some of the key research needs that could guide sound management and conservation of coral reefs, as well as offering some new insights into ways that reefs can be better managed using existing knowledge. Additionally, I hope that my findings may also contribute to a broader understanding of multiple-stressor interactions in other ecosystems, and help to formulate new research questions for ecologists everywhere.

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Appendix A Chapter 2 Supplementary Methods, Tables and Figures

Table A.1. Search terms used to identify studies using the Web of Science database.

Stressor search terms (all used with *and* coral*)
Acidification or calcification
Crown of thorns or Acanthaster*
Cyclone* or hurricane* or typhoon*
Disease*
Fishery or fisheries
Irradiance
Nutrient* or eutrophication
Pollution*
Salinity
Sediment* or Turbidity
Sea level
Temperature
Ultraviolet or UV

Supplementary Methods: Type II error and the two-interval method

Consider the hypothetical data in Table A.2, below, which I have contrived to make the conceptual problem associated with the two-interval method as transparent as possible. Notice that, in every individual study, the combined effect is larger than the additive effect (the sum of the two treatment effects when imposed separately). Thus, the evidence for a consistent interactive effect is very strong. However, the confidence intervals on the respective means for these treatments overlap almost completely, because the variation among studies in the values is large, relative to the within-study differences between treatments. Thus, using a confidence interval overlap approach is akin to using an unpaired t-test on these data (in this case yielding P=0.56), when a paired t-test (or, equivalently, a t-test on the difference between the treatment values) is appropriate (in this case, yielding P<0.001).

Table A.2. Table of hypothetical values illustrating the Type II error associated with using overlapping confidence intervals as indicator of significant differences.

Study	Additive Effect	Combined Effect	Difference (Synergy)
1	1	2	1
2	3	5	2
3	5	8	3
4	7	10	3
5	9	10	1
6	11	13	2
7	15	16	1
8	19	20	1
	Mean ± 95% CI		
	8.75 ± 4.22	10.5 ± 4.02	1.75 ± 0.61

Table A.3. Multiple-stressor studies with photosynthesis as the response variable. N.f.f. = not fully factorial, i.e., experiment not designed to detected synergistic effects. P = Gross photosynthesis. R = Gross respiration. [Chl a],[chl c2] = chlorophyll a and chlorophyll c2 concentrations, respectively. Fv/Fm = Maximum fluorescence yield.

			Response variable(s) measured									
Reference	Stressor 1	Stressor 2	F_v/F_m	F_o/F_m	F/F_m'	[chl a]	[chl c_2]	zoox density	P	R	Other	Synergistic effect(s) reported S=Synergistic A=Antagonistic N=None
(Anthony et al. 2008)	Irradiance	Acidification							x	x		S
(Stambler 1998)	Irradiance	Nutrients						x	x	x	x	N (except for Ec, Ek)
(Anthony & Connolly 2004)	Irradiance	Sedimentation							x	x	x	N
(Kinzie 1993)	Irradiance	UV				x		x			x	n.f.f.
(Sakami 2000)	Irradiance	Salinity	x			x			x			S
(Chauvin et al. 2011)	Nutrients	Acidification				x	x	x	x			n.f.f.
(Cervino et al. 2003)	Nutrients	Sedimentation	x									n.f.f.
(Jones & Hoegh-Guldberg 1999)	Pollution[7]	Irradiance	x		x			x			x	S
(Jones 2004)	Pollution[8]	Irradiance	x		x			x				S
(Cervino et al. 2003)	Pollution	Irradiance						x				n.f.f.

[7] Cyanide
[8] Herbicide (DCMU)

(Alutoin et al. 2001)	Pollution[9]	Salinity				x			x			N,A
(Shaw et al. 2012)	Pollution[10]	Salinity			x							n.f.f.
(Martinez et al. 2007)	Pollution[11]	UV			x							S
(Lirman & Manzello 2009)	Sedimentation	Salinity							x	x		S
(Fabricius et al. 2013)	Sedimentation	Temperature	x									S
(Rodolfo-Metalpa et al. 2010)	Temperature	Acidification			x			x	x	x		N
(Godinot et al. 2011)	Temperature	Acidification	x					x				N
(Cumbo et al. 2013)	Temperature	Acidification						x		x		N
(Ben-Haim et al. 2003)	Temperature	Pathogen				x		x			x	S
(Ferrier-Pages et al. 2010)	Temperature	Starvation				x		x	x	x	x	S
(Hoogenboom et al. 2012)	Temperature	Starvation				x			x	x	x	S
(Tolosa et al. 2011)	Temperature	Starvation				x	x	x			x	S
(Borell & Bischof 2008)	Temperature	Starvation	x		x			x			x	N

[9] Copper sulphate
[10] Diuron
[11] Fluoranthene

(Lenihan & Edmunds 2010)	Temperature	Flow	x								x	N[12]
(Banaszak et al. 2003)	Temperature	Irradiance			x						x	n.f.f.
(Bhagooli & Hidaka 2004)	Temperature	Irradiance	x									S. pistillata: S P. ryukyuensis: N
(Bhagooli & Hidaka 2003)	Temperature	Irradiance	x									S
(Bhagooli & Hidaka 2004)	Temperature	Irradiance	x			x	x	x			x	n.f.f.
(Brown & Dunne 2008)	Temperature	Irradiance	x			x		x				S
(Brown et al. 1999)	Temperature	Irradiance				x	x	x				n.f.f.
(Brown et al. 2002a)	Temperature	Irradiance	x			x		x				A
(Dove 2004)	Temperature	Irradiance	x					x				S
(Dunne & Brown 2001)	Temperature	Irradiance						x				n.f.f.
(Fine et al. 2005)	Temperature	Irradiance	x									S
(Fournie et al. 2012)	Temperature	Irradiance	x								x	N
(Franklin et al. 2004)	Temperature	Irradiance	x									n.f.f.
(Franklin et al. 2006)	Temperature	Irradiance	x					x			x	S
(Hill et al. 2005)	Temperature	Irradiance	x								x	S
(Hill & Ralph	Temperature	Irradiance	x			x	x	x				n.f.f.

[12] However, significant 3-way interaction effect of temperature, flow speed, physical injury on growth rate.

2006)												
(Hoegh-Guldberg & Smith 1989)	Temperature	Irradiance				x		x	x	x		n.f.f.
(Jacques et al. 1983)	Temperature	Irradiance						x	x			?
(Jones et al. 1998)	Temperature	Irradiance	x		x	x		x			x	S
(Karako-Lampert et al. 2005)	Temperature	Irradiance				x		x	x	x	x	N
(Kuguru et al. 2007)	Temperature	Irradiance	x			x		x			x	N
(Lesser et al. 1990)	Temperature	Irradiance	x			x					x	N
(Lesser & Farrell 2004)	Temperature	Irradiance			x						x	S
(Michalek-Wagner 2001)	Temperature	Irradiance						x				n.f.f.
(Nakamura et al. 2004)	Temperature	Irradiance							x	x		N
(Nakamura & Yamasaki 2008)	Temperature	Irradiance	x									A
(Papina et al. 2007)	Temperature	Irradiance						x			x	n.f.f.
(Piggot et al. 2009)	Temperature	Irradiance						x				n.f.f.
(Pillay et al. 2005)	Temperature	Irradiance						x				n.f.f.
(Robison & Warner 2006)	Temperature	Irradiance	x		x	x					x	N,S
(Rodolfo-	Temperature	Irradiance			x	x	x	x			x	n.f.f.

Metalpa et al. 2008)												
(Rowan 2004)	Temperature	Irradiance	x						x			n.f.f.
(Sakami 2000)	Temperature	Irradiance	x			x						S
(Sato et al. 2011)	Temperature	Irradiance	x									N
(Saxby et al. 2003)	Temperature	Irradiance	x			x	x	x			x	S
(Smith & Birkeland 2007)	Temperature	Irradiance	x					x				n.f.f.
(Strasser et al. 1999)	Temperature	Irradiance									x	n.f.f.
(Suwa et al. 2008)	Temperature	Irradiance	x					x				n.f.f.
(Takahashi et al. 2004)	Temperature	Irradiance	x			x		x				S
(Takahashi et al. 2009)	Temperature	Irradiance	x									S
(Venn et al. 2006)	Temperature	Irradiance				x	x	x				S
(Warner et al. 1996)	Temperature	Irradiance	x			x		x			x	n.f.f.
(Winters et al. 2006)	Temperature	Irradiance	x									S
(Winters et al. 2009)	Temperature	Irradiance	x			x		x				n.f.f.
(Yakovleva & Hidaka 2004b)	Temperature	Irradiance	x			x			x	x		N,S
(Yakovleva & Hidaka 2004c)	Temperature	Irradiance	x					x			x	N,S
(Wiedenmann et al. 2013)	Temperature	Irradiance	x			x			x			S

(Hill et al. 2012)	Temperature	Irradiance	x			x		x			x	n.f.f.
(Wiedenmann et al. 2013)	Temperature	Nutrients	x			x			x			S
(Nordemar et al. 2003)	Temperature	Nutrients				x		x		x	x	N,S
(Shick et al. 2011)	Temperature	Nutrients	x								x	S
(Uthicke & Klumpp 1998)	Temperature	Nutrients							x	x	x	N
(Beraud et al. 2013)	Temperature	Nutrients							x	x	x	A
(Fabricius et al. 2013)	Temperature	Nutrients	x									N
(Connolly et al. 2012)	Temperature	Nutrients[13]	x			x						A
(Porter et al. 1999)	Temperature	Salinity							x	x		A
(D'Croz et al. 2001)	Temperature	UV				x	x	x				N
(Drohan et al. 2005)	Temperature	UV						x				S
(Ferrier-Pages et al. 2007)	Temperature	UV	x			x					x	S
(Fitt & Warner 1995)	Temperature	UV	x			x		x	x	x	x	S
(Lesser 1996)	Temperature	UV	x			x					x	S

[13] "Nutrients" in this case consisted of live rotifers

Table A.4. Stressor-stressor interactions and direction of influence (↑ reinforcing, ↓ mitigating, ↔ mixed or no-effect). Empty rows/columns/rows omitted. The numbers in each cell indicate the number of studies reporting that finding. Empty cells indicate that I found no studies investigating that particular interaction. SLR = Sea level rise.

	Acidification	CoTS	Fishing	Irradiance	Nutrients	Pollution	Salinity	Sedimentation
CoTS			2↑ 1↔		1↑		1↑	
Fish Biomass/ Abundance	12↔					1↔		3↓ 1↔
Irradiance								7↓
Nutrients	1↔						17↑ 1↔	17↑
Pathogen growth and virulence	2↑ 1↔		1↔	2↑	8↑	6↑ 1↔		1↑
Pollution								10↑
Salinity								
Sedimentation					5↑1↔			
UV				1↑				2↓

Table A.4 continued.

	SLR	Storms	Temperature	UV
CoTS			2↔	
Fish		1↓2↔	3↓6↔	
Irradiance		1↓		
Nutrients		4↑		
Pathogen growth and virulence			18↑2↔	
Pollution				
Salinity		1↑		
Sedimentation	2↑	22↑1↓1↔		
Storms			4↑2↔	
Temperature		4↓		
UV			1↑	

Table A.5. Summary of multiple-stressor studies as listed in Table A.2. Response variable categories correspond to categories in Figure 2.2. The existence of interactions is only reported for studies that are designed to detect them. Studies may be listed more than once if they measured variables in a different category and/or reported different results for different measurement variables. Zoox. = zooxanthellae; NPQ = Non-photochemical quenching; P = Gross photosynthesis; R = Gross respiration; [chl a] = chlorophyll a concentration; [chl c_2] = chlorophyll c_2; P_{net}= Net photosynthesis; F_v/F_m = Variable fluorescence/Maximal fluorescence, a measure of Photosystem II efficiency.

Reference	Stressor 1	Stressor 2	Response	Measurement	Organism (O) Community (C) Ecosystem (E) Level	Factorial design	Significant interaction	Field (F) or Lab (L)	Synergistic (S), Antagonistic (A), or additive (+)
(Bruce et al. 2012)	Fishing	Pathogens	Algal cover	% cover	E	N	-	F	-
(Houk et al. 2012)	Fishing	Pollution	Reef condition	Coral cover, species richness, colony size, fish abundance	E	Y	Y	F	S
(Anthony et al. 2008)	Irradiance	Acidification	Coral bleaching	Change in luminance	O	Y	Y	L	S
(Anthony et al. 2008)	Irradiance	Acidification	Coral calcification	Buoyant weight	O	Y	Y	L	S[14]
(Anthony et al. 2008)	Irradiance	Acidification	Zoox. photosynthesis	P_{net}	O	Y	Y	L	S
(Suggett et al. 2013)	Irradiance[15]	Acidification	Coral calcification	Total alkalinity	O	Y	Y	L	A

[14] Species-dependent
[15] In this case, the experimental condition for irradiance was sub-saturating

(Suggett et al. 2013)	Irradiance	Acidification	Zoox. photosynthesis	P_{net}, P_{gross},R	O	Y	Y	L	A
(Comeau et al. 2013)	Irradiance	Acidification	Coral calcification	Buoyant weight	O	Y	N	L	+
(Renegar & Riegl 2005)	Nutrients	Acidification	Coral calcification	Buoyant weight	O	Y	N	L	+
(Silverman et al. 2007)	Nutrients	Acidification	Coral calcification	Community calcification	C	N	-	F	-
(Chauvin et al. 2011)	Nutrients	Acidification	Coral calcification	Total alkalinity	O	N	-	L	-
(Chauvin et al. 2011)	Nutrients	Acidification	Zoox. photosynthesis	P_{net}	O	N	-	L	-
(Holcomb et al. 2010)	Nutrients	Acidification	Coral calcification	Buoyant weight	O	Y	Y	L	A
(Thurber et al. 2009)	Nutrients	Acidification	Pathogenicity	Gene expression	O	N	-	L	-
(Remily & Richardson 2006)	Nutrients	Acidification	Pathogen growth	Growth rate	O	Y	Y	L	S
(Comeau et al. 2013)	Nutrients	Acidification	Coral calcification	Buoyant weight	O	Y	N	L	-
(Smith et al. 2010)	Nutrients	Fishing	Algal cover	% cover	E	Y	Y	F	S
(Muhando et al. 2002)	Nutrients	Fishing	Corallimorph cover	% cover	C	N	-	F	-
(Boyer et al.	Nutrients	Fishing	Herbivory	Grazing rate	E	N	-	F	-

2004)									
(Eklof et al. 2009)	Nutrients	Fishing	Sea urchin density	Predation	E	N	-	F	-
(Uthicke & Klumpp 1998)	Nutrients	Irradiance	Benthic microalgal production	Community production (P/R)	C	N	-	F	-
(Peirano et al. 2005)	Nutrients	Irradiance	Coral calcification	Extension rate	O	N	-	L	-
(Comeau et al. 2013)	Nutrients	Irradiance	Coral calcification	Buoyant weight	O	Y	N	L	+
(Hoogenboom et al. 2012)	Nutrients	Irradiance	Zoox. photosynthesis	P/R	O	Y	Y[1]	L	A
(Stambler 1998)	Nutrients	Irradiance	Zoox. photosynthesis	P/R, zoox density	O	Y	N	L	+
(Cooper & Fabricius 2012)	Nutrients	Irradiance	Coral pigmentation	[chl a], colour brightness	O	Y	Y	F/L	A
(Cervino et al. 2003)	Pollution	Irradiance	Coral mortality	% mortality	O	N	-	L	-
(Cervino et al. 2003)	Pollution	Irradiance	Zoox. photosynthesis	Zoox. density	O	N	-	L	-
(Jones & Hoegh-Guldberg 1999)	Pollution	Irradiance	Zoox. photosynthesis	F_v/F_m, zoox density	O	Y	Y	L	S

(Sakami 2000)	Salinity	Irradiance	Zoox. photosynthesis	F_v/F_m, [chl a],P	O	Y	n.r.	L	S
(Humphrey et al. 2008)	Salinity	Nutrients	Coral fertilization	% fertilization	O	Y	Y	L	S
(Faxneld et al. 2010)	Salinity	Nutrients	Coral mortality	% mortality	O	Y	Y	L	S
(Alutoin et al. 2001)	Salinity	Pollution	Zoox. photosynthesis	P/R	O	Y	Y	L	A
(Lambo & Ormond 2006)	Sedimentation	Fishing	Coral/algal cover	% cover	E	N	-	F	-
(Halpern et al. 2013)	Sedimentation	Fishing	Coral/algal cover, fish abundance/diversity	% cover	E	N	-	F	-
(Anthony et al. 2007)	Sedimentation	Irradiance	Coral mortality	Proportional hazard (relative increase in mortality)	O	Y	Y	L	A
(Anthony & Connolly 2004)	Sedimentation	Irradiance	Zoox. photosynthesis	P/R	O	Y	N	L	+
(Fabricius et al. 2005)	Sedimentation	Nutrients	Coral cover	% cover	E	N	-	F	-
(Fabricius & De'Ath 2004)	Sedimentation	Nutrients	Coral cover	% cover	E	N	-	F	-
(Weber et al. 2006)	Sedimentation	Nutrients	Zoox. photosynthesis	F_v/F_m	O	N	-	F	-

(Fabricius & Wolanski 2000)	Sedimentation	Nutrients	Coral mortality	% mortality	O	N	-	L	-
(Wittenberg & Hunte 1992)	Sedimentation	Nutrients	Coral mortality	Juvenile mortality	E	N	-	F	-
(Wielgus et al. 2004)	Sedimentation	Nutrients	Coral mortality	% cover	E	Y	n.r.	F	+
(Humphrey et al. 2008)	Sedimentation	Salinity	Coral fertilization	% fertilization	O	Y	Y	L	S
(Lirman et al. 2003)	Sedimentation	Salinity	Growth rate	Radial growth rate	O	N	-	F	-
(Adjeroud & Salvat 1996)	Sedimentation	Salinity	Coral cover	% cover	E	N	-	F	-
(Lirman & Manzello 2009)	Sedimentation	Salinity	Zoox. photosynthesis	P/R	O	Y	Y	L	S
(Lirman & Manzello 2009)	Sedimentation	Salinity	Coral mortality	% mortality	O	Y	Y	L	S
(Titlyanov 1991)	Sea level rise	Irradiance	Zoox. photosynthesis	P/R	O	N	-	F	-
(Mankiewicz 1995)	Sea level rise	Salinity	Growth rate	Stratigraphy	E	N	-	F	-
(Berumen & Pratchett	Storms	CoTS	Coral recovery	% coral cover	E	N	-	F	-

2006)									
(Done & Potts 1992)	Storms	CoTS	CoTS larval recruitment	Size structure	E	N	-	F	-
(Morton 2005)	Storms	Fishing	Physical damage	Beached corals	E	N	-	F	-
(Lapointe et al. 2006)	Storms	Nutrients	Algal cover	% algal cover	E	N	-	F	-
(Yu et al. 2013)	Storms	Nutrients	Fish abundance	Fish species number	E	N	-	F	-
(Silverman et al. 2007)	Temperature	Acidification	Coral calcification	Community calcification	C	N	-	F	-
(Edmunds 2011)	Temperature	Acidification	Coral calcification	Buoyant weight	O	Y	N	L	+
(Martin & Gattuso 2009)	Temperature	Acidification	Coral calcification	Buoyant weight	O	Y	Y	L	S
(Reynaud et al. 2003)	Temperature	Acidification	Coral calcification	Buoyant weight	O	Y	Y	L	S
(De'ath et al. 2009)	Temperature	Acidification	Coral calcification	Linear extension, density	E	N	-	F	-
(Edmunds et al. 2012)	Temperature	Acidification	Coral calcification	Buoyant weight	O	Y	N	L	+
(Rodolfo-Metalpa et	Temperature	Acidification	Coral calcification	Alkalinity anomaly Buoyant weight	O	Y	N	L	+

al. 2010)									
(Munday et al. 2009)	Temperature	Acidification	Fish aerobic performance	Resting, maximum O_2 uptake, aerobic scope	O	Y	N[16]	L	+
(Godinot et al. 2011)	Temperature	Acidification	Nutrient uptake	NH_4/PO_4/NO_3 uptake	O	Y	Y	L	S
(Remily & Richardson 2006)	Temperature	Acidification	Pathogenesis	Growth rate	O	Y	Y	L	S
(Thurber et al. 2008)	Temperature	Acidification	Pathogenesis	Viral gene expression	O	N	-	L	-
(Rodolfo-Metalpa et al. 2010)	Temperature	Acidification	Zoox. photosynthesis	P,R, Zoox density, F/Fm'	O	Y	N[17]	L	+
(Godinot et al. 2011)	Temperature	Acidification	Zoox. photosynthesis	Zoox density, F_v/F_m	O	Y	N	L	+
(Edmunds 2011)	Temperature	Acidification	Zoox. photosynthesis	Zoox density	O	Y	N	L	+
(Reyes-Nivia et al. 2013)	Temperature	Acidification	Bioerosion	Buoyant weight	O	N	-	L	-
(Albright & Mason 2013)	Temperature	Acidification	Coral fertilization	% fertilization	O	Y	Y	L	S

[16] Interaction term was non-significant for all variables and species except for one (resting O_2 uptake for *O. cyanosoma*)
[17] Interaction terms non-significant except for P_{net} in winter

(Chua et al. 2013)	Temperature	Acidification	Coral fertilization	% fertilization	O	Y	N	L	-
(Chua et al. 2013)	Temperature	Acidification	Coral larval mortality	% mortality	O	Y	N	L	-
(Cumbo et al. 2013)	Temperature	Acidification	Zoox. photosynthesis	Respiration, zoox. density	O	Y	N	L	+
(Cumbo et al. 2013)	Temperature	Acidification	Coral mortality	% mortality	O	Y	Y	L	S
(Banin et al. 2000)	Temperature	Pathogens	Zoox. photosynthesis	Zoox density	O	Y	Y	L	S
(Lesser et al. 1990)	Temperature	Irradiance	Antioxidant enzyme activity	SOD,ASPX,CAT	O	Y	Y	L	S
(MacKellar & McGowan 2010)	Temperature	Irradiance	Coral bleaching	Visual assessment	C	N	-	F	-
(Vinoth et al. 2012)	Temperature	Irradiance	Coral bleaching	Visual assessment, % mortality	C	N	-	F	-
(Drollet et al. 1994)	Temperature	Irradiance	Coral bleaching	Visual assessment	E	N	-	F	-
(Yee et al. 2008)	Temperature	Irradiance	Coral bleaching	Visual assessment	E	N	Y[12]	F	-
(Jokiel & Brown 2004)	Temperature	Irradiance	Coral bleaching	Visual assessment	E	N	-	F	-
(Dunne & Brown 2001)	Temperature	Irradiance	Coral bleaching	Visual assessment	O	N	-	F	-
(Jacques et	Temperature	Irradiance	Coral calcification	Alkalinity anomaly	O	Y	Y	L	S

al. 1983)									
(Peirano et al. 1999)	Temperature	Irradiance	Coral calcification	Growth rate	O	N	-	F	-
(Anthony et al. 2007)	Temperature	Irradiance	Coral mortality	Proportional hazard	O	Y	N	L	S
(Bena & van Woesik 2004)	Temperature	Irradiance	Coral mortality	% mortality	E	N	-	F	-
(Muller & van Woesik 2011)	Temperature	Irradiance	Coral disease	BBD prevalence	O	Y	Y	F	A
(Muller & van Woesik 2011)	Temperature	Irradiance	Coral disease	BBD incidence	O	Y	Y	F	A
(Muller & van Woesik 2011)	Temperature	Irradiance	Coral disease progression	BBD lesion size	O	Y	Y	F	S
(Sato et al. 2011)	Temperature	Irradiance	Coral disease progression	BBD lesion size	O	Y	N	L	+
(Kuehl et al. 2011)	Temperature	Irradiance	Cora disease progression	BBD lesion size	O	Y[18]	Y	L	A
(Papina et al. 2007)	Temperature	Irradiance	Fatty acid composition	[Polyunsaturated FA]	O	Y	Y	L	S
(Michalek-	Temperature	Irradiance	[MAA]	[MAA]	O	N	-	F	-

[18] Experiment lacked low-temperature, high-light treatment

Wagner 2001)									
(Yakovleva & Hidaka 2004a)	Temperature	Irradiance	[MAA]	[MAA]	O	N	-	L	-
(Jones et al. 1998)	Temperature	Irradiance	Zoox. photosynthesis	qP,qN, F_o/F_m	O	Y	Y	L	S
(Lesser et al. 1990)	Temperature	Irradiance	Zoox. photosynthesis	Zoox density, [chl a], [chl c_2]	O	Y	N	L	+
(Lesser & Farrell 2004)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m,F_o/F_m, [chl a], [chl c2], [MAA]	O	Y	Y	L	S
(Smith & Birkeland 2007)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, zoox density	O	N	-	L	-
(Strasser et al. 1999)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_0	O	N	-	L	-
(Fine et al. 2005)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	Y	Y	L	S
(Banaszak et al. 2003)	Temperature	Irradiance	Zoox. photosynthesis	F/F_m', [chl a], zoox density	O	N	-	F	-
(Bhagooli & Hidaka 2003)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	Y	n.r.	L	S
(Bhagooli &	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	Y	Y	L	S[19]

[19] Species-dependent

Hidaka 2004)									
(Bhagooli & Yakovleva 2004)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, ETR_{max}, zoox density, [chl a+c_2]	O	N	-	L	-
(Dove 2004)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, zoox density	O	Y[20]	Y	L	S
(Winters et al. 2006)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	Y	Y	F/L	S
(Takahashi et al. 2004)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, [chl a], zoox density	O	Y	Y	L	S
(Venn et al. 2006)	Temperature	Irradiance	Zoox. photosynthesis	[chl a], [chl c_2], other pigments, zoox density	O	Y	Y	L	S
(Brown et al. 1999)	Temperature	Irradiance	Zoox. photosynthesis	[chl a], zoox density	E	N	-	F	-
(Yakovleva & Hidaka 2004c)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, ETR_{max}, [chl a+c_2]	O	Y	Y	L	S
(Dunne & Brown 2001)	Temperature	Irradiance	Zoox. photosynthesis	Zoox density	O	N	-	F	-
	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, Zoox density, [chl a]	O	Y	Y	F	A
(Saxby et al. 2003)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, Zoox density, [chl a]	O	Y	Y	L	S

[20] Differences in irradiance were due to host pigments, not experimental treatment

(Jacques et al. 1983)	Temperature	Irradiance	Zoox. photosynthesis	Zoox density, net P	O	Y	n.r.	L	?
(Sato et al. 2011)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	Y	N	L	+
(Michalek-Wagner 2001)	Temperature	Irradiance	Zoox. photosynthesis	Zoox density	O	N	-	F	-
(Yakovleva & Hidaka 2004a)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, [chl a], ETR_{max}	O	N	-	L	-
(Franklin et al. 2004)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	N	-	L	-
(Hill et al. 2005)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	Y	Y	L	S
(Hill et al. 2005)	Temperature	Irradiance	Zoox. photosynthesis	NPQ	O	Y	Y	L	S
(Robison & Warner 2006)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, [chl a]	O	Y	n.r.	L	S
(Takahashi et al. 2009)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	Y	Y	L	S
(Yakovleva & Hidaka 2004b)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, [chl a]	O	Y	Y	L	S[21]

[21] Responses were species-specific

(Yakovleva & Hidaka 2004b)	Temperature	Irradiance	Zoox. photosynthesis	P_{max}, R	O	Y	Y	L	S[11]
(Kuguru et al. 2007)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, Zoox density, [chl a]	O	Y	N	F/L	+
(Kuguru et al. 2007)	Temperature	Irradiance	Zoox. photosynthesis	NPQ	O	Y	N	F/L	+
(Nakamura & Yamasaki 2008)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	Y	Y	L	A
(Sakami 2000)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m, [chl a]	O	Y	n.r.	L	S
(Brown et al. 2002b)	Temperature	Irradiance[22]	Zoox. Photosynthesis	F_v/F_m	O	N	-	F/L	-
(Brown et al. 2002b)	Temperature	Irradiance	Zoox. Photosynthesis	[chl a]	O	N	-	F/L	-
(Fabricius et al. 2004)	Temperature	Irradiance	Symbiont clade	Symbiont clade	E	N	n/a	F	-
(Fournie et al. 2012)	Temperature	Irradiance	Coral mortality	% mortality	O	Y	N	L	-
(Fournie et al. 2012)	Temperature	Irradiance	Coral Bleaching	Visual assessment	O	Y	N	L	-
(Fournie et al. 2012)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	Y	Y	L	S

[22] Experiment was to determine effect of irradiance history (acclimatisation) on bleaching susceptibility

(Hill et al. 2012)	Temperature	Irradiance	Zoox. photosynthesis	F_v/F_m	O	N	-	L	-
(Wooldridge & Done 2009)	Temperature	Nutrients	Coral bleaching	Visual assessment	E	N	-	F	-
(Zhu et al. 2004)	Temperature	Nutrients	Coral bleaching	Zoox. expulsion	O	N	-	L	-
(Wagner et al. 2010)	Temperature	Nutrients	Coral bleaching	Visual assessment	E	N	-	F	-
(Silverman et al. 2007)	Temperature	Nutrients	Coral calcification	Community calcification	C	N	-	F	-
(Beraud et al. 2013)	Temperature	Nutrients	Coral calcification	Total alkalinity	O	Y	Y	L	A
(Fabricius et al. 2013)	Temperature	Nutrients	Coral calcification	Buoyant weight	O	Y	N[23]	L	-
(Kruzic et al. 2012)	Temperature	Nutrients	Coral calcification	Linear extension rate	O	N	-	F	-
(Fabricius et al. 2013)	Temperature	Nutrients	Coral mortality	% Mortality	O	Y	N	L	-
(Rodriguez & Croquer 2008)	Temperature	Nutrients	Coral disease	Black band prevalence, incidence	E	N	-	F	-
(Rodriguez & Croquer	Temperature	Nutrients	Coral disease	Mortality	E	N	-	F	-

[23] Confounded with sedimentation effects

2008)									
(Nordemar et al. 2003)	Temperature	Nutrients	Zoox. photosynthesis	Zoox density, [chl a], [chl c], R	O	Y	N	L	+
(Nordemar et al. 2003)	Temperature	Nutrients	Zoox. photosynthesis	$P_{g,}$	O	Y	Y	L	S
(Borell & Bischof 2008)	Temperature	Nutrients[24]	Zoox. photosynthesis	F_v/F_m	O	Y	N	L	+
(Borell & Bischof 2008)	Temperature	Nutrients[13]	Zoox. photosynthesis	[chl a], zoox density	O	Y	Y	L	A
(Beraud et al. 2013)	Temperature	Nutrients	Zoox. photosynthesis	Zoox. density, [chl], NPQ	O	Y	Y	L	A
(Fabricius et al. 2013)	Temperature	Nutrients	Zoox. photosynthesis	F_v/F_m	O	Y	N	L	-
(Wiedenmann et al. 2013)	Temperature	Nutrients	Zoox. photosynthesis	F_v/F_m	O	Y	Y	L	S
(Negri & Hoogenboom 2011)	Temperature	Pollution	Coral larvae metamorphosis	% metamorphosis	O	Y	Y	L	S
(Negri et al. 2011)	Temperature	Pollution	Zoox. photosynthesis	F_v/F_m	O	Y	Y	L	S
(Negri et al. 2011)	Temperature	Pollution	Zoox. photosynthesis	$\Delta F/F_m$’	O	Y	N	L	+

[24] “Nutrients” in this case consisted of feeding of *Artemia salina* nauplii

(Berkelmans & Oliver 1999)	Temperature	Salinity	Coral bleaching	Visual assessment	E	N	-	F	-
(Chavanich et al. 2009)	Temperature	Salinity	Coral bleaching	Visual assessment	O	N	-	F/L	-
(Sakami 2000)	Temperature	Salinity	Zoox. photosynthesis	F_v/F_m, [chl a]	O	Y	Y	L	S
(Williams et al. 2010b)	Temperature	Sedimentation	Coral bleaching	Visual assessment of bleaching prevalence	E	N	-	F	-
(Anthony et al. 2007)	Temperature	Sedimentation	Coral mortality	Proportional hazard	O	Y	N	L	+
(Fabricius et al. 2013)	Temperature	Sedimentation	Zoox. photosynthesis	F_v/F_m	O	Y	Y	L	S
(Brandt et al. 2013)	Temperature	Storms	Coral disease	Disease prevalence	C	N	-	F	-
(Lesser et al. 1990)	Temperature	UV	Zoox. photosynthesis	Zoox density, [chl a], [chl c_2]	O	Y	N	L	+
(Gao & Zheng 2009)	UV radiation	Acidification	Coral calcification	Alkalinity anomaly	O	Y	Y	L	S
(Gao & Zheng 2009)	UV radiation	Acidification	Zoox. photosynthesis	[chl a]	O	Y	Y	L	S
(Kinzie 1993)	UV radiation	Irradiance	Zoox. photosynthesis	[chl a], zoox density	O	N	-	-	-
(Santas et al. 1998)	UV radiation	Irradiance	Productivity	Biomass productivity	C	N	-	F	-

(Fine et al. 2002)	UV radiation	Pathogen load	Coral bleaching	Visual assessment	O	Y	n.r.	F/L	A
(Martinez et al. 2007)	UV radiation	Pollution	Coral mortality	L_C50	O	Y	Y	L	S
(Martinez et al. 2007)	UV radiation	Pollution	Zoox. photosynthesis	$\Delta F/F_m'$	O	Y	Y	L	S
(Rogers et al. 2010)	UV radiation	Temperature	Growth rate	Symbiodinium growth rate	O	N	-	L	-
(Zeevi-Ben-Yosef & Benayahu 2008)	UV radiation	Temperature	Coral mortality	Time to 50% survival	O	Y	Y	L	S
(Drohan et al. 2005)	UV radiation	Temperature	Coral mortality	Mortality	O	Y	Y	L	S
(Drollet et al. 1995)	UV radiation	Temperature	Coral bleaching	Visual assessment	E	N	-	F	-
(Ferrier-Pages et al. 2007)	UV radiation	Temperature	Zoox. photosynthesis	F_v/F_m, [chl a]	O	Y	Y[25]	L	A
(Drohan et al. 2005)	UV radiation	Temperature	Zoox. photosynthesis	Zoox density	O	Y	Y	L	S
(Lesser 1997)	UV radiation	Temperature	Zoox. photosynthesis	P_{max}	O	N	-	L	-
(Gleason &	UV radiation	Temperature	Zoox. photosynthesis	Zoox density, [chl	O	Y	N	F	+

[25] Significant decreases occurred for all but one species.

Wellington 1993)				a]					
(Fitt & Warner 1995)	UV radiation	Temperature	Zoox. photosynthesis	F_v/F_m, P:R	O	Y	n.r.	L	S[26]
(Fitt & Warner 1995)	UV radiation	Temperature	Zoox. photosynthesis	Zoox density	O	Y	n.r.	L	S[15]
(Lesser 1996)	UV radiation	Temperature	Zoox. photosynthesis	F_v/F_m, [chl a]	O	Y	n.r.	L	S
(D'Croz et al. 2001)	UV radiation	Temperature	Zoox. photosynthesis	Zoox density, [chl a], [chl c_2]	O	Y	N	L	+
				Non-factorial design studies					
(Williams et al. 2010a)	Sedimentation	Fishing	Coral disease	Disease prevalence	E	N	Y[27]	F	-
(Hongo & Yamano 2013)	Temperature	Sedimentation	Coral cover	% cover	C	N	Y[28]	F	-
(Mumby et al. 2001)	Temperature	Irradiance[29]	Coral bleaching	Visual assessment	E	N	Y[30]	F	-
(Yee &	Temperature	Irradiance	Coral bleaching	Visual assessment	E	N	Y[31]	F	-

[26] Responses were species-specific
[27] Use of boosted regression tree analysis allowed detection of interaction effects without having a fully factorial experimental design
[28] Although not strictly factorial, the range of conditions between study sites provided evidence for a synergistic effect
[29] Irradiance as a function of cloud cover and wind speed
[30] Interaction effect detected using discriminant function analysis

Barron 2010)

[31] Interaction effect detected from multi-model selection of logistic regression models

Table A.6. Meta-regression of effect size for all photosynthetic response variables from multiple-stressor studies that examined both temperature and irradiance as stressors (n=26). A non-significant p-value means that a variable does not explain a statistically significant amount of variation in effect size between studies.

Predictor	Estimate ± 95% CI	p-value
Intercept	-2.18 ± 9.78	0.66
Genus	0.113 ± 0.141	0.55
Region	-0.149 ± 1.01	0.77
Dependent variable	1.40 ± 4.21	0.18
Size of temperature treatment	-0.974 ± 1.26	0.13
Size of irradiance treatment	-0.0010 ± 0.0035	0.56

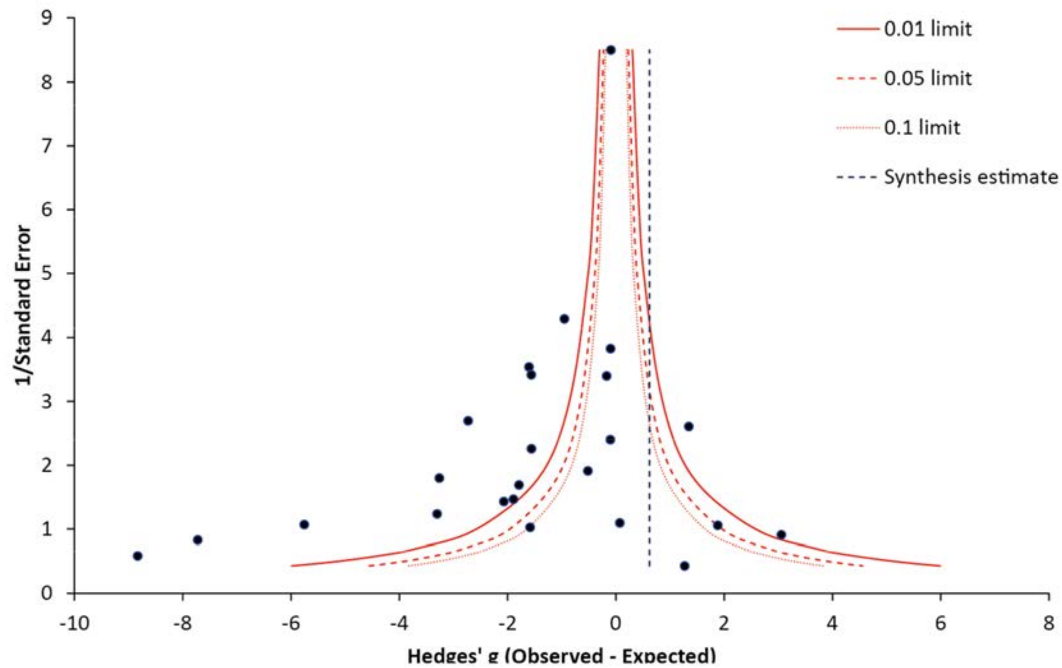

Figure A.1. Funnel plot of the light-temperature interaction term from studies with Fv/Fm, zooxanthellae density, or [chlorophyll a] as the response variable. Visually, the funnel plot appears to be slightly asymmetric in favour of studies reporting synergistic effects (larger positive values), but a linear regression test of asymmetry[1] was not statistically significant (p>0.05, d.f.=24), indicating no apparent publication bias. Also, there is no apparent hollowness to the plot (i.e., there is not a dearth of published studies with effect sizes near zero), indicating no tendency for underreporting where there is no significant synergistic effect. The preponderance of points on the left side of the plot with significant effect sizes also indicates that evidence in the literature is accumulating towards synergistic effects (at least where photosynthesis is concerned), although the random effect model shows that this evidence is not statistically distinguishable from a simple additive effect. The vertical dotted line represents the mean effect size for a random effect model. The solid, dashed, and dotted curved lines represent significant effects at the 0.01, 0.05, and 0.1 levels, respectively. Studies that did not detect a significant interaction effect between stressors fall inside these lines. Outside of these lines, more positive values represent larger synergistic (reinforcing) effects and more negative values indicate larger antagonistic (mitigating) interaction effects.

[1] Sterne, J.A.C., et al., *Recommendations for examining and interpreting funnel plot asymmetry in meta-analyses of randomised controlled trials.* British Medical Journal, 2011. **343**.

Appendix B Chapter 3 Supplementary Figures and Tables

a) White Syndrome

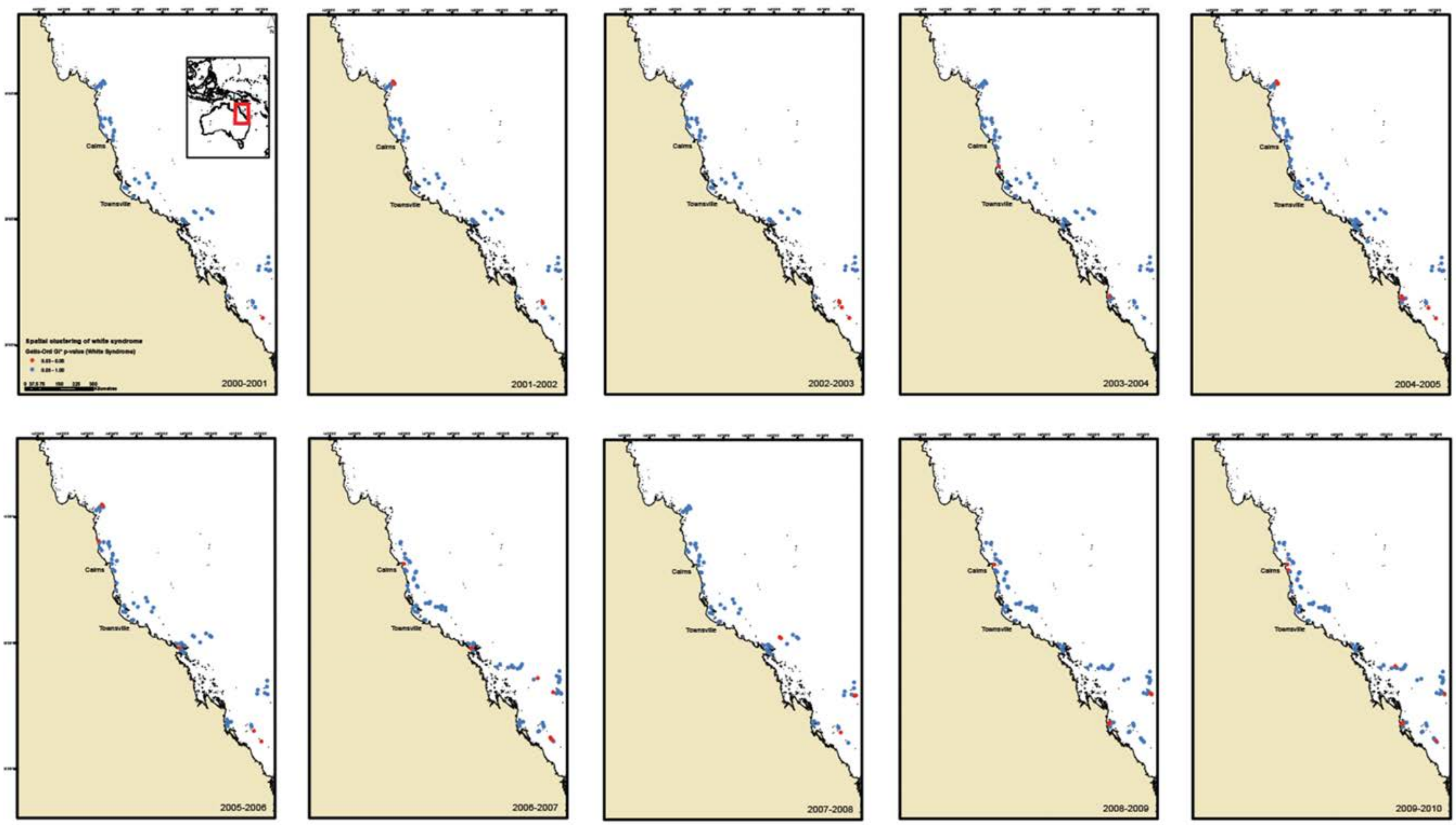

Figure B.1. Year-by-year cluster analysis of a) white syndrome and b) bleaching observations. Red dots indicate areas of significant clustering of high values. No clustering of low values was observed.

b) Bleaching

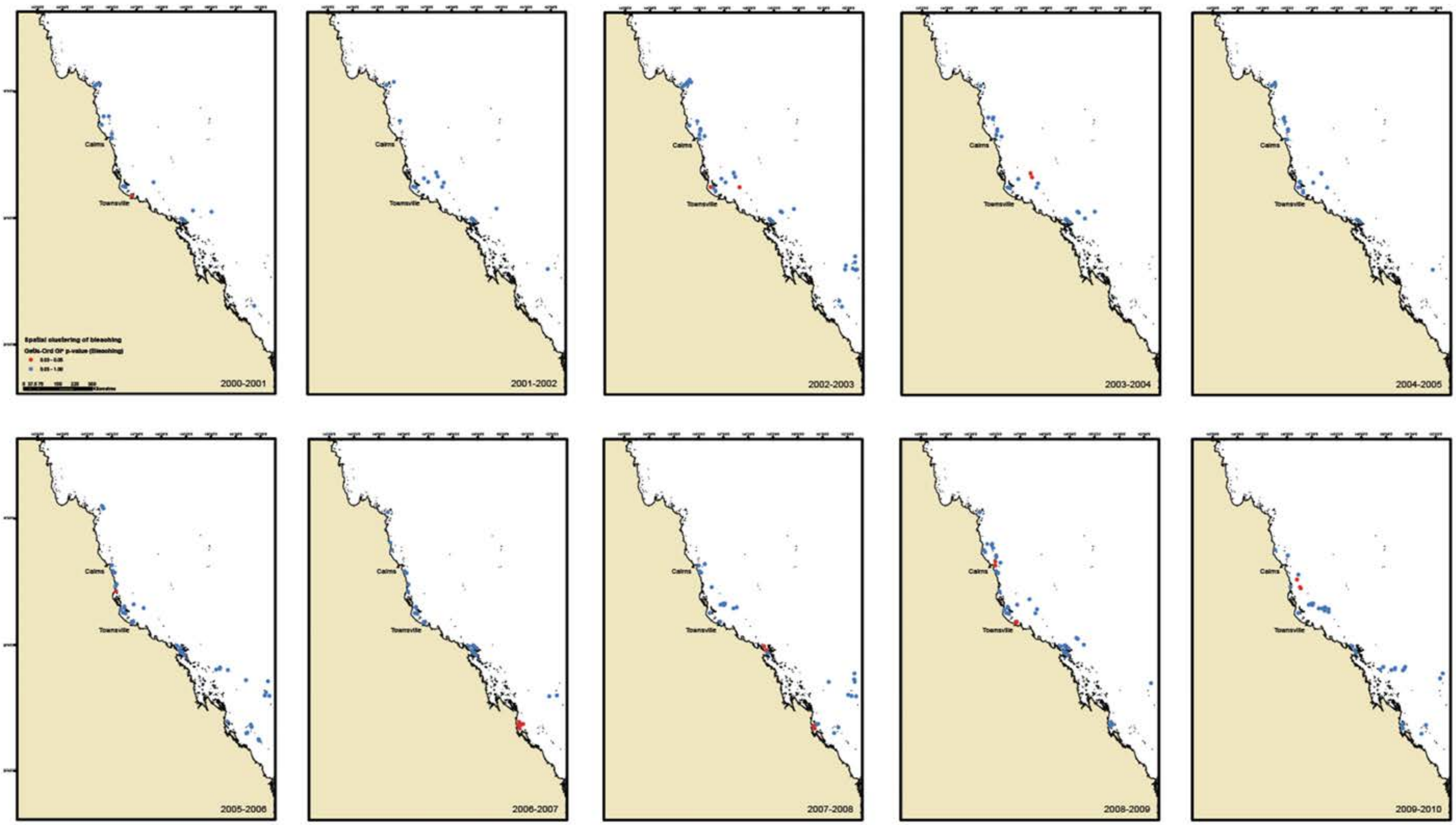
Spatial clustering of bleaching
Cairns
Townsville
2000-2001
2001-2002
2002-2003
2003-2004
2004-2005
2005-2006
2006-2007
2007-2008
2008-2009
2009-2010

Table B.1. Comparison of nested transect-level logistic models for presence of white syndrome with and without bleaching in the same/previous year as a predictor (Absence: 0/Presence: 1). For all effects, the effect size and standard errors are shown. Due to the use of generalized estimating equations for fitting of the transect-level data, PSS scores could not be calculated; instead, receiver-operating characteristic and quasilikelihood (QIC) scores are given. ROC scores below 0.5 indicate the model performs no better than chance.

	Model without bleaching		Model with bleaching		Model with bleaching, w/o temperature predictors		Model with previous year bleaching	
Parameter (standardized)	Estimate	Significance	Estimate	Significance	Estimate	Significance	Estimate	Significance
Hot Snap	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Winter Condition	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Cold Snap	**0.442 ±0.038**	**0.000**	**0.459 ±0.044**	**0.000**	n/a	n/a	**0.456 ±0.044**	**0.000**
Hot Snap*Acroporid cover	**-0.144 ±0.041**	**0.001**	**-0.134 ±0.022**	**0.000**	n/a	n/a	**-0.133 ±0.022**	**0.000**
Cold Snap*Acroporid cover	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Winter Condition*Acroporid cover	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
% Acroporid cover	**0.756 ±0.078**	**0.000**	**0.745 ±0.035**	**0.000**	n/a	n/a	**0.742 ±0.035**	**0.000**
Proportion bleached	n/a	n/a	0.037 ± 0.031	0.445	-0.011 ± 0.032	0.736	-0.016 ±0.033	0.635
Constant	**-1.016 ±0.030**	**0.000**	**-0.949 ±0.033**	**0.000**	**-0.805 ±0.038**	**0.000**	**-0.948 ±0.033**	**0.000**
QIC	6853.7		6854.1		7719.2		6855.53	
ROC Score	0.438		0.451		0.000 (Constant model)		0.428	

Table B.2. Comparison of mixed-effect models (negative binomial with log link) for white syndrome counts with and without bleaching in the same/previous year as a predictor at the transect level. For all effects, the effect size and standard errors are shown. Because generalized estimating equations (GEE) were used, quasilikelihood (QIC) statistics are reported for comparative goodness-of-fit measures; models with smaller QIC values are preferred.

	Minimal model		Full model		Model with bleaching, w/o temperature predictors		Model with previous year bleaching	
Parameter (standardized)	Estimate	Significance	Estimate	Significance	Estimate	Significance	Estimate	Significance
Hot Snap	0.091±0.076	0.233	**0.160±0.073**	**0.029**	n/a	n/a	n/a	n/a
Winter Condition	**-0.173±0.061**	**0.005**	**-0.212±0.062**	**0.001**	n/a	n/a	n/a	n/a
Cold Snap	**0.520 ±0.149**	**0.001**	**0.675 ±0.129**	**0.000**	n/a	n/a	**0.393 ±0.089**	**0.000**
MPSA	n/a	n/a	-0.034±0.065	0.595	n/a	n/a	n/a	n/a
Hot Snap*Acroporid cover	n/a	n/a	**-0.098 ±0.048**	**0.043**	n/a	n/a	**0.093 ±0.038**	**0.015**
Cold Snap*Acroporid cover	n/a	n/a	-0.103±0.101	0.305	n/a	n/a	n/a	n/a
Winter Condition*Acroporid cover	**0.253±0.057**	**0.001**	**0.305±0.041**	**0.000**	n/a	n/a	n/a	n/a
% Acroporid cover	**0.726 ±0.053**	**0.000**	**0.819 ±0.056**	**0.000**	**0.756 ±0.046**	**0.000**	**0.704 ±0.040**	**0.000**
Proportion bleached	n/a	n/a	0.067 ±0.038	0.080	0.047 ±0.033	0.145	-0.007 ±0.042	0.860
Constant	**-0.541 ±0.092**	**0.000**	**-0.598 ±0.094**	**0.000**	**-0.495 ±0.071**	**0.000**	**-0.554 ±0.072**	**0.000**
QIC	3847.8		3804.3		6938.1		6638.5	

Table B.3. Comparison of logistic models for presence/absence of bleaching with and without white syndrome in the same/previous year as a predictor at the transect level. The baseline model (first column) was derived by backwards-stepwise selection starting with all temperature variables.

	Model w/o WS disease		Model with WS disease		Model with WS disease (previous year)		Model with WS disease, w/o temperature variables	
Variable (standardized)	Estimate ±SE	Significance	Estimate ±SE	Significance	Estimate ±SE	Significance	Estimate ±SE	Significance
Hot Snap	**0.275 ±0.026**	**0.000**	**0.280 ±0.026**	**0.000**	**0.206 ±0.031**	**0.000**	n/a	n/a
Cold Snap	**0.181 ±0.037**	**0.000**	**0.185 ±0.037**	**0.000**	**0.250 ±0.042**	**0.000**	n/a	n/a
Winter Condition	-0.050 ±0.027	0.061	-0.049 ±0.027	0.065	**-0.082 ±0.032**	**0.010**	n/a	n/a
WS Count	n/a	n/a	-0.049 ±0.030	0.106	**-0.190 ±0.048**	**0.000**	**-0.169 ±0.042**	**0.000**
Constant	**-1.54 ±0.033**	**0.000**	**-1.54 ±0.033**	**0.000**	**-1.415 ±0.038**	**0.000**	**-1.390 ±0.037**	**0.000**
QIC	8579.92		8578.46		6187.19		6282.60	
ROC	0.586		0.587		0.589		0.534	
Hit Rate (H)	0%		0%		0%		0%	
False Positive % (F)	0%		0%		0%		0%	
False Negative % (1-H)	100%		100%		100%		100%	
Overall %	81.83%		81.83%		82.01%		80.55%	
PSS (H-F) ±SE	0±0		0±0		0±0		0±0	

Appendix C Chapter 4 Supplementary Methods and Figures

Methods

I created the initial list of experts through a literature search using the topic phrase "coral reef ecology" plus "Great Barrier Reef", and contacted the 10 people with the largest number of ecological publications related to the Great Barrier Reef in the previous five years. I then used a snowball approach to identify additional respondents with no constraints on the expertise or background of those identified, and asked interviewees demographic questions regarding their area of expertise and number of years of experience in the field (Supplementary Figure 2-4). I had a total of 21 respondents.

I provided a standard statement to all respondents that described the type of reef and type of physical environment I was considering:

- the model was intended to apply to a mid-shelf reef in the central GBR that was not subjected to chronic terrestrial stressors (sedimentation, nutrient loading, or flood plumes) but might experience such events in extreme years;
- the reef had not recently experienced acute disturbances such as cyclone damage, outbreaks of crown-of-thorns starfish, or bleaching mortality;
- the reef had a hard coral cover of approximately 30% - slightly above the current average coral cover on the GBR (De'ath et al. 2012), but consistent with the apparent minimum to facilitate disease outbreaks (Heron et al. 2010);
- the model time scale was annual to decadal, so the model did not explicitly account for chronic stressors such as ocean acidification and gradual increases in average water temperature, although it did recognise short-term (days to weeks) temperature anomalies.

Respondents were first asked for their assessment of overall model structure and whether nodes or links were missing or superfluous. I noted any suggested changes to assess the degree of consensus with the model structure. Then, because I had only one session with each participant, I asked him or her to parameterize only the initial model. The suggested changes to model structure were not incorporated into the subsequent questions to ensure that the surveys remained consistent between respondents.

Expert comments on model structure

Most experts agreed that the overall structure of the model represented a good abstraction of the reef system, although a few suggested alterations (Supplementary Fig. 6, and Supplementary Table 1). All but four of the suggested changes were suggested by only one expert each. Most of the changes suggested by more than one expert related to the influence of low-salinity events: addition of a linkage to bleaching (five responses) and disease outbreaks (two responses), and the removal of the linkage between salinity and crown-of-thorns starfish outbreaks (two responses). Additionally, two experts suggested a linkage between cyclones and disease outbreaks.

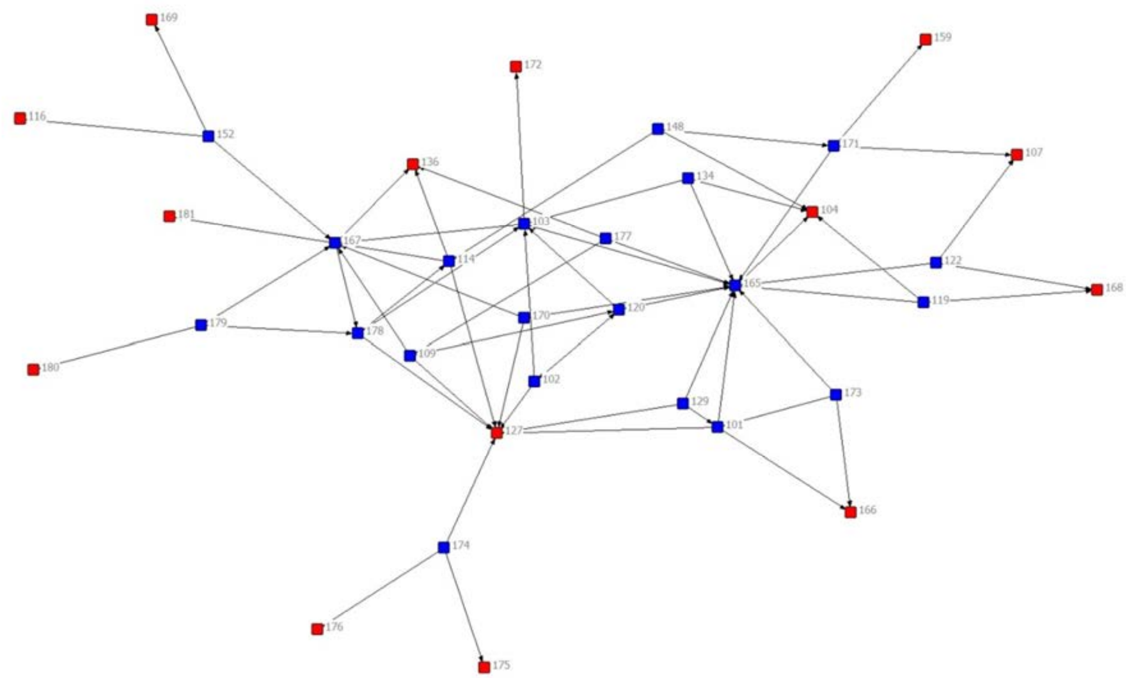

Figure C.1. Network diagram of respondents and those named as experts. Blue nodes are experts that were interviewed; red nodes are experts that were identified, but did not participate. Numbers are participant IDs.

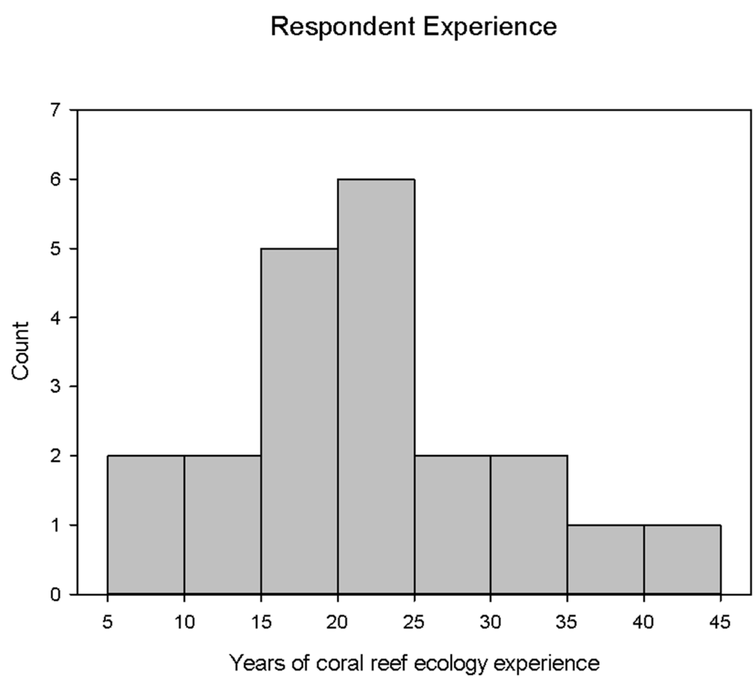

Figure C.2. Distribution of number of years of relevant experience of survey respondents.

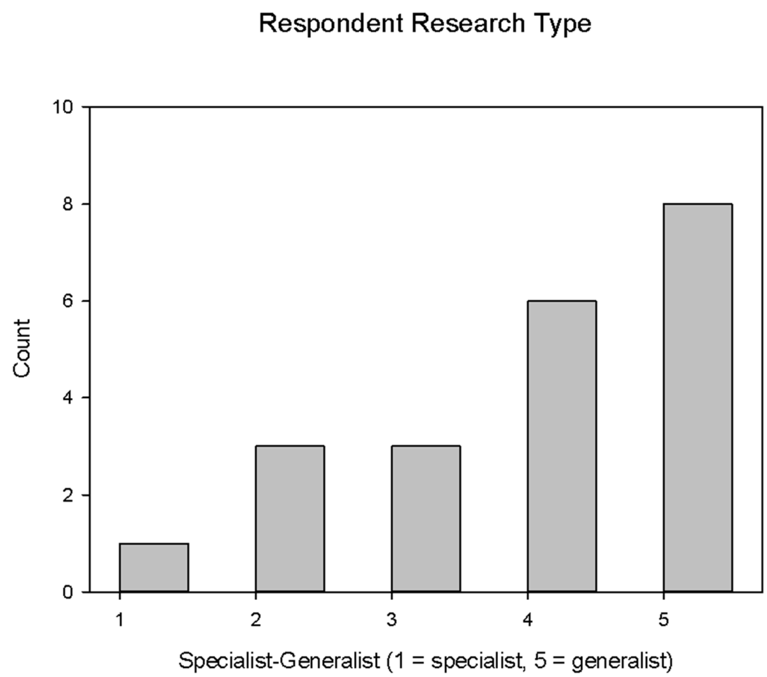

Figure C.3. Distribution of self-described research interests of survey respondents on a 5-point scale, where 1 represents highly specialized (e.g., taxon-specific) research, and 5 represents highly generalized (e.g., ecosystem-level) research.

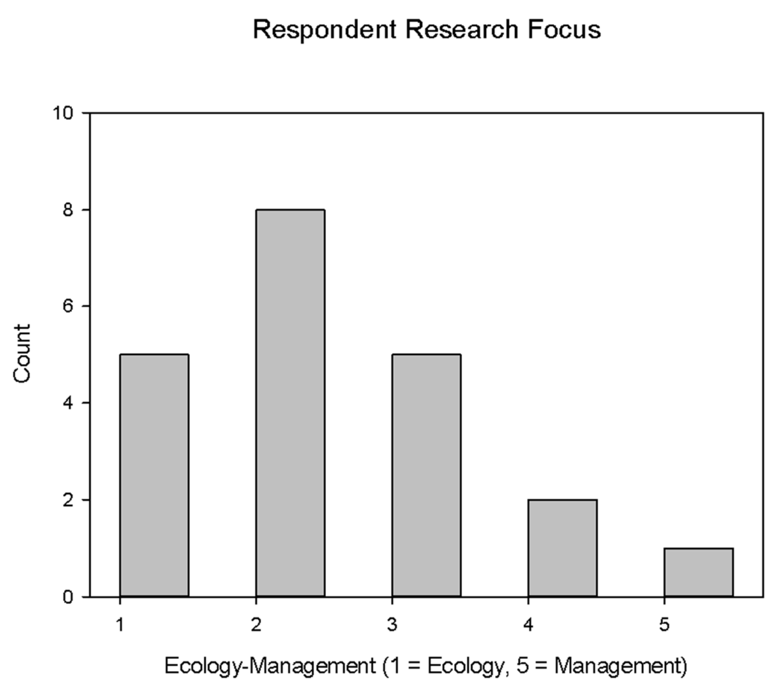

Figure C.4. Distribution of respondents' self-described research focus, with 1 representing completely ecology/biology-focused and 5 representing completely human/management focused.

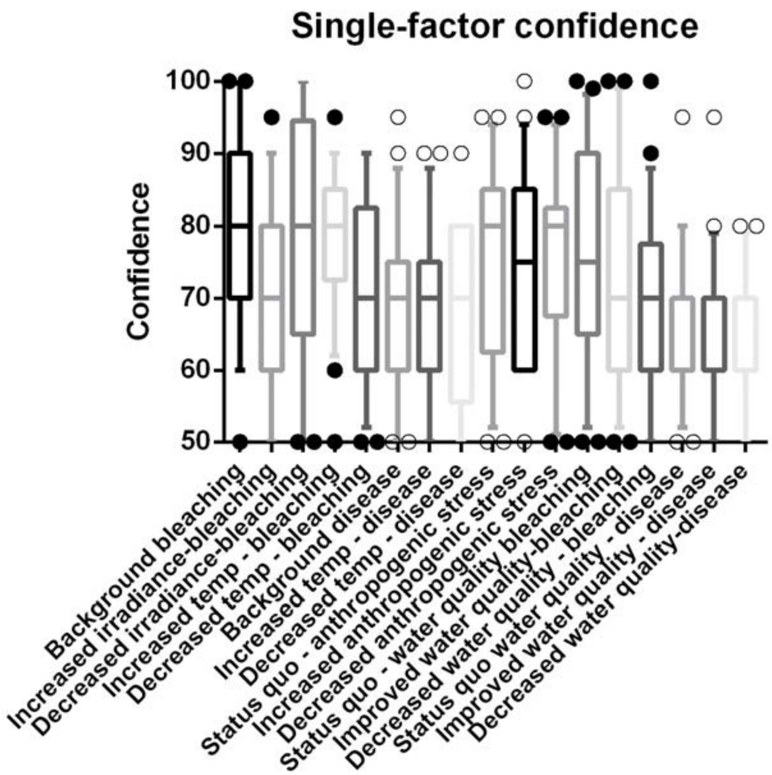

Figure C.5. Confidence levels associated with the effects of a single factor on an outcome. Boxes represent 75th and 25th percentile; whiskers represent 10th and 90th percentile; responses beyond 10th and 90th percentile represented by individual dots. Median value of responses represented by line.

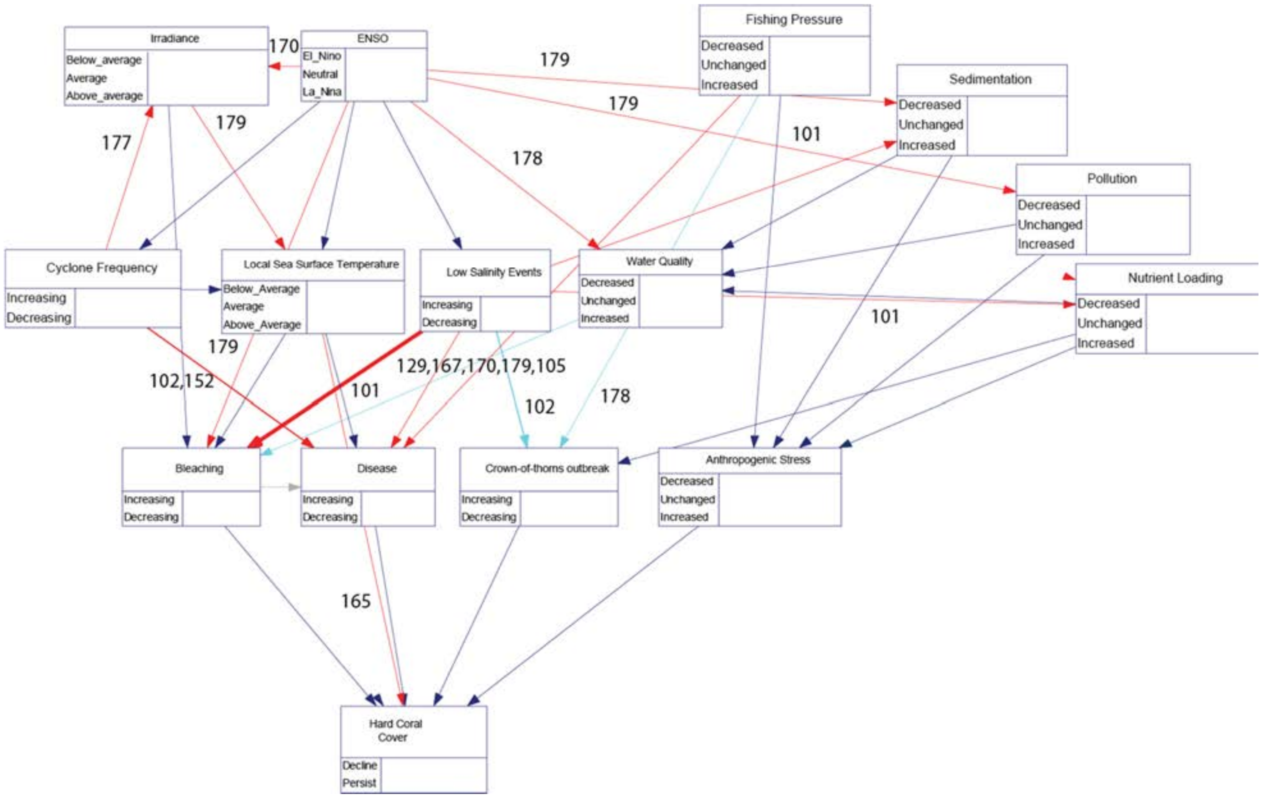

Figure C.6. Annotated model showing suggested modifications to model structure by experts. Lines in red denote links that respondents suggested were missing; lines in light blue denote links that respondents suggested could be removed. Thickness of lines indicates how many respondents suggested the addition/deletion. Numbers by each line indicate the identity of the respondent suggesting that change.

Table C.1. Suggested changes to model structure from respondents. Parent nodes are the factors exerting the influence; child nodes are factors that are being influenced.

Parent node	Child node	Number of respondents
	Additions	
Low salinity events	Bleaching	6
Low salinity events	Disease	2
Low salinity events	Sedimentation	1
Low salinity events	Pollution	1
Low salinity events	Nutrient loading	1
Low salinity events	Water quality	1
Cyclones	Disease	2
Cyclones	Irradiance	1
ENSO	Irradiance	1
ENSO	Water quality	1
ENSO	Bleaching	1
ENSO	Sedimentation	1
ENSO	Nutrient loading	1
Irradiance	Local SST	1
Bleaching	Disease	1
Water quality	CoTS Outbreaks	1
	Deletions	
Water quality	Bleaching	1
Low salinity events	CoTS outbreaks	2

Table C.2. Disease outbreak scenario descriptions. Shaded scenarios were directly elicited; unshaded scenarios were linearly interpolated from the elicited values.

Scenario #	Water quality (relative to present)	Temperature anomaly frequency (relative to present)
1	Improved	Decreased
2	Unchanged	Decreased
3	Decreased	Decreased
4	Improved	Unchanged
5	Unchanged	Unchanged
6	Decreased	Unchanged
7	Improved	Increased
8	Unchanged	Increased
9	Decreased	Increased

Table C.3. Mass bleaching scenario descriptions. Shaded scenarios were directly elicited; unshaded scenarios were linearly interpolated from the elicited values.

Scenario #	SST	Irradiance	Water quality
1	Below average	Below average	Improved
2	Below average	Below average	Unchanged
3	Below average	Below average	Decreased
4	Below average	Average	Improved
5	Below average	Average	Unchanged
6	Below average	Average	Decreased
7	Below average	Above average	Improved
8	Below average	Above average	Unchanged
9	Below average	Above average	Decreased
10	Average	Below average	Improved
11	Average	Below average	Unchanged
12	Average	Below average	Decreased
13	Average	Average	Improved
14	Average	Average	Unchanged
15	Average	Average	Decreased
16	Average	Above average	Improved
17	Average	Above average	Unchanged
18	Average	Above average	Decreased
19	Above average	Below average	Improved
20	Above average	Below average	Unchanged
21	Above average	Below average	Decreased
22	Above average	Average	Improved
23	Above average	Average	Unchanged
24	Above average	Average	Decreased
25	Above average	Above average	Improved
26	Above average	Above average	Unchanged
27	Above average	Above average	Decreased

Table C.4. Crown-of-thorns starfish (CoTS) outbreak scenario descriptions. Shaded scenarios were directly elicited; unshaded scenarios were linearly interpolated from the elicited values.

Scenario	Flood frequency	Fishing	Nutrients
1	Decreased	Decreased	Decreased
2	Decreased	Decreased	Unchanged
3	Decreased	Decreased	Increased
4	Decreased	Unchanged	Decreased
5	Decreased	Unchanged	Unchanged
6	Decreased	Unchanged	Increased
7	Decreased	Increased	Decreased
8	Decreased	Increased	Unchanged
9	Decreased	Increased	Increased
10	Increased	Decreased	Decreased
11	Increased	Decreased	Unchanged
12	Increased	Decreased	Increased
13	Increased	Unchanged	Decreased
14	Increased	Unchanged	Unchanged
15	Increased	Unchanged	Increased
16	Increased	Increased	Decreased
17	Increased	Increased	Unchanged
18	Increased	Increased	Increased

Table C.5. Hard coral persistence scenario descriptions. Shaded scenarios were directly elicited; unshaded scenarios were linearly interpolated from the elicited values.

Scenario	Cyclones	CoTS	Bleaching	Disease	Anthropogenic Stress
1	Decreasing	Decreasing	Decreasing	Decreasing	Decreasing
2	Decreasing	Decreasing	Decreasing	Decreasing	Unchanged
3	Decreasing	Decreasing	Decreasing	Decreasing	Increasing
4	Decreasing	Decreasing	Decreasing	Increasing	Decreasing
5	Decreasing	Decreasing	Decreasing	Increasing	Unchanged
6	Decreasing	Decreasing	Decreasing	Increasing	Increasing
7	Decreasing	Decreasing	Increasing	Decreasing	Decreasing
8	Decreasing	Decreasing	Increasing	Decreasing	Unchanged
9	Decreasing	Decreasing	Increasing	Decreasing	Increasing
10	Decreasing	Decreasing	Increasing	Increasing	Decreasing
11	Decreasing	Decreasing	Increasing	Increasing	Unchanged
12	Decreasing	Decreasing	Increasing	Increasing	Increasing
13	Decreasing	Increasing	Decreasing	Decreasing	Decreasing
14	Decreasing	Increasing	Decreasing	Decreasing	Unchanged
15	Decreasing	Increasing	Decreasing	Decreasing	Increasing
16	Decreasing	Increasing	Decreasing	Increasing	Decreasing
17	Decreasing	Increasing	Decreasing	Increasing	Unchanged
18	Decreasing	Increasing	Decreasing	Increasing	Increasing
19	Decreasing	Increasing	Increasing	Decreasing	Decreasing
20	Decreasing	Increasing	Increasing	Decreasing	Unchanged
21	Decreasing	Increasing	Increasing	Decreasing	Increasing
22	Decreasing	Increasing	Increasing	Increasing	Decreasing
23	Decreasing	Increasing	Increasing	Increasing	Unchanged
24	Decreasing	Increasing	Increasing	Increasing	Increasing
25	Increasing	Decreasing	Decreasing	Decreasing	Decreasing
26	Increasing	Decreasing	Decreasing	Decreasing	Unchanged
27	Increasing	Decreasing	Decreasing	Decreasing	Increasing
28	Increasing	Decreasing	Decreasing	Increasing	Decreasing
29	Increasing	Decreasing	Decreasing	Increasing	Unchanged
30	Increasing	Decreasing	Decreasing	Increasing	Increasing

31	Increasing	Decreasing	Increasing	Decreasing	Decreasing
32	Increasing	Decreasing	Increasing	Decreasing	Unchanged
33	Increasing	Decreasing	Increasing	Decreasing	Increasing
34	Increasing	Decreasing	Increasing	Increasing	Decreasing
35	Increasing	Decreasing	Increasing	Increasing	Unchanged
36	Increasing	Decreasing	Increasing	Increasing	Increasing
37	Increasing	Increasing	Decreasing	Decreasing	Decreasing
38	Increasing	Increasing	Decreasing	Decreasing	Unchanged
39	Increasing	Increasing	Decreasing	Decreasing	Increasing
40	Increasing	Increasing	Decreasing	Increasing	Decreasing
41	Increasing	Increasing	Decreasing	Increasing	Unchanged
42	Increasing	Increasing	Decreasing	Increasing	Increasing
43	Increasing	Increasing	Increasing	Decreasing	Decreasing
44	Increasing	Increasing	Increasing	Decreasing	Unchanged
45	Increasing	Increasing	Increasing	Decreasing	Increasing
46	Increasing	Increasing	Increasing	Increasing	Decreasing
47	Increasing	Increasing	Increasing	Increasing	Unchanged
48	Increasing	Increasing	Increasing	Increasing	Increasing

Appendix D Chapter 5 Supplementary Methods and Figures

Table D.1. Input data layers, associated spatial and temporal resolutions, and data sources.

Layer	Spatial Resolution	Temporal resolution	Source	Starting date	Ending date	Notes
Irradiance	$9km^2$	1 month	SeaWIFS/AQUA	Sep-1997	Dec-2010	AQUA data used for temporal gap-filling
ENSO	Non-spatial	1 month	Australian Bureau of Meteorology	Jan-1906	Sep-2012	
Cyclone frequency	Non-spatial	1 day	Australian Bureau of Meteorology	Jan-1906	Jan-2012	
Cyclone tracks	n/a	1 day	IBTRACS – International Best Tracks Archive for Climate Stewardship (Knapp et al. 2010)	Jan-1885	Dec-2008	>Cat 2 cyclone tracks, buffered 50km to the left and 30km to the right
Flood events	River basin	1 day	Australian Bureau of Meteorology	Apr-1901	Sep-2012	
Flood plume extent	$0.5km^2$	Yearly	(Alvarez-Romero et al. 2013)	2007	2011	
Sea surface temperature	$4km^2$	Monthly	NOAA Pathfinder/(Ban et al. 2012)	Jan-1985	Dec-2009	
Sedimentation	n/a	Yearly	(Alvarez-Romero et al. 2013)	2007	2011	
Nutrient loading	$0.5km^2$	Yearly	(Alvarez-Romero et al. 2013)	2007	2011	DIN only
Pollution		Yearly	(Maughan et al. 2008)	Modeled based on data up to 2006	Modeled based on data up to 2006	Herbicide (primarily diuron) loading only
Commercial fishing catch/effort	$6nm^2$ (~$11km^2$)	Yearly	Queensland Department of Agriculture, Forests, and Fisheries	2001	2012	Only line-caught species included; trawls and nets excluded

Table D.2. Modified environmental data layers for scenarios

	Sea surface temperature	Irradiance	Cyclone tracks	Flood plume extent	Sedimentation	Nutrients	Pollution	Fishing
Baseline	As is: Average 1-degree anomalies; 3-standard deviation cutoff	As-is: 1 SD climatology anomalies	Uniform average risk category	Average extent across 2007-2011	Averaged across 2007-2011	Averaged across 2007-2011	Averaged across 2007-2011	As-is; zero fishing assumed inside reserves
No climate change with local management	Same as baseline	Same as baseline	Uniform average risk category	30% decrease in flood plume extent	30% decrease in sedimentation extent	30% decrease in sedimentation extent	30% decrease in sedimentation extent	30% decrease in sedimentation extent
Climate change with local management	+0.2C to summer anomalies	Same as baseline	Uniform increased risk category	30% increase in flood plume extent	30% decrease in sedimentation extent	30% decrease in sedimentation extent	30% decrease in sedimentation extent	30% decrease in sedimentation extent
Climate change without local management	+0.2C to summer anomalies	Same as baseline	Uniform increased risk category	30% increase in flood plume extent	30% increase in sedimentation extent	Same as baseline	Same as baseline	Same as baseline

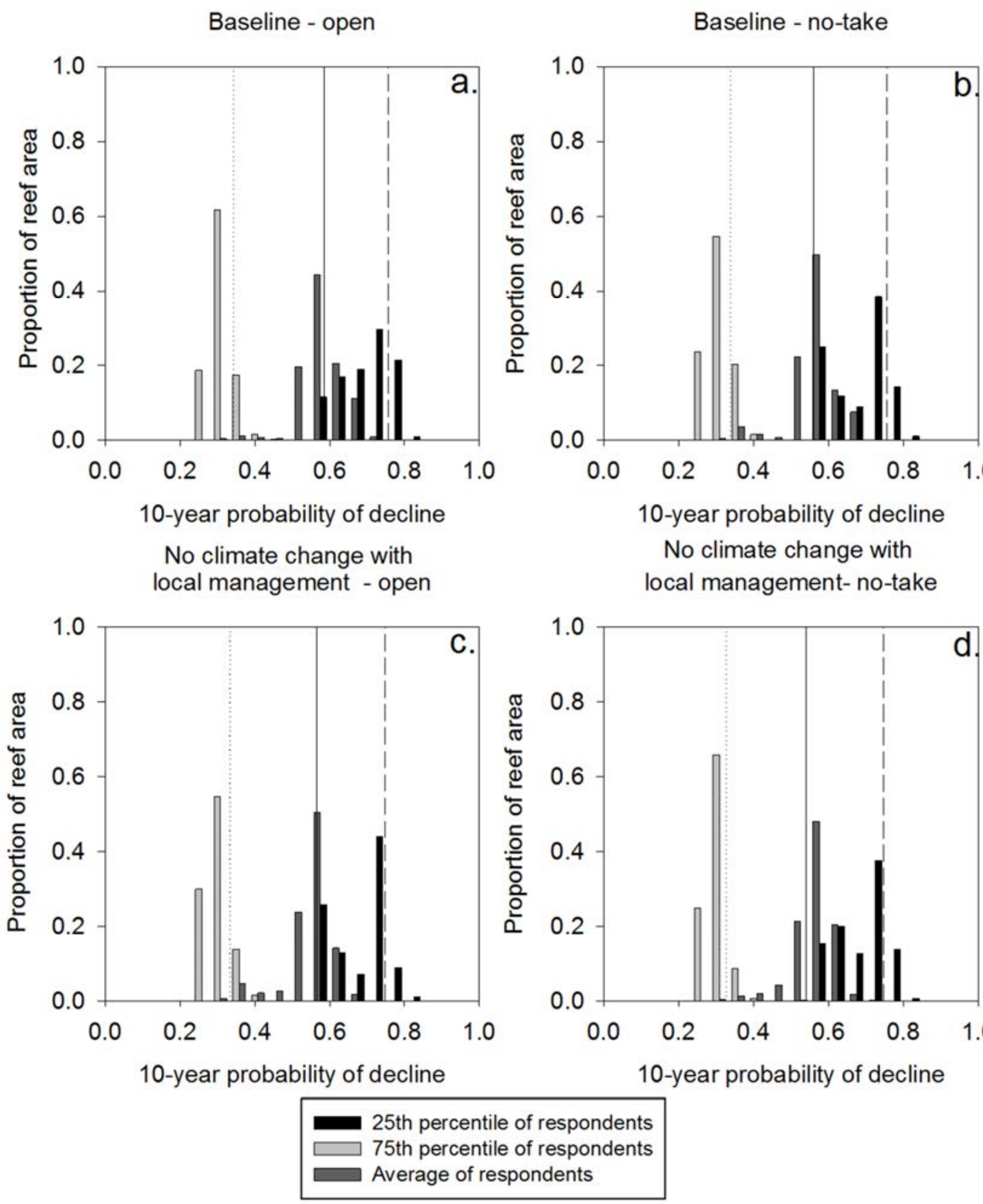

Figure D.1. Distribution of probabilities of decline in hard coral cover in relation to proportion of total reef area for models using 75th percentile (optimistic), 25th percentile (pessimistic), and mean expert parameters for: a) baseline scenario, reefs open to fishing; b) baseline scenario, no-take areas; c) local management without further climate change, open reefs; and d) local management without further climate change, no-take reefs. Dotted vertical line shows mean for 75th percentile estimates; solid vertical line shows mean for average estimates; dashed vertical line shows mean for 25th percentile estimates.

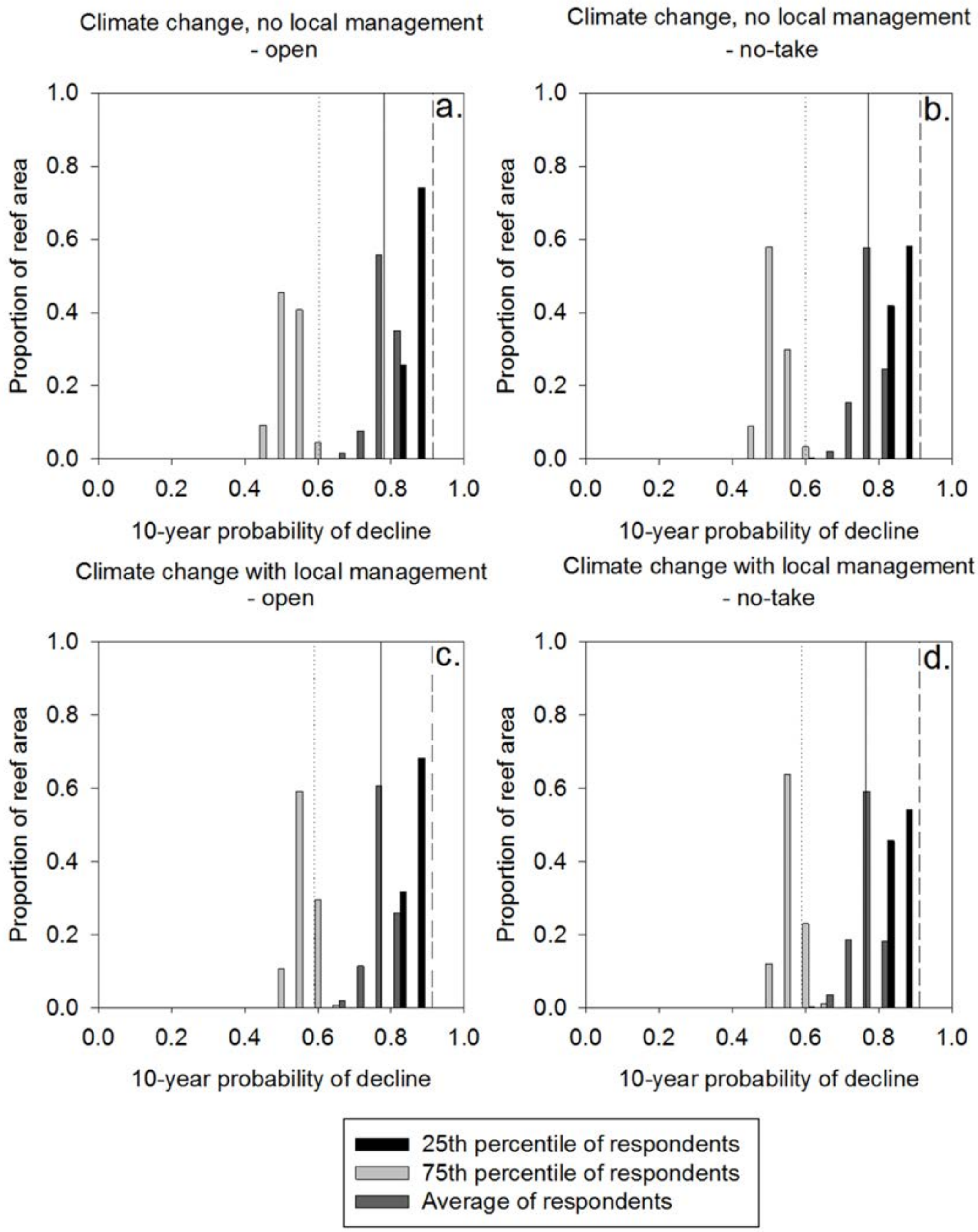

Figure D.2. Distribution of probabilities of decline in hard coral cover by reef area for models using 75th percentile (optimistic), 25th percentile (pessimistic), and average expert parameters for: a) climate change without local management scenario, reefs open to fishing; b) climate change without local management, no-take reefs; c) local management with climate change, open reefs; and d) local management with climate change, no-take reefs.

Appendix E Survey used for chapters 4 and 5

INFORMATION SHEET

Conceptual models of stressor impacts and ecological function on the Great Barrier Reef (Centre of Excellence for Coral Reef Studies)

You are invited to take part in a research project about the possible ecological and management scenarios for the Great Barrier Reef. I also am interested in how different kinds of experts perceive the different risks and relationships between stressors and components of the Great Barrier Reef, and how different management scenarios may be able to mitigate these stressors. The study is being conducted by **Stephen Ban** and will contribute to his **PhD** concerning multiple stressor effects on the GBR at James Cook University.

If you agree to be involved in the study, you will be invited to be interviewed. The interview should only take approximately 1 hour of your time. The interview will be conducted at a venue of your choice.

Taking part in this study is completely voluntary and you can stop taking part in the study at any time without explanation or prejudice. You may also withdraw any unprocessed data from the study.

Your responses and contact details will be strictly confidential. The data from the study will be used for the purposes of a doctoral thesis and subsequent research publications. You will not be identified in any way in these publications.

If you have any questions about the study, please contact **Stephen Ban**

Principal Investigator:
Stephen Ban, PhD candidate ARC CoE for Coral Reef Studies, James Cook University
QLD, 4811, Australia
Tel + Mobile 04 1492 2495
Email: Stephen.Ban@my.jcu.edu.au

If you have any concerns regarding the ethical conduct of the study, please contact: Tina Langford, Ethics Officer, Research Office, James Cook University, Townsville, Qld, 4811. Phone: 4781 4342, Tina.Langford@jcu.edu.au

JAMES COOK UNIVERSITY
AUSTRALIA

INFORMED CONSENT FORM

PRINCIPAL INVESTIGATOR	**Stephen Ban**
PROJECT TITLE:	Conceptual models of stressor impacts and ecological function on the Great Barrier Reef
SCHOOL	**Centre of Excellence for Coral Reef Studies**

I understand the aim of this research study is to find about how I conceptualize stressor interactions on the Great Barrier Reef, and how perceptions about these interactions may be affected by different research interests. I understand that any personal information will be kept strictly confidential and not be used without prior consent. I consent to participate in this project, the details of which have been explained to me, and I have been provided with a written information sheet to keep.

I understand that my participation will involve an **interview/ questionnaire** and I agree that the researcher may use the results as described in the information sheet.

I acknowledge that:

- any risks and possible effects of participating in the interview have been explained to my satisfaction;
- taking part in this study is voluntary and I am aware that I can stop taking part in it at any time without explanation or prejudice and to withdraw any unprocessed data I have provided;
- that any information I give will be kept strictly confidential and that no names will be used to identify me with this study without my approval;

(Please tick to indicate consent)

I consent to complete a questionnaire		**Yes**		**No**
I consent to be interviewed		**Yes**		**No**

Name: *(printed)*	
Signature:	**Date**:

For the following questions, assume that I are talking about a typical reef with hard coral cover of approximately 30% situated in the mid-shelf of the central Great Barrier Reef, in a location that is infrequently (~1 year in 10) exposed to terrestrial effects such as siltation, pollution, or flood plumes. Also assume that this hypothetical reef is healthy (i.e., has not recently experienced any acute disturbances such as bleaching, CoTS, disease, etc.).

Note that the confidence estimate must be higher than 50%, because it represents how confident you are that the values you provided contain the true value. If this number is less than 50%, it means that you are more confident that the true value is outside the range you have provided than inside it.

1.
   a. If irradiance is no higher or lower than normal, what's the probability of a bleaching event?

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

   b. If irradiance is higher than average, what's the probability of a bleaching event (in the absence of other stressors)?

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

   c. What about when irradiance is lower than average?

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

2.
   a. If local sea surface temperature is at least 1 degree C (but no more than 2) higher than average for 4-6 weeks in summer, how likely is a bleaching event to occur (in the absence of other stressors)?

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

   b. What about when temperature is 1 degree C (but no more than 2) below the average for 4-6 weeks in winter?

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

3.

a. What’s the probability of a disease outbreak event if local ocean temperatures remain at average?

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

b. If local sea surface temperature is more than 1 degree C (but no more than 2) higher than the (summer) average, how likely is a disease outbreak event to occur (in the absence of other stressors)?

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

c. What about when temperature is 1 degree C (but no more than 2) below the (winter) average?

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

4. In terms of the importance of anthropogenic stressors to coral persistence, weight the following 4 factors so that they sum to 100%:

a. Fishing pressure

b. Sedimentation

c. Pollution (herbicides, pesticides, heavy metals, etc)

d. Nutrient loading (phosphates, nitrates, etc)

5. How likely is hard coral cover to persist if the combined anthropogenic stresses from (4):

a. Stay the same as current levels

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

b. Increase above current levels

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

c. Decrease below current levels

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

6. In terms of overall water quality as it pertains to coral persistence, weight the following 3 factors so that they sum to 100% in terms of importance:
   a. Sedimentation

   b. Pollution

   c. Nutrient loading

7. In terms of the water quality I defined in (6), what's the likelihood of a bleaching event if water quality

a) remains at current levels;

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

b) improves over current levels;

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

c) declines over current levels.

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

8. As above, but for disease?
   a) Stays the same

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

b) Improves

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

c) Declines

Highest possible value	Lowest possible value	Best estimate	How confident are you? (50-100%)

9. Bleaching scenarios

SST anomaly	Irradiance	Water quality	Probability of bleaching (0-100)
↓	↓	↑(improved)	
↑	↑	↓(decreased)	
↔(status quo)	↓	↑	
↑	↓	↑	
↓	↔	↑	
↓	↑	↑	
↓	↓	↔	
↓	↓	↓	

10. Disease scenarios

SST anomaly	Water quality	Probability of disease outbreak (0-100)
↓	↑	
↑	↓	
↔	↑	
↑	↑	
↓	↔	
↓	↓	

11. Scenario: CoTS outbreak

Low salinity (flood) frequency	Fishing pressure	Nutrient loading	% CoTS outbreak frequency decreased	% CoTS outbreak frequency unchanged	% CoTS outbreak frequency increased
↓	↓	↓			
↑	↑	↑			
↑	↓	↓			
↓	↔	↓			
↓	↑	↓			
↓	↓	↔			
↓	↓	↑			

12. Scenario: Coral persistence

Cyclone frequency	CoTS outbreak frequency	Bleaching events	Disease outbreaks	Anthropogenic Stress Index	Probability of coral persistence
↓	↓	↓	↓	↓	
↑	↑	↑	↑	↑	
↑	↓	↓	↓	↓	
↓	↑	↓	↓	↓	
↓	↓	↑	↓	↓	
↓	↓	↓	↑	↓	
↓	↓	↓	↓	↔	
↓	↓	↓	↓	↑	

Finally, general background questions:

1. Approximately how many years of experience do you have in coral reef ecology?
2. On a scale of 1-5, with 1 being highly specialist and 5 being highly generalist, how would you describe your research interest(s)?
3. On a scale of 1-5, with 1 being ecology/biology-focused and 5 being management/human-focused, how would you describe your research interest(s)?
4. Name 3 people you would consider experts in the area of coral reef ecology on the Great Barrier Reef.

Appendix F Published manuscripts

Global Change Biology

Global Change Biology (2014) **20**, 681–697, doi: 10.1111/gcb.12453

REVIEW

Evidence for multiple stressor interactions and effects on coral reefs

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Abstract

Concern is growing about the potential effects of interacting multiple stressors, especially as the global climate changes. We provide a comprehensive review of multiple stressor interactions in coral reef ecosystems, which are widely considered to be one of the most sensitive ecosystems to global change. First, we synthesized coral reef studies that examined interactions of two or more stressors, highlighting stressor interactions (where one stressor directly influences another) and potentially synergistic effects on response variables (where two stressors interact to produce an effect that is greater than purely additive). For stressor-stressor interactions, we found 176 studies that examined at least 2 of the 13 stressors of interest. Applying network analysis to analyze relationships between stressors, we found that pathogens were exacerbated by more costressors than any other stressor, with ca. 78% of studies reporting an enhancing effect by another stressor. Sedimentation, storms, and water temperature directly affected the largest number of other stressors. Pathogens, nutrients, and crown-of-thorns starfish were the most-influenced stressors. We found 187 studies that examined the effects of two or more stressors on a third dependent variable. The interaction of irradiance and temperature on corals has been the subject of more research (62 studies, 33% of the total) than any other combination of stressors, with many studies reporting a synergistic effect on coral symbiont photosynthetic performance (n = 19). Second, we performed a quantitative meta-analysis of existing literature on this most-studied interaction (irradiance and temperature). We found that the mean effect size of combined treatments was statistically indistinguishable from a purely additive interaction, although it should be noted that the sample size was relatively small (n = 26). Overall, although in aggregate a large body of literature examines stressor effects on coral reefs and coral organisms, considerable gaps remain for numerous stressor interactions and effects, and insufficient quantitative evidence exists to suggest that the prevailing type of stressor interaction is synergistic.

Keywords: acidification, climate change, coral bleaching, coral disease, irradiance, meta-analysis, overfishing

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Coral Reefs
DOI 10.1007/s00338-012-0944-6

REPORT

Relationships between temperature, bleaching and white syndrome on the Great Barrier Reef

S. S. Ban · N. A. J. Graham · S. R. Connolly

Received: 19 February 2012 / Accepted: 31 July 2012

Abstract Coral bleaching and disease have often been hypothesized to be mutually reinforcing or co-occurring, but much of the research supporting this has only drawn an implicit connection through common environmental predictors. In this study, we examine whether an explicit relationship between white syndrome and bleaching exists using assemblage-level monitoring data from up to 112 sites on reef slopes spread throughout the Great Barrier Reef over 11 years of monitoring. None of the temperature metrics commonly used to predict mass bleaching performed strongly when applied to these data. Furthermore, the inclusion of bleaching as a predictor did not improve model skill over baseline models for predicting white syndrome. Similarly, the inclusion of white syndrome as a predictor did not improve models of bleaching. Evidence for spatial co-occurrence of bleaching and white syndrome at the assemblage level in this data set was also very weak. These results suggest the hypothesized relationship between bleaching and disease events may be weaker than previously thought, and more likely to be driven by common responses to environmental stressors, rather than directly facilitating one another.

Keywords Coral reef ecology · Multiple stressors · Synergy · Resilience · Coral bleaching · Coral disease

Communicated by Environment Editor Prof. Rob van Woesik

Electronic supplementary material The online version of this article (doi:10.1007/s00338-012-0944-6) contains supplementary material, which is available to authorized users.

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Assessing interactions of multiple stressors when data are limited: A Bayesian belief network applied to coral reefs

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ABSTRACT

Bayesian belief networks are finding increasing application in adaptive ecosystem management where data are limited and uncertainty is high. The combined effect of multiple stressors is one area where considerable uncertainty exists. Our study area, the Great Barrier Reef is simultaneously data-rich – concerning the physical and biological environment – and data-poor – concerning the effects of interacting stressors. We used a formal expert-elicitation process to obtain estimates of outcomes associated with a variety of scenarios that combined stressors both within and outside the control of local managers. There was much stronger consensus about certain stressor effects – such as between temperature anomalies and bleaching – than others, such as the relationship between water quality and coral cover. In general, the expert outlook for the Great Barrier Reef is pessimistic, with the potential for climate change effects potentially to overshadow the effects of local management actions.